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# Potato Greening

## A Literature Review

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# Foreword

The author would like to express his gratitude for the feedback, guidance and support provided by Wieneke van der Heide, Bram Knegt, Piet Haak, Ivana Imerovski, Jeroen Bakker and the other members of the graduation circle: Iris, Laura and Roy. This thesis would not have been possible without their help.

Due to the feedback provided by Bram Knegt, that the wording of the second and third sub-question implied that the author was able to predict future problems and the future developments of technology, the choice was made to slight alter the wording of these sub-questions to more accurately reflect the focus on current problems which might exacerbate the issues around greening and glycoalkaloid accumulation, and currently available technology which, while promising, is not widely used or available yet.

# Abstract

The potato is one of the most important staple crops for human consumption. However around 40 - 50% of the annual global potato production is thrown away. Two major causes of quality loss and the rejection of many potato tubers, by both the consumer and the processing industry, are greening and glycoalkaloid accumulation. Greening and glycoalkaloid accumulation are both caused by light exposure, but are regulated through two independent biological pathways.
This literature review shows growers and breeders what they can do to reduce greening and glycoalkaloid accumulation, the effect of climate change, promising technologies and available plant genetic resources.
Choosing less susceptible cultivars and reducing light exposure in the field, during harvesting and while the tubers are in storage is key for reducing greening and glycoalkaloid accumulation. Avoiding mechanical injury and excess nitrogen fertilization further reduces glycoalkaloid concentrations. Storing the tubers at temperatures below 5 °C and under low oxygen, elevated carbon dioxide conditions, has a positive impact on greening and glycoalkaloids.
Anthropogenic climate change will lead to more heat stress in potatoes, increasing glycoalkaloid content, while reducing greening. Precipitation will also increase due to climate change, leading to more soil erosion. Growers will need to adapt their irrigation strategies and use small dams between ridges, to retain water and reduce erosion.
Genome editing technology will be able to reduce SGA levels by regulating SGT genes, GAME genes, the SSR2 gene and the St16DOX gene. Precision agriculture tools, such as drones and AI, enable growers to more efficiently use irrigation and fertilization, leading to lower greening and glycoalkaloid levels. Breeders will be able to use these tools to create phenotyping datasets to optimize their breeding programs.
The potato reference genome, potato accessions in multiple gene banks and the information acquired through genome editing technology, are powerful tools for breeders. These tools can be used by breeders to breed commercial varieties with lower SGA contents and reduced greening.
This review also shows what is still unknown about greening and glycoalkaloid accumulation and recommends subjects which require further research.

# Samenvatting

De aardappel is één van de belangrijkste gewassen voor menselijke consumptie. Ieder jaar wordt echter 40-50% van de wereldwijde aardappel productie weggegooid. Twee belangrijke oorzaken van kwaliteitsverlies in aardappelknollen en hun uiteindelijke afwijzing, door zowel de consument als de aardappel verwerking industrie, zijn vergroening en glycoalkaloïde ophoping. Vergroening en glycoalkaloïde ophoping worden beide veroorzaakt door blootstelling aan licht, maar worden gereguleerd via twee verschillende biologische reactiepaden.
Dit literatuur onderzoek beschrijft hoe kwekers en veredelaars vergroening en glycoalkaloïde ophoping kunnen tegengaan, wat de effecten van klimaat verandering zijn, veelbelovende technologieën en beschikbare plant genetische bronnen.
Het kiezen van minder gevoelige rassen en het verminderen van blootstelling aan licht in het veld, tijdens het oogsten en in de opslagloods is essentieel om vergroening en glycoalkaloïde ophoping te verminderen. Het voorkomen van machinale schade en overmatige stikstof bemesting verlaagd de glycoalkaloïde concentratie nog verder. Het bewaren van de knollen bij temperaturen onder de 5 °C en onder lage zuurstof, verhoogde koolstofdioxide condities, heeft een positieve invloed op vergroening en glycoalkaloïden.
Antropogene klimaatverandering zal leiden tot meer hitte stress in aardappelen, wat to hogere glycoalkaloïde gehaltes zal leiden, maar vergroening verminderd. Neerslag zal ook toenemen door klimaatverandering, wat to meer grond erosie zal leiden. Telers zullen irrigatie strategieën hierop moeten aanpassen en gebruik moeten maken van kleine dammen tussen ruggen om zo water vast te houden en erosie te verminderen.
Genome editing technologie kan SGA gehaltes verlagen door het reguleren van SGT genen, GAME genen, het SSR2 gen en het St16DOX gen. Precisie agricultuur gereedschap, zoals drones en AI, stellen telers in staat om meer efficiënt te irrigeren en bemesten, wat vergroening verminderd en tot lagere glycoalkaloïde gehaltes leidt. Veredelaars kunnen dit gereedschap gebruiken om fenotype datasets te maken om daarmee veredelingsprogramma’s te optimaliseren.
Het aardappel referentie genoom, aardappel accessies beschikbaar in meerdere genenbanken en de informatie die via genome editing technologie beschikbaar is geworden, zijn geweldige hulpmiddelen voor veredelaars. Deze hulpmiddelen kunnen door veredelaars gebruikt worden om commerciële rassen te maken met lagere glycoalkaloïde gehaltes en verminderde vergroening.
Dit onderzoek beschrijft ook wat er nog niet bekent is over vergroening en glycoalkaloïden en raad onderwerpen aan waarnaar vervolg onderzoek nodig is.

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# Chapter 1: Introduction

The potato (*Solanum tuberosum L.*) is the third most important food crop for human consumption (Devaux, Kromann, & Ortiz, 2014). Over the last few decades, the total potato production has increased much faster then that of the other major staple crops, such as maize, wheat and rice (Kreuze, et al., 2020). As of 2018, an estimated 400 million metric tons of potatoes were produced globally (Haverkort, 2018), a significant increase compared to the estimated production of around 330 million metric tons in 2010 (Shahbandeh, 2020) and the 305 million metric tonnes produced in 2001 (FAO, 2020).

Because of the high yield, cheap price and the ability to be cultivated on a wide variety of soils and in many different climates, potatoes have become an important part of the diet of people in many parts of the world (Jadhav & Salunkhe, 1975). Potatoes also need a relative low amount of water compared to other staple crops, making the potato an interesting crop in dry and arid areas (Haak, 2019). Since 1960 potato production in the developing world has grown exponentially, with the developing world exceeding the potato production of the developed world in 2005. The biggest potato producing countries are China and India, producing almost a third of all the potatoes in the world (Food Innovation Online Corp, 2019).

The main source of energy in potatoes is starch, but sugars such as glucose, fructose and sucrose also contribute to its energy content. Potatoes contain about 1600Kj per 100 gram dry matter, this is comparable to other staple crops such as wheat and rice (Haverkort, 2018). It must be noted though, that the exact energy content will vary depending on the cooking method (Storey & Davies, 1992). Furthermore, potatoes also contain a significant amount phosphorus, potassium, calcium and vitamins, especially ascorbic acid (vitamin C) and thiamine (vitamin B1) (Jadhav & Salunkhe, 1975). Potatoes also contain more lysine, an essential amino acid, than most cereals (Maga & Fitzpatrick, 1980). However, potatoes have lower concentrations of the sulphur containing amino-acids, methionine and cystine (Woolfe, 1986).

## 1.1: Potato wastage

According to FAO estimates, approximately one-third of all the food produced for human consumption is either thrown away or wasted (FAO, 2013). Root and tuber crops, such as the potato, exceed that average. Annually, around 40-50% of the global production of potato is being thrown away (Plich, Zimnoch-Guzowska, Tatarowska, & Sliwka, 2020). A study by the Waste and Resources Action Programme (WRAP) found that the amount of potato waste in the supply chain was low compared to the waste in households, with potatoes contributing to around 40% of the total waste of fresh vegetable and salad products in households in the UK (Pritchard, et al., 2012).

### 1.1.1: Greening

One of the major causes of tuber quality loss and their rejection by both the consumer and processing industry is greening. Annual loses due to greening are being estimated at around 14-17% of total production (Plich, Zimnoch-Guzowska, Tatarowska, & Sliwka, 2020). According to polls of the Dutch Potato Association, greening is also one of the biggest quality problems associated with biological potatoes (Pereira da Silva & Otma, 2015). Furthermore, the processing industry does not accept potatoes if more then 2% of the batch shows signs of greening (Haak, 2020).
Greening is a defect in fresh and processed potato that can occur from the time the tubers form until their display in stores (Bamberg, Moehninsi, Navarre, & Suriano, 2015).

Greening is caused when potatoes are exposed to light, causing them to accumulate chlorophyll (Grunefelder, Hiller, & Knowles, 2006). One of the main contributors to this illumination of potatoes, is the importance of proper display and visibility of potatoes in the retail sector (Olsen & Brandt, 2005). This accumulation of chlorophyll is due to the transformation of amyloplasts to chloroplasts just beneath the tuber periderm as a result of the exposure of tubers to light (Plich, Zimnoch-Guzowska, Tatarowska, & Sliwka, 2020). A part of this process is the formation of an additional membrane between the envelope and the starch grain of the plastid (Tanios, Eyles, Tegg, & Wilson, 2018). This transformation is also characterized by changes in the biochemical and structural properties of the stomata, with the synthesis of Rubisco starting immediately after illumination (Muraja-Fras, Krsnik-Rasol, & Wrischer, 1994). This transformation will lead to the accumulation of the green photosynthetic pigment, chlorophyll, resulting in a green colour on the outside and inside of the potato tuber (Tanios, Eyles, Tegg, & Wilson, 2018). The rate of chlorophyll synthesis is affected by many pre- and post- harvest factors, such as genotype, planting depth, age of the tubers at harvest, the climatic and light conditions while in storage or on display (Tanios, Eyles, Tegg, & Wilson, 2018).

Through analysing crosses made between potatoes with a high and low tendency to greening, it has been shown that greening is an incompletely dominant polygenic trait (Akeley, Houghland, & Schark, 1962). A different study found that greening is a quantitative trait with both additive and epistatic effects, with the epistatic effect accounting for 59% of the observed genetic variance (Parfitt & Peloquin, 1981). It also seems that red varieties are more resistant to greening (Reeves, 1988).

The two main problems consumers associate with greening are marketability due to a change in taste and human health risks (Grunefelder, Hiller, & Knowles, 2006). Chlorophyll however is not toxic, nor does it change the taste of the tuber (Olsen & Brandt, 2005). The main reason why greening is considered so negatively by consumers, is because light not just induces greening, but also glycoalkaloid accumulation, which can be a health risk (Bamberg, Moehninsi, Navarre, & Suriano, 2015). Tuber greening and glycoalkaloid accumulation are regulated through two independent biological pathways and are not necessarily correlated (Edwards, 1998). Greening does provide a warning though that the potato tubers have been exposed to light and are thus less fit for consumption (Bamberg, Moehninsi, Navarre, & Suriano, 2015).

### 1.1.2: Glycoalkaloids

Steroidal glycoalkaloids (SGA) are secondary plant metabolites which function as biotoxins (Cahill, Caprioli, Vittori, & James, 2010). At appropriate levels, glycoalkaloids have been shown to be toxic to animals, bacteria, fungi, humans, insects and viruses (Friedman, 2006). The chemical structure of SGAs exhibits strong lytic properties and is able to inhibit acetylcholine-esterase activity (Manrique-Carpintero, Tokuhisa, Ginzberg, Holliday, & Veilleux, 2013). Symptoms of SGA poisoning include: coma, confusion, convulsions, gastrointestinal disorders, hallucinations, partial paralysis and even death (Krits, Fogelman, & Ginzberg, 2007).

Steroidal glycoalkaloids, even when compared to other common poisons, are relatively toxic, with an estimated lethal dose ranging from 1.75 mg/kg body weight to 6 mg/kg body weight (Grunenfelder, Knowles, Hiller, & Knowles, 2006). Furthermore, they are described as bitter tasting and leaving a burning, scratchy and/or acrid feeling in the mouth (Umemoto, et al., 2016). Once glycoalkaloids are formed, they do not degrade nor can they be destroyed through heating or cooking (Grunenfelder, Knowles, Hiller, & Knowles, 2006).

Commercial cultivars have been bred to contain low levels of SGAs, which in the tubers should not exceed 20mg per 100 grams fresh weight (Valkonen, Keskitalo, Vasara, & Pietilä, 1996). However, the tuber SGA content can be increased by several pre- and postharvest factors, such as drought, high temperature, high light intensity and wounding (Ginzberg, et al., 2012). The two major SGAs in cultivated potato are α-chaconine and α-solanine, accounting for up to 95% of the total glycoalkaloids found in potatoes, with α-chaconine usually being found in higher concentrations then α-solanine (Omayio, Abong, & Okoth, 2016).

The biosynthetic pathway and the factors that regulate the expression of SGAs are not yet fully understood (Umemoto, et al., 2016). SGAs are produced through the mevalonate/isoprenoid pathway, with the reductase HMGR catalysing the first step of isoprenoid synthesis (Ginzberg, et al., 2012). The synthesis of SGAs begins with the formation of cholesterol, yet little else is known about the metabolic steps which converts cholesterol to SGAs (Manrique-Carpintero, Tokuhisa, Ginzberg, Holliday, & Veilleux, 2013). The final reaction in the synthesis of the SGAs is the glycosylation of solanidine by SGT1 or SGT2 to form α-solanine and α-chaconine respectively (Krits, Fogelman, & Ginzberg, 2007). Our current understanding of the biosynthetic pathway and the enzymes involved is shown in figure 1.

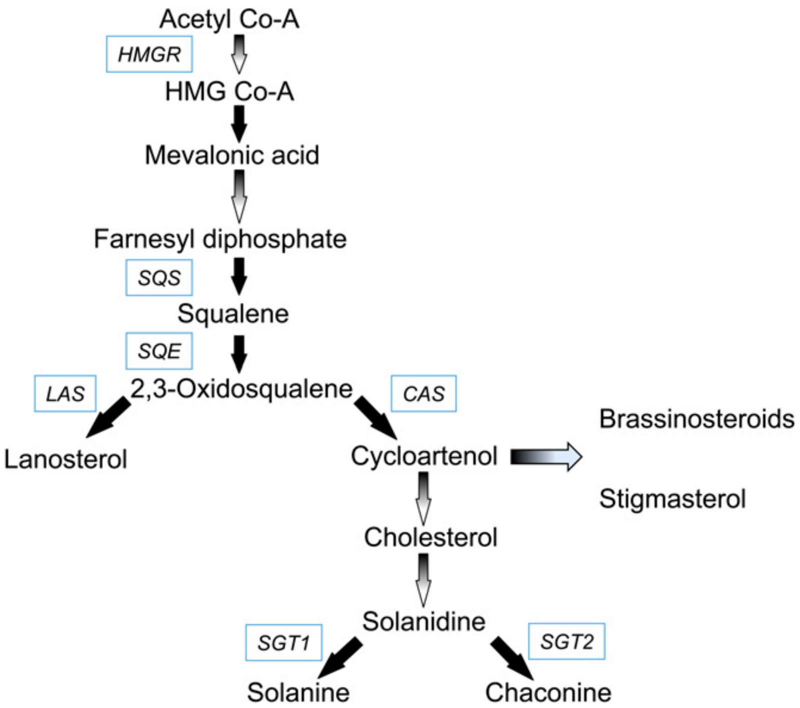


*Figure 1. Potato steroidal glycoalkaloid biosynthetic pathway (Manrique-Carpintero, Tokuhisa, Ginzberg, Holliday, & Veilleux, 2013)*

Glycoalkaloid concentrations seem to be genetically controlled, having a broad sense heritability somewhere between 86-89%. Yet few details are known about the genes regulating SGAs levels (Ginzberg, Tokuhisa, & Veilleux, 2009). It has been proposed that the expression of SGAs are at least partially regulated by two interacting loci in addition to a single locus effect (van Dam, Levin, Struik, & Levy, 2003). Many wild potato species contain higher SGA concentrations than cultivated varieties and thus introgressive hybridization of wild germplasm may increase the risk of high SGA levels (Umemoto, et al., 2016). Some wild species even contain concentrations of SGAs up to 100 times that of commercially available cultivars, with many of the glycoalkaloids being of unknown toxicity (Friedman, 2006).

## 1.2: Reducing potato wastage

As established earlier, the rejection of green potatoes by consumers can be, at least partially, attributed to both a loss in visual appeal and the perceived presence of glycoalkaloids.
While a lot of research has been conducted into combating both greening and glycoalkaloid accumulation, both still remain a significant problem for breeders, consumers and growers. Over the years many solutions have been proposed, using either pre- or post-harvest strategies, but these solutions have had either a negative impact on other quality attributes and/or limited commercial applications (Tanios, Eyles, Tegg, & Wilson, 2018). If good practices to combat greening and SGA accumulation can be established, either by raising the quality of cultivated potatoes or by specifically breeding for traits linked to either greening or SGA accumulation, potato wastage by consumers due to greening can potentially be prevented (Plich, Zimnoch-Guzowska, Tatarowska, & Sliwka, 2020).

The main aim of this study is the reduction of the amount of wasted and thrown away potatoes as a result of greening and glycoalkaloid accumulation. As of now, the information required to achieve this aim, is scattered over a wide variety of papers with many different subjects and targeted at different audiences, making this information harder to use for both breeders and growers. This review will attempt to unify this information and provide breeders and growers with the information required to breed less susceptible varieties and produce higher quality potatoes respectively, both in the present and in the future.

To achieve this aim, this thesis will attempt to answer the following research question:
*What can growers and breeders do to combat greening and glycoalkaloid accumulation in potato?*

To answer this question four sub-questions have been chosen:

- Sub-question 1: *What are the current practices used by growers and breeders to combat greening and glycoalkaloid accumulation?*
- Sub-question 2: *Will current problems, such as climate change, lead to more greening and glycoalkaloid accumulation?*
- Sub-question 3: *Which technologies will become available to growers and breeders for combating greening and glycoalkaloid accumulation?*
- Sub-question 4: *Which plant genetic resources can be used by growers and breeders to combat greening and glycoalkaloid accumulation in potato?*

## 1.3: Reading guide

Chapter 2: Methods will go into detail about the methods which have been used for researching these sub-questions. Chapter 3: Results will answer these four sub-questions and Chapter 4: Discussion, will then discuss the chosen methods and the acquired results. These results will be then used to answer the main research question in Chapter 5: Conclusions and recommendations.

# Chapter 2: Methods

Because food waste due to greening is a relevant subject, a lot of research has already been done. However, the information found about this subject is spread out over a large amount of papers and targeted at many different audiences. Here, a literature review has been conducted to compile this information and answer the main- and sub-questions. These answers have then been put it in a context applicable and understandable to both breeders and growers. This review has been conducted following a semi-systematic or narrative approach (Snyder, 2019). This chapter will detail which criteria will be used to determine whether or not a source would be considered relevant, for the purposes of this literature review. This chapter will also give a detailed account of which search procedures have been used and how the sources have been analysed.

## 2.1: Research procedure

For answering the main research question and the sub-questions, relevant key-words and google search operators have been used, e.g. for sub-question 1, a possible research query would be "Potato AND Greening AND Practices" (Müller, et al., 2020). A full list of relevant key-words, in no particular order, can be found in table 1.

*Table 1. Key-words used for the literature review*

| | | |
|---|---|---|
| "Potato" | "Pathway" | "Quality" |
| "Climate change" | "Practices" | "Production" |
| "Greening" | "Review" | "Glycoalkaloids" |
| "Gene" | "Agronomy" | "Climate" |
| "Drought" | "Cultivar" | "Soil" |
| "Light" | "Planting depth" | "Hilling" |
| "Irrigation" | "Erosion" | "Nutrition" |
| "Nitrogen" | "Pre-harvest factors" | "Post-harvest factors" |
| "Breeding" | "Resistance" | "Drones" |
| "Solanum tuberosum" | "Food waste" | "Screening technology" |

The search terms have been inputted in multiple search engines to find a variety of scientific and non-scientific sources. For the purposes of this review, the standard search engine Google, has been used to find most of the non-scientific sources used in this review. If for one reason or another a certain source was not available or had been removed, the internet archive has been used.
For scientific sources, the main search engine used was Google scholar. To a lesser extend the search engines of ScienceDirect, Springer and Wiley have also been used, mostly because Aeres University has access to their libraries.

## 2.2: Relevancy criteria

For the purpose of this review, a source has only been included if it is either a peer-reviewed article published in a scientific journal, a book relating to potato cultivation/breeding or a verifiable non-scientific source. A source was only considered a verifiable non-scientific source, if it was published by a recognised (non-)governmental organization, such as the FAO, WRAP or a national newspaper. All other sources have been excluded. Furthermore, if a source did not directly contribute to answering either the main research question or the sub-questions, then it was also excluded.

For this review, the year and/or location of publication were not considered as exclusion criteria. However, recent (2010 or later) sources relating to potato cultivation in the western world, were used over older sources or sources relating specifically to potato cultivation in the rest of the world, when the information within was contradictory. Finally, all sources had to either be in Dutch or in English, as these are the only two languages in which the author is sufficiently proficient.

## 2.3: Source analysis

First of all, the titles of the search results had been screened. When no more relevant titles could be found on a whole page of search results, all further pages were excluded. If the source did not belong in either of the three categories mentioned before: a peer reviewed article, a potato related book or a verifiable non-scientific source, then it was excluded.
After the relevant search results had been screened, the abstracts were assessed using the relevancy criteria. If no abstract was present due to the source being a book or non-scientific, comparable sections such as the summary were used.

Of the scientific sources, the main focus was put on the abstract, the introduction, the conclusion and the discussion. The material and methods, and the results, were most of the time considered irrelevant for the purposes of this review. Thus, they were only used if specific information from those chapters was needed. The reference list of all included sources was also searched for other possibly relevant sources. All included sources were downloaded if a PDF was available.

# Chapter 3: Results

There are many factors, which play a role when it comes to greening and glycoalkaloid accumulation. The main factors influencing these processes can be categorized in 3 different categories, pre-, during- and post-harvest factors (Nema, Ramayya, Duncan, & Niranjan, 2008).

The main pre-harvest factors which increase greening and SGA content are the genetics of the chosen cultivar, light exposure in the field and incorrect nitrogen fertilization (Ginzberg, Tokuhisa, & Veilleux, 2009). The most important during-harvest factors are the ambient temperature and intensity of sunlight during harvest, with higher temperature and sunlight intensities resulting in greener potatoes with higher SGA levels (Jadhav & Salunkhe, 1975). The maturity of the tubers during harvest also is an influential during-harvest factor, because immature tubers are more vulnerable to SGA accumulation (Pavlista, 2001). Finally the post-harvest factor with the greatest influence on greening and glycoalkaloid accumulation is exposure to light during storage (Tanios, Eyles, Tegg, & Wilson, 2018). Furthermore, atmospheric storage conditions also have an effect on both greening and SGA synthesis (Chang, 2013). Mechanical injury sustained during handling is also an influential post-harvest factor, but only on SGA levels (Valkonen, Keskitalo, Vasara, & Pietilä, 1996).The first of the pre-harvest factors, the genetics of the chosen cultivar, can also be considered a during- and pre-harvest factor, because the genetics also influences greening and SGA accumulation during- and after harvest (Chang, 2013). However, because the cultivar has to be chosen before planting, this will be considered as a pre-harvest factor in this review.

## 3.1: Current practices

By adopting practices that reduce or negate the effects of pre-, during- and post-harvest factors, breeders and growers can more effectively control greening and SGA accumulation in potatoes.

### 3.1.1: Pre-harvest practices

Most practices to combat greening and SGA accumulation involve preventing light exposure of the tubers (Wasukira, Walimba, Wobibi, & Owere, 2016). In the field potato tubers can be exposed to light through cracks in the soil, insufficient soil coverage or erosion, after which they will start to green and accumulate glycoalkaloids (Haverkort, 2018). The most effective way of combating light exposure is by planting seed potatoes at the appropriate depth and by using correct hilling practices (Bohl & Love, 2005). Many studies have looked into these effects and confirmed that increasing planting depth, leads to lower rates of greening and glycoalkaloids (Tanios, Eyles, Tegg, & Wilson, 2018). However, increasing the planting depth can lead to a reduced emergence rate and lower yields. Thus, it is very important that potatoes are planted at such a depth that tuber greening is negated as much as possible, while still maintaining an average emergence rate and yield (Pavek & Thornton, 2009). While the ideal planting depth depends on the specific cultivar, a planting depth of at least 15 centimetres is recommended (Pavlista, 2001). After emergence, forming a trapezoidal hilling structure will increase crop performance and quality (Jordan, Kelling, Lowery, Arriaga, & Speth, 2013). Furthermore, forming small dams or barriers in between the ridges created by hilling, retains significantly more rain water within these structures, reducing water runoff by around 70% and soil erosion by up to 90% (Europees Landbouwfonds voor Plattelandsontwikkeling, 2018). It is not completely clear if soil type influences SGA accumulation and/or greening. One study shows an increase in SGA levels on heavier soils, whereas another study shows the inverse, with higher SGA levels in potatoes grown on lighter soils (Sinden & Webb, 1974).

To further complicate the issue other studies seem to suggest that there are little to no differences in SGA content, between potatoes grown on sandy soil or clay (Friedman, McDonald, & Filadelfi-Keszi, 1997). No papers on the effect of soil type on potato greening have been found.
Fertilization also has an effect on greening and glycoalkaloid accumulation. Late or excessive addition of nitrogen to the soil might increase the SGA content in the potatoes, due to the fact that late application of nitrogen (Ojala, Stark, & Kleinkopf, 1990) and higher availability of nitrogen, delay tuber maturity (Hope, MacKay, & Townsend, 1960). An increase in soil nitrogen rates also seems to influence tuber greening (Braun, et al., 2010), this might be due to the high correlation between nitrogen and chlorophyll formation (Tanios, Eyles, Tegg, & Wilson, 2018).

There are significant differences in the rate of greening and glycoalkaloid accumulation between cultivars (Jadhav & Salunkhe, 1975). White skinned varieties tend to be more susceptible to greening than russet or purple skinned varieties (Haverkort, 2018). This has been attributed to the presence of accessory pigments, such as anthocyanin, affecting the quality of light penetrating the periderm (Grunefelder, Hiller, & Knowles, 2006). No studies researching the exact mechanics of these periderm properties on potato greening have been found.
Thus choosing the right cultivar is very important for reducing the rate of greening (Tanios, Eyles, Tegg, & Wilson, 2018) and regulating the SGA content (Nema, Ramayya, Duncan, & Niranjan, 2008). Choosing the right cultivar for either breeding or cultivation purposes is a very complex process, further complicated by the lack of a cultivar which is completely immune to either greening or glycoalkaloid accumulation (CGO, 2018). Because of these reasons this subject will be discussed in more detail in paragraph 3.4: “Available plant genetic resources”.

### 3.1.2: During-harvest practices

Greening and the glycoalkaloid content in potatoes are influenced by both high temperatures and bright sunlight. Harvesting very early in the morning or late in the afternoon, especially on an overcast day, will lead to less greening and SGA accumulation compared to harvesting at noon or during a very sunny day (Nema, Ramayya, Duncan, & Niranjan, 2008).

Immature tubers seem to be more susceptible than mature tubers to SGA accumulation, therefore early harvesting should be avoided expect when planting was also early (Pavlista, 2001). Whether maturity at harvest also influences greening is still unknown, with research into the subject giving contradictory results (Tanios, Eyles, Tegg, & Wilson, 2018) Some researchers found that mature tubers are more susceptible to greening (Buck & Akeley, 1967), while others claimed that immature tubers are more susceptible (Jadhav & Salunkhe, 1975). To further complicate this issue, in a slightly more recent study, no significant differences in greening rates were found, between immature and mature tubers (Griffiths, Dale, & Bain, 1994).

### 3.1.3: Post-harvest practices

Exposure to light is also the most important post-harvest factor, affecting both greening and glycoalkaloid formation (Jadhav & Salunkhe, 1975), while mechanical injury seems to have a significant influence on the accumulation of SGAs (Zhang, Zuo, Chen, Kang, & Qin, 2019). Once potatoes start to green or accumulate glycoalkaloids it is already too late as this process is irreversible (Salunkhe & Wu, 1979). Thus, avoiding or minimizing the usage of storage and handling methods that cause injury or exposes the tuber to light, will lead to less overall greening and glycoalkaloid accumulation (Nema, Ramayya, Duncan, & Niranjan, 2008). Keeping the storage room as dark as possible and only using the lights when it is strictly necessary, will reduce light exposure. Furthermore, not washing the potatoes will result in a protective layer of dirt remaining on the tubers which also reduces the exposure to light (Pavlista, 2001).

The temperature of the storage room also influences greening, with the rate of greening being lower in cold storage (<5 °C) then at room temperatures (Tanios, Eyles, Tegg, & Wilson, 2018). Glycoalkaloid accumulation also increases at higher storage temperatures, but only if the tubers suffer from mechanical injuries (Salunkhe & Wu, 1979).
The atmospheric conditions in storage can also be regulated to inhibit SGA accumulation and greening. Low oxygen ($O_2$) concentrations completely inhibit the synthesis of glycoalkaloids and chlorophyll in potato tubers, if the concentrations are lower then 5% and 1% respectively. Furthermore, Carbon dioxide ($CO_2$) levels higher then 6% and 12%, inhibit and reduce SGA accumulation and greening respectfully (Chang, 2013).

Research has been done into the effectiveness of using oil, wax and surfactant coatings, gamma-ray irradiation and chemical treatments, for combating greening and glycoalkaloid accumulation.
Oil coatings have been shown to reduce greening and SGA accumulation (Chang, 2013). However, due to the oily appearance of the tubers, the appeal of these tubers to consumers is reduced. Furthermore there are some concerns that using these oil coatings, may lead to potatoes becoming rancid (Jadhav & Salunkhe, 1975). When dipping the potatoes for half a second in paraffin wax at temperatures around 100 °C – 120 °C, chlorophyll formation and SGA accumulation was significantly reduced, compared to non-treated tubers. Waxing at 160 °C was even able to almost completely stop greening and glycoalkaloid formation. Just waxing the potatoes or just using heat treatments however, showed no effect (Wu & Salunkhe, Control of chlorophyll and solanine syntheses and sprouting of potato tubers by hot paraffin wax, 1972). Another study showed that immersing the tubers in a 3% detergent solution for 30 minutes, was able to reduce light induced greening and SGA accumulation by 92% for the first 2 days after treatment and by up to 50%, 10 days after treatment (Sinden, 1971). Spraying the potatoes with Tween 85 (4-5% concentration) and Tween 60 (10-15% concentration) reduced photoinduced greening of potato tubers for a period of around 13 days (Poapst & Forsyth, 1974). Gamma-ray irradiation can also be used to reduce greening in potatoes, subjecting the tubers to 0.5 and 2.5kGy, decreased greening in potatoes by around 75 and 85% (Schwimmer & Weston, 1958). However, another study showed that while increasing the dosage greatly reducing greening, subjecting the tubers to 2kGy also significantly reduced the quality of the tubers (Ziegler, Schandler, & Markakis, 1968). The chemical growth regulators Alar (Daminozide) and Ethral (Ethephon) were able to reducing greening and SGA accumulation (Patil, Salunkhe, & Singh, 1971). Another study showed the effectiveness of using 4 different brands of lecithin sprays: PAM, Mazola No Stick, Cooking ease and Griddle Mate. The lecithin sprays were able to reducing greening by 93-98% and SGA accumulation by 89-98%. Griddle Mate was the most effective at reducing greening, showing 98% less chlorophyll formation, whereas Cooking ease was most effective against glycoalkaloid accumulation ,inhibiting it by 98% (Wu & Salunkhe, 1977).
Using a calcium infiltration treatment on potato tubers, also reduced tuber greening by up to 80% using with a 2% $CaCl_2$ treatment (Arteca, 1982). Treating the potato tubers for 24 hours with a concentration of 600 µL/L ethanol in a 99% nitrogen environment significantly delayed greening and inhibited glycoalkaloid formation, showing the potential of ethanol fumigation as a post-harvest treatment. (Dong, Meng, Shi, Jiang, & Wang, 2017).
Other chemical treatments have also been tested, but they are either not approved for use on food crops, due to being categorized as herbicides or pesticides, or have not been shown to be effective (Tanios, Eyles, Tegg, & Wilson, 2018).

## 3.2: Current problems

Anthropogenic global warming is a problem which threatens global potato cultivation (Handayani, Gilani, & Watanabe, 2019). The average temperatures in areas important for the cultivation of potatoes are expected to increase by around 1.6 to 3.0 °C in the time period between 2040 and 2069 (Mori, Asano, Tamiya, Nakao, & Mori, 2015). Higher temperatures as a result of global warming, are one of the most devastating abiotic stresses influencing both potato yields and quality in many areas of the world (Levy & Veilleux, 2007). Most current potato cultivars have an inadequate tolerance for heat stress. This is due to a limited amount of introduced genetic variation in the foundation stock and a focus on enhancing yield and disease resistances in most potato breeding programs (Singh, Kukreja, & Goutam, 2019). One of the main quality defects associated with higher temperatures is increased glycoalkaloid content (Benavides, Diaz, Burgos, Felde, & Bonierbale, 2017). In contrast, heat stress decreases the rate of chlorophyll synthesis which lowers the speed of greening (Tiwara, Challam, Chakrabarti, & Feingold, 2020).

Another problem associated with global warming is a more vigorous hydrological cycle, which is characterized by an increase in total precipitation and more frequent high intensity precipitation events (Zhang & Nearing, 2005). In areas where the total rainfall increases, soil erosion and runoff is increasing at an even greater rate (Nearing, Pruski, & O'Neal, 2014). Especially higher intensity rainstorms during the warmer summer months accelerate soil erosion (Ochuodho, et al., 2013). The increase in temperature associated with global warming may even further complicate this issue, because warmer summers may lead to an increase in irrigation use. When rain falls on wet irrigated soil, it tends to run off quicker, leading to an further increase in soil erosion (Boardman & Favis-Mortlock, 1993). This acceleration of erosion could potentially become a big problem, because an increase in light exposure will induce greening and increase the glycoalkaloid content (Haverkort, 2018).

## 3.3: Technological possibilities

The current rapid increase in human population levels, will lead to an equal or even a proportionally greater increase in demand for food fit for human consumption (Hameed, Zaidi, Shakir, & Mansoor, 2018). Consumers increasingly demand higher quality food, putting further strain on our current agricultural system (Hewett, 2018). Potatoes will play a vital role in solving this problem, because it can provide more nutrition per hectare compared to any other staple food crop (Dangol, Barakate, Stephens, Çalıskan, & Bakhsh, 2019). To satisfy the demand for more and higher quality potatoes, breeders and growers will have to make use of new and upcoming technologies (Tanios, Eyles, Tegg, & Wilson, 2018).

### 3.3.1: Genome editing

One such technology that has great potential for creating higher yielding and higher quality potatoes, is genome editing (Nadakuduti, Buell, Voytas, Starker, & Douches, 2018). Techniques such as CRISPR-Cas9 and TALENs allow precise and targeted alterations to genomes through gene repair mechanisms, allowing the breeder to insert, remove, replace or modify genes at specific locations in the genome (Hewett, 2018). Through the use of these novel genome editing technologies, breeders will be able to greatly accelerate their breeding programs, using both gene knockout and gene knock-in approaches (Dangol, Barakate, Stephens, Çalıskan, & Bakhsh, 2019). Studies on the potato cultivar Lenape have shown that it is possible to use gene editing tools to manipulate the ratio of α-solanine and α-chaconine in potato tubers.

Through the knock-down of genes from the steroidal alkaloid glycosyl transferase (*Sgt*) gene family, scientists were able to reduce the accumulation of α-solanine, which was compensated by an increase in α-chaconine levels, thus only slightly lowering the total SGA content (McCue, 2009). Another study showed that by knocking out the St16DOX gene, it was possible to completely stop the accumulation of SGAs in the hairy roots of potatoes (Nakayasu, et al., 2018). Two other studies showed that modifying the glycoalkaloid metabolism genes (GAME) significantly decreased the SGA content in Solanaceous crops. Downregulating GAME1 led to an almost 50% reduction in α-tomatine levels in tomatoes (Itkin, et al., 2011), while silencing GAME4 led to an 74 fold decrease in SGAs in potato tubers (Itkin, et al., 2013). It was also shown that potatoes, in which the sterol side chain reductase 2 (SSR2) gene was silenced, had significantly lower levels of SGAs without influencing plant growth (Sawai, et al., 2014). Furthermore, the discovery of different versions of CRISPR-Cas, such as CRISPR-Cas12a and CRISPER-Cas13a and the availability of the whole genome sequence of the potato (The Potato Genome Sequencing Consortium, 2011), will allow breeders more tools to more efficiently edit the potato genome (Dangol, Barakate, Stephens, Çalıskan, & Bakhsh, 2019).

### 3.3.2: Precision agriculture

Other technologies which will greatly increase the yields and quality of potatoes, can be found within the fields of robotics and computer science, with unmanned aerial vehicles (UAVs) and artificial intelligence (AI) promising to revolutionize agricultural practices (Hewett, 2018). UAVs, more commonly known as drones, are pilotless aircraft systems, often controlled by an AI (Mahajan & Bundel, 2016). These drones can be outfitted with many different sensors, such as HD camera's, which allow them to be used for a wide variety of purposes (Stehr, 2015). To optimize yields and quality aspects, growers and breeders can use these tools to perform high throughput phenotyping on their crops, providing them with essential and target specific information. Drones can be used to perform soil and field analysis, mapping plant water and nutritional requirements, and for crop monitoring and health assessments (Puri, Nayyar, & Raja, 2017). Growers can then use this information, to optimize the usage of irrigation and nitrogen fertilization, reducing erosion (Janssens, et al., 2019) and quality loss due to excessive nitrogen fertilization (Kiril, 2019). Growers can also use drones to accurately measure soil erosion rates (Pérez & Garcia, 2017), which may be used to find the cause of differences in crop growth (Janssens, et al., 2019). Growers can even be assisted in certain cultivation actions, such as soil sampling, by drones and augmented reality tools, limiting the number of samples required, while still getting the information needed to properly fertilize their crops (Huuskonen & Oksanen, 2018).

Breeders can also use the information acquired through monitoring by drones, to create in-depth phenotype datasets. These datasets can be combined with genotyping data to optimize their breeding programs (Handayani, Gilani, & Watanabe, 2019). Furthermore, by combining climatology and information technology, breeders can more easily analyse genotype by environment (GxE) interactions, enabling them to more efficiently breed for traits which show a significant GxE effect (Singh, Kukreja, & Goutam, 2019), such as SGA accumulation (Sinden & Webb, 1972). While drones are currently the high-tech option for monitoring, satellites and manned aircraft can also be used for cheaper and lower resolution monitoring (Janssens, et al., 2019).

## 3.4 Available plant genetic resources

Cultivated potato has a very narrow genetic base which has led to the conservation of its landraces and wild relatives, in an effort to maintain and expand the collection of desirable genetic resources (Machida-Hirano & Niino, 2017). Historically, cultivated potato has been bred with these landraces and wild relatives, yet there are still many desirable traits left in landraces and wild relatives of the potato, which haven't been used for improving cultivated potato (Machida-Hirano, 2015).
Around 100.000 potato accessions are currently being conserved ex-situ with 80% of these accessions conserved in 30 different collections (Tiwara, Challam, Chakrabarti, & Feingold, 2020). Of these potato accessions, 23,169 are currently registered in Genesys, with the largest potato collections being located in the International Potato Center (CIP), the Leibniz-Institut für Pflanzengenetik und Kultupflanzenforschung (IPK) and the USDA-ARS gene banks (Genesys, 2020). The Dutch gene bank CGN (Centre for Genetic resources, the Netherlands) which holds 1471 potato accessions may also be used (CGN, 2020). The freely available online versions of the CGN, IPK and Genesys gene banks, do not have a filter available for sorting by either greening or SGA levels. The online version of the CIP gene bank however, does have an option to select for accessions with specific total glycoalkaloid (TGA) contents, although there is no option to select for greening here either.
The completion of the potato reference genome has created another resource which can be used by breeders to increase the efficiency of potato breeding efforts (Hirsch, Buell, & Hirsch, 2016). Dutch breeders can also make use of a CGO publication (Cultuur en gebruikwaardeonderzoek), this publication shows a list of available cultivars and their SGA content (CGO, 2018). Table 2 shows a list of promising cultivars found in this publication. All the cultivars in table 2 showed a SGA content of 2,0 mg/100g or less, under the protocol used for the CGO publication. All the potatoes designated as consumption varieties, had a SGA content of 20mg/100g or less, with most potatoes having less then 10mg/100g. Potato varieties designated as starch varieties however, had a much higher average SGA content with many potatoes exceeding 20mg/100g (CGO, 2018). Potato varieties having a SGA content higher then 20mg/100g has been linked to a burning sensation in the throat and potato varieties with higher SGA levels, such as Lenape and Magnum Bonum, have been banned from human consumption (Omayio, Abong, & Okoth, 2016).
Furthermore, table 3 shows a list of promising HZPC cultivars with a relatively slow speed to greening, being included if they scored higher than 70 points. A complete list of the speed to greening and TGA levels of specific HZPC cultivars can be found in Appendix I. It must be noted that only the cultivar Sunred can be found in both table 2 and 3, having both a low SGA content and a slow speed to greening.

*Table 2. Cultivars with low SGA content according to the CGO*

| CULTIVAR | GLYCOALKALOID CONTENT IN MG/100G | CATEGORY |
|---|---|---|
| *Monalisa* | 0,3 | Consumption |
| *Santera* | 1,3 | Consumption |
| *Essenza* | 1,4 | Consumption |
| *Sunred* | 1,4 | Consumption |
| *Remarka* | 1,5 | Consumption |
| *Sylvana* | 1,5 | Consumption |
| *Malika* | 1,6 | Consumption |
| *Aveka* | 1,6 | Starch |
| *Picobello* | 1,7 | Consumption |
| *Premium* | 1,7 | Consumption |
| *Sprint* | 1,8 | Consumption |
| *Bernadette* | 1,9 | Consumption |
| *Bimonda* | 1,9 | Consumption |
| *Disco* | 1,9 | Consumption |
| *Margarita* | 1,9 | Consumption |
| *Performer* | 1,9 | Consumption |
| *Saphire* | 1,9 | Consumption |
| *Elata KWS* | 2,0 | Consumption |
| *Levantina* | 2,0 | Consumption |

*Table 3. Speed to Greening of select HZPC cultivars*

| CULTIVAR | SPEED TO GREENING | CATEGORY |
|---|---|---|
| *Fenway Red* | 74 | Traditional |
| *Red Tinta* | 74 | N/A |
| *Carminelle* | 72 | Retail |
| *Sunred* | 72 | Traditional |
| *Baby Rose* | 71 | N/A |
| *Zarina* | 71 | N/A |
| *Annabelle* | 70 | Retail/Organic |
| *Rosi* | 70 | Organic |

# Chapter 4: Discussion

This study aims to reduce the amount of wasted and thrown away potatoes by unifying the available information about greening and glycoalkaloid in scientific literature and thus provide breeders and growers a powerful tool to breed less susceptible varieties and produce higher quality potatoes.

This review focusses mostly on scientific sources. Interviews with growers could potentially have been used to get a better picture about the practices used- and the problems experienced during potato cultivation.
No field trials have been performed by the author of this review. These field trials could potentially have given a better understanding about the effects of certain cultivars on greening and SGA accumulation, which would have resulted in more details in chapter 3.4.

The results indicate that, while there is at the moment, no way to completely eliminate either greening or SGA accumulation, there are certain cultivars, agricultural practices and promising technologies, which can greatly reduce both greening and glycoalkaloid accumulation. This review also shows which current problems might exacerbate the current issues around both greening and glycoalkaloids. Breeders and growers can make use of the cultivars, agricultural practices and technologies as described in this thesis, to combat both greening and SGA accumulation.

The key factor to control both greening and glycoalkaloid production seems to be light exposure (Pavlista, 2001). Light exposure is a problem during many different stages of cultivation, starting on the field and persisting during handling and in storage rooms (Wasukira, Walimba, Wobibi, & Owere, 2016). In the field light exposure can be caused by many factors outside the growers control, such as drought leading to cracks in the soil, ridges collapsing and heavy winds or rainfall leading to erosion. However, growers can use the agricultural practices described in this thesis to reduce the effects of some of these factors. The effects of drought can be reduced through irrigation and erosion caused by rainfall can be reduced by making small dams in between ridges (Europees Landbouwfonds voor Plattelandsontwikkeling, 2018).
Keeping a layer of dirt on potatoes by not washing them has shown to decrease light induced greening and SGA accumulation (Pavlista, 2001). This may however be more effective when planting on clay soils compared to sandy soils, due to the way clay sticks to tubers.
The relation between soil type and SGA accumulation is not clear, whereas no information about the relation of soil type and greening could be found.
Breeders can reduce the effects of light exposure, by breeding for cultivars with lower SGA accumulation rates and a slower speed to greening.
Harvesting immature tubers and mechanical injury have been show to also increase glycoalkaloid accumulation (Pavlista, 2001). While mechanical injury seems to have no effect on greening, it is unknown if tuber maturity has any effect.

There is still much unknown about the viability and safety of coatings, irradiation treatments and chemicals for reducing greening and SGA accumulation (Tanios, Eyles, Tegg, & Wilson, 2018). Recent advances in coating technology have proven that edible coatings are effective at increasing the storability of some fresh products (Wilson, Stanley, Eyles, & Ross, 2017). However, it is still unknown whether these edible coatings have an effect on light induced greening and SGA accumulation.

Irradiation treatment seems useable for reducing greening and SGA accumulation (Ziegler, Schandler, & Markakis, 1968). However, no information about commercial use of this technology, for reducing greening or SGA accumulation have been found. More then 40 countries, including The Netherlands, Belgium, France, China and Japan, have approved the use of irradiation to treat a variety of other problems though, such as sprouting of potatoes and controlling bacterial growth (Diehl, 2002). The energy levels used in these treatments are low, which means that only chemical changes are possible. Nuclear changes, which would make the food itself radioactive, are not possible (Andress, Delaplane, & Schuler, 1998). While food irradiation is seemingly safe, there is much opposition from vocal anti-irradiation groups and uncertainty about the consumer acceptance of the practice, has resulted in limited practical and commercial use of this technology (Diehl, 2002).
While a few select chemicals show potential for reducing greening and SGA accumulation, there is still much uncertainty about their safety, as shown by the controversy surrounding Daminozide (Jassanof, 1987). A recent study showed that Ethephon, another chemical mentioned in chapter 3.1.3, could be a potential mutagen (Yu, Gao, Zhao, Qi, & Yang, 2006). Lecithin, a chemical derived from soybean oil, has however been shown to have health benefits (Miller, 2002).

The effects global warming will have on tuber greening and SGA accumulation are also not completely clear yet. Heat stress seems to increase the rate of SGA accumulation (Benavides, Diaz, Burgos, Felde, & Bonierbale, 2017), while lowering the speed of chlorophyll synthesis, leading to a lowered speed to greening (Tiwara, Challam, Chakrabarti, & Feingold, 2020). The effect global warming will have on erosion is more clear. Global warming will increase the amount and intensity of precipitation, especially in the summer (Zhang & Nearing, 2005). Through weather forecasts and precipitation predictions, growers may be able to more efficiently plan their irrigation schedule, reducing soil erosion. The usage of small dams between ridges will also be a significant factor for reducing soil erosion caused by more intense precipitation.

Some early research has been conducted into reducing the rate of SGA accumulation through genome editing techniques and multiple genes which can be used to reduce SGA content, have been found. However, no studies showing the effect of specific genes on tuber greening have been found in this literature review. It must be noted however, that cultivars created through the use of genome editing techniques currently fall under the scope of European GMO legislation (Laaninen, 2019). This legislation means that any cultivars created through these techniques would need to go through a lengthy and expensive approval procedure, which makes these techniques seem uninteresting to breeding companies due to their limited commercial application (Callaway, 2018).
Breeding companies can still use these genome editing tools to acquire more information about the effects of certain genes on greening or SGA accumulation, by knocking these genes in or out. This information can then be used in combination with marker assisted selection (MAS) or classical breeding methods, to select for cultivars with or without these specific genes.

Drones and computer science also prove to be very promising technologies due to their potential for high throughput phenotyping, greatly increasing the available information for both breeders and growers. Growers can use this information to optimize their irrigation and nitrogen fertilization usage, reducing erosion (Janssens, et al., 2019) and tuber quality loss (Kiril, 2019), leading to lower greening rates and SGA levels. Whereas breeders can combine the acquired information with climatological and genotyping data, optimizing their breeding programs (Handayani, Gilani, & Watanabe, 2019). One of the biggest arguments for the use of drones is their cost, a starter kit can be bought for around €1000,- although there are much more expensive options available. Most drones will pay themselves back after just a few uses, due to the costs saved on labour, fertilizer and pesticides (Stehr, 2015).
Unlike with genome editing techniques, the use of drones is completely legal in the Netherlands, however due to the commercial nature of phenotyping crops, a license to fly the drone is required. Furthermore, the rules that also apply to recreational use of drones must be followed (Ministry of

Infrastructure and Water Management, 2020), meaning that there are some places where drones not allowed to fly (Ministry of Infrastructure and Water Management, 2016). These rules increase the cost of using a drone and due to the license required to fly the drone, it may be necessary to hire drone pilots from certain companies, who may cost up to €168 an hour. Because of these added costs, drones tend to be most effective for companies smaller then 25 hectares, as satellite and plane imagining tends to be cheaper for larger companies (de Jager, 2017).

Cultivars with a lower SGA accumulation and speed to greening rate have been found, these cultivars can be used by growers to produce tubers which are less vulnerable to green and SGA accumulation, while breeders can use these tubers as crossing parents for a breeding program focused on further reducing greening and SGA accumulation. The cultivars shown in table 2, 3 and Appendix I are all commercially available cultivars. The available sources only show a small list of resistances and some non-detailed information about yield and growing conditions. Thus, no accurate estimate about the quality of these cultivars are crossing parents or their viability to growers, outside of their greening rates and SGA levels, could be made.
It should however be noted that the cultivar Sunred has both a low SGA content and a low speed to greening making it an potentially an excellent candidate as a crossing parent. Sunred is an cross between Rodeo and Dakota Rose. It is an early maturing variety with good yield and big tubers, it has a red skin, light yellow flesh and has been bred for the traditional sector. It has some resistance against common scab, powdery scab and spraing (HZPC, 2020).
It must also be noted that the data provided by HZPC had multiple blank entries, which may skew the results slightly because some cultivars are potentially not being included in table 3. However there is still much genetic diversity to be found in landraces and wild relatives of potatoes which has not been exploited yet (Machida-Hirano, 2015).

# Chapter 5: Conclusions and recommendations

This study shows the best practices, cultivars and technologies available to breeders and growers for reducing greening and SGA accumulation. The current problems exacerbating these issues are also reviewed in this study. By unifying the information available on these subjects, this thesis provides breeders and growers a powerful tool to breed less susceptible varieties and produce higher quality potatoes. Which in turn will lead to a reduction in the amount of wasted and thrown away potatoes.

For growers, reducing light exposure in the field, during handling and while in storage is key. This can be achieved by planting at a sufficient depth (>15cm), using trapezoidal hilling structures, placing small dams between the ridges and harvesting early in the day or under cloudy conditions. Not washing the potatoes and leaving a layer of dirt on the skin, will further reduce the effects of photo-induced greening and SGA accumulation. The reviewed literature also shows that storing the potatoes at a sufficiently cold temperature (<5 °C) and under low oxygen (1-5%) and at elevated carbon dioxide(6-12%) conditions, greatly decreases greening and SGA accumulation. Choosing cultivars which are less susceptible to greening and SGA accumulation also makes a major difference. Furthermore, applying the correct amount of nitrogen fertilization at the right time, decreasing mechanical injury during harvest and harvesting when the tubers are mature, reduces SGA accumulation, making the tubers less likely to be discarded by consumers because of bitterness.

Anthropogenic climate change will increase the heat stress experienced by the potato, leading to an increase in SGA content. Conversely heat stress reduces speed to greening, due to its effect on chlorophyll synthesis. Another major consequence of climate change, will be the increase in total precipitation and high intensity precipitation events, especially during the summer months. This will lead to an increase in soil erosion. The use of irrigation during the warmer summer months will even further complicate this issue, because wet soil is more vulnerable to erosion.

Genome editing technologies, such as CRISPR-Cas9 and TALENs show potential. By regulating SGT genes, GAME genes, the SSR2 gene and the St16DOX gene, breeders will be able to more effectively reduce SGA accumulation. No specific genes with an effect on tuber greening have been found. The current legislation around genome editing limits its usability for breeders. Cultivars developed with these techniques fall under European GMO legislation, making them commercially unviable.

Precision agriculture can be used by growers to reduce greening and SGA accumulation in the field, because it enables them to more efficiently use irrigation and fertilization practices. Breeders will be able to make use of drones and AI, to create in-depth phenotyping datasets. These datasets can be combined with environmental and genotyping data to optimize their breeding program and more efficiently breed for traits with high GxE effects such as resistance to SGA accumulation.
Smaller companies can make use of drones, while satellite and plane imaging will be cheaper for larger companies.

Breeders can make use of the accessions available in multiple gene banks to select crossing parents showing favourable characteristics. These parents can then be crossed with high yielding varieties to create varieties more resistant to both greening and SGA accumulation. Growers can use the resulting varieties and also currently available varieties such as Sunred, to grow potatoes more resistant to greening and SGA accumulation.

By reducing light exposure as much as possible and using the correct practices to limit greening and SGA accumulation, growers will be able to provide higher quality potatoes to the consumer.
The ever increasing effects of global warming will force growers to adopt practices to better deal with soil erosion due to increases in precipitation. By planning irrigation strategies using weather forecasts and precipitation predictions, combined with small dams in between ridges, growers will be able to reduce erosion.
Precision agriculture can be used both by grower and breeders to more effectively phenotype their crops and thus take more informed actions and breed for more optimized cultivars. The potato reference genome, potato accessions in multiple gene banks and the information acquired through genome editing technology, provides powerful tools for breeders. These tools can be used by breeders to breed commercial varieties with lower SGA contents and a slower speed to greening. These higher quality potatoes and these varieties with reduced greening rates and low SGA levels, will be more attractive to consumers, reducing the amount of thrown away potatoes.

This review shows that the literature on greening and glycoalkaloids in potatoes can sometimes be contradictory and that there are still some elements which are not fully understood. This is not completely unexpected because greening and glycoalkaloid accumulation are influenced by multiple complex genetic and environmental factors. More research will be required to find out what the exact genetics behind greening are and how exactly the glycoalkaloid biosynthetic pathway works. The effects of soil type are also not completely clear yet, more research will be needed to understand what effect soil type has on greening and glycoalkaloids. Research into the effects of tuber maturity on greening is contradictory and more research will be required to confirm if tuber maturity has any effect on greening. The current research on drones shows that drones can be effective at dealing with factors related to glycoalkaloids and greening, but no specific research on how to best use drones to reduce greening and glycoalkaloid accumulation in the field has been conducted yet. Research also needs to be done to ascertain the viability and safety of coatings, irradiation treatments and chemicals for reducing greening and SGA accumulation. The current research on these treatments is decades old and is worth revisiting, due to advances in molecular biology, chemistry and statistical analysis software.

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# Appendix I: Speed to Greening and TGA of HZPC cultivars

| Variety | Stage | Set | Flesh Color | Skin Color | CTP | Speed to Greening | TGA(mg/100g) |
|---|---|---|---|---|---|---|---|
| ADORA | 1 | C | LY | Y | 26 - S. tuberosum | 57 | 4 |
| ALCANDER | 1 | C | LY | Y | 26 - S. tuberosum | 50 | 14 |
| ALLISON | 1 | C | CR | Y | 26 - S. tuberosum | 52 | 5 |
| ALTHEA | 1 | C | CR | DY | 26 - S. tuberosum | 51 | 6 |
| ALVERSTONE | 1 | C | W | Y | 26 - S. tuberosum | 51 | 7 |
| AMBRA | 1 | C | Y | Y | 26 - S. tuberosum | 57 | |
| ANIVIA | 1 | C | CR | LY | 26 - S. tuberosum | 66 | 3 |
| ANNABELLE | 1 | C | Y | Y | 26 - S. tuberosum | 70 | |
| ASTERIX | 1 | C | Y | R | 26 - S. tuberosum | 61 | 4 |
| AURUM | 1 | C | Y | Y | 26 - S. tuberosum | 64 | 4 |
| BABY ROSE | 1 | C | LY | DR | 27 - S. tuberosum Atlantic/Sagitta | 71 | 2 |
| BARAKA | 1 | C | LY | Y | 26 - S. tuberosum | 49 | |
| BARTINA | 1 | C | Y | R | 26 - S. tuberosum | 62 | |
| BERBER | 1 | C | Y | Y | 26 - S. tuberosum | 60 | 3 |
| BLUE STAR | 1 | C | P | P | 26 - S. tuberosum | 54 | 4 |
| CAESAR | 1 | C | LY | Y | 26 - S. tuberosum | 49 | 5 |
| CANBERRA | 1 | C | Y | R | 26 - S. tuberosum | 64 | 8 |
| CARDYMA | 1 | C | Y | DY | 26 - S. tuberosum | 49 | 9 |
| CARLITA | 1 | C | LY | Y | 26 - S. tuberosum | 51 | |
| CARMINELLE | 1 | C | LY | DR | 26 - S. tuberosum | 72 | 6 |
| CAROLINA | 1 | C | W | DR | 26 - S. tuberosum | 50 | 3 |
| CARRERA | 1 | C | Y | Y | 26 - S. tuberosum | 56 | |
| CECILE | 1 | C | Y | DR | 26 - S. tuberosum | 69 | 6 |
| CELANDINE | 1 | C | LY | Y | 26 - S. tuberosum | 64 | 5 |
| CHALLENGER | 1 | C | LY | Y | 26 - S. tuberosum | 66 | 6 |
| CICERO | 1 | C | LY | Y | 26 - S. tuberosum | 49 | |
| CLEOPATRA | 1 | C | LY | R | 26 - S. tuberosum | 64 | |
| COLOMBA | 1 | C | LY | Y | 26 - S. tuberosum | 63 | 3 |
| COURAGE | 1 | C | Y | R | 26 - S. tuberosum | 66 | 4 |
| CRISPS4ALL | 1 | C | LY | Y | 26 - S. tuberosum | 39 | 12 |
| DALI | 1 | C | Y | Y | 26 - S. tuberosum | 54 | 3 |
| DELIA RED | 1 | C | Y | DR | 26 - S. tuberosum | 69 | 3 |
| DERBY | 1 | C | LY | Y | 26 - S. tuberosum | 53 | 6 |
| DESIREE | 1 | C | LY | R | 27 - S. tuberosum Atlantic/Sagitta | 65 | 5 |
| DIONE | 1 | C | LY | BR | 26 - S. tuberosum | 53 | 12 |
| DOLCE VITA | 1 | C | DY | Y | 26 - S. tuberosum | 45 | 5 |
| DOUBLE FUN | 1 | C | MC | P | 27 - S. tuberosum Atlantic/Sagitta | 56 | 5 |
| DRAGA | 1 | C | CR | Y | 26 - S. tuberosum | | |
| ELVIRA | 1 | C | Y | Y | 26 - S. tuberosum | 45 | 9 |
| EMANUELLE | 1 | C | DY | DY | 25 - S. stoloniferum | 56 | 4 |
| EVORA | 1 | C | CR | Y | 26 - S. tuberosum | 55 | 5 |
| FABULA | 1 | C | LY | Y | 26 - S. tuberosum | 55 | 2 |
| FARIDA | 1 | C | LY | Y | 27 - S. tuberosum Atlantic/Sagitta | 50 | 5 |
| FELSINA | 1 | C | LY | Y | 26 - S. tuberosum | 47 | 2 |
| FENWAY RED | 1 | C | W | DR | 26 - S. tuberosum | 74 | 4 |
| FLAMENCO | 1 | C | W | DR | 27 - S. tuberosum Atlantic/Sagitta | 68 | 5 |
| FRANCELINE | 1 | C | LY | R | 26 - S. tuberosum | 68 | |
| FRISIA | 1 | C | CR | Y | 26 - S. tuberosum | 49 | |
| GENEROSA | 1 | C | LY | Y | 26 - S. tuberosum | 60 | 7 |
| GIOCONDA | 1 | C | Y | Y | 26 - S. tuberosum | 57 | 6 |
| HERACLEA | 1 | C | Y | Y | 26 - S. tuberosum | 53 | 7 |
| HERMOSA | 1 | C | LY | Y | 26 - S. tuberosum | 60 | 7 |
| HEROS | 1 | C | LY | Y | 26 - S. tuberosum | 53 | |
| INNOVATOR | 1 | C | LY | BR | 26 - S. tuberosum | 60 | 15 |
| IVORY RUSSE | 1 | C | W | BR | 26 - S. tuberosum | 63 | 4 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| JAERLA | 1 | C | LY | Y | 26 - S. tuberosum | 48 | 3 |
| JENNIFER | 1 | C | CR | LY | 26 - S. tuberosum | 68 | 5 |
| JESSICA | 1 | C | Y | Y | 6 - S. demissum (Starch) | 61 | 5 |
| JOLY | 1 | C | W | LY | 26 - S. tuberosum | 68 | 3 |
| LA VIE | 1 | C | DY | DY | 26 - S. tuberosum | 61 | 6 |
| LATONA | 1 | C | Y | Y | 26 - S. tuberosum | 45 | 4 |
| LEONARDO | 1 | C | Y | DY | 26 - S. tuberosum | 43 | 5 |
| LEONTINE | 1 | C | LY | Y | 26 - S. tuberosum | 58 | 7 |
| LISETA | 1 | C | LY | Y | 26 - S. tuberosum | 56 | 8 |
| LUCINDA | 1 | C | LY | Y | 26 - S. tuberosum | 60 | 3 |
| MARILYN | 1 | C | LY | Y | 26 - S. tuberosum | 66 | 5 |
| MARISOL | 1 | C | LY | Y | 26 - S. tuberosum | 59 | 7 |
| MEMPHIS | 1 | C | LY | R | 26 - S. tuberosum | 69 | 5 |
| MONALISA | 1 | C | Y | Y | 26 - S. tuberosum | 62 | |
| MONDIAL | 1 | C | LY | Y | 26 - S. tuberosum | 55 | 4 |
| MORGANA | 1 | C | CR | Y | 26 - S. tuberosum | 55 | 5 |
| MOZART | 1 | C | Y | R | 26 - S. tuberosum | 68 | 5 |
| MULBERRYBI | 1 | C | R | DR | 26 - S. tuberosum | 60 | 6 |
| MUSE | 1 | C | Y | Y | 25 - S. stoloniferum | 66 | 5 |
| NOBLESSE | 1 | C | Y | Y | 26 - S. tuberosum | 60 | 4 |
| ORIANA | 1 | C | LY | Y | 26 - S. tuberosum | 63 | 5 |
| ORLENA | 1 | C | Y | DY | 26 - S. tuberosum | 53 | 6 |
| PANAMERA | 1 | C | LY | Y | 26 - S. tuberosum | 57 | 4 |
| PANTHER | 1 | C | LY | Y | 26 - S. tuberosum | 65 | 10 |
| PARELLA | 1 | C | W | Y | 26 - S. tuberosum | 56 | 3 |
| PEE WEE RUS | 1 | C | LY | BR | 26 - S. tuberosum | 63 | 2 |
| PERDIZ | 1 | C | Y | Y | 26 - S. tuberosum | 60 | 4 |
| PRIMABELLE | 1 | C | LY | Y | 26 - S. tuberosum | 59 | 4 |
| PRIMURA | 1 | C | LY | Y | 26 - S. tuberosum | 35 | 7 |
| PRINCEOFOR | 1 | C | DO | R | 26 - S. tuberosum | 69 | |
| RED SCARLET | 1 | C | Y | R | 27 - S. tuberosum Atlantic/Sagitta | 65 | |
| RED TINTA | 1 | C | LY | DR | 26 - S. tuberosum | 74 | 10 |
| RODEO | 1 | C | LY | R | 26 - S. tuberosum | 65 | |
| RONALDO | 1 | C | LY | DR | 26 - S. tuberosum | 66 | 4 |
| ROSI | 1 | C | CR | R | 26 - S. tuberosum | 70 | 4 |
| ROYAL BLUE | 1 | C | Y | P | 26 - S. tuberosum | 63 | 4 |
| SABABA | 1 | C | CR | Y | 26 - S. tuberosum | 65 | 7 |
| SAGITTA | 1 | C | LY | Y | 27 - S. tuberosum Atlantic/Sagitta | 49 | 3 |
| SIFRA | 1 | C | CR | LY | 26 - S. tuberosum | 60 | 4 |
| SMART | 1 | C | DY | DY | 26 - S. tuberosum | 52 | 3 |
| SPUNTA | 1 | C | LY | Y | 26 - S. tuberosum | 54 | 7 |
| SUNDANCE | 1 | C | Y | DY | 25 - S. stoloniferum | 54 | 4 |
| SUNITA | 1 | C | Y | Y | 6 - S. demissum (Starch) | 52 | 5 |
| SUNRED | 1 | C | LY | DR | 26 - S. tuberosum | 72 | 1 |
| SYLVANA | 1 | C | Y | Y | 26 - S. tuberosum | 59 | 1 |
| TALENTINE | 1 | C | Y | Y | 6 - S. demissum (Starch) | 59 | 8 |
| TAURUS | 1 | C | LY | Y | 7 - S. demissum Taurus/ El mundo | 48 | 5 |
| TIGER | 1 | C | LY | BR | 26 - S. tuberosum | 65 | 16 |
| TRIPLE7 | 1 | C | LY | DY | 26 - S. tuberosum | 51 | 6 |
| VAN GOGH | 1 | C | Y | Y | - | 49 | |
| VICTORIA | 1 | C | Y | Y | 26 - S. tuberosum | 62 | 7 |
| VIOLET QUEE | 1 | C | P | P | 27 - S. tuberosum Atlantic/Sagitta | 54 | 5 |
| VIVALDI | 1 | C | LY | Y | 26 - S. tuberosum | 65 | |
| VOYAGER | 1 | C | Y | Y | 26 - S. tuberosum | 53 | 3 |
| WHITNEY | 1 | C | CR | LY | 26 - S. tuberosum | 65 | 9 |
| ZARINA | 1 | C | Y | Y | 26 - S. tuberosum | 71 | 5 |