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Investigating genetic and environmental factors impacting potato dormancy and assessing management strategies to control potato sprouting during storage

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Abstract

Sprouting during potato storage must be controlled as it leads to a decrease in tuber weight, a reduction in nutritional and processing quality, and consequently economic losses. To avoid losses during storage, chlorpropham (CIPC) has been extensively used for decades due to its high efficiency and affordability to mitigate potato sprouting. However, because CIPC and its major metabolite are a potential risk to human health, CIPC has recently been removed from the European market (EU regulation 2019/989).

Consequently, the main objective of this thesis was to find economically suitable and sustainable management strategies to control potato sprouting.

In this thesis, the influence of year, location and variety factors on potato dormancy was assessed. The analysis was performed using 3,379 records of multi-environment trials collected in Switzerland in five different locations with contrasting environments, over 25 years. In total, 537 genotypes were tested. The potential to predict potato dormancy of 247 predictors (i.e., environmental factors and management during the growing season variables) was evaluated using a forward selection approach to select a model predicting the duration of dormancy. Variety was the most important variable to explain the variability in dormancy (60.3 %), while year and location explained 13.9 % and 5.4 % of the dormancy variability, respectively. The selected predictive model used the variety class and a parameter related to the temperature of the growing season as predictors. The importance of the temperature parameter was confirmed by a greenhouse trial.

In order to find alternative anti-sprouting treatments, the potential to control potato sprouting of several synthetic pre- and post-harvest molecules was investigated (i.e., Maleic hydrazide (MH); 1,4-Dimethylnaphtalene (1,4-DMN); 3-decen-2-one and CIPC) and compared to an untreated control. The potential of 1,4-DMN and 3-decen-2-one post-harvest treatments to reinforce the efficacy of MH pre-harvest treatment was also investigated. Residue analyses were performed at the end of the storage. Results showed that all pre- and post-harvest treatments significantly mitigated sprouting for up to seven months of storage. The efficacy of the tested molecules to reduce the sprout weight in comparison to the untreated control was 86.9 %, 77.9 %, 73.6 % and 99.8 % for the MH, 3-decen-2-one, 1,4-DMN and CIPC molecules, respectively. The advantage of the 3-decen-2-one treatment is that it leads to complete necrosis of sprouts within 24 hours after treatment and it can be used as a curative treatment to save potato stocks that have already sprouted. In this study, results showed that there was no benefit to combine pre- and post-harvest treatments to mitigate sprouting. A variety-dependent effect of sprouting and treatment efficacy was observed. In addition, no residue of 1,4-DMN was observed in treated tubers (< limit of quantification), while residues of both CIPC and MH were found in treated tubers.

The efficacy of natural molecules to mitigate sprouting was also evaluated and compared to an untreated control. The tested natural molecules were L-carvone, D-

limonene (i.e., mint and orange essential oils, respectively) and ethylene. All the tested molecules efficiently controlled sprouting for up to five months of storage at 8 °C. These natural molecules are advantageous because they are authorized to treat potatoes in organic farming and they can so far be used without a maximum residue limit in the final product.

As an alternative or complementary approach, the potential of cold storage (i.e., at 4 °C) to mitigate sprouting after 4.5 months of storage in comparison to storage at a higher temperature (i.e., 8 °C) was evaluated for six processing potato varieties (Lady Claire, Verdi, Kiebitz, Pirol, Agria and Markies). Resistance to cold-induced sweetening (CIS) of these six potato varieties was evaluated by measuring relevant determinant parameters for the industry (e.g., acrylamide content, sucrose content, reducing sugars (RS) or crisp color quality) after two and/or four months of storage at 4 °C and 8 °C. The potential of reconditioning at 15 °C after a cold storage at 4 °C to decrease total RS, glucose and acrylamide contents in potato tubers was also evaluated. Vacuolar invertase (*VInv*) gene expression level was measured in tubers stored at 4 °C, at 8 °C and reconditioned at 15 °C. Results showed that a storage at 4 °C efficiently mitigates sprouting in the six tested varieties for up to 4.5 months of storage. Three CIS-resistant varieties were identified (i.e., Lady Claire, Verdi and Kiebitz) and displayed a low total RS and/or glucose content for up to four months of storage at 4 °C. In addition, the reconditioning efficiently reduced the glucose content and the *VInv* gene expression in the Markies variety after storage at 4 °C. Several correlations have been observed between glucose or RS content and *VInv* gene expression.

Based on the results obtained in this thesis, several potato management strategies are proposed to mitigate sprouting for different sprouting pressure scenarios.

Résumé

La germination pendant le stockage de la pomme de terre doit être contrôlée car elle entraîne une diminution du poids des tubercules, une réduction de la qualité nutritionnelle et de transformation, et par conséquent, des pertes économiques. Pour éviter les pertes pendant le stockage, le chlorprophame (CIPC) a été largement utilisé pendant des décennies pour sa grande efficacité et son coût abordable pour contrôler la germination. Cependant, en raison d'un risque potentiel pour la santé humaine de cette molécule et de son principal métabolite, le CIPC a récemment été retiré du marché européen (règlement UE 2019/989).

Par conséquent, l'objectif principal de cette thèse était de trouver des stratégies de gestion économiquement viables et durables pour contrôler la germination des pommes de terre.

Dans cette thèse, l'influence des facteurs année, lieu et variété sur la dormance de la pomme de terre a été évaluée. L'analyse a été réalisée à partir de 3 379 données d'essais multi-environnementaux collectés en Suisse dans cinq lieux différents avec des environnements contrastés et pendant 25 années. Au total, 537 génotypes ont été testés. Le potentiel de prédiction de la dormance de la pomme de terre de 247 prédicteurs (c'est-à-dire des facteurs environnementaux et des facteurs de gestion de la culture pendant la saison de croissance) a été évalué en utilisant une approche de type « forward selection » pour sélectionner un modèle prédisant la durée de la dormance. La variété était la variable la plus importante pour expliquer la variabilité de la dormance (60,3 %), tandis que l'année et le lieu expliquaient 13,9 % et 5,4 % de la variabilité de la dormance. Le modèle prédictif sélectionné comprend la classe de la variété et un paramètre lié à la température de la saison de croissance comme prédicteurs. Le modèle a été validé via un essai en serre.

Afin de trouver des alternatives au CIPC, le potentiel de contrôle de la germination des pommes de terre de plusieurs molécules synthétiques pré- et post-récolte a été étudié (hydrazide maléique (HM), 1,4-Diméthylnaphtalène (1,4-DMN), 3-decen-2-one et CIPC) et comparé à un contrôle non traité. Le potentiel des traitements post-récolte au 1,4-DMN et au 3-decen-2-one pour renforcer l'efficacité du traitement pré-récolte à l'HM a également été étudié. Des analyses de résidus ont été effectuées à la fin du stockage. Les résultats ont montré que tous les traitements pré- et post-récolte permettent d'atténuer significativement la germination jusqu'à sept mois de stockage. L'efficacité des molécules testées pour réduire la germination en terme de poids de germes par rapport au témoin non traité était respectivement de 86,9 %, 77,9 %, 73,6 % et 99,8 % pour les molécules : HM, 3-decen-2-one, 1,4-DMN et CIPC. L'avantage du traitement au 3-decen-2-one est qu'il entraîne une nécrose complète des germes dans les 24 heures suivant le traitement et qu'il peut être utilisé comme traitement curatif pour récupérer les stocks de pommes de terre déjà germées. Dans cette étude, les résultats ont montré qu'il n'y avait aucun avantage à combiner les traitements pré- et post-récolte pour atténuer la germination. Un effet variétal sur la germination et l'efficacité des traitements a été observé. De plus, aucun résidu de 1,4-DMN n'a été

observé dans les tubercules traités (< limite de quantification), alors que des résidus de CIPC et d'HM ont été détectés dans les tubercules traités.

L'efficacité de molécules naturelles pour atténuer la germination a aussi été évaluée et comparée à un témoin non traité. Les molécules testées étaient : la L-carvone, le D-limonène (huiles essentielles de menthe et d'orange, respectivement) et l'éthylène. Toutes les molécules testées ont été efficaces pour contrôler la germination jusqu'à cinq mois de stockage à 8 °C. Ces molécules naturelles présentent l'avantage d'être autorisées pour traiter les pommes de terre en agriculture biologique et elles peuvent, jusqu'à présent, être utilisées sans limite maximale de résidus dans le produit final.

En tant qu'approche alternative ou complémentaire, le potentiel du stockage au froid (4 °C) pour atténuer la germination après 4,5 mois de stockage par rapport au stockage à une température plus élevée (8 °C) a été évalué pour six variétés de pommes de terre de transformation, à savoir Lady Claire, Verdi, Kiebitz, Pirol, Agria et Markies. La résistance au « sucrage induit par le froid » ou « cold-induced sweetening » (CIS) de ces six variétés de pommes de terre a été évaluée en mesurant les paramètres déterminants pour l'industrie (par exemple, la teneur en acrylamide, la teneur en saccharose, les sucres réducteurs (SR) ou la qualité de la couleur des chips) après deux et/ou quatre mois de stockage à 4 °C et 8 °C. Le potentiel d'un reconditionnement à 15 °C après un stockage à froid à 4 °C pour diminuer la teneur en SR totaux, en glucose et en acrylamide des tubercules de pomme de terre a également été évalué. Le niveau d'expression du gène de l'invertase vacuolaire (*VInv*) a été mesuré dans des tubercules stockés à 4 °C, à 8 °C et reconditionnés à 15 °C. Les résultats ont montré qu'un stockage à 4 °C est efficace pour atténuer la germination dans les six variétés testées jusqu'à 4,5 mois de stockage. Trois variétés résistantes au « CIS » ont été identifiées (Lady Claire, Verdi et Kiebitz), présentant une faible teneur en sucres réducteurs totaux et/ou glucose jusqu'à quatre mois de stockage à 4 °C. De plus, le reconditionnement a été efficace pour réduire la teneur en glucose et l'expression du gène *VInv* pour la variété Markies après un stockage à 4 °C. Plusieurs corrélations ont été observées entre la teneur en glucose ou en SR et l'expression du gène *VInv.*

Sur la base des résultats obtenus dans cette thèse, plusieurs stratégies de gestion des pommes de terre sont proposées pour diminuer la germination pour différents scénarios de pression de germination.

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- °C: degrees Celsius
- µg kg^{-1}: microgram per kilogram
- µL: microliter
- µm: micrometer
- 1-MCP: 1-methylcyclopropene
- 3d2o: 3-decen-2-one
- ABA: abscisic acid
- a.i.: active ingredient
- ANOVA: analysis of variance
- bp: base pair
- Ca: calcium
- cDNA: complementary deoxyribonucleic acid
- CIPC: chlorpropham
- CIS: cold-induced sweetening
- cm: centimeter
- CO2: carbon dioxide
- DAH: days after harvest
- dCT: delta cycle threshold
- DMN: dimethylnapthalene
- DNA: deoxyribonucleic acid
- DNAse: deoxyribonuclease
- DW: dry weight
- e.g.: exempli gratia
- EFSA: European Food Safety Authority
- EMU: Ethylene Management Unit
- EU: European Union
- EU / EUs: experimental unit(s)
- FAO: Food administration Organisation
- FOAG: Federal office for agriculture
- FSVO: Food Safety and Veterinary Office
- FT: field treatment
- fwt: fresh weight
- g: gram
- g kg^{-1}: gram per kilogram
- g L^{-1}: gram per liter
- G x E x M: genotype by environment by management interaction
- GC-MS: gas chromatography-mass spectrometry
- GC-MS-TQ: gas chromatography-mass spectrometry triple quadrupole
- GMOs: genetically modified organisms
- h: hour
- ha: hectare

- i.e: id est
- IPCC : Intergovernmental Panel on Climate Change
- KB: Kiebitz
- kg: kilogram
- kg ha^{-1} of K2O: kilogram per hectare of potassium oxide
- kg ha^{-1} of Mg: kilogram per hectare of magnesium
- kg ha^{-1} of N: kilogram per hectare of azote
- kg ha^{-1} of P2O5: kilogram per hectare of phosphorus pentoxide
- L m^{-2}: liter per square meter
- LC : Lady Claire
- LC-MS/MS: liquid chromatography with tandem mass spectrometry
- LOQ: limit of quantification
- m: meter
- m asl: meter above sea level
- m.: months
- Mg: magnesium
- mg dL^{-1}: milligram per deciliter
- mg kg^{-1}: milligram per kilogram
- MH: Maleic Hydrazide
- MJ m^{-2}: megajoul per square meter
- mL: milliliter
- mL t^{-1}: milliliter per tonne
- mm: millimeter
- mm h^{-1}: millimeter per hour
- mmol L^{-1}: millimole per liter
- MO: main objective
- mol m^{-3}: mol per cubic meter
- MRL: maximum residue limit
- N: number of replicates
- NA: not analyzed
- Na_2SO_3: Sodium sulphite
- NaCl: Sodium chloride
- ng: nanogram
- NL: Netherlands
- nm: nanometer
- O_2: Dioxygen
- p: p-value
- PAI: Physiological Age Index
- pH: potential hydrogen
- qRT-PCR : quantitative Real Time Polymerase Chain Reaction
- QTL: qualitative trait loci
- R^2: coefficient of determination
- RH: relative humidity
- RMSE: root mean square error

- RMSEc: root mean square error of calibration
- RMSEv: root mean square error of validation
- RNA: ribonucleic acid
- rpm: rotations per minute
- RQ: Research Question
- rRNA: ribosomal ribonucleic acid
- RS: reducing sugars
- SDS: Sodium Dodecyl Sulfate
- SE: standard error
- StVinv: *Solanum tuberosum* vacuolar invertase
- t: tonne
- TBE: Tris-Borate-EDTA
- U.K: United Kingdom
- U.S: United State
- ULV: Ultra low volume
- VD: Vaud canton
- ZH: Zürich canton
- $\mu l.L^{-1}$: microliter per liter

Chapter 1

General introduction

1. Worldwide importance of potato and global challenges in potato storage management

1.1. The potato to face worldwide increasing food demand

The potato (*Solanum tuberosum* L.*)* is native to the Andean highlands of South America (Devaux et al. 2020). Domestication and breeding allowed its adaptation to various environments. Today, the potato is highly versatile and capable of high adaptability as potato is produced in more than 149 countries within a wide range of environmental conditions (i.e. temperate, subtropical, and tropical) (Devaux et al. 2020). Potato is a crop of high importance in developed and developing countries. According to the Food and Agriculture Organization (FAO), the potato is the fourth most important food crop worldwide in terms of quantity production after maize, wheat and rice with 370 million tonnes of potatoes produced in 2019 (Figure 1-1) (FAOSTAT 2021b). Among these four most important food crops, the potato has the highest potential for yield increase (Fengyi 2008). The total world potato production has substantially increased in the past decades, while the total area harvested decreased (Figure 1-1) (FAOSTAT 2021b).

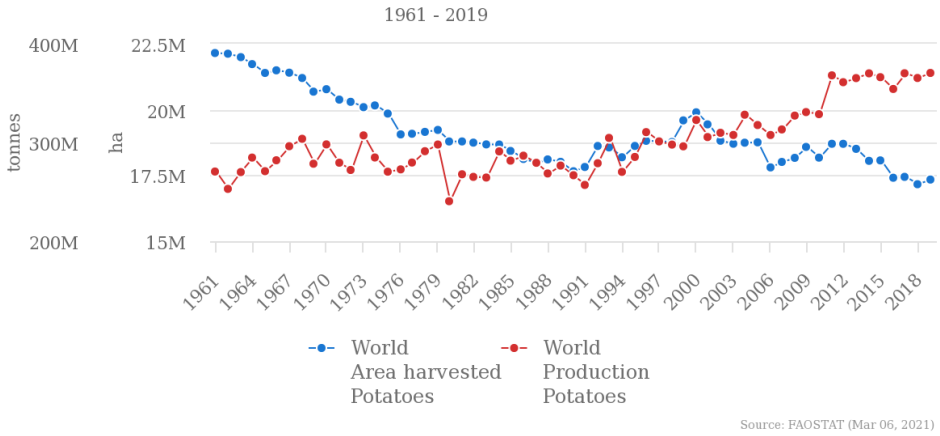

Figure 1-1. Worldwide potato production quantities and area (Retrieved from FAOSTAT (2021b))

This data indicates an increase in yields over time. According to the FAO, the average world potato yield was 12.2157 tonnes per ha in 1961 and 21.3619 tonnes per ha in 2019 (FAOSTAT 2021a). For example, in the U.K., potato yields have also almost doubled from 20 tonnes per hectare in 1960, to 40 tonnes per hectare in 2014 (Ritchie and Roser 2013). In contrast, potato production in developed countries has decreased over time with 183.13 million tonnes produced in 1991 and 159.89 million

tonnes produced in 2007, while potato production in developing countries has steadily increased over time from 84.86 million tonnes in 1991 to 165.41 million tonnes in 2019 (© FAO 2008). In 2005, the production in developing countries exceeded the production in developed countries (© FAO 2008). In fact, until the early 1990s, potatoes were mostly grown in North America, countries of the former Soviet Union and Europe, but since then an increase in potato demand and production has been observed in Africa, Asia and Latin America (© FAO 2008). In 2019, the top country in terms of potato production was China, followed by India, Russian Federation, Ukraine, United States of America, Germany, Bangladesh, France, Netherlands and Poland (FAOSTAT 2021a) (Table 1-1).

Countries	Potato production in 2019 (tonnes)
China	9.19E+07
India	5.02E+07
Russian Federation	2.21E+07
Ukraine	2.03E+07
United States of America	1.92E+07
Germany	1.06E+07
Bangladesh	9.66E+06
France	8.56E+06
Netherlands	6.96E+06
Poland	6.48E+06

Table 1-1. Top 10 countries in terms of potato production in 2019 (Data retrieved from: FAOSTAT (2021a))

However, productivity is much higher in developed countries than in developing countries. It has been reported that the yield in developing countries is below 20 tonnes per hectare and in some of them, below 10 tonnes per hectare. In European and North America countries, the yield is over 40 tonnes per hectare and 70 to 80 tonnes per hectare can be reached in experimental plots (Fengyi 2008); although, in agriculture, yield estimations in experimental trials are often overestimated (Laajaj et al. 2020). Consequently, there is a high potential to increase yields in developing countries. To increase potato yields in these regions, it would be necessary to use high quality seed tubers, to apply irrigation and fertilizers and to improve crop management (Fengyi 2008).

Food demand is expected to increase in the medium-term future mainly because of the world population growth (Bajželj et al. 2014). In addition, in the context of climate change and reduction of arable land, it is of high importance to increase the food supply (Fengyi 2008). To do so, the potato is the best candidate because of its

adaptability to various environments, its high nutritional value and its above-mentioned yield potential (Fengyi 2008). Consequently, potato will play an important role in food security in the future to match the increasing food demand.

This makes the potato a crop of economic and social significance, which is why the potato has been highly recommended as a food security crop by the FAO to overcome the world food demand and supply (FAO 2009). Potato provides a relatively inexpensive and high quantity source of high-quality nutrients (Devaux et al. 2020). Potato is a source of carbohydrates and high-quality proteins (Andre et al. 2007; Cotton et al. 2004). Potato contains a moderate level of iron and is rich in several micronutrients including vitamin C, which contributes to iron absorption (Andre et al. 2007; FAO 2008). Potato is also a good source of vitamins B1, B3 and B6 and minerals (e.g., magnesium, potassium and phosphorus). In addition, potato contains other vitamins such as: folate, riboflavin and pantothenic acid, as well as dietary antioxidants and fibers which make the consumption of potato beneficial for human health (FAO 2008). The role of potato in food security strategies is twofold, potato can be both a staple and cash crop making it particularly important for poor people as potato is sold in high-value markets (Devaux et al. 2014).

1.2. Challenges in potato storage management

The perishability of potatoes makes them fragile and easily damaged during harvest and post-harvest activities (FAO 2011). Adequate management of potato harvest and post-harvest activities is key to avoid potato post-harvest losses. Several steps such as sorting, cleaning, handling, packing, transportation, storage, distribution, marketing and processing can be optimized to limit post-harvest losses (Degebasa 2020). During the storage step, losses are mainly due to sprouting, diseases and weight losses caused by a decrease in moisture content (Magdalena and Dariusz 2018; Khanal and Bhattarai 2020). Sprouting induces shrinkage, softening and texture alterations, leading to a decrease in weight, processing and nutritional quality and consequently to non-marketable potatoes and economic losses (Alexandre et al. 2015; Sorce et al. 2005; Pinhero and Yada 2016). Water losses and shrinking of tubers is due to the remobilization of storage compounds, mainly proteins and starch, occurring during sprouting (Pinhero and Yada 2016). As sprouting increases respiration and moisture losses, it leads to physiological aging and accelerates the starch breakdown causing the accumulation of reducing sugars. The degradation of vitamins occurs during physiological aging in potato tubers (Pinhero and Yada 2016). Sprouting is also responsible for the production of toxic compounds in potato tubers as chaconine and solanine (Koffi et al. 2017).

The beginning of sprouting occurs after the break of dormancy (Coleman 1987; Daniels-Lake and Prange 2007) which is why, to improve potato storage management, it is important to identify and understand factors controlling the potato dormancy.

2. Theoretical background about potato dormancy

2.1. Definitions of dormancy

While it is commonly accepted that potato sprouting occurs only after the break of dormancy (Coleman 1987; Daniels-Lake and Prange 2007), the definition of potato dormancy is subject to discussions in the literature and has evolved over time (Delaplace 2007).

Emilsson (1949) considered two distinct periods: 1) the "rest period" beginning at harvest and during which tubers will not sprout even if potatoes are placed in optimal sprouting conditions as defined by Peacock (1934); and 2) the "dormant period" in which tubers do not sprout and do not break down physiologically although they are stored at temperatures suboptimal for sprouting (Figure 1-2). The author explained that the dormant period is related to the storage temperature and that if potatoes are stored at optimal conditions for sprouting, the "dormant period" and the "rest period" may coincide.

Reust (1982) described the dormancy duration in a single period from tuber formation to the appearance of the first sprouts (Figure 1-2). Thereafter, Reust (1986) defined dormancy as a physiological state of the tuber that does not allow it to germinate, even if tubers are placed under ideal conditions for sprout growth (i.e., darkness, temperature from 15 to 20 °C and relative humidity of about 90 %). However, Reust (1986) underlined that the dormancy period is often divided in two distinct parts in the literature: 1) the "vegetative rest" period during which no sprouting occurs even under favorable conditions; and 2) the "dormancy" period which is the period following the "vegetative rest". During this second period the conditions of the environment can inhibit sprout growth and this period ends when 80 % of tubers present one or several sprouts longer than 3 mm.

Later, Lang et al. (1987) reported the need to revise existing terminology about dormancy. Lang et al. (1987) emphasized that at the time of his study, several terms to describe dormancy existed in the literature (i.e., 54 terms) with duplication and equivocal meaning and that some of them were used to describe different types of dormancy. Based on existing terminologies and classifications of dormancy, Lang et al. (1987) defined a new classification of the dormancy with three distinct classes: endodormancy, paradormancy and ecodormancy. Endodormancy is regulated by physiological factors inside the affected structure, meaning that a signal within the affected structure (i.e., a specific signal from the environment or an endogenous signal) initiates the reaction leading to growth control (e.g., chilling responses or photoperiodic responses). Paradormancy is regulated by physiological factors outside the affected structure, meaning that a specific biochemical signal is necessary as an initial reaction and this signal does not come from the affected structure, i.e., signal triggered by environmental effect or signal not triggered by environment such as the inhibition of lateral bud meristems caused by morphogenic factors in nearby organs (e.g., apical dominance or photoperiodic responses). Ecodormancy is regulated by

environmental factors such as water stress, nutrient deficiencies or extreme temperatures, which do not have a specific effect on the meristematic or receptive structure but which have a large effect on plant function and growth.

Finally, Van Ittersum and Scholte (1992) used a more practical definition of dormancy, starting from haulm killing and ending when 80 % of tubers have at least one sprout longer than 2 mm (Figure 1-2).

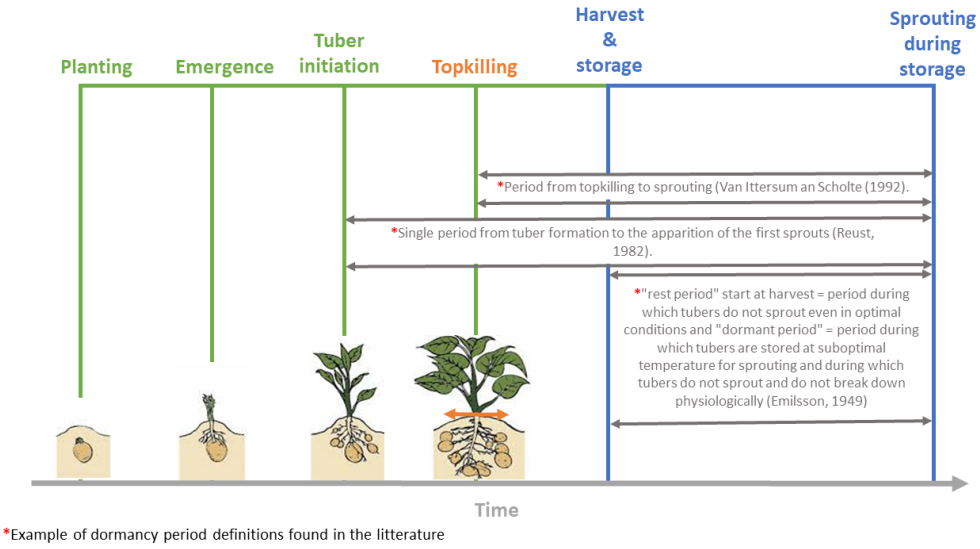

Figure 1-2. Scheme representing examples of potato dormancy definitions found in the literature, definitions are placed according to the potato cycle (Potato cycle pictures in this scheme are retrieved and modified from: © FAO (2008))

Potato dormancy mainly depends on the genetic background of tubers but is also under the influence of the stage of tuber development, of environment and management during both the growing season and storage (Aksenova et al. 2013; Muthoni et al. 2014), and of exposure to endogenous and applied dormancy-breaking compounds and tuber injury (Aksenova et al. 2013).

2.2. Evolution during dormancy installation in tubers

During the development of young tubers on the plant, dormancy gradually takes place (Claassens and Vreugdenhil 2000b). Potato dormancy is the first stage in the physiological ageing of potatoes. Then, ageing continues with sprouting stages and ends with senescence (Struik and Wiersema 1999; Johansen 2011). Buds in the eyes of young tubers successively become dormant, beginning at the stolon end and finishing with the apical eye (Es and Hartmans 1987; Claassens and Vreugdenhil 2000b). Tubers enter dormancy after reaching their final size and the dormancy stage

allows tubers to protect themselves under unfavorable growth conditions, as tubers are organs of vegetative reproduction (Aksenova et al. 2013).

At the dormancy break, when sprouts develop with roots at their basis, tubers, as storage organs, provide nutrients and energy for sprout formation (Struik 2007d; Aksenova et al. 2013). During tuber dormancy and sprouting, complex physiological processes occur and one of the most important is the active use of proteins and carbohydrates (Aksenova et al. 2013). As previously mentioned, this remobilization of starch and proteins during sprouting leads to water losses and shrinkage (Coleman 1987; Sonnewald and Sonnewald 2014).

Physiological processes occurring during tuber dormancy and sprouting are connected at molecular and biochemical levels and these connections are not completely understood (Aksenova et al. 2013). In addition, physiological ageing accompanied by dormancy break coincides with enhanced respiration and changes in the proteome and antioxidants in potato tubers (Delaplace et al. 2009).

2.3. Genetic and biochemical factors controlling dormancy

2.3.1. Genetic control

Among the factors influencing potato dormancy length and consequently sprouting during storage, genetic control is the most significant (Aksenova et al. 2013; Burton and Wilson 1978; Daniels-Lake and Prange 2007; Magdalena and Dariusz 2018; Muthoni et al. 2014; Suffle et al. 2016; Sonnewald 2001; Czerko and Grudzińska 2014). However, genetic control of potato dormancy is complex and not completely understood.

A review conducted by Muthoni et al. (2014) reports that studies of qualitative trait loci (QTL) showed quantitative inheritance of dormancy, and that this dormancy inheritance is controlled by at least nine loci.

Three out of the 9 QTLs are influencing Abscisic acid (ABA) level, suggesting a role in dormancy regulation (Claassens and Vreugdenhil 2000b). ABA has also been reported to control the CDK/Cyclin complexes which regulate transition from G1-phase to S-phase of the cell cycle (Del Pozo et al. 2005). Indeed, plant cell cycle consists of four main phases: DNA synthesis (S), mitosis (M) and two intervening gap phases (G1, G2) (Velappan et al. 2017) and the control of eukaryotic cell proliferation is governed by an accurate transition from G1-phase of the cell cycle to S-phase (Bertoli et al. 2013). It seems that transition from the G1-phase to the S-phase is blocked in cells of dormant tuber sprouts. Moreover, several genes and proteins, including D-cyclins, cyclin-dependent kinases and histones, have been identified as key factors controlling the transition from G1-phase to S-phase (Campbell et al. 2006; Berckmans and Veylder 2009; Aksenova et al. 2013). The activation of the gene cyclin D3 and other genes controlling cell cycle progression and DNA replication has been shown to be involved in transition from dormant stage to sprouting (Campbell et al. 2008; Senning et al. 2010; Hartmann et al. 2011; Aksenova et al. 2013).

2.3.2. Biochemical control

During the dormant stage, sprouts are isolated from the rest of the tuber by symplastic isolation, while in the sprouting stage; they are connected to the tuber through the vascular system. These connections allow the transport of metabolites from the tuber to sprouts and are important for the meristematic activity (Viola et al. 2001; Viola et al. 2007; Hancock et al. 2008; Aksenova et al. 2013). Aksenova et al. (2013) underlined that carbohydrate metabolism and particularly sucrose metabolism is important in regulation of dormancy and sprouting. During the dormancy break, authors also reported an increase in nucleic acid and protein synthesis, as well as changes in protein spectrum and an acceleration of the respiration rate (Aksenova et al. 2013; Delaplace 2007; Desire et al. 1995; Suttle 2004b).

During potato storage, several phytohormone modifications take place (Delaplace 2007; Coleman 2000). Phytohormones and their interactions are important regulators of potato dormancy, sprouting and sprout growth, among them: ABA; ethylene; brassinosteroids; auxins; cytokinins; jasmonates and gibberellins (Aksenova et al. 2013; Delaplace 2007; Fernie and Willmitzer 2001; Muthoni et al. 2014).

It is clear that exogenous application of gibberellins breaks potato dormancy (Fernie and Willmitzer 2001; Muthoni et al. 2014). In contrast, the role of ABA during potato storage is subject to discussion and remains unclear (Fernie and Willmitzer 2001). However, increasing evidence points to a role of ABA in potato dormancy (Claassens and Vreugdenhil 2000a; Muthoni et al. 2014). Aksenova et al. (2013) reported that both ethylene and ABA play a role to induce and maintain dormancy and underlined that ABA seems to be the most important phytohormone in dormancy initiation and maintenance, while other authors affirm that only ABA is needed to maintain sprout dormancy (Suttle 2004a; Muthoni et al. 2014).

Although genetic background of potatoes is the main factor influencing dormancy, other factors such as the environment during the growing season also influence the dormancy length of a given variety.

3. Impact of environmental conditions during the growing season on dormancy

Physiological age and consequently dormancy of potato tubers during storage is under the influence of the environment during the growing season (Muthoni et al. 2014; Van Dingenen et al. 2019; Caldiz et al. 2001b; Delaplace et al. 2008; Magdalena and Dariusz 2018; Reust 1982).

It is widely known that the temperature during the growing season influences potato dormancy and consequently potato sprouting during storage (Levy and Veilleux 2007; Magdalena and Dariusz 2018; Muthoni et al. 2014; Reust 1982; Zommick et al. 2014; Fernie and Willmitzer 2001). Several studies report that high air temperatures accelerate physiological aging and consequently reduce potato dormancy (Levy and Veilleux 2007; Magdalena and Dariusz 2018; Bodlaender et al. 1964; Rykaczewska

2015). Recently, Magdalena and Dariusz (2018) reported that a hot and rainy season tends to reduce the dormancy period and leads to early sprouting during storage. Over the three years tested (i.e., 2011, 2012 and 2013) with differences in terms of temperature and rainfall during the vegetation stage of plants, differences in the date of beginning of sprouting (i.e., more than two months) were observed between seasons of storage 2011-2012 and 2013-2014 (Magdalena and Dariusz 2018). In addition, climate change will lead to an increase in average temperature in several areas where potato is grown. Consequently, we can expect an increase in potato sprouting during storage in the future. It will be of interest to predict and quantify the impact of climate change on potato sprouting during storage (Figure 1-3).

The dormancy period also seems to be influenced by the photoperiod during the growing season (Fernie and Willmitzer 2001; Sonnewald 2001; Martínez-García et al. 2002b; Johansen 2011; Martínez-García et al. 2002a), however this effect is subject to discussion. Differences up to nine days in dormancy period have been observed between plants grown with two distinct photoperiod regimes with differences in the photoperiod effect between experiments and varieties. The first photoperiod regime consisted of a photoperiod of 12 hours of day and 12 hours of night, and the second photoperiod regime was a photoperiod of 12 hours of day and 12 hours of night, followed by an extension of the photoperiod to 18 hours for four to six weeks after tuber initiation using photosynthetically incandescent light (Van Ittersum et al. 1992). In contrast, in a recent study, no significant differences in dormancy length were observed in tubers grown under artificial light conditions with daylengths of 12, 18 or 24 h (Johansen 2011).

The water supply during the growing season also impacts potato sprouting during storage (Czerko and Grudzińska 2014; Muthoni et al. 2014). Among several climatic variables of the growing season, the sum of rainfall during vegetation has been reported to have the highest influence on the sprouting date, with an increased dormancy duration during seasons with high rainfall (Czerko and Grudzińska 2014). Conversely, as mentioned above, Magdalena and Dariusz (2018) reported that hot and rainy weather during the growing season leads to a shortened dormancy.

As the effect of photoperiod and water supply on potato dormancy duration is subject to discussion in the literature, it would be of interest to further evaluate the effect of these environmental parameters on dormancy duration. It would also be important to identify and quantify the effect of both environment and management parameters during the growing season in dormancy variability (Figure 1-3).

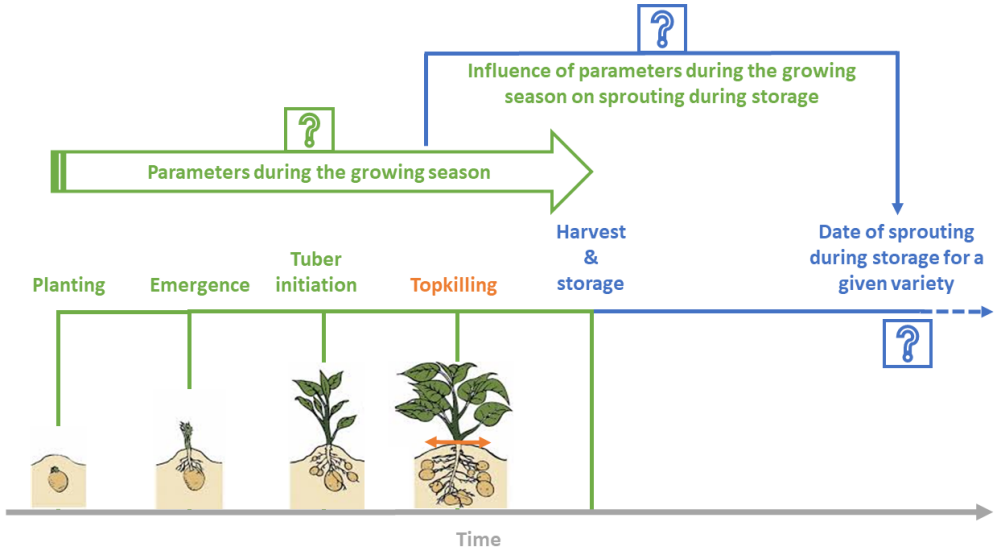

Figure 1-3. Simplified scheme of potato cycle and research questions (= "?") about influence of parameters during the growing season on potato sprouting in storage for a given variety (Scheme designed by Margot Visse-Mansiaux; potato cycle pictures on this scheme are retrieved and modified from: © FAO (2008))

4. Control of potato dormancy

As mentioned above, the most important parameter controlling dormancy of potatoes is the genotype. Consequently, the choice of the genotype will be the first strategy to improve storage management of ware potatoes. However, the dormancy duration is also governed by the above-mentioned environmental factors and by management during both the growing season and storage. Consequently, other pre- and post-harvest management strategies to mitigate sprouting are commonly used.

4.1. The use of dormancy to mitigate sprouting

Varieties display differences in dormancy duration. Magdalena and Dariusz (2018) reported that the sprouting date varied from 78 to 155 days among eight varieties tested and stored at 8 °C. Consequently, the first strategy to improve potato storage management using dormancy information would be to use only potato varieties with long dormancies and consequently with a spouting date as late as possible during storage. This would allow a sustainable storage of potatoes for months without using chemicals.

A second strategy would be to use the dormancy information of a given variety to help manage potato storage whatever the dormancy duration. Knowing the dormancy

duration of a given variety would allow priority to be given to selling stocks containing varieties with short dormancy first and to keep longer stocks with long dormancy. Using the dormancy information would also help to adapt, delay or avoid the use of anti-sprouting chemicals in potato storages.

However, the influence of the genotype on potato dormancy cannot be the only factor taken into consideration and the above-mentioned strategies are not always realistic in practice for several reasons. Firstly, the present panel of varieties with very long dormancies is not sufficient to respond to agricultural and market requirements. Furthermore, consumer preferences often guide the variety choices (Curty Personal communication). Swisspatat estimated the surface planted per variety in 2020 in Switzerland (Swisspatat 2020b) (Figure 1-4). The most planted varieties were: Agria (21 % in surface); Erika (8 % in surface); Innovator (6% in surface); Jelly and Fontane (5 % in surface); and Lady Rosetta and Victoria (4 % in surface) (Figure 1-4). Agria is a variety with a long to very long dormancy (European Cultivated Potato Database ; Agrico 2020); Fontane is also described as a potato variety with long or very long dormancy (Agrico 2020). Victoria is described as a variety with long dormancy (HZPC 2021). However, Erika has a medium to quite long dormancy period depending on the source (Solanum International Inc 2021; Agrico 2020), and Innovator (HZPC 2021) and Lady Rosetta (© C. Meijer B.V. 2021) have a medium dormancy. Finally, Jelly has a medium or long dormancy depending on the source (Europlan 2021; Sunrainseed 2021). These results show that in practice varieties commonly used by farmers have a relatively wide range of dormancy, and that farmers do not only use varieties with very long dormancy.

In addition, because potato varieties have different susceptibilities to diseases (Dupuis et al. 2017), and because yield differs between potato varieties (Haverkort and Struik 2015), it is not always possible to use only varieties with long dormancies. Consequently, varieties with short or medium dormancies are also used.

Furthermore, the dormancy information of a given genotype is not always well characterized, which limits the use of this characteristic to improve potato storage management. Dormancy data of potato varieties is not always available and the information supplied can be contradictory depending on the source (breeders, research institutes or other sources). In addition, methods, protocols and standard varieties used to assess the dormancy duration of a given variety vary within countries. For that reason, the dormancy information for a given variety is often highly heterogenous.

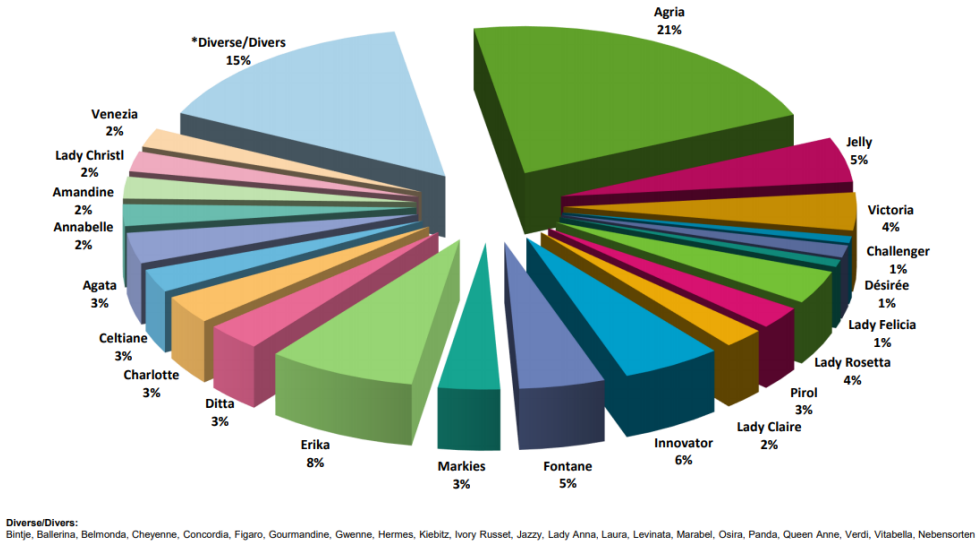

Figure 1-4. Estimation of potato variety surfaces in Switzerland in 2020 (retrieved from: Swisspatat (2020b))

To improve potato storage management, it will be necessary to improve characterization of potato dormancy for a large range of genotypes. In addition, it is necessary to standardize methods to assess the dormancy duration of varieties. The use of genetic tools, such as conventional genetic modification of organisms or epigenetic tools, to improve potato variety dormancy characteristics would assist in the development of a larger range of varieties with long dormancies.

Finally, to optimize the use of the dormancy duration to improve potato storage, genotype by environment by management (G x E x M) interactions should be considered, as the dormancy of a given genotype is subject to change according to the environment and management during the growing season. Consequently, the combined effect of the genotype and the environment on potato dormancy must be taken into account in dormancy characterization of a given variety to optimize the use of the dormancy information for managing potato storage. Sprouting of potato tubers during storage is also impacted by several crop management parameters, among them, fertilization, the haulm killing date or the use of pre-harvest anti-sprouting treatments.

4.2. Management during the growing season

4.2.1. Fertilization

Fertilization practices have been demonstrated to impact potato sprouting during storage. Van Dingenen et al. (2019) studied the effect of nitrogen availability on potato tuber yield and quality traits comprising sprouting. They found that growing tubers in low nitrogen content soil results in fewer tubers with a reduced weight, a

higher starch content, a lower sucrose content and a significant delay in sprouting for most of the tested varieties. For example, they showed that tubers from the Alegria variety grown in low nitrogen conditions started to sprout at 14 weeks of storage at room temperature, while the tubers of the same variety grown under optimal nitrogen conditions started to sprout only after seven weeks of storage. Authors explained that some observed differences in tubers grown in different nitrogen conditions could be explained by changes in hormone levels.

4.2.2. Haulm killing

Haulm killing means that the haulms of potatoes are killed or removed in the field a few weeks before harvest. Haulms can be killed using different technics (e.g., chemical or mechanical). Potato haulm killing is used in practice for several purposes such as: to reduce losses from diseases (e.g., late blight tuber rot), to reduce skinning of tubers during harvest or to control tuber size (Misener and Everett 1981). At the moment of haulm killing, young tubers become independent from the mother plant and starch translocation between primary and secondary tubers ends (Delaplace et al. 2008).

The haulm killing date plays a role in physiological ageing and a Physiological Age Index (PAI) using the haulm killing date was developed by Caldiz et al. (2001b) and is described as "a new, simple and reliable index to assess the physiological age of seed potato tubers based on haulm killing date and length of the incubation period". Delaplace et al. (2008) described variety-specific and harvest year-specific age variations using the PAI measured from the time of haulm killing in two varieties over two years and found that PAI values mainly depend on the duration of the period between haulm killing and the beginning of the storage. This influence of different haulm killing dates on potato physiological aging has been reported in the literature and early haulm killing results in earlier sprouting during storage, with sprouting date of 14 to 16 days earlier in tubers from plants defoliated six weeks before the other plants (Hutchinson 1978). This contradicts another study showing that early defoliation of two varieties ("Bonaerense" and "La Ballenera") over three seasons did not affect the sprouting capacity, the tuber yield or the physiological age of seed potatoes obtained (Panelo and Caldiz 1989).

It would be of interest to perform more studies to evaluate the effect of haulm killing on potato dormancy and sprouting to identify if this parameter could be used to mitigate potato sprouting during storage.

4.2.3. Pre-harvest anti-sprouting treatment

Management during growing season also include the use of pre-harvest anti-sprouting treatment to prevent sprouting during storage. Maleic Hydrazide (MH) is a systemic plant growth regulator used for several decades (Schoene and Hoffmann 1949). MH has been reported to control sprouting during storage (Caldiz et al. 2001a). This molecule is applied to potato leaves in the field and is transported to tubers (Kennedy and Smith 1951; Venezian et al. 2017; Hoffman and Parups 1964). Studies suggest that one mode of action of MH is by disruption of cell mitosis (Hoffman and

Parups 1964; Venezian et al. 2017). Several commercial MH based products are available, including Fazor® or Itcan SL270®.

Cunnington (2019) reported that MH use for sprout suppression is well developed in the US, however in Europe the adoption of MH as sprout suppression has been slower. Authors explained that one reason for this might be due to the complicated timing of application of MH based products. The treatment must be done at the right time to be effective, as the efficacy may vary according to the weather at the time of foliar application. Uniform uptake by the foliage is necessary for optimal efficacy (Cunnington 2019). To ensure proper absorption and migration of active ingredient from leaves to the tubers, MH based products must be applied to growing plants. The treatment needs to be done avoiding high temperatures and high humidity weather and a minimum period of 12 hours without rain is necessary after the treatment. In addition, treatment must be done when 80 % of tubers have reached a diameter greater than 25 mm to avoid altering the growth of the tubers and minimum two to three weeks before haulm killing (Martin 2011). Early MH applications have been associated with reduced yields, while late application may reduce the control of sprouting during storage (Cunnington 2019).

Some authors reported that MH-based product efficacy is time limited with a sprouting control of two to three months only, depending on the variety and the storage temperature (Martin 2020a). Other authors reported that MH is highly efficient and allows for sprout control for several months (Caldiz et al. 2001a; Visse-Mansiaux et al. 2020). The discrepancies in results could be due to differences in varieties used in the different studies. The efficacy of MH for different varieties and long storage duration should be further investigated and will be investigated in this thesis.

4.3. Post-harvest management

Management during storage plays an important role in dormancy variability and should be studied as well.

4.3.1. Effect of the storage environment

Several parameters of the storage chamber can be controlled to mitigate sprouting. It is reported that the temperature, relative humidity or atmospheric composition of the storage chamber may influence sprouting during storage (Caldiz 2009; Reust et al. 2001; Aksenova et al. 2013; Burton 1958; Struik 2007c; Claassens and Vreugdenhil 2000a; Reust 1982; Van Es and Hartmans 1987).

The temperature of storage is one of the main factors influencing the potato dormancy (Reust 1982; Muthoni et al. 2014; Sonnewald 2001; Czerko and Grudzińska 2014). The use of low temperatures to reduce sprouting during storage is a strategy commonly used as an alternative to the anti-sprouting molecules applied to delay sprouting. Burton (1989) reported that at storage temperatures ranging from 3 to 25 °C, the duration of the dormancy period is conversely proportional to the storage temperature. Consequently, decreasing the storage temperature (e.g., at 4 °C)

increases the dormancy duration and slows down physiological aging and respiration in potato tubers compared to storage at higher temperatures (e.g., 8 °C) (Blauer et al. 2013; Magdalena and Dariusz 2018; Muthoni et al. 2014; Burton 1978; Daniels-Lake and Prange 2007). Cheong and Govinden (1999) showed that after 12 weeks of storage at temperatures from 8 to 10 °C or at ambient temperature, weight losses due to sprouting were higher compared to a storage at temperatures from 2 to 4 °C. Czerko and Grudzińska (2014) showed that storage at 3 °C delays the beginning of sprouting by about two months in comparison to storage at 8 °C.

This strategy is commonly used for potatoes intended to the fresh market usually stored at low temperatures (e.g., 5-6 °C) (Bishop et al. 2012). However, potatoes intended for processing are usually stored at higher temperatures (e.g., 7-10 °C) (Bishop et al. 2012). It is not recommended to decrease the storage temperature for potatoes dedicated for processing due to the susceptibility of certain varieties to the accumulation of reducing sugars at low temperatures, which is called "cold induced sweetening" (CIS) (Sowokinos 2001) (Figure 1-5). The vacuolar invertase (*VInv*) gene has an important role in potato CIS as low transcript levels are found in CIS-resistant varieties, and silencing the *VInv* gene prevents the accumulation of reducing sugars in tubers (Bhaskar et al. 2010). CIS is a problem for the industry as high sugar content can lead to a decrease in potato quality with the production of toxic compounds such as acrylamide, which may pose a food safety hazard for consumers (Paul et al. 2016a; Wiberley-Bradford and Bethke 2017). CIS also leads to darkening and a bitter taste of crisps and French fries, which is commercially unacceptable (Amjad et al. 2020; Pinhero et al. 2011) (Figure 1-5).

However, to cope with the non-renewal of CIPC, cold storage should be used to mitigate sprouting. Consequently, it is of interest to find potato varieties that can be stored at low temperatures without sweetening. This would avoid risks of production of toxic compounds during frying after a storage at low temperature. A few varieties were identified as not susceptible to CIS such as Verdi, Sempra (Böhm et al. 2006) and White Pearl (Groza et al. 2006). However, the choice in CIS-resistant varieties is limited and not enough to fully use the potential of a cold storage strategy to mitigate sprouting for potatoes dedicated for processing. Consequently, it is necessary to find a larger range of varieties, which are not susceptible to CIS at low temperature. It would be of interest to search for genotypes with reduced *VInv* gene expression.

Reconditioning could be used as well to store potatoes at low temperature and maintain low reducing sugar levels before frying to avoid risks associated with CIS. Reconditioning after a cold storage consists of slowly increasing the storage temperature from a low temperature up to 15 °C, to decrease reducing sugars before frying (Jansky and Fajardo 2014). Cold-induced sugar accumulation is reversible and a decrease in reducing sugars during reconditioning is due to the equilibrium between starch degradation and starch resynthesis occurring at temperatures of 15-20 °C (Kyriacou et al. 2009; Sowokinos 2001). A drawback with this strategy is the variety-dependent potential of reconditioning to decrease reducing sugars (Kyriacou et al.

2009). Consequently, this strategy should also be studied to find varieties that respond positively to reconditioning.

Finally, studying the effect of conditions in the storage chamber such as the impact of storage temperature on potato dormancy and reducing sugar content; or potential interactions between genotype and storage temperature on sugars is important in the use of cold storage as an efficient and safe strategy to control sprouting (Figure 1-5). A better understanding of sugar metabolism in potato tubers is key to develop breeding and biotechnological strategies to limit CIS in potato varieties.

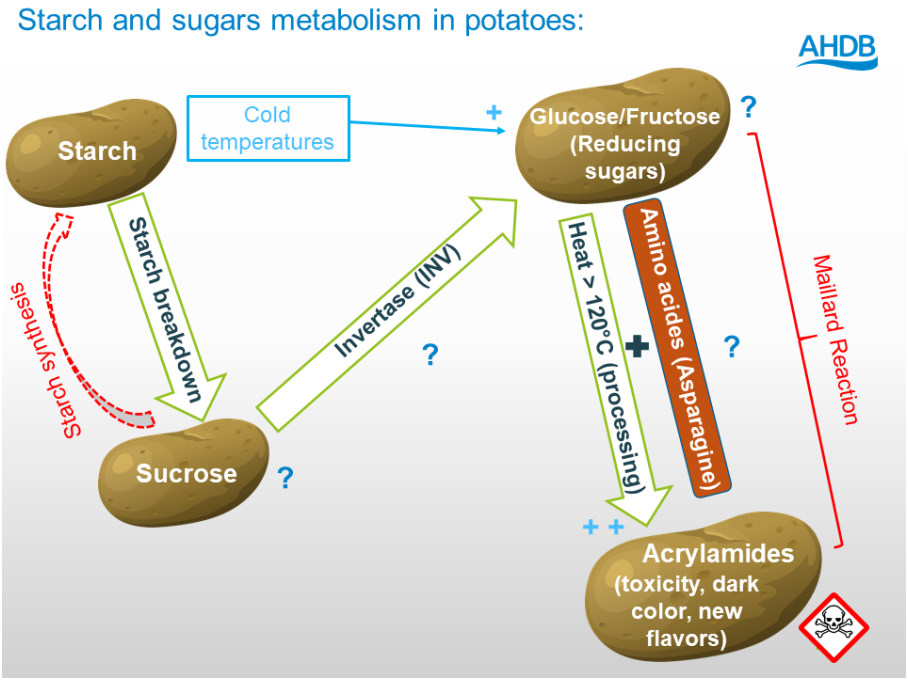

Figure 1-5. Simplified scheme of sugar metabolism in potatoes, influence of cold temperatures on sugar metabolism; the question marks represent the objectives of the chapter 5 research. (INV = vacuolar invertase gene expression) (retrieved from: Visse-Mansiaux et al. (2019)).

The gaseous composition of the storage chamber plays an important role in dormancy break and consequently in sprouting during storage (Muthoni et al. 2014). Different controlled atmosphere compositions were tested in tubers of the variety Record stored at 4 °C for six months, and several parameters were observed including the sprout growth and crisps fry color (Khanbari and Thompson 1994). Results showed that the exposure of tubers to high CO_2 and low O_2 combinations (i.e. 10.2 % CO_2 – 3.8 % O_2 or 9.7 % CO_2 - 2.0 % O_2) completely inhibited sprout growth (Khanbari and Thompson 1994). However, high CO_2 - low O_2 combinations led to

dark crisp color and rotting, while after reconditioning crisps were light, but the sprouting was similar to tubers stored under other atmospheric compositions after a reconditioning (Khanbari and Thompson 1994). The increase in reducing sugars caused by high CO_2 atmosphere composition has been reported to be dependent on the storage temperature, with increased reducing sugars in tubers stored at a high CO_2 level at 5 °C but not in tubers stored at a high CO_2 level at +0 °C (Workman and Twomey 1970). In addition, high CO_2 in the storage chamber may lead to tuber injuries and this effect is variety-dependent as Workman and Twomey (1970) showed that the variety Kennebec was more susceptible to CO_2 injury than the variety Russet Burbank. Tubers of the Kennebec variety did not tolerate added CO_2 at +0 °C and survived at 5 °C with 4% CO_2 (Workman and Twomey 1970). Consequently, it would be of interest to evaluate the potential of different atmospheric compositions in delaying sprouting for a large range of varieties, and within different storage temperatures for several reasons: 1) to find the best storage temperatures to avoid the increase in reducing sugars and injuries in certain varieties caused by high CO_2 levels in the atmosphere; and 2) to find a large range of varieties not susceptible to injuries at high CO_2 atmospheric levels.

Finally, the relative humidity in the storage chamber also plays a role in sprouting during storage (Muthoni et al. 2014). Increasing the relative humidity from 40 % to 100 % or supplying water to the basal cut end of tubers has been reported to lead to an increase in growth of apical sprouts in tubers of the variety Norland stored in the dark at 15 °C (McIntyre and Quick 1984). Growth of sprouts is probably determined by their water content and consequently by factors influencing the water supply from tubers to the sprouts and by the transpiration rate of sprouts (McIntyre and Quick 1984). Thus, reducing the relative humidity of the storage chamber would delay sprouting. However, low relative humidity during storage (e.g., 30-35 %) before the dormancy break is responsible for high weight losses (Singh and Ezekiel 2003). A relative humidity of 98–100% is reported to be optimum for long-term storage at +0-10 °C (Van Den Berg and Lentz 1973). Consequently, to avoid weight losses, potatoes are usually stored at a relative humidity of at least 90 % (Curty Personal communication).

4.3.2. Use of post-harvest treatments

4.3.2.1. Post-harvest treatments with synthetic molecules

4.3.2.1.1. CIPC and mechanisms of action

In the past decades, the anti-sprouting chemical chlorpropham (CIPC) applied as post-harvest treatment has been intensively used and is highly effective to prevent spouting during potato storage (Paul et al. 2016c). In addition to being highly effective, the cost related to the use of CIPC is low compared to the cost of most other anti-sprouting molecules (Curty Personal communication; Martin 2012). Another important benefit of CIPC use is that it requires little handling. Studies have shown that only one or two applications of CIPC are necessary to control sprouting depending on the duration of the storage period (Paul et al. 2016c). Usually the dose

is 18 g of CIPC (a.i.) per tonne of potatoes and for long-term storage two applications are made, with a total dose of 36 g (a.i.) of CIPC per tonne of potatoes (Paul et al. 2016c). Lewis et al. (1997) reported that only one application of CIPC at 22 mg a.i. per kg of potatoes (fresh weight) applied in hot fogging was enough to control sprouting for up to ten months of storage.

CIPC acts by inhibition of mitosis in potato cells (Wiltshire and Cobb 1996; Nurit et al. 1989). Nevertheless, the registration of the use of this molecule in potato storage has recently been removed from the European market by European Union (EU) authorities to due to a potential risk of toxicity for humans by the CIPC molecule and its metabolite 3-Chloroaniline (European Food Safety Authority (EFSA) et al. 2017; European Commission 2019a). The non-renewal of the CIPC in Europe is prompting the potato value chain to find sustainable alternative strategies to store potatoes without sprouting to avoid losses. To delay sprouting in potato storage without CIPC, several alternative anti-sprouting molecules, natural or chemical are already available and are described below.

4.3.2.1.2. Alternative synthetic molecules for post-harvest treatments

1,4-DMN is a natural compound originally discovered in the volatile profile of dormant potatoes (Jina Personal Communication). Only limited quantitative information is available on the natural background of 1,4-DMN in plants, however natural levels up to 0.061 mg/kg have been reported in potato tubers (European Food Safety Authority 2014). The compound was chemically synthesized and developed into a commercial product to be applied on potato (Jina Personal Communication). 1,4-DMN based products (e.g., 1,4SIGHT® or DORMIR®) are applied by hot fogging with several applications during the storage season. 1,4-DMN initiates transcriptional changes resulting in repression of genes associated with growth, and acts by prolonging potato dormancy (Jina Personal Communication).

3-decen-2-one compound is a 10-carbon unsaturated ketone that is naturally found in some mushrooms such as *Boletus edulis* (Burdock 2010) and *Lactarius hatsudake* (Miyazawa et al. 2010). 3-decen-2-one can also be found in tuna and many foods such as soy, ham, yogurt and spices (EPA 2013b) and in fermented milk (Patrignani et al. 2009). 3-decen-2-one is also used as a flavoring agent in food in the U.S. (EPA 2013b; Burdock 2010). This compound can be used to control potato sprouting. It is synthetized and commercialized under the name SmartBlock®, which contains 98% pure 3-decen-2-one as the active ingredient (©AMVAC Chemical Corporation 2016). This product is currently commercialized to control potato sprouting in the U.S., Canada and Israel. This product is already approved as a food additive in the EU (EC 2002) and has a pending registration as a plant protection product in the EU (Immaraju Personal communication). SmartBlock® is applied by hot fogging and depending on storage conditions, only one to three applications are generally required during the storage season to control sprouting of potatoes stored at 4 - 5 °C, however it is possible to make up to four applications to control sprouting of processing potatoes stored at higher temperatures (Immaraju Personal communication). This product presents the

advantage to act as an excellent curative product with long residual activity, when applied to tubers after dormancy break or when sprouts are small (< 5 mm) (Immaraju Personal communication). SmartBlock® should be applied only by a qualified technician, however there is no recommended temperature for application (©AMVAC Chemical Corporation 2016). 3-decen-2-one acts by inducing rapid necrosis of sprout tissue within 24 hours after application by destroying the rapidly-growing meristematic sprout tissue (Figure 1-6) (Knowles and Knowles 2015b, a).

Figure 1-6. Potatoes treated with SmartBlock® (left) vs. untreated potatoes (right) (source of the photo: Dr Lisa Knowles, Washington State University).

4.3.2.2. Natural post-harvest treatments

4.3.2.2.1. Phytohormones

Ethylene is a hormone naturally produced by plants. Continuous applications of ethylene have been demonstrated to inhibit sprout elongation of potatoes (Rylski et al. 1974). Ethylene can be applied directly in the storage chamber using the « Biofresh Safestore » system from the Biofresh Company (Biofresh Group Ltd.), consisting of pure ethylene (i.e. 99.95 %) stored in pressured cylinders. The application of ethylene is managed by the Biofresh Ethylene Management Unit (EMU) that delivers controlled concentrations of ethylene in the storage chamber (BioFresh 2020). Ethylene can also be applied using an ethylene generator (from the Restrain® Company Ltd.). The generator produces ethylene gas from liquid ethanol directly in the storage chamber (© Restrain 2021).

4.3.2.2.2. Essential oils

Spearmint oil active ingredient is registered as an anti-sprouting product for potatoes in several countries in Europe (i.e. in at least 18 countries) and outside Europe (e.g., in the U.S.) (De Barbeyrac Personal communication). Spearmint oil (referred as « mint essential oil» in the rest of the document) is commercialized thought the product Biox-M® containing 65 % to 85 % of L-carvone (Sardo Personal communication). One possibility to apply this product is by thermal fogging using a special fogger (e.g., Electrofog®). Another possibility is to apply Biox-M® by cold evaporation using a special device (e.g., Xedavap®). The Electrofog® and the Xedavap® are proposed by the Xeda company (Xeda International SA). Biox-M® cannot be applied with any conventional fogger, such as those used for CIPC application because their fogging temperature is too high and the fogging application temperature of Biox-M® must be around 180 - 190 °C to avoid product degradation (Sardo Personal communication); and to avoid fire hazards, as the auto-ignition temperature of Biox-M® is 301 ± 5 °C (Xeda Safety Data Sheet, n° 192). The application by hot fogging necessitates several applications during the season, while the application by cold evaporation consists of continuous application of low quantities of product, which are diffused in the storage chamber. Biox-M® acts as both a preventive and curative product by necrosis of existing sprouts (De Barbeyrac Personal communication; Sardo Personal communication).

The potato sprout inhibitor, ARGOS®, contains orange oil 843.2 g L^{-1} (D-Limonene) active substance. ARGOS® was recently registered in several European countries. ARGOS® can be applied during storage using hot fogging. When applied by hot fogging, the recommended dose is 100 ml of product per tonne of potatoes with an interval of three weeks and the first treatment should be applied three to six weeks after the beginning of the storage (note that the interval can be increased according to the variety, temperature and type of storage) (UPL Benelux BV 2020). ARGOS® acts as a preventive and curative product (Bonnet, Personal communication) as ARGOS® burns the sprouts and prevents them from growing (UPL Benelux BV 2020). ARGOS® prevents potato germ growth by acting upon contact with tubers and disrupting the growing point of newly emerging sprouts and burning them off (UPL 2021). For hot fogging application, it is critical to avoid fire risk by using only temperature-controlled equipment. ARGOS® has a self-ignition temperature of 248 °C and the fogging temperature must imperatively be no higher than 190 °C. The product can also be applied by cold fogging using specified equipment (UPL Benelux BV 2020).

In the literature, other natural compounds have been tested for the control of potato sprouting, such as components from the mint essential oil (other than carvone) (Coleman et al. 2001); peppermint and clove extracts (Kleinkopf et al. 2003) or Muña plant extracts (Manrique Klinge and Egúsquiza Palomino 2009). However, these molecules did not benefit from the same commercial distribution as the above-mentioned molecules.

Some of the above-mentioned alternative molecules to CIPC have been commercialized for a long time; however, their use was not significant in conventional farming because the CIPC cost-affordability and high efficacy made it the most used anti-sprouting molecule so far. Besides, these alternative molecules may present drawbacks; some of them have just been authorized in the EU or were not used as extensively as CIPC in the EU in the past decades. Consequently, trials are necessary to learn how to use these alternative molecules on a large scale and in industrial conditions and to have hindsight and anticipate eventual problems with the use of these molecules. It will be important to get familiarized with the method of application of these alternative molecules, which are often more constraining than CIPC application methods. It will be necessary to evaluate potential problems and challenges related to the use of these alternative molecules, such as potential variety-dependent interactions of product efficacy, induction of sweetening or residues in final products. Identifying potential problems will help to find solutions and adapt storage management strategies with these alternative molecules.

5. Research objectives

To increase sustainable potato production, farmers and potato industry will need to use new combined strategies and new tools to maintain high quality potato stocks for months and avoid important economic losses.

Sprouting of ware potatoes is governed by several above-mentioned complex parameters, from the choice of the genotype to the effect of pre- and post-harvest environment and management factors, as well as their interactions. To study and better understand the influence of these parameters on potato sprouting, we have introduced a new concept called the “storage system of ware potatoes” (Figure 1-7). To define this “storage system of ware potatoes”, we took inspiration from the “pathosystem” definition described as: “A pathosystem is comparable to an ecosystem. Indeed, a pathosystem is a subsystem of an ecosystem and is defined on the basis of parasitism. In particular, the term pathosystem emphasizes that the whole subject of crop loss due to parasites is one system, and not several, entirely distinct systems as implied by the disciplines of plant breeding, plant pathology, entomology, nematology, and so on.” (Robinson 1976).

As in a pathosystem, the undesirable potato sprout could be considered as the parasite and the potato as the host. The potato has properties of resistance to sprouting, meaning that according to the genotype, the dormancy may vary and the potato will be more or less resistant to sprouting.

The “storage system of ware potatoes” must be a multidisciplinary concept and should be studied in a large view with the study of the influence of genotype by environment by management (G x E x M) interactions on potato sprouting (Figure 1-7). In this “storage system of ware potatoes”, the sprouting of a potato tuber is controlled by the intrinsic properties of the potato and by its environment. In the

present thesis, the focus is on interactions within and between the genotype (G) of potato and the environment (E) during the growing season and during storage, as well as the influence of human intervention by management (M) both during the growing season and during storage (Figure 1-7). Studying the different parts of this "storage system of ware potatoes" is of high importance to understand sprouting of ware potatoes and to implement sustainable management strategies to mitigate sprouting during storage. In the present thesis, different aspects of this "storage system of ware potatoes" have been studied.

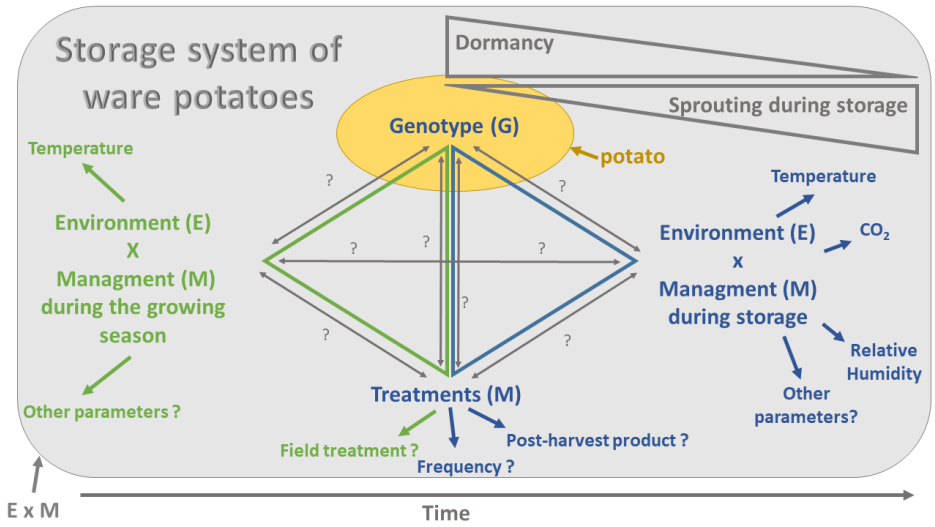

Figure 1-7. Conceptual diagram representing a potato storage system "storage system of ware potatoes" with main factors influencing sprouting during storage of potatoes; double grey arrows with a question mark (?) represent potential interactions between factors which must be studied.

Several above-mentioned strategies are available but present gaps and drawbacks and several questions related to the appropriate use of these strategies would still need to be determined. These strategies need to be improved and further scientific knowledge is required to fully unlock their potential. It will be necessary to further evaluate and quantify the effect of several factors influencing potato sprouting (e.g., genotype and pre- and post-harvest treatments). The effect of the environment and the management during the growing season and during storage on potato sprouting must also be studied further. Eventual interactions between these factors have to be evaluated to improve potato storage management (Figure 1-7).

The main objective of the thesis was to find economically suitable and sustainable management strategies to control potato sprouting. To efficiently answer to this main objective, four major emerging research questions (RQs) can be addressed.

RQ1- Is genotype the main factor influencing dormancy?

RQ2- Is it possible to predict potato dormancy to improve potato storage?

RQ3- Are there anti-sprouting molecules suitable to replace the CIPC in a sustainable way?

RQ4- What is the potential of cold storage to improve potato storage?

In this thesis, we will answer to those questions through five chapters (from chapter two to chapter six) as follows:

In the second chapter, the effect of the genotype and of several factors representative of management and environment during both the growing season and storage on potato dormancy was investigated. The aim was to identify and quantify the influence of several predictors on dormancy duration and to build a predictive model of dormancy. We performed an analysis with 3,379 records of multi-environment trials collected in Switzerland over 25 years in five different locations with contrasting environments, in which 537 genotypes were tested. To build the predictive model, about 250 predictors were tested using a forward selection approach. This chapter provides answers to RQs 1 and 2 (Figure 1-8).

In chapters 3 and 4, we evaluated the efficacy of pre- and post- harvest anti-sprouting treatments, natural or synthetic, to replace CIPC for potato storage. The objective was to identify treatments suitable to replace CIPC to control sprouting of processing potatoes and to get insight into the efficacy of these alternative treatments. Results will provide advice to farmers and to the potato industry in terms of choice of alternatives to CIPC. In this study, the efficacy of seven molecules was investigated (i.e. CIPC, MH, 1,4- DMN, 3-decen-2-one, ethylene, L-carvone and D-limonene) on several varieties and under different storage conditions (i.e. experimental, semi-industrial or industrial) according to the tested molecules. These chapters provide answers to RQ 3 (Figure 1-8).

The research performed in chapter 5 aimed at identifying varieties suitable for storage at low temperature (i.e. 4 °C) without CIS. Six processing varieties (i.e. Verdi, Lady Claire and Kiebitz, Agria, Markies and Pirol) were stored at three temperature regimes (i.e. 4 °C, 8 °C and 4 °C with reconditioning up to 15 °C). The effect of a reconditioning up to 15 °C after a storage at 4 °C was also evaluated in tubers of the varieties Verdi and Markies. Several parameters related to sweetening were analyzed after two and/or four months of storage (i.e. sucrose, total reducing sugars, glucose, crisps quality, asparagine and acrylamide content). To better understand the genetic metabolism involved in CIS, Vacuolar invertase (*VInv*) gene expression was measured in the six varieties stored at the three temperature regimes. This chapter answers RQ 4 (Figure 1-8).

The present thesis ends with a general discussion, which answers the main objective of the thesis (Figure 1-8) as we discuss the practical potential of the different strategies presented in chapters two, three, four and five and the implementation and combination of the strategies to cope with the CIPC non-renewal. The end of this discussion finishes with a conclusion and some future perspectives and gaps to fulfill to improve these strategies in the future.

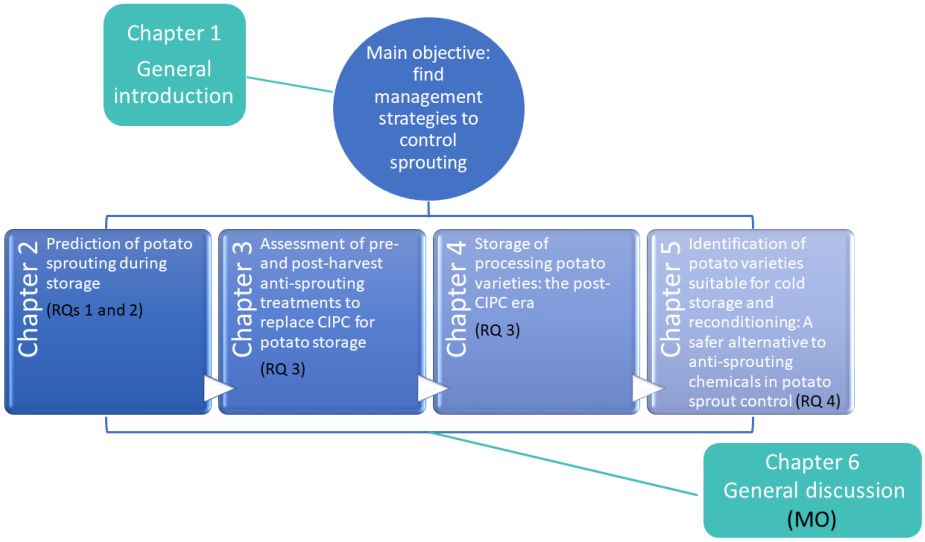

Figure 1-8. Diagram of the thesis chapters and main objective or research questions answered in the different chapters (i.e. main objective (MO) = to find economically suitable and sustainable management strategies to control potato sprouting & research questions (RQ): RQ1- Is genotype the main factor influencing dormancy?; RQ2- Is it possible to predict potato dormancy to improve potato storage?; RQ3- Are there anti-sprouting molecules suitable to replace the CIPC in a sustainable way? And RQ4- What is the potential of cold storage to improve potato storage?).

Chapter 2

Prediction of potato sprouting during storage

Adapted from: Margot Visse-Mansiaux*; Hélène Soyeurt*; Juan Manuel Herrera; Jean-Marie Torche; Hervé Vanderschuren; Brice Dupuis. Prediction of potato sprouting during storage. Article submitted to Field Crop Research. (*co-first authors)

Outline

The information of potato dormancy duration of a given variety for a given storage season is an important parameter within potato storage management. However, the dormancy information is not available for all varieties. In addition, the information for a given variety can be variable according to the source or to the year as previous studies reported that the dormancy is subject to change according to several parameters during the growing season. Therefore, improving potato storage management with an accurate forecast of the sprouting is a good option to reduce losses due to sprouting and the expenses generated by the treatments with anti-sprouting products. Previous research studied the effect of some parameters during the growing season on potato dormancy during storage, however these studies have been conducted on small data sets and further research is required to improve knowledge of this trait for a better management of potato storage. This chapter two aims to identify and quantify the effect of both management and environment during the growing season on potato dormancy duration. This study also aims to propose a robust predictive tool of potato dormancy based on parameters during a given growing season for a given variety to support farmers in improving their potato storage management. This study presents the advantage of using a large data set with more than 500 varieties tested with records from multi-year and multi-environment trials. In a context of climate change, understanding genotype by environment interactions driving the potato dormancy will be of interest to avoid crop losses.

Abstract

Potato sprouting during storage occurs after a break in dormancy, leading to a decrease in quality and consequently economic losses. We used 3,379 records from multi-year and multi-environment trials of 537 potato varieties to identify the main factors driving potato dormancy and to develop predictive models for an efficient sprouting forecast. The variety explained the majority of the dormancy variability (60.3%), followed by the year (13.9%) and the location (5.4%). About 250 predictors were considered to develop a predictive model of potato dormancy. The best model had a validation precision of 14.59 days; it used the variety class and the sum of the daily maximum temperatures in the air during the period from planting to harvest as predictors. The predictions of the best model were validated in vivo using dormancy measurements from potato varieties grown under different temperature regimes in greenhouse conditions. With the growing impact of climate change on crop production, predictive models as developed here can provide an efficient and cost-effective tool to optimize the control of potato sprouting during storage.

Keywords: potato dormancy, multi-environment trials, weather, predictive analytics, climate change, models

1. Introduction

After harvest, the potato value chain requires long-term storage to supply high-quality potatoes for year-long processing to satisfy market requirements. The evolution of physiological age leads to the breaking of dormancy and thus to the sprouting of potatoes during storage (Delaplace et al. 2008). Sprouting alters potato quality by causing shrinkage, weight loss, and a decrease in turgidity (Alexandre et al. 2015; Sonnewald and Sonnewald 2014; Teper-Bamnolker et al. 2010) and therefore must be controlled.

Various approaches are used to control potato sprouting, such as decreasing storage temperature (Blauer et al. 2013; Magdalena and Dariusz 2018; Muthoni et al. 2014), using chemicals to delay sprouting (Corsini et al. 1979; Mahajan et al. 2008; Paul et al. 2016b), or using the dormancy length of potato varieties to manage storage (Magdalena and Dariusz 2018). The first approach may not be adequate for the storage of potatoes dedicated to processing, as most varieties are susceptible to sweetening when stored at low temperatures. This phenomenon of sweetening due to the accumulation of reducing sugars is also called "cold-induced sweetening" (CIS) (Hou et al. 2017; Sowokinos 2001). High sugar levels induce browning of the potato after frying and produce toxic compounds such as acrylamide that may raise concerns for human health (Paul et al. 2016b; Wiberley-Bradford and Bethke 2017). The advantage of using anti-sprouting products is their broad effectiveness for any variety at any temperature. However, some products are associated with a risk of toxicity for the consumer, and there is an increasing demand from consumers and national agencies for food free of chemical products. Indeed, chlorpropham (CIPC) has been used for decades to control sprouting in potatoes, but the European Union recently decided to not renew the approval of this molecule due to concerns raised for consumers regarding this active substance and its metabolite 3-chloroaniline, and due to the identification of data gaps preventing to perform a final consumer risk assessment (European Commission 2019a; European Food Safety Authority (EFSA) et al. 2017). The metabolites of CIPC, such as aniline, have further increased concerns for consumers since those molecules have been detected in the potato's skin (Orejuela and Silva Poma 2005; Paul et al. 2014; Smith and Bucher 2012). Molecules that pose fewer health risks have been recently commercialized, and they seem promising as replacements for CIPC, but their costs remain high; some require several applications to be effective during the entire storage season, which is time-consuming (Curty Personal communication), and it is unclear whether consumers and authorities will accept them in the future. Therefore, using potato varieties with a long dormancy period could be a sustainable solution to avoid or delay the sprouting of potatoes, thus avoiding or eliminating the use of anti-sprouting products and consequently increasing the benefits for human health and the environment. However, the dormancy of potato varieties is not known for all varieties, or information found about dormancy is sparse and conflicting (Agriculture and Horticulture Development Board (AHDB) 2019). Therefore, in this context, predicting potato dormancy is of great interest for

the management of storage. For instance, the capacity to predict potato dormancy may allow the processing of priority batches of short-dormancy varieties, thus minimizing or avoiding the use of chemicals and optimizing the management of stocks.

Potato sprouting appears during storage after a break in the dormancy period (Coleman 1987; Daniels-Lake and Prange 2007), but the definition of dormancy is subject to discussion. Reust (1982) described dormancy as the "period between tuber initiation and the development of the first sprouts". Emilsson (1949) mentioned a «rest period» where the potatoes are unable to sprout and a «dormancy period» where the tuber is maintained without sprouting under optimal conditions. Three periods were also defined: endodormancy regulated by physiological factors internal to the meristem, paradormancy regulated by external physiological factors, and ecodormancy. During this last period, dormancy can be maintained under specific environmental conditions (Delaplace 2007; Lang et al. 1987). It is necessary to take into consideration that the length of this period depends on complex mechanisms to predict potato dormancy. In the literature, authors have reported that varieties display differential responses in dormancy length (Aksenova et al. 2013; Burton 1978; Danieli et al. 2018; Daniels-Lake and Prange 2007; Magdalena and Dariusz 2018; Muthoni et al. 2014; Suffle et al. 2016). However, dormancy is also influenced by phytohormones, metabolites, and environmental conditions during both the growing season and storage (Aksenova et al. 2013; Delaplace 2007; Delaplace et al. 2009; Muthoni et al. 2014; Reust 1982; Sonnewald and Sonnewald 2014). Factors related to the growing season that influence dormancy include the temperature (Levy and Veilleux 2007; Magdalena and Dariusz 2018; Muthoni et al. 2014; Reust 1982; Zommick et al. 2014), the water supply (Czerko and Grudzińska 2014; Muthoni et al. 2014), the soil humidity (Firman et al. 1992), the soil fertility (Muthoni et al. 2014), and the photoperiod (Fernie and Willmitzer 2001; Muthoni et al. 2014). Firman et al. (1992) studied the importance of soil moisture and physiological age on the emergence of seed tuber sprouts in the field. They showed that temperature influenced the growth rate of sprouts and demonstrated that the growth rate is different in dry soil compared to wet soil. After harvest, the temperature and the atmosphere composition during storage also play important roles in dormancy duration (Aksenova et al. 2013; Burton 1958; Caldiz 2009; Celis-Gamboa et al. 2003; Czerko and Grudzińska 2014; Daniels-Lake and Prange 2007; Magdalena and Dariusz 2018; Muthoni et al. 2014; Reust 1982; Reust et al. 2001; Struik 2007b, a; Struik et al. 2006; Suttle 2007).

The dormancy of the different potato varieties is subject to change depending on the above-mentioned factors. Most of these environmental parameters will be affected in the future by climate change; therefore, it is of interest to identify and quantify the main variables influencing dormancy duration. This would allow the building of a robust predictive model of dormancy parametrized with predictors that are easy to record in the field. The limitations of previous studies conducted on the same topic include the small sizes of the datasets used and the use of only a few varieties, or only a few years of trials. In the present study, we took advantage of an unprecedented large dataset containing dormancy observations obtained from field trials managed

under contrasted environmental conditions by Agroscope (Nyon, Switzerland) over a period of 25 years.

Given the increasing climate variability, dormancy models can enable the improvement of potato storage management and reduce losses caused by sprouting.

2. Materials and methods

2.1. Data collection and preparation

2.1.1. Field trials

Field trials have been conducted during 25 growing seasons (from 1990 to 2014) by Agroscope, the Swiss agricultural research center, in five experimental sites located at different altitudes in Switzerland, namely "La Frêtaz" (elevation of 1200 m asl), "Les Mottes" (elevation of 455 m asl), "Grangeneuve" (elevation of 680 m asl), "Goumoëns" (elevation of 609 m asl), and "Changins" (elevation of 420 m asl). A total of 537 varieties were tested, and each was included in at least three different experiments, allowing the acquisition of 3,379 records. All varieties tested were varieties registered in the official European variety catalog. They are listed in the table A-1 in appendix. Potatoes were planted from March to June and harvested from August to September, depending on the year and location. The soils were fertilized when necessary following the usual agricultural practices. Before potato emergence, a herbicide was applied according to the best management recommendations each year. Haulm destruction was implemented with a combination of chemicals (various products) and mechanical treatments (the EnviMaxX machine from Rema environmental machinery B.V., the Netherlands). Potatoes were treated to prevent late blight (*Phytophtora infestans*) approximately once a week from emergence to haulm killing, using various fungicides. After harvest, potatoes were stored at room temperature (around 15 °C) for two weeks in the dark to promote healing. Then, the potato tubers were calibrated, weighed, and stored in wooden crates (0.6 x 0.4 x 0.18 m) at a rate of 10 kg per crate for each variety, trial, and location. The tuber diameter used for the post-harvest trials ranged from 42.5 mm to 70 mm. The temperature was gently decreased from 15 °C to 8 °C at a rate of 3°C every 48 hours, and potatoes were kept at 8 °C and 85% relative humidity (RH).

During the 25 studied growing seasons, the following weather data were collected from Agrometeo (https://www.agrometeo.ch/, accessed 2017) and from MeteoSwiss (Federal Office of Meteorology and Climatology MeteoSwiss, Switzerland): the daily average temperature (°C) in the air at two meters above the soil; the daily minimum temperature (°C) in the air at two meters above the soil; the daily maximum temperature (°C) in the air at two meters above the soil; the daily average temperature (°C) at the level of the soil (i.e., at five cm above the soil); the daily average soil temperature (°C) at a depth of 10 cm; the daily average relative humidity (%); the daily precipitation (mm); the daily maximum precipitation intensity (= maximum precipitation per hour registered in the day) (mm h^{-1}); and the daily average insolation

(= solar irradiance) (MJ m-2). Plots were only irrigated for a few growing seasons and only at the "Changins" location. Irrigation data were handled by adding the water amounts per day to the daily precipitation data. The tuber initiation date was recorded for one location (Goumoëns), eight years and 67 varieties, which allowed the acquisition of 126 records. To fill this data gap, we set 16 days after the emergence as the date of theoretical tuber initiation for all locations in the dataset where this information was missing. This value was obtained by averaging the period from emergence to tuber initiation date from the tuber initiation recorded for the 67 tested varieties (average = 16.37 days). The standard deviation of tuber initiation was 4.05 days, representing less than 5% (3.04%) of the entire growing period (from planting to harvest), which was on average equal to 132.94 days in the dataset. The date of the main physiological stages of the crop (i.e., planting, emergence, tuber initiation, and maturity) and the dates of crop management operations (e.g., haulm killing and harvest) were also recorded and used to define the following periods: from planting to emergence, from planting to tuber initiation, from planting to haulm killing, from planting to harvest, from emergence to haulm killing, from emergence to harvest, from tuber initiation to haulm killing, from tuber initiation to harvest, and from haulm killing to harvest. For all these periods, the above-mentioned weather data (e.g., temperature, precipitation, or relative humidity) were summed and/or averaged for each period and recorded in the database (list in the Table A-2 in appendix). During storage, potatoes were considered sprouted when 80% of tubers in the crate had visible sprouts of a minimum length of three mm, according to the definition of the end of dormancy established by Reust (1982, 1986). The sprouting date was recorded at the time that the tubers first displayed the characteristics described the abovementioned definition. In this study, we will consider the dormancy period as follows: the period between the harvest and the sprouting date during storage.

2.1.2. Greenhouse trial

A greenhouse trial was conducted in which seed tubers of the Bintje variety were placed at 18 °C and under light for 18 days to stimulate germination before planting. A total of 42 tubers were planted in square pots of 10 liters following good practices for greenhouse trial management. A standard soil was used (Swiss mixture from the company RICOTER Erdaufbereitung AG, mixture for organic gardening, Switzerland; composition: 30% white peat 0–30 mm; 30% country soil sterile and 40% Coco-Peat) and mixed with substrate for plant cultivation (Gerbr. Brill Substrate GmbH & Co. KG, Typ 4, Germany) (ratio 2:1). Ammonium nitrate fertilizer was added and mixed into the soil mixture; about 30 g of fertilizer were mixed with 100 liters of soil mixture (ammonium nitrate fertilizer composition: total N = 27% + total Mg = 2.5% and Ca = 9%, LANDOR fenaco Genossenschaft, Switzerland). Plants were kept in the same room at ambient temperature for 10 days, corresponding to 99% emergence (average temperature of 17°C). The 42 plants were divided into seven greenhouse chambers and grown at two different temperatures (15 or 20°C), with four chambers at 15 °C (four replicates) and three chambers at 20°C (three replicates). Data loggers (LogTag® temperature recorder, model: TRIX-8, Amatempérature Sàrl,

Switzerland) were placed close to the plants from planting to harvest to measure the air temperature for each replicate (one record per hour). Plants were irrigated manually two or three times a week, and a photoperiod of 12 hours of light and 12 hours of dark was applied. To prevent infestation by thrips (*Thrips tabaci, Frankliniella occidentalis*), we placed *Amblyseius cucumeris* auxiliaries in each plant (Andermatt Biocontrol Suisse AG). Potatoes were haulm killed 67 days after emergence and harvested 34 days after haulm killing to allow proper skin set. The harvested tubers were calibrated for each plant to identify the proportion of tubers (number and weight) smaller and larger than 32 mm. The average weight per tuber of each caliber and from each plant was calculated by dividing the total weight of tubers per plant by the number of tubers per plant. The tubers were then stored in a storage chamber at 12 °C and 85% RH for one week to stimulate healing, and then the temperature was lowered to 8 °C at a rate of 2 °C every four days. Sprouting assessment was performed every two weeks. The length of the biggest sprout of each tuber and from each plant was measured.

2.2. Data analysis

The R software version 3.6.3 (R Core Team, 2019) was used for data preparation and statistical analysis.

2.2.1. Field trials

An analysis of variance (ANOVA) was conducted to confirm the effect of the factors variety, location, and year on the potato dormancy duration. In this analysis, the 25 years of trials were considered, as well as the five locations and the 537 tested varieties. A given variety for a given year was considered as the experimental unit, and the dormancy duration from harvest until sprouting date was accessed for each experimental unit. This allowed the acquisition of 3,379 records (see section 2.1.1.). The percentage of the variability explained by each factor was calculated by the ratio of the sum of squares for the considered effect to the total sum of squares.

As some varieties were only tested three times during the 25 years of testing, the prediction of the dormancy for those varieties could be less reliable due to a lack of sufficient reference dormancy values. Therefore, the estimates for the variety effect given by the ANOVA model were used to define an additional explanatory variable called “variety class”. Based on these estimates, varieties tested fewer than ten times during the 25 years of testing were placed in the same variety class as the varieties closest in dormancy that were tested more frequently. However, all varieties that were tested at least 10 times were kept to limit the bias that could come from the effect of combination with other varieties less tested. Finally, 143 different variety classes were identified: 85 classes containing grouped varieties and 58 classes containing individual varieties (i.e., tested at least 10 times).

A validation was performed using one third of the records (randomly selected) for each variety class (N = 1,102) to assess the accuracy of the developed prediction model. The remaining samples were used to calibrate the model (N = 2,277). This

splitting was done using the CARET package version 6.0-86 in R (Kuhn 2020) that ensures the presence of all varieties in both the validation and calibration sets. The predictors used in the regression were previously mentioned in the data section; however, variety class was used instead of variety. Moreover, the location and the year of testing were not retained in the prediction model because they were characterized by the weather predictors. Consequently, 247 predictors were considered to develop the model predicting potato dormancy. All predictors were not available for all records. The completeness of the calibration set varied from 44.1% (N = 1,005) to 100% (N = 2,277) as follows: 94 predictors had a completeness of at least 75%, 131 predictors had a completeness ranging from 50% to less than 75%, and 22 predictors had a completeness of less than 50% (Table A-2 in appendix).

The predictive model was built using a forward selection approach for the predictors. So, the predictors were added to a linear model one by one. First, 247 univariate regressions were performed. For each model, the following statistical parameters were calculated: the coefficient of determination (R^2c), the root mean square error (RMSEc) of the calibration, the RMSE (RMSEv), and the R^2 of the validation (R^2v). The predictor included in the univariate model with the highest R^2v was kept. Then, bivariate regressions were developed by fixing the first retained predictor and testing the remaining 246 variables as the second predictor. Again, the second predictor was selected based on the model that gave the highest R_2v. This procedure was repeated until the inclusion of an additional predictor in the model explained less than 1% of the additional variability in dormancy. This allowed us to avoid the potential problem of overfitting. Finally, all estimates of the prediction model were studied to determine whether the model generated an expected weight for all selected predictors.

2.2.2. Greenhouse trial

The sum of daily maximum temperatures in the air from planting to harvest for each replicate (3 replicates for plants grown at 20 °C and 4 replicates for plants grown at 15 °C from emergence to harvest) was calculated using the maximum temperature recorded per day (one record per hour).

Data for all measured variables of the six plants per greenhouse chamber were averaged before the analysis. Our experiment was conducted using a nested design. We used a one-way linear mixed model with the temperature of growth as a fixed effect (15 and 20 °C) to evaluate the number of small and large tubers and the average weight of small or large tubers after harvesting. The length of sprouts was fitted to a two-way linear mixed model that included temperature (two levels: 15 and 20°C) and the period of observation (days after harvest = DAH, four levels) as fixed effects. Models were adjusted using the lme4 R package version 1.1-23 (Bates et al. 2015). The data for the length of the sprouts were transformed using “log (x+1)” to ensure the homogeneity of the variance and normality. The greenhouse chambers were considered a random factor for all the models. The effect of the greenhouse chambers was removed to improve the model when this effect was not significant. We performed significance tests for the fixed effects for the measured variables (with a

confidence interval of 95%) using a Chi-square test or an F-test in cases where the effect of the random factor was not significant. Calculations were performed using the "car" R package (Fox and Weisberg 2019). The marginal post hoc Tukey test (emmeans method) using the "emmeans" R package (Lenth 2020) was used to compute the multiple comparison post hoc tests to identify mean differences within factors and interactions. For data summary and graphics, we used various R packages ("ggplot2", "plyr", "Rmisc", "lattice", and "cowplot" packages) (Hope 2013; Sarkar 2008; Wickham 2011, 2016; Wilke 2019).

3. Results

3.1. Main factors influencing potato dormancy

In this study, we considered dormancy as the period between the harvest and the sprouting date during storage. This definition is generally used in practice by the potato sector. The dormancy period varied from 27 days to 179 days, with an average of 96.29 days in the dataset (all varieties, years, and locations taken together). The variety effect explained 60.3% of the dormancy variability ($p < 0.001$). Among the 537 studied varieties, the dormancy period of the varieties varied on average from 50 (Lucera [N = 3]) to 158 days (Taurus [N = 3]). Several popular varieties had short dormancies (e.g., Agata, Annabelle, Nicola, or Amandine, which displayed an average dormancy of 57 days [N = 22], 57 days [N = 16], 72 days [N = 25], and 75 days [N = 20], respectively), while other popular varieties had long dormancies (e.g., Agria, Panda, Lady Claire, or Verdi, which displayed an average dormancy of 131 days [N = 96], 130 days [N = 24], 120 days [N = 68], and 120 days [N = 10], respectively) (Figure 2-1).

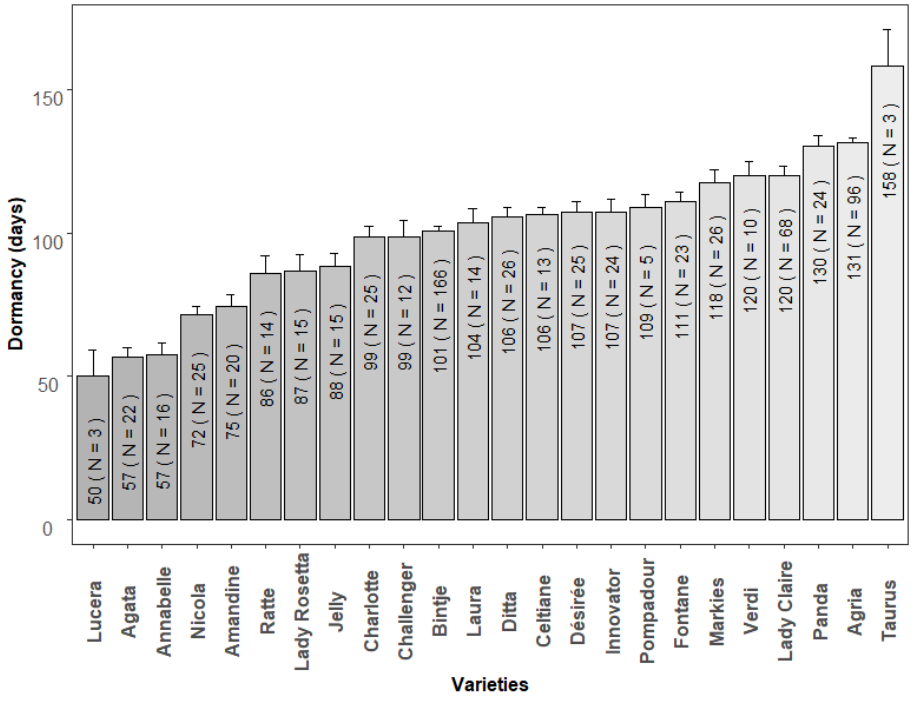

Figure 2-1. Average days of dormancy with their standard errors observed for popular tested varieties. The number of records (N) available for each variety is indicated on the bars.

The year effect explained 13.9% of the dormancy variability ($p < 0.001$). For instance, during the 25 years of testing for the Bintje variety, the observed dormancy ranged from 67 days (N = 7) to 125 days (N = 9) (Figure 2-2).

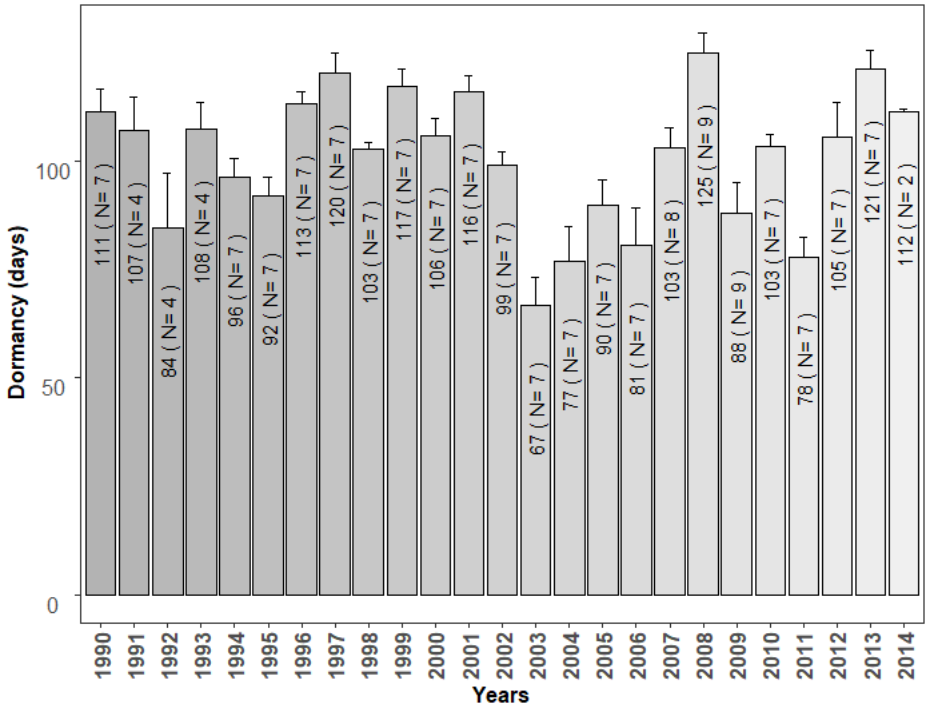

Figure 2-2. Average days of dormancy (days) with their standard errors observed for the Bintje variety during the 25 years of tests. The number of records (N) available for each year is indicated on the bars.

The location effect was less important than the two above-mentioned effects and explained 5.4% of the dormancy variability ($p < 0.001$). The average dormancy observed in the location "Changins" was 93 days (N = 2,138), while in the "La Frêtaz" (N = 576), "Goumoëns" (N = 219), "Grangeneuve" (N = 330), and "Les Mottes" (N = 116) locations, the average dormancies were 110, 100, 92, and 88 days, respectively.

3.2. Prediction model of potato dormancy

A total of 247 univariate linear regressions were initially performed using the calibration set and then applied to the validation set. R^2v ranged from 0.00 to 0.52, and RMSEv varied between 18.49 and 27.53 days. For the sake of conciseness, all models are not shown; only the five best models are presented (Table 2-1). The model explaining the majority of the dormancy variability included the variety class as a fixed effect. The corresponding R_2v was 0.52, which is well ahead of all other models (Table 2-1). The R2c was close to R_2v (0.58 and 0.52), suggesting good model robustness. The RMSEv was 18.49 days. The univariate model including the sum of the daily maximum temperatures from tuber initiation to harvest had the highest R_2v after the model that included the variety class (Table 2-1). The different sample sizes

used in the calibration and validation set between the predictors are related to data availability, which may vary for the predictors used. The 247 predictors and the corresponding number of records for each predictor are listed in the Table A-2 in appendix.

Table 2-1. Calibration and validation prediction performance of the five best univariate models predicting potato dormancy.

Dormancy ~ predictor	Calibration			Validation		
	N	R^2	RMSE (days)	N	R^2	RMSE (days)
Variety class	2,277	0.58	17.90	1,102	0.52	18.49
Sum of the daily maximum temperatures in the air for the period from tuber initiation to harvest	1,754	0.17	23.98	839	0.16	24.24
Sum of the daily average temperatures in the air for the period from tuber initiation to harvest	1,746	0.16	24.12	835	0.16	24.25
Sum of the daily maximum temperatures in the air for the period from emergence to harvest	1,730	0.16	24.06	822	0.16	24.23
Sum of the daily average temperatures in the air for the period from emergence to harvest	1,722	0.15	24.23	818	0.15	24.27

N = number of samples, R^2 = coefficient of determination, RMSE = Root mean squared error.

For the second step in the development of the predictive model, bivariate models that always included the variety class plus one of the 246 remaining explanatory predictors were evaluated. R^2v ranged from 0.41 to 0.70. RMSEv varied between 14.59 and 20.94 days. The five bivariate models with the best values for goodness of fit are presented in Table 2-2. It is important to note that the five predictors represent temperature parameters. The differences in prediction performance between models (Table 2-2) were less important than those observed between variety class and other tested predictors in the univariate models (Table 2-1). The model with the highest goodness of fit for validation (R^2v and RMSEv) relied on data with few missing records. This model included the sum of the daily maximum temperatures in the air during the period from planting to harvest as a second predictor (Table 2-2) and explained 70% of the variability in dormancy ($R^2v = 0.70$). The RMSEv was 14.59 days. By subtracting the part of the variability explained by the univariate model including only the variety class, we can conclude that this second predictor explained an additional 18% of dormancy variability. Based on the regression coefficient (-0.02), the sum of the daily maximum temperatures in the air during the period from planting to harvest had a negative influence on potato dormancy.

A second validation analysis was performed to assess the robustness of the above-mentioned bivariate model. The bivariate models were run with a smaller set of data used for the validation containing the same amount of data for all the tested variables (N = 454 instead of N = 1,048). We observed that the bivariate model with the highest goodness of fit for validation is the same for both dataset (RMSEv = 14.92 and RMSEv = 14.59). This validation analysis confirms the robustness of the selected bivariate model with the sum of the daily maximum temperatures in the air during the period from planting to harvest as second predictor.

Table 2-2. Calibration and validation prediction performance of the five best fitted bivariate models predicting potato dormancy.

Dormancy ~ variety class + predictor	Calibration			Validation		
	N	R^2	RMSE (days)	N	R^2	RMSE (days)
Sum of the daily maximum temperatures in the air for the period from planting to harvest	2,175	0.72	14.32	1,048	0.70	14.59
Sum of the daily maximum temperatures in the air for the period from tuber initiation to harvest	1,753	0.73	14.31	839	0.69	14.75
Sum of the daily maximum temperatures in the air for the period from emergence to harvest	1,729	0.73	14.25	822	0.69	14.70
Sum of the daily average temperatures in the air for the period from planting to harvest	2,167	0.72	14.50	1,044	0.69	14.75
Sum of the daily average temperatures in the air for the period from tuber initiation to harvest	1,745	0.72	14.42	835	0.69	14.83

N = number of samples, R^2 = coefficient of determination, RMSE = Root mean squared error.

The third step in the development of the predictive model consisted of developing 245 models including three explanatory variables. The first and second predictors were the ones selected from the univariate and bivariate models, respectively. For the third step, the remaining predictors were evaluated. R^2v and RMSEv for the 245 developed models ranged from 0.66 to 0.71 and between 14.33 and 15.83 days, respectively. Table 2-3 summarizes the five best fitted three-trait models.

Table 2-3. Calibration and validation prediction performance of the five best fitted models predicting potato dormancy using three predictors.

Dormancy ~ variety class + sum of the daily maximum temperatures in the air for the period from planting to harvest + predictor	Calibration			Validation		
	N	R^2	RMSE (days)	N	R^2	RMSE (days)
Average of the daily average insolation data for the period from emergence to tuber initiation	1,546	0.75	13.80	736	0.71	14.33
Average of the daily maximum temperatures in the air for the period from planting to harvest	2,175	0.73	14.09	1,048	0.70	14.46
Average of the daily average insolation data for the period from haulm killing to harvest	1,901	0.74	14.17	919	0.70	14.60
Period from planting to harvest	2,175	0.73	14.18	1,048	0.70	14.51
Average of the daily average temperatures in the air for the period from planting to harvest	2,167	0.73	14.12	1,044	0.70	14.50

N = number of samples, R^2 = coefficient of determination, RMSE = Root mean squared error.

As already observed with the bivariate models, the differences in goodness of fit between the best candidate models were small. The model showing the highest R^2v included the average of the daily average insolation data for the period from emergence to tuber initiation as the third explanatory variable. This combination of variables explained 71% of the dormancy variability.

This corresponds to an increase of only 1.20% of R^2v compared to the bivariate model (Table 2-4). Therefore, the prediction accuracy of a model including three predictors was not highly improved compared to the selected bivariate model. Moreover, the average of the daily average insolation data for the period from emergence to tuber initiation that was included as the third explanatory variable in the model is not easy to collect in the field.

Table 2-4. Performance of the models including one to five predictors within the forward selection.

Number of predictors	Variable added to the model	Validation R^2	% of variability explained by the added predictor	RMSEv (days)
1	Variety	0.52	51.82	18.49
2	Sum of the daily maximum temperatures in the air for the period from planting to harvest	0.70	17.82	14.59
3	Average of the daily average insolation data for the period from emergence to tuber initiation	0.71	1.20	14.33
4	Average of the daily maximum temperatures in the air for the period from emergence to tuber initiation	0.73	1.75	13.90
5	Sum of the daily average soil temperatures at a depth of 10 cm for the period from maturity to harvest	0.74	1.30	14.01
6	Average of the daily maximum temperatures in the air for the period from planting to emergence	0.75	0.72	13.82

R^2 = coefficient of determination, RMSE = Root mean squared error.

Models with four, five, and six predictors were also tested, and we found R^2v values of 0.73, 0.74, and 0.75, respectively. Their respective RMSE values were 13.90 days, 14.01 days, and 13.82 days (Table 2-4). We did not go further than six predictors because the additional predictor explained less than 1% of the dormancy variability (Table 2-4). As observed for the models including three predictors, the models with four, five, and six predictors had only a marginal increase in R^2v and improvement of prediction accuracy compared to the selected bivariate model (Table 2-4). Thus, since the most robust model is always the most parsimonious, the best model is the one including two explanatory variables (Table 2-2). Moreover, this model had the advantage of including variables that are easy to record in the field.

3.3. Varietal differences in dormancy

The effect of variety was modeled as a categorical variable, and it was studied using the selected bivariate model. To improve the clarity of the variety estimates obtained by the ANOVA model, the estimate of the Bintje variety was used as a reference (i.e., estimate equal to 0), as this variety is the most tested in our dataset. The estimates for the main 58 individual varieties tested in our dataset are presented in Figure 2-3. Several varieties had estimates close to the estimate of the Bintje variety fixed at zero for this analysis, meaning that the dormancy of these varieties is close to the dormancy of Bintje. For instance, the dormancy of the varieties "Charlotte" (estimate = -2.26), "Gourmandine" (estimate = 0.64 days), "Granola" (estimate = 4.25 days), "Challenger" (estimate = - 2.87 days), "Erika" (estimate = 2.50 days), or "Juliette" (estimate = 3.47 days) were similar to the reference dormancy of the Bintje variety. In contrast, the variety "Agata" had a shorter dormancy of 42.57 fewer days compared to the Bintje variety. For the variety "Agria", dormancy was 30.09 days longer than the dormancy of the Bintje variety (Figure 2-3).

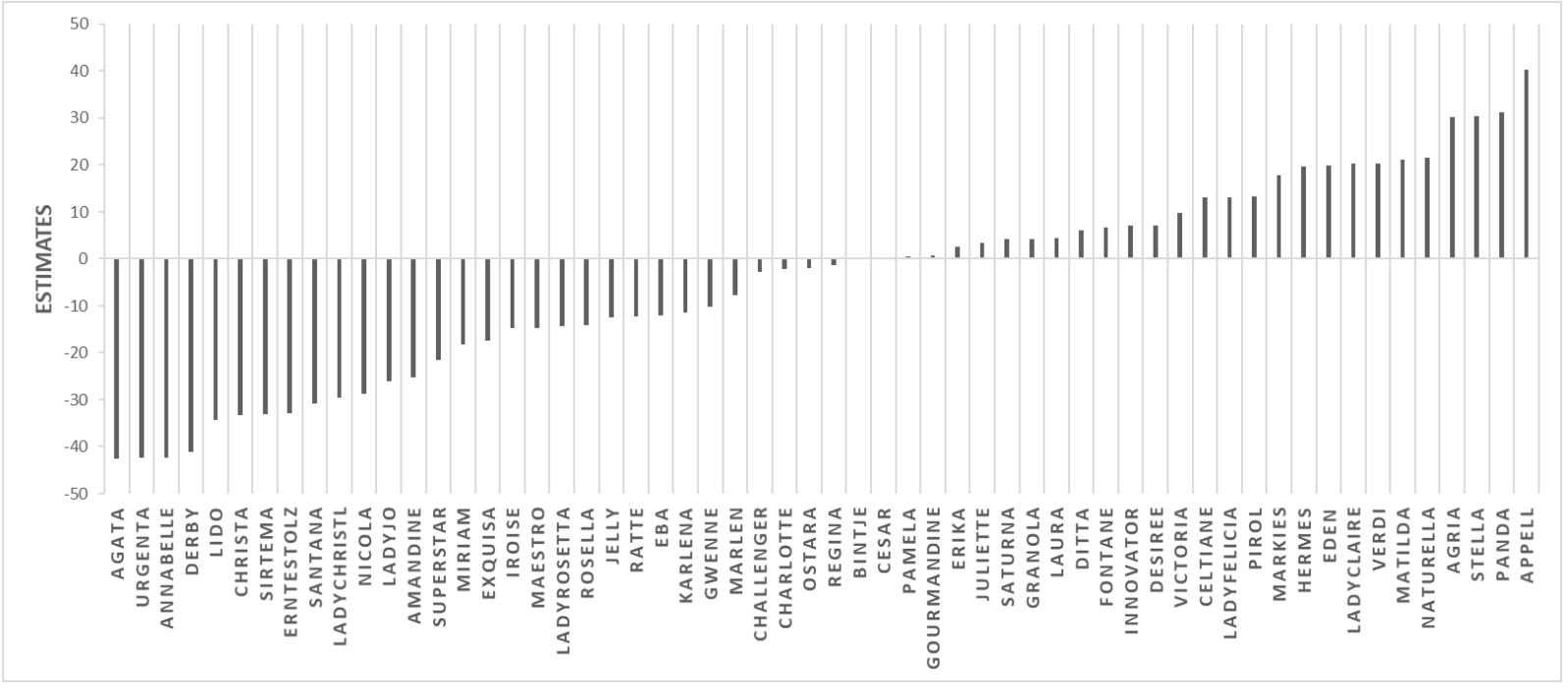

Figure 2-3. Dormancy estimates in days compared to Bintje obtained from the selected bivariate model for the 58 main tested varieties

3.4. In vivo validation of the model

Based on the composition of the bivariate model, after variety, the sum of the daily maximum temperatures in the air for the period from planting to harvest is the environmental factor that most influences dormancy variability. To test the relevance of this effect, different temperatures were applied under controlled conditions in the greenhouse trial from emergence to harvest. This resulted in obtaining two distinct average sums of daily maximum temperatures in the air from planting to harvest. The average sum of daily maximum temperatures in the air from planting to harvest was 2706 °C ± 122 (mean ± standard error, N = 4) for plants grown at 15 °C and 3223 °C ± 144 for plants grown at 20°C (mean ± standard error, N = 3).

After harvest, the average number and weight of the large tubers (caliber > 32 mm) were not significantly different between the plants grown at 15 °C (6.8 tubers/plant and 44.7 g) and 20°C (7.1 tubers/plant and 53.5 g) (P values = 0.75 and 0.16). The average number and weight of the small tubers (caliber < 32 mm) were also not significantly different for plants grown at 15 °C (10.6 tubers/plant and 12.1 g) and at 20°C (7.1 tubers/plant and 11.1 g) (P values = 0.16 and 0.50). The length of the sprouts during storage was significantly impacted by the temperature during the growing period between emergence and harvest (P value = 0.02) and by the time of observation measured in days after harvest (P value < 0.001). We also observed an interaction between the temperature during the growing season and the time of observation (P value = 0.02). At the beginning of the storage period (74 DAH), sprouting was absent or low, and the length of the sprouts from tubers grown at 20°C (average of 0.2 mm) was not significantly different from the length of the sprouts of tubers grown at 15 °C (average of 0.0 mm) (P value = 0.52). At 103 days after the harvest, the length of the sprouts of the large tubers was significantly higher for plants grown at 20°C (average of 1.6 mm of sprouts) when compared to 15 °C (average of 0.3 mm of sprouts) (P value = 0.01). The length of the sprouts of the large tubers at 88 and 119 days after harvest was also higher for plants grown at 20°C (average of 0.6 and 4.4 mm) compared to 15 °C (average of 0.0 and 2.4 mm). However, it should be noted that the differences for these last two observation periods were not significant, even though the P values were low (0.08 and 0.07) (Figure 2-4).

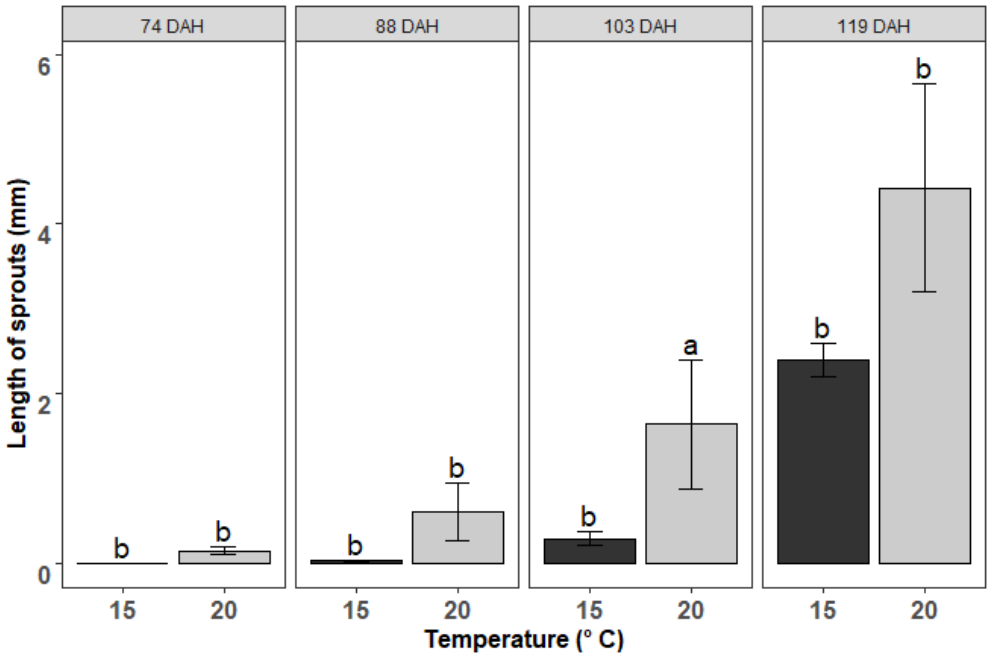

Figure 2-4. Average length of the sprouts for the large tubers (caliber > 32 mm) from plants grown at two average sums of daily maximum air temperature from planting to harvest, i.e. 2706 °C ± 122 (plants grown at 15 °C, mean ± SE, N = 4) and 3223 °C ± 144 (plants grown at 20 °C, mean ± SE, N = 3) for each observation in days after harvest (= DAH). For a given observation, groups sharing the same letter are not significantly different (Tukey test, confidence level of 95%).

We also observed a faster increase in sprout length during storage for plants grown at 20°C compared to plants grown at 15 °C. Sprouting from tubers grown at 20°C started to significantly increase at 103 DAH. The length of the sprouts at 103 DAH was significantly higher (average of 1.6 mm) compared to the length of the sprouts at 74 days and 88 days after harvest (average of 0.2 and 0.6 mm) (P values < 0.001 and 0.01) and continued to significantly increase at 119 DAH (average of 4.4 mm) compared to sprouting at 103 DAH (P value < 0.001). Sprout length at 74 and 88 DAH was not significantly different (P value = 0.11). Sprouting of potatoes grown at 15 °C started to increase later, at 119 DAH. The length of the sprouts was significantly higher at 119 DAH (average of 2.39 mm) compared to the length of the sprouts for the first three observations at 74, 88, and 103 DAH (average of 0.0, 0.0, and 0.3 mm)

(P value < 0.001) for which sprouting was low and not significantly different (lowest P value = 0.13).

4. Discussion

With the non-renewal of the most used anti-sprouting product CIPC in Europe (European Commission 2019a), a proper management of potato storage will be vital to avoid economic losses. Anti-sprouting products that are replacing CIPC on the market often require more treatments during the storage season and thus are time-consuming and have a higher cost compared to CIPC (Curty Personal communication). Therefore, the use of dormancy should be considered to improve potato storage management, and the model built in our study could be an instrumental tool to help farmers in their decisions and to avoid losses during potato storage.

The main factor determining the duration of potato dormancy highlighted by this study was the variety. This explained 60.3% of the variability and was the most critical variable used to predict the duration of dormancy. We observed a range of 108 days between varieties. The lowest dormancy was 50 days for the Lucerna variety; the longest was more than three-fold higher: 158 days for the Taurus variety (see Figure 2-1). Our results are in line with Magdalena and Dariusz (2018); they observed dormancy periods ranging from 78 to 155 days, depending on the variety, among six potato varieties tested during three seasons of storage at 8 °C.

The second important factor determining the duration of potato dormancy is related to environmental conditions. Indeed, the year and location together explained almost 20% of the variability in dormancy duration (19.3%), while 13.9% was explained by the year. Thus, year had a higher impact on the duration of dormancy than location. In our trials, the dormancy of the Bintje variety ranged from 67 to 125 days, depending on the year. Magdalena and Dariusz (2018) also observed significant differences in sprouting date between different years of testing and varieties, and underlined that these differences were due to the effect of weather conditions during the growing period of the potato plants. It has been reported in the literature that the water supply (Czerko and Grudzińska 2014; Muthoni et al. 2014), the temperature (Levy and Veilleux 2007; Magdalena and Dariusz 2018; Muthoni et al. 2014; Reust 1982; Zommick et al. 2014), the soil humidity (Firman et al. 1992), the photoperiod (Fernie and Willmitzer 2001; Muthoni et al. 2014), or the soil fertility (Muthoni et al. 2014) during the growing season greatly influences the length of the potato dormancy period. These interactions between dormancy and weather conditions were also present in our dataset. The response of the Bintje variety illustrates this; after a growing season with a heatwave (year 2003), the dormancy was only 67 days, while after a colder growing season (year 2008), the dormancy was almost two-fold longer– 125 days (Figure 2-2). Our results show that variety x environment interactions drive the length of potato dormancy and underline the effect of climate change on potato dormancy. The expected temperature increase over the next 30−50 years is predicted to be in the range of 2−3°C (Hatfield and Prueger 2015; IPCC 2007a). With such an

increase in average temperatures during the growing season of potatoes, we can expect a shortening of the dormancy of tubers during storage, with practical consequences for storage management. Among those consequences, we can mention the necessity of early anti sprouting treatments, or the necessity to lower the average temperatures of storage, with consequences for tuber quality with enhanced CIS.

Thanks to our large dataset, we built models to predict the sprouting date of a given potato variety considering its dormancy length and the environmental factors related to its growing season. Within our models, we used weather variables of the different years and locations instead of year and location as categorical factors, which have no predictive power themselves. Of all the models for predicting potato dormancy length tested in our study, the bivariate model including the variety and the sum of daily maximum temperatures during the period from planting to harvest showed a good fit explaining 70% of the variability of the observed dormancy, which is 18% better than the univariate model with only variety as a predictor. This model predicted the dormancy period with a precision of 14.59 days. This level of precision can be considered sufficient in comparison with the average duration of potato storage, which may extend up to eight months (Curty Personal communication). The robustness of the selected bivariate model was confirmed by a second analysis performed with a smaller set of data used for the validation containing the same amount of records for all variables (N = 454 instead of N = 1,048). Other bivariate models with different variables were presenting similar performances in term of prediction (Table 2-2). The added value of the selected model, in addition to its highest goodness of fit, is that it offers the advantage of using variables that are easy to collect in the field and therefore is easy to use in practice by the growers.

The study of the regression coefficient showed a negative impact of the sum of the daily temperatures from planting to harvest (-0.02). This means that the dormancy length decreases when this temperature increases. This temperature effect was confirmed by our in vivo experiment. Indeed, we conducted a greenhouse trial to check the effect of the environmental variable that most influenced the dormancy duration after the variety factor and selected through the models. The Bintje variety was chosen because it was the most represented variety in our trials. We found that at 103 DAH, the length of the sprouts of the large tubers from plants grown at 20°C was significantly higher (average of 1.6 mm of sprouts) than the ones grown at 15 °C (average sprout length of 0.3 mm). In this greenhouse experiment, we also observed an effect of temperatures during the growing season on the speed of growth of the sprouts during storage. Faster sprouting was observed for tubers from plants grown at 20°C for which the increase in sprouting significantly began at 103 DAH, compared to tubers harvested from plants grown at 15 °C for which the increase in sprouting was only significant at 119 DAH. These results are consistent with our models as well as with the literature since authors conducted studies on different varieties and showed that high temperatures during the growing season lead to reduced dormancy (Levy and Veilleux 2007; Magdalena and Dariusz 2018; Zommick et al. 2014). This impact of temperatures during the growing season on the dormancy length can be explained

because high temperatures during the growing season are known to accelerate the physiological aging of the tubers (Caldiz et al. 2001b) leading to several physiological and biochemical modifications related to the end of dormancy (Delaplace et al. 2009; Fukuda et al. 2019).

The variety is a qualitative effect; therefore, in our model, it is represented through 143 estimates of the selected bivariate model. Thus, to verify the relevance of these estimates, we have made a comparison of the dormancy information for a few varieties found in the literature. To facilitate the interpretation of these estimates, we have shown those results compared to the Bintje variety (Figure 2-3). Bintje is usually described as a variety with medium to long dormancy according to the references (European Cultivated Potato Database; Le plant de pomme de terre Français; NIVAP, 2011). Varieties with an estimate in Figure 2-3 close to zero also have a medium to long dormancy period (e.g., Gourmandine, Granola or Erika). We noticed that for some varieties, such as Agria, Agata, or Erika, the dormancy length in our model and in the literature were comparable (Agrico 2020; European Cultivated Potato Database ; Le plant de pomme de terre Français ; NIVAP 2011), while for other varieties, the dormancy length was slightly different. For instance, the dormancy of the Granola variety is described in the literature as long to very long (European Cultivated Potato Database ; Solana GmbH & Co. KG), while according to our bivariate model, this variety has a medium to long dormancy (4.25 days longer than Bintje, see Figure 2-3). The small differences between the estimate of dormancy given by our model and the dormancy provided by the breeders can be explained by the fact that our estimates are based on a large dataset with multi-environmental trials, while the dormancy provided by the breeders is generally based on trials managed in less contrasted environmental conditions. This highlights the need to collect information related to the weather conditions during the growing season and to harmonize the dormancy characterization of potato varieties.

In addition to its sufficient accuracy, this model was chosen as the most appropriate because it was robust (i.e., calibration and validation results were close) and the predictors included in the model are easy to collect in the field. Indeed, the planting and harvest dates are obviously known, and the daily maximum temperature is readily available from weather stations located in the surrounding area of the field or through simple temperature sensors that can be placed in the field during the growing season. Furthermore, in the context of pesticide reduction, using the dormancy information provided by our model to avoid or delay the use of chemicals to store potatoes is also of great interest.

Several practical storage strategies should be undertaken according to the final use of the potato (processing or fresh market) and depending on the dormancy duration of the varieties (short, medium, or long), as well as the desired storage duration (short-term storage or long-term storage).

The ideal scenario to prevent the use of anti-sprouting products would be to use varieties with long dormancies that can be stored for a long period at 8 °C and that do not require the application of anti-sprouting products for several months. Our model

does not allow estimation of the dormancy of a variety for which the variety class of dormancy is unknown or not properly characterized. Therefore, it would be necessary to define the average dormancy of such varieties by testing them in the field and comparing their dormancy period with one of the control varieties for which the variety class is well characterized (e.g., the Bintje variety). This would enable us to integrate those varieties in our model to estimate the date of sprouting for a given storage season.

However, using varieties with long dormancies cannot be the only solution given that market requirements are driving the choice of varieties to be produced (Curty Personal communication); therefore, it is advisable to also store varieties with medium and short dormancies. For short- and medium-dormant varieties, storage must be carefully planned for each season of storage to avoid food and thus economic losses. Based on the weather during the growing season, our model could be used to predict the dormancy period of these varieties and provide advice on which of the varieties will sprout first and therefore should be sold first, and which varieties will sprout later and can be retained. Another challenge for the adoption of this model by interested stakeholders is the collection of representative data for validation. Indeed, to maximize the accuracy and applicability of a model, it is important to collect large amounts of data using standardized protocols.

Depending on the predicted sprouting date, cold storage could be used to extend the dormancy of potato varieties. However, this is usually not possible for processing varieties because such storage induces sweetening at low temperatures, leading to a risk of production of toxic compounds during potato frying that may raise concerns for human health (Paul et al. 2016a; Wiberley-Bradford and Bethke 2017). Nevertheless, some varieties that are not sensitive to sweetening can be stored at low temperatures without any problems (Visse-Mansiaux et al. 2019). Since our model was developed based on potatoes stored at 8 °C, it is not appropriate to predict sprouting for potatoes stored at lower temperatures (e.g., 4 °C). Such a prediction would require a revision of the model with new data for dormancy from tubers stored at lower temperatures. A correction coefficient or a new model could then be calculated. Such a corrected model dedicated to cold storage may be effective for the management of the storage of varieties for fresh markets that are usually stored at low temperatures.

Finally, trials are being conducted worldwide in which the potato dormancy date is recorded, and for which weather information is often readily available. This large amount of data from different countries could be collected and would allow for a better characterization of the dormancy of many varieties and a better prediction of the dormancy for a wider range of environmental conditions. This would facilitate the use of the dormancy information for storage management in the future. This tool will help anticipate the consequences of climate change on potato storage losses caused by sprouting and thus improve long-term food security. It could also effectively contribute to the development of a more sustainable agriculture sector by decreasing

the use of chemicals through better management of potato storage and consequently answer the demands from consumers to avoid chemicals in food.

In conclusion, our study confirms the important impact of temperatures during the growing season on the dormancy period and shows that a bivariate model can predict with an acceptable level of accuracy the dormancy period for a given variety according to specific weather predictors during the growing season (i.e. sum of daily maximum temperatures during the period from planting to harvest). Our bivariate model has been validated by an in vivo experiment and has the advantage of being based on a large dataset, taking into consideration various environments across a wide range of conditions and varieties with many predictors. Consequently, predictive models can improve potato storage management and can help anticipate the consequences of climate change on potato storage.

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The authors have not stated any conflicts of interest.

Chapter 3

Assessment of pre- and post-harvest anti-sprouting treatments to replace CIPC for potato storage

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Outline

Potato storage is a crucial step in the potato value chain and a good management is necessary to mitigate sprouting and thus to avoid losses during storage. For the past decades, the chlorpropham (CIPC) has been the most anti-sprouting molecule used to control sprouting for its cost-effectiveness. The CIPC has been recently banned by the EU authorities. In chapter two presented above, we proposed a modelling tool, which will allow to predict the sprouting date during storage. Knowing the sprouting date will allow to improve potato storage management and to sell stocks with a short predicted dormancy duration first and to keep longer stocks with a long predicted dormancy duration. However, for long-term storages or after seasons leading to high sprouting pressure, it will be necessary to use other storage management strategies. To do so, this chapter three aims to test and to identify advantages and drawbacks of anti-sprouting alternative molecules to CIPC to mitigate sprouting during storage. In this study, trials were conducted using four processing potato varieties and were repeated during three years. Sprouting of treated tubers was evaluated after seven months of storage to access the efficacy of synthetic pre- and post-harvest anti-sprouting treatments (i.e. maleic hydrazide, 1,4-DMN, 3-decen-2-one and CIPC molecules) and compared to an untreated control. The potential of pre- and post-harvest combination of treatments was evaluated as well as potential residues in tubers at the end of the storage. The novelty of this this study is that we evaluated the efficacy of several treatments in the same trials and that tubers were stored in small automatized experimental chambers (i.e. with 200 kg of potatoes per chamber and one post-harvest treatment per chamber) placed in the same cold storage allowing to have the exact same storage conditions between treatments. This research will contribute to improve knowledge about the efficacy of these synthetic molecules to mitigate sprouting. This will also help farmers to get insights on the use of these molecules and thus, to improve potato storage management and to avoid economic losses.

Abstract

To avoid losses from sprouting during potato storage, the anti-sprouting agent chlorpropham [CIPC] has been widely used over the past few decades. However, the European Union recently decided not to authorize the renewal of CIPC, prompting the value chain to find alternative treatments. We assessed for three years the potential of pre- and post-harvest anti-sprouting treatments to replace CIPC using four potato-processing varieties. Pre-harvest application of maleic hydrazide [MH] and post-harvest applications of 3-decen-2-one, 1,4-dimethylnapthalene [1,4-DMN] and CIPC were performed following supplier's recommendations. In addition, we evaluated the potential of 3-decen-2-one and 1,4-DMN to prolong the efficacy of pre-harvest MH treatment anti-sprouting activity during storage. All molecules significantly reduced sprouting after seven months of storage compared with the untreated control group. MH, 3-decen-2-one, 1,4-DMN and CIPC displayed respectively 86.9 %; 77.9 %, 73.6 % and 99.8 % of efficacy to control sprout weight and 79.4 %; 73.4 %, 68.4 % and 96.9 % of efficacy to control sprout length. Our results suggest that using 3-decen-2-one and 1,4-DMN in combination with MH do not bring additional benefit to control sprouting. Because differences in dormancies could be observed between varieties, we also showed that the efficacy of post-harvest treatments is genotype-dependent, while MH pre-harvest treatment is effective equally for all varieties. Applications of CIPC and MH led to detectable residues in tubers, while no residue of 1,4-DMN has been detected in tubers treated with this molecule (< LOQ). We concluded that treatments with MH, 1,4-DMN and 3-decen-2-one are valuable alternatives to CIPC to control sprouting of processing potatoes.

Keywords: potato; sprouting; maleic hydrazide; post-harvest treatments; genotypes

1. Introduction

Potatoes (*Solanum tuberosum L.)* are an economically important crop. According to FAO, potato was the fourth largest food crop worldwide with 377 x 10^6 t produced in 2016 is the fourth largest in the world, after rice (741 x 10^6 t), wheat (749 x 10^6 t), and maize (1.06 x 10^9 t) (FAO 2018).

During potato storage, losses occur mainly due to water loss, disease, and sprouting (Magdalena and Dariusz 2018). The evolution of potatoes' physiological age coincides with an increase in sprouting (Delaplace et al. 2008), which alters potato quality in different ways. Sprouting modifies potatoes' physical properties by reducing turgidity, inducing shrinkage, and accelerating weight loss (Alexandre et al. 2015; Teper-Bamnolker et al. 2010; Sonnewald and Sonnewald 2014). Premature sprouting also leads to a reduction in nutritional and processing qualities, thereby eliciting economic losses (Alexandre et al. 2015; Sorce et al. 1997; Suttle et al. 2016). Moreover, potato sprouting can result in the production of toxic compounds in the potato flesh, such as solanine and chaconine (Koffi et al. 2017). To prevent the aforementioned problems, it is important to delay potato sprouting during the storage period.

As soon as tuber formation begins, the young tuber is in a dormant condition, during which it imports sucrose from photosynthetic organs. During the dormancy period, the tuber cannot sprout, even under favorable conditions (Reust 1982; Delaplace 2007). Potato sprouting appears during storage when the dormancy period is broken progressively (Coleman 1987; Daniels-Lake and Prange 2007). Several parameters can be controlled to delay potato sprouting during long-term storage, including the use of varieties with long dormancy periods, low temperature storage, and the application of sprouting inhibitors. Despite the availability of varieties with good performance under long-term storage, it is not always possible for growers and retailers to use them because they do not necessarily comply with potato value chain requirements. Cold-induced sweetening (CIS), which occurs in most processing varieties, also limits the possibility of using cold-temperature storage to mitigate sprouting. CIS leads to dark color, alteration of potato quality, and an increase in acrylamide content after frying, which may pose risks to human health (Paul et al. 2016a; Wiberley-Bradford and Bethke 2017). In this context, the potato value chain has relied heavily on the use of chemicals such as chlorpropham [CIPC], which was released commercially in 1951 and so far has been viewed as the most effective potato-sprouting suppressant (Paul et al. 2016c). CIPC is applied in post-harvest treatments and acts as an anti-sprouting molecule by inhibiting mitosis in potato cells (Nurit et al. 1989; Wiltshire and Cobb 1996; Kleinkopf et al. 2003; Campbell et al. 2010). Studies have demonstrated that single or multiple applications with 18 to 36 g of CIPC per tonne of potatoes allow for potato storage without sprouting for five to 12 months at temperatures between 8 and 12 °C (Mahajan et al. 2008; Corsini et al. 1979; Paul et al. 2016b).

Maleic hydrazide [MH] is a systemic plant growth regulator first reported by Schoene and Hoffmann in 1949 (Schoene and Hoffmann 1949). MH-based products are applied on the field during vegetative growth (Kennedy and Smith 1951; Paterson et al. 1952) and are transported from leaves to growing progeny tubers, where they build up (Hoffman and Parups 1964; McKenzie 1989; Dias and Duncan 1999a; Venezian et al. 2017). MH's mode of action is not fully characterized. It has been suggested that it disrupts mitosis and/or interacts with the metabolism of hormones such as auxin and gibberellin (Venezian et al. 2017; Hoffman and Parups 1964). Treating potatoes with MH-based products allows for delaying initial sprouting and inhibiting sprout growth for six to eight months without affecting sugar content (Caldiz et al. 2001a; Yada et al. 1991).

1,4-dimethylnapthalene [1,4-DMN] is a product from the naphthalene group of chemicals found naturally in potatoes and has been found to control potato sprouting (Lewis et al. 1997; Kleinkopf et al. 2003; Campbell et al. 2010; Campbell et al. 2012). Lewis et al. (1997) showed that one application of DMN molecules (isomer mixture) at 100 mg kg^{-1} (expressed on a fresh weight basis) was sufficient to suppress sprout growth for six months during storage of the Russet Burbank variety. So far, 1,4-DMN's action mechanisms to control sprouting are not completely understood, but recent studies suggest that 1,4-DMN readily could inhibit plastid development at the initial stages, whereas this molecule also may lead to lasting transcriptional changes (Campbell and D'Annibale 2016).

The α,β-unsaturated aliphatic aldehydes and ketone compounds have been described as having the ability to cause necrosis in potato sprouts during storage. It also has been reported that among these compounds, 3-decen-2-one, an α,β-aliphatic unsaturated ketone molecule, has been shown to control sprouting (Knowles and Knowles 2012, 2015a). The 3-decen-2-one treatment usually is vaporized on potatoes when their dormancy breaks, leading to necrosis in sprout tissue within 24-36 h (Immaraju Personal communication). It also induces a transient increase in tuber respiration rate, rapid desiccation of sprouts, and an overall reduction in the tissue's ability to modulate oxidative stress (Knowles and Knowles 2012, 2015a). It is important to note that 3-decen-2-one vapor is active only when the sprouts' fast-growing meristematic tissues are exposed to the product. This destruction and desiccation of external sprout tissue also elicit internal cell structure breakdown, leading to a "burnt out" appearance (Immaraju Personal communication).

Because of its high efficacy and cost-affordability, CIPC so far has remained the preferred anti-sprouting treatment in the potato value chain. However, due to the presence of data gaps in the application file for the renewal of the CIPC registration, and due to the raise of concerns for the consumer regarding a potential risk of this active substance and the metabolite 3-chloroaniline, the European Union recently decided not to authorize the renewal of this molecule (European Food Safety Authority (EFSA) et al. 2017; European Commission 2019a).

This non-renewal indicates an urgent need for safe alternative treatments and procedures to reduce potato sprouting during storage. The aforementioned molecules appear to be promising and are already or coming onto the market as anti-sprouting products.

Contrary to CIPC, 1,4-DMN and 3-decen-2-one molecules require more than one or two treatments to elicit sprouting control during an entire storage season. These molecules also necessitate stricter monitoring of potatoes during storage. For instance, as mentioned earlier, to be effective, the 3-decen-2-one molecule needs to be applied on fast-growing meristematic tissues, i.e., the potatoes' sprouting state needs to be monitored carefully. Furthermore, sprouting control for processing varieties needs to be followed closely, as they usually are stored between 7 and 10 °C to avoid CIS, i.e., temperatures more conducive to sprouting, compared with potatoes headed for fresh markets, which usually are stored between 5 and 6 °C (Bishop et al. 2012).

Therefore, this study's purpose is to propose new suitable strategies for processing potatoes to cope with the CIPC non-renewal while maintaining good quality during storage. To reach this goal, this study focusses on different points. Potato variety's effect on sprouting was assessed to evaluate genetic factors' influence on sprouting. Therefore, two crisp varieties and two French fries varieties were compared. The following molecules' efficacy was evaluated for different genotypes to propose anti-sprouting treatments to replace CIPC that are suitable for processing potatoes, and are easy to use: MH (pre-harvest treatment); 3-decen-2-one; 1,4-DMN; and CIPC (post-harvest treatments). Combinations of pre-and post-harvest treatments also were tested to verify potential benefits from combinations in sprouting control. Finally, residues in treated and untreated potatoes were assessed at the end of the storage period to evaluate potential health concerns from treated potatoes and potential cross-contamination.

The main limitation of previous studies undertaken to assess anti-sprouting products' efficacy is that each product usually is tested in a different storage chamber. This implies that storage conditions are not exactly the same among the tested products, inducing a risk of unexpected bias in the results. In our study, we solved this technical problem by having a separated experimental chamber for each post-harvest product tested to avoid cross-contamination, while all the experimental chambers were located in the same cold storage chamber, i.e., all the storage conditions were equal for all tested products. Furthermore, all the tubers used for the experiments were produced in the same location the previous year, guaranteeing homogeneity in the physiological age of the tubers tested in the experiment. To our knowledge, this is the first experiment to evaluate the efficacy of 3-decen-2-one, 1,4-DMN, and CIPC molecules alone, and in combination with the MH pre-harvest treatment, coping with the aforementioned experimental precautions.

2. Materials and methods

2.1. Plant material, growing conditions, and field treatments

Field trials have been conducted by Agroscope, a center for agricultural research in Switzerland. Two crisp varieties (Lady Claire and Verdi) and two French fries varieties (Markies and Fontane) were planted in April and harvested at the end of August or beginning of September over three consecutive years: 2015; 2016; and 2017 (planting dates: 13 April 2015, 11 April 2016 and 18 April 2017; harvest dates: 3 September 2015, 30 August 2016 and 29 August 2017, respectively). The following fertilizers were used: 120 kg ha^{-1} of N; 85 kg ha^{-1} of P_2O_5; 450 kg ha^{-1} of K_2O; and 25 kg ha^{-1} of Mg.

After planting, an herbicide treatment was performed for weed control. Haulm destruction was implemented in two phases. A first treatment was performed using the Reglone® (active ingredient: 200 g L^{-1} Diquat) in accordance with the supplier recommendations (Syngenta 2018a), combined with mechanical destruction (using an EnviMaxX machine from Rema Environmental Machinery B.V. [NL]). The dates of treatments are the following: 3 August 2015, 9 August 2016 and 7 August 2017. A second treatment was applied using the product Spotlight® Plus (active ingredient: 60 g L^{-1} Carfentrazone-ethyl) in accordance with the supplier recommendations (Syngenta 2018b). The dates of treatments are the following: 10 August 2015, 12 August 2016 and 14 August 2017. During the period from planting to haulm killing, water deficit was monitored and calculated according to pluviometry and evapotranspiration, and corrected with a crop coefficient. In case of drought (a water deficit above 40 mm), the potatoes were irrigated with at least 30 L m^{-2}. Altogether, the potatoes were irrigated with 180, 65, and 138 L m^{-2} in 2015, 2016, and 2017, respectively. The potatoes were treated to protect them from potato blight (*Phytophtora infestans*) approximately once a week after emergence until haulm killing, with different products following recommendations from the PhytoPRE decision support system (PhytoPRE+ 2000). The plot was separated in two blocks and one of the two blocks was treated with Fazor®, which contains 60 % of maleic hydrazide [MH]. Five kilograms of Fazor® in 400 liters of water were applied per hectare with a Birchmeier® backpack sprayers equipped with a pump driven by a combustion engine. This treatment has been performed when 80 % of the potato tuber size reached 25 mm (dates of treatments: 26 June 2015, 23 June 2016 and 26 June 2017) in accordance with the supplier recommendations (Leu+Gygax AG 2018).

2.2. Harvest and grading

At harvest, the potatoes were stored at about 15 °C for two weeks in the dark to promote healing. Potato tubers then were weighed and calibrated to assess the tuber

size. The tuber size used for the post-harvest trials was between 42.5 and 70 mm in diameter.

2.3. Experimental design

The potatoes were stored in small experimental chambers (0.8 m x 1.2 m x 2.0 m), with a total capacity of approximatively 200 kg of potatoes per experimental chamber (Figure 3-1).

Figure 3-1. Picture of one experimental chamber (0.8 m x 1.2 m x 2.0 m) with a total capacity of 200 kg of potatoes.

Each experimental chamber contained a tray on which two piles of stacked plastic crates were placed: one pile for potatoes treated with MH on the field and one pile for potatoes untreated on the field. Each pile is composed of four varieties disposed in four distinct plastic crates (experimental unit [EU]) (0.6 m x 0.4 m x 0.18 m), and each crate was filled with 100 tubers of a given variety. There were eight EUs per experimental chamber (4 varieties x 2 field treatments). Each experimental chamber was covered with an airtight plastic sheet inside a plastic structure and hermetically sealed on the tray using magnet bands. Anti-sprouting molecules were tested individually in each experimental chamber placed in the same storage chamber, which allows for having the same temperature for all experimental chambers. The storage chamber's temperature was 12 °C for one week, and then the temperature was brought

to 8 °C with a decrease of 1 °C per week and kept at 8 °C for the remaining duration of the storage period. At the end of the storage period, a reconditioning was applied with an increase of 1 °C per week to reach 15 °C by the end of May.

Each chamber was equipped with fans, an air extractor, and CO_2 sensors (CozIR®-A CO_2 Sensor) connected to a microcomputer (Raspberry Pi 3, B Model) to control temperature, humidity, and CO_2 parameters. During storage, potatoes were stored in a controlled atmosphere with the following characteristics: 80 % RH; continuous ventilation; and air renewal to keep CO_2 concentration in the air below 0.124 mol m^{-3} (= 3000 ppm). The air extracted from the experimental chambers was expelled outside the storage chamber to avoid air contamination among chambers.

The following active molecules were tested and applied in post-harvest treatments: 3-decen-2-one (SmartBlock® - global registration owner: AMVAC Chemical Corporation); 1,4-Dimethylnaphthalene [1,4DMN or DMN] (1,4SIGHT® / DORMIR® - European registration owner: DormFresh Ltd); and chlorpropham [CIPC] (Neo-Stop Starter® - Global registration owner: UPL Benelux). These molecules were tested on potatoes treated or untreated on the field with MH. An experimental chamber containing the untreated control was also added to the experimental design. Anti-sprouting molecules were applied following commercial recommendations (Table 3-1).

Table 3-1. Dosage and frequency of treatments for the tested molecules and the device used for treatments

	Concentration of the active ingredient	**Treatment quantity (mL t^{-1})**	**Frequency and total number of treatments during each entire season of storage**	**Dates of first treatments for each season of storage**	**Number of treatments before sprouting assessment**	**Dates of the last treatments for each season of storage**	**Application device**
SmartBlock®	98 % pure 3-decen-2-one (AMVAC Chemical Corporation)	100	When all varieties had sprouts > 3 mm, 4 treatments	16 November 2015; 8 November 2016; 20 November 2017	3	15 May 2016; 27 April 2017; 1 May 2018	Burgess® 982 Electric Professional Thermal Fogger
1,4SIGHT®	98 % pure 1,4-DMN (DormFresh Ltd)	20	Every 6 weeks, 6 treatments	28 October 2015; 18 October 2016; 20 October 2017	4	23 May 2016; 15 May 2017; 24 May 2018	Burgess® 982 Electric Professional Thermal Fogger
Neo-Stop Starter®	300 g L^{-1} Chlorpropham (UPL Benelux)	60	One treatment	27 October 2015; 18 October 2016; 10 October 2017	1	27 October 2015; 18 October 2016; 10 October 2017	MAFEX® ULV Fine Spray Unit for application of liquid products

After each treatment, an air circulation (without renewal) was applied for 24 h to allow the proper distribution of the product. After that period, the air was automatically renewed when the CO_2 concentration exceeded 0.124 mol m^{-3} (= 3000 ppm). The CIPC post-harvest treatment was applied using a MAFEX® Ultra-Low Volume (ULV) Fine Spray Unit for application of liquid products. 1,4-DMN and 3-decen-2-one post-harvest treatments were applied by hot fogging in each chamber using an electric fogger (Burgess® 982 Electric Professional Fogger, Model 16982150). To allow the fogging, the products were heated at a temperature ranging from 232 to 274 °C (The Fountainhead Group company Personal communication).

This experimental design followed a split-split plot design comprising four anti-sprouting molecule levels (three molecules and an untreated control). Within each chamber are two distinct field treatment (FT) groups (treated or untreated on the field), and within each FT group are four EUs (four varieties), each containing 100 individual tubers. This design was repeated during three years and the year is considered as a random factor.

2.4. Observations

2.4.1. Tuber size at harvest

The total yield at harvest (weight of potatoes) was recorded, as well as potatoes' tuber sizes for different varieties and field treatment groups. The following tuber sizes were considered: tubers smaller than 42.5 mm in diameter (small tubers) and larger than 42.5 mm (large tubers) (N = two years).

2.4.2. Sprouting during storage

For the three years of trial, sprouting was assessed after seven months of storage (end of March or early April), by sampling 25 tubers for each treatment and variety. This assessment was done by measuring the following parameters on sprouts with a minimum size of 1 mm: weight of sprouts from the 25 tubers and average length of the longest sprout of each tuber.

2.4.3. Sugar content

Sugar analysis was conducted using the ion chromatography method with conductivity detector (Zweifel Pomy-Chips AG 2018) to assess the effect from products on potatoes' sugar content after seven months of storage (end of March or early April). Sucrose, fructose, and glucose levels were also measured for each sample (results are expressed on a fresh potato weight basis). The sum of glucose and fructose is viewed as the "reducing sugars" in potatoes. This observation was performed for two consecutive years (2017 and 2018) on two varieties (Verdi and Lady Claire).

2.4.4. Residues

Residues analysis were performed during two consecutive storage seasons (2016-2017 and 2017-2018) at the end of the storage period and after the reconditioning from

8 to 15 °C for all the tested molecules, except 3-decen-2-one. At least one month after the last treatment (Table 3-1), potatoes of the variety Fontane were washed with tap water for 30 seconds and sampled for residue analysis (dates of sampling: 15 June 2017 and 25 June 2018). The period between the last treatment and the sampling for residues analysis varies among products. Sampling for residue analysis were performed one month after the last treatment with 1,4-DMN, 8 to 8.5 months after the last treatment with CIPC and 12 months after the field treatment with MH. One kilogram of tubers was sampled and kept with the skin and another kilogram was peeled before analysis. Each sample was then cut into pieces and blended (Moulinex® - Ovatio 3 Duo Press) and disposed in plastic bags (Domédia kitchen, six liters zip lock bags). Then, the samples were kept in the freezer (- 80 °C) until the analysis.

A method based on the Dutch mini-Luke ("NL") extraction method was used for the extraction of the sample (EURL-FV 2014; Balleix personal communication). Then, the Gas Chromatography - Mass Spectrometry - Triple Quad (GC-MS-TQ) method was used to detect the molecules 1,4-DMN, CIPC and 3-chloroaniline (limit of quantification [LOQ] = 0.01 mg kg^{-1}). The liquid chromatography-tandem mass spectrometry (LC-MS/MS) method was used to analyze the MH (LOQ = 0.1 mg kg^{-1}), according to the European Union guidance documents for pesticide residues [SANTE/11945/2015 for samples of the year 2017 and SANTE/11813/2017 for samples of the year 2018] (EURL 2015; Balleix personal communication; European Commission 2017).

2.5. Statistical analysis

R software, Version 3.6.3 (R Core Team 2019), was used for the statistical analysis. A linear mixed model was used to analyze the measured variables: sprout weight and length; sugars in potatoes; total yield weight; and small and large tubers' weight. Due to the wide variability of the data and to fulfill parametric model assumptions, it was decided to transform the average sprout length and weight variables with (log +1) to ensure variance homogeneity and response variable normality when necessary. The year is viewed as a random factor. Significance tests were performed using chi-square tests provided by the "car" R package, Version 3.0-7 (Fox and Weisberg, 2019). To analyze the effect from significant variables, the marginal post hoc Tukey's test (emmeans method) was used as a multiple comparison test to identify mean differences within factors and interactions. To perform the aforementioned analysis, we used different R packages ("lme4," "emmeans," "Matrix," and "nlme") (Bates and Maechler 2019; Bates et al. 2015; Lenth 2020; Pinheiro et al. 2019). For data summary and graphics, we used different R packages ("ggplot2", "plyr", "Rmisc", "lattice," and "cowplot") (Wickham 2011, 2016; Wilke 2019; Sarkar 2008; Hope 2013).

3. Results and discussion

3.1. Varieties have differences in dormancy length

After seven months of storage, we observed a significant effect from potato variety on dormancy in terms of sprout weight (Table 3-2). The Fontane variety had the highest sprout development, at 22.4 g, followed by Lady Claire, at 16.6 g; Markies, with 10.5 g; and Verdi, with 7.4 g. Sprout weight is significantly different for the Fontane ($p = 0.019$; Tukey's test) and Lady Claire ($p = 0.043$; Tukey's test) varieties compared with the Verdi variety (Figure 3-2). It should be noted that no significant difference in sprout length was observed between the four varieties (Table 3-2).

Dormancy differences between varieties are a phenomenon that is well-characterized in the literature. Daniels-Lake and Prange (2007) and Magdalena and Dariusz (2018) reported that the dormancy period's length is mainly variety-dependent and modulated by other parameters, such as storage temperature and weather conditions during growing season. However, in our study, this result must be treated with caution because there is little interaction ($p = 0.0496$) between the variety and product factors for sprout weight (Table 3-2). This interaction is described in section 3.5.

Among the two varieties tested, we observed that sucrose content was not significantly different (average of 2.3 g kg^{-1} for Verdi and 2.2 g kg^{-1} for Lady Claire), and reducing sugar content also was nearly equal for both varieties (average of 0.3 g kg^{-1} for Verdi and 0.2 g kg^{-1} for Lady Claire) (Table 3-2). Verdi and Lady Claire are crisp varieties known to be less susceptible to sweetening, explaining why sugar content is low for both.

At harvest time, total yield and tuber size balances were different between varieties (Table 3-3). Tukey's test did not allow for distinguishing between varieties in terms of total yield and small tuber yield ($p > 0.05$); however, we observed a higher yield of large tubers for the Fontane variety (average of 50.69 kg) compared with the Lady Claire variety (average of 35.58 kg) ($p = 0.028$; Tukey's test) (Figure 3-3).

Table 3-2. ANOVA P-values (Pr[>chi-sq]) for the measured parameters in response to the different factors and their interactions after seven months of storage (* = statistically significant)

Factors	Weight of sprouts	Length of sprouts	Reducing sugars	Sucrose
Product	<0.001***	<0.001***	0.874	0.039*
Field treatment	<0.001***	<0.001***	0.859	0.432
Variety	0.005**	0.111	0.192	0.050
Product x Field treatment	<0.001***	<0.001***	0.214	0.012*
Product x Variety	0.0496*	0.092	0.419	0.543
Field treatment x Variety	0.963	0.995	0.408	0.553

Table 3-3. ANOVA P-values (Pr[>chi-sq]) of the linear mixed model for the measured parameters in response to the different variables and their interactions at harvest time (* = statistically significant)

Variables	Yield	Small tuber size	Large tuber size
Variety	0.005**	0.008**	< 0.001***
Field treatment	0.462	0.759	0.539
Field treatment x Variety	0.273	0.603	0.451

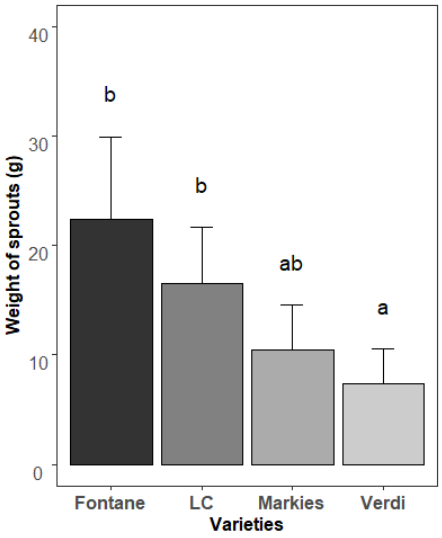

Figure 3-2. Average sprout weight for each variety; over four products, two field treatments, and three years (n = 24) after seven months of storage (80 % RH); error bars represent standard error of the mean; (LC = Lady Claire). Groups sharing the same letter are not significantly different (Tukey's test, confidence level of 95 %).

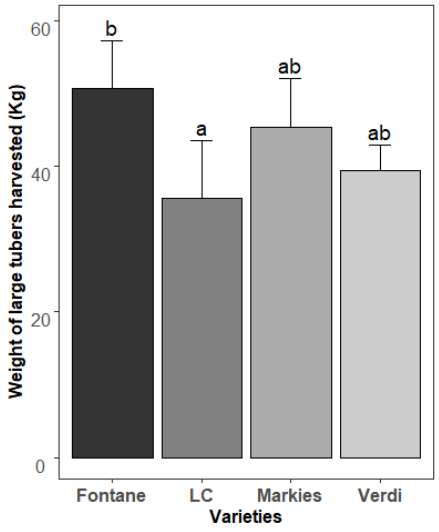

Figure 3-3. Average yield's weight for large tubers at harvest time for each variety over two field treatments and two years (n = 4); error bars represent standard error of the mean; (LC = Lady Claire). Groups sharing the same letter are not significantly different (Tukey's test, confidence level of 95 %).

3.2. All post-harvest treatment products are effective, but CIPC remains the most effective one

3.2.1. Effect from post-harvest products on sprouting

Our results revealed a significant effect from post-harvest products on sprouting measurements (sprout length and weight). We also observed interactions between post-harvest and MH field treatments (Table 3-2). These interactions will be examined in section 3.4. As there is a low interaction ($p = 0.0496$) between the variety and product factors for sprout weight (Table 3-2), the effect of post-harvest products for each variety is detailed in section 3.6.

Our results suggest that all tested molecules (used without prior MH field treatment) effectively control sprouting for up to seven months of storage, as both sprout length and weight were lower in treated potatoes compared with the untreated control group (Table 3-4).

The sprouts' weight and length were higher for the untreated control group (an average of 64.0 g and 44.8 mm) than for potatoes treated with CIPC (an average of 0.1 g and 1.4 mm), with the 3-decen-2-one (average of 14.1 g and 11.9 mm), and with 1,4-DMN (average of 16.9 g and 14.2 mm) (Figure 3-4 A and B).

As expected and already indicated in extant literature (Mahajan et al. 2008; Corsini et al. 1979; Paul et al. 2016b), our results confirmed that CIPC's efficacy is high (96.90 % efficacy for sprout length and 99.80 % for sprout weight compared with the untreated control group). The 3-decen-2-one and 1,4-DMN efficacies were similar: both molecules controlled sprouting at 73.38 % and 68.37 % efficacy for sprout length and 77.94 % and 73.60 % efficacy for sprout weight, respectively, compared with the untreated control group.

Our results correspond with those of Lewis et al. (1997), who tested DMN's efficacy to control sprouting and showed that one application of DMN molecules (a mixture of isomers) at 100 mg $^{Kg\text{-}1}$ (expressed on a fresh weight basis) was sufficient to suppress sprout growth for six months in storage. Furthermore, similar to results in the literature (Knowles and Knowles 2012, 2015a), in our study, the 3-decen-2-one molecule controlled sprouts by causing desiccation and necrosis of sprouts in 24 h, confirming that 3-decen-2-one acts as a curative product, ensuring flexible, long-term management of potato sprouting during storage.

Table 3-4. Tukey's test P-values (emmeans method) describing the products' effect on the measured parameters for potatoes treated or not treated with MH after seven months of storage (* = statistically significant) (FT = field treatment; MH = maleic hydrazide)

	Comparison between products	Effect on sprout weight	Effect on sprout length	Effect on sucrose
With FT	(Control + MH) - (1,4-DMN + MH)	0.391	0.419	0.974
	(Control + MH) - (CIPC + MH)	0.045*	0.012*	0.975
	(Control + MH) - (3-decen-2-one+ MH)	0.425	0.228	0.710
	(1,4-DMN + MH) -(CIPC + MH)	0.130	0.059	0.845
	(1,4-DMN + MH) - (3-decen-2-one+ MH)	0.958	0.882	0.513
	(CIPC + MH) - (3-decen-2-one+ MH)	0.739	0.710	0.894
Without FT	Control - 1,4-DMN	0.007**	0.023*	0.114
	Control - CIPC	< 0.001***	< 0.001***	0.070
	Control - 3-decen-2-one	0.042*	0.036*	0.157
	1,4-DMN - CIPC	0.002**	0.001**	0.925
	1,4-DMN - 3-decen-2-one	0.721	0.921	0.981
	CIPC - 3-decen-2-one	0.220	0.132	0.775

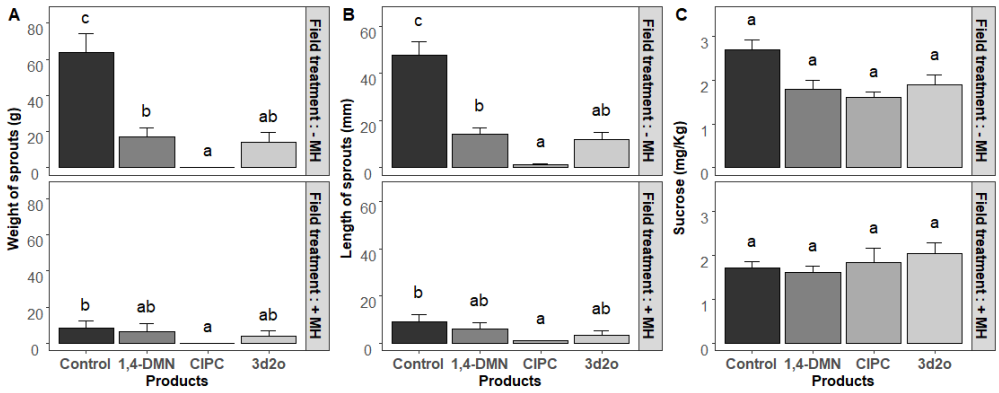

Figure 3-4. Average sprout weight (A), sprout length (B), and sucrose content in potatoes (C) for each post-harvest treatment; with (+ MH) or without (- MH) MH field treatment after seven months of storage (80 % RH); over four varieties and three years for sprout weight and length measurements (n = 12) and over two varieties and two years for sucrose measurement (n = 4); error bars represent standard error of the mean; (3d2o = 3-decen-2-one; MH = maleic hydrazide). For a given observation and within each field treatment, groups sharing the same letter are not significantly different (Tukey's test, confidence level of 95 %).

3.2.2. Post-harvest products do not affect sugar content

No significant effect on sucrose content was recorded (Table 3-4), although lower sucrose content was observed in about 40 %, 30 % and 34 % for potatoes treated with CIPC, 3-decen-2-one, and 1,4-DMN, respectively, compared with untreated potatoes (Figure 3-4 C). It is reported in the literature that sprouting increases respiration and water loss of potato tubers and accelerates physiological aging (Pinhero and Yada 2016). Therefore, treated tubers, which are less sprouted, have a reduced physiological aging. Consequently, the lower sucrose content observed in treated potatoes in our study is probably due to reduced physiological aging for treated potatoes compared with untreated ones. Our results correspond with those of Mehta and Singh (2015), who showed that sucrose concentration increased linearly during storage in both untreated and CIPC-treated potatoes and that the increase is lower in potatoes treated with CIPC. In their study, both reducing sugar and sucrose content remain low compared with the freshly harvested control group. The authors noted that the lower sugar content in CIPC-treated potatoes may be due to lower physiological aging compared with the control group (Mehta and Singh 2015; Mehta et al. 2012).

We found that the anti-sprouting products tested in this study did not affect the reducing sugar content in potatoes (Table 3-2). The results are consistent with studies conducted with CIPC by Blenkinsop et al. (2002) and Mehta et al. (2012), who found that CIPC did not significantly affect crisp color quality or reducing sugars content in potatoes.

3.3. The MH field treatment controls sprouting and sucrose content effectively

3.3.1. Effect from MH field treatment on sprouting

The MH field treatment controlled sprouting very effectively. After seven months of storage, both sprout weight and length appeared to be significantly higher for tubers from untreated plants (average weight of 64.0 g and average length of 44.8 mm) than for tubers from plants treated only with MH (average weight of 8.4 g and average length of 9.2 mm) (Table 3-5) (Figure 3-5 A and B). The MH was highly effective, with 86.94 % efficacy for sprout weight and 79.38 % for sprout length, compared with the untreated control.

Similar efficacies also were found in a previous study by Caldiz et al. (2001a), who reported that MH treatments delay the initial sprouting date and inhibit sprout growth for up to eight months.

3.3.2. Effect from MH field treatment on sugars

In our study, sucrose content in tubers harvested from untreated plants (average of 2.68 g kg^{-1}) was significantly higher than in tubers harvested from plants treated only on the field with MH (average of 1.72 g kg^{-1}) (Table 3-5) (Figure 3-5 C). However, the field treatment did not affect the reducing sugar content in potatoes (Table 3-2). Our results are consistent with results from Sabba et al. (2009), who showed that MH did not lower glucose concentration at harvest or after a storage period of 25 weeks at 9 °C. However, in their study, MH treatment did not impact sucrose concentration, which contradicts our findings, as we observed a decrease in sucrose content for potatoes treated with MH compared with untreated potatoes. The increase in sucrose content during storage of untreated potatoes that we observed could be due to potato aging, as sucrose accumulates in potatoes during long storage periods (Ezekiel et al. 2011; Mehta et al. 2012). This increase can be explained by the formation of invertase inhibitor or the inhibition of the invertase activity at higher temperatures (Uppal and Verma 1990; Mehta and Singh 2015), but one of these mechanisms should have been mitigated by MH in our study. Another explanation of the differences observed between our study and Sabba et al. (2009) could be that the metabolism of the invertase is variety-dependent, as different varieties were used in both studies.

Table 3-5. Tukey's test P-values (emmeans method) describing the effect of the MH field treatment on the measured parameters for each product after seven months of storage (* = statistically significant) (FT = field treatment; MH = maleic hydrazide)

Comparison: molecules used alone or with MH	FT effect on sprout weight	FT effect on sprout length	FT effect on sucrose
(CIPC + MH) - CIPC	0.795	0.658	0.540
(3-decen-2-one + MH) - 3-decen-2-one	0.019*	0.005**	0.679
(1,4-DMN + MH) - 1,4-DMN	0.006**	0.006**	0.640
(Control + MH) - control	< 0.001***	< 0.001***	0.0498*

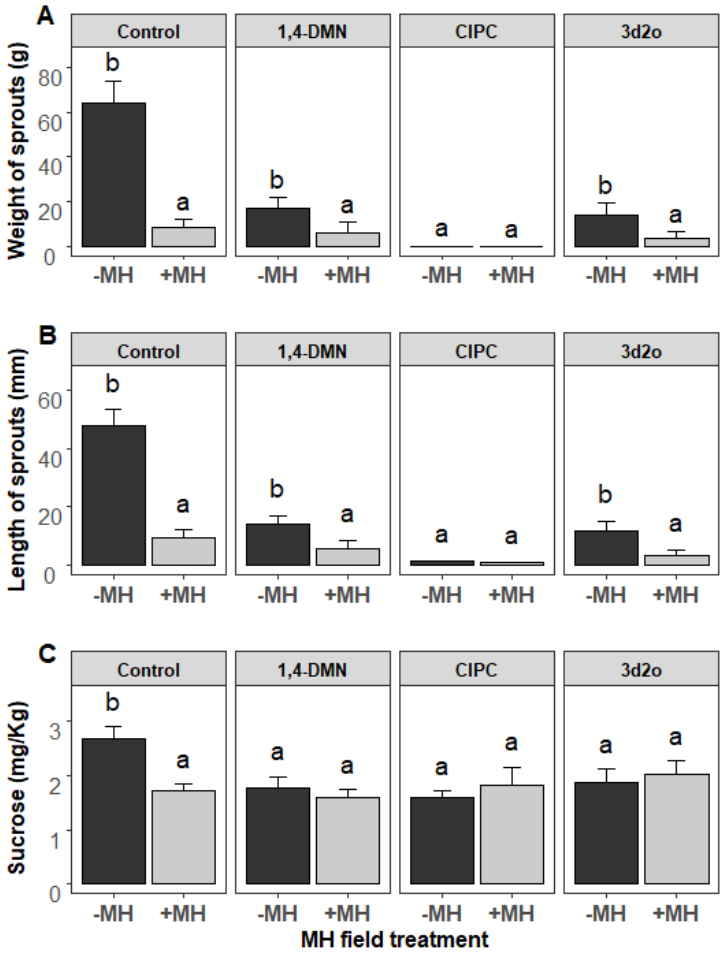

Figure 3-5. Average sprout weight (A), sprout length (B), and sucrose content (C) of potatoes treated with maleic hydrazide (+ MH) or not (- MH) in the field and for potatoes treated with different post-harvest treatments after seven months of storage (80 % RH); over four varieties and three years for sprout weight and length measurements (n = 12) and over two varieties and two years for sucrose measurement (n = 4); error bars represent standard error of the mean; (3d2o = 3-decen-2-one; MH = maleic hydrazide). For a given observation and within each post-harvest treatment, groups sharing the same letter are not significantly different (Tukey's test, confidence level of 95 %).

3.3.3. Effect from MH field treatment on yield and tuber size

In our study, MH field treatment did not affect the yield and size of tubers at harvest (Table 3-3). Our results correspond with previous research by Yada et al. (1991) and Caldiz et al. (2001a) in showing that MH has no effect on yield. However,

Ravichandran et al. (2012) reported an increase in the number of tubers in their experimental conditions. Our results showed no effect from MH treatments on tuber size, while Sabba et al. (2009) and Ravichandran et al. (2012) showed that MH field treatment can lead to a decrease in the production of large tubers by lowering potato weight.

The discrepancy with our study might be explained by varietal differences in the response to MH treatment, as it has been reported previously that the effect from MH on potato yield is variety-dependent (Sabba et al. 2009).

3.4. Combining post-harvest products and MH field treatment does not come with a systematic added value

3.4.1. Benefit from using combinations of post-harvest treatment and MH field treatment to control sprouting

Our results highlighted that potato-sprouting control was greater in potatoes treated with a combination of CIPC post-harvest treatment and MH field treatment (average sprout weight of 0.0 g and 1.0 mm in length) than for potatoes treated only with MH field treatment (average sprout weight of 8.4 g and 9.2 mm in length) (Table 3-4) (Figures 3-4 A and B). However, we observed that treating potatoes with the CIPC-MH combination does not significantly control sprouting more than treating potatoes only with a CIPC post-harvest treatment (average sprout weight of 0.1 g and 1.4 mm in length) (Figures 3-5 A and B) (Table 3-5). These results show that the CIPC-MH combination does not provide any additional benefit, as the CIPC treatment alone already enables nearly complete inhibition of sprouting.

Sprouting levels in potatoes treated with a combination of MH field treatment and post-harvest molecules 3-decen-2-one and 1,4-DMN (average length of 3.5 mm and 5.9 mm and weight of 3.8 g and 6.3 g, respectively) were not significantly different from sprouting levels in potatoes treated only with MH on the field (average length of 9.23 mm and weight of 8.4 g) (Figures 3-4 A and B) (Table 3-4). However, combinations of the molecules 3-decen-2-one or 1,4-DMN with a MH field treatment significantly control sprouting better than treatments with molecules 3-decen-2-one and 1,4-DMN alone (average sprout length of 11.9 mm and 14.2 mm, and weight of 14.1 g and 16.9 g, respectively) (Figures 3-5 A and B) (Table 3-5).

These results showed that in this case, it was not possible to improve sprouting control significantly in potatoes already treated on the field with MH by performing post-harvest treatment with 1,4-DMN and 3-decen-2-one molecules.

Our results contradict Harper (2019), who tested combinations of post-harvest sprout suppressants and MH field treatment, and concluded that combinations that include MH are effective sprout suppressants, but in their study, they noted that this result could not be categorically established because they used potatoes from different stocks.

3.4.2. No influence from combinations on sugar content in potatoes

A combination of MH field treatment and post-harvest treatments with CIPC, 3-decen-2-one, and 1,4-DMN does not influence the reducing sugars in potatoes (Table 3-2), as well as sucrose content, compared with pre- and post-harvest treatments used alone (Tables 3-4 and 3-5) (Figures 3-4 C and 3-5 C).

3.5. Variety effect varies according to post-harvest treatment

We observed little interaction ($p = 0.0496$) between the product and variety factors (Table 3-2) for sprout weight. We performed a separate supplementary Tukey's test analysis of this interaction to check the effect from factor variety on sprout weight for each product.

Sprout weight is not significantly different between varieties in the control group and in potatoes treated with CIPC ($p > 0.05$; Tukey's test), while for potatoes treated with 1,4-DMN, sprout weight is significantly higher for the Lady Claire variety (average of 29.8 g) compared with the Verdi variety (average of 9.4 g) ($p = 0.002$; Tukey's test), with no significant differences observed between the other varieties ($p > 0.05$; Tukey's test) (Figure 3-6). When potatoes are treated with 3-decen-2-one, sprout weight is significantly higher in the Fontane variety (average of 22.6 g) compared with the Markies variety (average of 1.2 g) ($p = 0.017$; Tukey's test), with no significant differences observed between the other varieties ($p > 0.05$; Tukey's test) (Figure 3-6). The higher sprout development in the Fontane variety, compared with Markies, for potatoes treated with 3-decen-2-one can be explained because we applied the 3-decen-2-one treatment when sprouts reached a minimum length of 3 mm for all varieties. The Fontane variety has the shortest dormancy period, so the sprouts were bigger than 3 mm at the time of treatment. We think that the product was applied too late for this variety, as it is a product with a curative effect that works better when applied on small sprouts (< 3 mm).

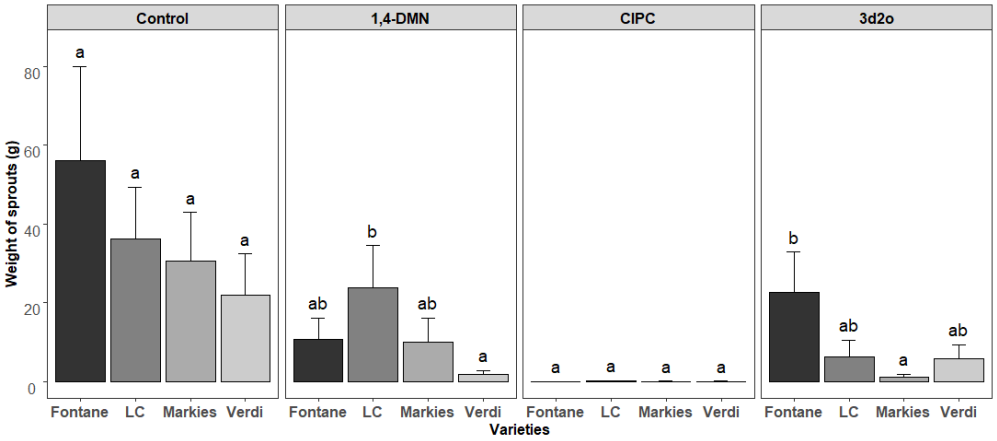

Figure 3-6. Average sprout weight for each variety and for potatoes treated with different post-harvest treatments; over two field treatments and three years (n = 6); after seven months of storage (80 % RH); error bars represent standard error of the mean; (LC = Lady Claire; 3d2o = 3-decen-2-one). Within each post-harvest treatment, groups sharing the same letter are not significantly different (Tukey's test, confidence level of 95 %).

3.6. Effect from products is genotype-dependent

The effect from post-harvest treatments (without previous MH pre-harvest treatment) varies according to variety. Treating potatoes with CIPC, 3-decen-2-one, and 1,4-DMN significantly decreases sprout weight among the Fontane ($p < 0.001$; $p = 0.046$ and $p = 0.005$) and Markies ($p < 0.001$, $p = 0.006$ and $p = 0.036$) varieties compared with the untreated control group, but it should be noted that the effect from 3-decen-2-one on sprout weight for the Fontane variety is low ($p = 0.046$) (Tukey's test, Figure 3-7). This low effect is probably due to the fact that the Fontane sprouts were too big at the time of the first treatment with 3-decen-2-one (see 3.5).

For the Lady Claire variety, only the CIPC and 3-decen-2-one treatments decreased sprout weight ($p < 0.001$ and $p = 0.009$), while sprout weight for potatoes treated with 1,4-DMN was not significantly lower than the control (Tukey's test). Finally, treating Verdi potatoes with CIPC and 1,4-DMN significantly decreased sprout weight compared with the control group ($p < 0.001$ and $p = 0.002$), while 3-decen-2-one did not significantly decrease sprout weight for this variety ($p = 0.112$) compared with the untreated control group, probably due to the data variability and because sprouting in the Verdi variety was relatively low in the control group (Tukey's test) (Figure 3-7).

These results show that the effect from post-harvest treatments on sprout weight is genotype-dependent. When potatoes are treated on the field with MH, among tested post-harvest treatments, only CIPC significantly reduces sprout weight in the Fontane and Lady Claire varieties compared with the control group treated on the field with MH ($p = 0.012$ and $p = 0.031$, Tukey's test).

Post-harvest treatments of the Markies and Verdi varieties already treated with MH on the field did not significantly reduce sprout weight compared with potatoes treated with MH only ($p > 0.05$, Tukey's test) (Figure 3-7). Thus, the effect from post-harvest treatments used in combination with an MH pre-harvest treatment is also genotype-dependent.

Therefore, the choice of pre- and post-harvest products to control potato sprouting will necessitate considering choice of variety and adapting and monitoring potato storage accordingly.

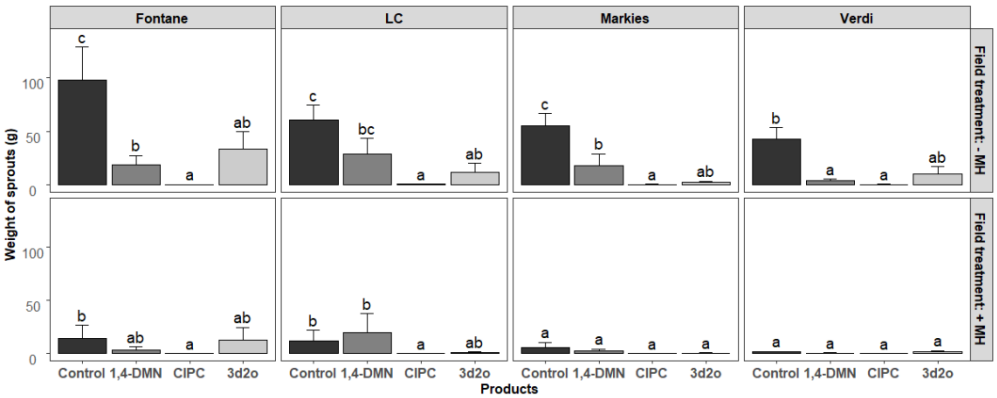

Figure 3-7. Average sprout weight for each post-harvest treatment; with (+ MH) or without (- MH) MH field treatment and for different varieties after seven months of storage (80 % RH); over three years (n = 3); error bars represent standard error of the mean; (LC = Lady Claire; 3d2o = 3-decen-2-one; MH = maleic hydrazide). Within each variety and each field treatment, groups sharing the same letter are not significantly different (Tukey's test, confidence level of 95 %).

3.7. CIPC and MH residues found in treated potatoes

The European Commission established maximum residue levels (MRLs) for the tested molecules in potatoes at 10 mg kg^{-1}, 15 mg kg^{-1}, and 60 mg kg^{-1} for CIPC, 1,4-DMN, and MH, respectively (European Commission 2019b). 3-decen-2-one is registered as post-harvest treatment on potatoes in the USA and Canada, but not in the European Union. In the USA and Canada, there is an exemption from the requirement of a tolerance (= MRL) for this product (EPA 2013b; Health Canada 2014).

CIPC residue was detected and was greater on average in potatoes analyzed with skin (22 mg kg^{-1} in 2016-2017 and no residue in 2017-2018 [<LOQ]) than in skinless potatoes (1.4 mg kg^{-1} in 2016-2017 and 1.3 mg kg-1 in 2017-2018).

Our results are consistent with those of Ezekiel and Singh (2008), who showed that CIPC residue is higher in the peel than in the flesh. Furthermore, 48 h after CIPC treatment, they found that CIPC residue in the peel was about 4.7 mg kg^{-1}, whereas in

peeled potatoes, it was 0.1 mg kg^{-1}. Mahajan et al. (2008) also reported that peeling potatoes lowers residue levels, as they found negligible residue levels in peeled potatoes. Moreover, it was reported that the residue level of CIPC was significantly lower in cooked potatoes (crisps and jacket potato crisps), which was due to the nature of this product, though it is not systemic. Thus, residue remained on the tuber surface, and most of it was removed by peeling the potatoes before processing (Lewis et al. 1996; Mahajan et al. 2008). We observed cross-contamination in our study (2017-2018 trial), as we detected low CIPC residue levels in potatoes that did not receive CIPC treatment (0.012 mg kg^{-1} of CIPC in potatoes treated with the molecule 1,4-DMN and 0.042 mg kg^{-1} of CIPC in untreated potatoes, both analyzed with skin). Furthermore, 3-chloroaniline, the metabolite of CIPC, was not found in the potatoes in our trials (< LOQ).

We found MH residue in potatoes analyzed without skin and in potatoes analyzed with skin. In the potato flesh, 14 and 9.8 mg kg^{-1} of MH residue were found in 2016-2017 and 2017-2018, respectively, while in unpeeled potatoes, no residue was detected in 2016-2017 (<LOQ) and 10 mg kg^{-1} were found in 2017-2018. Previous studies showed similar results. Newsome (1980) found 3.3 ± 0.9 mg kg^{-1} of MH residue in treated potatoes after eight weeks of storage, analyzed with skin. The authors reported that because MH is applied on the field and translocated from the leaves to the potato tubers through the phloem (Hoffman and Parups 1964; McKenzie 1989; Dias and Duncan 1999b), residue is expected to be located within the flesh of the potato tuber and distributed evenly throughout the tuber (Lewis et al. 1998; McKenzie 1989).

Molecules of 1,4-DMN were not found in treated potatoes in 2016-2017 and 2017-2018 (<LOQ).

4. Conclusions

Despite the high efficiency of CIPC, a need exists to develop new sprouting-control strategies in the wake of the European Union's non-renewal of CIPC due to gaps in the renewal application file, and to the raise of concerns for the consumers regarding the CIPC and its major metabolite (European Food Safety Authority (EFSA) et al. 2017; European Commission 2019a). CIPC residues were detected in our study in potato tubers 8 to 8.5 months after CIPC treatments. The level of residues detected exceeded the authorized level (MRL = 10 mg kg^{-1}) in one sample of tubers analyzed with the skin. Besides, cross-contamination with CIPC were also found in our study. Such cross-contamination can be due to the high persistence of CIPC in the concrete of potato storage chambers (Douglas et al. 2018) and in devices such as ventilation systems (Martin 2020b).

Our experiments confirmed that MH field treatment is also effective in controlling potato sprouting and, therefore, can be viewed as a good alternative to CIPC. Nevertheless, using MH also resulted in the presence of residues in the potatoes. MH

residues may be a problem, as this molecule elicits cytotoxic effects in mammal cells, carcinogenic effects in both mice and rats, and reportedly decreases fertility in rats (Swietlińska and Zuk 1978; Ponnampalam et al. 1983; Epstein et al. 1967; Yurdakok et al. 2014). Nevertheless, in our trials, maximum MH residue levels were below the authorized level of 60 mg kg^{-1}. However, MH field treatment should be used for potato varieties with a short dormancy period, when drastic sprouting control is needed to avoid losses during storage. For the other varieties, it is possible to avoid field treatment and schedule post-harvest treatments according to the duration of the variety's dormancy period and the expected storage duration (Visse-Mansiaux et al. 2018). For instance, the Verdi variety displayed a longer dormancy period than the Fontane variety because after seven months of storage, Verdi showed significantly lower sprout development in our study. Thus, the first post-harvest treatment for the Verdi variety could be delayed compared with Fontane. Using varieties with medium to long dormancies could allow for the use of anti-sprouting molecules that are less effective than CIPC, but less persistent in potato tubers, to avoid residue problems.

Our results showed that post-harvest treatments with 1,4-DMN and 3-decen-2-one reduce sprouting effectively during seven months of storage compared to the untreated control, but with lower efficacy compared with CIPC.

However, acceptation level of sprouting is higher for potatoes dedicated to processing compared with potatoes dedicated to the fresh market. In the present study, we concluded that both 1,4-DMN and 3-decen-2-one post-harvest treatments allowed to maintain a good control of sprouting up to seven months for processing potatoes and represent valuable alternative to CIPC. Moreover, no residue of 1,4-DMN has been detected in tubers treated with this molecule in our study (< LOQ). The benefit of the 3-decen-2-one post-harvest treatment is that this molecule allows to burn and dry out sprouts and can be used to save potato stocks that already have sprouted, as the study authors reported that applying 3-decen-2-one on potatoes leads to necrosis in sprouts within 24-36 h of exposure (Knowles and Knowles 2015a). Such necrosis after treatments with 3-decen-2-one also was observed in our experiments. Nevertheless, 3-decen-2-one treatments should be performed on tubers with small sprouts (< 3 mm), as the efficacy of this product drops for tubers with bigger sprouts. For example, we observed this phenomenon with the Fontane variety.

Our results showed that combining MH field treatment with post-harvest treatments does not improve sprout control compared with pre-harvest or post-harvest treatments used alone. For instance, our results suggest that performing a post-harvest treatment with the molecules 3-decen-2-one or 1,4-DMN on potatoes already treated on the field with MH does not improve sprout control. These findings indicate that these combinations are not economically sustainable and that in this case, pre-harvest treatment with MH alone is sufficient to control sprouting.

Other products on the market have been touted as effective to control post-harvest potato sprouting, such as mint essential oil and ethylene gas, which have the advantage of being authorized for organic farming (Martin 2012), but they also present drawbacks.

Nebulizing of mint essential oil may increase sprouting-control expenses during storage because a large quantity is required during the storage period, and its price is generally higher than the other chemicals available on the market (Martin 2012; Curty Personal communication).

Costs associated with ethylene gas treatments are in the range of those reported for CIPC; nevertheless, this product often is not recommended for the storage of processing potatoes (Martin 2012) because ethylene gas is reported to increase reducing sugars in potatoes and thus leads to a risk of darkening of potatoes after frying (Daniels-Lake 2013). Harper and Stroud (2018) reported that ethylene's effect on processing fry color was variety-dependent; therefore, ethylene could be used for some varieties. However, the authors recommend testing each variety's fry-color response to ethylene before using it on a larger scale. Further research in this area would allow for screening current and future processing-potato varieties suitability for ethylene treatment. Prange et al. (2005) reported that the 1-methylcyclopropene (1-MCP) molecule can be used in combination with ethylene treatment to reduce ethylene-induced fry-color darkening.

Finally, cold storage (at 4 °C) to delay sprouting could be an option for some varieties with a higher tolerance to CIS, either through conventional breeding or genetic engineering. For instance, the Lady Claire, Kiebitz, and Verdi varieties reportedly have limited CIS abilities after being stored at 4 °C (Visse-Mansiaux et al. 2019). Such varieties could be stored at low temperatures and used for processing with a lower risk of acrylamide production. Furthermore, anti-sprouting treatments would be requested only for very long storage periods.

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The authors have not stated any conflicts of interest.

Chapter 4

Storage of processing potato varieties: the post-CIPC era

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Outline

This chapter aims to find anti-sprouting suitable alternatives to CIPC. The novelty of this research compared to chapter three, is that the efficacy of natural molecules to mitigate sprouting was evaluated as well (i.e. L-carvone from mint essential oil, D-limonene from orange essential oil and ethylene). In addition, the efficacy of L-carvone and D-limonene molecules was assessed in both semi- and industrial conditions of storage close to the practice (i.e. 5 tonnes and > 300 tonnes of potatoes per storage chamber respectively). The efficacy of ethylene alone or in combination with the 1-MCP molecule, was evaluated in experimental chambers (i.e. 200 Kg). 1-MCP is a synthetic molecule used to limit the development of reducing sugars in potatoes stored in an ethylene-rich atmosphere. This research could contribute to help farmers to face the CIPC removal in Europe, especially for organic farming with natural alternatives proposed in this chapter.

Abstract

For decades, chlorpropham (CIPC) has been the most commonly used product for controlling potato sprouting during storage. The non-renewal of the authorization of this molecule came into effect in January 2020 within the European Union. In Switzerland, its use has been banned since 30 September 2020. Anticipating this situation, Agroscope performed trials over a five-year period, from 2015 to 2020, to find alternatives to CIPC for the storage of commercial potato varieties. The efficacy of five anti-sprouting molecules applied in post-harvest treatments was evaluated for at least two consecutive years: 1,4-dimethylnaphtalene (1,4-DMN), 3-decen-2-one, ethylene alone or in combination with 1-methylcyclopropene (1-MCP), L-carvone, and D-limonene. In addition, the efficacy of maleic hydrazide (MH), which is applied in the field to crops, was also evaluated. The efficacy of the active molecules was evaluated up to five or seven months of storage and compared to an untreated control and to the efficacy of CIPC. Reducing sugars were measured in tubers of the trial that evaluated the efficacy of ethylene alone or in combination with the 1-MCP molecule.

The results show that all the tested molecules are effective in controlling sprouting, but with varying degrees of efficacy within the tested molecules and the experimental conditions. Moreover, the efficacy of certain molecules (MH and ethylene) can vary depending on the variety. We also observed that the active molecule 1-MCP inhibited the increase in reducing sugars caused by an ethylene treatment. In general, the molecules tested were not as effective as CIPC. The use of these molecules should be combined with innovative storage strategies in order to meet the dual challenge of keeping stocks sprout-free for several months and preventing an increase in reducing sugars.

Keywords: potatoes, sprouting, maleic hydrazide, essential oils, synthetic molecules

1. Introduction

Chlorpropham (CIPC) is a highly effective molecule that has been used worldwide for decades to control potato sprouting during several months of storage (Paul et al. 2016c).

The use of pesticides within the European Union (EU) and Switzerland has increasingly been subject to constraints for safeguarding human health and promoting environmental sustainability. In this context, the use of CIPC is in its final days. In fact, the decision not to renew the authorization of this molecule came into effect in the EU in January 2020 (European Commission 2019a). The use of CIPC stocks is being phased out, and is already prohibited in several European countries such as Belgium (Martin Personal communication). In Switzerland, the sale of CIPC was still authorized up to 15 August 2020, and 30 September 2020 was set as the use-by date for the remaining stocks (FOAG 2020). This means that the 2020–2021 storage season will be CIPC-free in the majority of European countries. Switzerland was theoretically still able to treat potatoes with CIPC in September 2020, but this was discouraged to avoid residues in the tubers and storage cells, given the high persistence of the product. Indeed, although the maximum residue limit (MRL) for CIPC currently remains unchanged in the EU (MRL = 10 mg kg^{-1}) (European Commission 2019b), it is expected to change rapidly. A vote is scheduled for autumn 2020 that is expected to endorse a temporary MRL of 0.4 mg kg^{-1} which will be implemented in spring or summer 2021. This temporary MRL will be further reduced at a later stage (Martin Personal communication). In Switzerland, the Federal Food Safety and Veterinary Office (FSVO) has decided that the current MRL of 30 mg kg^{-1} will remain in force until 1st July 2021, at which point it will change to 10 mg kg^{-1}. Like the EU, Switzerland is expected to subsequently fix a temporary MRL of 0.4 mg kg^{-1}; however, the date of this revision for Switzerland is not yet known (Swisspatat 2020a). CIPC is a product that remains in facilities for a long time; it has been shown to persist in the concrete of storage rooms, as well as in their ventilation systems (Douglas et al. 2018; Martin 2020b). Consequently, it is important to anticipate the risks of product persistence in storage facilities. The first measure would be to stop using CIPC, and the second would be to clean the storage facilities to remove as much of the residues from the previous years of treatment as possible.

The ban on using CIPC implies a genuine need to find new anti-sprouting solutions. Several molecules that can be applied post-harvest as an alternative to CIPC are already on the market worldwide, such as:

- **1,4-dimethylnaphtalene (1,4-DMN)**

The molecule 1,4-DMN is a hormone that is naturally present in potatoes (Campbell et al. 2012). Chemically synthesized to be used as a sprout inhibitor, 1,4-DMN is approved in six European countries, as well as in the United States, Canada, New Zealand, Mexico, and Kenya (Jina Personal Communication). It has just been approved in Switzerland (FOAG 2020). The MRL of the molecule 1,4-DMN in

potatoes is fixed at 15 mg kg^{-1} in the EU (European Commission 2019b) and in Switzerland (FSVO 2020).

- **3-decen-2-one**

The molecule 3-decen-2-one is a natural biochemical compound (EPA 2013a) found in certain mushroom species of the genus Boletus and authorized as a food additive in the EU. This molecule is chemically produced and is approved as a sprout inhibitor in the United States, Canada and Israel. It is expected to be registered in the EU in 2022 (Immaraju Personal communication).

- **Ethylene**

Ethylene is a hormone that is naturally present in numerous fruits and vegetables. This molecule is approved as a sprout inhibitor with different modes of application. The first is via a so-called 'Biofresh Safestore' system, which uses 99.95% pure ethylene supplied in compressed-gas cylinders. Ethylene is released in the storage room in a controlled manner by a Biofresh Ethylene Management Unit (EMU) (BioFresh 2020). Offered by the company Biofresh (Biofresh Group Ltd.), this system is approved in six European countries, the United States, and Japan (Caisley 2020). The second delivery mode, offered by the firm Restrain® Company Ltd., is via a generator that transforms ethanol into ethylene directly in the storage room. The Restrain® system is also approved in numerous European countries, particularly in Switzerland, where it is marketed by Netagco (Netagco Suisse Sàrl).

- **L-carvone**

Mint essential oil, which primarily consists of the molecule L-carvone, has been approved as a sprout inhibitor in 18 European countries (including Switzerland) as well as in the United States (De Barbeyrac Personal communication).

- **D-Limonene**

Orange essential oil, the main active molecule of which is D-limonene, was recently approved as a sprout inhibitor in the Netherlands (Bonnet Personal communication).

- **Maleic hydrazide (MH)**

Maleic hydrazide-based products applied in the field are available in several countries and in Switzerland, and help slow sprouting during storage (Caldiz et al. 2001a). This molecule is very old, given that it was first approved in the late 1940s (Schoene and Hoffmann 1949).

This research project aimed to explore all alternative treatment solutions to CIPC for controlling potato sprouting and maintaining the quality of goods during storage. The efficacy of the different aforementioned molecules was tested under experimental conditions for some molecules (200 kg potatoes) and under semi-industrial (five tonnes) and industrial conditions (> 300 tonnes) for others. The trials were conducted at facilties owned by Agroscope and/or at those of our partner, Fenaco.

2. Materials and methods

2.1. Anti-sprouting treatment in the field

2.1.1. Maleic hydrazide (MH)

We tested the efficacy of maleic hydrazide (MH) up to seven months of storage to study the efficacy of this molecule over time in controlling sprouting during storage. The efficacy of MH was compared to an untreated control and to the efficacy of CIPC. Sprouting (the weight of the sprouts from 25 tubers) was observed after three and five months of storage at 8 °C as well as at seven months of storage after a gradual increase in temperature of 1 °C per week, ultimately reaching 15 °C after seven months. This process of gradually increasing the temperature is referred to as 'reconditioning' in the rest of this article. Nine varieties (Agria, Bintje, Fontane, Innovator, Lady Claire, Markies, Panda, Pirol, and Verdi) were tested for two seasons of consecutive trials (2016–2017 and 2017–2018). The treated tubers (100 kg per product) and the control tubers (100 kg) were stored in a cold room at 8 °C and 80% relative humidity.

The molecules were applied according to the suppliers' recommendations (Table 4-1).

2.2. Anti-sprouting treatments in storage

2.2.1. 1,4-DMN and 3-decen-2-one

The efficacy of the 1,4-DMN and 3-decen-2-one molecules was tested in experimental chambers developed by Agroscope containing 200 kg potatoes and allowing control of the CO_2 level. These experimental chambers were placed in a single cold room at 8 °C and 80% relative humidity, allowing the molecules to be tested under identical temperature and humidity conditions (Figure 4-1).

The molecules were tested on nine varieties (Agria, Bintje, Fontane, Innovator, Lady Claire, Markies, Panda, Pirol, and Verdi) for two seasons of consecutive trials (2016–2017 and 2017–2018). In order to evaluate the efficacy of the molecules, sprouting (the weight of the sprouts from 25 tubers) was observed after three and five months of storage at 8 °C for the treated tubers as well as for an untreated control. The sprout control efficacy of 1,4-DMN and 3-decen-2-one was compared to that of CIPC and the untreated control.

The molecules were applied according to the suppliers' recommendations (Table 4-1).

2.2.2. Ethylene alone or in combination with 1-MCP

We also evaluated the efficacy of ethylene for controlling sprouting (the weight of sprouts from 25 tubers), alone or in combination with the molecule 1-MCP (trade name: SmartFresh™). These tests were conducted under the same experimental conditions as for the molecules 1,4-DMN and 3-decen-2-one, and compared to an untreated control. The efficacy of these molecules was also compared to that of CIPC.

The 'control' and 'CIPC' chambers were placed in a different cold room from the 'ethylene' and 'ethylene + 1-MCP' chambers. The ethylene was released into the cold room via the Restrain® system (Restrain® Company Ltd.), which continuously released 10 ppm of ethylene into the atmosphere (after a progressive increase). Given that the ethylene generator was not fitted directly into the experimental chambers and that said chambers did not continuously draw air from the cold room, the ethylene concentration in the experimental chambers was variable (less than or equal to 10 ppm). The 1-MCP was applied at the end of October and then once a month at a concentration of 2 g SmartFresh™ powder diluted in 20 ml distilled water. When mixed with water, 1-MCP produces a gas that volatilizes in the storage room. We followed the dosage recommended in the publication of Prange *et al.* (2005), which uses 1-MCP via the product EthylBloc®, which we adapted for the volume of our experimental chambers in order to obtain the same dosage (0.9 μl.L^{-1}) with the SmartFresh™ used in our study.

We also observed the impact of these molecules on potato sugar content. Our partner Zweifel (a crisp manufacturer in Switzerland) conducted the analyses of the reducing sugars (glucose + fructose) on four varieties (Markies, Agria, Verdi, and Lady Claire) after three and five months of storage and for two consecutive years (2015–2016 and 2016–2017).

The molecules were applied according to the suppliers' recommendations (Table 4-1). Since 1-MCP is not authorized for the treatment of potatoes, it is not listed in Table 4-1.

2.2.3. Essential oils

The efficacy of the essential oils of mint and orange (L-carvone and D-limonene) was evaluated after three and five months of storage over two years of trials on three varieties (Agria, Verdi, and Innovator) and compared with that of an untreated control. The first year of trials was conducted under semi-industrial conditions (five tonnes for the year 2017–2018) and the second year under industrial conditions (> 300 tonnes for the year 2018–2019). The tubers of the different varieties came from the same batch, except for the tubers of the control from the year 2017–2018, which came from a different batch. The molecules were applied according to the suppliers' recommendations (Table 4-1).

Table 4-1. Information on the application of the molecules tested for Switzerland (*information given for guidance only; other suppliers, dosages, or application methods may exist).

Trade name of products used	Molecules	Modes of action	Product supplier in Switzer-land*	Amount to be applied*	Frequency of treatments*	Date of first application*	Modalities of application in our trials	Witholding period (waiting time before removal of potatoes	Method of application
Fazor®	60% maleic hydrazide	Inhibits cell division (*inter alia*)	Arysta LifeScience Switzerland Sàrl	5 kg / ha	Single treatment	Size greater than 25–30 mm	When the size was > 25 mm (1 treatment)	-	Liquid spraying
SmartBlock®	98% 3-decen-2-one	Curative: necrosis via destruction of the internal structure of the sprout cells	Not yet approved	100 mL/t	Application when the sprouts reach 3 mm in size (max. 4 treatments)	When the sprouts reach 3 mm	End of November or December according to the trials (4 treatments)	Unknown, as not approved in Europe	Hot-fogging
Dormir®	98 % 1,4-DMN	Preventive : prolongs potato dormancy	AGROLINE (Fenaco**)	10 to 20 mL/t)	Every 6 weeks (max.120 ml over season)	Possible as of entry into storage	Mid-October (treatments every 6 weeks)	30 days (EU)	Hot-fogging
Neo-Stop Starter®	300g/l Chlorpropham	Inhibits cell division	Arysta LifeScience Switzerland Sàrl	60 mL/t	Single treatment for liquid application	At the beginning of storage	Mid-October (1 treatment)	Four weeks after last treatment	Liquid spraying***
Argos®	843.2 g/L D-limonene	Preventive and curative (necrosis)	Not yet approved	100 mL/t	Every 3 weeks	1 month after entry into storage	Variable from mid-October to mid-November, depending on the trials (treatment every 3 weeks)	No withholding period	Hot-fogging (190 °C) ***
Biox-M®	65 to 85% L-carvone	Preventive and curative (necrosis)	Andermatt Biocontrol SA	90 ml/t (1st treatment) then 30 to 45 ml/t	Every 3 weeks (30 ml/t) or 4 weeks (45 ml/t) and a maximum 360 ml/t in total	6 to 20 days after harvest	Variable from mid-October to mid-November, depending on the trials (treatment every 3 weeks)	No withholding period	Hot-fogging (180-190 °C)***
Éthylène	Ethylene	Preventive – slows the growth of the sprouts and their speed of elongation	Netagco Suisse sàrl	Progressive increase, then 10 ppm continuously	Continuously	At the beginning of storage	From the beginning of storage (Restrain® generator)	No withholding period	Restrain® generator

**The product Dormir® was approved in Switzerland in September 2020 and will be marketed by Fenaco's new AGROLINE unit (https://www.agroline.ch/fr).
***Other application methods exist: check with the suppliers.

Figure 4-1. Automated experimental unit manufactured by Agroscope, which allowed potatoes to be treated independently in the same cold room. (Photo: Margot Visse-Mansiaux, Agroscope)

2.3. Experimental design and statistical analyses

The software program R, version 3.6.3 (R Core Team 2019) was used to perform the statistical analyses. Experimentation on the field treatments followed a repeated-measures linear mixed model with the fixed factors 'variety' and 'molecule' and the repeated factor 'observation date'. Year was considered a random factor. Post-harvest trials followed a linear mixed model with the fixed factors 'variety' and 'molecule', and 'year' was considered the random factor. For these post-harvest trials, statistical analyses were performed separately for the observations after three and five months of storage.

The aforementioned models were constructed using the 'lmer' function of the R package 'lme4' (Bates et al. 2015). For each model, the random factor 'year' was removed when it was found to be insignificant. The models were analyzed with the 'Anova' function of the R 'car' package version 3.0-7, which uses the chi-squared significance test for the linear mixed models (Fox and Weisberg 2019) or the F test

for the linear models without random effects. Variables were 'log (x + 1)' transformed when necessary to ensure normality and homogeneity of variance. A Tukey test (multiple comparisons of marginal means using the 'emmeans' method) was performed on the factors or interactions with a significant effect using the R 'emmeans' package (Lenth 2020). The significance threshold for all statistical tests was fixed at 5%.

3. Results and discussion

The results of the significance tests showing the effect of the factors 'treatment', 'variety' and 'observation period' as well as the effect of the interactions between the different factors are summarized in Table 4-2.

Table 4-2. *P-values* from the significance test (chi-squared test or F test according to the trials) showing the effects of the different factors and their interactions; statistics over two years of trials; *statistically different; NA = not analyzed.

Factors	**Period (months)**	**P-values for the trials with different treatments:**				
		Effect on sprouting (weight of sprouts from 25 Tubers in g)				Effect on the reducing sugars
		MH, CIPC, control	1,4-DMN, 3-decen-2-one, CIPC, control	Ethylene, ethylene + 1-MCP, CIPC, control	L-carvone, D-limonene, control	Ethylene, ethylene + 1-MCP, CIPC, control
Treatment	3 m.	p < 0.001*	p < 0.001*	p < 0.001*	p < 0.001*	p < 0.001*
	5 m.		p < 0.001*	p < 0.001*	p < 0.001*	NA
Variety	3 m.	p < 0.001*	p < 0.001*	p < 0.001*	p > 0.05	p < 0.001*
	5 m.		p < 0.01*	p > 0.05	p > 0.05	NA
Treatment x variety	3 m.	p < 0.001*	p > 0.05	p < 0.05*	P > 0.05	p < 0.01*
	5 m.		P > 0.05	P > 0.05	P > 0.05	NA
Observation period	_	p < 0.001*	NA	NA	NA	NA
Observation period x treatment	_	p < 0.001*	NA	NA	NA	NA
Observation period x variety	_	p > 0.05	NA	NA	NA	NA

The p-values presented in the sections below correspond to the p-values from the Tukey tests.

3.1. Anti-sprouting treatment in the field

3.1.1. Maleic hydrazide (MH)

The efficacy of the treatments varied depending on the variety and observation period (Table 4-2); consequently, we studied the effects of the treatments for each observation period and variety (Figure 4-2).

The results show that, compared to the control, MH provides good sprout control up to seven months of storage with temperature reconditioning ranging from 8 °C to 15 °C. After three months of storage at 8 °C, the efficacy of MH is similar to that of CIPC for the majority of varieties. After five months of storage at 8 °C, CIPC is more effective than MH for the majority of varieties. After seven months of storage with temperature reconditioning, CIPC is more effective than MH for all the varieties tested.

After three months of storage, the sprout weight was significantly lower for the CIPC and MH treatments than for the untreated control for the varieties 'Bintje', 'Fontane', 'Lady Claire', 'Markies', 'Panda', 'Pirol' and 'Verdi' ($p < 0.05$). For the 'Innovator' variety, the two molecules enabled significant sprout suppression compared to the control ($p < 0.001$), although CIPC achieved better control than MH ($p < 0.001$). For the 'Agria' variety, a significant but weak sprout-suppressant effect was observed for the CIPC-treated tubers ($p = 0.046$), and a marginally significant effect was observed for the tubers from plants treated with MH ($p = 0.050$) compared to the control (Figure 4-2).

After five months of storage, the sprout weight of the CIPC and MH treatments was significantly lower for the 'Pirol' and 'Verdi' varieties compared to the sprout weight of the untreated control ($p < 0.001$). For the seven other varieties, CIPC and MH achieved better sprout suppression than in the untreated control ($p < 0.001$), but the sprout weight of the CIPC-treated tubers was systematically lower than that of the tubers from plants treated with MH ($p < 0.05$) (Figure 4-2).

Finally, after seven months of storage and reconditioning at 15 °C, we observed that the molecules CIPC and MH had a better sprout-suppression effect for the nine varieties than in the control group ($p < 0.001$), and that for all varieties, MH was significantly less effective than CIPC ($p < 0.05$).

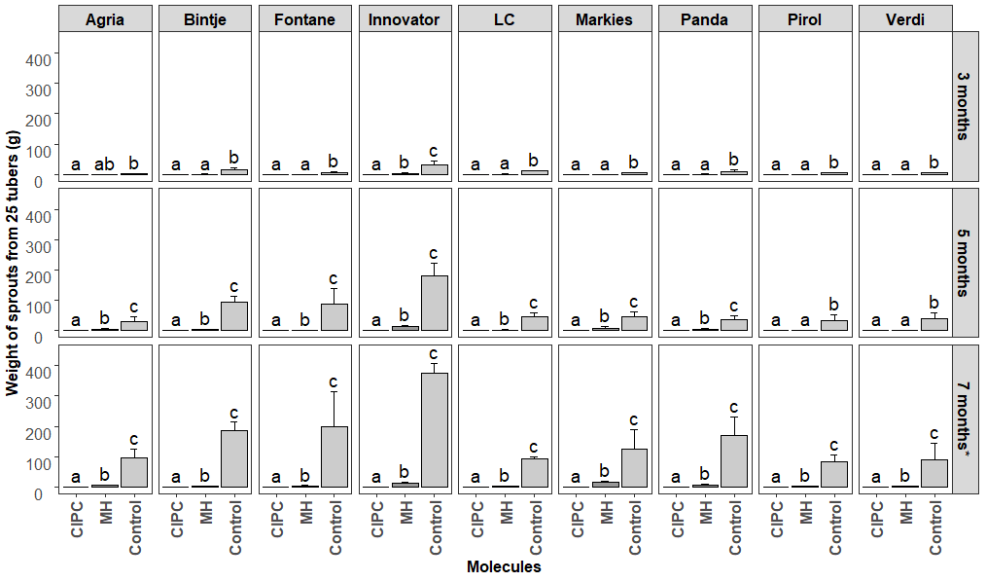

Figure 4-2. Sprout weight of 25 tubers treated with maleic hydrazide (MH) and CIPC and for the tubers of the untreated control after three and five months of storage at 8 °C and after seven months of storage (*seven months of storage with temperature reconditioning starting at 8 °C and ending at 15 °C at seven months) for the nine varieties tested during the two years of trials under controlled experimental conditions (200 kg of potatoes) (mean ± standard error). Means not sharing the same letter are significantly different according to the Tukey test. (LC = Lady Claire).

3.2. Anti-sprouting treatments during storage

3.2.1. 1,4-DMN and 3-decen-2-one

The molecules 1,4-DMN and 3-decen-2-one permit effective sprout control for up to at least five months of storage compared to the untreated control ($p < 0.001$). After three months of storage the efficacy of the two molecules is equivalent, and after five months 3-decen-2-one is more effective than 1,4-DMN ($p < 0.01$). Nevertheless, the efficacy of both active molecules was lower than that of CIPC for the two observation periods ($p < 0.001$; Figure 4-3).

The molecule 3-decen-2-one has a curative action, completely necrotizing and desiccating sprouts in just 24 hours (Figure 4-4). This explains the lower sprout weight of the potatoes treated with 3-decen-2-one compared with that of the tubers treated with 1,4-DMN after five months of storage. Sprout necrosis and desiccation 24 to 36 hours after application of 3-decen-2-one is reported in the literature (Knowles and Knowles 2015b, a; Immaraju 2020). The advantage of 3-decen-2-one lies in its curative action, which allows it to rescue potato stocks that have already sprouted. This product actually destroys the internal structure of the sprout cells; tissues are completely necrotized and desiccated down to the base of the sprouts. . 3-decen-2-one

works very well when applied by hot-fogging on small sprouts (< 3 mm). It is even more effective when the treatment is done at the first signs of dormancy break (sprouts at the 'white dot' stage), since the product vapors can then penetrate inside the sprouts and kill the developing meristematic tissues (Immaraju Personal communication, 2020). In our trials, the efficacy of this product is probably understated for certain varieties, since several varieties had variable dormancies in the same experimental chamber. Certain varieties that had sprouted more than others should thus have been treated sooner in order to achieve a better curative action. The number of 3-decen-2-one treatments for a complete storage season (seven to eight months) varied depending on the variety and temperature. On average, one to two treatments are necessary for the storage of long-dormancy varieties at low temperatures, and three to four treatments are required for short-dormancy varieties stored at higher temperatures (Immaraju Personal communication).

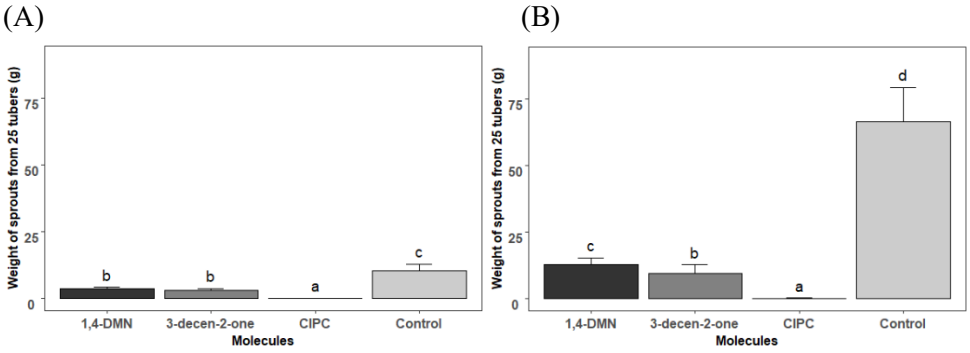

Figure 4-3. Efficacy of the molecules 1,4-DMN and 3-decen-2-one after three months (A) and five months (B) of storage over two years of trials under controlled experimental conditions (200 kg of potatoes) and for nine varieties (mean ± standard error). Means not sharing the same letter are significantly different according to the Tukey test.

Figure 4-4. Tubers of the 'Verdi' variety treated with the molecule 3-decen-2-one, after five months of storage under experimental conditions. Note the complete necrosis and desiccation of the sprouts. (Photo: Carole Parodi, Agroscope).

3.2.2. Ethylene alone and in combination with 1-MCP

Ethylene alone or in combination with the molecule 1-MCP reduces sprouting for at least up to five months of storage compared to the untreated control ($p < 0.05$; data not presented).

After three and five months of storage, the weight of the sprouts from the tubers treated with CIPC, ethylene, and the combination of ethylene + 1-MCP was significantly lower than the weight of the sprouts from the control ($p < 0.001$; $p < 0.05$ and $p < 0.05$).

Note that the efficacy of ethylene (alone or in combination with 1-MCP) may have been underestimated in our trials, owing to the fact that our experimental chambers did not allow the tubers to be exposed to a constant concentration of ethylene, which is normally recommended for this molecule. This is why we decided not to present the efficacy results obtained with ethylene in this article. However, we did note that the efficacy of ethylene depends on the variety of potato. We observed a less rapid progression of sprouting for the 'Markies' variety than for the three other varieties tested. This difference in efficacy between varieties was also observed in other trials. Flesch and Martin (2019) also observed excellent sprouting control for the 'Markies' variety stored under ethylene, while the sprouting control was less effective for the varieties 'Agria', Fontane' and 'Challenger' and was even less effective for the 'Innovator' variety.

We analyzed the amounts of reducing sugars in the tubers treated with the different molecules and in the untreated tubers of the control after three and five months of

storage at 8 °C. Given that the tested tubers had been exposed to a variable concentration less than or equal to the recommended dose (10 ppm), it is possible that the effect of ethylene on the increase in the reducing-sugar content of the treated tubers may have been underestimated in this study. The results are presented in Table 4-3. Statistical analyses were only performed for the data at three months of storage, for which we had the results for all molecules and all varieties for the two consecutive years of trials (Table 4-4).

As previously shown in the literature (Harper and Stroud 2018), our study showed that the impact of ethylene on sugar levels depends on the variety (Table 4-2). We therefore studied the effect of ethylene on sugars after three months of storage for each of the varieties (Table 4-4). Our results showed that the varieties 'Lady Claire' and 'Verdi' are not susceptible to sweetening under ethylene, while the varieties 'Agria' and 'Markies' are susceptible. Our study showed that 1-MCP helps to limit ethylene-induced potato sweetening. Our results are in line with the study of Prange et al. (2005), which showed that 1-MCP can be used to limit ethylene-induced fry-color darkening without inhibiting ethylene's sprout-suppressant effect.

Indeed, after three months of storage, reducing-sugar levels in the varieties 'Lady Claire' and 'Verdi' were low and did not vary much according to the molecules tested, while for the varieties 'Agria' and Markies' reducing-sugar levels varied depending on the treatment (Table 4-4). For the 'Agria' variety, reducing sugars were significantly higher in tubers stored in an ethylene-rich atmosphere (mean: 1.97 g kg^{-1}) compared to the reducing sugars measured in the tubers treated with ethylene + 1-MCP (mean: 0.72 g kg^{-1}) and those measured in the control (mean: 0.29 g kg^{-1}). Nevertheless, they were not significantly different from the sugars in the CIPC-treated tubers (mean: 1.18 g kg^{-1}) (Tables 4-3 and 4-4), because the reducing-sugar concentration was particularly high in the CIPC-treated tubers during the second year of trials (Table 4-3). The reducing sugars for the 'Markies' variety were not significantly different in the tubers treated with CIPC, ethylene + 1-MCP and in the control (means: 0.31, 0.82 and 0.39 g kg-1, respectively) but were significantly higher in the tubers treated with ethylene alone (mean: 1.77 g kg^{-1}) (Table 4-4).

After five months of storage, trends showed that the reducing-sugar levels were still low for the varieties 'Verdi' and 'Lady Claire', regardless of the treatment undergone, while for the varieties 'Agria' and 'Markies', reducing-sugar levels were relatively high in the ethylene-treated tubers (mean: 1.85 g kg-1 and 2.27 g kg^{-1}) compared with those of the control (mean: 0.89 g kg-1and 1.15 g kg^{-1}) or with those treated with CIPC (mean: 0.94 g kg^{-1} and 0.52 g kg^{-1}). The decrease in reducing-sugar levels in the tubers treated with ethylene + 1-MCP seemed to be greater after five months of storage than after three. Indeed, after five months of storage, treatment with 1-MCP seems to prevent an increase in reducing-sugar content in tubers of the varieties 'Agria' and 'Markies' (mean: 1.13 g kg^{-1} and 0.54 g kg^{-1}) (Table 4-3).

The molecule 1-MCP is not yet authorized in the European Union for use on potatoes. Consequently, although it cannot be used at present to decrease sugar levels in tubers stored under ethylene, authorization of this molecule in the EU for use on

potatoes is expected for 2022. A high level of reducing sugars increases the risk of darkening and of production of toxic compounds during frying (Wiberley-Bradford and Bethke 2017). For this reason, our partner Zweifel has fixed a very strict authorized pre-processing limit for reducing sugars (0.4 g kg^{-1}) to avoid any risk of darkening and of the presence of toxic compounds (mainly acrylamide) in the final product. Our results showed that this threshold can be exceeded for tubers stored in an ethylene-enriched atmosphere, including for the least susceptible varieties, such as Lady Claire, and even in the case of storage under ethylene in combination with the active substance 1-MCP (Table 4-3).

This reducing-sugar threshold may vary depending on the final product (crisps or French fries), the country, and the company. At Frigemo, a French fry manufacturer in Switzerland, the threshold varies depending on the variety. Before processing the potatoes into French fries, a fry test is performed with a visual rating of French-fry color (Swisspatat 2018), after which a correspondence chart allows for the evaluation of the corresponding level of reducing sugars in the French fries (Grob 2003). For example, the 'Markies' variety can be processed into French fries if it does not exceed the average threshold of 0.76 g kg^{-1} of reducing sugars, while the 'Agria' variety can be processed into French fries if it contains a level less than or equal to 0.95 g kg^{-1} (Schertenleib 2020).

In our study, these thresholds were systematically exceeded for potatoes stored under ethylene and were sometimes also exceeded for potatoes stored under ethylene + 1-MCP (Table 4-3). Consequently, the systematic performance of these fry and/or reducing-sugar tests before processing the potatoes into crisps or French fries is crucial, to avoid the risk of producing toxic compounds during frying.

Table 4-3. Reducing-sugar levels (g kg^{-1} of fresh weight) after three and five months of storage in the tubers treated with the molecules CIPC, ethylene, and ethylene + 1-MCP, as well as in the untreated control, for the four varieties tested during two years of trials.

			Reducing sugars (g kg^{-1}) for the different varieties:			
Molecules	Period	Trial year	Agria	Lady Claire	Markies	Verdi
CIPC	3 mos.	2015-2016	0.39	0.06	0.1	0.06
		2016-2017	1.97	0.07	0.51	0.14
	5 mos.	2015-2016	0.74	0.13	0.46	0.13
		2016-2017	1.14	0.29	0.58	0.18
Ethylene	3 mos.	2015-2016	1.77	0.43	1.36	0.18
		2016-2017	2.17	0.41	2.17	0.36
	5 mos.	2015-2016	1.04	NA	2.1	NA
		2016-2017	2.65	0.73	2.43	0.35
Ethylene + 1-MCP	3 mos.	2015-2016	0.66	0.22	0.31	0.09
		2016-2017	0.78	0.29	1.32	0.26
	5 mos.	2015-2016	0.71	0.53	0.69	0.17
		2016-2017	1.54	0.24	0.38	0.51
Control	3 mos.	2015-2016	0.12	0.18	0.08	0.08
		2016-2017	0.45	0.14	0.7	0.12
	5 mos.	2015-2016	0.68	0.08	0.39	0.15
		2016-2017	1.09	0.51	1.91	0.33

Table 4-4. P-values from the Tukey test comparing the effects of the treatments on the level of reducing sugars (glucose + fructose) after three months of storage for the four varieties tested (statistics for two years of trials: * = statistically different, (*) = cutoff).

Compared treatments	**Agria**	**Lady Claire**	**Markies**	**Verdi**
CIPC – Ethylene	>0.05	>0.05	<0.01*	>0.05
CIPC – Ethylene + 1-MCP	>0.05	>0.05	>0.05	>0.05
CIPC – Control	0.055(*)	>0.05	>0.05	>0.05
Ethylene – Ethylene + 1-MCP	<0.01*	>0.05	0.034(*)	>0.05
Ethylene – Control	<0.001*	>0.05	<0.01*	>0.05
Ethylene + 1-MCP – Control	>0.05	>0.05	>0.05	>0.05

3.2.3. Essential Oils

The study showed that the molecules L-carvone and D-limonene also provide good control of sprouting after three and five months of storage compared to the untreated control ($p < 0.01$ and $p < 0.05$) and with a similar efficacy. Furthermore, no significant difference was observed between the efficacy of the molecules L-carvone and D-limonene ($p > 0.05$; Figure 4-5).

In our trials, the essential oils caused localized necroses on the tips of the sprouts.

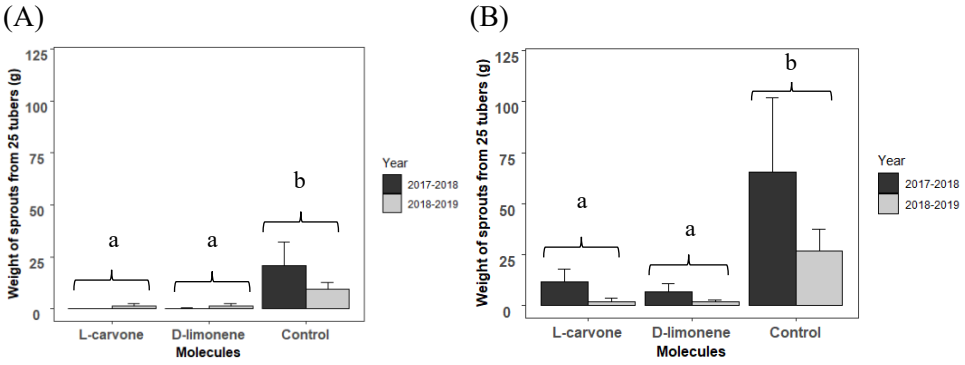

Figure 4-5. Efficacy of the essential oils at three months (A) and five months (B) during two years of trials, one year under semi-industrial conditions (five tonnes = year 2017–2018) and one year under industrial conditions (> 300 tonnes = year 2018–2019) for three tested varieties: Agria, Verdi and Innovator (mean ± standard error). In 2017–2018, the tubers from the untreated control were from a different batch. The means not sharing the same letter are significantly different according to the Tukey test.

3.3. Advantages and drawbacks of the different molecules

The various aforementioned molecules are likely to replace CIPC with more or less efficacy. The drawback of ethylene is its good-to-unsatisfactory efficacy as a sprout inhibitor, depending on the variety (Flesch and Martin 2019) and its negative effect on reducing-sugar content for certain varieties. The drawback of hot-applied essential oils is the high frequency of treatments (every three to four weeks), which require time and additional labor to carry out compared to the other products. The essential oils can also be automatically diffused by evaporation using a device such as the Xedavap®. This type of device should limit labor costs, but we have not tested its efficacy in our trials. Nevertheless, ethylene and essential oils offer certain advantages. Two of these molecules are already approved in Switzerland: the mint essential oil (L-carvone, approved under the name Biox-M®) and ethylene (approved for application on potatoes with the Restrain® generator). These products are compatible with organic farming, and are therefore not subject to an MRL. Ethylene has the advantage of an equivalent price of use to CIPC (Martin 2012; Visse-Mansiaux

et al. 2017). The other alternatives to CIPC are generally more expensive; for example, the cost of using the mint essential oil is at least two times greater than that of CIPC (Visse-Mansiaux et al. 2017; Curty Personal communication; Martin 2012).

The molecules 1,4-DMN and MH are highly effective and easy to use. However, they are not authorized for use in organic agriculture, and they are subject to an MRL in the final products (MRL = 15 mg kg^{-1} for 1,4-DMN and MRL = 60 mg kg^{-1} for MH in the EU (European Commission 2019b) and Switzerland (FSVO 2020). The molecule 3-decen-2-one is also highly effective and easy to use; our results showed that four treatments are sufficient to ensure control of sprouting throughout a storage season. Furthermore, this product has a curative effect, enabling the rescue of potato stocks that have already sprouted. Nevertheless, this molecule has not yet been approved in the EU and Switzerland. Once it has been approved, placing varieties with comparable dormancies in the same cold room will be the preferable approach to optimize product use. Given that the product is applied when the tubers start to sprout (Immaraju 2020), there is no benefit in treating varieties with a long dormancy and thus not yet showing any signs of sprouting at the same time as the tubers of varieties with shorter dormancy that are already showing sprouts.

CIPC can be applied in a single liquid-spray application at the beginning of storage, while the candidate replacement products are either applied several times by fogging, or continuously (by vaporization or gassing) during the storage season (Table 4-1). Thus, suitable storage buildings with powerful ventilation systems for proper distribution of the products are preferable for optimizing the efficacy of these products. The storage facilities must also be sufficiently airtight to prevent product loss, which would lead to reduced efficacy of the product and a direct financial loss. Given that these molecules are less effective than CIPC, wherever possible it would be preferable to favor varieties with medium-to-long dormancies.

CIPC was withdrawn from the market owing to risks of residues in the peel of the tubers (Ezekiel and Singh 2008) sometimes exceeding the authorized MRL of 10 mg kg^{-1} in the EU (European Commission 2019b). Nevertheless, this product had the advantage of being partially or totally eliminated during the peeling of the potatoes prior to their industrial processing. Conversely, maleic hydrazide is a systemic product found in the flesh of the tuber, and hence is only partially eliminated during processing; howerver, MH residues are in general well below the MRL of 60 mg kg^{-1} authorized in the EU. Compared to CIPC and MH, the molecules 1,4-DMN and 3-decen-2-one have the advantage of leaving very little residue on the tubers, thereby avoiding health and environmental risks. The CIPC, MH, 1,4-DMN, and 3-decen-2-one residue analyses conducted in our trials on treated tubers confirm the information presented above (data not presented).

4. Conclusions

It is important to combine the use of different alternative molecules to CIPC with new storage strategies in order to prevent loss of goods during potato storage and maintain high-quality stocks for several months without sprouting. Agroscope researchers are developing different innovative solutions for controlling sprouting.

- A sprouting model was developed to predict the dormancy date (and hence the sprouting date) of a given variety during a given season, based on weather parameters during the potato growth period (Visse-Mansiaux et al. 2018). This model will be used as a decision-support system for better potato-storage management based on the expected sprouting date. It will also help reduce or avoid the application of sprout-suppressant products depending on the length of expected dormancy, and thus reduce both treatment costs and the risk of product residues.
- In partnership with Swisspatat, Agroscope is also working on identifying industrial varieties that would not be susceptible to sweetening during storage at low temperatures. This would enable these varieties to be stored at 4 °C or 6 °C to delay tuber sprouting. With such varieties, it would be possible to extend storage and/or reduce or even avoid the application of sprout-suppressant products. This work has already allowed the identification of three varieties with low susceptibility to sweetening for storage at 4 °C: Lady Claire, Verdi, and Kiebitz (Visse-Mansiaux et al. 2019).
- Agroscope is also testing the effect of low storage temperature (4 °C) for varieties susceptible to sweetening, followed by reconditioning. We observed that reconditioning allowed a significant reduction of the reducing-sugar levels of certain varieties that are susceptible to sweetening (data not presented). However, sugar levels can vary (even in varieties with a low susceptibility to sweetening at low temperatures) depending on the year and the growing location (data not presented). We therefore recommend the systematic performance of reducing-sugar analyses and/or a fry test before processing potatoes stored at 4 °C with or without reconditioning, in order to limit the risk of darkening and acrylamide production during frying.

In response to the CIPC ban, the various aforementioned strategies must be implemented and combined in order to maintain high-quality storage and guarantee the sustainability of potato storage in Switzerland.

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The authors have not stated any conflicts of interest.

Chapter 5

Identification of potato varieties suitable for cold storage and reconditioning: a safer alternative to anti-sprouting chemicals for potato sprouting control

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Outline

To avoid or reduce the use of anti-sprouting treatments presented in chapters three and four, another storage management strategy would be to use storage at low temperatures to mitigate sprouting. This would reduce the use of chemical treatments that lead to the risk of residues in potatoes and lower the costs associated with those treatments. Cold storage may also be used to reinforce the efficacy of these anti-sprouting treatments to mitigate sprouting during long-term storage or after seasons leading to high sprouting pressure. Consequently, the main objective of this chapter was to identify potato varieties suitable for storage at low temperature (i.e. 4 °C) without Cold Induced Sweetening (CIS), with good processing quality and without production of toxic acrylamide. Six processing potato varieties (Lady Claire, Verdi, Kiebitz, Pirol, Agria and Markies) were tested in the present study. Firstly, the potential of cold storage to mitigate sprouting was studied for the six selected varieties stored at both 4 °C and 8 °C for up to 4.5 months. Secondly, to understand the CIS behaviour of these six potato varieties, the effect of cold storage on several parameters was evaluated after two and/or four months of storage at 4 and 8 °C. Parameters measured were the following: sucrose, total reducing sugars, glucose, crisp quality, asparagine, acrylamide content in crisps and expression of the Vacuolar Invertase (VInv) gene. In addition, the potential of reconditioning up to 15 °C after storage at 4 °C to improve the above-mentioned parameters was assessed in varieties Markies and Verdi after four months of storage. This study will help farmers to get insights on the CIS behaviour of potato varieties and consequently will improve the use of cold storage to mitigate sprouting, while lowering the risks of acrylamide production. Identifying CIS-resistant potato varieties will also help to avoid or delay treatments with synthetic anti-sprouting molecules. Consequently, using CIS-resistant varieties will have a two-fold benefit for human health.

Abstract

Low temperature storage as an alternative to anti-sprouting chemicals in potato storage may induce reducing sugars (RS) accumulation (i.e. glucose and fructose) in potato tubers. This phenomenon is called "cold induced sweetening" (CIS) and occurs in certain varieties. CIS leads to a decrease in the organoleptic qualities and darkening of processed potato and the accumulation of toxic molecules such as acrylamide. To identify potato varieties suitable for storage at low temperatures, we screened six commercial processing varieties: Lady Claire (LC), Verdi, Kiebitz (KB), Pirol, Agria and Markies for their CIS characteristics and sprout-forming potential after storage at 4 °C and 8 °C. Our findings reveal that 4 °C storage allows for efficient sprout reduction in all six tested varieties for up to 4.5 months of storage. Three CIS-resistant varieties, namely Verdi, Lady Claire and Kiebitz, were identified as able to be stored for up to four months at 4 °C with limited increase in glucose content. Conversely, Pirol, Agria and Markies showed an increase in glucose content with decrease in storage temperature and can be considered as CIS-susceptible varieties. After processing into crisps, the CIS-susceptible varieties displayed poor crisp color quality (brown to black color crisps) after storage for two months at 4 °C compared to the storage at 8 °C, whereas the CIS-resistant varieties had good crisp color quality (pale yellow color crisps) after storage at both 4 and 8 °C. Interestingly, the trends of total RS and/or glucose content in the CIS-resistant and in the CIS-susceptible varieties were correlated with the trends in Vacuolar Invertase (*VInv*) gene expression for most varieties, as well as with the trends in acrylamide content after processing. In addition, reconditioning of Markies variety after storage at 4 °C by gradually increasing the temperature to 15 °C resulted in reduced *VInv* transcript levels and reduction in glucose and acrylamide contents.

Keywords: potato, Cold Induced Sweetening, CIS-resistant genotype, acrylamide, sugars, vacuolar invertase gene

1. Introduction

Potato (*Solanum tuberosum* L.) is the fourth most important food crop worldwide in terms of annual production with 370 million tonnes in 2019 (FAOSTAT 2021b). To avoid losses caused by sprouting during potato storage, chlorpropham, commonly called CIPC, has been used for decades as the anti-sprouting agent of choice in the EU and Switzerland and is highly efficient to keep potatoes free of sprouts for months at storage temperatures ranging from 8 to 12 °C (Paul et al. 2016c; Corsini et al. 1979; Mahajan et al. 2008). Nevertheless, the European Union recently voted for the non-renewal of the use of CIPC in potato storage due to a potential risk of CIPC and its metabolite 3-chloroaniline for the consumer (EU regulation 2019/989). Alternative chemicals controlling sprouting are available, however these molecules are often less effective than CIPC (Visse-Mansiaux et al. 2020; Visse-Mansiaux et al. 2021) and residues of treatments could persist in tubers. Visse-Mansiaux et al. (2021) reported that residues of the maleic hydrazide anti-sprouting molecule have been detected in tubers at the end of the storage period, even though these residues were below the authorized maximum residue limit (MRL).

Other storage strategies can be used to keep potatoes free of sprouts without relying on anti-sprouting molecules such as using varieties with long dormancies. However, because of market and agricultural requirements, varieties with short- and medium-dormancies are frequently used (Curty Personal communication). To use varieties with a large range of dormancies while avoiding the use of chemicals to control sprouting, storage at low temperatures can be used to prolong the dormancy period and to delay sprouting (Paul et al. 2016b; Sonnewald 2001; Sowokinos 2001; Burton and Wilson 1978; Gichohi and Pritchard 1995). Potatoes intended for the fresh market are usually stored at low temperatures ranging from 5 to 6 °C (Bishop 2012). Storage at low temperature is generally not recommended for potato varieties dedicated for processing. Due to their susceptibility to sweetening, varieties dedicated for processing are usually stored at temperatures ranging from 7 to 10 °C (bishop 2012). Sweetening of tubers at low temperatures is caused by the accumulation of reducing sugars (RS) (i.e. glucose and fructose), also called “cold-induced sweetening” (CIS) (Hou et al., 2017; Sowokinos, 2001) and controlled by complex mechanisms. During storage at low temperatures, potato starch is degraded mainly through phosphorylase in hexose-phosphates (Morrell and Rees 1986; Davis and Viola 1992; Hill et al. 1996; Sowokinos 2001) leading to the accumulation of sucrose free sugar (Sowokinos 2001; Sowokinos 1990). Sucrose is then cleaved by acid invertase to RS (McKenzie et al. 2013). During the CIS phenomenon in potato tubers, the rate of conversion of starch into RS is accelerated through several enzymatic reactions (Sowokinos 2001). CIS leads to a decrease in quality of processed potatoes (e.g., crisps and French fries) and is partly responsible for bitter-tasting and dark coloration of crisps and French fries, which is unacceptable to consumers (Pinhero et al. 2011; Amjad et al. 2020; Mottram

et al. 2002). CIS also leads to the production of toxic compounds such as acrylamide during frying, which may raise concerns for human health (Paul et al. 2016b; Wiberley-Bradford and Bethke 2017; Wiberley-Bradford et al. 2016) as acrylamide is classified as a probable human carcinogen (FAO/WHO 2002). Undesirable flavor, dark color and acrylamide are produced through the Maillard reaction. The Maillard reaction occurs during heat treatment and consists of a reaction between amino acids and RS leading to the above-mentioned undesirable flavor, dark color and acrylamide. Asparagine has been demonstrated to be a major amino acid involved in the production of acrylamide in potatoes (Mottram et al. 2002).

Two main metabolic pathways control the CIS phenomenon: the sucrose synthesis controlled by several enzymes and the hydrolysis of sucrose to reducing sugars mainly controlled by the level of acid invertase activity (Stitt and Sonnewald 1995; Sowokinos 2001; Pressey and Shaw 1966). The vacuolar invertase (*VInv*) gene seems to play an important role in potato CIS. Bhaskar et al. (2010) demonstrated that silencing this gene prevents the accumulation of RS in potatoes stored at low temperature and that the transcript levels of *VInv* were low in tubers resistant to CIS. At low temperatures, sucrose concentrations increase and sucrose becomes the substrate for vacuolar invertase leading to accumulation of RS (Duplessis et al. 1996).

In the context of pesticide reduction, storing potatoes at low temperature to avoid sprouting instead of using chemicals seems to be a good practice to promote. To avoid CIS and human health risks associated with the presence of acrylamide in processed potatoes, potato varieties with limited accumulation of RS at low temperature (CIS-resistant varieties) should be used for cold storage. A few varieties with low accumulation of reducing sugars at low temperatures are available such as White Pearl (Groza et al. 2006), Sempra or Verdi (Böhm et al. 2006). With the CIPC non-renewal, it would be of interest to have a larger panel of CIS-resistant varieties, which can be stored at low temperatures. Therefore, it is necessary to describe the CIS-characteristics of several varieties before considering storage at low temperature and proposing CIS-resistant varieties with large ranges of dormancy.

Another strategy commonly used by the industry is to use cold storage followed by warming the tubers for one to several weeks at temperatures between 12 and 15 °C before processing. This allows the RS content to decrease. This practice is also called "reconditioning" (Jansky and Fajardo 2014; Fitzpatrick and Porter 1966; Schippers 1975).

Reconditioning could be used to reduce RS in CIS-susceptible varieties, improve the quality of crisps and French fries after cold storage, and consequently decrease the risk of acrylamide formation in deep-fried products. However, the reconditioning potential to decrease RS has been reported to be genotype-dependent (Kyriacou et al. 2009; Blenkinsop et al. 2002). Consequently, the potential of reconditioning should be evaluated for different potato varieties.

The main objectives of the present study are to identify potato varieties adapted to storage at low temperatures in relation to CIS, to evaluate the efficacy of

reconditioning to reduce the RS content in potatoes after storage at low temperature, and to characterize genetic and enzymatic mechanisms involved in CIS.

For this research, six processing potato varieties, namely Verdi, Lady Claire (LC), Kiebitz (KB), Pirol, Agria and Markies were stored at low temperature (i.e. 4 °C) and the commonly used temperature (i.e. 8 °C). To understand the interaction between variety and storage temperature on potato tuber quality, several parameters such as tuber dormancy, sugar composition, asparagine content and *VInv* gene expression in tubers, as well as crisp color quality and acrylamide content in crisps were determined. In addition, the potential of reconditioning at 15 °C after storage at 4 °C was evaluated in tubers of the varieties Markies and Verdi.

2. Materials and methods

2.1. Plant material and experimental design

The six potato varieties: LC, Verdi, KB, Pirol, Agria and Markies were planted in April, harvested at the end of August, or beginning of September in Reckenholz (ZH, Switzerland) and stored for three seasons (2016-2017, 2017-20018 and 2018-2019). Upon harvest, tubers were stored at room temperature (about 15 °C) for two weeks to promote healing and afterwards storage trials were performed at two sites: Changins (VD, Switzerland) for two storage seasons 2017-2018 and 2018-2019, and Reckenholz for the three seasons: 2016-2017, 2017-20018 and 2018-2019. At each site, half of the tubers of each potato variety were stored in two different chambers at 12 °C and 85-90 % RH until the end of October or beginning of November. Then, the temperature was gradually decreased to 4 °C for the first chamber and to 8 °C for the second chamber with a decrease of 1.5 °C per week. Both final temperatures were reached at the end of November, date of the beginning of the storage. Tubers were stored at both temperatures until mid-April. In addition, for some of the tubers of Markies and Verdi varieties stored at 4 °C, a reconditioning treatment was applied from 4 to 15 °C with an increase of 1.5 °C per week to reach 15 °C after four months of storage (at the end of March). Tubers of the different tested varieties were sampled in chambers at 4 °C, 8 °C or after reconditioning at 15 °C at different periods to perform several measurements described in the sections below.

The storage trials described above were conducted with tubers from the same batch, all grown at the "Reckenholz" site. The tubers stored at 8 °C for four months at the Reckenholz site were treated with CIPC while tubers stored at 4 °C (with or without reconditioning) were untreated. Tubers stored at the Changins site at 8 °C and 4 °C remained untreated (with or without reconditioning). This experiment follows a split plot experimental design with two fixed effects: temperature and variety and was repeated over two to three seasons of storage.

2.2. Measurements performed on the stored potatoes

2.2.1. Physiological measurement: sprouting evaluation

Sprouting of potatoes was evaluated on tubers stored in the "Changins" site, after 4.5 months of storage at 4 and 8 °C (until Mid-April) for the six potato varieties. Sprouting evaluation was performed by measuring the total weight of sprouts for one year of testing (2018-2019 season) and on four replicates of five tubers each and for each variety and temperature (sum of the weight of sprouts from five tubers, measurements performed on sprouts with a minimum size of 1 mm). Data of sprouting observation were analyzed using a two-way Anova. The fixed effects were the variety and the temperature. Sprouting variable was transformed to "log (x+1)" to ensure the homogeneity of the variance and normality of the response variable. Significance test was performed with the F test provided by the "car" R package, version 3.0-7 (Fox and Weisberg, 2019). To analyze the effect of significant variables, the marginal post hoc Tukey's test (emmeans method) was used as a multiple comparison test to identify mean differences within factors and interactions (Lenth 2020).

2.2.2. Measurements after processing: frying test and acrylamide content

Frying test and acrylamide content were measured on samples stored in the "Reckenholz" site during three seasons (2016-2017, 2017-20018 and 2018-2019). For each sample, a slice of two mm was cut at the center of 10 potato tubers. A frying test with color evaluation of 10 crisps per sample using a scale ranging from four (=crisps fully dark) to seven (=crisps clear) was performed (refer to Table A-3 in Appendix). In general, a score of seven is considered as an acceptable result and a score from four to six is usually not acceptable for the potato processing industry. We adjusted a two-way binomial generalized linear mixed model on the number of crisps with acceptable color (note = seven) among the 10 tested crisps using the lme4 package version 1.1-23 (Bates et al. 2015). The fixed effects of this analysis were the variety and the temperature, and the year was considered as the random factor. The effect of the year was removed from the model when the variance of the year was not significant.

We generated the Anova table corresponding to our model using the "car" R package, Version 3.0-7, and using the chi-square significance test or the F test in cases where the effect of the random factor was not significant (Fox and Weisberg, 2019). Analyses were performed separately for the different periods: after two months of storage on six varieties and two storage temperatures (i.e. at the end of January at 4 and 8 °C) (N = 3 years); after four months of storage on six varieties and two storage temperatures (i.e. at the end of March at 4 and 8 °C) (N = 2 years); and after four months of storage in two varieties and three temperature regimes (i.e. at the end of March at 4 °C, 8 °C and 4 °C with a reconditioning to reach 15 °C at four months of storage) (N = 2 years). Tukey's post-hoc test (emmeans method) was performed to decompose significant fixed effects (Lenth, 2020). For the sake of conciseness, in cases of significant interaction between factors variety and temperature, the Tukey's test was performed directly on the interaction.

Acrylamide content analyses were performed on crisp samples for the six varieties obtained from the season of testing 2018-2019 after four months of storage at 4 and 8 °C, and after four months of storage with a reconditioning from 4 to 15 °C on two potato varieties (Verdi and Markies). Crisp samples (10 crisps per sample) were stored in double sealed plastic bags in the freezer at -20 °C for one month before the analysis. Before acrylamide extraction, the samples were crushed and ground to a powdery material with a rolling pin. After homogenization, each sample was extracted in duplicate by addition of deuterated acrylamide as internal standard. GC-MS analysis on a Trace GC/Trace DSQ instrument (Thermo Scientific, Dreieich, Germany) was performed in the chemical ionization mode by the use of a Restek Stabilwax Integra-guard column (Restek GmbH, Bad Homburg, Germany, 30 m x 0.25 mm i.d., 0.25 µm film thickness). Detailed description of the extraction and measurement is given by Haase et al. (2012).

2.2.3. Biochemical measurements: sugar analysis

All biochemical measurements were performed on tubers stored in the "Changins" site.

To analyze sugar content (glucose, total RS and sucrose) in potatoes, five biological replicates of three tubers were sampled for each variety, temperature of storage and observation period (i.e. after two months = end of January, and four months of storage = end of March) over two years of testing (tubers from the seasons 2017-2018 and 2018-2019).

Glucose analysis was performed on fresh tubers using a glucose titer measurement device (Accu-Check® Active glucometer, Roche) and with at least two analytical glucose measurements per tuber. We used the protocol of Olsen et al. (2011) with some modifications. For one analytical measurement, the potato was cut in two parts; a knife was used to macerate the tissue at the center of one potato part to obtain enough juice. Then, a test strip (suitable for this glucometer) was introduced in the glucometer, and a drop of juice was sampled using a 200 µL micropipette and placed on the test strip to obtain the measurement. The glucometer allows measurements ranging from 10 mg dL^{-1} to 600 mg dL^{-1} (0.6 mmol L^{-1} – 33.3 mmol L^{-1}) and outside this interval, the device indicates "low" or "high". Olsen et al. (2011) reported that, in the more stringent cases, glucose levels of 0.05 % on a fresh weight (fwt) basis are required in tubers before processing to avoid unacceptable fry color. In their study, glucose level of 0.05 % fwt corresponded to values of 75 mg dL^{-1} with the glucometer. Based on these results, we considered glucose values greater than 75 mg dL^{-1} as unacceptable for processing and glucose values $\leq$ 75 mg dL^{-1} as acceptable for processing. Consequently, the raw data were transformed into binary categories: 0 = acceptable sugar content in potatoes ($\leq$ 75 mg dL^{-1}) and 1 = unacceptable sugar content in potatoes ($>$ 75 mg dL^{-1}). The percentages of unacceptable samples for each variety and temperature over two years were calculated and asymmetrical confidence level estimated by the specific formula of the Agresti-Coull function in R (lower or upper Agresti-Coull confidence limits) appropriate for the analysis of binary data was added

to the graphics using the "binom" R package version 1.1-1 (Dorai-Raj 2014) (Agresti and Coull 1998).

Analysis of glucose content results was performed separately for the different periods: after two months of storage (end of January) for six varieties and two storage temperatures (4 and 8 °C); after four months of storage (end of March) for six varieties and two storage temperatures (4 and 8 °C); and after four months of storage for two varieties and three temperature regimes (4 °C, 8 °C and 4 °C with a reconditioning to reach 15 °C at four months of storage) (N = 2 years).

Total RS (glucose + fructose) and sucrose were analyzed on freeze-dried samples. Five biological replicates (one biological replicate = three tubers) were sampled for each variety, temperature, and observation period over two years of testing. Tubers of each biological sample were peeled, cut in pieces and frozen in liquid nitrogen. Samples were stored at – 80 °C until lyophilized, after which they were kept at ambient temperature until the analysis. RS content was analyzed in tubers of the six tested varieties after four months of storage at 4 or 8 °C and on two varieties stored at 4 °C and reconditioned from 4 to 15 °C to reach 15 °C at four months of storage. The sucrose content was measured only in tubers of two varieties (Verdi and Markies) stored at 4 °C over 3 months to verify the effect of the variety on sucrose content in tubers stored at low temperature over two seasons of storage.

Sucrose, glucose and fructose were measured using a K-SUFRG kit (Megazyme, Ireland). Sucrose, D-Fructose and D-Glucose were quantified according to the manufacturer's protocol (Megazyme, K-SUFRG 04/17) with some modifications. Lyophilized samples were crushed in powder and 200 mg of each powder sample were suspended in 1 mL distilled water, vortexed and centrifuged at 15000 rpm for 10 minutes at 4 °C. The supernatant of each sample was collected, and sucrose, glucose and fructose content were measured using the microplates protocol of the Megazyme K-SURFG assay procedure 04/17. The 96 wells F-Bottom Microplates (Greiner bio321 one, Germany) were used. The Microplate path length was adjusted to 1 cm by dividing the absorbance by 0.625 (= function of the diameter of the well and the total reaction volume). Contents of different sugars (glucose, fructose and sucrose) were calculated as described in the K-SURFG assay procedure 04/17 (Megazyme, Germany).

To analyze RS content, a two way linear mixed model was built with the fixed effects: temperature and variety using the "lme 4" R package version 1.1-23 (Bates et al. 2015). The fixed effects were the variety and the temperature. To analyze the sucrose content, a one-way linear model with the variety as fixed effect was used. In both models, the year was considered as the random factor (N = 2) and the effect of the year was removed from the model when the variance of the year was not significant. The "RS" variable was transformed with "log (x+1)" to ensure the homogeneity of the variance and normality of the response variable. Analysis of RS results were performed separately for the periods: after four months of storage (end of March) in six varieties and two storage temperatures (4 and 8 °C); and after four

months of storage in two varieties and three temperature regimes (4 °C, 8 °C and 4 °C with a reconditioning to reach 15 °C at four months of storage) (N = 2 years).

To observe the effect of the fixed effects and interactions for both reducing sugars and sucrose content, we performed significance tests (with a confidence interval of 95 %) using the chi-square test or the F test when the effect of the random factor was not significant, from the "car" R package version 3.0-7 (Fox and Weisberg 2019).

Tukey's post-hoc (emmeans method) test was performed to decompose significant fixed effects (Lenth, 2020). For the sake of conciseness, in case of significant or low interaction between the factors variety and temperature, the Tukey's test was performed directly on the interaction.

2.2.4. Biochemical measurements: Asparagine content

Asparagine measurements were performed on tubers stored in the "Changins" site. 200 mg of each freeze-dried powder sample was suspended in 1.6 mL of 1 M perchloric acid, mixed and centrifuged at 15000 rpm for 10 minutes at 4 °C. 1 mL of supernatant of each sample was collected and transferred into a 2 mL tube. 2 M KOH was used to adjust the pH to 8 and the volume of each tube was made up to 1.5 mL with distilled water. The Microplate procedure was used for asparagine quantification and calculations were performed following the protocol described in the assay procedure K-ASNAM 376 07/17 (the path length was adjusted to 1 cm).

2.2.5. Molecular characterization: *VInv* transcript levels

Transcript levels of *VInv* measurements were performed on tubers stored in the "Changins" site.

The freeze-dried tuber samples were used for RNA extraction according to the protocol of Kumar et al. (2007) with slight modifications. Around 100 mg of freeze-dried tubers were sampled, and the volumes of reagents (NaCl SDS, Na2SO3, TBE, and beta-mercaptoethanol) were scaled down 5-fold.

RNA quality was verified by agarose gel electrophoresis using a 1 % agarose gel, followed by DNAse treatment using DNAse I (Bioke, Netherlands) according to the manufacturer's protocol. To guarantee the total removal of genomic DNA, aliquots of DNAse-treated RNA were again checked on a 1 % agarose gel by electrophoresis. cDNA was synthesized from 500 ng of each DNA-free RNA sample using the GoTaq Reverse Transcription, Oligo dT kit (Promega, USA) following the manufacturer's instructions. The cDNA was diluted in distilled water 5-fold and 2 µl of each diluted sample was used for a single qRT-PCR reaction with 1x GoTaq qRT-PCR master mix (Promega, USA) and 10 nM primers for RT-qPCR (StVInv-F, StVInv-R, rRNA-F and rRNA-R). The Primer sequences used are the following: 1) StVinv (forward primer sequence (5'-3') = GGGTATGTGGGAGTGTGTGG; reverse primer sequence (5'-3') = ATTCCACAATCCAATTCCGGGT; size = 201 bp) and 2) 18S rRNA (forward primer sequence (5'-3') = GGGCATTCGTATTTCATAGTCAGAG; reverse primer sequence (5'-3') = CGGTTCTTGATTAATGAAAACATCCT; size =101 bp).

Three technical replicates were performed for each sample, and the thermal cycle was performed on a CFX96 Real-Time System (Bio-Rad, USA) using the following program: 95 °C for 3 mins initial denaturation, followed by 40 cycles of 95 °C for 10 seconds (denaturation), 60 °C for 30 seconds (Annealing) and 72 °C for 30 seconds (elongation), followed by a plate read. Melting curves were generated at temperatures between 65 °C and 95 °C with 0.5 °C increments. The comparative cycle threshold method was employed to calculate the relative gene expression and the expression levels of candidate genes were normalized to the mean delta cycle threshold (dCT) of the housekeeping gene (rRNA). rRNA has been shown to be the best housekeeping gene in conditions of cold treatment of potato tubers (shumbe et al., 2020).

Transcript levels of *VInv* were assayed for tubers of the 2017-2018 testing season. Five biological replicates for each variety, temperature and observation period were analyzed. Each biological replicate was composed of a pool of three tubers. We used a two-way Anova to analyze *VInv* transcript data, with fixed effects being temperature and variety. We transformed this variable with "log (x+1)" to ensure the homogeneity of the variance. Significance tests were performed using F test provided by the "car" R package version 3.0-7 (Fox and Weisberg, 2019). Tukey's post-hoc (emmeans method) test was performed to decompose significant fixed effects (Lenth, 2020). For the sake of conciseness, in case of significant or low interaction between factors variety and temperature, the Tukey's test was performed directly on the interaction.

2.2.6. Statistical analysis

The R software version 3.6.3 (R Core Team, 2019) was used for the statistical analysis. Several R packages were used: "ggplot2", "plyr", "Rmisc", "lattice," and "cowplot" packages for graphics and data summary (Wickham 2011, 2016; Wilke 2019; Sarkar 2008; Hope 2013) and packages for the statistical analysis are described in the sections bellow. For the different tests, the significance level has been fixed at 5 %.

3. Results

3.1. Low temperature storage delays sprout development

After four and half months of storage (mid-April), sprouting of potatoes was variety-dependent and varied according to the temperature of storage (p-value < 0.001). An interaction was observed between the temperature and variety factors (p-value < 0.001).

Sprout weight was systematically lower in tubers stored at 4 °C compared to the sprout weight of tubers stored at 8 °C, this result was observed for all the tested varieties (p-value <0.001). Five tubers of LC, Verdi, KB, Pirol, Agria and Markies varieties displayed an average sprout weight of 2.62, 0.17, 1.00, 1.44, 0.00 and 0.21 g, respectively, while five tubers of the same varieties stored at 8 °C had an average

sprout weight of 11.42, 8.69, 27.87, 17.71, 3.27 and 8.13 g, respectively (figure 5-1 A).

The variety effect on sprout weight for tubers stored at 4 °C was different from the variety effect for tubers stored at 8 °C. For tubers stored at 4 °C, the average sprout weight was relatively low for all varieties but the LC variety had a higher sprout weight compared to Verdi, Agria, Markies (p-value < 0.001) and KB varieties (p-value = 0.026). No significant difference in sprout weight was observed between LC and Pirol varieties (p-value = 0.379). In tubers stored at 8 °C, KB was the most sprouted variety with an average sprout weight significantly higher than the sprout weight of other varieties (p-values < 0.001), except for the Pirol variety (p-value = 0.142), probably because the Pirol variety displayed a high sprout weight itself (figure 5-1 B).

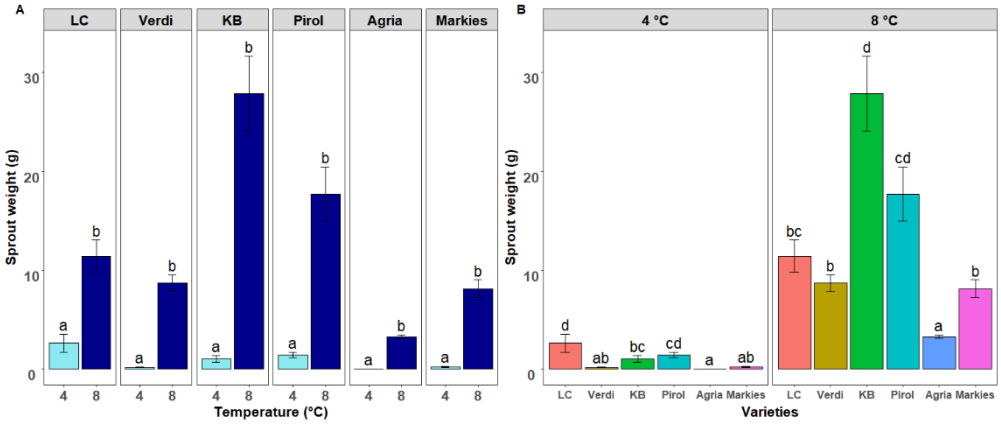

Figure 5-1. Effect of the temperature of storage on the sprout weight for each variety (A) and effect of the variety on the sprout weight for the different temperatures of storage (B) after 5.5 months of storage at 4 or 8 °C (80 % RH); over 4 biological replicates (N = 4), mean ± standard error. For a given observation, groups sharing the same letter are not significantly different (Tukey's test, confidence level of 95 %); (LC = Lady Claire; KB = Kiebitz)

3.2. Storage temperature and variety modulate crisp color and acrylamide content

3.2.1. Crisp color quality

After two (end of January) and four months of storage (end of March), the color of crisps was impacted by temperature and variety factors. A significant interaction between temperature and variety effects was detected after two months of storage and disappeared after four months of storage with or without reconditioning (Table 5-1).

Table 5-1. P-values from significance tests (Pr[>chi-sq] or P[F test]) for the measured parameters in response to the different factors and their interactions after two and four months of storage at 4 and 8 °C on six varieties and after a storage at 4 °C with reconditioning from 4 to 15 °C to reach 15 °C at four months of storage on two varieties (* = statistically significant; (*) = low significance; NA = not analyzed)

Factors	Period of observation in months (m.) (+ number of varieties tested)	Crisp color	Reducing sugars content	Sucrose content	Vacuolar invertase gene expression	Asparagine content
Temperature	2 m. (6 varieties)	<0.001*	NA	NA	<0.001*	0.177
	4 m. (6 varieties)	<0.001*	<0.001*	NA	0.003*	NA
	4 m. + reconditioning (2 varieties)	<0.001*	0.001*	NA	<0.001*	NA
Variety	2 m. (6 varieties)	<0.001*	NA	<0.001*	0.005*	0.023*
	4 m. (6 varieties)	<0.001*	<0.001*	NA	0.107	NA
	4 m. + reconditioning (2 varieties)	<0.001*	<0.001*	NA	0.011*	NA
Temperature X variety	2 m. (6 varieties)	0.027*	NA	NA	0.083(*)	0.040*
	4 m. (6 varieties)	0.535	0.005*	NA	0.200	NA
	4 m. + reconditioning (2 varieties)	0.326	0.009*	NA	0.052(*)	NA

Tubers from the six tested varieties displayed a good crisp color quality after two months of storage at 8 °C with an average of at least seven crisps with an acceptable color among 10 crisps evaluated, and no difference in crisp color quality was observed between varieties (lowest p-value = 0.589) (figure 5-2 A). In contrast, the crisp color quality from tubers stored for two months at 4 °C varied according to the variety. Lower numbers of crisps with an acceptable color were obtained with Agria and Markies varieties compared to the numbers of crisps with an acceptable color obtained from the varieties LC, Verdi and KB, stored for two months at 4 °C (highest p-value = 0.012) (figure 5-2 A). Agria and Markies varieties displayed averages of 0.67 and 1.67 crisps, respectively, with an acceptable color among the ten crisps tested; while varieties LC, Verdi and KB displayed averages of 6.67, 7.33 and 7.00 crisps, respectively, with an acceptable color among the ten crisps tested (Figure 5-2 A).

The crisp color quality of the Pirol variety was not significantly different to the crisp color quality of varieties LC; KB; Agria; Markies (lowest p-value = 0.106) and Verdi (p-value = 0.055) stored for two months at 4 °C. It should be noted that the crisp color quality from tubers of the Verdi variety seemed higher than that from tubers of the Pirol variety stored at 4 °C, and that even though the effect was not significant, the p-value was low (p-value = 0.055) (Figure 5-2 A). The Verdi variety displayed an average of 7.33 crisps with an acceptable color among the ten crisps tested, while Pirol variety displayed an average of 3.00 crisps with an acceptable color among the ten crisps tested (Figure 5-2 A).

Crisps obtained from tubers of LC, Verdi and KB varieties stored at 4 °C had a similar quality compared to crisps obtained from tubers of the same varieties stored at 8 °C for two months (lowest p-value = 0.471). In contrast, the varieties Pirol, Agria and Markies displayed a lower number of crisps with an acceptable color after two months of storage at 4 °C compared to the crisp color from tubers of the same varieties stored for two months at 8 °C (p-values = 0.006; 0.001 and 0.001) (Figure 5-2 A). Varieties Pirol, Agria and Markies displayed an average of 3.00; 0.67 and 1.67 crisps respectively, with an acceptable color among 10 crisps tested after two months of storage at 4 °C, and of 9.67; 7.33 and 8.00 crisps, respectively, with an acceptable color among 10 crisps tested after two months of storage at 8 °C (Figure 5-2 A).

After four months of storage, trends were similar to the observation at two months of storage; however, the interaction between temperature and variety factors could not be shown statistically (Table 5-1). The number of crisps with an acceptable color was almost two-fold higher in crisps from tubers stored at 8 °C compared to crisps from tubers stored at 4 °C for four months (Table 5-1). On average, tubers of the six varieties displayed 8.75 and 4.42 crisps with an acceptable color among the 10 crisps tested after four months of storage at 8 °C and 4 °C, respectively. The crisp color quality varied according to the variety after four months of storage (Table 5-1).

The number of crisps with an acceptable color quality obtained from tubers of the Verdi variety after four months of storage was significantly higher than the number of crisps with an acceptable color quality obtained from tubers of the Agria and Markies varieties (p-values = 0.004 and 0.024). Verdi displayed an average of 7.75

crisps with an acceptable color among the 10 crisps tested, while Agria and Markies displayed an average of 3.50 and 4.25 crisps, respectively, with an acceptable color among the 10 crisps tested (Figure 5-2 B).

The Pirol variety had a significantly higher number of crisps with an acceptable color (average of 7.00 crisps with an acceptable color among the 10 crisps tested) compared to the variety Agria (p-value = 0.018) (Figure 5-2 B).

The varieties LC and KB also had high numbers of crisps with acceptable color (average of 8.75 and 8.25 crisps with an acceptable color among 10 crisps tested, respectively). However, the Tukey's test did not discriminate the crisp color quality of these varieties from the other varieties (lowest p-value = 1.000) (Figure 5-2 B).

The crisp color quality of the varieties Markies and Verdi after four months of storage at three temperature regimes: 8 °C, 4 °C and at 4 °C with a reconditioning from 4 to 15 °C (Figure 5-2) was affected by the temperature and variety factors (Table 5-1). There was no interaction between those two factors (table 5-1). On average, the crisp color quality was significantly higher for tubers stored at 8 °C (average 8.28 crisps with an acceptable color among the 10 crisps tested) than at 4 °C (average of 3.75 crisps with an acceptable color among the 10 crisps tested) (p-value = 0.000).

The crisp color quality from tubers reconditioned from 4 to 15 °C (average of 5.25 crisps with an acceptable color among the 10 crisps tested) seemed higher than the crisp color quality from tubers stored at 4 °C (p-value = 0.234), however Tukey's test did not discriminate the color quality of crisps stored at these two temperature regimes (p-value = 0.234) (Figure 5-2 C).

On average, the variety Verdi displayed a higher crisp color quality compared to the crisp color quality of the Markies variety (p-value = 0.000). Verdi had an average of 7.5 crisps with an acceptable color among the 10 crisps tested and Markies had an average of 4.0 crisps with an acceptable color among the 10 crisps tested (Figure 5-2 C).

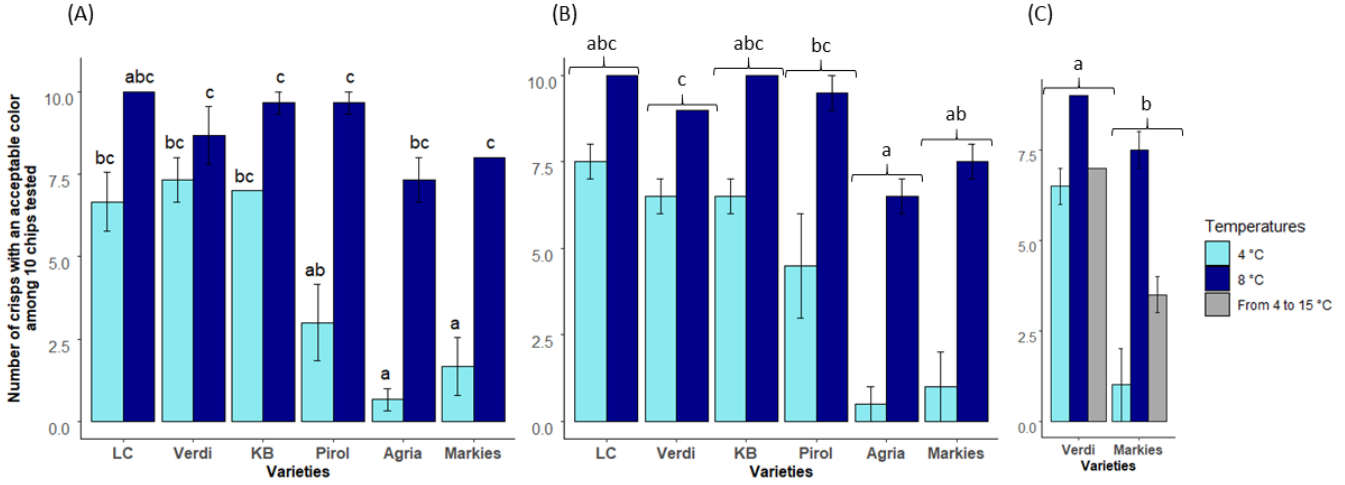

Figure 5-2. Average number of crisps with an acceptable color among the 10 crisps tested for the six varieties stored at 4 or 8 °C during two months (A) (N = 3 years, Tukey's test, groups sharing a letter are not significantly different, confidence level of 95 %), four months (B) (N = 2 years) and for two varieties stored at 4, 8 °C and reconditioned from 4 to 15 °C to reach 15 °C at four months of storage (C) (N = 2 years), +- standard error, LC = Lady Claire and KB = Kiebitz.

3.2.2. Acrylamide content in crisps

Trends indicate that for the six tested varieties, the acrylamide content was lower in crisps from tubers stored at 8 °C (average of 627.25 µg kg^{-1}) than in crisps from tubers stored at 4 °C (average of 3611.08 µg kg^{-1}). This difference was less pronounced in crisps from the varieties LC, Verdi and KB in which the acrylamide content remained relatively low and similar after four months of storage at 4 °C (average of 1339.00, 334.50 and 1234.00 µg kg^{-1} respectively), compared to the acrylamide content in crisps from tubers of the same varieties stored at 8 °C (average of 560.50, 220.00, 354.50 µg kg^{-1}respectively). In contrast, in tubers from Pirol, Agria and Markies varieties, the acrylamide content was higher in crisps from tubers stored at 4 °C (average of 2486.00, 7924.00 and 8349.00 µg kg^{-1}respectively) compared to crisps from the tubers stored at 8 °C (average of 364.00, 1400.50 and 864.00 µg kg^{-1}).

Trends also suggest that the reconditioning from 4 to 15 °C decreases the acrylamide content in crisps from tubers of Markies variety (average of 2100.00 µg kg^{-1}) compared to the acrylamide content in crisps from tubers of the same variety stored for four months at 4 °C without reconditioning (average of 8349.00 µg kg^{-1}). However, the reconditioning did not allow tubers to reach an acrylamide content as low as in crisps from tubers of the variety Markies stored at 8 °C (average of 864.00 µg kg^{-1}). The reconditioning had a lower impact on the acrylamide content in crisps from tubers of the Verdi variety (average of 178.67 µg kg^{-1}) because the acrylamide content in this variety was already low even after storage at 4 °C (Figure 5-3).

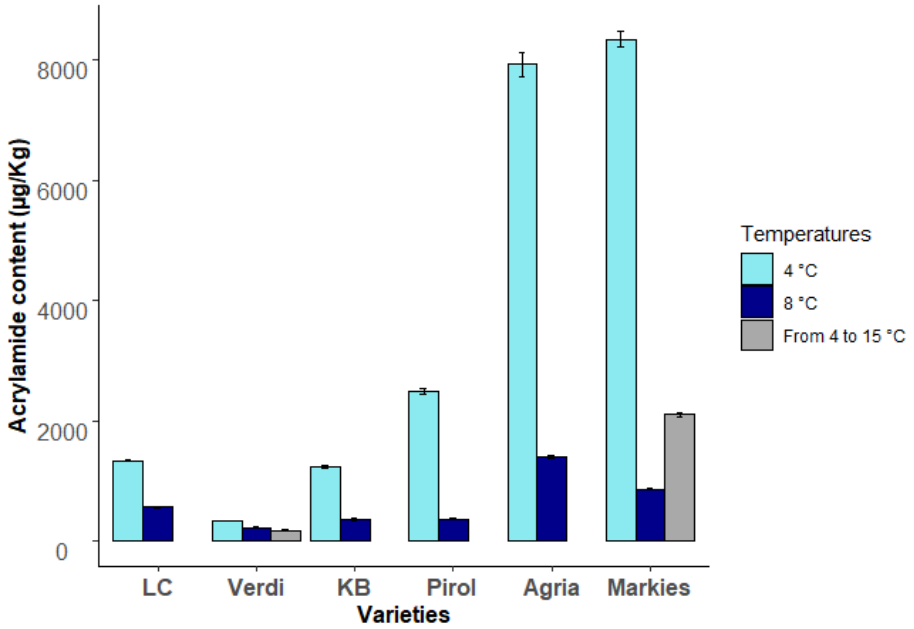

Figure 5-3. Average acrylamide content in crisps from the season 2017-2018 (N = 2 to 3 analytical replicates), in six varieties stored at 4 or 8 °C for four months and in crisps from Markies and Verdi varieties stored at 4 °C and reconditioned from 4 to 15 °C to reach 15 °C at four months of storage, +- standard error, LC = Lady Claire and KB = Kiebitz

3.3. Biochemical measurements: sugar content in tubers is variety and temperature dependent

3.3.1. Glucose analysis in tubers

The glucose content in tubers from varieties Agria, Pirol and Markies after two months of storage at 4 °C was high and unacceptable in most tubers (70 %, 100 % and 100 % of data indicated a glucose content > 75 mg dL^{-1}). Conversely, tubers of the same varieties stored at 8 °C had a low and acceptable glucose content (≤ 75 mg dL^{-1}) (0 % of data indicated a glucose content > 75 mg dL^{-1}). For these three varieties, the confidence intervals at 4 or 8 °C did not overlap, meaning that there is a clear difference in glucose content between the two temperatures of storage (Figure 5-4 A).

Tubers of LC and Verdi varieties displayed a low and acceptable glucose content at both 4 and 8 °C (0 % of data indicated a glucose content > 75 mg dL^{-1}). In tubers of the KB variety, the glucose content was low and no clear difference in glucose content was observed in tubers of this variety stored at 4 °C (20% of data indicated a glucose content > 75 mg dL^{-1}) or at 8 °C (0 % of data indicated a glucose content > 75 mg dL^{-1}), the confidence intervals at 4 and 8 °C overlap (Figure 5-4 A).

After four months of storage, tubers of the Pirol, Agria and Markies varieties stored at 4 °C had an unacceptable glucose content (70 %,100 % and 100 % of data, respectively, indicating a glucose content > 75 mg dL^{-1}), while tubers of the same varieties stored at 8 °C had an acceptable glucose content (≤ 75 mg dL^{-1}) (0 %, 10 % and 10% of data indicated a glucose content > 75 mg dL^{-1} respectively). For these three varieties, the confidence intervals estimated by the Agresti-Coull function at 4 or 8 °C did not overlap. Based on this method (Agresti and Coull 1998), this suggests that there is a clear difference in glucose content between the two temperatures of storage (Figure 5-4 B). In contrast, the varieties LC, Verdi and KB stored for four months have an acceptable glucose content at both 4 and 8 °C (0 % of data indicated a glucose content > 75 mg dL^{-1} for the three varieties).

After four months of storage, the glucose content was always low in tubers of the Verdi variety stored at 4 °C, 8 °C and 4 °C with a reconditioning at 15 °C (0 % of data indicated a glucose content > 75 mg dL^{-1} for the three varieties) (Figure 5-4 C). Conversely, the glucose content in tubers of the Markies variety was unacceptable after a storage of four months at 4 °C (100 % of data indicated a glucose content > 75 mg dL^{-1}), while the glucose content was lower in tubers of this variety stored at 8 °C or at 4 °C with a reconditioning at 15 °C (only 10 % of data indicated a glucose content > 75 mg dL^{-1}) (Figure 5-4 C).

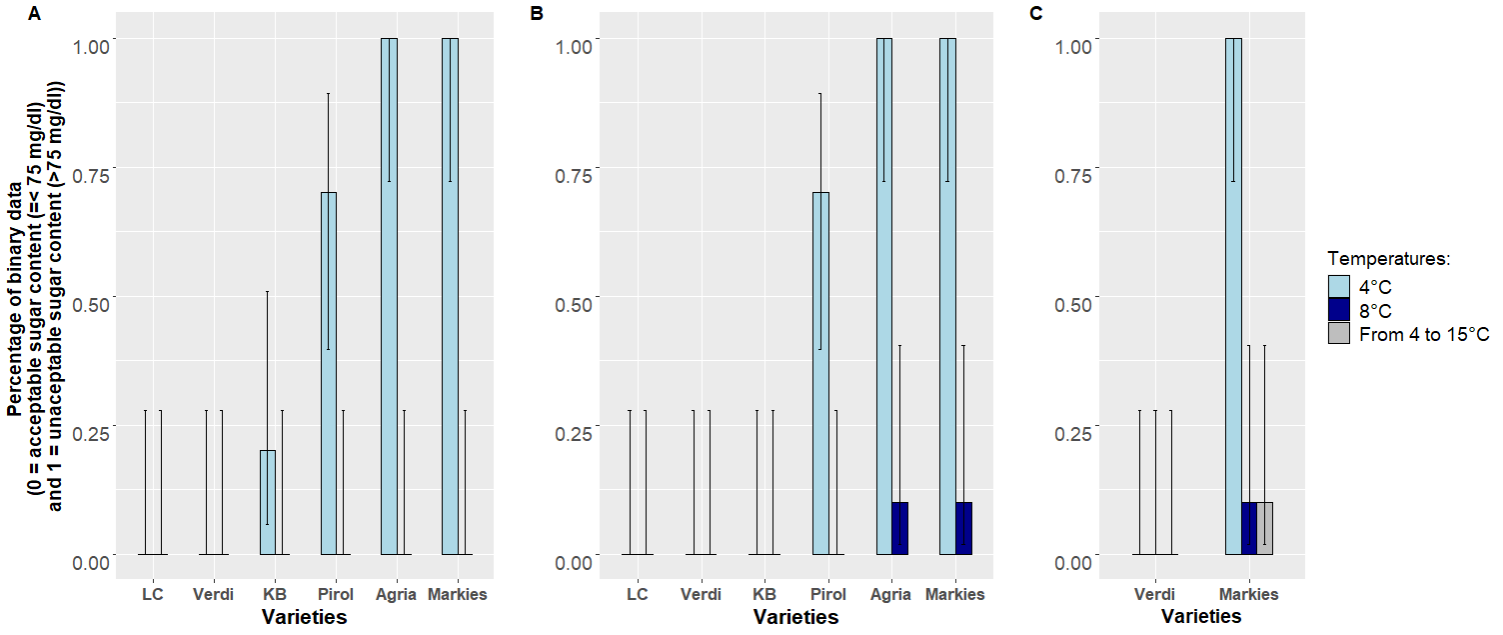

Figure 5-4. Glucose content represented by the percentage of binary data with an unacceptable glucose content (> 75 mg dL-1) (N = 10, 5 biological replicates x 2 years), for the six varieties tested varieties stored at 4 and 8 °C for two months (A), four months (B) and for the two tested stored at 4, 8 °C and reconditioned from 4 to 15 °C at four months of storage (C) + lower and upper confidence intervals estimated by the Agresti-Coull function (Agresti and Coull 1998).

3.3.2. Reducing sugars in tubers

RS content (glucose + fructose) was analyzed in tubers of the six varieties after four months of storage at 4 and 8 °C and in tubers of the varieties Markies and Verdi after a reconditioning from 4 to 15 °C.

After four months of storage with or without reconditioning, RS content was significantly affected by the temperature of storage and varied according to the variety. There was an interaction between temperature and variety factors (Table 5-1).

In tubers stored at 8 °C, the RS content was lower in tubers of the LC variety compared to the RS contents in tubers of the Verdi, Agria and Markies varieties (p-value = 0.013, p-value < 0.001 and p-value < 0.001) and was not different to the RS contents in tubers of the KB and Pirol varieties (p-value = 0.237 and p-value = 0.116).

The RS content in tubers of the Agria variety stored at 8 °C was higher than that in tubers of the LC, Verdi, Pirol and Markies varieties (p-value < 0.001; p-value < 0.001; p-value <0.001 and p-value = 0.004) and was not different from that in tubers of the KB variety (p-value = 0.253) (Figure 5-5 A).

RS contents in tubers of LC, Verdi and KB varieties were low and equal in tubers stored at both 4 °C (average of 71.97; 103.73 and 274.30 mg / 100 g DW) and 8 °C (average of 37.48; 95.63 and 138.13 mg / 100 g DW) (lowest p-value = 0.409).

Conversely, RS contents in tubers of Pirol and Markies varieties stored at 4 °C (average of 328.25 and 266.92 mg / 100 g DW) were significantly higher compared to the RS contents in tubers of the same varieties stored at 8 °C (average of 82.98 and 150.05 mg / 100 g DW) (p-value < 0.001 and p-value = 0.042). RS content in tubers of the Agria variety stored at 4 °C seemed higher (average of 633.92 mg / 100 g DW) compared to RS content in tubers of the same variety stored at 8 °C (average of 322.76 mg / 100 g DW), however the Tukey's test did not discriminate differences in RS content between storage at 4 or 8 °C for this variety (p-value = 0.298) (Figure 5-5 A).

After four months of storage at 4 °C, the RS contents in tubers of the LC and Verdi varieties were equivalent and low (p-value = 0.782) and were significantly lower than the RS content in tubers of the KB, Pirol, Agria and Markies varieties stored at the same temperature (p-value < 0.001) (Figure 5-5 A).

Figure 5-5 B shows that the RS content was low and equal in tubers of the Verdi variety stored at 4 °C, 8 °C and 4 °C with a reconditioning from 4 to 15 °C over four months (lowest p-value = 0.533). RS content was higher in tubers of the Markies variety stored at 4 °C compared to the RS content in tubers of the same variety stored at 8 °C and compared to the RS content in tubers of the Verdi variety stored at 4 °C or 8 °C (p-value = 0.001). RS content was not significantly lower in tubers of Markies variety reconditioned from 4 to 15 °C compared to RS in tubers of Markies stored at 4 °C (p-value = 0.408).

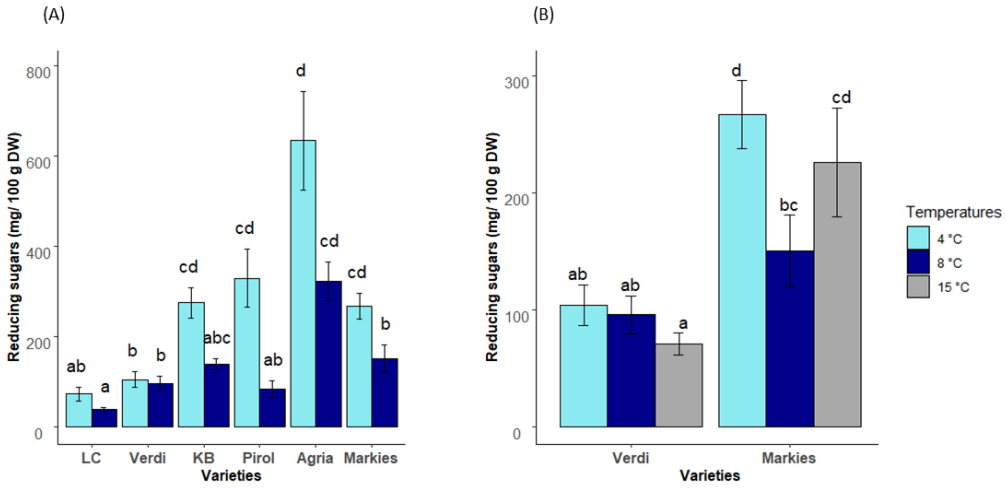

Figure 5-5. Average reducing sugars content in six potato varieties stored at 4 or 8 °C for four months (A) (N = 2 years, Tukey's test, groups sharing a letter are not significantly different, confidence level of 95 %), and in two varieties stored at 4, 8 °C and reconditioned from 4 to 15 °C during four months (B) (N = 2 years), +- standard error, LC = Lady Claire and KB = Kiebitz.

3.3.3. Sucrose content in tubers

The sucrose content in tubers of the Markies and Verdi varieties after two months of storage at 4 °C (until end of January) was measured to evaluate the sugar "stocks" in these varieties stored at low temperature. The sucrose content was significantly lower in tubers of the Markies variety (average of 460.70 mg / 100 g DW) than in tubers of the Verdi variety (average of 1385.92 mg / 100 g DW) (Table 5-1).

3.4. Genetic and enzymatic measurements

3.4.1. Vacuolar invertase gene expression is temperature and variety dependent

The transcript levels of *VInv* were evaluated by RT-qPCR after two months (until end of January) and four months (until end of March) of storage at 8 °C and 4 °C, and after a storage at 4 °C with a reconditioning to reach 15 °C at four months of storage. After two months of storage (during the 2017-2018 season of storage), transcript levels of *VInv* varied according to the temperature of storage, the variety, and there is a marginal interaction between these two factors (p = 0.083) (Table 5-1). Transcript levels of *VInv* were relatively low and similar in tubers stored at both 4 °C and 8 °C for varieties LC and Verdi (p-values = 1.000 and 0.999 respectively). Transcript levels of *VInv* for the KB variety were similar in tubers stored at both 4 and 8 °C (p-value = 0.707). However, transcript levels of *VInv* in tubers of the KB variety seemed high

after two months of storage at both 4 °C and 8 °C, compared to other varieties. Indeed, transcript levels of *VInv* in tubers of the KB variety stored at 8 °C for up to two months was significantly higher than the transcript levels in tubers of the Agria variety stored at the same temperature (p-value = 0.042). After a storage at 4 °C, the transcript levels of *VInv* in tubers of the KB variety was significantly higher than in tubers of the LC variety stored at 4 °C (p-value = 0.047). Finally, the Tukey's test did not discriminate the transcript levels of *VInv* in tubers of the KB variety from the transcript levels of *VInv* in tubers of the other varieties for storage at 4 °C (lowest p-value = 0.188) or 8 °C (lowest p-value = 0.334) (Figure 5-6 A).

The transcript levels of *VInv* in tubers of the Agria variety stored at 4 °C were significantly higher compared to the *VInv* gene expression in tubers of the same variety stored at 8 °C (p-value = 0.01). The transcript levels of *VInv* in tubers of the Markies variety seemed higher in tubers stored at 4 °C compared to the transcript levels of *VInv* in tubers of the same variety stored at 8 °C. However, the Tukey's test did not discriminate the transcript levels of *VInv* in tubers of the Markies variety stored at 4 °C from the transcript levels of *VInv* in tubers of this variety stored at 8 °C (p = 0.534). No significant differences in transcript levels of *VInv* were observed in tubers of the Pirol variety stored at 4 °C compared to the transcript levels of *VInv* in tubers of the same variety stored at 8 °C (p-value = 0.772) (Figure 5-6 A).

After four months of storage, the transcript levels of *VInv* varied according to the temperature of storage. There was no impact of the variety and no interaction between variety and temperature factors (Table 5-1). The transcript levels of *VInv* were significantly higher in tubers stored at 4 °C (average relative mRNA of *VInv* of 6.38) compared to 8 °C (average relative mRNA of *VInv* of 3.96) (Table 5-1).

The study of the effect of four months of storage at 4 °C, 8 °C and 4 °C with a reconditioning at 15 °C in tubers of Verdi and Markies varieties showed that the transcript levels of *VInv* varied according to the temperature and variety, and that there is a low interaction between the temperature and the variety (Table 5-1). After four months of storage, the transcript levels of *VInv* were significantly higher in tubers of the Markies variety stored at 4 °C compared to the transcript levels of *VInv* in tubers of Markies stored at 8 °C or 4 °C with a reconditioning at 15 °C. Transcript levels of *VInv* in tubers of Markies variety stored at 4 °C were also higher compared to the transcript levels of *VInv* in tubers of the Verdi variety stored at 4 °C, 8 °C and at 4 °C with a reconditioning at 15 °C (highest p-value = 0.029) (Figure 5-6 B).

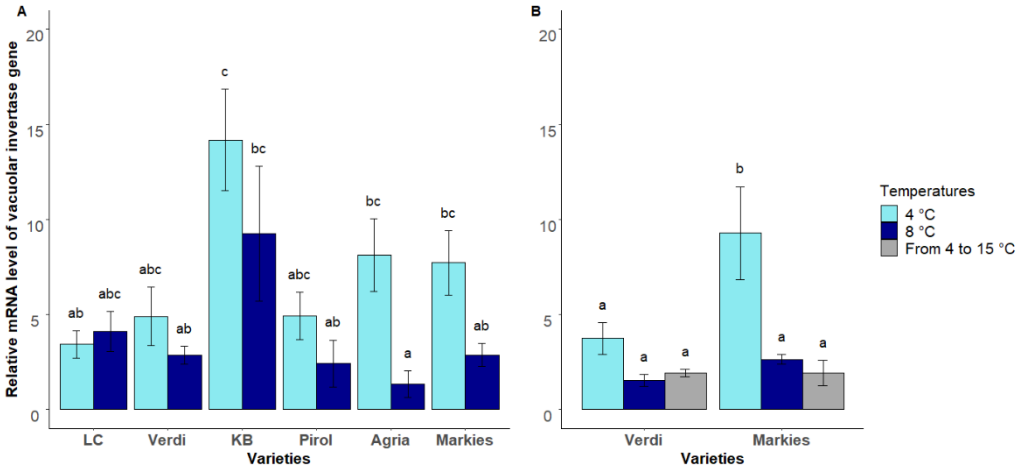

Figure 5-6. Relative mRNA level of vacuolar invertase gene (*VInv*) in six potato varieties stored at 4 or 8 °C over two months (A), and in two varieties stored at 4, 8 °C and reconditioned from 4 to 15 °C after four months (B), +- standard error, LC = Lady Claire and KB = Kiebitz, (N = 5 biological replicates over one season of storage, Tukey's test, groups sharing a letter are not significantly different, confidence level of 95 %)

3.4.2. Asparagine content in tubers

After two months of storage (season 2017-2018), the asparagine content was not affected by the storage temperature (Table 5-1), however it was affected by the variety and this effect was temperature-dependent (Table 5-1). In tubers stored at 4 °C, the asparagine content was similar among the six tested varieties (lowest p-value = 0.216), while in tubers stored at 8 °C, the asparagine content was significantly higher in tubers of the KB variety (average of 512.64 mg / 100 g DW) compared to asparagine content in tubers of the Pirol and Agria varieties (average of 355.35 and 350.30 mg / 100 g DW respectively) (p = 0.039 and 0.050 respectively). The asparagine content in tubers of the KB variety stored at 8 °C was equivalent to the asparagine content in tubers of LC, Verdi and Markies varieties stored at the same temperature (average of 475.20, 436.51 and 411.99 mg / 100 g DW respectively) (lowest p-value = 0.415) (Figure 5-7).

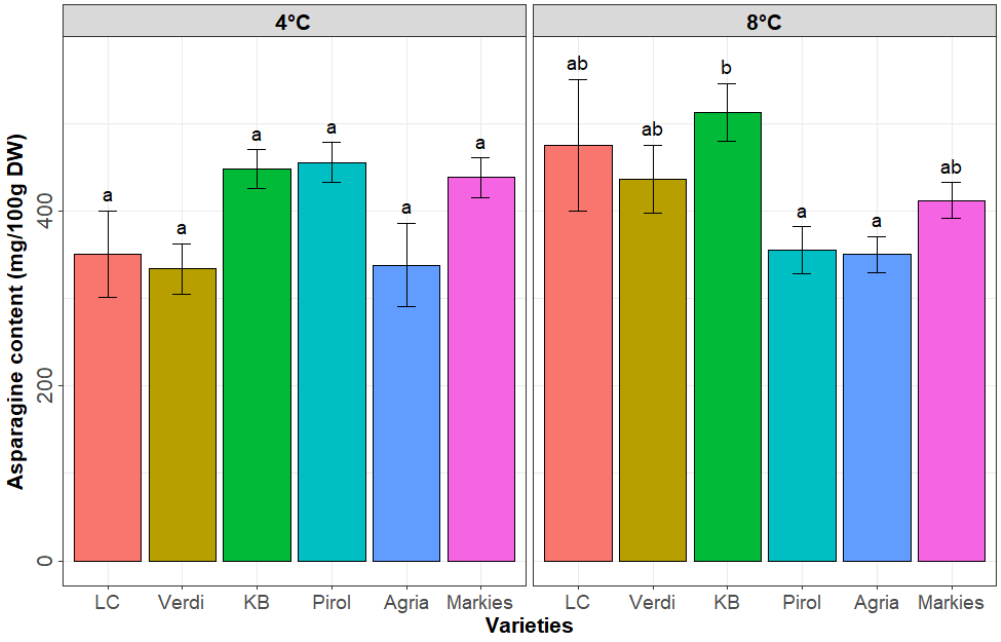

Figure 5-7. Effect of variety on the asparagine content in tubers stored at 4 °C, and effect of the variety in tubers stored at 8 °C during two months; mean +- standard error, Tukey's test, groups sharing a letter are not significantly different (confidence level of 95 %), (N = 5 biological replicates over 1 year)

4. Discussion

The recent non-renewal of the use of chlorpropham molecule to control potato sprouting in Europe is prompting the potato value chain to find storage alternatives to control sprouting (European Commission 2019a; European Food Safety Authority (EFSA) et al. 2017). To avoid using other anti-sprouting chemicals, often less efficient than CIPC (Visse-Mansiaux et al. 2020), the storage at low temperatures to control sprouting should be considered for certain varieties.

Potato dormancy is mainly influenced by the genotype and the temperature of storage (Sharma et al. 2020; Daniels-Lake and Prange 2007; Magdalena and Dariusz 2018). This has been confirmed in our study as varieties displayed differences in sprout weight after 4.5 months of storage (until mid-April) and the effect of the variety on sprouting was shown to be temperature-dependent. The storage at low temperature (i.e. 4 °C) was more efficient in reducing sprouting compared to storage at higher temperature (i.e. 8 °C) for the six tested varieties up to 4.5 months of storage. LC, Verdi, KB, Pirol, Agria and Markies varieties displayed 77, 98, 96, 92, 100 and 97 % of sprout weight reduction, respectively. Our results are in line with the literature

reporting that low temperatures during storage allow efficient sprout control (Paul et al. 2016b; Sonnewald 2001; Sowokinos 2001; Burton and Wilson 1978). For example, Gichohi and Pritchard (1995) reported that sprouting of the Shepody potato variety was delayed by 15 weeks when the temperature was lowered from 8 to 5 °C.

To store potatoes at low temperatures, the variety should be selected with caution due to the susceptibility of certain varieties to CIS, which can lead to dark color and bitter-tasting of French fries and crisps (Pinhero et al. 2011; Amjad et al. 2020; Mottram et al. 2002). CIS may also lead to the production of toxic compounds such as acrylamide in tubers during frying, which may raise concerns for human health (Paul et al. 2016b; Wiberley-Bradford and Bethke 2017; Wiberley-Bradford et al. 2016; FAO/WHO 2002).

The frying quality was influenced by the storage temperature for certain varieties. The varieties Agria, Pirol and Markies obtained poor results with a higher number of dark crisps after two months of storage (until end of January) at 4 °C compared to 8 °C. Conversely, the LC, Verdi and KB varieties had better crisp quality results with good crisp color quality after two months of storage at both 4 and 8 °C. After four months of storage, trends were similar, although the effect of variety by temperature interaction on crisps color quality could not be statistically proven. This lack of significance at four months of storage is probably because of the use of binomial data, which are less powerful than conventional data. Consequently, after four months of storage, only the global negative effect of temperature and the effect of the variety on crisps color quality was demonstrated.

Our results are in line with the literature as the variety by temperature interaction effect on fry color has been previously reported. Groza et al. (2006) reported that the White Pearl variety produced light crisps after a storage at 3.3 °C, while four other varieties tested in their study produced darker crisps after storage at the same temperature. They also reported that a 1-month reconditioning at 12.8 °C following storage at 3.3 °C for 6 months returned the crisps color quality of the White Pearl variety to the same level than after storage at warmer temperatures. Our results obtained with the variety Markies also suggest that a reconditioning from 4 to 15 °C increases the crisp color quality. However, this effect was not statistically significant.

The darkening of crisps was associated with an increase in acrylamide content. After four months of storage, trends indicated that the acrylamide content was higher in crisps from tubers stored at 4 °C compared to 8 °C. In addition, differences in acrylamide content between a storage at 4 °C and a storage at 8 °C were much higher in crisps obtained from tubers of Pirol, Agria and Markies varieties, than in crisps obtained from tubers of LC, Verdi and KB varieties. Higher acrylamide contents in crisps of 583, 466, 866, 139, 52 and 248 % have been observed from tubers stored at 4 °C compared to acrylamide in crisps from tubers stored at 8 °C for four months for varieties Pirol, Agria, Markies, LC, Verdi and KB, respectively. The reconditioning from 4 to 15 °C allowed a decrease in acrylamide content in tubers of the Markies variety of 78 % compared to the acrylamide content in tubers of this variety stored at

4 °C for four months. However, the acrylamide content in reconditioned tubers is 143 % higher than the acrylamide content in tubers of this variety stored at 8 °C.

The poor crisp color quality displayed by varieties Pirol, Agria and Markies after two months of storage, with similar trends after four months of storage, was correlated with the trends that indicated a high acrylamide content in these varieties after four months of storage at 4 °C. Our results are in line with those of Matsuura-Endo et al. (2006). They studied the effect of storage temperature on four potato varieties and reported an increase of dark brown crisp color, acrylamide and RS for all varieties, when stored at temperatures lower than 8 °C.

Reaction between amino acid (mainly asparagine) and RS through the Maillard reaction during frying of potatoes is responsible for the increase in acrylamide content and for the darkening after frying (Mottram et al., 2002).

In our study, the asparagine content in tubers did not explain the differences observed in crisp color and acrylamide content between tubers stored at 4 °C instead of 8 °C, as the asparagine content was not affected by the temperature of storage. However, the asparagine content was affected by the genotype in a temperature-dependent manner. After two months of storage at 4 °C, the asparagine content in tubers was not different between varieties, while at 8 °C, the asparagine content was higher in the variety KB compared to the varieties Pirol and Agria.

Our findings suggest that darkening of crisps is correlated with high acrylamide, high glucose and/or high total RS sugar content in tubers stored at low temperature.

In addition to displaying good crisp color quality after storage at both 4 and 8 °C after two months, with similar trends after four months, LC, Verdi and KB varieties had low glucose content after two and four months of storage at 4 °C ($\leq$ 75 md dl^{-1} for 100 % of data). For these varieties, the glucose content, as well as the total RS content were not higher in tubers stored at 4 °C than in tubers stored at 8 °C. Furthermore, LC and Verdi displayed low RS content after four months of storage at 4 °C. For the KB variety, even if the RS content was not higher after storage at 4 °C than at 8 °C; RS content in this variety stored at 4 °C was higher than in LC and Verdi varieties stored at 4 °C.

Based on these results, we concluded that LC, Verdi and KB varieties can be identified as not susceptible to CIS, or "CIS-resistant varieties". Verdi has been reported in the literature to be a CIS-resistant variety (Böhm et al. 2006; Shumbe et al. 2020; Fischer et al. 2013), as well as LC variety (Fischer et al. 2013). To our knowledge our study is the first study identifying the KB variety as CIS-resistant.

Inversely, the three varieties Pirol, Agria and Markies displayed poor crisp color quality after two months of storage at 4 °C compared to 8 °C, with similar trends after four months. In addition, in tubers of these three varieties, the storage at low temperature led to an unacceptable glucose content (i.e. > 75 mg dl-1) in comparison with glucose content in tubers of the same varieties stored at 8 °C (i.e. $\leq$ 75 md dl-1) for up to four months of storage. Levels higher than 75 mg dL^{-1} of glucose in potatoes are not acceptable by the industry for processing potatoes (Olsen et al. 2011). Based

on these results, we concluded that Pirol, Agria and Markies are susceptible to CIS and can be considered as "CIS-susceptible varieties". Furthermore, higher total RS content was also observed in tubers of Pirol and Markies CIS-susceptible varieties stored at 4 °C compared to 8 °C but not in tubers of the CIS-susceptible Agria variety. Our results are in line with the literature stating that crisp color quality is inversely correlated with the glucose content in tubers (Coleman et al., 1993).

The reconditioning after storage at low temperature could be used as a strategy to decrease the RS content in tubers stored at low temperature and to improve the quality of fried potatoes. De Wilde et al. (2005) showed that a reconditioning from 4 to 15 °C was efficient to decrease the RS content in potato tubers after storage at low temperature, and Schippers (1975) reported a positive effect of reconditioning after storage at 5 °C on the crisp quality. In our study, the positive effect of reconditioning on the glucose content was also observed with the variety Markies. This CIS-susceptible variety could be stored at 4 °C with a limited sweetening by applying a reconditioning in temperature from 4 to reach 15 °C after four months of storage. The glucose content in tubers of the Markies variety was unacceptable after a storage of four months at 4 °C (i.e. > 75 mg dL^{-1}), while the glucose content was lower and similar in tubers of this variety stored at 8 °C or at 4 °C with a reconditioning at 15 °C. At the opposite end of the glucose content results, the reconditioning of tubers from the CIS-susceptible Markies variety did not result in a significant decrease in RS content.

In general, our results underline a variety-dependent effect of the storage temperature on glucose content, acrylamide content and crisp color quality. Our results are in line with De Wilde et al. (2005) who reported that Saturna was the least susceptible variety to acrylamide formation during frying compared with Bintje and Ramos. The authors further showed that storage at low temperature (i.e. 4 °C) increases RS content and acrylamide formation compared to storage at 8 °C. In our study, the impact of low temperature as well as the effect of the reconditioning on the glucose content was clearer than the effects on the total RS content. These results are in line with Pritchard and Adam (1994) who showed that the fry color of the Russet Burbank variety correlated with the glucose content and that the relation with the glucose content was stronger than with the fructose or total RS content.

The increase in glucose content observed after two and four months of storage at low temperature in CIS-susceptible varieties probably originates from the cleavage of sucrose in RS by acid invertase (McKenzie et al. 2013). The sucrose content in tubers of the CIS-susceptible Markies variety stored at 4 °C for two months was lower than the sucrose content in tubers of the CIS-resistant Verdi variety stored at the same temperature. The sucrose "stock" in Markies has probably been converted in RS under the effect of low temperature. Conversely, in tubers of the Verdi variety, the sucrose "stock" was maintained high, probably because a low amount of sucrose was converted in RS, as this variety is CIS-resistant. Our results are in line with Sowokinos (2001) who reported that during the CIS phenomenon in potato tubers, several

enzymatic reactions occur and the rate of starch conversion to sucrose and of sucrose to RS is accelerated.

The acid invertase activity level mainly controlled the hydrolysis of sucrose to RS (Stitt and Sonnewald 1995; Sowokinos 2001; Pressey and Shaw 1966) and the *VInv* gene has been reported to play an important role in potato CIS (Bhaskar et al. 2010). After two months of storage, in tubers of LC and Verdi, the transcript levels of *VInv* were low and similar in tubers stored at 4 or 8 °C, consequently the conversion of sucrose to RS was probably mitigated, which could explain the low glucose content in these CIS-resistant varieties. Our results are in line with Shumbe et al. (2020), reporting that transcript levels of *VInv* in the CIS-resistant variety Verdi were lower than in CIS-susceptible varieties.

Surprisingly, the transcript levels of *VInv* in tubers of the CIS-resistant KB variety stored for two months at 4 or 8 °C seemed high. Indeed, the *VInv* gene was overexpressed in tubers of the CIS-resistant variety KB stored for two months at 4 or 8 °C, compared to the transcript levels of *VInv* in tubers of the CIS-susceptible variety Agria stored at 8 °C. This result means that even if the transcript levels of *VInv* were high, the invertase enzyme was not produced systematically. One possibility is that invertase inhibitors blocked the activity of the enzyme invertase even if the *VInv* gene was overexpressed. Greiner et al. (1999) reported that an invertase inhibitor from tobacco reduced cold-induced hexose accumulation by up to 75%.

After two months of storage, the *VInv* gene was overexpressed in tubers of the CIS-susceptible Agria variety after storage at 4 °C compared to 8 °C, and thus the increase in glucose content observed in tubers of this variety stored at low temperature was probably due to a high conversion of sucrose to RS through the invertase protein under control of the *VInv* gene.

No overexpression of the *VInv* gene was observed in tubers of the Pirol CIS-susceptible variety stored at 4 °C for two months compared to the gene expression in tubers of the same variety stored at 8 °C. This implies that other mechanisms may be involved in the increase of glucose content observed after storage at low temperatures with this variety. Indeed, it is reported that invertases are involved in the regulation of the ratio of hexose to sucrose but do not control the total amount of soluble sugars in potatoes stored at low temperature (Zrenner et al. 1996).

After four months of storage, higher transcript levels of the *VInv* gene were observed in tubers of the CIS-susceptible Markies variety stored for four months at 4 °C, compared to the transcript levels of *VInv* in tubers of this variety stored at 8 °C. In addition, results revealed that a reconditioning at 15 °C after a storage at 4 °C significantly reduced the transcript levels of *VInv*. The reconditioning resulted in transcript levels of *VInv* after four months of storage in tubers of the Markies variety similar to the level of transcripts of *VInv* in tubers of the same variety stored at 8 °C, or in tubers of the CIS-resistant Verdi variety stored for four months at 4 °C or 8 °C.

In addition to a decrease in the glucose and acrylamide content in tubers, results showed that the reconditioning from 4 to 15 °C after four months of storage also

significantly decreased the transcript levels of *VInv* in the CIS-susceptible Markies variety in comparison to storage at 4 °C without reconditioning. Our results are in line with Knowles et al. (2009), who reported that a reconditioning at 16 °C allows a RS decrease by accelerating the catabolism of RS and thus restoring processing quality.

However, it would be necessary to study the reconditioning potential of potato varieties before storage at low temperatures with a reconditioning, as it is reported that the effect of reconditioning is limited, depending of the variety (Schippers 1975; Kyriacou et al. 2009; Knowles et al. 2009). Knowles et al. (2009) reported that a reconditioning at 16 °C had a lower effect in reducing RS accumulation in tubers of the 'Umatilla Russet' variety compared to 'Ranger Russet' and 'Russet Burbank' varieties. In another study, Kyriacou et al. (2009) reported that in varieties accumulating high RS levels, the potential of reconditioning to decrease RS is low and suggests using the RS accumulation level and the chipping performance of potato tubers stored at low temperatures (< 5 °C) during the first 30 days of storage to evaluate the potential of a reconditioning of potato varieties.

The storage duration needs to be considered as well, since it is well known that potato tuber ageing leads to an irreversible senescent sweetening (Isherwood and Burton 1975). Driskill et al. (2007) studied the effect of a reconditioning on three potato varieties and showed that even if the reconditioning improved the processing quality for all the tested varieties, the potential of reconditioning was decreased for one cold sweetened variety due to earlier onset of irreversible senescent sweetening over 230 days of storage.

5. Conclusion

Three CIS-resistant varieties have been characterized (i.e. Lady Claire, KB and Verdi), that are suitable for storage at low temperature conducive to sprout reduction (i.e. 4 °C) with limited sweetening and low acrylamide content for up to four months of storage.

After two months of storage at low temperature, CIS-resistant varieties exhibited high crisp quality, while the three CIS-susceptible varieties displayed poor crisp quality and similar trends were observed after four months of storage. After four months of storage at 4 °C, low acrylamide content was observed in crisps of CIS-resistant varieties, while high acrylamide content was observed in crisps of CIS-susceptible varieties.

Correlation between high transcript levels of *VInv* and high conversion of sucrose to glucose at low temperature has been observed in tubers of the CIS-susceptible Markies variety after four months of storage. Similar correlation has been observed in the CIS-susceptible Agria variety, which had high transcript levels of *VInv* and high glucose content after two months of storage at 4 °C. These correlations were not observed in the CIS-susceptible Pirol variety, meaning that other mechanisms are

responsible for RS accumulation in CIS-susceptible varieties, such as the increase of sucrose synthase occurring at low temperature (Stitt and Sonnewald 1995; Sowokinos 2001; Pressey and Shaw 1966; Duplessis et al. 1996).

The CIS-resistance of Verdi and LC varieties can be explained by low transcript levels of *VInv* observed after two months of storage. Surprisingly, the CIS-resistant KB variety had high levels of the *VInv* transcript, meaning that the production of the invertase enzyme has probably been blocked by invertase inhibitors (Greiner et al. 1999) or that there is a rapid reconversion of the reducing sugars produced to sucrose.

Finally, the Markies CIS-susceptible variety responds positively to reconditioning up to 15 °C at four months of storage allowing a decrease of the transcript levels of *VInv* and consequently, a reduction in glucose accumulation and in acrylamide content.

Our study has helped in the identification of CIS-resistance in potato varieties and in the characterization of the genetic and enzymatic mechanisms involved in CIS.

It is of high importance to determine the ability of several potato varieties to tolerate cold storage without sweetening to expand potato storage management strategies and to use cold temperatures to reduce sprouting instead of using anti-sprouting chemicals.

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The authors have not stated any conflicts of interest.

Chapter 6

General discussion and perspectives

Outline

The aim of this chapter is to discuss the results of the thesis. Focus is placed on the implementation of management strategies to control sprouting assessed in the present thesis, in particular their strengths, limitations, practical use, potential combination and improvement. The potential of the new modelling tool proposed in the thesis is also discussed. Chapter 6 ends with a conclusion section summarizing the work and a section discussing research perspectives for alternative post-harvest management strategies.

1. Main challenges and management strategies to mitigate sprouting

As detailed in the Chapter 1, EU farmers and potato retailers are facing important challenges due to the removal of the CIPC from the European market (European Commission 2019a). Several solutions to improve potato storage within the potato storage system have been investigated and presented in the thesis. The potato management strategies tested in the different chapters of the thesis (i.e. chapters 2, 3, 4 and 5) should be used alone or in combination to mitigate sprouting according to the sprouting pressure of a given season. Management strategies based on those findings are presented in this section. The main findings of the thesis and the corresponding research questions are summarized in Table 6-1 below.

1.1. Main limitations of using the dormancy for a given genotype to manage potato storage

Sprouting of ware potatoes relies mainly on the genotype as potato varieties display differences in dormancy duration. Consequently, the starting point for farmers to mitigate sprouting would be the selection of genotypes that are less prone to sprouting during storage. However, farmers also have to choose the genotype according to the processors' and/or consumers' requirements. The final use of the potato tubers, for fresh market or for processing, also has to be taken into account. In the present study, the variety explained 60.3 % of the dormancy variability and the dormancy period varied from 50 to 158 days among the 537 tested varieties in this study (chapter 2, Table 6-1). Our results are in line with reports in the literature on the impact of variety on dormancy period (Magdalena and Dariusz 2018).

Table 6-1. Table summarizing the main findings of the thesis for each chapter and the corresponding research questions answered by each chapter

Chapters	Main findings of the thesis	Research questions
Chapter 2	- Variety, year and location factors explained 60.3 %, 13.9 % and 5.4 % of the dormancy variability, respectively - The environment and management during the growing season must be considered to define the dormancy of a given variety - We proposed a predictive bivariate model tool to predict potato dormancy with a precision of 14.59 days - This model uses the variety class and the sum of the daily maximum air temperature from planting to harvest as predictors	RQ1- Is genotype the main factor influencing dormancy? & RQ2 - Is it possible to predict potato dormancy to improve potato storage?
Chapter 3	- Synthetic molecules (MH, 1,4- DMN and 3-decen-2-one) are efficient in controlling sprouting for up to seven months in storage - The efficacy of the tested molecules is lower than the CIPC efficacy - Combinations of pre- and post-harvest treatments did not provide additional benefits to mitigate sprouting - MH and CIPC residues have been found in treated tubers	RQ3 - Are there anti-sprouting molecules suitable to replace the CIPC in a sustainable way?
Chapter 4	- Ethylene, mint and orange essential oils are efficient in mitigating sprouting for up to 5 months at 8 °C - Costs associated with the use of mint and orange essential oils treatments are higher than costs associated with the use of CIPC - The frequency of treatment with oils applied by hot fogging is relatively high - Ethylene may lead to an increase in reducing sugars in tubers - No MRL for these natural treatments and no or only a very short withholding period (a few days) before commercialization is required	RQ3 - Are there anti-sprouting molecules suitable to replace the CIPC in a sustainable way?
Chapter 5	- Storage at 4 °C was efficient in reducing sprouting in six tested varieties compared to storage at 8 °C - Three CIS-resistant varieties (i.e. Verdi, Lady Claire and Kiebitz) have been identified - Agria, Pirol and Markies were identified as CIS-susceptible varieties - A reconditioning at 15 °C after storage at 4 °C resulted in a decrease of glucose and acrylamide content in the CIS-susceptible Markies variety	RQ4 - What is the potential of cold storage to improve potato storage?

A precise characterization of the dormancy for the currently used potato varieties would be very relevant to improve potato storage management in the future. However, there is a lack of information about the dormancy duration of certain potato varieties (Visse-Mansiaux et al. 2018; Agriculture and Horticulture Development Board (AHDB) 2019). Moreover, discrepancies exist in the existing dormancy information for a given variety, depending to the source. This sparse, heterogeneous and conflicting dormancy information for a given variety can be partially explained by the variability in methods to measure dormancy (Visse-Mansiaux et al. 2018; Agriculture and Horticulture Development Board (AHDB) 2019).

Consequently, there is a need to request breeding companies to provide growers with detailed information about sprouting, but also a need to standardize sprouting behavior of potato genotypes.

The heterogeneous dormancy information is also due to the fact that, even if sprouting of ware potatoes relies mainly on the genotype, it is also under the influence of both environment and management factors during the growing season and at storage (Chapters 2, 3, 4 and 5, Table 6-1). We showed that the intrinsic dormancy period for a given variety varies according to the year and location of the trial, which explained 13.9 % and 5.43 % of the variability of dormancy, respectively (Chapter 2, Table 6-1). Location and year are qualitative factors represented by the management and environment (i.e. weather) of the growing season.

The weather during the growing season is something we cannot control, however the effect of genotype by environment interactions must be considered to predict the dormancy duration of a given variety and to implement appropriate management strategies to improve potato storage.

To avoid losses due to sprouting during storage, which may increase because of the non-renewal of CIPC and climate change, these management strategies must be combined and adapted according to the effect of genotype by environment interactions, which may lead to different sprouting pressures.

1.2. Environmental conditions during the growing season lead to different sprouting pressures

At the beginning of the storage period, the choice of the genotype has already been made, and sprouting pressure for a given variety will vary according to the effect of the environment during the growing season.

In the study conducted in chapter 2, it was demonstrated that predictors related to the temperature during the growing season have the highest influence on the dormancy variability, after the variety class. The best selected model to predict dormancy includes the sum of daily maximum air temperatures from planting to harvest and the variety class as predictors. The temperature predictor has a negative influence on the potato dormancy (Chapter 2, Table 6-1). For example, varieties with contrasting dormancies, e.g., Amandine, Bintje and Agria, displayed a longer dormancy duration after a season with an environment optimal for a maximal dormancy duration (i.e. low

sum of daily maximum air temperatures during the growing season), compared to the average dormancy after a hot season decreasing the dormancy duration (Figure 6-1). Within the different trials conducted in our study in several locations, we observed that 2008 was a season with a low sum of daily maximum air temperature during the growing season (Figure 6-1 B). Amandine, Bintje and Agria varieties displayed an average dormancy of 94, 125 and 137 days in 2008, respectively (Figure 6-1 A). In contrast, because of the heat wave, the 2003 season resulted in a higher sum of daily maximum air temperature during the growing season (Figure 6-1 B) and the dormancy durations of Amandine, Bintje and Agria varieties were much lower than in 2008 with 48, 67 and 112 days, respectively (Figure 6-1 A).

Consequently, the environment of the 2003 season led to high sprouting pressure while the environment of the 2008 season led to a low sprouting pressure. Different management strategies have to be implemented according to the sprouting pressure of the season.

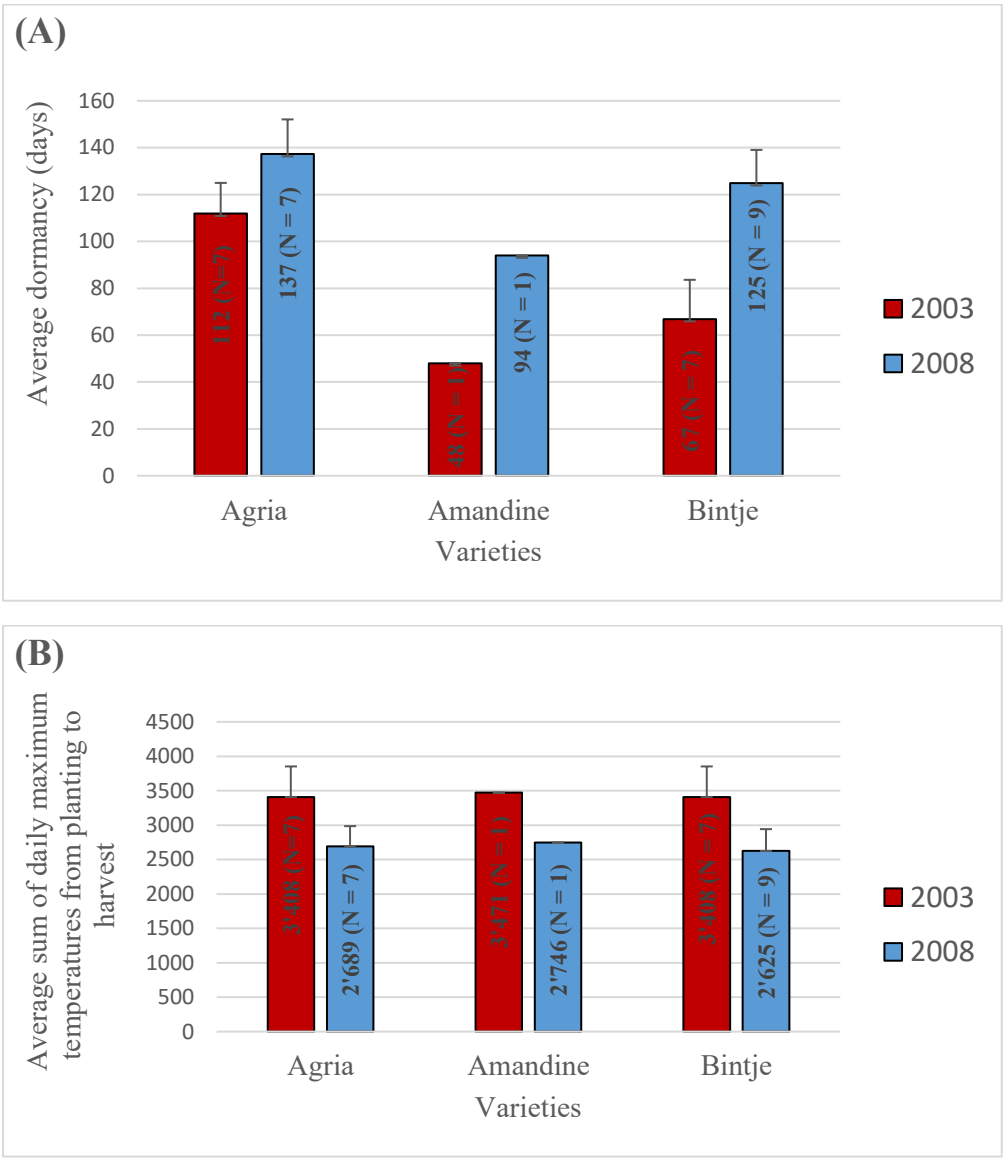

Figure 6-1. Average dormancy duration (A) for varieties grown under contrasting seasons; the 2003 season leading to high sprouting pressure (i.e. high sum of daily maximum temperatures from planting to harvest) and the 2008 season leading to low sprouting pressure (i.e. low sum of daily maximum temperatures from planting to harvest) (B). Average ± SD, data of one or several trials with one or several locations (N are indicated on the bars).

1.3. Management strategies to mitigate sprouting considering the sprouting pressure of the storage season

1.3.1. Modeling tool to predict dormancy and evaluate the sprouting pressure of the season

The second management strategy (after the variety choice) to improve potato storage management should be the use of the predictive tool of potato dormancy developed in chapter 2 to determine the sprouting pressure of a given season and a given genotype (See management strategies 1 and 2 in Figure 6-2).

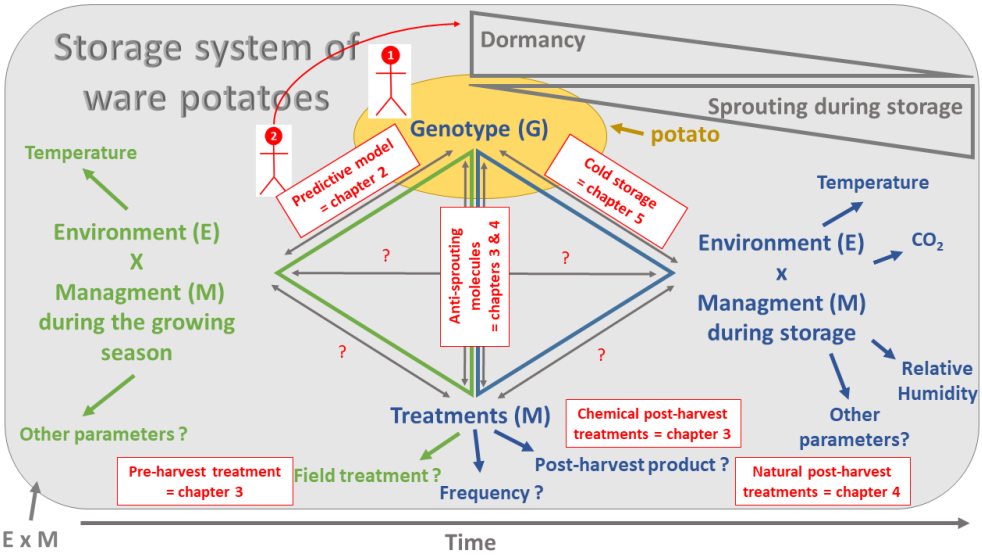

Figure 6-2. Conceptual diagram representing a potato storage system "storage system of ware potatoes" with main factors influencing sprouting during storage of potatoes; = potential management strategies to mitigate sprouting.

As previously mentioned, the predictive model of potato dormancy (Chapter 2) uses the variety class and the sum of the daily maximum air temperature during the period from planting to harvest as predictors (Table 6-1, Figure 6-3). It represents a decision support system tool that is easy to use as the temperature in the field can be easily obtained through a weather station or temperature recorder. The model enables the prediction of dormancy with a precision of ± 15 days, which is acceptable for the potato industry compared to the months of storage (Curty Personal communication). In addition, it would be of interest to test the model and to predict dormancy duration using data from trials in different countries. The model will help to improve the quality of the dormancy characterization of different varieties. The predictive model could be used as a cost-effective tool for farmers to predict the potato dormancy duration of a given variety according to the temperatures during the growing season of a given year and location (Figure 6-3). If we had used the model in previous years, we would have

been able to anticipate and improve the storage management. In 2008, we would have known that varieties with medium to long dormancy such as Bintje (European Cultivated Potato Database ; Le plant de pomme de terre Français ; NIVAP 2011) could have been kept for up to 125 days without sprouting using a simple storage at 8 °C, without any other human intervention required. While if we had used the model in 2003, we would have known that the sprouting pressure was high and we would have been able to anticipate other management strategies to mitigate sprouting and avoid losses due to the heat wave (Figure 6-3). Once the dormancy duration for a given genotype, year and location is predicted by the model, different management strategies can be implemented to further extend the storage duration according to the sprouting pressure.

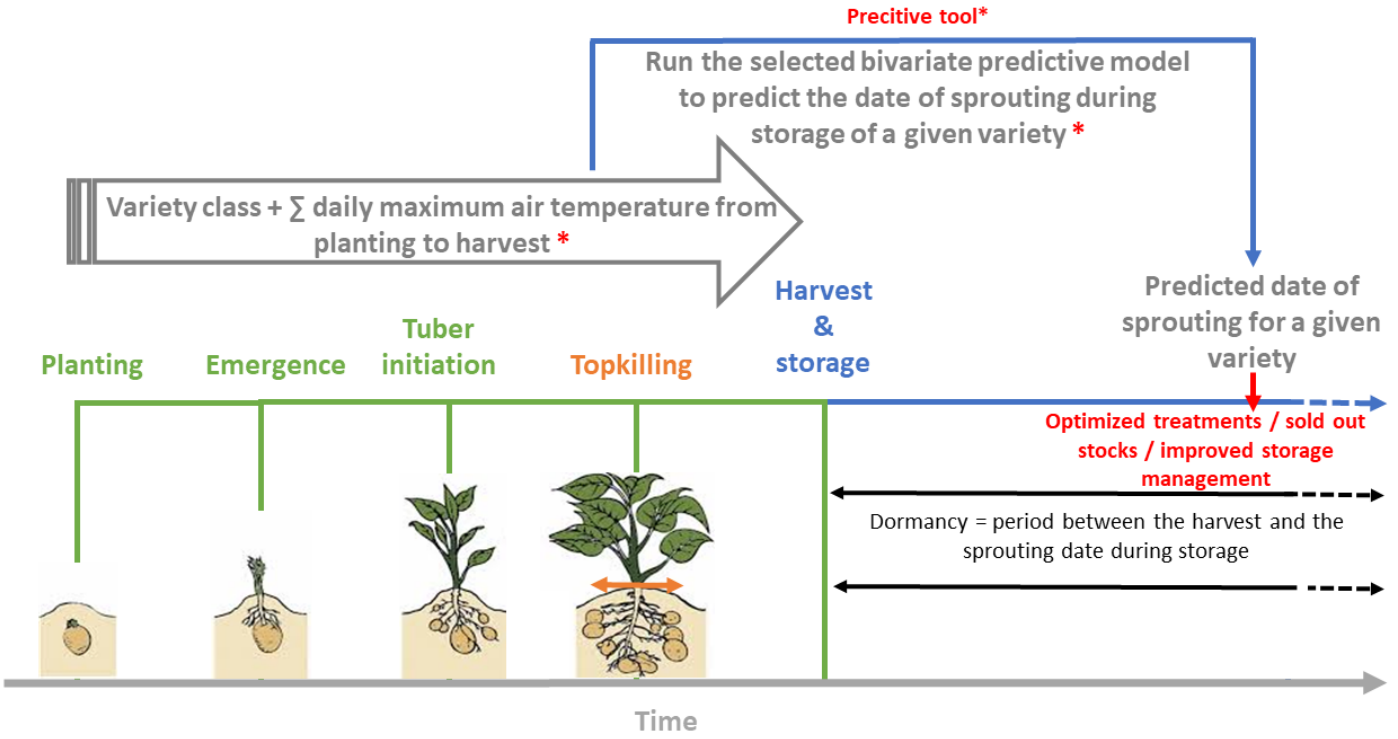

Figure 6-3. Schematic illustration of the predictive tool based on the two combined most influencing variables on dormancy variability issues from the selected bivariate predictive model (Chapter 2). Note the definition of potato dormancy defined and used in this thesis and in chapter 2. (Schematic illustration designed by Margot Visse-Mansiaux; potato cycle pictures on this scheme are retrieved and modified from: © FAO (2008))

1.3.2. Management strategies to mitigate sprouting during season with low sprouting pressure

After a season leading to low sprouting pressure (see above example of the 2008 season, Figure 6-1), a storage at 8 °C might be enough without using other management strategies to mitigate sprouting. According to the dormancy's information predicted by the model (Chapter 2, Figure 6-3), potato varieties with the lowest predicted dormancy's duration can be sold first, while potato varieties with the highest predicted dormancy's duration can be kept longer.

To further extend the storage duration of a given genotype grown during a season leading to low sprouting pressure, others management strategies can be implemented to delay sprouting such as the use of anti-sprouting treatments or of low temperatures during storage (See management strategies 3 and 4 on Figure 6-4).

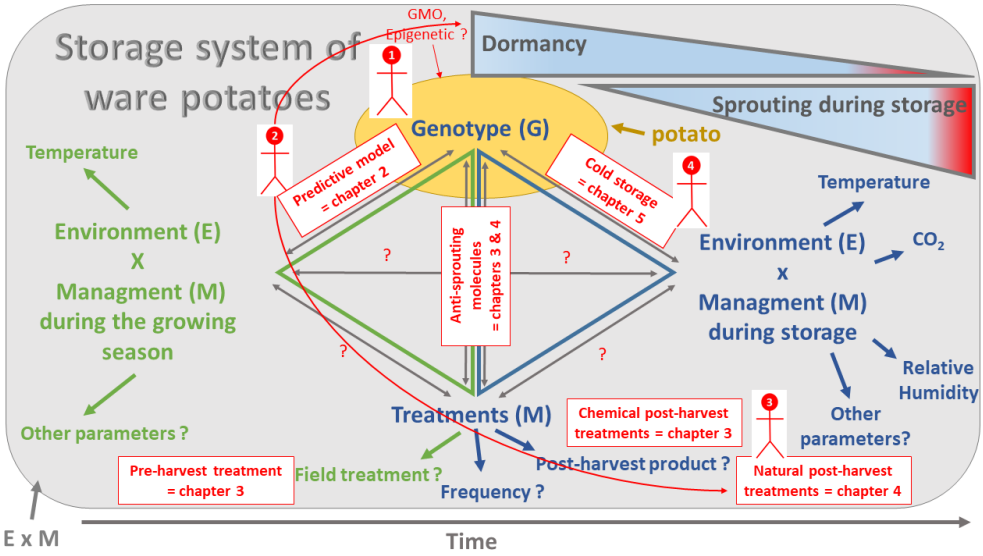

Figure 6-4. Diagram representing a potato storage system "storage system of ware potatoes" under a low sprouting pressure (i.e. high dormancy's duration and low sprouting during storage), with main factors influencing sprouting during storage of potatoes; = potential management strategies to mitigate sprouting under low sprouting pressure. Potential combinations of management strategies are represented by red arrows.

Synthetic post-harvest molecules could be used to further extend the storage without sprouting, however, for such low sprouting pressure, we recommend focussing on natural post-harvest anti-sprouting molecules (See management strategy 3 on Figure 6-4). Natural active ingredients such as spearmint oil (= mint essential oil, containing L-carvone molecule) and D-Limonene from orange essential oil should be used (Chapter 4, Table 6-1 and Table 6-2). These molecules present the advantage to be

authorized for stored potatoes in organic farming, and no or only a very short withholding period (a few days) before commercialization is required for these natural products (Chapter 4, Table 6-1 and Table 6-2), allowing the sale of potato stocks shortly after application of the anti-sprouting treatment. In addition, these natural molecules are not subject to an MRL in the EU (Table 6-2). Ethylene could be used as well as it presents the same advantages as essential oils (Chapter 4, Table 6-1 and Table 6-2).

We showed that these essential oils are efficient alternatives to CIPC as they reduced sprouting during storage for up to five months, in comparison to an untreated control, and caused localized sprout necrosis on the apical part of the sprouts (Visse-Mansiaux et al. 2020) (Chapter 4, Table 6-1). Other studies reported similar results in terms of efficacy and necrosis of sprouts on tubers treated with mint essential oil (Teper-Bamnolker et al. 2010; Kleinkopf et al. 2003; Sanli et al. 2010). A major drawback associated with the use of these natural essential oils is that their application by hot fogging generally requires high frequency of treatments and large quantities of product to efficiently control sprouting for an entire storage season. Consequently, these natural essential oils generally lead to a lot of handling and high costs of treatments (Curty Personal communication) (Table 6-2). Furthermore, as essential oils are highly volatile, the storage chamber must be sealed to avoid product losses and consequently a loss of efficacy. Finally, a good ventilation system is necessary to allow the proper distribution of the product (Martin 2020b). However, for such a low sprouting pressure scenario, these essential oils could be used to mitigate sprouting without using the maximal frequency of treatments, to reduce the costs and handling time to treat potatoes. This means that, as these oils cause localized sprout necrosis (Chapter 3), the first treatment could be delayed and applied just before sprouting instead of being applied during the first few weeks of storage, with the proviso of knowing the sprouting date of the stored tubers. In a season with low sprouting pressure such as the 2008 season, the Agria variety stored at 8 °C displayed an average dormancy duration of 137 days without any treatment (Figure 6-1 A). This means that for the Agria variety, tubers could have been treated with oils only a few days or weeks before the end of the dormancy to extend the storage and reduce costs associated with the high frequency of treatments. To do that, the predictive model (Chapter 2) will be useful to predict the sprouting date during storage to determine the right time to treat (Figure 6-3 and management strategies 2+3 on Figure 6-4). This strategy needs to be further tested and validated.

Besides presenting the same advantages as essential oils in terms of flexibility with the possibility to sell potato stocks quickly and the absence of MRL, the cost related to the use of ethylene presents the advantage of being relatively cheap compared to the cost of use of other products on the market (Martin 2020b) (Table 6-2). Martin (2020b) reported that the cost associated with the use of ethylene to treat potatoes is 4 to 5 euros per tonne, while the cost of mint essential oil and orange essential oil is 13 to 20 euros and 10 to 18 euros per tonne, respectively (indicative cost for France, may vary according to the germination pressure of the year and management of the

storage conditions) (Table 6-2). In comparison, the cost of the use of CIPC varied from 3 to 6 euros per tonne of potatoes (indicative past cost for France) (Table 6-2).

Table 6-2. Table summarizing information about the different anti-sprouting treatments (the sources of information are indicated below the table)

Active ingredient	Trade name of products or of the system ǂ	Modes of action	Company ǂ	Dose and frequency of treatment ǂ	Date of first application ǂ	Withholding period (waiting time before removal of potatoes)	Method of application ǂ	MRL (in the EU) ǂ	Authorized in organic farming ǂ	Indicative cost (excluding tax) ǂ
Maleic hydrazide	Fazor star / Itcan SL 270*	Preventive*, inhibits cell division (*inter alia*)**	UPL / Kreglinger*	Fazor star: 2 treatments, max. 5 kg/ha* / Itcan SL 270: 1 treatment, 11l/ha*	Size greater than 25–35 mm*	21 days*	Liquid spraying** Application in the field*	60 ppm*	No*	2 to 3 €/t*
3-decen-2-one	SmartBlock ®	Curative: necrosis via destruction of the internal structure of the sprout cells**	AMVAC Netherlands B.V.**	100 mL/t**, application when the sprouts reach 3 mm in size (max. 4 treatments)**	When the sprouts reach 3 mm**	Unknown, not approved in the EU**	Hot-fogging**	Unknown, not approved in the EU**	Unknown, not approved in the EU**	Unknown, not approved in the EU**
1,4-DMN	Dormir®	Preventive : prolongs potato dormancy**	Dormfresh Ltd.*	20 mL/t*, every 28 days* Max. 6 treatments*	Possible as of entry into storage**	30 days (EU)**	Hot-fogging**	15 ppm*	No*	8 to 14 €/t*
CIPC	Several commercial names and formulations ***	Preventive - Inhibits cell division**	Several companies*	Variable depending on the formulation, 36g/t max.* Not authorized in EU***	At the beginning of storage or during storage according to the formulation***	Not authorized in the EU*	In powder, liquid spraying or hot fogging depending of the formulation***	10 ppm until 2 september 2021 and then 0.4 ppm in the EU*	No***	3 to 6 €/t*in the EU***
D-limonene (orange essential oil)	Argos®	Preventive and curative (necrosis)**	UPL*	100 ml/t*, every 3 to 4 weeks, max. 9 treatments*	White spot stage*	None** or a few days*	Hot fogging (180-190 °C)*	None*	Yes*	10 to 18 €/t**
Spearmint oil	Biox-M®	Preventive and curative (necrosis)**	Xeda*	Hot fogging: 90ml/t and 9 x 30 ml/t *; evaporation: 1 to 2 ml/t/day. Max. 360 ml/t*	White spot stage*	None** or a few days*	Hot fogging (180-190 °C) or cold evaportation (Xeadvap)*	None*	Yes*	13 to 20 €/t*
Ethylene	System to apply: Biofresh safestore or Restrain®*	Preventive – slows the growth of the sprouts and their speed of elongation*	Biofresh or Restrain®*	Progressive increase, then 10 ppm continuously*	At the beginning of storage*	None*	With Restrain® generator or Biofresh safestsore*	None*	Yes*	4 to 5 €/t*

* Information retrieved and modified from Martin (2020a) and from Martin (Personal communication) for France and/or EU, the author notes that the costs are indicative and may vary according to the germination pressure of the year and management of the storage conditions. The indicative costs are estimated for about 6 months of storage and for France, this estimation takes in consideration the varietal diversity and different storage conditions.

** Information retrieved and modified from Visse-Mansiaux et al. (2020), other products, dosage, frequency or application methods may exist

*** Earlier information because the CIPC molecule is forbidden in EU since 8 October 2020

ǂ Other products, suppliers or application methods may exist and all the information in this table is subject to variation according to the storage conditions (e.g., temperature or length of storage), the product used, the country, etc. Please check with the suppliers.

Studies reported that continuous application of ethylene at a rate of 10 ppm suppressed sprout growth for up to six months after harvest in all tested varieties (Harper and Stroud 2018). In addition, the application is easy and requires almost no handling. A major drawback with ethylene is that it can induce the increase and accumulation of sugars in certain potato varieties (Harper and Stroud 2018; Martin 2012). We have observed this negative effect on Markies variety (Visse-Mansiaux et al. 2020) (Chapter 4). This result was also observed by Harper and Stroud (2018) reporting commercially unacceptable fry color values (= darker colours) for Markies stored up to height months under ethylene atmosphere compared to tubers in an ethylene-free atmosphere. This contradicts Martin (2020b) reporting that tubers from Fontane and Markies varieties could be stored under ethylene without a high risk of degradation of their frying-ability. However, the author reported that the use of ethylene for processing varieties is not recommended except for varieties such as Fontane and Markies. To cope with the increase in reducing sugars caused by ethylene, a solution would be to use treatments combining ethylene with 1-methylcyclopropene (1-MCP). 1-MCP treatment prevents the increase in reducing sugar content caused by ethylene treatment (Visse-Mansiaux et al. 2020) (Chapter 4). Prange et al. (2005) reported that 1-MCP can be used as a treatment to prevent ethylene-induced fry color darkening while maintaining the efficacy of ethylene to mitigate sprouting.

Another solution to further mitigate sprouting in tubers during seasons with low sprouting pressure would be to use low storage temperatures (Management strategy 4 on Figure 6-4). The storage at low temperature (i.e. 4 °C) decreased sprouting of potatoes compared to storage at higher temperature (i.e. 8 °C) for six tested varieties (Chapter 5, Table 6-1). Our result is in line with the literature as Gichohi and Pritchard (1995) reported that lowering the storage temperature from 8 °C to 6 °C and 5 °C delayed sprouting by 3 and 15 weeks respectively in the Shepody variety.

This solution is suitable for tubers designated for the fresh market, however low storage temperature may lead to an increase in RS content for certain varieties (Matsuura-Endo et al. 2006). Consequently, the use of CIS-resistant varieties with long dormancy period should be favored over cold storage conditions for the potato processing industries in order to limit the unwanted byproducts of the Maillard reaction.

For example, CIS-resistant varieties identified in chapter 5 such as Lady Claire, Verdi or Kiebitz could be used for storage at 4 °C to extend the storage duration with limited CIS (Table 6-1). In the literature, a few other varieties have been reported to be CIS-resistant such as Sempra (Böhm et al. 2006) or White Pearl (Groza et al. 2006). However, the limited number and availability of CIS-resistant varieties are a major constraint to meet the demand and requirements of the potato industry. To face the CIPC non-renewal, it would be of interest to find a large range of CIS-resistant potato varieties with diverse traits to offer enough choice in terms of agricultural and market requirements (e.g., large genetic basis or resistance to diseases and water stress). In addition, the sugar content in potato may vary depending on several parameters of the

growing season such as maturity, temperature, irrigation or mineral nutrition (Kumar et al. 2004), consequently, to avoid any risk, we recommend performing a RS measurement and a frying test before processing for tubers stored at low temperatures.

Genetic engineering could be used (Figure 6-4) to create new CIS-resistant varieties using gene knockout or silencing of the *Vinv* gene as demonstrated in the varieties Russet Burbank and Ranger Russet (Zhu et al. 2014) and in the variety Katahdin (Bhaskar et al. 2010; Shumbe et al. 2020). However, public acceptance remains a major constraint for the homologation and adoption of GM potato in the EU where only genetically modified organism (GMO) maize MON810 is currently authorized. Consequently, new breeding technologies such as CRISPR/Cas9 could be used to generate CIS-resistant traits by knocking out the *VInv* genes in the potato varieties currently used by growers and industrial processors (Hameed et al. 2020). Epigenetic modifications could also be used to generate modified tubers with CIS-resistance. Shumbe et al. (2020) identified that the CIS-resistance of the Verdi variety could be due to hypermethylation of the *Vinv* promoter in the 1.0-1.7kb region. It would be of interest to evaluate if this mechanism occurs in the CIS-resistant varieties identified in our study and to use this information to create genetic lines with CIS-resistance.

For CIS-susceptible varieties such as Markies, the cold storage could be used as well using a solution explored in chapter 5 and called "reconditioning" (Table 6-1). The CIS-susceptible Markies variety can be stored at low temperature (i.e. 4 °C), which significantly reduced sprouting compared to storage at 8 °C, followed by a reconditioning period. The reconditioning resulted in a reduced quantity of glucose produced by the tuber compared to the glucose in the same variety stored at 4 °C without reconditioning. Our results are in line with the literature, as De Wilde et al. (2005) reported that a reconditioning at 15 °C after a storage at low temperature decreased RS in tubers. Consequently, reconditioning presents a valuable solution to circumvent the limitations of CIS-susceptible varieties. However, the potential of reconditioning to reduce RS content in potatoes is variety-dependent (Kyriacou et al. 2009; Schippers 1975) and it would be of interest to test a large range of varieties for the potential of reconditioning.

1.3.3. Management strategies to mitigate sprouting under high sprouting pressure season

During the 2003 season with high sprouting pressure due to the heat wave, among 80 varieties tested in our trials, the longest dormancy durations were observed for the varieties "Noe 963-96" and "Agria" with 115 and 112 days, respectively (data not presented in chapter 2). Consequently, after a season leading to high sprouting pressure as in 2003 (Figure 6-1), whatever the genotype and the desired storage duration, several management strategies might be necessary to efficiently mitigate sprouting and avoid losses during storage caused by early sprouting.

Once the dormancy duration has been predicted (management strategy 2 on Figure 6-5), the same previously mentioned management strategies can be used (management

strategies 3 or 4 in Figure 6-4 or Figure 6-5), but might not be enough to keep potatoes free of sprouts for several months under such high sprouting pressure seasons.

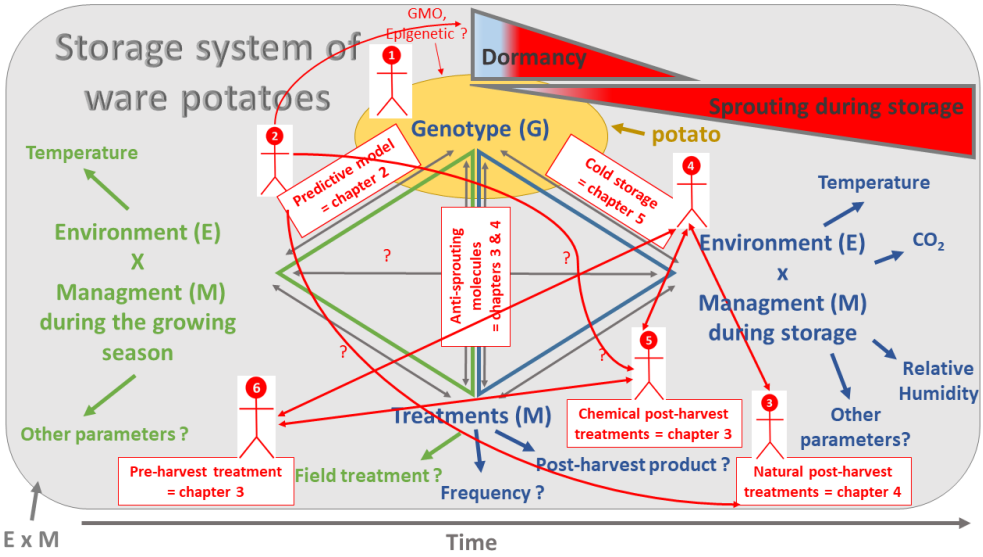

Figure 6-5. Conceptual diagram representing a potato storage system "storage system of ware potatoes" under high sprouting pressure (i.e. low dormancy duration and high sprouting during storage), with main factors influencing sprouting during storage of potatoes; = potential management strategies to mitigate sprouting under high sprouting pressure. Potential combinations of management strategies are represented by red arrows.

In the case of a high sprouting pressure season, it would be possible to combine the above-mentioned management strategies. A solution would be to combine the use of natural anti-sprouting treatments with cold storage (management strategies 3 + 4 in Figure 6-5) to reinforce the control of sprouting. A few studies demonstrated the efficacy of mint essential oil to control sprouting during storage at 8 °C or 10 °C (Teper-Bamnolker et al. 2010; Coleman et al. 2001), however to our knowledge, there is no study evaluating the effect of the storage temperature on the efficacy of both orange and mint essential oils. It would be of interest to compare the efficacy of these molecules in storage at both 4 °C and 8 °C in further studies to assess the potential of combining cold storage and the use of natural anti-sprouting molecules to mitigate sprouting during seasons with high sprouting pressure.

In addition, it would be of interest to study the potential of these combined strategies (i.e. using natural treatments with cold storage) to decrease the frequency of treatment with essential oils and consequently to decrease the cost of treatments during seasons with high sprouting pressure. For example, it has been reported that for the product

ARGOS® (i.e. orange essential oil) applied by hot fogging, the recommended dose is 100 ml of product per tonne of potatoes, with a first treatment three to six weeks after the beginning of the storage and then an interval of three weeks between treatments, but that the interval can be increased according to the variety, temperature and type of storage (UPL Benelux BV 2020). This strategy would need to be further investigated.

However, during seasons with high sprouting pressure, even with the use of cold storage, it may not be possible to delay the first application or the frequency of essential oil treatments to decrease the cost of treatments as suggested above. If it is not possible to delay the frequency of treatments using a cold storage during a high sprouting pressure season, this will necessitate the use of the maximum authorized frequency of product to control sprouting and consequently, this will lead to high cost of use and high handling during the season (Curty Personal communication; Martin 2012). This could be an option for farmers producing potatoes in organic farming, where synthetic anti-sprouting molecules cannot be used.

To mitigate sprouting during a season leading to high sprouting pressure in conventional farming, a solution to decrease handling and cost of treatments would be to use pre- and post-harvest synthetic molecules (Chapter 3, Table 6-1) alone or in combination (management strategies 5 and 6 or 5+6 in Figure 6-5), or to combine the use of pre- or post-harvest treatments with cold storage (management strategies 4 + 5 or 4 + 6 in Figure 6-5).

During the growing season, if farmers identify that the environment is favorable to high sprouting pressure (e.g., pressure similar to 2003 season), they can choose to use MH pre-harvest treatment in the field to mitigate sprouting during storage (management strategies 6 in Figure 6-5). Pre-harvest treatment with MH is highly efficient to control sprouting for up to seven months of storage, as in our study MH displayed 86.9 % efficacy to control sprout weight in comparison to the untreated control (Visse-Mansiaux et al. 2021) (Chapter 3, Table 6-1). Similar efficacies have been demonstrated in the literature. Varieties Ranger Russet and Russet Burbank were shown to have delayed sprout growth 8 months after haulm killing following MH treatment (Caldiz et al. 2001a). The advantage of MH is that, aside from controlling sprouting during storage, it also provides control of volunteers in potato crops (Cunnington 2019). MH can also help limit the risk of internal sprouting (Martin 2020a). Blauwer et al. (2012) reported the beneficial effect of MH in limiting internal sprouting in the Innovator potato variety. In addition, the cost related to the use of MH is relatively low compared to the cost of most anti-sprouting treatments. Martin (2020b) reported that the cost associated with the use of MH pre-harvest treatment is 2 to 3 euros per tonne (indicative cost for France, may vary according to the germination pressure and the management of the storage conditions) (Table 6-2).

To help farmers decide about the importance of performing a pre-harvest MH treatment during the growing season, the predictive model built in chapter 2 (Table 6-1) could help identifying the sprouting pressure of the season based on the variety class, the records of the temperature predictor of the season (past records and estimation of future records, as the season will be ongoing) and of an estimated harvest

date. This strategy would need to be further investigated. To further reinforce the control of sprouting, potatoes treated with MH could be stored at low temperature (management strategies 4 + 6 in Figure 6-5).

A drawback with the use of MH-based products is the presence of residues in tubers at the end of the storage period reported by several independent studies (Visse-Mansiaux et al. 2021; Dias and Duncan 1999a; Harper 2019) (Chapter 3, Table 6-1). However, the MRL for MH in potatoes in the EU is relatively high (= 60 mg kg^{-1}) (European Commission 2019b) and in our study the detected residues were below this limit (Chapter 3) (Visse-Mansiaux et al. 2021). In addition, as mentioned in chapter 1, treatment with MH must be done at the right time to be effective as the efficacy may vary according to the weather at the time of foliar application (Cunnington 2019).

If farmers did not apply MH during the growing season because of the above-mentioned constraints and if sprouting pressure is high, chemical post-harvest treatments can be used alone (management strategy 5 in Figure 6-5), or in combination with cold storage (for CIS-resistant varieties) (management strategies 5 + 4 in Figure 6-5) to efficiently mitigate sprouting.

In chapter 3, we showed that post-harvest 1,4-DMN and 3-decen-2-one molecules are efficient to control sprouting for up to seven months after harvest with 73.6 % and 77.9 % efficacy in controlling sprout weight, respectively, in comparison to an untreated control (Visse-Mansiaux et al. 2021). Our results are in line with the literature as the efficacy of both 1,4-DMN and 3-decen-2-one have been confirmed by recent studies. 1,4-DMN has been reported to effectively control sprouting in five processing varieties stored for 9 months at 9 °C (Harper 2019). The 3-decen-2-one molecule has also been reported to be highly effective in controlling sprouting for eight months after storage in six tested varieties stored at 6.5 °C and with only three treatments during the season (Demeulemeester et al. 2019). In particular, the 3-decen-2-one molecule showed a better efficacy compared to other tested active ingredients (Demeulemeester et al. 2019). A key advantage of the aforementioned chemical post-harvest treatments is the relatively low frequency of treatments necessary to control sprouting as compared to treatments with essentials oils.

In addition, as 1,4-DMN initiates transcriptional changes resulting in repression of genes associated with the sprout growth and acts by prolonging potato dormancy (Jina Personal Communication), the predictive model presented in chapter 2 could be useful to adapt treatments with the 1,4-DMN molecule during seasons with very high sprouting pressure (management strategies 2 + 5 in Figure 6-5). This would allow prediction of a sprouting date for a given variety and planning to treat potatoes a few days before this date to prolong the dormancy period using the 1,4-DMN molecule. As with most CIPC-alternative products, the use of 1,4-DMN based products to control sprouting is more expensive than CIPC. According to Martin (2020b), the costs associated with the use of post-harvest 1,4-DMN treatment is 8 to 14 euros per tonne (indicative cost for France, may vary according to the germination pressure of the year and the management of the storage conditions), while the past cost of use of CIPC varied from 3 to 6 euros per tonne of potatoes (Table 6-2).

Therefore, it is key to implement the predictive model in order to delay the application of 1,4-DMN and thereby reducing the costs associated with 1,4-DMN applications. The drawback with this strategy is that it offers less flexibility in terms of reducing stocks than with natural molecules as for 1,4-MDN currently there is a delay of 30 days after treatment to wait before commercialization in the EU, which makes the management of stocks complicated (Curty, Personal communication). However, a proposal to reduce this delay to three days was performed by the company supplying the product (Jina Personal Communication). In addition, the current MRL in the EU for 1,4-DMN based products is 15 mg kg^{-1} (European Commission 2019b). It should be noted that no residue of 1,4-DMN were found in tubers one month after the last treatment (Chapter 3) (Visse-Mansiaux et al. 2021).

The 3-decen-2-one molecule acts as a curative treatment and will be useful to control sprouting and/or to save potato stocks already sprouted during season with a very high sprouting pressure. This molecule has the advantage to provide complete desiccation and blackening of sprouts. Longer sprouts, up to 2.5 cm can also be removed as part of a rescue treatment later in the storage cycle, if necessary (Immaraju 2020). This is a key asset of this 3-decen-2-one molecule as it allows saving potato stocks as this molecule acts as a curative product with a complete necrotize of sprouts within 24 hours (Chapters 3 and 4) (Figure 6-6). Similar results have been reported in the literature (Knowles and Knowles 2015b). SmartBlock® is exempt from the requirement of an MRL in the U.S., Canada (EPA 2013b; Health Canada 2014) and Israel, however it is not registered in the EU at the moment. It is anticipated that this molecule will soon be registered in the EU. Our study (Chapter 3) confirmed the efficacy of SmartBlock® and it can serve as a basis for the implementation of SmartBlock® treatments in the EU. Since SmartBlock® is chemically synthesized, it will probably not be authorized for use in organic production, and a final decision on the exemption for the requirement of an MRL for 3-decen-2-one in the EU has yet to be established. There is no waiting period listed on existing SmartBlock® labels however, it is likely that similar to other sprout control products in the EU, a withholding period will be required. In addition, SmartBlock® will necessitate regular monitoring of potato stocks because SmartBlock® is most effective after tubers break dormancy.

As we showed that 1,4-DMN and 3-decen-2-one are effective to mitigate sprouting up to seven months of storage at 8 °C (Chapter 3), using these molecules in combination with cold storage (i.e. at 4 °C) we can expect a reinforced efficacy of these molecules (management strategies 5 + 4 on Figure 6-5). Consequently, to further support and promote the use of these post-harvest alternative treatments (i.e. 1,4-DMN and 3-decen-2-one molecules), it would be of interest to test the efficacy of these treatments within different storage environments. For example, it might be useful to test the efficacy of these molecules under different temperatures of storage, including cold storage, to evaluate their potential efficacy according to the storage temperature.

For CIS-susceptible varieties that cannot be stored at low temperatures, another strategy to face very high sprouting pressure seasons would be to combine MH pre-harvest treatment and post-harvest treatment with 1,4-DMN or 3-decen-2-one (management strategies 5+6 on Figure 6-5). We showed that combining pre- and post-harvest treatments is not economically feasible as the MH efficacy is high enough itself for storage up to seven months (Chapter 3, Table 6-1) (Visse-Mansiaux et al. 2021). However, Martin (2020b) reported that using MH pre-harvest treatment offers flexibility in terms of management at the beginning of the storage by delaying the beginning of sprouting.

In the study presented in chapter 3, the sprouting pressure was not extreme as in the 2003 season and the storage duration was seven months. It would be of interest to test these combinations for a storage season with very high sprouting pressure and for a very long storage season up to 8 months. As the 3-decen-2-one showed a high curative effect (chapter 3, Table 6-1, Figure 6-6), a combination which might be particularly useful would be to treat potato plants with MH in the field and then to treat potatoes during storage with the 3-decen-2-one molecule only if the MH treatment is not sufficient and sprouts appear. It would be necessary to evaluate the added economic value of using these combinations, i.e. compare the economic costs associated with losses due to sprouting in tubers treated with pre- and post-harvest treatments used alone or in combination, with the cost of use of these molecules used alone or in combinations.

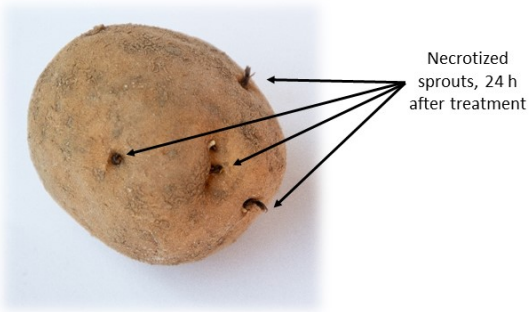

Figure 6-6. Tubers of the Verdi variety treated with the molecule 3-decen-2-one, after five months of storage under experimental conditions. Complete necrosis and desiccation of sprouts can be observed (Source: extract and modified from Visse-Mansiaux et al. (2020), chapter 4).

2. General conclusion

Results of the thesis allow us to understand and quantify the effect of genetic, management, and environmental factors during the growing season on potato dormancy duration during storage (Table 6-1). Through these results, the different research questions have been answered (Table 6-1). Results showed that the genotype is not the main factor influencing dormancy and that factors year and location are important as well (Chapter 2, RQ1, Table 6-1). The predictive model proposed in chapter 2 will allow improvement of potato storage management by predicting the sprouting date during storage of a given variety according to the growing environment. This tool will allow producers to anticipate the sale of potato stocks according to the sprouting pressure of the season and avoid losses during storage (Chapter 2, RQ2, Table 6-1).

Once the duration of dormancy is predicted, other management strategies can be implemented and combined to keep potato varieties from sprouting in seasons with higher or lower sprouting pressure. Pre- and post-harvest anti-sprouting treatments have been evaluated in this thesis and are a valuable alternative to CIPC since they control sprouting for several months (Chapters 3 and 4, RQ3, Table 6-1). However, these products are less efficient than CIPC, more costly, and some of them require more handling; consequently, their use is more time-consuming.

Combinations with other strategies are necessary to decrease the cost associated with these alternative treatments and high sprouting pressure, which will be more frequent in the context of climate change. The predictive model can help by delaying the date of the first anti-sprouting treatment, thus reducing storage costs associated with sprouting control. Depending on the sprouting pressure, storage at low temperature can also be used to mitigate sprouting. Results of the thesis show that storage at cold temperatures is a suitable solution to cope with the non-renewal of CIPC in the EU provided that producers use CIS-resistant genotypes and/or reconditioning to avoid CIS. Our study identified CIS-resistant varieties suitable for storage at low temperature without the risk of sweetening and production of toxic compounds during frying. Finally, we showed that the reconditioning strategy reduces glucose content in potatoes before frying (Chapter 5, RQ4, Table 6-1). In addition, to reinforce the anti-sprouting effect of cold storage, it could be combined with anti-sprouting treatments.

In seasons with very high sprouting pressure and without CIPC, we recommend combining the above-mentioned potato storage management strategies to mitigate sprouting and avoid losses during storage. Based on the results of the different chapters, sustainable management strategies to control potato sprouting are proposed in this thesis.

3. Perspectives

3.1. Future research to face the impact of climate change on potato dormancy

Climate change is expected to impact potato dormancy by increasing year-to-year variability as well as the number of years with high sprouting pressure. To improve potato storage management without CIPC, further studies are necessary to investigate gaps and fully understand the "storage system of ware potatoes".

For instance, it is of interest to study potential interactions between the environment and management during the growing season and the efficacy of treatments during storage. For example, hot seasons lead to an increase in sprouting during storage (Magdalena and Dariusz 2018) (Chapter 2), and with the effect of climate change, hot seasons will become more frequent in the coming years. Consequently, we can expect an increase in sprouting pressure during storage and a decrease in the efficacy of anti-sprouting molecules at the current recommended dosages. In chapter 2, we demonstrated that the 2003 heat wave drastically reduced dormancy duration during storage (see example for the Bintje variety in chapter 2). In addition, the greenhouse trial reported in chapter 2 confirmed that high temperatures during the growing season lead to faster sprouting during storage. However, in this greenhouse trial, the temperatures of growth were 15 °C or 20 °C and thus not extreme. Consequently, it would be of interest to simulate the effect of future climatic conditions during the growing season on potato sprouting during storage. A trial could be implemented to simulate the effect of different prediction scenarios under global temperature increases reported by the Intergovernmental Panel on Climate Change (IPCC 2007b) on: 1) the duration of dormancy during storage, and 2) the efficacy of the above-mentioned anti-sprouting molecules. Several varieties commonly used in Europe should be tested such as Agria, Amandine, Innovator or Markies. Potatoes could be grown in greenhouse trials with different temperature regimes representing the best- and worst-case scenarios of global temperature increases. Then, some of the tubers could be stored in a chamber at 8 °C without anti-sprouting molecules to observe the dormancy duration of the different cultivars. The remainder of the tubers should be stored in a second storage chamber at 8 °C using the above-mentioned pre- and post-harvest treatments to access their efficacy after growing seasons with different temperature scenarios. The experiment should be repeated over at least 3 years. Other experiments could be designed to adapt the frequency and quantity of anti-sprouting products in order to obtain an acceptable efficacy under the worst-case scenarios of climate change.

Another solution to predict the impact of climate change on potatoes grown in Europe would be to collect dormancy data from potato grown at other latitudes with higher average temperatures.

With climate change, we can expect an increase of stresses on tubers during the growing season such as drought or heat stress, but also excess water stress (e.g.,

flooding). Stress is known to increase the PAI and to reduce the dormancy duration of potatoes (Delaplace et al. 2008), thus it would be of interest to further study the effect of different stresses on potato dormancy.

In addition, plant-microbiome interactions are of high importance as plants are able to interact with their surrounding microbial communities and to select natural microbiomes with specialized strains to mitigate stresses (Rodriguez and Durán 2020). Consequently, it would be of interest to study the impact of these interactions on potato dormancy via a reduction of the stresses incurred by the plant.

3.2. Evaluating the efficacy of the different pre- and post-harvest treatments under different storage conditions

Another area of concern is the potential interaction between variation in storage conditions (e.g., various temperature or humidity conditions) and the efficacy of pre- and post-harvest treatments during storage. For instance, it is of interest to evaluate the efficacy of pre- and post-harvest treatments under different temperatures of storage since, to our knowledge, there is no study evaluating the efficacy of the different pre- and post-harvest treatments (i.e. treatments studied in chapters 3 and 4) with different storage temperatures within the same trial. Varieties with contrasting dormancies should be used for the trials (e.g., Amandine, Bintje and Agria) in order to assess the efficacy of products for a large range of dormancies. Potatoes should be grown at the same location for at least three years to obtain representative results. Using at least three years would allow identification of a potential effect of the environment and of the year, which may lead to differences in physiological age. This may result in differences in sprouting during storage and in the efficacy of sprouting treatments during storage at different temperatures. After harvest, tubers should be stored at different temperatures (e.g., 4 °C, 6 °C and 8 °C) for at least five months and treated with the different anti-sprouting treatments. Sprouting evaluation should be performed by assessing the weight of sprouts (see chapters 3 and 4) at different periods of storage (e.g., after three and five months) to evaluate the efficacy of each product at these different storage temperatures. This would facilitate the choice of pre- and/or post-harvest treatment according to the desired temperature of storage. Once the efficacy of a given anti-sprouting treatment at the different storage temperatures is known, this could also help to adjust and decrease the frequency of treatments and thus, to decrease the costs associated with the use of anti-sprouting alternatives to CIPC.

3.3. Evaluate the efficacy of combinations between post-harvest treatments

In chapter 3, we studied the potential of combining pre-harvest treatment with MH and post-harvest treatments with 1,4-DMN and 3-decen-2-one molecules, however we did not study the potential of combining several post-harvest treatments for a reinforced control of sprouting during storage. Some combinations between CIPC and

alternatives to CIPC post-harvest treatments to mitigate sprouting have already been studied (Cunnington 2019). However, to our knowledge, there is no study evaluating the efficacy of the combinations of all the alternative treatments studied in chapters 3 and 4 (i.e., mint and orange essential oils and ethylene, 1,4-DMN and 3-decen-2-one molecules). Therefore, it would be of interest to test the efficacy of different combinations to mitigate sprouting. For instance, as the 3-decen-2-one has a strong curative effect (chapter 3), it would be of interest to test combinations with the 1,4-DMN molecule which acts by prolonging potato dormancy (Jina Personal Communication) with a treatment with 3-decen-2-one when the dormancy breaks and the sprouts appear. It would be necessary to further study these strategies of combinations to evaluate their relevance and economical added value.

3.4. Perform an economical analysis of costs associated with sprout control and potato losses during storage

In the discussion of this thesis, we briefly compare the costs associated with the use of pre- and post-harvest anti-sprouting treatments to the cost of use of CIPC. However, we only present the price based on a study of Martin (2020b) and other personal communications and we did not evaluate the cost associated with potato losses during storage. It would be of interest to perform an in-depth analysis about the economical benefit of using pre- and post- harvest treatments alone or in combination and to study the economic losses due to sprouting during storage in treated or untreated tubers.

A study could also be performed to provide farmers with a guideline to follow according to the sprouting pressure (e.g., compare high vs. low sprouting pressure), with different solutions to mitigate sprouting throughout the storage (e.g., treatments or cold storage) and associated costs due to anti-sprouting treatments used for each sprouting pressure.

3.5. Perform studies on CIS-resistance for better use of cold storage

We identified three CIS-resistant processing varieties that allow for the use of cold storage without the risk of sweetening or production of toxic compounds during frying (i.e., Verdi, Lady Claire and Kiebitz). In the literature, only a few other varieties were identified as CIS-resistant. The choice in CIS-resistant varieties is not great enough to extensively use cold storage for sprout control while also considering market and agricultural requirements. Consequently, further screening to find additional CIS-resistant varieties should be performed. In addition, it is of interest to study the effect of the environment during the growing season on RS content in tubers of these CIS-resistant varieties during storage. Ezekiel et al. (2008) reported that the growing location can influence RS content during storage. These differences are probably due to the differences in growing season environment, since the temperature during the growing season, the mineral nutrition, and the maturity have been reported to

influence sugar content during storage (Kumar et al. 2004). The impact of environmental conditions during the growing season on sugar content and conversion during storage should be studied further. Finally, in order to improve the use of cold storage to control sprouting while simultaneously avoiding sweetening, the reconditioning should be evaluated for a larger range of varieties as studies reported that the potential of reconditioning is genotype-dependent (Kyriacou et al. 2009).

One potential experimental design to address the above-mentioned knowledge gaps is to use a large panel of potato varieties that are popular across Europe (several hundred varieties). These varieties would then be stored at three different temperature regimes (as in chapter 5): low temperature (i.e., 4 °C), conventional temperature (i.e., 8 °C) and at 4 °C with a reconditioning at 15 °C. Several parameters including starch, reducing sugar content, sucrose content, acrylamide, and invertase genes or invertase inhibitors could be measured to fully assess the effect of the three temperature regimes on sugar metabolism and identify a large range of CIS-resistant varieties. To capture the gene and sugar dynamics for the three storage temperature regimes, measurements should ideally be performed at the beginning of the storage, and after one, two, three, four and five months of storage. The experiment should be repeated over at least three years. Finally, to investigate the effect of the environment during the growing season on the sugar content in tubers during storage, the above-mentioned proposed experiment could be done at different contrasting locations that display differences in temperatures during the growing season.

In addition, potato-breeding programs should prioritize the introduction of CIS resistance in potato varieties with long dormancy to increase the choice in varieties with good processing quality and reduced sprouting. Introducing these characteristics in potato-breeding programs would probably take time and bring some difficulties as other characteristics such as resistance to diseases or yield should be considered as well. In addition, as mentioned in chapter 1, the dormancy characterization is heteregenous depending on the source and it would be necessary to find standard methods to assess the dormancy of potato varieties.

Genetic tools could be used as well to improve potato varieties. The use of conventional genetic tools (i.e., GMOs) could help improve the CIS-ability of potatoes, thereby allowing storage at cold temperature to control sprouting in potatoes varieties with short dormancies. However, the introduction of GMOs in EU is a relatively long process and other tools can be used. For instance, the epigenetic tools such as CRISPR/Cas9 breeding technology could be used to introduce new CIS-resistant varieties to the EU market (Shumbe et al. 2020). It is of interest to perform studies to better understand sugar metabolism in potatoes and to fill knowledge gaps in this area.

3.6. Potential of the predictive model of dormancy

The model is a predictive tool that could be used worldwide to predict dormancy of a large range of varieties and under contrasting environmental conditions. This predictive model could be developed into a smartphone or web application aimed at helping farmers make management decisions for improving potato storage management. As the model is built exclusively on data collected in Switzerland, it will be important to test and to adjust the model with data from other trials around the world in order to cover a wider range of environmental conditions. Among predictors of the growing season used to build the predictive model (Chapter 2), only "physical" predictors were tested (e.g., rainfall, date of main physiological stages, temperature or solar radiation) and it would be important to evaluate the effect of "chemical" predictors that may influence potato dormancy (e.g., nitrogen fertilization, soil composition or soil pH). In addition, as to build the predictive model, we used a forward selection approach using linear regressions; it would be of interest to use the same dataset and to build a model with a "machine learning" approach to consider the non-linear effects and to attempt to improve the predictive model.

Furthermore, the predictive model is based on dormancy data from storage at 8 °C and should be adapted to predict the duration of dormancy for a given variety stored at 4 °C. This would allow the model to be used to predict the sprouting date during storage at low temperatures and would further improve the management strategy for potato storage. For example, predicting the sprouting date during storage at 4 °C will allow producers to plan to sell potato stocks that will sprout first and keep potato stocks that will sprout later. To adapt the model for a prediction during storage at 4 °C, it is necessary to collect a large amount of dormancy data from potatoes stored at 4 °C and to adjust the equation of the model using those data. Then, a new validation of the model should be performed.

This data could come from variety testing trials worldwide, or trials could be performed to obtain dormancy data from potatoes stored at 4 °C. Trials should be performed under controlled conditions. At least six commonly used varieties with contrasting duration of dormancy should be selected. The selection should include varieties used to create the initial predictive model. A selection could be: a variety with a short dormancy (e.g., Amandine), a variety with a medium dormancy (e.g., Innovator) and a variety with a long dormancy (e.g., Agria). The three varieties could be obtained from potato growers in Switzerland at different locations. It would be better to choose locations with weather stations close by to obtain the temperature parameters during the growing season, which are necessary for prediction. The potatoes would then be stored at Agroscope at both 4 °C and 8 °C under the same conditions used to generate data of the model (Chapter 2). Observations could be performed every week to identify the sprouting date for a given variety and a given location, stored at both 4 °C and 8 °C. The initial model should be used to predict the sprouting date of tubers stored at 8 °C based on the variety class and on the sum of maximum daily air temperature from planting to harvest predictors. The observed

sprouting date should be compared with the predicted sprouting date at 8 °C. Then, the equation may be adjusted using the sprouting date for tubers stored at 4 °C.

Finally, and based on the predicted sprouting date, the model can be used to optimize the application of alternative anti-sprouting molecules and delay the application of the first treatment. Since alternative molecules are more expensive than CIPC, this would result in reduced costs associated with treatments. Further experiments in collaboration with companies that provide alternative molecules may be beneficial in order to evaluate the efficacy of the predictive model (chapter 2) and adjust the application of post-harvest treatments.

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Appendix

Table A-1. List of varieties used in our study and number of field trials for each variety over 25 years and five locations

Varieties	Number of field trials	Varieties	Number of field trials	Varieties	Number of field trials
Accent	3	Fiesta	3	Oriana	3
Action	3	Figaro	3	Osira	3
Agata	22	Filea	3	Ostara	15
Agave	3	Fioretta	3	Palma	3
Agila	9	Flavia	3	Pamela	12
Agnes	3	Fleur de mai	3	Pamir	3
Agria	96	Flora	3	Panda	24
Aida	3	Floréal	3	Parli	4
Albata	3	Florette	3	Pasha	3
Albatros	3	Folva	3	Passion	3
Alert	3	Fontane	23	Pepite	3
Alexandra	9	Forza	6	Pepo	9
Allians	3	Francine	4	Performer	3
Aloha	9	Fregate	3	Perline	3
Altesse	3	Fresco	3	Piccolo Star	6
Alwara	3	Freya	4	Pirol	16
Amadeus	3	Fribona	6	Platina	3
Amandine	20	Fridor	3	Pomfine	3
Amany	3	Futura	9	Pompadour	5
Ambassador	3	G01TT0114004	3	Pomqueen	3
Ambrine	3	G02TT165008	3	PR89-2097	3
Ampera	3	G89TT299_9	3	Preciosa	3

Andante	7	G95TD19009	3	Priamos	3
Angela	3	G97TD002006	3	Princess	3
Annabelle	16	G97TT013004	3	Prior	9
Anoe	3	G99TT028004	3	Privileg	3
Antina	9	Gabriella	6	Processor	6
Antoinet	3	Gala	9	Protea	4
Antonia	3	Galante	3	Puccini	3
Anuschka	3	Georgina	3	Punika	3
Apolline	3	Gervioline	3	PW99-013	3
Appell	11	GO93RS23	3	Quarta	3
AR8101	3	Goldstar	3	Raisa	3
AR91-492	3	Golf	9	Ratte	14
AR96-1120	3	Goliat	3	RDZ95-1859	3
AR96-560	3	Goulvéna	3	Red Baron	3
Arendenta	3	Gourmandine	17	Red Lady	3
Arielle	6	Gourmeta	3	Red Scarlett	3
Arietis	3	Granada	3	Red Star	6
Arosa	5	Grandeur	3	Regina	12
Artis	7	Granola	11	Rembrandt	3
Assia	3	Gredine	3	Ricarda	3
Asterix	9	Grot Arkadia	3	RJC24	3
Astoria	3	Gwenne	10	Robinata	3
Asva	3	Hamlet	3	Rodriga	3
Aula	7	Hegge85-807-1	3	Romanze	3
Aurelia	3	Heidi	3	Romie	3
Avondale	3	Helena	9	Roncalla	3

B00_244_51	3	Henrike	3	Rosa Gold	3
B99_603_513	3	Hermes	24	Rosella	10
Baby Boomer	3	Hertha	6	Royal	3
Bafana	3	Hommage	3	RS_RCH	3
Ballade	3	Huaycha	5	RS_RDP	3
Ballerina	3	Hz-03-1458	3	Rubinia	3
Ballys	3	Ibis	3	Rumba	9
Baril	3	Impale	4	RZ87-169	3
Bastion	3	Innovator	24	RZ90-316	3
Belana	7	Inova	3	RZD84-1028	3
Belladonna	3	Irga	3	Sagitta	3
Bellini	9	Iroise	17	Saline	3
Berber	9	Jade	3	Salome	9
Bernadette	3	Jaqueline	9	Samba	3
Bintje	166	Jazzy	3	Sandy	3
Biogold	9	Jelly	15	Santana	20
Biola	3	Jen86-5	3	SARA1240_09	3
Birgit	3	Jenny	3	SARA1278_06	3
Blaue Schweden	4	Juliane	3	Sara2674_83	3
Blaue St. Galler	5	Juliette	13	Sara95-145-2	3
Bleue d'Artois	3	Jutlandia	3	Sara97-364-3	3
Blondy	9	JWM94-2	3	SaraH2711_83	3
Blue Belle	3	Karin	3	Sarpo Mira	3
BM82-344	3	Karlena	10	Satina	3

Boe300_86_4300	3	Kiebitz	3	Satu	3
Boe320_A88	3	Kiwi	3	Saturna	14
Boe4120_13	3	Krone	3	Sempra	7
Boe546_89	3	Kuroda	3	Serafina	3
Bondeville	3	KWS06-547	3	Servane	3
Bonell	3	L3479_55	3	Signal	3
BP94K69_2	3	L348_94_401	3	Simone	3
Bridget	3	Lady Amarilla	3	Sinora	3
Brodick	3	Lady Lenora	3	Sirius	3
Caesar	3	Lady Amarilla	6	Sirtema	91
Calypso	3	Lady Anna	3	Sissi	3
Campina	3	Lady Christl	21	SL78-447	3
Canelle	3	Lady Claire	68	Sl87-27	3
Cantate	3	Lady Felicia	76	Sofia	3
Caprice	3	Lady Jo	15	Solide	9
Cardinia	3	Lady Olympia	9	Solist	3
Careca	3	Lady Rosetta	15	Sonate	3
Carmona	9	Laguna	3	Soraya	3
Carolus	3	Lanorma	3	Sprint	9
Carrera	3	Latona	3	St684_94	3
Caruso	9	Laura	14	ST89-57-106	3
CB84-11-15	3	LD88-1815	3	ST98-11-1	3
CB87012-072	3	Leonardo	3	Stefanie	3

CB88-7506	3	Leoni	9	Stella	30
Cécile	9	Leontine	3	Subito	3
Celtiane	13	Leyla	3	Sunbeam	9
Cerbella	6	Lido	10	Superstar	12
Cesar	10	Liliane	3	Sv82149	3
Challenger	12	Liva	3	Sv83115	3
Champion	3	Lolita	3	Sv83122	3
Charisma	3	Lucera	3	Sv88109	3
Charlotte	25	Lucie	3	Sv88113	3
Charmante	3	Luciole	3	SW89-1363	3
Chérie	9	Ludmilla	9	SW94134	3
Chipie	3	Lutetia	3	Symfonia	6
Chista	3	Madeline	3	Tal82-040-4	3
Christa	11	Madison	3	Talent	3
Clairette	3	Maestro	12	Tasso	3
Claret	3	Magda	3	Taurus	3
Clarina	3	Magnum	9	TerraGold	3
CMK1997-022-017	3	Malou	6	Tessa	3
CMK2002-055-010	3	Manuela	9	Tiara	3
CN89-3-2	3	Marabel	7	Timate	3
Colomba	3	Marella	9	Tivoli	3
Compass	3	Marena	6	Toluca	4
Concordia	3	Marilyn	9	Tomensa	9
Coquine	3	Marine	3	Toscana	3
Corolle	9	Mariska	3	Trabant	6
Corsa	3	Markies	26	Tresor	3
Courage	3	Marlen	12	Trias	9
Crebella	3	Marlene	3	Triplo	3
Crisper	3	Martina	3	Tristant	3
Crispy	3	Matilda	12	Triumpf	3
Cycloon	3	Melina	3	Troja	3
Cynthia	3	Melody	3	Ukama	6

D_HKK80-48-08	3	Mira	3	Umatilla_Russet	3
Daisy	9	Mirage	3	Uno	3
Dali	3	Miranda	9	UP2_302_1	3
Daniela	3	Miriam	12	UP2_320_3	3
Dario	3	Miss Bianca	3	UP2_328_180	3
Debora	3	Miss Malina	3	UP2_332_10	3
Delikat	3	Miss Mignonne	3	UP2_346_19	3
Derby	18	Mozart	9	UP4_406_8K	3
Desiree	25	Musica	9	Urgenta	20
Destiny	3	Mustang	9	v_d_W82-101	3
Diana	3	Nathalie	7	Valentine	3
Dione	3	Naturella	16	Valeria	3
Disco	3	Nazca	3	Van Gogh	9
Ditta	26	Nena	3	Vdz01-413	3
Dobra	3	Nicola	25	Vdz03-139	3
Dolly	9	Nika	3	Velox	9
Donald	3	Nikita	9	Venezia	9
Dorado	5	Niska	3	Vento	3
Doremi	3	Noe1025_84	3	Verdi	10
Doris	3	Noe1176_94	3	Verona	9
Drop	3	Noe1209_02	3	Victoria	23
Dukata	3	Noe129_84	3	Vitabella	3
E82_280	3	Noe14_92	3	Vitesse	3
E88_8	3	Noe1944_02	3	Vivaldi	3

E94_83_10	3	Noe2077_91	3	Vivi	3
E96_423	3	Noe2178_85	3	VR808	6
E98_226_189	3	Noe2226-95	3	VR84-149	3
E99-318-644	3	Noe2335_85	3	VR86-44	3
Eba	94	Noe2415_89	3	VR90-44	3
Edelstein	3	NOE2672_95	3	VR90-52	3
Eden	12	Noe2782_97	3	VR90-61	3
Eldena	7	Noe2828_91	3	VR90-708	3
Electra	3	Noe3060_93	3	VR92-17	3
Elfe	3	Noe3063_99	3	VR92-216	3
Ellie	3	Noe31_88	3	VR92-465	3
Erika	10	Noe3266_97	3	VR94-268	3
Erntestolz	114	Noe3356_93	3	VR98-72	3
Esmeralda	3	Noe3793_05	3	VR98-808	3
Estrella	3	Noe447_02	3	Wal82-161	3
Eurobeta	6	Noe722_94	3	Wal84-43	3
Europa	3	Noe775_96	3	White Lady	3
Eurostar	3	NOE961_94	3	WJ88-2002	3
Excellent	7	Noe963-96	3	YP85-100	3
Expova	3	Noe989_84	3	YP85-115	3

Exquisa	12	Nora	9	YP89-070	3
F8123	3	Novara	3	YP91-123	3
Falko	3	Novella	3	YP94-067	3
Fanchette	3	Novita	3	YP99-016	3
Farmer	9	Omega	3	YP99-044	3
Felicitas	3	Opal	9	Yvonne	3
Felsina	4	Opaline	3	Zalta	3
Fianna	6	Operle	3	Zorba	9

Table A-2. List of the predictors used in our study and number of records for each variable

247 predictors	Total number of records for each predictor	Number of records used in the calibration set	Number of records used in the validation set	Completeness of the calibration set (%)
Planting date	3'379	2'277	1'102	100.0
Variety class	3'379	2'277	1'102	100.0
Harvest date	3'365	2'267	1'098	99.6
Period from planting to harvest	3'365	2'267	1'098	99.6
Sum of the daily maximum temperatures in the air for the period from planting to harvest	3'224	2'176	1'048	95.6
Sum of the daily minimum temperatures in the air for the period from planting to harvest	3'224	2'176	1'048	95.6
Average of the daily maximum temperatures in the air for the period from planting to harvest	3'224	2'176	1'048	95.6
Average of the daily minimum temperatures in the air for the period from planting to harvest	3'224	2'176	1'048	95.6
Sum of the daily average temperatures in the air for the period from planting to harvest	3'212	2'168	1'044	95.2
Average of the daily average temperatures in the air for the period from planting to harvest	3'212	2'168	1'044	95.2
Average of the daily average relative humidity data for the period from planting to harvest	3'208	2'162	1'046	94.9
Haulm killing date	3'163	2'133	1'030	93.7
Period from planting to haulm killing	3'163	2'133	1'030	93.7
Period from haulm killing to harvest	3'149	2'123	1'026	93.2
Average of the daily maximum temperatures in the air for the period from haulm killing to harvest	3'122	2'106	1'016	92.5
Average of the daily average relative humidity data for the period from haulm killing to harvest	3'122	2'106	1'016	92.5

Sum of the daily maximum temperatures in the air for the period from haulm killing to harvest	3'122	2'106	1'016	92.5
Sum of the daily minimum temperatures in the air for the period from haulm killing to harvest	3'122	2'106	1'016	92.5
Sum of the daily average temperatures in the air for the period from haulm killing to harvest	3'122	2'106	1'016	92.5
Average of the daily minimum temperatures in the air for the period from haulm killing to harvest	3'122	2'106	1'016	92.5
Average of the daily average temperatures in the air for the period from haulm killing to harvest	3'122	2'106	1'016	92.5
Average of the daily minimum temperatures in the air for the period from planting to haulm killing	3'113	2'102	1'011	92.3
Average of the daily maximum temperatures in the air for the period from planting to haulm killing	3'113	2'102	1'011	92.3
Sum of the daily minimum temperatures in the air for the period from planting to haulm killing	3'113	2'102	1'011	92.3
Sum of the daily maximum temperatures in the air for the period from planting to haulm killing	3'113	2'102	1'011	92.3
Sum of the daily average temperatures in the air for the period from planting to haulm killing	3'101	2'094	1'007	92.0
Average of the daily average temperatures in the air for the period from planting to haulm killing	3'101	2'094	1'007	92.0
Average of the daily average relative humidity data for the period from planting to haulm killing	3'097	2'088	1'009	91.7
Average of the daily average temperatures at the level of soil for the period from planting to harvest	2'905	1'960	945	86.1
Sum of the daily average temperatures at the level of soil for the period from planting to harvest	2'905	1'960	945	86.1
Average of the daily average insolation data for the period from planting to harvest	2'899	1'951	948	85.7
Average of the daily precipitation data for the period from planting to harvest	2'896	1'949	947	85.6

Sum of the daily precipitations for the period from planting to harvest	2'896	1'949	947	85.6
Average of the daily average temperatures at the level of soil for the period from haulm killing to harvest	2'862	1'932	930	84.8
Sum of the daily average temperatures at the level of soil for the period from haulm killing to harvest	2'862	1'932	930	84.8
Average of the daily precipitation data for the period from planting to haulm killing	2'860	1'930	930	84.8
Average of the daily average insolation data for the period from planting to haulm killing	2'860	1'930	930	84.8
Sum of the daily precipitations for the period from planting to haulm killing	2'860	1'930	930	84.8
Average of the daily precipitation data for the period from haulm killing to harvest	2'857	1'926	931	84.6
Sum of the daily precipitations for the period from haulm killing to harvest	2'857	1'926	931	84.6
Average of the daily average temperatures at the level of soil for the period from planting to haulm killing	2'841	1'921	920	84.4
Sum of the daily average temperatures at the level of soil for the period from planting to haulm killing	2'841	1'921	920	84.4
Average of the daily average insolation data for the period from haulm killing to harvest	2'844	1'916	928	84.1
Average of the daily maximum precipitation intensity data for the period from planting to harvest	2'837	1'912	925	84.0
Average of the daily maximum precipitation intensity data for the period from planting to haulm killing	2'823	1'908	915	83.8
Average of the daily maximum precipitation intensity data for the period from haulm killing to harvest	2'827	1'904	923	83.6
Average of the daily average soil temperatures at a depth of 10 cm for the period from planting to harvest	2'753	1'858	895	81.6
Sum of the daily average soil temperatures at a depth of 10 cm for the period from planting to harvest	2'753	1'858	895	81.6
Period from planting to tuber initiation	2'723	1'839	884	80.8

Tuber initiation date	2'723	1'839	884	80.8
Average of the daily average soil temperatures at a depth of 10 cm for the period from haulm killing to harvest	2'707	1'834	873	80.5
Sum of the daily average soil temperatures at a depth of 10 cm for the period from haulm killing to harvest	2'707	1'834	873	80.5
Period from tuber initiation to harvest	2'709	1'829	880	80.3
Period from planting to emergence	2'693	1'821	872	80.0
Period from emergence to harvest	2'693	1'821	872	80.0
Emergence date	2'693	1'821	872	80.0
Period from emergence to tuber initiation	2'693	1'821	872	80.0
Average of the daily average soil temperatures at a depth of 10 cm for the period from planting to haulm killing	2'689	1'819	870	79.9
Sum of the daily average soil temperatures at a depth of 10 cm for the period from planting to haulm killing	2'689	1'819	870	79.9
Sum of the daily minimum temperatures in the air for the period from planting to tuber initiation	2'624	1'771	853	77.8
Average of the daily average relative humidity data for the period from planting to tuber initiation	2'624	1'771	853	77.8
Sum of the daily maximum temperatures in the air for the period from planting to tuber initiation	2'624	1'771	853	77.8
Sum of the daily average temperatures in the air for the period from planting to tuber initiation	2'624	1'771	853	77.8
Average of the daily maximum temperatures in the air for the period from planting to tuber initiation	2'624	1'771	853	77.8
Average of the daily minimum temperatures in the air for the period from planting to tuber initiation	2'624	1'771	853	77.8
Average of the daily average temperatures in the air for the period from planting to tuber initiation	2'624	1'771	853	77.8
Average of the daily average relative humidity data for the period from planting to emergence	2'619	1'769	850	77.7
Sum of the daily maximum temperatures in the air for the period from planting to emergence	2'619	1'769	850	77.7

Sum of the daily minimum temperatures in the air for the period from planting to emergence	2'619	1'769	850	77.7
Sum of the daily average temperatures in the air for the period from planting to emergence	2'619	1'769	850	77.7
Average of the daily maximum temperatures in the air for the period from planting to emergence	2'619	1'769	850	77.7
Average of the daily minimum temperatures in the air for the period from planting to emergence	2'619	1'769	850	77.7
Average of the daily average temperatures in the air for the period from planting to emergence	2'619	1'769	850	77.7
Sum of the daily maximum temperatures in the air for the period from tuber initiation to harvest	2'593	1'754	839	77.0
Sum of the daily minimum temperatures in the air for the period from tuber initiation to harvest	2'593	1'754	839	77.0
Average of the daily maximum temperatures in the air for the period from tuber initiation to harvest	2'593	1'754	839	77.0
Average of the daily minimum temperatures in the air for the period from tuber initiation to harvest	2'593	1'754	839	77.0
Average of the daily average relative humidity data for the period from emergence to tuber initiation	2'594	1'753	841	77.0
Sum of the daily maximum temperatures in the air for the period from emergence to tuber initiation	2'594	1'753	841	77.0
Sum of the daily minimum temperatures in the air for the period from emergence to tuber initiation	2'594	1'753	841	77.0
Sum of the daily average temperatures in the air for the period from emergence to tuber initiation	2'594	1'753	841	77.0
Average of the daily maximum temperatures in the air for the period from emergence to tuber initiation	2'594	1'753	841	77.0
Average of the daily minimum temperatures in the air for the period from emergence to tuber initiation	2'594	1'753	841	77.0
Average of the daily average temperatures in the air for the period from emergence to tuber initiation	2'594	1'753	841	77.0

Sum of the daily average temperatures in the air for the period from tuber initiation to harvest	2'581	1'746	835	76.7
Average of the daily average temperatures in the air for the period from tuber initiation to harvest	2'581	1'746	835	76.7
Average of the daily average relative humidity data for the period from tuber initiation to harvest	2'577	1'740	837	76.4
Average of the daily minimum temperatures in the air for the period from emergence to harvest	2'552	1'730	822	76.0
Average of the daily maximum temperatures in the air for the period from emergence to harvest	2'552	1'730	822	76.0
Sum of the daily minimum temperatures in the air for the period from emergence to harvest	2'552	1'730	822	76.0
Sum of the daily maximum temperatures in the air for the period from emergence to harvest	2'552	1'730	822	76.0
Sum of the daily average temperatures in the air for the period from emergence to harvest	2'540	1'722	818	75.6
Average of the daily average temperatures in the air for the period from emergence to harvest	2'540	1'722	818	75.6
Average of the daily average relative humidity data for the period from emergence to harvest	2'536	1'716	820	75.4
Period from tuber initiation to haulm killing	2'507	1'695	812	74.4
Period from emergence to haulm killing	2'477	1'677	800	73.6
Average of the daily minimum temperatures in the air for the period from tuber initiation to haulm killing	2'457	1'664	793	73.1
Average of the daily maximum temperatures in the air for the period from tuber initiation to haulm killing	2'457	1'664	793	73.1
Sum of the daily minimum temperatures in the air for the period from tuber initiation to haulm killing	2'457	1'664	793	73.1
Sum of the daily maximum temperatures in the air for the period from tuber initiation to haulm killing	2'457	1'664	793	73.1

Sum of the daily average temperatures in the air for the period from tuber initiation to haulm killing	2'445	1'656	789	72.7
Average of the daily average temperatures in the air for the period from tuber initiation to haulm killing	2'445	1'656	789	72.7
Average of the daily average relative humidity data for the period from tuber initiation to haulm killing	2'441	1'650	791	72.5
Average of the daily minimum temperatures in the air for the period from emergence to haulm killing	2'427	1'646	781	72.3
Average of the daily maximum temperatures in the air for the period from emergence to haulm killing	2'427	1'646	781	72.3
Sum of the daily minimum temperatures in the air for the period from emergence to haulm killing	2'427	1'646	781	72.3
Sum of the daily maximum temperatures in the air for the period from emergence to haulm killing	2'427	1'646	781	72.3
Sum of the daily average temperatures in the air for the period from emergence to haulm killing	2'415	1'638	777	71.9
Average of the daily average temperatures in the air for the period from emergence to haulm killing	2'415	1'638	777	71.9
Average of the daily average relative humidity data for the period from emergence to haulm killing	2'411	1'632	779	71.7
Average of the daily precipitation data for the period from planting to tuber initiation	2'355	1'588	767	69.7
Average of the daily average insolation data for the period from planting to tuber initiation	2'355	1'588	767	69.7
Sum of the daily precipitations for the period from planting to tuber initiation	2'355	1'588	767	69.7
Average of the daily precipitation data for the period from planting to emergence	2'350	1'586	764	69.7
Average of the daily maximum precipitation intensity data for the period from planting to emergence	2'350	1'586	764	69.7
Average of the daily average insolation data for the period from planting to emergence	2'350	1'586	764	69.7

Sum of the daily precipitations for the period from planting to emergence	2'350	1'586	764	69.7
Average of the daily average temperatures at the level of soil for the period from planting to tuber initiation	2'336	1'579	757	69.3
Sum of the daily average temperatures at the level of soil for the period from planting to tuber initiation	2'336	1'579	757	69.3
Average of the daily average temperatures at the level of soil for the period from planting to emergence	2'331	1'577	754	69.3
Sum of the daily average temperatures at the level of soil for the period from planting to emergence	2'331	1'577	754	69.3
Average of the daily maximum precipitation intensity data for the period from planting to tuber initiation	2'333	1'573	760	69.1
Average of the daily average temperatures at the level of soil for the period from tuber initiation to harvest	2'324	1'571	753	69.0
Sum of the daily average temperatures at the level of soil for the period from tuber initiation to harvest	2'324	1'571	753	69.0
Average of the daily average temperatures at the level of soil for the period from emergence to tuber initiation	2'325	1'570	755	69.0
Average of the daily precipitation data for the period from emergence to tuber initiation	2'325	1'570	755	69.0
Average of the daily average insolation data for the period from emergence to tuber initiation	2'325	1'570	755	69.0
Sum of the daily average temperatures at the level of soil for the period from emergence to tuber initiation	2'325	1'570	755	69.0
Sum of the daily precipitations for the period from emergence to tuber initiation	2'325	1'570	755	69.0
Average of the daily maximum precipitation intensity data for the period from emergence to tuber initiation	2'303	1'555	748	68.3
Average of the daily average insolation data for the period from tuber initiation to harvest	2'299	1'553	746	68.2
Average of the daily precipitation data for the period from tuber initiation to harvest	2'296	1'551	745	68.1

Sum of the daily precipitations for the period from tuber initiation to harvest	2'296	1'551	745	68.1
Average of the daily average temperatures at the level of soil for the period from emergence to harvest	2'283	1'547	736	67.9
Sum of the daily average temperatures at the level of soil for the period from emergence to harvest	2'283	1'547	736	67.9
Average of the daily maximum precipitation intensity data for the period from tuber initiation to harvest	2'273	1'539	734	67.6
Average of the daily average insolation data for the period from emergence to harvest	2'258	1'529	729	67.1
Average of the daily precipitation data for the period from emergence to harvest	2'255	1'527	728	67.1
Sum of the daily precipitations for the period from emergence to harvest	2'255	1'527	728	67.1
Average of the daily average temperatures at the level of soil for the period from tuber initiation to haulm killing	2'235	1'516	719	66.6
Average of the daily precipitation data for the period from tuber initiation to haulm killing	2'235	1'516	719	66.6
Average of the daily average insolation data for the period from tuber initiation to haulm killing	2'235	1'516	719	66.6
Sum of the daily average temperatures at the level of soil for the period from tuber initiation to haulm killing	2'235	1'516	719	66.6
Sum of the daily precipitations for the period from tuber initiation to haulm killing	2'235	1'516	719	66.6
Average of the daily maximum precipitation intensity data for the period from tuber initiation to haulm killing	2'212	1'504	708	66.1
Average of the daily maximum precipitation intensity data for the period from emergence to harvest	2'210	1'500	710	65.9
Average of the daily precipitation data for the period from emergence to haulm killing	2'205	1'498	707	65.8
Average of the daily average temperatures at the level of soil for the period from emergence to haulm killing	2'205	1'498	707	65.8

Average of the daily average insolation data for the period from emergence to haulm killing	2'205	1'498	707	65.8
Sum of the daily average temperatures at the level of soil for the period from emergence to haulm killing	2'205	1'498	707	65.8
Sum of the daily precipitations for the period from emergence to haulm killing	2'205	1'498	707	65.8
Average of the daily average soil temperatures at a depth of 10 cm for the period from planting to tuber initiation	2'213	1'494	719	65.6
Sum of the daily average soil temperatures at a depth of 10 cm for the period from planting to tuber initiation	2'213	1'494	719	65.6
Average of the daily average soil temperatures at a depth of 10 cm for the period from planting to emergence	2'199	1'489	710	65.4
Sum of the daily average soil temperatures at a depth of 10 cm for the period from planting to emergence	2'199	1'489	710	65.4
Average of the daily maximum precipitation intensity data for the period from emergence to haulm killing	2'182	1'486	696	65.3
Average of the daily average soil temperatures at a depth of 10 cm for the period from emergence to tuber initiation	2'183	1'476	707	64.8
Sum of the daily average soil temperatures at a depth of 10 cm for the period from emergence to tuber initiation	2'183	1'476	707	64.8
Average of the daily average soil temperatures at a depth of 10 cm for the period from tuber initiation to harvest	2'176	1'470	706	64.6
Sum of the daily average soil temperatures at a depth of 10 cm for the period from tuber initiation to harvest	2'176	1'470	706	64.6
Average of the daily average soil temperatures at a depth of 10 cm for the period from emergence to harvest	2'160	1'462	698	64.2
Sum of the daily average soil temperatures at a depth of 10 cm for the period from emergence to harvest	2'160	1'462	698	64.2
Average of the daily average soil temperatures at a depth of 10 cm for the period from tuber initiation to haulm killing	2'112	1'431	681	62.8
Sum of the daily average soil temperatures at a depth of 10 cm for the	2'112	1'431	681	62.8

period from tuber initiation to haulm killing				
Average of the daily average soil temperatures at a depth of 10 cm for the period from emergence to haulm killing	2'082	1'413	669	62.1
Sum of the daily average soil temperatures at a depth of 10 cm for the period from emergence to haulm killing	2'082	1'413	669	62.1
Maturity date	2'035	1'373	662	60.3
Period from planting to maturity	2'035	1'373	662	60.3
Period from maturity to harvest	2'022	1'364	658	59.9
Average of the daily average relative humidity data for the period from maturity to harvest	1'963	1'328	635	58.3
Sum of the daily maximum temperatures in the air for the period from maturity to harvest	1'963	1'328	635	58.3
Sum of the daily minimum temperatures in the air for the period from maturity to harvest	1'963	1'328	635	58.3
Sum of the daily average temperatures in the air for the period from maturity to harvest	1'963	1'328	635	58.3
Average of the daily maximum temperatures in the air for the period from maturity to harvest	1'963	1'328	635	58.3
Average of the daily minimum temperatures in the air for the period from maturity to harvest	1'963	1'328	635	58.3
Average of the daily average temperatures in the air for the period from maturity to harvest	1'963	1'328	635	58.3
Average of the daily minimum temperatures in the air for the period from planting to maturity	1'965	1'327	638	58.3
Average of the daily maximum temperatures in the air for the period from planting to maturity	1'965	1'327	638	58.3
Sum of the daily minimum temperatures in the air for the period from planting to maturity	1'965	1'327	638	58.3
Sum of the daily maximum temperatures in the air for the period from planting to maturity	1'965	1'327	638	58.3

Sum of the daily average temperatures in the air for the period from planting to maturity	1'956	1'321	635	58.0
Average of the daily average temperatures in the air for the period from planting to maturity	1'956	1'321	635	58.0
Average of the daily average relative humidity data for the period from planting to maturity	1'953	1'316	637	57.8
Period from maturity to haulm killing	1'911	1'287	624	56.5
Average of the daily average relative humidity data for the period from maturity to haulm killing	1'889	1'274	615	56.0
Sum of the daily maximum temperatures in the air for the period from maturity to haulm killing	1'889	1'274	615	56.0
Sum of the daily minimum temperatures in the air for the period from maturity to haulm killing	1'889	1'274	615	56.0
Sum of the daily average temperatures in the air for the period from maturity to haulm killing	1'889	1'274	615	56.0
Average of the daily maximum temperatures in the air for the period from maturity to haulm killing	1'889	1'274	615	56.0
Average of the daily minimum temperatures in the air for the period from maturity to haulm killing	1'889	1'274	615	56.0
Average of the daily average temperatures in the air for the period from maturity to haulm killing	1'889	1'274	615	56.0
Period from tuber initiation to maturity	1'853	1'254	599	55.1
Period from emergence to maturity	1'827	1'238	589	54.4
Average of the daily minimum temperatures in the air for the period from tuber initiation to maturity	1'783	1'208	575	53.1
Sum of the daily maximum temperatures in the air for the period from tuber initiation to maturity	1'783	1'208	575	53.1
Sum of the daily minimum temperatures in the air for the period from tuber initiation to maturity	1'783	1'208	575	53.1
Average of the daily maximum temperatures in the air for the period from tuber initiation to maturity	1'783	1'208	575	53.1

Sum of the daily average temperatures in the air for the period from tuber initiation to maturity	1'774	1'202	572	52.8
Average of the daily average temperatures in the air for the period from tuber initiation to maturity	1'774	1'202	572	52.8
Average of the daily precipitation data for the period from planting to maturity	1'783	1'200	583	52.7
Average of the daily average insolation data for the period from planting to maturity	1'783	1'200	583	52.7
Sum of the daily precipitations for the period from planting to maturity	1'783	1'200	583	52.7
Average of the daily average temperatures at the level of soil for the period from maturity to harvest	1'781	1'199	582	52.7
Sum of the daily average temperatures at the level of soil for the period from maturity to harvest	1'781	1'199	582	52.7
Average of the daily average relative humidity data for the period from tuber initiation to maturity	1'771	1'197	574	52.6
Average of the daily average temperatures at the level of soil for the period from planting to maturity	1'769	1'194	575	52.4
Sum of the daily average temperatures at the level of soil for the period from planting to maturity	1'769	1'194	575	52.4
Sum of the daily maximum temperatures in the air for the period from emergence to maturity	1'757	1'192	565	52.3
Sum of the daily minimum temperatures in the air for the period from emergence to maturity	1'757	1'192	565	52.3
Average of the daily maximum temperatures in the air for the period from emergence to maturity	1'757	1'192	565	52.3
Average of the daily minimum temperatures in the air for the period from emergence to maturity	1'757	1'192	565	52.3
Sum of the daily average temperatures in the air for the period from emergence to maturity	1'748	1'186	562	52.1
Average of the daily average temperatures in the air for the period from emergence to maturity	1'748	1'186	562	52.1

Average of the daily average relative humidity data for the period from emergence to maturity	1'745	1'181	564	51.9
Average of the daily precipitation data for the period from maturity to harvest	1'753	1'179	574	51.8
Average of the daily average insolation data for the period from maturity to harvest	1'755	1'179	576	51.8
Sum of the daily precipitations for the period from maturity to harvest	1'753	1'179	574	51.8
Average of the daily maximum precipitation intensity data for the period from planting to maturity	1'750	1'178	572	51.7
Average of the daily average temperatures at the level of soil for the period from maturity to haulm killing	1'738	1'172	566	51.5
Average of the daily precipitation data for the period from maturity to haulm killing	1'738	1'172	566	51.5
Sum of the daily average temperatures at the level of soil for the period from maturity to haulm killing	1'738	1'172	566	51.5
Sum of the daily precipitations for the period from maturity to haulm killing	1'738	1'172	566	51.5
Average of the daily average insolation data for the period from maturity to haulm killing	1'727	1'164	563	51.1
Average of the daily maximum precipitation intensity data for the period from maturity to harvest	1'732	1'163	569	51.1
Average of the daily maximum precipitation intensity data for the period from maturity to haulm killing	1'717	1'156	561	50.8
Average of the daily average soil temperatures at a depth of 10 cm for the period from maturity to harvest	1'658	1'120	538	49.2
Sum of the daily average soil temperatures at a depth of 10 cm for the period from maturity to harvest	1'658	1'120	538	49.2
Average of the daily average soil temperatures at a depth of 10 cm for the period from planting to maturity	1'648	1'110	538	48.7
Sum of the daily average soil temperatures at a depth of 10 cm for the period from planting to maturity	1'648	1'110	538	48.7

Average of the daily average soil temperatures at a depth of 10 cm for the period from maturity to haulm killing	1'615	1'093	522	48.0
Sum of the daily average soil temperatures at a depth of 10 cm for the period from maturity to haulm killing	1'615	1'093	522	48.0
Sum of the daily average temperatures at the level of soil for the period from tuber initiation to maturity	1'612	1'089	523	47.8
Average of the daily average temperatures at the level of soil for the period from tuber initiation to maturity	1'612	1'089	523	47.8
Average of the daily precipitation data for the period from tuber initiation to maturity	1'612	1'089	523	47.8
Average of the daily average insolation data for the period from tuber initiation to maturity	1'612	1'089	523	47.8
Sum of the daily precipitations for the period from tuber initiation to maturity	1'612	1'089	523	47.8
Average of the daily maximum precipitation intensity data for the period from tuber initiation to maturity	1'603	1'084	519	47.6
Average of the daily average temperatures at the level of soil for the period from emergence to maturity	1'586	1'073	513	47.1
Average of the daily average insolation data for the period from emergence to maturity	1'586	1'073	513	47.1
Average of the daily precipitation data for the period from emergence to maturity	1'586	1'073	513	47.1
Sum of the daily average temperatures at the level of soil for the period from emergence to maturity	1'586	1'073	513	47.1
Sum of the daily precipitations for the period from emergence to maturity	1'586	1'073	513	47.1
Average of the daily maximum precipitation intensity data for the period from emergence to maturity	1'563	1'059	504	46.5
Average of the daily average soil temperatures at a depth of 10 cm for the period from tuber initiation to maturity	1'517	1'021	496	44.8
Sum of the daily average soil temperatures at a depth of 10 cm for the period from tuber initiation to maturity	1'517	1'021	496	44.8

Average of the daily average soil temperatures at a depth of 10 cm for the period from emergence to maturity	1'491	1'005	486	44.1
Sum of the daily average soil temperatures at a depth of 10 cm for the period from emergence to maturity	1'491	1'005	486	44.1

Table A-3. Extract of the color scale for quality evaluation of crisps (Swisspatat scale, Edition 2013, Swiss Potato Comission CH-3186 Düdigen, retrieved from: https://www.patate.ch/)