Investigation of starch metabolism in Cassava (Manihot esculenta Crantz)

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Investigation of starch metabolism in Cassava (*Manihot esculenta* Crantz)

A dissertation submitted to the

ETH ZURICH

For the degree of Doctor of Sciences

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2014
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Summary

Cassava (*Manihot esculenta* Crantz) is a perennial shrubby plant grown in the tropical and subtropical regions for its starchy roots. In South America and Africa it is mainly grown as a security food and feed stock whereas in Asia the starch industry is the major consumer. In the last decades the economic interest of cassava as a starch crop increased markedly. However, cassava is vegetatively propagated and limited in germplasm.

Starch is the major carbohydrate in plants and an important raw material used for food and non-food industry for mankind. Plants store carbohydrates in form of starch, a polyglucan consisting of linear α-1,4 linked glucose units with α-1,6 branch points. The insoluble, semi-crystalline starch granules are either stored transiently in autotrophic (source) leaf tissues or as reserve compound in heterotrophic storage organs (sink; i.e. seeds and tubers). Transitory starch is synthesised during the day in source tissues from photosynthetically assimilated carbon. During the subsequent night transitory starch is degraded to meet the demand for carbohydrates in sink tissues. In most plants carbohydrates are transported through the phloem from source to sink in form of sucrose, a non-reducing disaccharide. In sink tissues sucrose is unloaded and converted to starch and stored as a carbohydrate reserve for long term. In the process of starch biosynthesis multiple enzymes are involved. Starch metabolism in source and sink tissues share some common features, however there are some differences in which enzymes are involved. Differences also occur depending on the botanical source, in respect of starch architecture, granule size and shape. These characteristics define physico-chemical properties. For the diverse industrial applications (i.e. pharmaceuticals, instant food, paper-making) starches of different characteristics are desired.

In order to increase the value of cassava as a starch crop the subject of my thesis was to identify possible key enzymes involved in cassava root starch metabolism. With the help of profound knowledge about starch metabolism and improved biotechnology tools, transgenic cassava plants can be engineered with better starch properties or increased yield.

In my first part of the thesis I have investigated the growth performance of cassava (cv. 60444) grown under defined greenhouse conditions. The interest was to study the photosynthetic capacity and the allocation of assimilated carbon in form of starch and soluble sugars. In the first part the main focus was on leaf and stem tissue at different developmental stages. Hence, photosynthetic capacity and non-structural carbohydrates were visualized and measured from leaf and stem tissue at different developmental stages. Integration of photosynthetic rate and accumulated carbohydrate revealed a high source capacity of cassava leaves. Hence, more carbohydrates are accumulated than needed throughout the day.
In a second part of my thesis I asked the question what key enzymes are involved in remobilizing root starch. Therefore, storage roots, harvested from untreated cassava plants and 10 days after cutting off the aerial plant material were compared. Analysed starch levels and amylolytic enzyme activity revealed a negative correlation. Further, a large scale proteome analysis indicated a metabolic transition from sink to source. This analysis elucidated the involvement of an α-amylase, AMY3 to be a major enzyme responsible for starch mobilization.

In my third part of the thesis I focused on the attempt to modify starch properties in order to add economic value to cassava starch. Phosphorylated starches, the only naturally occurring modification, are used in paper-making industry to increase paper-strength. Depending on the botanical source the degree of starch-bound phosphate varies from high (i.e. 0.5% in potato) to low (i.e. 0.05 % in cassava). Phosphorylation of starch in plants is executed by a glucan, water dikinase (GWD) and dephosphorylated by two glucan phosphatases (SEX4, LSF2). Activity of GWD is redox regulated. Thus either the potato StGWD or the redox-insensitive and constitutively active StGWD_{C1084S} were transformed into cassava. Preliminary analysis revealed a positive functionality hence, an increase in total phosphate content. Secondly, cassava plants were transformed with an RNAi constructs targeting SEX4 or LSF2 transcript. The constructs were specifically expressed in root tissue to avoid manipulation of starch metabolism in other tissues. In order to increase starch yield an RNAi construct was made targeting AMY3 as I could show that this is the major enzyme involved in starch mobilization.
Zusammenfassung


Um Cassava als Kulturpflanze einen Mehrwert zu verleihen, war das Thema meine Doktorarbeit die Identifizierung möglicher Schlüsselenzyme die im Stärkemetabolismus von Cassava beteiligt sind. Mit Hilfe von fundiertem Wissen über den Stärkemetabolismus und den verbesserten biotechnologischen Werkzeugen kann eine Wertsteigerung von Cassava als Kulturpflanze für Stärke erreicht werden.

In meinem ersten Teil der Dissertation habe ich das Wachstumsverhalten von Cassava (cv. 60444) Pflanzen untersucht, die bei definierten Gewächshaus Bedingungen angezogen wurden. Das
Zusammenfassung


Im dritten Teil meiner Doktorarbeit habe ich mich damit beschäftigt in Cassava Stärke mit modifizierten Eigenschaften herzustellen um der Stärke aus Cassava einen wirtschaftlich höheren Wert zu verleihen. Phosphorylierte Stärke – die einzige natürlich vorkommende Modifizierung, wird in der Papierherstellung gebraucht um das Papier zu stärken. Abhängig von der botanischen Quelle kann der Grad von Stärkegebundenem Phosphat von hoch (Bsp. 0.5% in Kartoffeln) und niedrig (Bsp. 0.05%, in Cassava) variieren. Die Pflanzenstärke wird durch die glucan, water dikinase (GWD) phosphoryliert und durch zwei glucan phosphatasen (SEX4, LSF2) dephosphoryliert. Die Aktivität von GWD ist Redox reguliert. So wurden das Kartoffel StGWD Protein oder die redox-insensitive konstitutive aktive StGWDc1084S Form in Cassava transformiert. Erste Ergebnisse zeigen eine positive Funktionalität und somit einen erhöhten Phosphatgehalt. Weiter, Cassava Pflanzen konnten mit einem RNAi Konstrukt gegen die Transkripte von SEX4 und LSF2 transformiert werden. Die Konstrukte wurden wurzelspezifisch exprimiert um das Verändern auf den Stärkemetabolismus in anderen Geweben zu verhindern. In einem dritten Ansatz mit dem Ziel den Stärkeertrag zu erhöhen habe ich ein RNAi Konstrukt entwickelt gegen das AMY3 Transkript, da ich zeigen konnte das dieses ein wichtiges Enzym ist um gespeicherte Stärke abzubauen.
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<td>AGPase</td>
<td>ADPglucose pyrophosphorylase</td>
</tr>
<tr>
<td>AMY3</td>
<td>α-amylase 3</td>
</tr>
<tr>
<td>ANOVA</td>
<td>analysis of variance</td>
</tr>
<tr>
<td>ATP</td>
<td>adenosine triphosphate</td>
</tr>
<tr>
<td>BAP</td>
<td>6-benzylaminopurine</td>
</tr>
<tr>
<td>BCA</td>
<td>bicolchominic acid</td>
</tr>
<tr>
<td>BE</td>
<td>branching enzyme</td>
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<tr>
<td>Bp</td>
<td>base pairs</td>
</tr>
<tr>
<td>BSA</td>
<td>bovine serum albumin</td>
</tr>
<tr>
<td>CBM</td>
<td>carbohydrate-binding module</td>
</tr>
<tr>
<td>DEPC</td>
<td>diethylpyrocarbonate</td>
</tr>
<tr>
<td>DHAP</td>
<td>dihydroxyacetonephosphate</td>
</tr>
<tr>
<td>DP</td>
<td>degree of polymerization</td>
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<tr>
<td>DTT</td>
<td>dithiothreitol</td>
</tr>
<tr>
<td>EDTA</td>
<td>ethylenediaminetetraacetic acid</td>
</tr>
<tr>
<td>EoD</td>
<td>end of day</td>
</tr>
<tr>
<td>EoN</td>
<td>end of night</td>
</tr>
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<td>EtOH</td>
<td>ethanol</td>
</tr>
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<td>Expt</td>
<td>experiment</td>
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<tr>
<td>F1,6BPase</td>
<td>fructose-1,6-bisphosphatase</td>
</tr>
<tr>
<td>F6P</td>
<td>fructose-6-phosphate</td>
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<tr>
<td>FBA</td>
<td>fructose-1,6-bisphosphate aldolase</td>
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<tr>
<td>FEC</td>
<td>friable embryonic callus</td>
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<td>FK</td>
<td>fructokinase</td>
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<td>FR</td>
<td>fibrous root</td>
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<td>Fru</td>
<td>fructose</td>
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<td>FW</td>
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<td>G1P</td>
<td>glucose 1-phosphate</td>
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<td>G6P</td>
<td>glucose 6-phosphate</td>
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<td>G6PDH</td>
<td>glucose-6-phosphate dehydrogenase</td>
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<td>GAP</td>
<td>glyceraldehyde-3-phosphate</td>
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<td>GBSS</td>
<td>granule bound starch synthase</td>
</tr>
<tr>
<td>Glc</td>
<td>glucose</td>
</tr>
<tr>
<td>GPT1</td>
<td>plastidial hexose-phosphate translocater</td>
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<tr>
<td>GWD</td>
<td>glucan, water dikinase</td>
</tr>
<tr>
<td>H+</td>
<td>proton</td>
</tr>
<tr>
<td>HXK</td>
<td>hexokinase</td>
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<td>HPAEC</td>
<td>high pH anion exchange chromatography</td>
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<tr>
<td>IITA</td>
<td>International Institute for Tropical Agriculture</td>
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<tr>
<td>Int</td>
<td>internodium</td>
</tr>
<tr>
<td>INV</td>
<td>invertase</td>
</tr>
<tr>
<td>IRGA</td>
<td>infrared gas analyser</td>
</tr>
<tr>
<td>ISA</td>
<td>Isoamylase</td>
</tr>
<tr>
<td>LC</td>
<td>liquid chromatography</td>
</tr>
<tr>
<td>LDA</td>
<td>limit-dextrinase (pullulanase)</td>
</tr>
<tr>
<td>LSF2</td>
<td>like sex4 2</td>
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<td>Abbreviation</td>
<td>Full Form</td>
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<tr>
<td>Mal</td>
<td>maltose</td>
</tr>
<tr>
<td>MeOH</td>
<td>methanol</td>
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<tr>
<td>Mops</td>
<td>3-(N-morpholino)propanesulfonic acid</td>
</tr>
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</tr>
<tr>
<td>NAD+/NADH</td>
<td>nicotinamide adenine dinucleotide</td>
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<tr>
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<td>phosphoglucomutase</td>
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<td>PPD</td>
<td>post-harvest physiological deterioration</td>
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<td>Ppi</td>
<td>inorganic pyrophosphate</td>
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<td>PWD</td>
<td>phosphoglucon water dikinase</td>
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<td>starch excess</td>
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<td>SEX4</td>
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<td>SnRK1</td>
<td>Snf1-protein kinase</td>
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<td>SPS</td>
<td>sucrose phosphate synthase</td>
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<td>SR</td>
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<td>T6P</td>
<td>trehalose-6-phosphate</td>
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<td>TCA</td>
<td>tricarboxylic acid</td>
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<td>TCA cycle</td>
<td>ten days of pruning</td>
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<td>TEMED</td>
<td>tetramethylethylenediamine</td>
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<td>TPS</td>
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<td>Tris</td>
<td>tris(hydroxymethyl)aminomethane</td>
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<td>TTBS</td>
<td>tris-buffered saline with tween-20</td>
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<td>ZDP</td>
<td>zero days of pruning</td>
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1. Introduction

1.1. Cassava – an important starch crop

Cassava (Manihot esculenta Crantz) belongs to the five important starch crops beside, rice, wheat, potato and maize. In recent years, its commercialization increased markedly. World market assessment revealed a 9% increase in cassava productivity within the years 2006-2010 (www.fao.org/giews; Food outlook 2008 and 2012). While in Africa cassava is mainly a strategic crop in terms of food security and poverty reduction, an increased industrial interest is observed on the Asian market. Especially in Thailand, one of the leaders for cassava starch production, this market is supported by the government (www.fao.org/giews; Food outlook May 2012). Hence, the interest in cassava biology in respect of starch production increased during the last decades. One main focus in cassava research is the improvement of cassava as a starch crop by investigating storage root production, starch properties and to increase yield in order to attribute more value to this crop.

1.2. Physiology of cassava

Manihot esculenta Crantz or cassava is perennial, shrubby crop that belongs to the family of Euphorbiaceae. It originates from South America, most likely from Brazil, and is grown for its starchy roots in tropical and subtropical regions as a food and feed crop. As a crop it shows several good characteristics like stress tolerance, tolerance for limited soil-nutrient and, as it is a perennial crop, there is no defined harvesting time. Thus, in South America and Africa, cassava is grown by small-scale farmers as a security food crop along with other crops in intercropping systems. Cassava is vegetatively propagated from stem cuttings. Older parts of mother plants are cut into 20-30 cm sticks which are transplanted to soil. The performance of a new plant depends on the fitness of the mother plant. Harvesting of storage root is performed between seven and twelve months after planting. Cassava roots can be harvested when needed. However, fresh roots need to be used immediately or further processed due to rapid post-harvest physiological deterioration (PPD). This process happens within 24-72h where after storage root become unpalatable (Sanchez et al., 2006). With respect to its economic use, PPD is a major drawback as harvested roots have a short shelf live. Hence, harvested storage roots are often further processed to chips or flour.

Cassava synthesizes cyanogenic glycosides (CG), linamarin and lotaustral in all plant tissues. Cyanogenic glycosides are involved in herbivour defence, where tissue damage brings together CG with specific enzymes. In subsequent enzymatic reactions linamarin and lotaustral are converted to the neurotoxic cyanide (Mcmahon et al., 1995; Du et al., 1995). Hence, before consumption cassava tissues need to be prepared to detoxify them. Depending on the CG content cassava varieties are
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broadly categorized into being sweet (low CG content) or bitter (high CG content) (Ceballos et al., 2004).

Cassava has two types of roots; fibrous roots involved in nutrient uptake and thick storage roots containing high starch levels (up to 80% of dry weight). Fibrous roots are built at the lateral side of stem cuttings. During growth some fibrous roots undergo a developmental transition to form starchy storage roots. This occurs by radial thickening and starch deposition in the phloem and xylem parenchyma cells (Teerawanichpan et al., 2008).

1.3. Starch – an important raw material

For the diverse applications in the starch industry, a raw material is needed that shows a number of specific properties. Knowledge about starch metabolism is growing, through many ground-breaking studies performed on model plants like Arabidopsis thaliana. Thanks to such studies, many of the enzymes involved and the regulatory mechanisms controlling them have been described. This knowledge comes from leaf tissue which synthesises starch during the day and degrades during the following night to meet the metabolic needs of the plant and fuel growth in the dark (reviewed in Streb and Zeeman, 2012; Stitt and Zeeman, 2012; Smith and Stitt, 2007; Zeeman et al., 2010).

Two kinds of starches can be distinguished in plants which fulfil different storage requirements. Transitory starch in photosynthetic tissues like Arabidopsis leaves undergoes a diurnal cycle of synthesis and degradation. In non-photosynthetic tissues (i.e. potato tubers, cassava storage roots, maize kernels) carbohydrate is translocated from the photosynthetic tissue, imported into the amyloplast and converted to starch. Starch in amyloplasts is built-up and stored over a long-term period (Geigenberger, 2003; Sonnewald and Kossmann, 2013). Cassava produces both transient and storage starch, but neither process has been studied in depth at the molecular genetic level in this species.

Starch originating from different botanical sources behave in a different physico-chemical way. The tissue as well as the species it is extracted from defines the properties of starch. The granule size and the amylose to amylopectin ratio both contribute to defining the starch properties. In pharmaceutical industries, starch is used as a filling material in tablets, for which starch with a small granule size is ideal. In the food industry, starch is used as a binding agent in processed foods in addition to being a carbohydrate source. For this, starches with low amylose contents are often preferred for their stable gelling properties when heated in water (i.e. gelatinised). Native starches are often pre-treated either chemically or physically in order to improve or deliver the required properties required by the various branches of the food industry. In the paper industry starch is used as a coating agent. For this, starches are pre-treated with harsh chemical methods to insert charged
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groups. In this context, naturally phosphorylated starch is used for paper industry. Starch phosphorylation is the only natural modification of the glucose units that introduces a charged group. For this reason, there is an interest in increasing in total phosphate bound to native starches. This could potentially decrease the pre-treatments or even make them unnecessary. Omitting such harsh chemical treatments would reduce processing costs and be better for the environment.

1.4. Composition of starch and its architecture

Starch is an inert polyglucan composed of two molecules, amylose and amylopectin. Amylose has an estimated molecular weight of $10^5$-$10^6$ Daltons (Perez and Bertoft, 2010) consists of essentially linear $\alpha$-1,4 linked glucose chains with a low proportion of $\alpha$-1,6 linkages (branch points). Amylopectin has an estimated molecular weight of $10^7$-$10^9$ Daltons (Yoo and Jane, 2002) and consists of shorter, linear $\alpha$-1,4 linked chains with high degree of $\alpha$-1,6-branches (~5%; Perez and Bertoft, 2010). Amylopectin is responsible for the crystalline structure of starch granules. The branches of $\alpha$-1,6 linkages lay within a specific layer, the so called amorphous layer. Amorphous layers alternate with crystalline layer that contain mainly linear $\alpha$-1,4 linked glucan chain segments. These linear chains form double helices then pack in an ordered pattern. This arrangement gives starch its insoluble, semi-crystalline properties as water molecules are expelled. These alternating layers make up the crystalline zones of starch granules which can be viewed as a ring-like structure (Figure 1.1). The formation of helices and their arrangement differ depending on the starch type and plant species. The helices arrange either in an A-, or B- type crystallinity. In an A-type starch, typically found in cereals, the helices are packed together densely in a monoclinic unit cell, whereas in a B-type starch, characteristic for tuberous starch, is arranged in an open hexagonal way with water-filled space between the helices (Blennow and Engelsen, 2010). In some species, a mixture of A- and B-type packing is observed. This so-called C-type starch is found in pea and cassava (reviewed in Damager et al., 2010).
1.5. Carbon assimilation and storage: From source to sink tissue

Starch is a storage compound found in many plant tissues. In leaves carbon for starch biosynthesis comes from the assimilated CO₂ during photosynthesis. In contrast, in heterotrophic tissues, the carbon for starch biosynthesis comes from sucrose transported from the leaves. Despite the differences in the way of carbon is supplied, there are many similarities in how starch itself is synthesized. In the following part, the two pathways will be described.

1.6. Carbon assimilation by photosynthesis

Plants assimilate carbon during the day via photosynthesis. Photosynthesis is partitioned into light-dependent and light-independent reactions. In the light reactions light energy is captured and converted into chemical energy, used to catalyse the light-independent reactions where atmospheric carbon dioxide is incorporated into carbon compounds that fuel cellular metabolism and biomass production. Light is captured in the chloroplast thylakoid membranes by chlorophyll and accessory pigments of the light harvesting complexes. This energy is transferred to the photosystem II, where it excites electrons derived from the splitting of water molecules. Electrons flow along the photosynthetic electron transport chain, a series of redox reactions, transports protons across the thylakoid membrane into the lumen, creating a proton gradient. This gradient is used by the proton-
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Driven ATPase to synthesise ATP from ADP and inorganic phosphate. The electrons are further energised in photosystem I and then used to reduce NADP to NADPH.

The generated chemical energy and reducing power is primarily used in the assimilation of atmospheric CO\(_2\) via the Calvin Cycle (the light-independent reactions of photosynthesis).

The cycle has 3 parts: carboxylation, reduction and regeneration. During carboxylation atmospheric CO\(_2\) is assimilated by the enzyme Ribulose-1,5-bisphosphate-carboxylase/oxygenase (RuBisCo) yielding 2 molecules of 3-phosphoglycerate (3-PGA). This is converted to triose-phosphates (TP), a fraction of which can be transported to the cytosol for sucrose synthesis or retained in the chloroplast for starch synthesis. Most TP is used to regenerate RuBP via several enzymatic steps. One of the intermediates generated is fructose 6-phosphate (F6P) that is used for starch synthesis.

Assimilated carbon is partitioned between starch and sucrose synthesis. Sucrose is the primary product, synthesized in the cytosol and exported to heterotrophic tissues via the phloem. Starch in the chloroplast is transiently stored during the day and degraded during the subsequent night, when no photosynthesis occurs. The extent of partitioning into starch depends on the need of the plant and on the species. For Arabidopsis it was reported that during the day up to 50% of the assimilated carbon is subjected into starch (Zeeman and Ap Rees, 1999).

1.7. **Starch synthesis in chloroplasts**

In the starch synthesis pathway (Figure 1.2), F6P is first isomerized by phosphoglucoseisomerase (PGI) to glucose-6-phosphate (G6P). Then, G6P is converted to glucose 1-phosphate (G1P) by phosphoglucomutase (PGM). ADPglucose pyrophosphorylase (AGPase) catalyses the committed step in starch biosynthesis, using G1P and ATP to generate ADP-glucose and inorganic pyrophosphate (PPI). AGPase is highly regulated and, although it catalyses a reversible reaction, the action of inorganic pyrophosphatase hydrolyses pyrophosphate rendering ADPglucose production essentially irreversible *in vivo*. AGPase is regulated by redox regulation on the one hand (Hendriks et al., 2003). On the other hand, its activity is controlled allosterically by the levels of inorganic phosphate (Pi), an inhibitor, and triose-P, an activator (Preiss et al., 1988).
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![Figure 1.2 Pathway of starch synthesis in chloroplasts](image)

Carbon assimilated via the Calvin cycle is partitioned with a fraction exported to the cytosol for sucrose synthesis and a fraction retained in the chloroplast for starch synthesis. Redox activation and allosteric regulation of AGPase controls the flux of carbon into starch. Abbreviations: Fru6P, fructose 6-phosphate; Glc1P, glucose 1-phosphate; Glc6P, glucose 6-phosphate; TPT, triose-phosphate/phosphate translocator. (Zeeman et al., 2007)

The ratio of these two metabolites changes according to supply of photo-assimilates and the demand for them, helping to regulate partitioning into starch. It was also shown that T6P, a compound involved in sucrose signalling, is able to promote the redox-activation of AGPase. Evidence for the linear pathway of starch synthesis comes from Arabidopsis mutants lacking each of the three enzymes (PGM, PGI, AGPase; Caspar et al., 1985; Lin et al., 1988; Yu et al., 2000). Compared to wild-type plants these mutants are unable to accumulate significant amounts of starch in their leaves. Instead they accumulate 4-5 times more soluble sugars during the day than wild-type plants (Caspar et al., 1985; Gibon et al., 2002).

Starch itself is synthesized by the coordinated activities of three enzymes. Linear chains of amylopectin and amylose are synthesized by starch synthases. Starch synthases transfer the activated glucosyl moiety of ADP-glucose to the non-reducing end of a pre-existing glucan chain, elongating it by one glucose unit. There are five classes of starch synthases in plants (Ball and Morell, 2003). Four of these starch synthases are soluble (SS1-4) whereas the fifth is termed granule bound starch synthase (GBSS). The granule bound starch synthase (GBSS), as the name
implies is found within the starch granules and is responsible for amylose synthesis. Mutant plants (e.g. maize _waxy_ mutant) lacking the GBSS activity are amylose free (Shure et al., 1983).

The synthesis of amylopectin involves several steps in order to achieve its semi-crystalline structure. Soluble starch synthases (SS1-SS3) elongate existing glucan chains. Mutant analysis revealed that each isoform prefers to elongate glucan chains of different lengths. The SS1 isoform is thought to synthesis short glucan chains with a degree of polymerization (DP) of around 10 glucose units (Delvalle et al., 2005). The SS2 and SS3 isoforms elongate longer glucan chains. Pea mutants lacking SS2 have amylopectin with an altered structure, containing excessive small (DP<10) and long (DP>25) glucan chains (Craig et al., 1998), but deficient in intermediate length chains. The SS2 knock-out mutant of _Arabidopsis_ also has amylopectin with decreased numbers of intermediate-length chains (DP12 to DP28; Zhang et al., 2005). For SS3 no change in amylopectin synthesis was observed in Arabidopsis mutant (Zhang et al., 2005), though the double mutant _Atss2ss3_ displayed a strong reduction in DP12 to DP28 chains, and it was suggested that these two isoforms have some redundancy in their activities (Zhang et al., 2008).

The SS4 isoform is somewhat unique in that it appears to have a role in starch granule initiation. Arabidopsis mutants lacking SS4 had a decreased number and altered morphology of starch granules compared to the wild type, even though no change in amylopectin structure was observed. Interestingly, the double mutant _Atss3ss4_ is essentially starch free suggesting that SS3 can partially compensate for SS4 in granule initiation (Roldan et al., 2007; Szydlowski et al., 2009). Starch granule initiation is far from understood.

To introduce α-1,6-branch points, branching enzymes (BE) act on the linear substrates generated by starch synthases. Branching enzymes cut α-1,4 linked glucan chains and transfer the cut segment to a C6 hydroxyl of a glucose unit on the same or an adjacent chain, introducing an α-1,6 linkage. In plants, two classes of branching enzyme exist, SBEI and SBEII. The BEs act on linear glucan chains with a minimum length of DP12, transferring at least 6 glucose units (Takeda et al., 1993). A third enzyme class helps to give starch its semi-crystalline structure by selectively removing some branch points. This is done by the debranching enzymes (DBE), which hydrolyse α-1,6 glucose linkages. The DBEs can be classified into two sub-groups; isoamyloses (ISA) and limit-dextrinases (LDA). LDA acts preferentially on substrates with small side chains, like the yeast pullulan (α-1,4 linked maltotriose linked together with α-1,6 bond) and limit dextrins produced during starch breakdown. ISAs do not act on pullulan, probably needing longer linear chains before the branch point. However, ISAs can further be divided into three sub-classes ISA1-3. For starch synthesis, ISA1 and ISA2 are most relevant. Mutants lacking ISA1 have been described in several species. All accumulate a glycogen-like glucan polymer as well or instead of insoluble granules. Thus, ISA1 is proposed to trim the glucans to
promote the formation of semi-crystalline structures. In most species examined, ISA2 is non-catalytic and acts in a complex with catalytic ISA1 subunits (Hussain et al., 2003). ISA3 is, by contrast, implicated in starch degradation (see below).

1.8. Starch degradation in leaves

1.9. Starch phosphorylation

To meet the carbon need in the dark, leaf starch is degraded. The initial step of starch degradation requires glucan phosphorylation. In potato, the isolation of proteins capable of binding starch led to the identification of glucan, water dikinase (GWD). Repression of this enzyme in potato led to an 85% drop in total starch bound phosphate and increased starch levels in leaves (Lorberth et al., 1998). Similarly, the Arabidopsis gwd mutant (sex1) displays elevated starch levels and slow growth, as the plants lack carbon supply during the dark period (Yu et al., 2001). GWD catalyses the transfer of the β-phosphate of ATP to the glucose moieties while the γ-phosphate of ATP is concomitantly released (transferred to water) to produce orthophosphate (Pi) and AMP (Mikkelsen et al., 2005). It was shown that GWD phosphorylates the C6 position of the glucose residues (Ritte et al., 2006). Upon phosphorylation by GWD, a second kinase, phosphoglucan water dikinase (PWD) catalyzes the phosphorylation of the C3 position of different glucose residues (Baunsgaard et al., 2005; Kotting et al., 2005). PWD, as its name implies, needs the pre-phosphorylation by GWD. Starch phosphorylation was shown to solubilize starch granule surface, presumably by disrupting and unwinding the helical structures of amylopectin (Blennow and Engelsen, 2010). This solubilisation renders starch granules accessible for hydrolytic enzymes involved in starch degradation, such as exoamylases (i.e. BAM1, BAM3) and debranching enzymes (i.e. ISA3) (Edner et al., 2007) (Figure 1.3).
Figure 1.3 The pathway of starch degradation in chloroplasts and the role of transient glucan phosphorylation

Maltose and malto-oligosaccharides are released from the surface of the starch granule during degradation. Maltooligosaccharides are metabolized in the stroma. Maltose and glucose are exported to the cytosol. Estimated fluxes are indicated by relative arrow size. Dashed arrows represent the minor steps in Arabidopsis. Inset is a model depicting the role of phosphorylation by GWD and PWD in disrupting the packing of amylopectin double helices (gray boxes). This allows the release of maltose and malto-oligosaccharides (black lines) by β-amylases (BAMs) and DBE (ISA3). Phosphate (red dots) is concomitantly released by SEX4 to allow complete degradation (Zeeman et al., 2010).

It was shown many years ago that β-amylases are not able to act past phosphate residues on glucan chains (Takeda and Hizukuri, 1981). Thus, for efficient starch degradation phosphate residues introduced by GWD and PWD need to be released again. In Arabidopsis two genes have been shown to encode active phosphoglucan phosphatases. Functional characterization of these enzymes in Arabidopsis (AtSEX4, AtLSF2) showed that sex4 mutants have high starch levels and slow growth compared to wild-type plants, and also accumulate phospho-oligosaccharides. Total glucan-bound phosphate (starch and phospho-oligosaccharides) was six times higher in sex4 mutants than in wild type plants. SEX4 preferentially removes phosphate residues from C6-position of glucose residues (Kotting et al., 2005; Hejazi et al., 2010). The second isoform, LSF2 was shown to specifically release phosphate from the C3 position of the glucose residues (Santelia et al., 2011). Interestingly, the single mutant lsf2 behaves like wild-type plants with respect to starch and phospho-oligosaccharide.
levels. However, total starch bound phosphate levels are 25% higher than in the wild type, specifically due to an increase in C3-bound phosphate. Although no starch excess phenotype was observed for lsf2, the double mutant sex4lsf2 showed an even more severe starch-excess phenotype and the accumulation of phosphor-oligosaccharides (Santelia et al., 2011). This shows that in the sex4 mutant lines LSF2 activity contributes to starch breakdown even if it cannot substitute for the lack of SEX4.

1.10. **Starch hydrolysis in chloroplasts**

The opening of the double helical chains makes the glucans accessible for hydrolyzing enzymes like α- and β-amyloses and debranching enzymes (LDA, ISA3). In Arabidopsis leaves starch degradation is predominantly catalyzed by the plastidial exoamyloses BAM1 and BAM3, which release maltose from the non-reducing ends of α-1,4 glucan chains. Maltose is the major degradation product from β-amylolytic hydrolysis of transitory starch (Weise et al., 2004; Fulton et al., 2008), which is transported to the cytosol through the maltose exporter 1 (MEX1; Niittyla et al., 2004). However, β-amyloses are not able to hydrolyse α-1,6 glucan bonds. Thus, they act no further than few glucose units close to the branch point.

Characterization of starch degrading enzymes in cereal endosperm revealed that α-amyloses are important upon germination. The situation appears to be different in Arabidopsis. There are three α-amylase isoforms in Arabidopsis, but only one is localized to the plastid (AMY3). In contrast to the cereal endosperm, it was shown that α-amyloses play a minor role in starch degradation. Mutants lacking α-amylases metabolize starch normally (Yu et al., 2005) suggesting that α-amyloses are not crucial in starch degradation. Only in plants already deficient in starch metabolism due to the lack of other proteins was a contribution of AMY3 observed. For example, it was shown that phospho-oligosaccharides were reduced while starch content was elevated in the double mutant sex4amy3, compared to the sex4 single mutant (Kotting et al., 2009). This suggests that AMY3 releases branched oligosaccharides from the starch granule, at least in the sex4 mutant background.

Branch points on the granule surface and in branched oligosaccharides are hydrolysed by debranching enzymes ISA3 and LDA resulting in linear glucan chains which can be further hydrolysed by β-amyloses. In the chloroplast, a disproportionating enzyme (DPE1) recycles short maltooligosaccharides to release glucose (Critchley et al., 2001; Lu et al., 2006). Glucose is also transported to the cytoplasm by the plastidial glucose transporter (pGlcT; Cho et al., 2011). Another enzyme thought to be involved in starch mobilisation is starch phosphorylase (PHS1). PHS1 catalyses the reversible reaction which releases G1P from linear glucans. It has long been speculated that
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starch phosphorylases are involved in starch degradation, however mutant analysis only displayed a phenotype under stress conditions (Zeeman et al., 2004).

Maltose, once exported to the cytosol, is further metabolized to provide substrates for downstream pathways (e.g. sucrose synthesis). The cytosolic glucosyltranferase (DPE2) splits maltose, releasing one and transferring the other to an acceptor, probably a cytosolic heteroglycan (Chia et al., 2004; Fettke et al., 2006). The free glucose is phosphorylated by hexokinase and enters the hexose-P pool. A cytosolic starch phosphorylase (PHS2) acts on the heteroglycan, releasing or adding G1P. Thus, supply of substrates for various metabolic processes is maintained during the night.

1.11. Sucreose synthesis

Sucrose, a non-reducing disaccharide consisting of one molecule glucose and one fructose, is synthesized in the cytosol. In most plants, sucrose is transported from the source to the sink or stored in the vacuoles. Furthermore, plants often accumulate sucrose upon cold, drought or salt stress to maintain osmotic balance and to help stabilize proteins and membranes.

As described earlier, triose-phosphates (TP) synthesized during photosynthesis are exported from the chloroplast by the triose-phosphate/phosphate translocator (TPT) in exchange for orthophosphate (Pi). In the cytosol, TP provides substrates for diverse pathways (protein synthesis, organic acid or cell wall synthesis) but most is utilized to synthesize sucrose, at least in fully expanded leaves. First, TP is condensed to fructose-1,6-bisphosphate (F1,6BP) by aldolase. F1,6BP is then dephosphorylated by fructose-1,6-bisphosphatase (F1,6BPase) to F6P. In the cytosol F6P, G6P and G1P are equilibrated by the cytosolic phosphoglucoisomerase (cPGI) and phosphoglucomutase (cPGM), respectively. G1P is converted to UDP-glucose (UDPGlc) by UDPGlc pyrophosphorylase, using UTP and releasing PPi. The hexose-phosphate F6P and UDPGlc are then utilized to synthesize sucrose by the sequential reactions of sucrose-6-phosphate synthase (SPS) and sucrose-6-phosphate phosphatase (SPP).

The synthesis of sucrose is strongly regulated. The activity of SPS is regulated via complex allosteric feed forward and feedback mechanisms that integrate the availability of substrates for sucrose synthesis with the demand for sucrose in sink tissues. A decreased demand in sink tissues leads to an accumulation of sucrose in leaf mesophyll cells. An increase in sucrose leads to inhibition of SPS which causes an increase in F6P since this is not further utilized. This in turn influences levels of the regulatory metabolite fructose 2,6-bisphosphate (F2,6BP) - produced from F6P by fructose 2,6-bisphosphatase (F2,6BPase). F2,6BP inhibits F1,6BPase activity, limiting hexose-P production. As Pi is released in various steps of sucrose synthesis, inhibition of the pathway leads to less Pi in the cytosol, which restricts the export of triose-phosphate from the chloroplast. Increasing stromal TP and lowered Pi concentrations promotes starch synthesis through allosteric activation of
AGPase as described above. In addition, the accumulation of sucrose frequently correlates with an increase of trehalose-6-phosphate, which redox-activates AGPase (Kolbe et al., 2005). Thus, partitioning between sucrose and starch is both flexible but also tightly regulated to allow fast responses to changes in environmental conditions, and the supply of and demand for photoassimilates.

1.12. Sucrose transport

Sucrose is transported by the phloem from the site of synthesis (mature leaves; source) to the site of utilization (growing leaves, heterotrophic tissues; sink). From the mesophyll cells, sucrose diffuses symplastically through plasmodesmata, to the bundle sheath cells adjacent to the phloem, after which it is loaded into the phloem by one of three mechanisms (see below). The difference in concentration of solutes between the source, where sugars are synthesized and the sink, where sugars are unloaded and utilized, results in a hydrostatic pressure gradient that leads to a bulk flow of assimilates between the source and sink tissues.

In plants three mechanisms of phloem loading exist; apoplastic loading, symplastic loading and polymer trapping (reviewed in De Schepper et al., 2013). Species that transport raffinose instead of sucrose use polymer trapping, where sucrose is symplastically transported to specialized companion cells – intermediary cells - via plasmodesmata. There sucrose is converted to a higher molecular carbohydrate, raffinose or stachyose. Because of the higher molecular size of raffinose and stachyose, it is proposed that these carbohydrates cannot diffuse back through the plasmodesmata and are thus trapped in the companion cells and then transported in the phloem. In many woody species, phloem is symplastically loaded down a concentration gradient, without up-concentration, hence a completely passive way. However, the most common phloem loading is via the apoplast where the phloem cells are symplastically isolated from the mesophyll. Sucrose is transported symplastically to the phloem parenchyma transported into the apoplast by an efflux transporter (SWEET; Chen et al., 2012).

Sucrose is then actively loaded into the companion cells via sucrose/H⁺ co-transporters (SUT1, AtSUC2; Stadler and Sauer, 1996; Sauer, 2007). The proton motive force is built up via an H⁺-ATPase in the companion cell membrane.

In sink tissues sucrose unloading can be apoplastically or symplastically. For potato tuber it was shown that during tuberization the unloading changes from apoplastic to symplastic. In the tuberization initiation phase, when the stolon tip starts to grow, phloem tubers are symplastically isolated hence phloem unloading occurs via the apoplast (Viola et al., 2001). In contrast, phloem loading occurs symplastically in the developing potato tubers themselves. However, in detached
potato tubers exhibiting bud outgrowth, the phloem function shifts to apoplastic loading (Viola et al., 2007).

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1.13. Sucrose metabolism in heterotrophic tissues

Sucrose produced in the source tissues is transported to non-photosynthetic tissues and unloaded according to the demand of these sink tissues. In sink cells sucrose is either hydrolysed by an invertase (INV) to fructose and glucose or metabolized by sucrose synthase (SUS) to fructose and UDP-glucose using UDP (Koch, 2004). Alternatively it can be transported to the vacuole. There are 3 types of invertases: cell wall (cwINV), cytosolic (cINV), and vacuolar (vINV) invertases. SUSs are localized to the cytosol.

Depending on the developmental stage or ongoing physiological processes, sucrose may be preferentially cleaved by INVs or by SUSs. In general, hexoses favour cell division and expansion and INV is often seen to mediate the initiation and expansion of many new sink structures, often with vacuolar activity preceding that in cell walls. The action of cwINV coincides with the elevated expression of hexose transporters in some systems (Koch, 2004). Later, transition to storage and maturation phases is facilitated by changes in the hexose/sucrose ratio, and by shifts from INV to SUS mediated sucrose cleavage (Koch, 2004). SUS activity in mature storage tissues may be advantageous because it is energy-efficient compared with INVs. SUS releases only one hexose in contrast to INV which releases two this means that double the ATP is used in order to phosphorylate the hexose products of INVs. It was observed that O$_2$ concentration decreases within solid tissues in a potato tuber (Geigenberger et al., 2000), and correlating with this was a decrease in ATP/ADP ratio. This suggests that respiration and hence ATP synthesis may be lower. Hence, releasing only one free hexose by SUS might save energy within the glycolytic pathway. On the other hand, INV is thought to play a role in delivering hexose based signals and it can define the osmotic strength for sucrose unloading or in the vacuole.

In order to investigate the possibility to increase sink strength transgenic potato tubers expressing yeast INV either in the apoplast or in the cytosol were analysed. This analysis revealed that cytosolic expression led to large changes of metabolites, decrease in starch and increase of respiration. The apoplastic INV increased potato tuber size due to increase in water content. The authors of these studies suggested that the sucrose/hexose ratio depends on how and where sucrose is cleaved. This can lead to unpredicted changes in sugar signalling. Thus, an increase in extracellular hexose promoted respiration rather than increasing starch synthesis (Ferreira and Sonnewald, 2012).
1.14. Starch synthesis in amyloplasts
In heterotrophic tissues, starch synthesis occurs in the amyloplast via a similar pathway as in chloroplasts (see above). Unlike in chloroplasts, carbohydrates need to be transported from the cytosol across the plastid membrane to fuel starch synthesis. Cleavage of sucrose by SUS in the cytosol results in UDPGlc and fructose. Fructose is phosphorylated by hexokinases (HXK) or fructokinase (FK) yielding F6P, which is equilibrated with G1P and G6P by the activity of PGI and PGM. Carbohydrate is imported in form of G6P (or occasionally G1P) from the cytosol into the amyloplast (Hill and Smith, 1991; Kosegarten and Mengel, 1994; Kammerer et al., 1998). In the amyloplast stroma, subsequent steps convert G6P to ADPglucose as described above. The cereal endosperm is an exception as the precursor for starch synthesis; ADPG is also produced by a cytosolic AGPase and transported into the plastid from the cytosol. Indications that G6P is the major compound transported to the amyloplast in other species comes from transgenic or mutant plants lacking PGM in the plastid, which leads to decreased starch content in heterotrophic tissues (Caspar et al., 1985; Harrison et al., 1998; Fernie et al., 2002). The activity of AGPase in the amyloplast relies on the availability of ATP. This is maintained by an ADP/ATP translocator (Neuhaus et al., 1997).

1.15. Starch degradation in heterotrophic tissue upon germination and re-growth
Starch mobilization in heterotrophic tissue was shown to be different from the transitory starch degradation like cereals where starch degradation was described to occur by an amylolytic enzyme activity (Fincher, 1989). Thereby the accumulated starch in the endosperm is degraded upon the gibberellic acid signal released by the germinated seed. This signal stimulates the aleurone cell layer to initiate the production and secretion of α-amylase and other hydrolytic enzymes. Free glucose released in the endosperm space is taken up by the embryo, phosphorylated by hexokinases to hexose phosphates which supply the non-photosynthetic seedling with respiratory substrates and carbon skeletons for diverse cellular structures. However, knowledge about starch mobilization in heterotrophic tissues apart from cereals is very poorly understood.

1.16. Adding value to cassava as a starch crop
Cassava starch is low in protein and fat content compared to seed crops like rice, or wheat (Jobling, 2004). As aforementioned (Chapter 1.1) both its good, low-input growth and the physico-chemical properties of its starch make cassava a valuable starch crop. One drawback of cassava, though, is limited genetic variation, as it is multiplied by vegetative propagation. To introduce new desirable traits to cassava by breeding is challenging. In general, inbreeding by consecutive self-pollination is used to identify useful recessive traits. However, cassava is a monoecious plant where flowering time of female and male at the same branches is often separated in time. Hence, it is
challenging to define the right time to be able to perform crosses (Jennings and Iglesias, 2002; Ceballos, 2004). Moreover, generating seeds is slow, taking up to a year.

To increase cassava germplasm and to add value to it as a starch crop, identification of new lines was performed earlier, either by mutant screening (Carvalho et al., 2004; Ceballos et al., 2007; Ceballos et al., 2008) or by transgenic modification (Raemakers et al., 2005). Through genetics, plant lines affected in GBSSI (Raemakers et al., 2005; Ceballos et al., 2007), and putatively in ISA (Ceballos et al., 2008) and BE2 (Carvalho et al., 2004) have been described. All of these lines show differences in starch architecture and starch properties, potentially suitable for various industrial applications. With the progress made in biotechnology during the last decades it is now possible to generate transgenic lines (Bull et al., 2009) in cassava in which foreign genes are expressed or endogenous genes are repressed. This method provides the possibility to study the biochemical roles of one or more gene in more detail. However, in order to analyse gene functions in cassava starch metabolism knowledge about the basic growth behaviour and metabolic pathways are first needed. On the biochemical level very few genes involved in cassava starch metabolism were studied to date. It was shown that SBE2 transcript expression undergoes a diurnal oscillation and is induced upon sugar supply (Baguma et al., 2003; Baguma et al., 2008). Transcriptional analysis revealed the presence of a plastidic ATP/ADP transporter in a wide range of cassava plant tissues (Yuen et al., 2009). Moreover, a gene encoding for an α-amylase (designated as MeAMY2) was isolated from cassava storage roots (Tangphatsornruang et al., 2005). The authors reported that the sequence contains the active site and a carbohydrate binding domain. However, sequence analysis revealed closer homology to AtAMY2-like (At1g76130) than AMY3 from Arabidopsis.

1.17. Scope of the work

The increased use of cassava in starch industry leads to increased demand for variation in starch traits. Although some genes involved in cassava starch metabolism were isolated, information about biological relevance is missing thus far. To generate and analyse transgenic cassava plants basic knowledge about the carbohydrate metabolism is needed.

I first analysed cassava plants grown in a greenhouse, monitoring growth performance, the capacity for carbon assimilation and carbon allocation. Second, I sought to identify key enzymes involved in starch metabolism, with the main focus on starch mobilization. This is important in understanding the biological background on the one hand and to unravel target enzymes for future biotechnological applications on the other. Third, I attempted to introduce new starch traits to the cassava germplasm through biotechnology. Transgenic lines were designed based partly on current knowledge and partly according to my new findings.
2. Material and Method

All studies were performed with the African Cassava variety *Manihot esculenta* Crantz (cv. 60444) form the International Institute for Tropical Agriculture (IITA), Ibadan, Nigeria.

2.1. Greenhouse grown cassava

Cassava plants were propagated by taking stem cuttings from the lower, hardwood part of the stem of mother plants. The cuttings contained at least 2 axillary buds or a stem with 15 cm length. The stem cuttings were planted in soil (70% Klasmann Substrat 2 [pH 5.5 (CaCl2), fertilization 2.0 g/L], 30% Perlite) in a squared pot size (7x7x6 cm, V=195 cm³). Within 2 months, the rooted cuttings were transferred to bigger round pots (diameter 13 cm, V = 880 cm³) containing 40% Klasmann Substrate 2, 10 % Perlite, 50% lawn soil from Ricoter (40 % sand, 10% Perlite, 25% garden compost, 25% “Weisstorf”, 5kg m⁻³ chipples made of horn) and 6 g Osmocot extract from Scotts (11% N, 11% P, 18% K, 2% MgO). Mother plants grown for cuttings were cultivated and grown in 5-L pots containing 40% Klasmann Substrate 2, 10% Perlite, 50% lawn soil from Ricoter and 16 g Osmocot extract from Scotts. The plants were grown under greenhouse conditions under a 14 h light period at 20 kilolux minimal light intensity, 24°C, 60% humidity, and 10 h night period, 17°C and 50% humidity.

2.2. Growth analysis

2.2.1. Age determination

The developmental stage of cassava plants were determined by the height, number of axillary buds and leaves. The height was determined from the origin of sprouting to the apex. The number of nodes and leaves were counted from the apex leaf down to the origin of sprouting. The apex leaf (being visible from top view) was considered as youngest leaf 1 (L1) (Figure 3.1 A).

2.3. Photosynthetic capacity

Photosynthetic capacity of greenhouse grown cassava plants was determined using a portable Li-6400XT from Li-COR. The Li-6400XT device was connected to an infrared gas analyser (IRGA). Calibration of the device was performed as described in the manual. For each series of measurement a new CO2 cylinder (Licor Environmental GmbH, Bad Homburg, Germany) was used and the soda lime and the desiccant were exchanged if necessary. All measurements were performed with the following parameter settings: a stomata ratio of 0.5, an air flow of 250 µmol m⁻² s⁻¹ and a CO2 concentration of 400 ppm at ambient air humidity in the chamber. The light intensity varied
depending on the experimental set up (see paragraphs 2.3.1 and 2.3.2.). For the measurements, a chamber with integrated LED source is clamped over a single leaf and the gas exchange of a defined area (6 cm²) of the leaf was measured. As the area of cassava leaves is greater than 6 cm², the measurements were performed on each of the three middle lobes of a specific leaf.

2.3.1. Photosynthesis at different light intensities
To determine the photosynthetic rate at different light intensities, a series of light quanta was applied to a mature leaf (L4). The light series comprised 0, 25, 50, 100, 200, 400, 600, 800, 1200, 1500 µmol quanta m⁻² s⁻¹. For each position of the chamber, three measurement points per light intensity were logged with an interval of 10 s and a dead time of 90 s after the intensity changes. The three middle lobes per leaf were analysed for three individual plants.

2.3.2. Photosynthesis of leaves at different developmental stages
To measure the photosynthetic rate dependent on leaf age, the measurements were performed at a constant light intensity of 100 µmol quanta m⁻² s⁻¹. On each of the three middle lobe of the leaf, three independent measurement points were logged when the value was stable. The data was collected from leaves of different developmental stage (L4, L7, L10, L13, L16, L19) of three individual plants.

2.4. Iodine staining, microscopy
Starch visualization by iodine staining was performed as described in Hostettler et al. 2011. Briefly, leaf material was destained in hot 80% ethanol and submerged in iodine solution (I₂–KI) solution (0.34% (w/v) I₂ and 0.68% (w/v) KI) for staining. Stem and storage root tissue was stained directly with iodine.

2.4.1. Microscopy
The plant tissue samples (leaf, stem, storage root) were cut into lateral sections of 20 µm using a Vibratom (Leica VT1200 S) and stained with iodine. The samples were analysed under a Zeiss Axio Imager Z2 microscope.

2.5. Carbohydrate extraction
Insoluble and soluble carbohydrate extraction was performed as described in Hostettler et al. 2011. Plant material of leaf, stem and storage root was harvested and immediately frozen in liquid nitrogen. For leaf tissue, 8 discs with an area of 3.41 mm² each were punched out of the lobes. Except for the youngest leaf, which was too small, the disks did not contain the middle vein. Each tissue sample
consisted of 100-200 mg plant material. Stem and storage root samples were pulverized with the Geno/Grinder® 2010 from SPEX SamplePrep prior to further extraction. All tissue samples were grinded in an ice-cold 5-mL all-glass homogenizer with 3 mL ice-cold 0.7M perchloric acid. 2.7 mL of the homogenate were transferred into a 13-mL culture tube and spun down (3,000 g, 10 min, 4°C). After centrifugation, 2.2 mL of the supernatant was transferred into a new tube and neutralized to pH 6-7 by adding the appropriate volume of neutralization buffer (2 M KOH, 0.4 M MES). After precipitation of the potassium perchlorate (14.000 g, 10 min, 4 °C), aliquots were taken from the supernatant and stored at -20°C. The insoluble fraction was washed with 4 mL ddH₂O and spun down (3,000 g, 10 min, 4 °C). The supernatant was discarded and the pellet was washed 3 times with 80% ethanol. Between the washing steps the suspension was spun down as before. The pale or colourless pellet was dried and re-suspended in water to a final volume of 1 mL. The insoluble fraction was stored at -20 °C.

2.6. Carbohydrate measurements

2.6.1. Insoluble carbohydrate determination

For the carbohydrate measurements, the starch in the samples was first hydrolysed to glucose. This involved a gelatinization step at 95°C for 10 min after which the samples were mixed with digestion buffer (220 mM Na-acetate pH 4.8, 10 units α-amylace [EC 3.2.1.98, Roche Diagnostics], 12.6 units amyloglucosidase [EC 3.2.1.3, Roche Diagnostics]) or control digestion buffer (220 mM Na-acetate pH 4.8) in a 1:1 (v:v) ratio and incubated at 37°C for 4 h. The digest was spun down at 16,000 g for 10 min at 20°C. For glucose quantification 100 µL sample (for ΔOD340 0.2-0.5) was mixed in a 200 µL assay containing 25 mM Hepes-KOH pH 7.5, 1 mM MgCl₂, 1 mM ATP, 1 mM NAD⁺, 1.4 units hexokinase (EC2.7.1.1, Roche Diagnostics). The initial OD at 340 nm (OD₃₄₀) was determined. The addition of 1 unit glucose-6-phosphate dehydrogenase (EC1.1.1.49, Roche Diagnostics) to the assay triggers the conversion of glucose-6-phosphate to 6-gluconolactone thereby reducing NAD⁺ to NADH which was spectrophotometrically detected with a microplate reader (TECAN Infinite® M1000). The amount of NADH detected corresponds to the equivalent amount of glucose.

2.6.2. Soluble carbohydrate determination

2.6.2.1. Enzymatically

The contents of soluble sugars such as glucose, fructose and sucrose were analysed spectrophotometrically using an enzymatic assay. The enzymatic assay was comprised of three steps.
2. Material and Method

The first steps of the assay involved the measurement of glucose levels and were already described before (Chapter 2.6.1.). When the kinetic reaction for glucose reached the endpoint, fructose levels were determined by adding 0.7 units phosphoglucoisomerase (PGI, 2mg/mL, EC5.3.1.9, Roche Diagnostics). PGI converts fructose 6-phosphate (F6P) to glucose 6-phosphate (G6P) that then enters the same reaction pathway as described before and NADH is released and measured. When fructose kinetic reaction reached the saturation 10 units invertase (INV, EC3.2.1.26, baker yeast Fluka) was added to hydrolyse sucrose into glucose and fructose. Both, glucose and fructose then enter again the reaction pathway via G6PDH either directly or through PGI and can be monitored indirectly via the formation of NADH.

2.6.2.2. HPLC-PAD

Soluble sugars (glucose, fructose, sucrose and maltose) in the supernatant were measured using high pH anion exchange chromatography coupled to pulsed amperimetric detection (HPAEC-PAD) as described in Fulton et al. (2008) with minor modifications. Samples of the neutralized soluble fraction (100 µL) were applied to sequential 1.5-mL columns of Dowex 50 W and Dowex 1 (Sigma-Aldrich, Buchs, Switzerland). The neutral compounds were eluted with 4 mL of water, lyophilized, and re-dissolved in 100 µL of water. The sugars were separated on a Dionex PA-20 column according to the following conditions: eluent A, 100 mM NaOH; eluent B, 150 mM NaOH and 500 mM sodium acetate. The gradient was as follows: 0 to 7 min, 100% A; 7 to 26.5 min, a concave gradient to 20% A, 80% B (elution of sugars); 26.5 to 32 min, 20% A, 80% B (column wash step); 32 to 40 min, 100% A (column re-equilibration). Peaks were identified by co-elution with known sugar standards. Peak areas were determined using Chromeleon software (Dionex, Olten, Switzerland).

2.7. Protein extraction

2.7.1. Soluble protein extraction for Immunoblot analysis and native PAGE

Three hundred mg of frozen, pulverized tissue was homogenized with 1 mL ice-cold extraction buffer (100 mM Mops pH 7.2, 1 mM EDTA, 10% [v/v] ethanediol, 1% [w/v] PVPP, 1mM DTT, 1x proteinase inhibitor [Complete, Mini, EDTA-free, Roche Applied Science]). The proteins were homogenized using ice-cold all-glass homogenizer. The homogenate was sedimented by centrifugation (10min, 16.000g, 4°C) and the supernatant immediately used for native protein activity assays or stored at -80°C for further experiments.
2.7.2. Protein amount determination by Bradford

For total protein content determination, the BioRad Protein Assay (BioRad, Herculaeus, California) was performed following the manufacturer’s instruction. Bovine serum albumin (BSA, Sigma-Aldrich) served as a standard.

2.8. SDS PAGE

Soluble proteins were separated by SDS-PAGE. The stacking gel was composed of 3.75% (w/v) acrylamide/ bisacrylamide (37.5/1), 125 mM Tris-HCl pH 6.8, 0.1% (w/v) SDS, 0.05% (w/v) ammonium persulfate, 0.1% (v/v) TEMED and the separating gel of 7.5% (w/v) acrylamide/bisacrylamide (37.5/1), 375 mM Tris-HCl pH 8.8, 0.1% (w/v) SDS, 0.05% (w/v) ammonium persulfate, 0.05% (v/v) TEMED.

Proteins were mixed in a 1:9 (v/v) ratio with SDS sample buffer (0.1 M Tris-HCl pH 6.8, 40% [v/v] glycerol, 3% [w/v] SDS, 0.015% [w/v] bromophenol blue, 1.1% [w/v] DTT). Electrophoresis was performed in running buffer (25 mM Tris-HCl pH 8.3, 192 mM glycine, 0.1% [w/v] SDS) at 22°C at constant current of 15 mA per gel. PrecisionPlusProtein™ Standards (Biorad) were used as molecular weight markers. To visualize proteins on SDS gel the proteins were first fixed in 12% trichloroacetic acid (TCA) solution for 30 min and then the staining solution (5% [v/v] MeOH, 12.5% Ammonium sulfate, 2.5% ortho-phosphoric acid, (1-2 mL) 5% Coomassie blue G250) was added.

2.9. Western Blot

Proteins separated by SDS PAGE were transferred onto a PVDF-membrane by electroblotting in 119 mM Tris, 40mM glycine, pH8.3, 10% (v/v) methanol (blotting buffer) at constant 100V for 1 h at 4°C. Following transfer, the membrane was washed in TBS (20mM Tris-pH7.5, 500mM NaCl) for 10 min and incubated for 1h at 25°C in blocking solution (2% or 3% (w/v) non-fat dry milk in TTBS (TBS with 0.1% Tween-20) to block unspecific binding sites. After the blocking step the membranes were rinsed in TTBS for 1 min and subsequently the membrane was washed 3 times 10 min. The blots were incubated overnight with the primary antibody against GWD (Eurogentech, Cologne, Germany) or against the FLAG Tag (M2, Sigma Aldrich) in a dilution of 1/3000 or 1/1000, respectively. The antibodies were raised in rabbit (GWD) and mouse (M2). The corresponding secondary antibodies tagged with horse radish peroxidase (HRP) were mixed with 3% non-fat dry milk in TTBS and incubated at 20°C for 2h. The membrane was washed with TTBS once for 1 min and subsequently three times for 10 min. Chemiluminescence was detected using the Chemiglow West substrate following the manufacturers protocol (Proteinsimple, Santa Clara, California).
2.10. Determination of amylolytic activity

2.10.1. Native PAGE

For native gels, soluble proteins were mixed 1:9 (v/v) with 10x native sample buffer (50% [v/v] glycerol, 0.05% [w/v] bromophenol blue) and separated using 1 mm thick gels consisting of a stacking gel (3.75% [w/v] acrylamide/bisacrylamide (37.5/1), 125 mM Tris-HCl pH 6.8, 0.05% [w/v] ammonium persulfate, 0.1% [v/v] TEMED) and a separating gel (6% [w/v] acrylamide/bisacrylamide (37.5/1), 375 mM Tris-HCl pH 8.8, 0.05% [w/v] ammonium persulfate, 0.05% [v/v] TEMED). Electrophoresis was performed in running buffer (25 mM Tris pH 8.3, 192 mM Glycine) at 4°C, 100 V for 20 min followed with 20 mA constant current for 1 h. To detect amylolytic protein activity, the following substrates were added to the gel: 0.1% (w/v) amylpectin from potato starch (Sigma-Aldrich), 0.1% (w/v) β-limit dextrin (Megazyme International, Bray, Ireland) or 1% (w/v) red-pullulan (Megazyme International).

2.11. Proteome analysis, sample digestion, mass spectrometry and spectra analysis

2.11.1. Protein preparation

Total proteins were extracted according to a modified protocol from (Saravanan and Rose, 2004). Briefly, root material was homogenize on ice using a glass homogenizer in 1% (w/v) PVPP, 0.7 M sucrose, 0.1 M KCl, 0.5 M Tris-HCl, pH 7.5, 100 mM EDTA, 2% (v/v) β-mercaptoethanol, 2x protease inhibitor cocktail (Roche Applied Science, Penzberg, Germany). 1:1 ratio (v/v) phenol, pH 8.0 (Sigma-Aldrich) was added and spun down at 30 min at 4,000 g, 4°C. Proteins in the phenol phase were precipitated overnight at -20°C in 5 volumes of 0.1 M ammonium-acetate-100% methanol and after centrifugation (5 min at 4,000 g, 4°C) washed in 100% methanol and subsequently in 80% acetone. The air-dried precipitated proteins were resuspended in 4% SDS, 40 mM Tris pH 6.8, 2x protease inhibitor cocktail (Roche Applied Science). Protein concentration was determined using a BCA Protein Assay Kit (Thermo Scientific, Waltham, Massachusetts) before adding 40 mM DTT. Proteins were boiled 5 min at 95°C and 100 μg proteins were subjected to SDS-PAGE on 12% gels. The Gels were Coomassie-stained according to standard procedures and subsequently sliced into 14 fractions. Each gel slice was diced into small pieces. In-gel protein digestion was performed according to a modified protocol from Shevchenko et al (1996). After digestion, dried peptides were resuspended in 3% (v/v) acetonitril 0.2% (v/v) trifluoretic acid and
cleaned up using Sep-Pak Cartridges (Waters, Milford, Massachusetts, USA). Clean samples were dried and resuspended in 12 μL 3% (v/v) acetonitril, 0.2% (v/v) formic acid for mass spectrometry.

2.11.2. Mass spectrometry
Mass spectrometry analysis and database searches were done accordingly to Bischof et al., 2011 and Bischof et al., 2013. Peptides were analyzed on a LTQ Orbitrap mass spectrometer (Thermo Fischer Scientific, Bremen, Germany) coupled to an Eksigent-Nano-HPLC system (Eksigent Technologies, Dublin (CA), USA). Peptide mixtures were loaded onto laboratory-made capillary columns (75 μm inner diameter [BGBAnalytik, Böckten, Switzerland], 8 cm length, packed with Magic C18 AQ beads, 3 μm, 100 Å [Michrom BioResources, Auburn, CA, USA]). Peptides were eluted from the column by an increased acetonitrile concentration in the mobile phase from 5% (v/v) acetonitril, 0.2% (v/v) formic acid to 40% (v/v) acetonitril, 0.2% (v/v) formic acid over 74 min, followed by a 10 min wash step at 5% (v/v) acetonitril, 0.2% (v/v) formic acid. Full-scan MS spectra (300–2000 m/z) were acquired with a resolution of 60000 at 400 m/z after accumulation to a target value of 500000. Collision induced dissociation (CID) MS/MS spectra were recorded in data dependent manner in the ion trap from the six most intense signals above a threshold of 500, using a normalized collision energy of 35% and an activation time of 30 ms. Charge state screening was enabled and singly charge states were rejected. Precursor masses already selected for MS/MS were excluded for further selection for 120 s and the exclusion window was set to 20 ppm. The size of the exclusion list was set to a maximum of 500 entries.

2.11.3. Protein identification and label-free peptide quantification.
MS/MS spectra were searched with Mascot (Matrix Science, London, UK) version 2.3 against the cassava protein database Mesculenta_147_peptide.fa (ftp://ftp.jgi-psf.org/pub/JGI_data/phytozome/v7.0/Mesculenta/) with a concatenated decoy database supplemented with contaminants. Information about Arabidopsis AGI-homologue and protein description were obtained from the file Mesculenta_147_annotation_info.txt. (download from ftp://ftp.jgi-psf.org/pub/JGI_data/phytozome/v7.0/Mesculenta/) using a small awk script. The search parameters were: requirement for tryptic ends, one missed cleavage allowed, mass tolerance of ± 5 ppm. Beside carbamidomethylation of cysteines as fixed modification, oxidation of methionine was included as variable modification. Peptide identification was accepted with a minimal Mascot ion score of 23 and a Mascot expectation value ≤ 0.05. To increase protein identification confidence, a minimum of two unique peptides for each identified protein was required. The spectrum false discovery rate was calculated by dividing the number of decoy database spectrum assignments by
2. Material and Method

the number of spectrum assignments in the final dataset. The false positive rate was below 1% for all measured biological replicates. For the Progenesis analysis, a merged peaklist was generated.

Progenesis LC-MS analysis was done according to (Greer et al., 2012). Peptides were detected and quantified with Progenesis LC-MS software (version 2.5; Non Linear Dynamics) using default settings (no deconvolution/deisotoping, 200 most intense MS/MS peaks). Peak areas were calculated by Progenesis from imported Thermo RAW mass spectrometry files. The 14 gel lanes, each containing six biological samples were analysed separately and resulting quantification information was merged to obtain final protein abundances. For peak alignment, one sample was set as reference and the retention times of all other samples within the same gel lane were aligned. Around 20 manual landmarks were set before automatic alignment to create a maximal overlay of the two-dimensional feature maps. Features with only one charge or more than 3 charges were excluded from further analyses and all remaining features were used to calculate a normalization factor for each sample that corrects for experimental variation. For quantification, all unique peptides (with Mascot score ≥ 25 and p < 0.05, see above) of an identified protein were included and the total cumulative abundance was calculated by summing the abundances of all peptides allocated to the respective protein. No minimal thresholds were set for the method of peak picking or selection of data to use for quantification. Finally, quantification information of all 14 analyzed gel lanes were merged and statistical analysis of variance (ANOVA) was used to calculate p-values based on the sum of the normalized abundances across all 84 runs.

2.12. Construct design

2.12.1. Overexpression of potato StGWD in cv. 60444
Two pCAMBIA2300 plasmid constructs harbouring either the wild-type (pCAMBIA2300::StGWD) or redox-insensitive (pCAMBIA2300::StGWD<sub>C1084S</sub>) coding sequence (CDS) of potato GWD were obtained from Mikkel Glaring (University of Copenhagen, Copenhagen, Denmark). In both cases, the constructs were under the control of the 35S promoter and contained the native transit peptide of StGWD (JG388473; NCBI database) at the N-terminus. At the C-terminus, a FLAG-tag (Einhauer and Jungbauer, 2001) was added. The redox-insensitive sequence contains a nucleotide modification (5′-GC-3251-CT-3′) leading to an amino acid substitution of cysteine 1084 to a serine (C1084S) at the peptide level. Genotyping and verification of mutation sequence was performed with primers as indicated in Table 2.1.
2. Material and Method

### Table 2.1 Primer list for genotyping and sequencing the wild-type and redox-insensitive StGWD constructs (in bold the sequence for restriction sites).

<table>
<thead>
<tr>
<th>Primer</th>
<th>Sequence (5′-3′)</th>
</tr>
</thead>
<tbody>
<tr>
<td>StGWD_BamHI_rv</td>
<td>gcggatcTCACCTTATCATCAT</td>
</tr>
<tr>
<td>StGWD_BamHI_fw2</td>
<td>cgggatcATGAGTAATTCCCTTAG</td>
</tr>
<tr>
<td>StGWDSF</td>
<td>TCCAATGGTGAGACAAACCA</td>
</tr>
</tbody>
</table>

2.1.2.2. RNAi: Hairpin design

For RNA interference (RNAi), a hairpin construct was designed against three genes: *MeSEX4*, *MeLSF2* and *MeAMY3*. For each gene, a 190- 205 bp long template was amplified from the coding sequence which was prior tested to be unique to the specific transcript by performing a nucleotide BLAST search on the cassava genome database (www.phytozome.net). Accession numbers and sequence positions of the hairpin templates are given in Table 2.2. The target sequence of *MeSEX4* was first cloned in the pCR8 vector using the TOPO® TA Cloning® Kit from Life Technologies (Carlsbad, California). The *MeAMY3* sequence was first cloned in the pJET1.2 vector using the CloneJET PCR Cloning kit from Thermo Scientific. All primers are given in Table 2.3, set A). In a second step, the *MeSEX4* and *MeAMY3* sequences were re-amplified (primers in set B, Table 2.3) in the forward and reverse orientation and cloned into a modified plasmid of pBluescriptSKII (from H. Vanderschuren, ETH Zurich, Switzerland) containing a synthetic plant intron sequence forming a loop (57-165 bp of the M27939 sequence; Goodall and Filipowicz, 1989). The hairpin construct of *MeLSF2* (target sequence in both orientations linked with the loop) was de novo synthetized and ligated in the pBluescriptSKII by Eurofins MWG Operon (Ebersberg, Germany). All RNAi constructs were each subcloned into a modified pCAMBIA1301 vector containing the *Solanum tuberosum* class I patatin promoter (GQ352473.1 aligning 11-970bp, Naumkina et al., 2007) at the 3′ end (Figure 2.1).

### Table 2.2 Sequence position of the RNAi hairpin construct

<table>
<thead>
<tr>
<th>Construct</th>
<th>Accession (Phytozom.org)</th>
<th>CDS (bp)</th>
<th>Sequence position for hairpin construct (bp)</th>
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<tr>
<td>SEX4 RNAi</td>
<td>cassava4.1_009735m.g</td>
<td>1140</td>
<td>197-402</td>
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<tr>
<td>LSF2 RNAi</td>
<td>cassava4.1_013314m</td>
<td>858</td>
<td>41-231</td>
</tr>
<tr>
<td>AMY3 RNAi</td>
<td>cassava4.1_001362</td>
<td>2691</td>
<td>1-210</td>
</tr>
</tbody>
</table>
2. Material and Method

Table 2.3 Primer list used for hairpin cloning and genotyping (in bold the sequence for restriction sites).

<table>
<thead>
<tr>
<th>Primer name</th>
<th>Sequence (5’-3’)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Set A</strong></td>
<td></td>
</tr>
<tr>
<td>MeS4fw2</td>
<td>ATGAGAACATGAGAAAAATTT</td>
</tr>
<tr>
<td>MeS4rv8</td>
<td>ATTCTGCTTGCAACAGGACC</td>
</tr>
<tr>
<td>AMY3 forward</td>
<td>ATGTGCACCGTTGCCATTGAG</td>
</tr>
<tr>
<td>AMY3 reverse</td>
<td>AAAAGTTTCAAGAAGAGCGGT</td>
</tr>
<tr>
<td><strong>Set B</strong></td>
<td></td>
</tr>
<tr>
<td>AMY3 anti-sense forward (ClaI)</td>
<td>ATATCGATAATCTTACCTCAGAGTGGTACATGTCACCAGGTTGAG</td>
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<tr>
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<tr>
<td>AMY3-sense reverse (ClaI)</td>
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<tr>
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</tr>
<tr>
<td>terminatorRV</td>
<td>AGC GCA ACG CAA TTA ATG TGA</td>
</tr>
</tbody>
</table>
2. Material and Method

2.1.2.3. Agrobacterium tumefaciens transformation

Electrocompetent Agrobacterium tumefaciens strain LBA4404 (Rif<sup>50</sup> Strep<sup>100</sup>) were transformed with an RNAi construct or the full length CDS of StGWD-Flag tag, respectively. One µL the plasmid of interest was added to a 50 µL aliquot of competent cells of A. tumefaciens, hold on ice. The mix was transferred to pre-cooled Gene Pulser cuvettes (BioRad) and an electro shock of 1.5kV, 200 Ω was applied. After transformation, the cells were put back on ice and 750 µL of YEB liquid medium (5 g/L Beef extract, 1 g/L yeast extract, 5 g/L peptone, 5 g/L sucrose, 0.5 g/L MgCl<sub>2</sub>) was added. After 90 min, the cells were grown on YEB medium containing the respective antibiotics at 28°C for 2 days.

2.12.4. Tissue culture and FEC transformation

Cassava plantlets of the African genotype cv. 60444 were grown in a SANYO plant growth facility (Type MLR, Panasonic Biomedical Sales Europe B.V.) under a day-night regime (16h light, 8h dark, 27°C, 50 µmol m<sup>−2</sup> s<sup>−1</sup>). Transgenic cassava lines were obtained with Agrobacterium-mediated friable embryonic callus (FEC) transformation described in (Bull et al., 2009; Niklaus et al., 2011). The important steps of transformation are illustrated in a scheme in Figure 2.2. After transformation with A. tumefaciens harbouring the plasmid of interest, the transformed FECs were pre-selected on regenerating medium containing hygromycin antibiotics (Figure 2.2, step 2 and 3). Until step 4 the growth media are supplied with antibiotics for selection though in step 4 and 5 the media contain no antibiotics (Figure 2.2). In these steps (4, 5) new plantlets are regenerated. To confirm that the re-generated cassava plantlets contain the construct of interest a rooting test was performed on
growth media containing selection antibiotics (Figure 2.2, step 6). DNA was extracted and the insertion of the construct verified by PCR amplification using primers listed in Table 2.3 (set C).

2.13. Construct functional analysis

2.13.1. Starch isolation from transgenic cassava storage root and $^{31}$P NMR analysis
To measure the content of starch-bound phosphate, starch granules were purified from cassava storage roots according to Hostettler et al., 2011. The frozen material was first pulverized using a
2. Material and Method

Geno/Grinder® 2010 from SPEX SamplePrep. After resuspension in ice-cold starch extraction buffer (50 mM Tris-HCl, pH 8.0, 0.2 mM EDTA, 0.5% (v/v), the mix was homogenized for 3 min using a Waring blender. The homogenate was filtered through a 100 µm nylon mesh and the filtrate was spun down (15 min, 3.000 g, 20°C). The pellet was resuspended in starch extraction buffer and filtered through a 75 and 60 nylon mesh. The filtrate was overlaid on a 10 ml cushion of 95% (v/v) Percoll and 5% (v/v) 500 mM Tris-HCl, pH 8.0 and after centrifugation (15 min at 2.500g), the pellet was resuspended in SDS buffer (0.5% SDS [w/v]). The samples were spun down at 20.000g for 1 min and washed again in 1ml SDS buffer. The centrifugation and re-suspension steps with SDS buffer were repeated several times to get a clean, white pellet of starch granules. After this, SDS was washed away by five centrifugation/resuspension steps with water and a final wash with 80% EtOH. The starch pellet was dried under vacuum for 48 h.

Sample preparation for 31P-NMR analysis was done according to Santelia et al. (2011). Briefly, the starch samples were resuspended in a salt solution (3 mM NaCl, 1 mM CaCl2, pH6) and digested with α-amylase from pig pancreas (Roche Applied Science) and amyloglucosidase from Aspergillus niger (Roche Applied Sciences). 31P-NMR analysis was performed on an Avance III 600-MHz spectrometer equipped with a QCI CryoProbe (Bruker) at 303K.

2.13.2. Genomic DNA extraction

Leaf material was harvested and frozen in liquid nitrogen. After pulverisation with a mixer mill (MM301, Retsch) in a 1.5-mL Eppendorf tube containing glass beads, the plant material was resuspended in 900 µL DNA extraction buffer (7M Urea, 0.3 M NaCl, 50 mM Tris-HCl, pH 8.0, 20 mM EDTA, pH 8). Following centrifugation (13.000g, 20 °C, 15 min), the supernatant was mixed in a 1:1 (v/v) ratio with phenol: chloroform: isoamylalcohol (25:24:1; Carl Roth, Karlsruhe, Germany) and spun down for 15 min, 13.000g, at 20°C. Six hundred µL from the aqueous phase was transferred to a 1.5-mL Eppendorf tube containing 1:10 (v/v) 3 M Sodium Acetate, pH 5.2 and 1 µL RNaseA (20 mg/mL) was added and mixed well. To precipitate the DNA, isopropanol in a 1:1 (v/v) was added to the mixture and incubated for 1 h at -20°C. The precipitated DNA was spun down at 13.000g for 15 min at 20°C. The pellet was washed twice with 1 mL 70% ethanol and once with 100% ethanol. Between the washing steps the sample was spun down 13.000g, 15 min at 20°C. After drying the pellet under the air-flow it was re-suspended in 30 µL ddH₂O.

2.13.3. RNA extraction

Up to 200 mg of pulverized storage root samples (using a GenoGrinder, described in 2.6) were mixed with 600 µL of RNA extraction buffer (150 mM Tris-boric acid, pH 7.5, 2% SDS, 50 mM EDTA, pH 8.0)
2. Material and Method

during 2-5 min using a vortex. After adding 150 µL of 100% EtOH and mixing for 1 min on a vortex, 66 µL 5M potassium acetate were added and mixed for 1 min. Following the addition of 750 µL chloroform to denature proteins, the samples were mixed for 1 min and spun down at 13.000 g for 3 min at 20°C. Of the RNA containing aqueous phase, 500 µL was transferred to a new 2-mL Eppendorf tube. To the aqueous phase phenol: chloroform was added in a 1:1 (v/v) ratio. The mixture was spun down at 13.000 g, 1 min, 20°C. From the upper aqueous phase 400 µL was transferred to a new 2-mL Eppendorf tube. One mL of 100% RNase-free EtOH was added and mixed well. The RNA was precipitated at -80°C for 30 min and pelleted by 13.000 g, 30 min, 4°C. The supernatant was removed and 170 µL 80% RNase-free EtOH was added. The RNA was subsequently pelleted at 13.000 g, 3 min, 20°C. The supernatant was removed and the pellet re-suspended in DEPC water. To precipitate RNA, 25 µL 8M DEPC LiCl was added and incubated at -20 °C overnight. The RNA was pelleted at 13.000 g, 30 min, 4 °C and the supernatant was removed. To wash the pellet 170 µL 80% RNase-free EtOH was added and spun down (13.000 g, 3 min, 20 °C). The supernatant was removed and the pellet air dried under the flow hood for 5 min. Then the pellet was re-suspended in 25-50 µL DEPC water.
3. Cassava growth carbon assimilation and allocation analysis

3.1. Introduction

In plants two kinds of starches can be distinguished which fulfil different storage requirements. Transitory starch in photosynthetic tissues like Arabidopsis leaves undergoes a diurnal cycle of synthesis and degradation. In non-photosynthetic tissues (i.e. potato tubers, cassava storage roots, maize kernels) carbohydrate is translocated from the photosynthetic tissue, imported into the amyloplast and converted to starch. Starch in amyloplasts is built-up and stored over a long-term period (Geigenberger, 2003; Sonnewald and Kossmann, 2013). Cassava produces both transient and storage starch, but neither process has been studied in depth at the molecular genetic level in this species.

I first studied carbohydrate metabolism in leaves and storage root of cassava with the aim of drawing a basic framework of starch and carbohydrate metabolism. I measured physiological parameters and correlate them with the carbohydrate metabolism. My experiments were performed with greenhouse-grown cassava plants, grown under defined conditions to reduce environmental influences on the metabolism (such as variability in water availability, temperature, light intensities or soil-nutrient availability). Cassava physiological characteristics and yield performance in response to natural growth conditions as well as stress conditions were investigated in several studies performed on field grown cassava plants (El-Sharkawy et al., 1984; El-Sharkawy, 1990; Angelov et al., 1993). Comparisons of biomass with parameters such as photosynthetic rate and stomatal conductance revealed a positive correlation between the root biomass and photosynthesis (El-Sharkawy, 1990). Only few studies are reported dealing with greenhouse grown cassava plants (Edwards et al., 1990; Calatayud, 2000; Cruz, 2003).

To investigate the general performance of cassava in our greenhouse conditions, experiments were performed to unravel the general performance, in respect of growth and carbon assimilation. Therefore, the characteristics of several batches of greenhouse grown cassava plants was assessed and compared with photosynthetic capacity and the distribution of carbohydrates in different tissues at various developmental stages.
3.2. Growth analysis of greenhouse-grown cassava plants

3.2.1. Growth analysis of plant batches grown at different time points

Manihot esculenta Crantz plant batches were generated by stem cuttings from different mother plants. The plants were grown in a greenhouse for 4-5 months under defined light, climate, and soil-nutrient conditions (Chapter 2.1). For this thesis, six batches of plants were harvested at different times of the year for six individual experiments. Although the conditions were controlled, minimal variation of external, environmental influences like day length and light intensity could not be excluded. For the harvested batches, the homogeneity of the plants was determined. Individual plant height was measured from the apex - the emerging point of the youngest visible leaf - to the sprouting initiation site at the bottom. The number of leaves was assigned by the top-down counting, starting with the youngest leaf (number one) down to the initiation of sprouting (Figure 3.1 A). The number of leaves was determined by counting them from top to bottom. The numbering of internodes was done the same way where the first internode section was that between the first and second leaf. Although at the point of harvesting the plants were at a similar developmental stage, differences in height, number of leaves and of internodes were observed. Therefore, the above definition of tissue age facilitated the comparisons of plants and tissues at the same developmental stages in the different experiments (i.e. young, developing, mature, and aged leaves).
Figure 3.1 *Manihot esculenta* Crantz (cv. 60444) grown under greenhouse conditions for 4-5 months

A) The tissue was numbered according to the age and counted from the young, undeveloped to the old, mature tissue (L = leaf). B) Enlargement of the apex of cassava plant showing the youngest leaves, arrow pointing at the youngest leaf. C) Cassava fibrous roots (FR) and storage roots (SR).

Comparing the growth of the six plant batches, the mean plant height of the different batches was 110 cm ranging between 57 ± 5.97 cm (Photosynthesis Expt 1) to 137.79 ± 19.72 cm (RNAseq) (Figure 3-2 A). Variation in the number of internodes was between 24.3 ± 0.67 (Photosynthesis Expt 1) and 34.3 ± 1.2 (Photosynthesis Expt 2) (Figure 3-2 B). And the number of leaves ranged from 14.6 ± 2.01 (Proteome) to 25.83 ± 3.41 (RNAseq) (Figure 3-2 C).
For the six plant batches used in the different experiments for this thesis the three measures height (cm), number of internodes and number of leaves were determined. Mean ± SD (N = 3, 10, 24 as indicated).

Although the average of leaf number varied between batches, minimal variation was observed within each batch. An eventual connection between the parameters they were plotted against each other to reveal any dependency. Thus, a pairwise-comparison was performed on the collected data and linear regression was investigated (Figure 3-3). The comparison revealed that, within the harvested plants, none of these parameters were strongly correlated.
Figure 3.3 Pairwise comparisons over all six plant batches used for the described experiments

The comparison was performed between A) height (cm) vs. number of leaves, B) Number of internodes vs. number of leaves, C) number of internodes vs. height (cm). \( R^2 \) = linear correlation coefficient (N = 60).

3.3. Photosynthetic capacity measurements

I measured the photosynthetic capacity of greenhouse grown cassava plants using a LI-COR 6400 XT device connected to an integrated infrared-gas analyser (IRGA). This device has a chamber with integrated LED source, which is clamped over a single leaf and the gas exchange of a defined area (6 cm\(^2\)) of the leaf is measured. Cassava leaves are hand-shaped with multiple lobes and a surface area larger than 6 cm\(^2\). Thus, photosynthetic measurements were performed on the 3 middle lobes in triplicate (i.e. nine measurements) and the mean value taken as a representative value for photosynthetic performance. I investigated the influence of both light intensity and leaf age on the photosynthetic capacity so as to be able to relate this to carbohydrate content. For the analysis, CO\(_2\) concentration and air flow were kept constant (400 ppm; 250 mol s\(^{-1}\)).

3.3.1. Photosynthetic capacity of cassava leaves in dependence of light and age

The dependency of photosynthesis on light was investigated by applying a series of light intensities (photosynthetically active radiation [PAR] from 0 to 1500 \( \mu \)mol quanta m\(^{-2}\) s\(^{-1}\)) to a fully-expanded leaf (L4) and measuring gas exchange (Figure 3.4 A). As expected, photosynthetic rate increased with increasing light intensity. In the dark, respiration led to negative photosynthetic rate (i.e. an increased \( \Delta \text{CO}_2 \)). At a PAR of 25 \( \mu \)mol quanta m\(^{-2}\) s\(^{-1}\) photosynthetic rate was close to zero, and the
acquired data allowed me to calculate a light compensation point of PAR 24 µmol quanta m⁻² s⁻¹ (where the rate of photosynthesis equals that of respiration/photorespiration). Between PAR 50 to 200, the photosynthetic rate increased in a near-linear way ($R^2 = 0.9853$), reaching 7.48 µmol CO₂ m⁻² s⁻¹. The positive influence of light intensity on the photosynthetic rate was limited beyond PAR 400 and the CO₂-assimilation curve flattened reaching a maximum of 13.84 µmol CO₂ m⁻² s⁻¹ as photosynthesis became light-saturated (Figure 3.4 A).

The influence of leaf age on photosynthesis was measured at a light intensity of 100 µmol quanta m⁻² s⁻¹, which was similar to that measured within the leaf canopy in the greenhouse on a typical day. The youngest fully developed leaves measured (L4 and L7) showed highest photosynthetic rates (around 5 µmol CO₂ m⁻² s⁻¹; Figure 3.4 B). From leaf 10 to the oldest leaves, photosynthetic capacity decreased progressively to 1.43 µmol CO₂ m⁻² s⁻¹. Thus, leaf age indeed has a major negative influence on the photosynthetic rate even with the same, non-saturating PAR.
3.4. Carbohydrate accumulation in cassava leaves and stem

3.4.1. Carbohydrates in cassava leaves of different developmental stage and time points

Based on my measurements of photosynthetic rate, I calculated the theoretical accumulation of carbohydrate for a defined light period. These calculations revealed that in mature leaves up to 298.76 mg hexoses g⁻¹ FW at high light intensities (PAR 1500) could be assimilated in a 14 h light period (Table 3.1). While at low light intensities the theoretical assimilation of hexoses decreases 89% (PAR 50; Table 3.1). The potential of hexose assimilation depends on leaf age where the theoretical carbohydrate accumulation was lower in older leaves with L20 having only 29% the assimilation rate of L4 (Table 3.2).

<table>
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<th>Light intensity (µmol quanta m⁻² s⁻¹)</th>
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<tr>
<td>25</td>
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<td>1500</td>
<td>298.76</td>
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Table 3.1 Theoretical carbon assimilation according the photosynthetic rate measurements Calculation was based on both the photosynthetic rate measurements in dependency of light intensity and the measurement that 1 g leaf tissue has an area of 0.01414 m².

<table>
<thead>
<tr>
<th>Leaf</th>
<th>9h light period</th>
<th>14h light period</th>
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<td>L4</td>
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<td>106.61</td>
</tr>
<tr>
<td>L7</td>
<td>66.77</td>
<td>103.86</td>
</tr>
<tr>
<td>L10</td>
<td>54.53</td>
<td>84.83</td>
</tr>
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<td>L13</td>
<td>47.98</td>
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<tr>
<td>L16</td>
<td>35.36</td>
<td>55.01</td>
</tr>
<tr>
<td>L20</td>
<td>19.72</td>
<td>30.68</td>
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</table>

Table 3.2 Theoretical carbon assimilation according the photosynthetic rate measurements Calculation was based on both the photosynthetic rate measurements in dependency of light intensity and the measurement that 1 g leaf tissue has an area of 0.01414 m².

PAR: 100 µmol quanta m⁻² s⁻¹
Figure 3.5 Visualisation of starch in cassava leaves by iodine staining
Whole leaves stained with iodine, harvested 4h into the light period. L1= leaf one, L4=leaf 4, L7= leaf 7, L10= leaf 10, L13= leaf 13, L16= leaf 16, L20= leaf 20. Scale bar 10 cm.

The theoretical hexose accumulation during the light period leads to the question about real level of carbohydrates in cassava leaves at different developmental stages. The finding of reduced photosynthetic rate in older leaves suggests that they might have a lower degree of starch and soluble sugar accumulation during the day. To investigate this, I harvested every 3rd leaf – from the first, undeveloped leaf (L1) down to the oldest leaf (L20) (Figure 3.1). Initially, whole cassava leaves harvested 4h into the light were stained with iodine to visualize starch. This showed no obvious differences in starch levels between the differently aged leaves, except that the youngest leaf hardly stained (Figure 3.5 A). This suggests that starch is either not fully degraded during the night or starch
synthesis is very rapid during the first 4h light period. To complement this semi-quantitative iodine staining, leaf material was harvested in two experiments to quantify insoluble and soluble carbohydrates. In the first experiment, leaves of different ages (every 3rd leaf) were sampled both at midday (9h into the light) and in the second experiment the comparable leaves were sampled both at the end of the day (EoD) and end of the night (EoN). Insoluble (starch) and soluble (sucrose, glucose, fructose and maltose) carbohydrates were extracted and measured as described (Chapter 2.6.). For these measurements leaves of plants from ‘carbohydrate Expt1’ and ‘carbohydrate Expt2’ were analysed (Figure 3.2).

The measurement of starch at midday showed that carbohydrate allocation into this storage pool differed depending on the leaf age and position. In L4 the starch level was highest (13.76 ± 1.98 mg glu eqv. g⁻¹ FW) whereas only in the youngest, undeveloped leaf (L1) it was lowest (0.142 ± 0.08 mg glu eqv. g⁻¹ FW). For the other leaves investigated (L7-L21), starch levels varied between 3.50 ± 1.51 mg (L10) and 10.52 ± 2.01 (L19) mg glu eqv. g⁻¹ FW (Figure 3.6 A). The analysis of soluble sugars revealed a pattern similar to that described by Angelov et al. (1993) where sucrose levels are low in the very youngest (~6 mg suc g⁻¹ FW) and oldest (~11 mg suc g⁻¹ FW) leaves but higher in the most of the fully-expanded leaves in between (~14-15 mg suc g⁻¹ FW). In comparison to the sucrose levels the amount of glucose and fructose are low with maximal values in L4 (2.1 ± 0.25 mg gluc g⁻¹ FW; 1.16 ± 0.13 mg fruc g⁻¹ FW) (Figure 3.6 B-D). Generally, in my analysis the carbohydrate levels were slightly lower than what was measured in field studies, but comparable in terms of the division between the different carbohydrate pools. The carbon partitioned into starch after 9h in cassava leaves, is comparable to the amounts typically observed in Arabidopsis at the end of the day (in a 12h light period) (Gibbon et al., 2004; Fulton et al., 2008).
Figure 3.6 Analysis of insoluble (starch) and soluble (sucrose, glucose, fructose and maltose) carbohydrate allocation in leaves at different developmental stages
A-D) harvested at the 9h into the light period and E-I) harvested at end of the day (grey, stripe bar) and end of the night (black bar) A, E) starch, B, F) sucrose, C, G) glucose, D, H) fructose I) maltose. L1=young, newly emerged leaf at the top, L21=oldest leaf at the bottom. Mean ± SE, N = 5, 4, 3.
To investigate the extent of leaf starch accumulation during the day and degradation in the subsequent night, leaf tissue was harvested at the EoD and EoN. These measurements give insight into the extent of diurnal, transitory starch turnover in a 14h light regime. For these measurements leaves from plants ‘carbohydrate Exp2’ were analysed (Figure 3.2). Higher starch levels were observed at the EoD, with the highest value of 20.01 ± 3.78 mg glu eqv. g⁻¹ FW in L4 and the lowest in L1 (8.03 ± 1.89 mg glu g⁻¹ FW). As in the previous experiment, starch levels in the older leaves (L7, L10 and L20) were comparable to each other and lower than in L4. At the end of the night between 80.1 % (L1) and 52.3 % (L7) of the transient starch level was degraded. Interestingly, the levels for soluble sugars (sucrose, glucose and fructose) were unchanged at EoD and EoN (Figure 3.6 F-H). These data are consistent with the idea that leaf starch is degraded to maintain sugar levels during the dark.

Lower amounts of starch at the EoN than at the end of the previous day suggests that in cassava leaves, diurnal starch metabolism is occurring in a similar way as has been described in the model plant Arabidopsis (Gibon et al., 2004; Fulton et al., 2008). In Arabidopsis, transient leaf starch is degraded during the night by a cascade of enzymes (see Chapter 1.6). In the main transient starch degradation pathway, β-amylases are involved, producing maltose as an intermediate metabolite (Niittyla et al., 2004; Weise et al., 2004). The comparison of maltose levels at the EoD and EoN showed increased maltose levels at the EoN in all leaves except L1, where maltose levels remained unchanged. (Figure 3.6 I) This finding suggests that in cassava leaves, maltose is an intermediate metabolite in transitory starch metabolism, as in Arabidopsis.

### 3.4.2. Carbohydrates in cassava stem at different developmental stages and time points

In daily life cassava is propagated by stem cuttings from mother plants. The older part of the stem is cut into 15-30 cm long sections and planted vertically to soil. This is because this lower part is full of nutrients needed to fuel re-growth of new leaves and stem (El-Sharkawy, 2004).
I stained the laterally bisected stem with Lugol to reveal a positive correlation between tissue age and starch accumulation. This is in accordance with the stem being a storage organ. Starch accumulates mainly in the pith ray at the outermost layers of the stem. In the younger stem tissue, the middle pith remains unstained, whereas in older tissue, the staining is observed in all layers (Figure 3.7). Analysis of differently aged transverse stem sections under the light microscope (Int1, Int10, Int15, Int20, and Int25) confirmed the preliminary finding of starch accumulation in different cell layers. In the youngest part of the stem (Int1), starch granules are formed in the chlorenchyma (Figure 3.8). In internode 10, starch granules appear in the cells around the phloem, and start to accumulate at the margins of the pith. From Int10 to Int15, radial growth from the cambium is observed. The cell layer containing the pith ray and xylem are enlarged and starch granules start to accumulate in pith ray close to the cambium, and eventually also in the pith cells (Figure 3.8). Within the pith ray and the central pith layer, starch granules increase in number and volume.
The accumulation of starch in the older part of the stem was also shown quantitatively; every 5\textsuperscript{th} internode section (counting from the top to the bottom) was harvested from 5 replicate cassava plants. For these measurements stem sections of plant batch ‘carbohydrate Expt1’ (Figure 3.2) were analysed. I observed that the starch content increased with the age of the tissue (Figure 3.9 A). Starch levels below 10 mg glu eqv. g\(^{-1}\) FW were detected in Int1, Int5 and Int10. From Int15 down to Int30, close to the sprouting initiation site, starch levels doubled from 35.05 \pm 3.3 mg to 73.93 \pm 17.79 mg glu eqv. g\(^{-1}\) FW (Figure 3.9 A).
Sucrose levels showed quite similar levels throughout the analysed samples, ranging from 4.2 ± 0.3 mg to 7.95 ± 0.2 mg suc g⁻¹ FW. Int1 and Int5 had the lowest levels of sucrose. Compared to the younger stem part sucrose levels were higher in the middle of the stem (Int10 to Int20) and the oldest stem sections (Int25 and Int30) (Figure 3.9 B). The levels of glucose and fructose behaved in a reciprocal manner compared to starch accumulation. These soluble sugars were considerably lower in the older stem tissue. For example, glucose levels were 87% lower in Int30 compared with Int1. Fructose levels, like those of glucose were highest in the youngest part of the stem (Figure 3.9 C-D).

Analysis of insoluble and soluble carbohydrate accumulation at the end of the day and at the end of the night, measured from stem sections of plant batch ‘carbohydrate Expt2’ (Figure 3.2), revealed little or no diurnal fluctuation in stem carbohydrate levels. Diurnal starch turnover was not observed in investigated parts of the stem (Figure 3.9 E-H). The values for starch at the end of the day were comparable to the values measured in samples harvested after the following dark period. Except for Int25 where a difference in starch levels at the indicated time points was determined though below significance (t-test > 0.05) (Figure 3.9 E). No major differences were observed between the end of the day and the end of the night for sucrose, glucose and fructose (Figure 3.9 F-G). Only in Int10 were sucrose levels 30% lower at the end of the night than at the end of the day. Glucose and fructose levels showed a similar pattern of accumulation to each other; levels increased from Int1 to Int10 and were lower again in Int25 (Figure 3.9 G-H). In comparison to the measurements on plant batch ‘carbohydrate Expt1’, lower soluble sugar levels were determined. For the two hexoses, glucose and fructose the levels differed between 2 and 80% in younger internode sections compared to the previous measurements. In contrast for Int25 the analysed hexoses were 60% higher. The changes in sucrose levels were between 16-35% lower compared to the ‘carbohydrate Expt1’.
Figure 3.9 Analysis of insoluble (starch) and soluble (sucrose, glucose, and fructose) carbohydrate allocation in stem at different developmental stages. A-D) harvested at the 9h into the light period and E-H) harvested at the end of the day (grey, stripe bar) and end of the night (black bar) A, E) starch, B, F) sucrose, C, G) glucose, D, H) fructose. Int1 = youngest internode section, on the top Int25 = oldest internode section at the bottom. Mean ± SE, N=5, 4, 3.
3.5. Conclusions drawn from the analysis of carbohydrate assimilation in cassava plants

3.5.1. Analysis of plant batches used for subsequent experiments

In this chapter I showed that small differences in height, number of internodes and leaves were observed between the batches of plants used for my individual experiments (Figure 3.2). However, considering that the plants were grown from cuttings of different mother plants and grown under semi-controlled greenhouse conditions at different times of year, the batches used for experiments were broadly homogenous. The number of internodes is a good parameter to define the plants developmental stage and showed the least variation. The variation of leaf number between the batches can be explained by the fact that in cassava, the oldest leaves undergo senescence and are eventually shed (Alves, 2002). Nevertheless, for most of the plants, the number of leaves, plant height and the number of internodes was the same. Even in the batches where one parameter varied (e.g. plant height in the batch for the photosynthesis experiment) the other two parameters were still similar to other batches. Therefore, it is reasonable to conclude that the developmental stage of the batches was similar and that the results from the different experiments can be compared with each other.

3.5.2. Capacity of cassava plants to perform photosynthesis and carbon assimilation

The photosynthetic rate measurements accurately quantified the influence of light intensity on the carbon assimilation rate in my material (Figure 3.4 A). The light intensity inevitably varied in my plants, depending on the season, although this was augmented to some extent by supplementary lighting in the glasshouses. The maximal photosynthetic rates reported here are lower than was found in other studies (Edwards et al., 1990; Angelov et al., 1993; Calatayud et al., 2000). This might be because my measurements were gained on greenhouse-grown plants and/or because the variety used (cv. 60444) is rather a model than an agricultural cultivar. A clear negative correlation between leaf age and the capacity to assimilate carbon could also be shown (Figure 3.4 B). This was also observed in field grown plants (Angelov et al., 1993). The collected photosynthetic rate data are important as they allowed me to calculate the potential carbon assimilation, which can be compared with the absolute measurements of non-structural carbohydrates in the leaves. For example, comparing the theoretical assimilation of carbon with the starch accumulation during a day suggests that young, fully expanded leaves partitioned only 5-11% of assimilated carbon into starch. In the oldest leaf (L20) as much of 22% goes into starch. However, these values are somewhat speculative as light intensity is likely to have varied throughout the day and throughout the leaf canopy.
All leaves degraded their starch to some extent during the night, although some degraded more than others, and most contained residual starch at the end of the dark period (Figure 3.6 E). This is in contrast to findings in the model plant Arabidopsis, which partitions a higher proportion of its assimilates into starch and degrades almost all of it at night. Nevertheless, as in Arabidopsis, I observed increased maltose levels at the end of the night (Figure 3.6 I) suggesting that cassava leaves metabolise their starch via a comparable pathway.

Cassava differs from Arabidopsis in another important way, accumulating about 10 times more sucrose (Gibon et al., 2004), together with high levels of glucose and fructose. In fact, the levels of total soluble carbohydrates were comparable to the amount of starch in the leaves. It is likely that much of this sugar is stored in the vacuoles of the palisade and sponge mesophyll cells. Interestingly, the levels of these sugars were almost unchanged at the end of the night, suggesting that starch is degraded to support night-time metabolism and maintain sugar levels (Figure 3.9 E-H).

Total non-structural carbohydrate levels were lowest in the oldest leaves (i.e. those close to senescence and with low photosynthetic rates) and the very youngest leaves (i.e. those that are still actively growing; Figure 3.6). The highest levels were observed in the fully expanded leaves at the top of the canopy (L4 and L7; Figure 3.6), which can be partly explained by their location (exposed to more light) and their high photosynthetic rate. Moving down the stem, the older leaves are more prone to being shaded by the upper canopy (Figure 3.1) and display lower photosynthetic rates, possibly as the process of senescence begins and the photosynthetic machinery is degraded (Figure 3.4 B). These findings are in agreement with the data shown by Angelov et al. (1993) where a similar trend of carbohydrate levels in different aged leaves was found, although the absolute values they observed were higher than those reported here. Again, these differences in absolute amounts could be explained by the growth conditions and the model cultivar used in our studies.

Carbohydrate levels measured for the developmental stages and diurnal fluctuations revealed differences in absolute values and pattern in respect of tissue age. Especially soluble sugars were lower in the diurnal analysis compared to the levels seen for the developmental stages. Depending on the analysed tissue and the age variation was up to 80% i.e. in stem sections Int1 at the end of the day compared to middle of the day (Figure 3.9). A reason for these substantial differences might be explained by differences in light conditions in the greenhouse and the difference in plant material (carbohydrate Expt1 and Expt2, Figure 3.2). Another reason for the observed differences might be explained by a diurnal fluctuation of carbohydrates throughout the day night cycle. Here I present three time points thus, it might be that soluble sugars throughout the light period are accumulated at midday and decrease towards the end of the day. To test this hypothesis a 24-h harvesting
experiment could be performed. However, the experimental-setup I present here was designed in such a way that the results can be considered to be valuable.

Fully-expanded leaves serve as source tissue delivering carbohydrates to sink tissues. Export is probably highest during the day in cassava, but might continue during the night. However, if the calculated partitioning into starch is correct, it suggests that only a small fraction of the day-time assimilates is stored for night-time metabolism. Clearly, the developing root and shoot apices represent strong sinks, as does the starch-accumulating storage root. However, my data also show that starch accumulates in the stem – particularly the older parts (Figure 3.9 A) – to very high levels (up to 74 mg glu eqv. g\textsuperscript{-1} FW). This suggests that the stem is also a strong sink tissue. The stem starch does not appear to follow the diurnal fluctuations observed for transitory starch in leaves, and can be considered as a storage starch pool that accumulates over time in the pith (Figure 3.8). This starch probably serves an important role during the propagation of cassava from stem cuttings, fuelling regrowth of new roots and shoots.

Further evaluation of the pattern and amounts of carbon partitioned between storage in the leaf and export to the various sinks would be valuable. This could be evaluated by feeding cassava leaves with \textsuperscript{14}C-labelled CO\textsubscript{2}. After supplying a pulse of \textsuperscript{14}CO\textsubscript{2}, the amount of \textsuperscript{14}C label in the insoluble or soluble carbohydrate fractions in different plant parts could be determined during a chase period. Performing such experiments for differently aged leaves could reveal also where carbon, fixed in different parts of the canopy are primarily exported to. In Arabidopsis and other species, it was shown that the phloem network between leaves is established in with a defined way, related to the phyllotaxis of the plant. Thus, sucrose exported from a specific source leaf ends up in sink leaves defined by the vascular connections (Busse and Evert, 1999).
4. Carbohydrate metabolism in Cassava storage roots after induction of sink-to-source transition

4.1. Introduction

As described in the General Introduction, transitory leaf starch metabolism has already been studied in detail and well-described in the literature (Smith and Stitt, 2007; Streb and Zeeman, 2012). In contrast, storage starch metabolism in heterotrophic tissues - especially starch remobilization - is less well understood. Early biochemical studies dealing with starch remobilization in cereal grains revealed major differences between the degradation pathways of transitory and storage starch. For example, whereas the breakdown of transitory starch in Arabidopsis leaves is highly dependent on the hydrolytic activity of β-amylases, storage starch remobilization in the cereal endosperm is mainly catalysed by α-amylases (Fincher, 1989). Although other starch metabolizing enzymes are found to be present in the endosperm of germinating seeds (i.e. LDA, α-glucosidase, β-amylase) a large increase in α-amylase production is observed upon germination. This led to the general acceptance that cereal starch mobilization is initiated by α-amyloytic hydrolysis. On the other hand, in potato tubers evidence was presented showing that β-amylases may be the main hydrolytic enzymes, responsible in remobilizing starch (Nielsen et al., 1997; Viola et al., 2007). It is well known that potato tubers stored at cold temperatures for several days increase break down some of their starch and accumulate soluble sugars, a process called cold-sweetening. Studies to investigate the molecular mechanism and discover the enzymes involved revealed a correlation between increased β-amylase activity and cold-sweetening. For white clover, it was also shown that starch mobilization upon defoliation leads to increase in soluble sugars and decrease in starch content in the storage roots. This was shown to correlate with an increase in α-amylase activity (Gallagher et al., 1997). Other studies showed that α-amylase activity can be isolated from starch granules of poplar wood ray cells and potato tubers (Witt and Sauter, 1994; Witt and Sauter, 1996). Although no detail about the functional involvement of these hydrolytic enzymes in heterotrophic starch metabolism are provided, the results give indications that starch remobilization differs from what is described in leaf tissue.

The aim of this study was to identify key proteins involved in the remobilization of starch in cassava storage roots using a proteomics approach. Therefore a simple method was developed to shift the metabolism in cassava roots from starch synthesis to degradation - or in other words to induce a sink to source transition. In potato tubers, studies involving sink-source transition are performed on tubers detached from the mother plants. By doing so, bud dormancy is released and new sprouts are made (Viola et al., 2007). In this process, starch is remobilized and sucrose is made and transported
4. Metabolic shift in cassava storage root from sink-to-source

to the bud, indicating that new sink is created. Unlike potato tubers, which derive from modified stems, cassava roots do not sprout once detached from the mother plant. In contrast, detached cassava roots undergo a rapid post-harvest physiological deterioration (PPD) within 24-48h (Sanchez et al., 2006). The first step is black discoloration of the vascular parenchyma and later of the storage parenchyma. This is followed by a secondary PPD, attributed to microbial infection. Thus, to study starch remobilization in cassava storage roots, another experimental setup was needed to provoke the transition from sink-source in cassava roots. Studies aiming to delay PPD showed that pruning before the harvest minimises deterioration. Additionally, it was shown that starch content of storage roots decreased near linearly up to 26 days, after which starch starts to accumulate again (van Oirschot et al., 2000). Thus, pruning seems to be a valuable method to study starch remobilization in cassava storage roots, and was used here.

In the past decades, mass spectrometry-based proteomics has become an important method to monitor metabolic network components at a system-wide level (Domon and Aebersold, 2010; Schulze and Usadel, 2010). Nevertheless, peptide and therefore protein identification depends upon available genome sequence information. Sequencing of the cassava genome began 2003 and resulting EST sequences were used for pioneer transcriptomics and proteomics studies (Lopez et al., 2004; Sheffield et al., 2006; Reilly et al., 2007; Li et al., 2010; Mitprasat et al., 2011; Owiti et al., 2011). Proteomics studies based on 1 or 2 dimensional gel electrophoresis analysed several cassava tissues including fibrous and storage root (Sheffield et al., 2006), secondary somatic embryos (Baba et al., 2008), leaves at different growth stages (Mitprasat et al., 2011) and storage roots subjected to post-harvest deterioration (Owiti et al., 2011). These studies successfully identified up to 1110 proteins in storage roots by combining available EST sequences with bioinformatics approaches to optimize protein identification in non-sequenced organisms (Owiti et al., 2011). Recently, the first annotated draft of the cassava genome, predicted to contain 30666 protein-coding loci, was released (ftp://ftp.jgi-psf.org/pub/JGI_data/phytozome/v5.0/Mesclulenta; reviewed in Prochnik et al., 2012) thus paving the way for the application of large-scale shotgun proteomics.

Various methods have been developed to provide absolute or relative quantitative information for identified proteins (Domon and Aebersold, 2010; Schulze and Usadel, 2010). First, protein abundances can be determined prior to analysis by peptide isobaric labelling, during acquisition by multiple reaction monitoring or in a post-acquisition manner by label-free strategies (Vaudel et al., 2010; Owiti et al., 2011). Second, it has been shown that the number of identified peptides is to some extent proportional to the protein abundance, enabling protein quantification by label-free spectra counting (Lu et al., 2007). Third, softwares such as SuperHirn or Progenesis LC-MS
have been developed to determine peptide and protein abundances according to the intensity of eluting ions (Azimzadeh et al., 2012; Fischer et al., 2012; Greer et al., 2012). Implementation of statistical tests in Progenesis LC-MS has proven to be excellently suited for obtaining sensitive and robust quantification of proteomics data (Azimzadeh et al., 2012; Fischer et al., 2012; Greer et al., 2012), and this approach was used here to identify proteins involved in the remobilization of starch in cassava storage roots.

4.2. Remobilization of carbohydrates from storage organs

![Figure 4.1 Pruning of cassava plants and the influence on the carbohydrates](image)

A) Cassava plants were pruned and storage roots harvested immediately (ZDP) or ten days after pruning (TDP). Within this time-period a new shoot appeared (red arrow); Greenhouse, 14h light. A-D) Carbohydrate allocation in stem at the cutting side ZDP and TDP. E-G) Carbohydrate allocation in cassava storage roots ZDP and TDP, A,E) starch, C,F) sucrose and D,G) soluble sugar level glucose (dark grey), fructose (light grey). Values are mean ±SE (N=5), *t-test < 0.01
To investigate starch catabolism in cassava storage roots, I analysed changes in carbohydrate levels and amyloolytic activity upon cutting off the photosynthetic above-ground tissues. The storage roots of greenhouse-grown cassava plants (plant batch ‘Proteome’, Figure 3.2) were harvested either uncut as a control (Control; zero days of pruning, ZDP) or 10 days after cutting off the above-ground photosynthetic part (ten days of pruning, TDP) (Figure 4.1 A). The emergence of new shoots from internodes could be observed within this time period, but the leaves were tiny and not yet photosynthetic source tissues (Figure 4.1 A).

To investigate the remobilization of carbohydrates from both stem and root storage tissues, levels of starch, sucrose, glucose, and fructose were determined at both time points. Starch levels in stem tissue (immediately below the cutting side) and storage roots were decreased by 44.6% and 48.1%, respectively (Figure 4.1 B, E). The level of sugars remained unchanged for the two time points in both tissues (Figure 4.1 C, D, F, G).

Activities cannot be determined unambiguously. Ceballos et al. (2008) performs similar analyses and suggested that ISA and SBE activities migrate at the top of the gel (Figure 4.2 A). However, isoforms of both α- and β-amylases also run in this location in Arabidopsis leaf extracts. A faint activity band appears further down in the gel for the TDP protein samples, which may represent limit dextrinase (LDA) activity. The substrate β-limit dextrin (amylopectin digested with an excess of commercial β-amylases; Figure 4.2 B) cannot be digested by β-amylase. As seen on amylopectin, the enzymatic activities on β-limit dextrin were increased TDP in comparison to the control samples. Activity of the top two bands appeared the same as on amylopectin and were increased in TDP samples, as was the lowest band. Two minor bands visible on amylopectin were not visible on β-limit dextrin, suggesting that they may be β-amylases. The chromogenic substrate red-pullulan (partially depolymerised pullulan containing Procion MX-SB dye) is a specific substrate to reveal LDA activity (Figure 4.2 C). For LDA activity, 3 times more total protein was loaded per lane (7.5 µg) compared to the native PAGE containing amylopectin and β-limit dextrin. The activity of LDA on red-pullulan also appeared to be increased in the TDP samples compared to ZDP control samples (Figure 4.2 C). With the exception of LDA activity, these analyses do not reveal clearly which hydrolytic enzymes are involved in the process of starch degradation upon the sink-source-transition.
I was interested if the decrease in starch levels is caused by a changed hydrolytic activity of starch degrading enzymes. Therefore, protein extracts from two replicate cut and control storage roots were analysed by native PAGE containing 0.1% amylopectin, 0.1% β-limit dextrin or 1% red pullulan (Figure 4.2 A-C). Using amylopectin as a substrate reveals starch hydrolysing/modifying enzyme activity. Activity bands appeared at the top of the native PAGE with a markedly increased activity in storage root extract after cutting compared to the control (Figure 4.2 A). The identity of these The decrease in starch levels and the increase in amylolytic activity show that storage starch is mobilized in stems and storage roots for the production of new leaf tissue. Therefore, this treatment appears as a suitable system in which to further analyse the switch from a sink to a source tissue.

**Figure 4.2 Amylolytic enzyme activity PAGE**
Total storage root protein extract from ZDP and TDP were subjected on a 6% native PAGE containing A) 0.1% potato amylopectin, B) 0.1% β-limit dextrin and C) 1% red pullulan. Protein loading was 2.5 µg for A and B, and 7.5 µg for C. D) 6% SDS-PAGE stained with co-omassie for protein loading control, either 2.5 µg or 7.5 µg per lane.
4.3. Cassava storage root proteome comparison: Unravelling enzymes involved in carbohydrate metabolism in storage roots before and after pruning

A large-scale proteome study of storage roots was performed and conducted by Dr. Sylvain Bischof, primarily to identify important proteins involved in storage starch metabolism. Therefore, proteins from storage roots harvested before (ZDP) and after pruning (TDP) were extracted and equivalent concentrations of total proteins were separated by 1-dimensional SDS-PAGE (Figure 4.3 A). Each lane was cut into 14 fractions to decrease the sample complexity, thereby increasing the probability to identify individual proteins. Proteins in each fraction were in-gel digested with trypsin and analyzed by mass spectrometry (MS) using an Orbitrap mass spectrometer. Three biological replicates were analysed for each time point. Measured spectra were identified using the cassava genome database (www.phytozome.net) and quantitative information for each identified peptide and protein was obtained using the software Progenesis LC-MS.

![Figure 4.3 Evaluation of proteomics data set](image)

A) Total protein separated on a SDS-PAGE for proteomics and the slices subjected for digestion  
B) Correlation analysis between the biological replicate represented in a PCA plot. Before Cutting = ZDP; After Cutting = TDP  
C) Total number of proteins indicating the significantly up- and down-regulated as a percentage in respect of fold changes. Data obtained by Dr. Sylvain Bischof, ETH Zürich.
In total, 20177 peptides were identified across all six datasets analysed. Peptide identification was accepted with a minimal Mascot ion score of 23 and a maximum expectation value of ≤ 0.05. To increase protein identification confidence, a minimum of two unique peptides for each protein was required. Proteins identified with only a single peptide hit were excluded. This led to a total of 2410 proteins identified with a high confidence (Supplemental Table 4.1). Of these, 2409 proteins were found in both time points while only one protein (cassava4.1_005818m; homologue to Arabidopsis CYTOCHROME P450 86 A1) was found only at ZDP (Supplemental Table 4.1).

To investigate homogeneity among the biological replicates, a principle component analysis (PCA) was performed. PCA analysis revealed a clear separation of the biological replications of “Before Cutting” (ZDP) and “After Cutting” (TDP) (Figure 4.3 B). In PC1, which contributes 53% of the variance, clearly separates the six replicates according the treatment “Before cutting” and “After cutting”. While the replicates for “Before Cutting” cluster together for PC2 (20.9%) and PC3 (11.6%) “After Cutting” B separates from the two other replicates for PC3 (Figure 4.3 B). However, the clear separation between the treated and untreated samples indicates clear protein regulation.

To identify proteins significantly differently expressed after pruning (compared to the untreated control), an analysis of variance (ANOVA) test was performed (Supplemental Table 4.2). To reveal proteins that were de-regulated (up or down) after pruning, the mean average of protein abundance TDP was compared to mean average of protein abundance of the untreated control samples. This comparison reveal a total of 315 proteins with ANOVA p-values ≤ 0.05 (Figure 4.3 D). Investigations of the fold change of the deregulated proteins revealed that 127 proteins were up-regulated, 105 and 33 of which were at least 1.5-fold or 2-fold higher, respectively. One hundred and eighty proteins were down-regulated, 101 and 68 of which were at least 1.5-fold or 2-fold lower, respectively. (Figure 4.3 D; Supplemental Table 4.2).

Next, I used the publicly-available functional annotations of Arabidopsis thaliana proteins to identify the cassava proteins (see Material and Methods for details). Several Arabidopsis proteins had more than one close cassava protein homolog suggesting that DNA duplications have resulted in multiple gene copies in the cassava genome. Sixteen out of 2410 cassava proteins could not be assigned to any Arabidopsis homolog, suggesting that they are specific to cassava (Supplemental Table 4.1).

To gain insight into the metabolic processes affected by pruning, I categorized the 2394 genes according to their metabolic functions using the MapMan software (Supplemental Table 4.1; mapman.mpimp-golm.mpg.de; Usadel et al., 2009). As some proteins are involved in more than one metabolic pathway, several cassava homologs were found to be allocated to two or more functional
categories. In order to identify processes significantly altered by pruning, the proportion of deregulated proteins in each category was compared with the proportion of total proteins in the same category. After pruning (TDP), proteins belonging to the functional categories ‘cell wall’ and ‘hormone metabolism’ were significantly under-represented compared to the control (ZDP; Figure 4.4 A). In contrast, proteins assigned to the categories ‘major CHO metabolism’, ‘TCA/Organic acid transformation’, ‘amino acid metabolism’, and ‘protein’ were significantly over-represented after pruning (Figure 4.4 A).

![Image of Figure 4.4 Evaluation of the MapMan categorization]

**Figure 4.4 Evaluation of the MapMan categorization**
The relative pathway abundance was calculated by the number of features assigned to a MapMan category in relation to the total number of features found over all categories (Black bar). White bar reflect the relative abundance of significantly up-regulated features TDP to the total number of features significantly up-regulated TDP. Grey bar reflect the relative abundance of significantly down-regulated features TDP to the total number of features significantly down-regulated TDP. The probability of features found to be over- or underrepresented within one category was determined with a Hypergeometric distribution test. *p-value ≤0.01

### 4.3.1. Investigation of metabolic pathway changes after pruning

#### 4.3.1.1. Changes in the abundance of proteins involved in primary carbon metabolism

The transition of cassava root from sink-to-source is connected to significant changes in starch and sucrose metabolism. This is not surprising as storage roots, as a sink tissue, relies on carbohydrates (sucrose) transported from the photosynthetic source tissues. The sucrose is unloaded from the phloem and can either be cleaved by invertase (into fructose and glucose) or by sucrose synthase (SUS; which converts UDP and sucrose into fructose and UDP-glucose). In subsequent steps the generated hexoses are metabolised further giving substrates for diverse metabolic pathways (e.g.
respiration), or they are transported to the vacuole for storage, or transported into the amyloplast and converted into starch. In heterotrophic tissues that have switched into a source tissue, some of these reactions are reversed. For example, starch is degraded and the products are used to synthesise sucrose, which then is exported to new sink tissue via phloem transport. Sucrose is synthesised in the cytoplasm from F6P and UDP-glucose by consecutive activities of sucrose-6-phosphate synthase (SPS) and sucrose-6-phosphate phosphatase (SPP). To elucidate differences in storage root primary carbohydrate metabolism in untreated (sink) and pruned (source) roots, I investigated the protein levels for enzymes involved in starch and sucrose metabolism in more detail.

**Starch metabolism**

In *Arabidopsis thaliana*, 53 proteins are known to be directly or indirectly involved in starch metabolism (Streb and Zeeman, 2012). The obtained cassava proteome data were mined for cassava homologs of *Arabidopsis* proteins involved in starch metabolism. A total of 31 cassava proteins were found (Table 4.1). For the other 22 proteins assigned to the starch metabolism in *Arabidopsis* no peptides corresponding to a cassava homolog were identified. Of the 31 proteins identified, six pairs were each annotated to the same Arabidopsis protein. A closer investigation of the cassava genome revealed that these cassava homologs are duplicate. Hence a total of 25 starch related proteins were found in this proteome analysis. The duplicates were indicated with a prefix “a” or “b”. The case of LDA was an exception; a closer analysis showed that the two cassava sequences (cassava4.1_004771; cassava4.1_024672) lie next to each other on the same scaffold. An alignment of these two peptide sequences to the AtLDA as a query reveald sequence homology of either the N- or C-terminus without common sequence overlaps. Therefore, the two samples were taken together. From these 25 proteins 8 were identified to be involved in starch synthesis and 15 in degradation, (Table 4.1; Streb et al., 2012).

Of the 30 proteins involved in starch metabolism, five were significantly (p-value = ≤ 0.05) deregulated in the TDP sample compared to the ZDP control (Table 4.1). Of these, three proteins were up- and two proteins were down-regulated.

Among the proteins induced by pruning was a protein containing a starch-binding domain and a coiled-coil domain (COC, cassava4.1_012932) which was increased in abundance by 1.7 fold. The Arabidopsis homolog was shown to be a chloroplast-localized protein which binds to starch, preferentially to amylose (Lohmeier-Vogel et al., 2008). Furthermore, starch synthase 1 (SS1; cassava4.1_004619) was significantly more abundant TDP (1.2-fold) compared to the ZDP control. However, the most striking change was a 6.3-fold increase in the plastidial endoamylase α-amylase 3 (AMY3; cassava4.1_001362). AMY3 is involved in the release of branched malto-oligosaccharides
from the starch granule. Analysis of down-regulated proteins in TDP samples revealed APL3 (a large-subunit of AGPase cassava4.1_005409) and PWD (phosphoglucon water dikinase, cassava4.1_000497) to be 2-fold and 1.3-fold less abundant, respectively. APL3 is specific for root tissue in Arabidopsis, while APL1 is more abundant in leaves (Crevillen et al., 2005). PWD (cassava4.1_000497) plays a role in starch phosphorylation, acting on starch granules after pre-phosphorylation by GWD (Baunsgaard et al., 2005; Kotting et al., 2005).

The other proteins assigned to the starch synthesis pathway include the plastidial PGM1 isoform, three isoforms of starch synthases (SS2, cassava4.1_002278; SS4, cassava4.1_003800; and GBSSI, cassava4.1_003884), two branching enzymes isoforms (SBE2-a cassava4.1_003773; SBE2-b, cassava4.1_001686; and SBE3, cassava4.1_001595), and the debranching enzymes ISA1 and ISA2 (cassava4.1_001932; cassava4.1_001414). Amongst the proteins assigned to starch degradation were the debranching enzymes ISA3 (cassava4.1_008945) and LDA (cassava4.1_004771, cassava4.1_024672), the phosphoglucon phosphatase SEX4 (cassava4.1_009735) and its homolog LSF1 (cassava4.1_025886). Both plastidial and cytosolic disproportionating enzymes, DPE1 (cassava4.1_008552) and DPE2 (cassava4.1_001086), which recycle short maltooligosaccharides to release glucose were identified. Homologs of the plastidial and cytosolic α-glucan phosphorylase (PHS1, cassava4.1_004717, cassava4.1_002614 and PHS2, cassava4.1_001626, cassava4.1_004717) were identified. PHS1 and PHS2 catalyze the reversible reaction of glucose-1-phosphate release from linear glucans (Steup and Schachtel, 1981; Shimomura et al., 1982). In addition, a plastidial hexose-phosphate translocater (GPT1, cassava4.1_009268) and a glucose transporter (GlcT, cassava4.1_004822) could be identified. GPT1 was described in maize and Arabidopsis heterotrophic tissues and transports glucose-6-phosphate across the amyloplast membrane (Kammerer et al., 1998; Andriotis et al., 2010), providing substrates for either starch synthesis or the plastidial oxidative pentose phosphate pathway. GlcT was shown to be important to export glucose from the Arabidopsis chloroplasts during the dark period (Cho et al., 2011).
Table 4.1 Starch related proteins: Up- or down-regulation of starch–related proteins TDP. Significant ANOVA p-value ≤ 0.05 are indicated in bold. Fold change is represented in respect of TDP (N=3).

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Amongst the significantly deregulated proteins were several enzymes involved in sucrose metabolism. A set of 100 proteins involved in sucrose metabolism and transport in Arabidopsis was used to identify homologs in cassava. I could assign 49 cassava proteins to Arabidopsis homologs (Table 4.2). After correcting for duplicated (or triplicated genes), a total of 34 Arabidopsis homologs were found in the cassava proteome (Table 4.2). Amongst the 49 proteins, four were significantly up-regulated and two significantly down-regulated (p-value ≤ 0.05) in TDP samples compared the ZDP control samples (Table 4.2). After pruning fructokinase (FK; cassava4.1_011584) and cytosolic fructose-1,6-bisphosphatase (F1,6BPase; cassava4.1_011197) (which produce fructose 6-phosphate from free fructose or from fructose 1,6-bisphosphate respectively) were down-regulated compared to the control. Mutant analysis in Arabidopsis showed that F1,6BPase is involved in fructose sensing and signalling, independent to the catalytic activity (Cho and Yoo, 2011). After pruning, there was significant up-regulation of plastidial fructose-1,6-bisphosphate aldolase (FBA3; cassava4.1_009233), cytosolic invertase2 (cINV2; cassava4.1_005201), cytosolic/nuclear hexokinase1 (HXK1; cassava4.1_006138) and plastidial hexokinase3 (HXK3; cassava4.1_007221). FBA3 converts fructose 1,6-bisphosphate into dihydroxyacetone phosphate (DHAP) and glyceraldehyde-3-phosphate (GAP; triose-phosphate). The metabolites DHAP and GAP are substrates for diverse metabolic pathways in different subcellular compartments (OPPP, glycolysis and TCA cycle, sucrose synthesis). The cINV2 hydrolyses sucrose into glucose and fructose. HXK1 and HXK3 phosphorylate various hexoses (e.g. fructose and glucose) (Claeyssen and Rivoal, 2007). As for F1,6BPase, HXK1 is involved in sugar-signalling in Arabidopsis, sensing glucose independently of its catalytic activity (Moore et al., 2003).
### Table 4.2 Sucrose related proteins

Proteins involved in sucrose metabolism up- or down regulated TDP. Significant ANOVA p-value ≤ 0.05 are indicated in bold. Fold change is represented in respect of TDP (N=3).

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4. Metabolic shift in cassava storage root from sink-to-source
Sugar signalling is well known and certain sugars and some enzymes are involved in translating the metabolic state of the cell into a transcriptional response. As mentioned, glucose can be sensed by HXK1 (Jang et al., 1997; Moore et al., 2003) and fructose can be sensed by F1,6BPase (Cho and Yee, 2011), both of which were up-regulated after pruning. Also up-regulated after pruning was KIN1 (cassava4.1_008188), the γ-regulatory subunit (Bouly et al., 1999) of the heterotrimeric SnRK1 (Snf1-protein kinase), which was 11-fold more abundant. Proteins homologous to SnRK1 in mammals (AMPK) and yeast (Snf1) have been described to be up-regulated under starving conditions (reviewed in Hardie et al., 1998). In plants, the role of SnRK1 proteins is still controversial. However, there are reports that SnRK1 inhibits the activity of enzymes involved in energy consuming pathways (Sugden et al., 1999). Sugden et al. (1999) showed that SPS is inactive in the phosphorylated state (Huber et al., 1989). I also identified KIN10, the catalytic α-subunit of the SnRK1 (Baena-Gonzalez et al., 2007), though no change in abundance was observed.

4.3.1.2. Changes in different metabolic pathways accompany the metabolic shift from sink-to-source

Energy derived from catabolic processes (in form of ATP and reducing equivalents i.e. NAD[P]H) are required for cell maintenance and to drive energy-consuming anabolic processes. To provide energetic compounds carbohydrates and other energy-rich metabolites are respired by various pathways. Depending on the metabolite source (e.g. lipid, sugar, protein, amino acids) different pathways are involved. For example, glycolysis consumes hexose-phosphates generating pyruvate, ATP and NADH, while lipids are metabolized by β-oxidation to acetyl Co-A. Both pyruvate and acetyl CoA provide substrate for the tricarboxylic acid (TCA) cycle. As shown in Figure 4.4 A, proteins of the functional categories, ‘protein’, ‘amino acid’, ‘gluconeogenesis’ and ‘TCA/ organic acid’ were statistically overrepresented in the dataset TDP (Table 4.3).

Energy producing pathways

Energy to fuel metabolism can be obtained by degradation of lipids. Interestingly, an enrichment of proteins functionally categorized in lipid metabolism was observed after pruning (Figure 4.4 A). Seven proteins were down-regulated in TDP compared ZDP samples, five of which are known to act in lipid synthesis. On the other hand of the ten proteins up-regulated, six are known to play a role in lipid degradation (Table 4.3). These observations indicate an induction of lipid degradation after pruning.
I observed an increased abundance of several peroxisomal proteins involved in β-oxidation and the glyoxylate cycle: the acyl-CoA oxidase ACX3 (cassava4.1_002966), the multifunctional protein MFP2 (cassava4.1_002479) and the peroxisomal ketoacetyl-CoA thiolase PKT3 (cassava4.1_007022). Ten additional proteins involved in fatty acid breakdown were also identified (Supplemental Table 4.1; Penfield et al., 2006). Tricarboxylic acid cycle proteins were also significantly enriched and up-regulated TDP (Figure 4.4 A). Metabolites derived from sugars, fatty acids, and proteins all feed into the TCA and are metabolized to produce reducing equivalents to fuel ATP production. In total, 49 proteins of the TCA cycle were identified (Supplemental Table 4.1), of which nine were up-regulated TDP compared to the ZDP control samples. In contrast, only one TCA protein was down-regulated TDP (Table 4.3).

Gluconeogenesis allows the de-novo synthesis of glucose from non-carbohydrate carbon substrates (i.e. pyruvate, lactate, glycerol, gluconeogenic amino acids). The two gluconeogenic enzymes phosphoenolpyruvate carboxykinase PCK1 (cassava4.1_004362; cassava4.1_030131) and peroxisomal malate dehydrogenase pMDH1 (cassava4.1_010585) were both found to be up-regulated in TDP samples (Table 4.3; Supplemental Table 4.1). In a sequential reaction, MDH catalyses the oxidation of malate to oxaloacetate which is further converted by PCK1 to phosphoenolpyruvate. Phosphoenolpyruvate can then be converted to hexose phosphates through gluconeogenesis, or to pyruvate through the last steps of glycolysis. In addition, the glyoxylate cycle enzyme citrate synthase CSY2 (cassava4.1_005825; Pracharoenwattana et al., 2005) was detected but its abundance did not change.

Twenty proteins involved in the oxidative pentose phosphate pathway (OPPP) were identified, eighteen of which were unchanged (Supplemental Table 4.1). However, the glucose-6-phosphate dehydrogenase isoform G6PD4 (cassava4.1_003566), which generates NADPH at the start of the pathway was up-regulated TDP (Table 4.3).
### 4. Metabolic shift in cassava storage root from sink-to-source

#### Table 4.3 Significant regulated proteins of the MapMan categorization with the largest changes. MapMan categories that showed highest changes and the proteins that changes most (p-value ≤ 0.05).

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**Glucose transporter**

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- AT4G37870
- AT2G22780
- AT2G22780
- AT3G54110

**Cassava**

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- cassava4.1_030131
- cassava4.1_010585
- cassava4.1_009952
- cassava4.1_014824

**Arabidopsis**

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**Max fold change**

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- 2.560662975
- 1.768182403
- 1.213384973
- 1.306196433

**Anova (p)**

- 0.015794126
- 0.029497669
- 0.028130428
- 0.000655903
- 0.007485635
- 0.026417829
4. Metabolic shift in cassava storage root from sink-to-source

Protein and amino acid metabolism

I observed changes in proteins associated with protein and amino acid biosynthesis. There was an increase in proteins assigned to protein ubiquitination and modification TDP compared to the ZDP controls (Table 4.4). The protein ubiquitination pathway served to conjugate ubiquitin to Lys residues within substrate proteins, thereby targeting them for degradation by proteasomes (Smalle and Vierstra, 2004). Amongst the functional category for amino acid metabolism 18 proteins were up-regulated TDP. Four of the proteins are assigned to the central amino acids metabolism like aspartate aminotransferase that catalyses the reversible transfer of the amino group from aspartate to β-ketoglutarate yielding glutamate and oxaloacetate. Furthermore, it was described that they are responsible to recycle carbon skeleton during ammonia assimilation (Ryan and Fottrell, 1974).

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4. Metabolic shift in cassava storage root from sink-to-source
4. Metabolic shift in cassava storage root from sink-to-source

Cell wall biosynthesis

The plant cell wall consists of cellulose, hemicellulose and pectins. These different polymers make up the cell wall layers, giving it the rigidity. Plant cell walls undergo constant modifications in order to allow cell expansion and division in growing tissues. Biosynthesis of the cell wall includes polymerization and several modification steps. Of the proteins described to be involved in cell wall synthesis and hemicellulose modifications, 12 were down-regulated (e.g. RHM1, UDP-GlcNAc) TDP compared to the ZDP controls, while five others were up-regulated (like expansin-like 1 pectin methylesterase inhibitor [PME inhibitor] and xylanase 1; Table 4.5). PME was shown to be involved in cell wall modifications required for pollen tube growth (Jiang et al., 2005). The finding that a putative PME inhibitor is up-regulated, while most other cell wall biosynthetic proteins were down-regulated, indicates that cell wall modifications and growth may be reduced.

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</table>
4. Metabolic shift in cassava storage root from sink-to-source

Changes in strigolactone biosynthesis- release of bud outgrowth

According to our analysis the MapMan category ‘hormones’ was significantly down-regulated after pruning. Interestingly, investigations of this functional category revealed that two proteins involved in strigolactone biosynthesis, MAX1 and MAX4 (cassava4.1_005510 and cassava4.1_005134), to be down-regulated 2.3 and 9.4 times, respectively. For Arabidopsis it was shown that strigolactone is involved in maintaining axillary bud dormancy. It was shown that strigolactone-deficient mutant plants, max (more axillary growth), exhibit increased branching (Stirnberg et al., 2002; Sorefan et al., 2003; Booker et al., 2005). Recently, a strigolactone transporter ABCG40 (also known as PDR12 that transports strigolactone in petunia; cassava4.1_027677; cassava4.1_000229) was described (Kretzschmar et al., 2012) ABCG40 was 1.7 times more abundant after cutting (Table 4.6; Supplemental Table 4.1).

<table>
<thead>
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4.4. Discussion

4.4.1. Robustness of proteomics data analysis

Here, I show that shotgun proteome analysis proved helpful in elucidating the changes in protein abundance when cassava storage roots are transformed from a sink to a source and induced to mobilize their starch. The PCA analysis showed that one of the TDP biological replicates separated apart from the other two, while the ZDP control group clustered together closely. However, the treated samples were clearly separated from the controls along the main axis of the PCA analysis, suggesting that changes caused by pruning occurred in all three TDP samples. It is likely that after
pruning, the plants are more stressed than the control plants, and therefore in a less uniform state. It is also likely that, because of the TDP sample separation, the statistical significance of individual protein changes are less pronounced than they could be with further replication. Nevertheless, the data I present here are valuable, and their analysis provides insight into storage root signalling and metabolism.

When analysing my proteome data, it became apparent that cassava frequently has multiple homologs to a given Arabidopsis protein suggesting that gene duplication might have since the evolutionary divergence of the two species. However, for some cases it transpired that the cassava genome database is not correctly annotated. For example, an incorrect annotation was found for LDA, where the single gene locus is interrupted and incorrectly given as two loci in the database. Thus, in order to analyse protein families in more detail, it will be crucial to carefully verify that the gene annotation is correct.

4.4.2. Changes in starch metabolism caused by pruning

As expected, I could show that pruning off the cassava shoots induces starch remobilization in storage roots. The decrease in starch content, both at the site of stem pruning and in subterranean storage roots, was highly significant after 10 days (Figure 4.1 B, C). This is in accordance with previous studies of pre-harvest pruning experiments (van Oirschot et al., 2000). I could show using various native gels that there was an increase in amylolytic activity in storage roots accompanying the change in starch. However, with the exception of LDA, it was not possible to really say which enzymes are responsible for the activity bands I observed, hence the use of proteomics.

My data reveal that there are changes in starch metabolic proteins, but these changes are not as widespread as one might have expected. Furthermore, not all of the changes can be simply interpreted. The down-regulation of the root specific large subunit of AGPase (APL3) after pruning is in agreement with the idea that the rate of starch synthesis is decreased upon transition from sink-to-source. AGPase is widely accepted to be the step at which the flux into starch is controlled in plants. The down-regulation of PWD after pruning is more surprising as the enzyme has a designated role in starch degradation (Baunsgaard et al., 2005; Kotting et al., 2005). That said, it was shown that glucan phosphorylation not only occurs during starch degradation, but also during synthesis (Nielsen et al., 1994), explaining the presence of PWD in control storage roots. Furthermore, it should be pointed out firstly, that the change in PWD abundance was small and secondly, that it is not known whether phosphorylation is really required for the degradation of starch in cassava root, as it is in Arabidopsis leaves or potato tubers.
Despite the red-pullulan gels suggesting a higher LDA activity at TDP compared to ZDP (Figure 4.2), at the proteome level no significant change was observed. It is possible that the increase in activity was due to posttranslational modification rather than an increase in protein abundance. However, the semi-quantitative native gels also need to be backed up with accurate assays. In contrast, the proteomic analysis showed that AMY3 protein abundance is substantially increased in starch-mobilizing roots TDP. It is not clear whether this activity is reflected on the native gel analysis, and further work will be needed to determine if there is an increase in α-amylase activity. In Arabidopsis, mutant analysis revealed that AMY3 is not essential for transitory starch degradation (Yu et al., 2005). However, for cereals it is well described that α-amylases are the main hydrolytic enzymes involved in degrading storage starch for germination (Fincher, 1989). Furthermore, in other systems, an increase in α-amylase activity correlates with re-mobilization of storage starch (e.g. in defoliated white-clover and poplar wood ray cells; Baur-Höch et al., 1990; Witt and Sauter, 1994; Gallagher et al., 1997). This supports the idea that storage starch degradation in some heterotrophic tissues involves α-amylases. If the main pathway to degrade cassava storage starch does involve AMY3, it implies that branched and linear maltooligosaccharides are released from the granule surface. Branched maltooligosaccharides will serve as substrates for debranching enzymes (LDA and ISA3) to generate more linear maltooligosaccharids (Delatte et al., 2006; Streb et al., 2008). Linear maltooligosaccharides can be further processed by stromal enzymes. In the pathway described in Arabidopsis leaves β-amylases would be one of the key stromal enzymes degrading both the granule surface and linear maltooligosaccharides. It is surprising that in the proteome analysis, I could not identify any β-amylase homologs. The reason for this might be that β-amylases are not involved in storage starch mobilization in cassava or the proteins were below the detection limit.

To strengthen my hypothesis that AMY3 is a key player in cassava root starch breakdown, functional analyses are needed. A transgenic cassava line with repressed AMY3 is in development, and will give allow the functionality of AMY3 in storage root to be tested directly (see Chapter 5). If it is involved, changing its expression may offer an opportunity to increase starch yields in cassava storage roots by preventing the post-harvest decline in starch levels.

4.4.3. Changes in sucrose metabolism caused by pruning

Although I interpret the changes in proteins detected on the assumption that the sink-source transition occurred, it is interesting that the actual sucrose amount did not change (Figure 4.1). In sink tissues sucrose is unloaded from the phloem and transported to the cell, where it is hydrolysed by SUS or cytosolic INV depending on how sucrose is cleaved UDPG and fructose (SUS) or glucose and fructose (INV) are generated. The free hexoses are then phosphorylated either by HXK or FK in order to feed the hexose-P pool. In the proteomic analysis I observed more of FK in untreated samples
(sink). This suggests that fructose is phosphorylated predominantly by FK to increase F6P levels. In subsequent steps F6P can be equilibrated by PGM to G6P that then can be transported to the amyloplast by the pG6PT where it can be converted to starch. Interestingly, I could identify more of cytosolic F1,6BPase before pruning. This enzyme catalyses the dephosphorylation of F1,6BP to F6P by releasing Pi. As a result again F6P is produced that could be subjected towards the amyloplast, and hence starch synthesis. A recent screen for fructose insensitive mutants in Arabidopsis identified the cytosolic F1,6BPase as a sensor for fructose availability. It was shown that similar to HXK1 signalling this is not dependent on the catalytic activity. This finding suggests that potentially in heterotrophic tissues similar mechanism exists. On the other hand after pruning and thus during transition from sink to source metabolism, cINV2 increased suggesting that sucrose is hydrolysed in the cytosol to glucose and fructose. This might be beneficial as high sucrose export rate to the new emerging leaves might not be required yet. The concomitant increase of hexokinases (HXK1 and HXK3) suggests that potentially the demand for hexose-P increased in the root that can feed into diverse metabolic pathways. Furthermore, a plastidic fructose-1,6 bisphosphatealdolase (FBA) that catalyses the reversible reaction of F1,6BP to DHAP and triose-P. Further DHAP can enter the oxidative pentose phosphate pathway generating NADPH. Thus, these findings suggest that the sucrose metabolism has changed. There are good evidences that sucrose pathway generates F6P that is likely converted to G6P and hence starch in the amyloplast in untreated storage roots. On the other hand the high abundance of cINV suggests that there is an increased demand for hexose-Ps that can supply various metabolic pathways.

4.4.4. Evidence for sugar signalling in cassava storage roots

It might be that the concentration of sucrose is finely controlled and is kept constant despite large changes in fluxes. After pruning, the influx of sucrose must have stopped abruptly and, after a time, sucrose production in the root must occur to support regrowth. It is also possible that there were significant changes between ZDP and TDP but that after ten days, a new homeostasis has been reached. That said there were relatively few changes in sucrose metabolic proteins detected ten days after pruning compared to control plants, suggesting that perhaps the storage root has already the enzymatic capacity to synthesise sucrose.

In potato tubers, where transition of sink to source was studied upon tuber sprouting, a correlation between activity of either SUS or cINV and developmental stage of the tissue was observed. Thus, INV activity is predominant in the tuber initiation phase, where growth occurs. Sucrose cleavage by SUS on the other hand is the main sucrolytic pathway in developed tubers (Ross et al., 1994; Appeldoorn et al., 1997). The up-regulation of cINV2 TDP might also indicate a change in how sucrose is degraded in cassava roots. The concomitant up-regulation of two hexokinases, HXK1 and HXK3,
4. Metabolic shift in cassava storage root from sink-to-source

point into the direction that there is an increased capacity to feed hexoses (potentially generated by cINV2) into the hexose-P pool. Hexose-Ps are intermediates used for diverse catabolic and anabolic pathways. An increase in HXK activity and in biosynthetic activities associated with transition to a source tissue would also lead to an increased demand of ATP consistent with my findings of a significant increase of proteins involved in respiration (Table 4.3). Although not measured here, I anticipate that there would be an increase in respiration in the storage roots of pruned plants.

In roots TDP, there was a significant up-regulation of KING1, a regulatory subunit of SnRK1, while the catalytic α-subunit remained unchanged. SnRK1, a homolog to AMPK in mammals and Snf1 in yeast, is reported to be involved in sucrose signalling and up-regulated upon starvation. Expression analysis showed that SnRK1 is up-regulated in growing potato stolons, whereas in mature tuber tissue fewer transcripts were detected suggesting that SnRK1 is active during tuber maturation (Man et al., 1997). In addition it was shown that the transcript of γ-subunit (KING1) is highly expressed in stems and root tissue of Arabidopsis (Bouly et al., 1999). SnRK1 is proposed to act in two ways; it directly inhibits target enzymes involved in isoprenoid synthesis, nitrogen assimilation and sucrose synthesis (Sugden et al., 1999) by phosphorylating them. For Arabidopsis, it was also shown that overexpression of the catalytic α-subunits (AtKIN10 and AtKIN11) increases the transcription of target enzymes involved in starvation and/or stress responses via a transcriptional cascade involving factors like GBF5 and bZIP (Satoh et al., 2004; Baena-Gonzalez et al., 2007). Amongst up-regulated transcripts, were genes repressed by sugars. In addition, for wheat endosperm it was shown that the wheat TaAMY2 promoter is induced by SnRK1, supporting the hypothesis that SnRK1 is involved in low sugar-signalling. In contrast, overexpression of SnRK1 in potato tubers as well as rice led to an increase in starch content as well as an increase in sucrose synthase and ADGPase activity (Mckibbin et al., 2006). Given the strong data implicating SnRK1 in the response to starvation, the finding that the KING1 subunit is greatly up-regulated is exciting and makes it an excellent target for further experimental analysis.

Also in the context of sucrose signalling, it was shown that the sucrose signalling pathway of SnRK1 is linked to the signalling pathway via the metabolite trehalose 6-phosphate (T6P). It was shown in Arabidopsis that T6P increases after sucrose feeding and re-illumination at the end of the night (Schluempmann et al., 2004; Lunn et al., 2006). These findings have led to the suggestion that T6P serves as a signal for high carbon availability. It was further shown that T6P can stimulate redox activation of AGPase (Kolbe et al., 2005; Lunn et al., 2006) and that supplying exogenous trehalose increases APL3 transcription (Wingler et al., 2000). My proteomics data revealed the presence of four homologs of trehalose-6-phosphate synthase (TPS; Supplemental Table 4.1), but they were unchanged during the experiment.
4. Metabolic shift in cassava storage root from sink-to-source

The pruning of my cassava plants clearly had a big impact on other metabolic pathways that were not the primary focus of my work, with changes of proteins involved in lipid, protein and amino acid metabolism and in the biosynthesis of hormones such as strigolactones. Clearly such changes can be interpreted in the context of this study. For example, the fact that strigolactones act as inhibitors of apical dormancy release is consistent with re-sprouting of lateral buds (Figure 4.1 A, Table 4.6). Such findings suggest that in cassava, as in other plants, strigolactones are involved in regrowth and branching. My work therefore provides further gene targets for investigation that could ultimately be used to improve plant vigour or to alter plant architecture.

The extent of re-mobilization of starch after pruning however, cannot only be explained only by the transition of the storage root to a source tissue supplying newly-developing sinks (i.e. the new leaves). The strength of these sinks is not likely to be strong enough to require all the carbon lost from the starch pool. The decrease of 48% in starch content 10 days after pruning (Figure 4.1 E) additionally reflects the needs of storage roots to maintain its own cellular homeostasis through respiration. Without the support of the autotrophic leaf tissues, stored carbohydrates are converted into CO₂ through the OPPP and the TCA cycle. In addition to supplying energy (e.g. for housekeeping metabolism and membrane energization) these pathways will also supply various intermediates which are needed to feed other biochemical processes (i.e. protein metabolism, gene transcription, general metabolic pathways) throughout the day and night.

4.4.5. General conclusion and outlook

Overall, the analysis of changes in the primary carbohydrate metabolism together with the overall proteome changes occurring after pruning lead me to the conclusion that a transition from sink to source did indeed occur. The finding that AMY3 levels correlated with starch remobilization, places it as a main candidate in the starch degradation pathway depends. Moreover, the absence of β-amylase homologs in the proteome data supports this idea. To confirm the hypothesis that AMY3 is the key enzyme in cassava to mobilize starch a functional analysis using an RNAi construct to suppress AMY3 expression is underway (Chapter 5).

It might be that some proteins (e.g. the β-amylases) are missing as their abundance is below detection limit. Our laboratory recently conducted a combined proteome and transcriptome study in the non-model plants Cecropia peltata. More detailed information was gained with a transcriptome analysis (Bischof et al., 2013) than with the proteome analysis, but the combination of both was optimal. In order to strengthen the data I present here, a whole transcriptome analysis using the RNAseq is underway. As transcript levels respond faster than protein levels, I performed a time-course harvest of storage roots after pruning. At the time of writing, storage roots were harvested 4h,
4. Metabolic shift in cassava storage root from sink-to-source

24h, 2 days, 6 days and 10 days after pruning, with control samples (uncut plants) at time points 0h, 4h and 24h. The outcome of this experiment is still under investigation, but when completed, will be directly comparable with my proteome study.
5. Increasing starch bound phosphate level: A transgenic approach

5.1. Introduction

Depending on the end use in food or non-food industries, starches with different properties are needed. Apart from processed food, confectionary and drinks, starch is used to make corrugated board and paper. For most of these processes, starches are modified post-extraction to obtain the required properties. Many modifications are gained by substitution of hydroxyl groups. Substitutions are gained through esterification (e.g. phosphate, acetate), oxidation, etherification (e.g. hydroxypropyl, hydroxyethyl) or cross-linking (e.g. phosphate diester). These chemical alterations confer properties such as increased water retention, better retrogradation, starch structure stabilisation, or improved pasting properties. In the paper industry, cationic starches are used for paper strengthening (Tharanathan, 2005). Native starches from various botanical sources differ in their physico-chemical properties. Several studies have shown that parameters like amylose:amylopectin ratio, granule size, protein and lipid content, and the degree of starch phosphorylation are responsible for influence key functional characteristics such as peak viscosity, paste clarity, or retrogradation (Tester and Morrison, 1990; Jobling et al., 2002). The degree of phosphorylation was reported to influence peak viscosity and gel formation. This was shown by the analysis of physico-chemical properties of potato wild-type starch compared to Stgwd suppressor lines which have low levels of starch-bound phosphate (see below and Chapter 1). This revealed that high maximum viscosity derives from starch phosphorylation (Vikso-Nielsen et al., 2001). Potato tuber starch, which has a high degree of phosphorylation (0.5%), shows a much higher viscosity peak compared to cassava root starch, which has only 0.05% starch phosphorylation (Blennow et al., 1998).

Early studies of GWD down-regulation in potato revealed a starch excess phenotype in leaves, while tubers exhibited a reduction in cold sweetening. These findings indicated that StGWD is involved in starch degradation in both tissues. As these studies also showed that the lack of StGWD leads to a reduced G6-phosphorylation (Lorberth et al., 1998; Vikso-Nielsen et al., 2001), they provided the first indication that phosphorylation is important for the initial step in starch degradation. Subsequent studies in the model plant Arabidopsis supported this finding. Thus, a model has emerged in which amylopectin on the starch granule surface is phosphorylated by GWD during degradation, rendering it more soluble. Phosphate-ester bound to the starch granule is suggested to open the packing of
double helical chain structures by altering the steric conformations. It may also destabilise the double helices themselves. This is proposed to make the glucan chains more accessible for hydrolysing enzymes like α- and β- amylases, and the debranching enzymes (ISA3, LDA) involved in starch degradation (Edner et al., 2007). Through studies of Arabidopsis, another glucan dikinase (PWD, phosphoglucon, water dikinase) was subsequently discovered and shown to phosphorylate glucose units of amylopectin at the C3 position after pre-phosphorylation of GWD (Baunsgaard et al., 2005; Kotting et al., 2005). GWD was also shown to be specific for the 6-carbon of the individual glucose units (Ritte et al., 2002).

Limited proteolysis revealed that StGWD, a 155 kDa protein, consists of 5 stable fragments. Analysis of these fragments showed that GWD contains three major domains important for successful amylopectin phosphorylation. GWD contains two CBM domain that are involved in binding amylopectin and a pyruvate-phosphate dikinase-like domain is involved in phototransfer via an autocatalytic histidine residue (Mikkelsen et al., 2005; Mikkelsen et al., 2006). Investigation of the third domain through site-directed mutagenesis of cysteine residues revealed a redox regulation motif. Functional analysis revealed that GWD is active by reduction of a disulphide bridge in a reducing environment which is predominant during the light phase in chloroplasts. Although the main function of starch phosphorylation was shown to be important during starch mobilisation, Nielsen et al. (1994) reported that during starch biosynthesis phosphate is incorporated into starch. In potato tubers discs 0.5% of the glucosyl residues in newly synthesised starch are phosphorylated (Nielsen et al., 1994). This finding also explains why starch granules are phosphorylated not only at the surface but also in the inner layers. This was recently visualized by synchrotron X-ray microfluorescence mapping in potato starch granules (Buleon et al., 2014).

For efficient hydrolysis of starch granules to maltose and oligosaccharides, phosphate esters need to be removed. In higher plants two glucan phosphatases – SEX4 and LSF2 - have been described (Zeeman and Ap Rees, 1999; Niittyla et al., 2006; Kotting et al., 2009; Santelia et al., 2011). The characterisation of these phosphatases in Arabidopsis revealed that both enzymes are responsible for removing phosphate residues both from the starch granules and from soluble phospho-oligosaccharide released from the starch granule. Recombinant AtSEX4 protein efficiently removes phosphate residues from both the C-6 and C-3 position of the glucose units. The Atsex4 mutant has increased starch levels as well as high phospho-oligosaccharide content. The accumulation of phospho-oligosaccharide revealed the importance of removing phosphate contents as some hydrolysing enzymes
5. Increasing starch-bound phosphate level: A transgenic approach

(including the important maltose-producing exoamylase, β-amylase) are blocked by phosphate residues (Kotting et al., 2009). In contrast, AtLSF2 removes preferentially C3- bound phosphate (Santelia et al., 2012). In contrast to Atsex4 mutants, Atlsf2 mutants show no difference in starch levels to the wild type, and nor do phospho-oligosaccharides accumulate. This suggests that side-specificity of AtSEX4 for C3-bound phosphate may be sufficient to mediate its removal during starch breakdown. However, the loss of LSF2 was reflected at the level of total starch-bound phosphate, which was increased by 25%, specifically due to an increase at the C3 position. In addition, it was shown that although Atlsf2 seems to have only little effect on starch metabolism, the double mutant Atsex4lsf2 had a more severe starch-accumulating phenotype than the Atsex4 single mutant. This showed that although AtLSF2 is dispensable for normal rates of starch degradation, its activity becomes important in the Atsex4 mutant background (Santelia et al., 2011).

In recent studies, transgenic plants overexpressing StGWD were described and published in the scientific literature and in patent applications. StGWD was expressed in barley (Carciofi et al., 2011), wheat and corn (Sonnewald and Kossmann, 2013). Carciofi et al. (2011) showed that StGWD overexpression leads to more than a 7-fold increase of starch-bound phosphate. This corresponds to 3 times more phosphate than what is found for cassava native starch. Here, we aimed to increase the degree of starch-bound phosphate in cassava starch granules, as well as to increase starch yield. Therefore, three approaches were followed. Two aimed at increasing starch-bound phosphate and one at increasing starch levels in cassava storage root. Firstly, potato StGWD was overexpressed either in its wild-type form or as a modified, redox-insensitive form (StGWDc1084). This was done with the expectation that, if the wild type form was inactive in vivo through oxidation, the redox-insensitive form would be constitutively active. Secondly, RNAi constructs were designed against each of the two endogenous genes encoding glucan phosphatases SEX4 and LSF2 in order to reduce their activity. Both RNAi constructs are driven by a root-specific promoter to limit dephosphorylation activity specifically in cassava storage roots. Third, an RNAi construct was designed against the plastidial alpha amylase gene (AMY3) to decrease starch degradation in storage root and thereby increasing starch yields in an agricultural setting. As shown in the previous chapter, AMY3 is highly induced at both gene and protein levels during starch remobilisation in cassava storage roots.
5. Increasing starch-bound phosphate level: A transgenic approach

5.2. Transformation and regeneration of cassava

5.2.1. Overexpression of potato glucan, water dikinase in cassava tissue culture

5.2.2. Construct description, in vitro analysis

As described, potato starch is highly phosphorylated compared to other plant species. To investigate if the potato StGWD would be as efficient in phosphorylating starch granules in other species and to investigate the impact of the mutated, redox-insensitive StGWD in vivo, constructs for expression of StGWD or the redox-insensitive StGWD_{C1084S} were transformed into cassava friable embryonic cell cultures (FECs; see Chapter 2.12; Figure 2.1). In subsequent steps, the transformed FECs were successfully regenerated on selective media, containing the antibiotic geneticin. The last steps for regenerating plantlets are performed on media without antibiotics. Thus, the regenerated plantlets were subsequently re-tested by growing them on selective rooting media containing the antibiotic geneticin. In this test, only transformed plantlets containing the construct produce roots. For the StGWD construct, 22 individual plant lines were isolated and for the StGWD_{C1084S}, 43 plant lines were isolated. The insertion of the transformation construct in the cassava plantlets was further verified by insert-specific PCR (Figure 5.1, Chapter 2.12.1) and DNA sequencing of the products. For StGWD lines, this revealed an 81% positive transformation rate. For the StGWD_{C1084S} lines, all lines selected in the rooting test were positive by PCR and sequencing. For further analysis, 13 individual StGWD lines and 35 individual StGWD_{C1084S} were selected.

![Figure 5.1](image.png)

**Figure 5.1** Representative PCR reactions to test positive StGWD and StGWD_{C1084S} transgene insertion. Primers annealing in the promoter and insert region were chosen for the PCR. Here the transgenic StGWD #5 line was loaded on a 1% Agarose gel together with wild-type, plasmid and water as template. For DNA control the PP2A was amplified.
5. Increasing starch-bound phosphate level: A transgenic approach

The expression levels of StGWD and StGWD<sub>C1084S</sub> proteins in the selected transgenic lines were investigated by immunoblot analysis, compared to untransformed wild-type plants. As both proteins were tagged with a FLAG-tag at the C-terminus, the protein level was investigated using two antibodies; an anti-GWD antiserum raised against recombinant StGWD protein (Eurogentec) and a commercially-available anti-FLAG antibody raised against the FLAG-tag (α-M2, Sigma). The anti-GWD antibody recognised both the overexpressed StGWD/StGWD<sub>C1084S</sub> (162 kDa) protein and another protein of similar molecular weight – presumably the endogenous MeGWD (155 kDa). This second band was variable in intensity, but was observed in both transformed plants and the wild type. As shown in Figures 5.2 and 5.3, the expression level of the recombinant protein in leaf tissue varied from high to undetectable between the individual transformed lines. The antibody against the FLAG tag was used to discriminate between the endogenous and overexpressed StGWD protein. Immunoblots incubated with the anti-FLAG antibody showed that it was specific (i.e. the second band was not visible), but the overall sensitivity was much lower than for the anti-GWD antibodies. Considering both the anti-GWD and the anti-FLAG immunoblots, the transgenic lines were divided into three groups of high, intermediate and low/non-expressing lines. High expression refers to clear protein detection with both antibodies; intermediate when protein expression detected with the anti-GWD, but not the anti-FLAG antibodies; low when neither antibodies detected the overexpressed proteins. For the StGWD over-expressing lines, four (lines 18, 17, 5 and 2) were identified with high, two with intermediate (lines 16 and 11) and seven with low (lines 6, 9, 1, 20, 3, 21, and 19) protein expression levels (Figure 5.3). For the transgenic StGWD<sub>C1084S</sub> cassava lines tested, there were 18 with high (lines 48, 52, 45, 43, 53, 46, 41, 9, 13, 20, 30, 27, 22, 39, 6, 34, 10, and 24), 15 with intermediate (50, 51, 47, 42, 44, 35, 36, 8, 40, 33, 5, 32, and 11), and four with low (lines 3, 15, 4, and 49) protein expression (Figure 5.3).
5. Increasing starch-bound phosphate level: A transgenic approach

**Figure 5.2** StGWD expression levels in transgenic Cassava lines

Thirty µg of total leaf protein from individual transgenic Cassava lines were subjected to immunoblot analysis. Replicate blots were performed using anti-StGWD (top panel) or anti-FLAG (bottom panel) primary antibodies. The black arrow indicates the 162 kDa StGWD protein. The grey arrow may represent the endogenous 155 kDa MeGWD protein.
5. Increasing starch-bound phosphate level: A transgenic approach

**Figure 5.3 StGWDC1084S expression levels in transgenic Cassava lines**

Immunoblot analysis as in Figure 5.1 of individual transgenic cassava lines using anti-StGWDC or anti-FLAG antibodies. The black arrow indicates the 162 kDa StGWDC1084S protein. The grey arrow may represent the endogenous 155 kDa MeGWD protein.
5.2.3. Growth analysis of transgenic StGWD and StGWD\textsubscript{C10845} lines compared to wild-type plants

To describe any effects of expression of either the StGWD or the StGWD\textsubscript{C10845} constructs on growth, yield and starch-bound phosphate, a set of transgenic lines were transferred to soil and grown under greenhouse conditions. The selection of lines for analysis was performed according the protein levels detected in leaves. Transgenic lines were selected with either high or low expression, the latter serving as transgenic controls. Thus, for StGWD-9 overexpressing lines (18, 17, 5, 2, 16, 11, 3, 21 and 19) (Figure 5.2), and 12 for StGWD\textsubscript{C10845} the lines (48, 52, 45, 46, 41, 49, 44, 9, 13, 33, 5, 3, 15) (Figure 5.3) were grown in the greenhouse for storage root formation. As an additional control, in-vitro grown wild type (cv. 60444) was transferred on soil. Four months after transplantation of the transgenic lines, plant height, leaf numbers and internode numbers were determined as described in Chapter 3.2.1. Figures 5.4 and 5.5 show the transgenic StGWD and StGWD\textsubscript{C10845} lines (ordered according transgene expression levels; see Figures 5.2 and 5.3), compared to wild-type plants. For the transgenic lines expressing the wild-type StGWD construct the number of internodes and leaves showed a tendency to be higher than in wild-type plants though, only for line 2 a significant difference in number of internode was observed (Figure 5.4 B-C). The analysis of leaf number shows a tendency that transgenic plants – StGWD and StGWD\textsubscript{C10845} - retain the leaves compared to wild type plants, though only for the StGWD\textsubscript{C10845} – lines 33, 41, 5, and 9 a significant difference was seen. Older leaves were curled and bent downwards, while the newly developing leaves at the apex were apparently unaffected. Although this seemed to be a general phenotype for transformed cassava plants, in StGWD lines 17 and 5, the effect was more severe and seemed to be consistent for all leaves as they aged. The other plants showed the leaf-phenotype for a certain period, but it then well as disappeared at a later stage in development. This leaf phenotype was not observed when the plants were grown in vitro. The StGWD lines, when compared to wild-type plants, grew less well shown by plant height (Figure 5.4 A). This reduced growth effect was statistically significant (Student’s t-test ≤ 0.05) for the lines 11, 16 and 17. For these transgenic lines the protein expression levels were high. This suggests that the protein expression might influence growth of the internodes as the plants otherwise appear to be at the same developmental stage. The negative influence was obvious in two plant lines with high expression (17, 5), which showed a pronounced stunted growth (Figure 5.4 D). Three out of four lines with highest protein expression levels (18, 17 and 5) showed decreased growth as the two lines with intermediate protein expression (16 and 11) (Figure 5.4 A). However, the transgenic
5. Increasing starch-bound phosphate level: A transgenic approach

Figure 5.4 Growth analyses of transgenic StGWD cassava lines

In vitro grown plantlets were transferred into soil and grown in the greenhouse. The general growth parameters were determined after 4 months. The transgenic lines were arranged according the protein loading in Figure 5.1 (from high in dark grey to low in light grey; Figure 5.1). A) Height (cm), B) number of internodes, C) number of leaves. Transgenic lines (grey bars), cv. 60444 wild type (black bar). Mean ± SE (N=1-5). Asterisk shows significant difference (t-test < 0.05) D) Pictures of representative transgenic plants and a wild-type plant.

lines with low or non-detectable expressed protein (3, 21, and 19) grew comparably to wild-type plants. From the analysis of the redox-insensitive StGWDC1084S lines, no clear correlation between plant growth parameters and recombinant protein expression could be made. None of the lines showed a significant difference compared to wild-type plants (Figure 5.5).
5. Increasing starch-bound phosphate level: A transgenic approach

Figure 5.5 Growth analyses of transgenic StGWDC1084S cassava lines

*In vitro* grown plantlets were transferred into soil and grown in the greenhouse. The general growth parameters were determined after 4 months. The transgenic lines were arranged according the protein loading in Figure 5.2 (from high in dark grey to low in light grey; Figure 5.2). A) Height (cm), B) number of internodes, C) number of leaves. Transgenic lines (grey bars), cv. 60444 wild type (black bar). Mean ± SE (N=1-5). Asterisk shows significant difference (t-test < 0.05).

D) Pictures of representative transgenic plants and a wild-type plant.
5. Increasing starch-bound phosphate level: A transgenic approach

5.2.4. Starch visualization in leaf and determination of storage root growth in the transgenic plants

To provide a first insight in impact of StGWD or StGWD_{C1084S} expression on starch metabolism, the tips of leaf 4 or 5 were stained with iodine at the end of the day and end of the night (Figure 5.6). As shown in Chapter 3 (Figure 3.5), leaf starch in the wild type is not fully degraded at the end of the night. Wild-type leaves stained in a brown-reddish colour at both time points. For the transgenic lines, leaf tissue was harvested from two plants representing high, intermediate and low protein expression levels. Starch stained a brown-reddish colour as in the wild type. For the transgenic StGWD lines with high protein expression (18, 17), starch had accumulated at the end of the day and a residual amount still seen at the end of the night. The two StGWD transgenic lines with intermediate protein expression level (16, 11) had starch at the end of the day, but less starch could be seen at the end of the night than in the wild type. For one low expressing line (21) starch was detected at both time points where for another (19) less starch was observed at the end of the night compared with the end of the day. Interestingly, the transgenic lines expressing the redox insensitive StGWD_{C1084S} starch stained darker in contrast to the brown-reddish colour of the wild type and the StGWD overexpressing lines. The redox insensitive lines expressing high protein levels (9, 13) and intermediate protein level (5) had starch at the end of the day but did not stain at the end of the night. The leaves of a second line expressing intermediate protein levels (33) stained for starch at both time points. The two non-expressing StGWD_{C1084S} lines stained for starch at the end of the day but not at the end of night (Figure 5.6). Overall preliminary results hint at a difference in the starch in the StGWD_{C1084S} lines, but these differences (either qualitative or quantitative) need to be confirmed by further measurements and analyses.
5. Increasing starch-bound phosphate level: A transgenic approach

Figure 5.6 Iodine staining of transgenic StGWD/STGWDC1084S leaves at the end of the day (EoD) and end of the night (EoN). Leaf tips from transgenic StGWD and StGWDC1084S lines, with different protein expression levels were harvested at EoD and EoN were stained with iodine.
5. Increasing starch-bound phosphate level: A transgenic approach

To investigate the phosphorylation activity of StGWD and StGWD<sub>C1084S</sub> on cassava starch, the storage roots of the transgenic plants were harvested after 6 months. The mean storage root fresh weight of the transgenic lines was in all cases lower than in wild-type plants (Figure 5.7). On average, the storage root fresh weight of StGWD lines was 68% lower than in the wild type, varying between 0.93 g and 37.67 g (Figure 5.7 A). On average, the storage root biomass production of StGWD<sub>C1084S</sub> lines was 81% less than in the wild-type, varying between 0.85 g and 10.37 g (Figure 5.7 B). In some of the individual transgenic line no storage roots had developed. No correlation was observed between storage root development and transgenic protein expression (Figure 5.7).

![Figure 5.7 Storage root of transgenic StGWD and StGWD<sub>C1084S</sub> cassava lines](image)

The fresh weight of the storage roots from transgenic (grey bars) and wild-type (black bars) plants was determined after 6 months of growth. A) StGWD lines B) StGWD<sub>C1084S</sub> lines. The transgenic lines are arranged according the protein expression levels (high to low) given in Figures 5.1 and 5.2. Mean ± SD. (N=1-5).
5. Increasing starch-bound phosphate level: A transgenic approach

5.2.5. Storage starch: \(^{31}\text{P}\)-NMR reveals increased phosphate bound to C6 and C3 position in StGWD\(_{C10845}\)

Starch was isolated from the StGWD and StGWD\(_{C10845}\) lines and subjected for \(^{31}\text{P}\)-NMR analysis to get information about the ratio of C3 and C6 phosphorylation, as was described by Santelia et al. (2011). For these measurements, starch was isolated from the storage roots of representative transgenic lines as well as from the wild type. The non-expressing StGWD line (21) was used as a transformation control (Figure 5.2). Representative lines with high protein expression for StGWD (#18) and StGWD\(_{C10845}\) (#9) were chosen (Figure 5.2, Figure 5.3). \(^{31}\text{P}\)-NMR gives a relative percentage of C3 and C6 phosphorylation within a sample, and is also semi-quantitative for phosphate abundance. All analysed samples revealed similar C3:C6 phosphorylation ratio between 2.1 and 2.7 (Figure 5.8). The peak intensity was similar for all samples except for the StGWD\(_{C10845}\) line 9 highly expressing the redox insensitive form. For this sample the peak was more intense (the y-axis scale in Figure 5.8 D is double that of the other spectra in A-C). This suggests that more total phosphate was present. However, for quantification of total bound phosphate other, more quantitative experimental approaches are needed.
5. Increasing starch-bound phosphate level: A transgenic approach

5.2.6. Increase in total starch phosphate: RNAi construct design against MeSEX4 and MeLSF2

Another approach to increase phosphate content bound to starch is to knock-out the glucan phosphatases SEX4 and LSF2 using the RNAi technique. In Arabidopsis, it was shown that Atsex4 mutants lead to stunted growth. This stunted growth is caused by the fact that Atsex4 mutant plants accumulate starch that is not degraded during the night, thus the supply of carbon during the night is blocked (Zeeman et al., 1999; Kotting et al., 2005). Thus,
it is possible that down-regulation or knocking-out of MeSEX4 transcript might lead to a comparable impact on whole plant growth in cassava, and negatively affect biomass production. Furthermore, the propagation of plants by stem cuttings might also be negatively affected when starch can’t be degraded to fuel regrowth. Therefore, an RNAi construct was designed driven by a potato patatin class I promoter, which was shown to be tuber specific in potato and root-specific in Arabidopsis (Naumkina et al., 2007).

The protein sequences of AtSEX4 and AtLSF2 were used as a query to search for the orthologous proteins in cassava. A BLASTP search was performed against the cassava proteome database (www.phytozome.net; Prochnik et al., 2012). The translation product of gene accession number cassava4.1_009735m showed highest homology to the AtSEX4 protein sequence and the translation product of gene accession number cassava4.1_013314m showed highest homology to the LSF2 protein. For the production of the RNAi hairpin constructs, sequences unique to the individual transcripts (205 bp for SEX4-RNAi and 190 bp for LSF2-RNAi) were chosen (Figure 5.9 A, B). All RNAi constructs were cloned into a modified pCAMBIA1301 vector with a patatin class I promoter and Nos-terminator (Figure 2.1).

**Figure 5.9 Sequences used for RNAi construction**
The indicated sequence form the corresponding CDS was used as a template to design a hairpin construct
Increasing starch-bound phosphate level: A transgenic approach

Both constructs were successfully cloned and transformed into cassava FECs according the protocol described previously (Bull et al., 2009; see also Chapter 2). For the SEX4-RNAi lines 155 and for LSF2-RNAi lines 133 individual plants were grown on selective growth media containing hygromycin. Under these conditions, only transgenic plantlets produced roots. For the SEX4-RNAi construct 46 and for the LSF2-RNAi construct, 57 plantlets made roots (Table 5.1). Using PCR reactions with primer combinations specific for the promoter and terminator sequences present in the T-DNA insertion, integration of the construct into the genomic DNA was confirmed (Figure 5.10). The confirmation PCR analysis revealed that for SEX4-RNAi lines the majority (84%) were positive for both PCR reactions. Four lines were positive for only promoter or terminator sequence PCRs and one line showed no insertion. For the LSF2-RNAi lines, 86% were positive for both sequences, 17% were positive for either promoter or terminator sequence, and two lines showed no insertion. Preliminary observations suggest that the SEX4-RNAi lines have a pronounced slow-growth phenotype in tissue culture and that the leaves for several independent lines are abnormally narrow. In contrast, LSF2-RNAi lines are comparable to the wild type plants grown in tissue culture.
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Figure 5.10 Representative PCR reaction to test positive RNAi-lines
Promoter (Patatin) and terminator (Terminator) sequence were amplified to verify the insertion of the hairpin construct. For each line a positive transgenic line, wild-type and plasmid containing the respective RNAi insert and water was loaded as indicated. For DNA control the PP2A was amplified. A) SEX4-RNAi, positive line #155 B) LSF2-RNAi line, positive control line #4.

5.2.7. RNAi construct design against MeAMY3

As described in Chapter 4, AMY3 was identified as a likely candidate enzyme involved in starch degradation in heterotrophic storage root tissue. In order to test this biological role of AMY3 in storage starch degradation and potentially increase storage root biomass by preventing unwanted starch breakdown, I designed a hairpin construct against the MeAMY3 transcript. Although AMY3 is dispensable for starch degradation in Arabidopsis leaves, we do not know if this is the case for cassava. Furthermore, down-regulation of AMY3 could block starch degradation in heterotrophic tissue such as the stem. Thus, expressing a hairpin construct against the MeAMY3 transcript on a whole plant level could potentially have a negative impact on plant growth and propagation, as described for SEX4 down-regulation above. Thus, the MeAMY3 RNAi hairpin was also designed to be driven by the patatin class I promoter (Naumkina et al., 2007).
The AtAMY3 protein sequence was used as a query to search for the orthologous protein in cassava. A BLASTP search revealed that the protein encoded by the gene accession number cassava4.1_001362m has the highest sequence homology to AtAMY3. For the RNAi hairpin construct, a unique 210-bp sequence matching the 5’ end of the MeAMY3 coding sequence was chosen (Figure 5.9 C). The RNAi construct was cloned into a modified pCAMBIA1301 vector (Figure 2.1).

At the time of writing, the AMY3-RNAi construct the plasmid has been transformed into FECs. The transformed FECs are growing on selection media (Figure 2.2, step 4 and 5) and 22 individual plantlets are currently regenerating on growth medium (Table 5.1). Next, these plants will be transferred and tested for rooting capacity on a medium containing hygromycin (Figure 2.2, step 6).

5.3. Discussion

5.3.1. Analysis of Cassava plants expressing StGWD and StGWD_{GWDC1084S}

Here, I describe the successful isolation of multiple independent StGWD and StGWD_{GWDC1084S} overexpressing lines with different protein levels. Preliminary characterisation of growth parameters showed no persistent correlation between protein expression and growth behaviour. Though, three out of 4 high expressing StGWD lines were significantly smaller than wild-type plants (Figure 5.3 A). A reason might be that the insertion sites of the transgene disrupt endogenous genes affecting growth. However, this would be unlikely to occur at the relatively high frequency with which we observed reduced growth. In addition it might be that the plantlets coming from in vitro culture need some time to recover after changed conditions. However, transformed plants without transgene expression seemed not to be affected during this environmental change and grew as well as wild-type plants. The correlation between transgene expression and growth behaviour needs to be investigated in subsequent generations. In addition, the data for transgene protein expression level comes from leaf tissue. Although the transgene is driven by the ubiquitous 35S promoter it is possible that the protein expression in storage root differs. Thus, in order to correlate aspects of the phenotypes it will be crucial to determine transgenic protein expression level in storage roots as well. Then the overexpression of a key enzyme involved in starch metabolism could potentially influence the performance of any starch synthesising tissue, which further might have secondary effects on the whole plant.
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It is known that repression of AtGWD leads to starch accumulation and stunted growth, caused by the reduced remobilization of starch during the dark period (Yu et al., 2001). Starch accumulation and hypo-phosphorylation was found in potato tubers with repressed StGWD (Lorberth et al., 1998). However, overexpressing StGWD in cassava could render starch more accessible to hydrolytic degradation because of phosphate-esters bound to starch solubilize the granule surface by disrupting the packing of double helical structure of amylopectin. In this case, the carbohydrate supply essential for growth would not be limited. Thus, I assume that overexpression of StGWD in cassava plants doesn’t change growth phenotype substantially. As shown in Figure 5.4 the staining of transgenic StGWD and especially the StGWD_{C10845} lines degrade as much, if not more starch during the night compared to wild-type plants. An indication for facilitated starch remobilization caused by GWD overexpression was shown by Carciofi et al., (2011), where starch granules were visualized by Scanning Electron Microscopy (SEM). The starch granules from the endosperm of StGWD overexpressing barley lines had pores and irregularities on their surface that were not seen in the starch from the wild type. Similar pore like structures were shown for barley starch granules after partial α-amylolytic hydrolysis (Li and Yeh, 2001). Thus, additional phosphate-esters on starch granules may indeed render the amylopectin more accessible to hydrolytic enzymes (Edner et al., 2007). Whether this occurs in my cassava lines and has an influence on starch levels will need to be tested. An increased phosphate-level bound to starch is also likely to change the starch properties as the granule architecture might be less densely packed and thus, exhibiting differences in physico-chemical behaviour. In addition, the staining of starch for the transgenic StGWD/ StGWD_{C10845} shows differences in metabolizing starch efficiency indicating that starch hydrolysis is facilitated. However, a more detailed investigation with quantitative measurements of the starch content at the end of the day and end of the night will be needed to confirm the preliminary finding with iodine staining.

The aim of the transgenic lines was to increase total phosphate content on starch and potentially to modify starch properties. In barley, StGWD overexpression increased the total starch-bound phosphate content in the endosperm by 7-fold (Carciofi et al., 2011). Preliminary analysis of C3- and C6-bound phosphate by $^{31}\text{P}$-NMR measurements revealed that although there was no shift in C3:C6 ratio, the high peak intensity in the starch sample from a plant highly expressing the redox insensitive form of GWD seems highly promising (Figure 5.8). As $^{31}\text{P}$-NMR is not a quantitative method to determine total starch bound phosphate levels further experiments will need to support these preliminary analyses. At the
time of writing, analyses of total phosphate using assays based on the Malachite Green reagent seem to confirm a doubling of the phosphate content of the starch from this line (Wuyan Wang, unpublished results). Furthermore, the results I present here were gained from just one biological replicate. Thus, in order to unravel the functional effect of the transgenic lines these first results need to be corroborated by the analysis of other transgenic lines expressing the two versions of the GWD protein. However, taken together, the preliminary data of staining leaves with iodine and the \(^{31}\text{P}\)-NMR analysis of the redox-insensitive StGWD\textsubscript{C1084S} suggests that the starch in the transgenic line potentially has an altered structure (i.e. amylopectin) as visualized by iodine (Figure 5.6) and phosphate content.

It will now be essential to perform further experiments to reveal the full effect of StGWD and its redox-insensitive version on cassava root starch metabolism. The first thing will be to confirm the increase in total phosphate content, which can be measured using one of three different ways: Firstly, the aforementioned Malachite Green assay can be performed to determine total phosphate content after enzymatic glucan dephosphorylation. Secondly, it will be important to determine with additional NMR analyses whether there is a shift in the ratio of C3:C6 phosphorylation. On the one hand, one might expect an increase in C6 phosphorylation, given that GWD specifically mediates this reaction. However, as PWD depends on previous action of GWD, an increase in C3-bound phosphate might also occur as a consequence. A third method to discriminate between C6- and C3- bound phosphate quantitatively is by HPLC after acid-hydrolysis of the starch to release Glucose 6-P and Glucose 3-P. If an increase in phosphate is achieved, further structural analyses on the starches from the transgenic plants will be required to determine if starch granule morphology, composition (amylose:amylopectin ratio), or architecture (amylopectin chain length distribution) are affected. Furthermore, it will be crucial to analyse the physico-chemical properties to elucidate whether characteristics of commercial interest (i.e. paste clarity, viscosity, retrogradation) are improved.

5.3.2. RNAi-constructs transformed to Cassava cv. 60444 under investigation

All three RNAi constructs described here have been transformed into cv. 60444 plantlets. For all three constructs SEX4-RNAi, LSF2-RNAi and AMY3-RNAi lines, plantlets could successfully be re-generated. For SEX4- and LSF2-RNAi genotyping revealed positive lines (Table 5.1). Whereas the phenotype of in vitro grown LSF2-RNAi lines is comparable to
wild-type plants SEX4-RNAi lines show growth retardation and reduced leaf area. This phenotype might be caused by the transformation process, as suggested for \textit{StGWD/\textit{StGWD}_C1084S} expressing plants grown on soil. However, the LSF2-RNAi lines would then also be expected to show this phenotype; the transformed plasmid is the same and the transformation process was done in parallel. This implies that the growth phenotype, if substantiated, is caused by the SEX4 RNAi construct. As shown for Arabidopsis, loss of SEX4 reduces growth as a consequence of being unable to degrade transitory starch at night, restricting carbohydrate supply (Kotting et al., 2009). The observation of retarded growth of my SEX4-RNAi lines, although not yet quantified, may reflect a similar metabolic perturbation. However, it is important to stress that the construct is driven by the class I patatin promoter which is supposedly root specific. The possibility exists that the promoter is leaky or that, in cassava, it is not exclusively expressed in roots. Furthermore, there are reports that the patatin promoter is induced by sucrose (Naumkina et al., 2007), which is supplied to the growth media at this stage in the transgenesis process. That said, it is questionable whether such a metabolic defect, as described above for Arabidopsis, would restrict growth in material grown in such sugar-rich culture medium.

Careful evaluation of promoter function is important when considering starch remobilization to avoid negatively influencing growth the propagation of material through stem cuttings. This will need to be investigated in further detail, for instance by transcript analysis in leaves and by analysis of transgenic plantlets transferred to soil (where no exogenous sucrose is supplied). Staining leaf tissue to detect a possible starch-excess phenotype will give a first indication as to whether the construct is expressed and functional in tissues other than storage roots.

Concerning the RNAi-LSF2 lines, after positive genotyping it will be crucial to analyse transcript levels in leaves and storage roots, once the lines are transferred on soil. \textit{In vitro} grown LSF2-RNAi plantlets do not show any growth defects. This is unsurprising as this was also the case for \textit{Atlsf2} mutants (Santelia et al., 2012). To confirm the functionality of this construct it will be critical to investigate storage starch directly to see whether there is a change in phosphate content and distribution like that seen in Arabidopsis \textit{Atlsf2} mutants. This will be highly novel as the role of LSF2 in storage starch metabolism has never been studied. Furthermore, though it is well known that the level of starch phosphorylation has an impact on starch properties, it is not known what influence a changed ratio of C6:C3 bound phosphate has. The physico-chemical properties of Arabidopsis starches were not
investigated, presumably because of the difficulties in obtaining adequate amounts. This should not be a problem with cassava and if my transgenic plants exhibit the desired effects on starch bound phosphate, it may have real potential for future industrial applications.

Analysis of the AMY3-RNAi lines will give new information about starch mobilization in cassava storage roots. The finding that AMY3 has a minor role in Arabidopsis leaf starch metabolism (Yu et al., 2005) has dampened interest in this protein, but the high expression in cassava storage roots upon transition from sink to source tissue (Chapter 4) renews the question of how important AMY3 might be in this and other systems. The minor role in leaf starch metabolism, if also the case for cassava, makes AMY3 a good potential candidate for repression in that it may affect specifically root starch, though the aforementioned question about whether stem starch metabolism will also be affected remains. Thus, analysis of the AMY3-RNAi line will be important to reveal the importance of α-amylolytic activity in heterotrophic tissue, and to what extent other hydrolysing enzymes are able to compensate for the loss of AMY3.

5.3.3. Outlook

In the longer term, there may be still more to gain by combining the modifications I have initiated here. In respect of generating phosphorylated starch in cassava I would think that generating a double transgenic overexpressing StGWD and repressing SEX4 and/or LSF2 could potentially increase starch yield as well as phosphorylation of starch further than any of the single modifications can.

In Atsex4 mutant lines, glucan-bound phosphate accumulates as phospho-oligosaccharides rather than phosphorylated starch. It was shown that these phospho-oligosaccharides are released from the starch granule by the debranching enzyme ISA3 and by AMY3 (Kotting et al., 2009). The double mutant Atsex4amy3 revealed a decrease in phospho-oligosaccharides and increase starch levels. Thus, repressing both AMY3- and SEX4/LSF2 might again increase starch yield and starch bound phosphate in cassava storage roots.

As described earlier, before the harvesting of cassava storage roots is performed, the aboveground plant part is cut off. This cutting was shown to increase shelf-life of the roots, as PPD response is delayed. However, during this process starch is degraded and thus yield is affected. It might be of interest to investigate if blocking starch degradation in SEX4-RNAi or AMY3-RNAi has any effect on the PPD response. If it does, such lines could of substantial interest for cassava growers.
6. General Discussion

In the first part of my PhD thesis I described growth analysis of greenhouse-grown cassava plants to gain information about experimental reproducibility and showed that the plants behaved in a comparable way. The absolute values of carbon assimilation and non-structural carbohydrates were lower than what has been described in the literature. This is likely because the previous measurements were mostly gained from agronomic cassava cultivars grown in the field (Angelov et al., 1993). It is not surprising that the absolute values differ. Unlike greenhouse experiments, growth in field is not limited in respect of soil space and the environmental conditions are not equally comparable. However, the advantage of our experimental design lies in the high reproducibility between experiments, which is important for this kind of basic research. I could show that under the given conditions, cassava accumulates similar starch levels in leaves during the day as does Arabidopsis (Gibon et al., 2004). Further, I could show that starch is synthesised during the day degraded during the night, as reported for Arabidopsis (Gibon et al., 2004; Fulton et al., 2008). Interestingly, in contrast to Arabidopsis, the synthesised starch is not fully remobilized at the end of the night and the residual starch content varies, depending on leaf age. (Figure 3.6 E). This is an important observation as it shows that single time point measurements or single leaf analysis have to be treated carefully. Further, the incomplete remobilisation suggests that the demand during the night is for less than the available stored carbohydrate. This would be an interesting point to follow up, because it could mean that cassava could grow faster with the available stored resources, which in turn opens possibilities for cassava varieties with more biomass production. Soluble sugar analysis revealed high levels of sucrose; far more than what is reported in Arabidopsis (Figure 3.6 F-H) (Gibon et al., 2004).

Combining the photosynthetic rate measurements and the levels of starch accumulated during a photo period in young leaves, a hypothetical carbon portioning rate was calculated. This revealed that only 5-11% of the assimilated carbon is subjected into starch (Table 3.1 and Table 3.2). In contrast high levels of sucrose were measured. However, the photosynthetic rate and determination of carbohydrate levels were not performed with the same plant batch and not at the same time. This could potentially influence absolute values as suggested by comparing two carbohydrate measurements from two different plant batches analysed for the influence of leaf development and diurnal starch turnover (Figure3.6). Thus the actual carbon flux is yet unknown. As mentioned in ‘Chapter 3’ 14C-labelling experiments could substantiate this calculated value for carbon partitioning.
Nevertheless, in terms of source capacity (e.g. carbon assimilation and transport), the residual starch levels at the end of the night and high sucrose levels 9h into the day strongly indicate that cassava plants grown in the greenhouse are not restricted in carbohydrate availability (Figure 3.6 B,E). The carbon assimilated and stored throughout the day exceeds the demand of sink tissues. This is highly interesting in the context of biotechnological applications, where approaches are considered in order to increase source capacity. Hence, from the results I present here I conclude that the source capacity of cassava canopy is already high. As mentioned above for the carbohydrate analysis, plant batches used for analysis were grown at different times of the year. Comparing the absolute values and the pattern of carbohydrate allocation reveals that in terms of soluble sugars absolute levels differ whereas starch levels remain comparable amongst the plant batches (Figure 3.6). Therefore, sucrose and hexose pools could potentially serve as a buffering system to meet the needs for non-structural carbohydrates. It is likely that under stressful environmental conditions where low carbon assimilation occurs (i.e. scarce environmental conditions like water limitation, low light conditions, and high temperature), accumulated soluble sugars could compensate for the carbon deficiency. This hypothesis needs further investigation, for instance labelling experiments in combination with stress analysis might reveal changes in soluble carbohydrate availability and flux. It is also possible that the non-structural carbohydrate levels follow a species-specific pattern different to what has been described for Arabidopsis (Gibon et al., 2004). This could be tested with a 24h experiment where plant material is harvested throughout the day and night at different time points.

6.1. Integrating Proteomics and carbohydrate metabolism

As cassava is an important starch crop, strategies to increase yield in storage roots could potentially achieved by increasing source capacity or sink strength or by preventing starch mobilization.

An increase in source strength could potentially provide increased carbohydrates for transport to sink tissues. The finding of residual starch levels at the end of the night and high soluble sugar content in leaves (Figure 3.6) suggests that the carbohydrate available for transport exceeds the need during the night. Thus, a more promising approach to increase starch yield in heterotrophic tissue could be to increase sink strength in storage roots. In the past attempts to increase sink strength in various crop species was shown to be challenging, because sucrose or sugar availability revealed to be tightly regulated. This was shown by overexpression of yeast INV in the apoplast or cytosol of potato tubers, which increased
tuber water content, but not starch levels (Ferreira and Sonnewald, 2012). For the cytosolic INV expressing lines, increased glucose levels were observed, whereas sucrose and starch levels decreased. Further analysis revealed that high levels of hexose-phosphate were not imported to the amyloplast for starch synthesis but rather subjected to glycolysis (Sonnewald et al., 1997; Hajirezaei et al., 2000). This illustrated that the increase in hexoses derived from the hydrolytic activity of INV is channelled in an unexpected way. It is likely that the changes in hexose availability mimic the situation of high sugar availability. As mentioned before sucrose and hexoses are sensed by various proteins that trigger specific responses at the molecular level. Evidence for sugar signalling occurring in cassava storage root upon pruning (sugar starvation) are given by the identification of overrepresented key signalling proteins (e.g. SnRK1, HXK1). This suggests that a response to changes of metabolite availability does occur. Strategies to increase sink strength in cassava simply by increasing sucrose hydrolysis may also trigger a cellular response to carbohydrate availability as they did in potato.

It was shown that starch yield can be increased by SUS overexpression. Evidence for the correlation of SUS activity and starch synthesis came from transgenic potato plants where SUS was repressed. A lack of SUS led to decrease of starch levels, whereas StSUS4 overexpressing lines accumulated up to double the starch amount detected in wild-type plants (Baroja-Fernandez et al., 2009). Thus, these findings suggest that SUS overexpression has a potential to increase starch yield in storage organs. Successful transformation of cassava lines were performed in another project, though the analysis is still under investigation (Miyako Keller, unpublished).

As an alternative to increasing yield, I decided to block starch degradation. As cassava storage roots accumulate up to 85% starch per dry weight, this yield already is high. However, as described, cassava plants are pruned before harvesting in order to minimize post-harvest physiological deterioration. To inhibit starch mobilization in a targeted way I performed a proteomic analysis to reveal important starch mobilizing enzymes in heterotrophic tissues.

My experimental setup showed that 10 days after pruning off the aerial parts of cassava there was a decrease in starch levels by half in storage roots to support regrowth of new leaves (Figure 4.1). The decreased starch levels correlated with higher total amylolytic activity as detected by native gels. Although the individual activity bands could not be
assigned to a defined enzymatic activity, proteomics provided a way to elucidate potential proteins responsible that would then be suitable targets for a transgenic approach.

The analysis of deregulated proteins between untreated control samples and roots 10 days after pruning revealed major changes in a wide range of metabolic pathways. Of the starch metabolizing enzymes, the high abundance of AMY3 protein after pruning leads me to conclude that starch remobilization may be highly dependent on this α-amylase activity. This is quite novel as, thus far, α-amylases were not clearly attributed to be involved in starch degradation of roots. Hopefully, the transgenic lines AMY3-RNAi I generated will provide definitive evidence for the importance of this α-amylase in cassava starch mobilization one way or the other.

The activity of LDA on red-pullulan native PAGE also appeared to increase upon pruning (Figure 4.2). This enzyme was easy to assay because red-pullulan is a specific substrate it. However, although the protein was detected in the proteomics, an increase in abundance was not observed. Nevertheless, I propose a working model where the initial steps of starch mobilization in cassava storage root occurs by the interplay of AMY3 attacking the granule and LDA helping to debranch the limit dextrins it releases. According to the other proteins I found in the proteome, the glucosyl tranferase DPE1 and the starch phosphorylase PHS1 could also be involved in subsequent metabolism of linear oligosaccharides. The resulting Glc and Glc1P could then enter metabolic pathways such as the oxidative pentose phosphate pathway (OPPP) or be transported to the cytosol for further down-stream metabolism (e.g. sucrose synthesis, glycolysis). Proteomics data give good broad evidence as to which pathways may have changed. However, to substantiate the findings it is crucial to perform further experiments. For example, the increased abundance of AMY3 does not necessarily mean that also the activity is also increased, although it is likely. Hence, specific enzyme assay is needed to substantiate the hypothesis. Moreover, the fact that I did not identify any β-amylases in the proteomics approach does not necessary lead to the conclusion that they are not present. Indeed, cassava, like Arabidopsis, has several β-amylase genes and some minor bands visible on the native gel with amylpectin could not be seen on the native gel with β-limit dextrin – a hallmark of a β-amylase. Thus, together with the analysis of α-amylase activity it will be crucial to determine if there is any β-amylase activity present after all, and if pruning changes it.

Due to the sink-source transition where sucrose is exported rather than imported, a change in sucrose pathway was expected. The investigation of the sucrose pathway revealed
6. General Discussion

underrepresentation of F1,6BPase and FK after pruning. In contrast, a cytosolic INV2 and HXK1 and HXK3 were found to be more abundant after pruning compared to the control. The high abundance of both cINV and HXK1 in accordance with an increased abundance of the respiration pathway shows similarities to the finding that high cytosolic INV expression in potato tubers leads to increased respiration (Appeldoon et al., 1997). In agreement with this hypothesis is the finding of proteins involved in glycolysis found to be highly abundant. Hence, while this strongly indicates that after sink-source transition cINV helps to meet the changed cellular demand for energetic compounds, it does not really provide insight into changes in sucrose biosynthesis.

The identification of a major component SnRK1 being increased after pruning is an exciting result. As discussed in chapter 4, this indicates that the metabolic reconfiguration in the storage roots of pruned plants is switched by starvation, potentially via this kinase. This also represents a good target for transgenic repression, as blocking its activity might keep the root in a dormant state and prevent unwanted regrowth.

The comparison of the proteomic analysis of storage roots before and after pruning has thus proved to be an excellent tool to identify major changes in metabolic pathways and revealed potential targets for future transgenic approaches. However, only 25 cassava proteins homologous to the 53 known Arabidopsis proteins involved in starch metabolism were identified. This is surely because protein detection is limited to the more abundant proteins. Previously it was shown that a combined analysis of proteome and transcriptome can be highly complementary (Bischof et al., 2012). Hence, I initiated an RNAseq analysis. Although these data are still under investigation, first results showed high induction of AMY3 transcript after pruning, consistent with the data presented in this thesis.

6.2. Potential of modified starch in industry

In the third part of my PhD, three transgenic approaches were pursued to increase the value of cassava as starch crop. The main focus was to engineer starch with altered starch composition and architecture. Manipulating starch composition can confer improved physico-chemical properties. For the diverse industrial applications, both in the food and non-food branches, a diversity of starches raw materials is desired. Rather than modify native starches post-harvest, genetically modified plants could provide native improved starches directly to replace chemical treatments. For instance, it was shown that genetically modified amylose-free and short-chain potato amylopectin starch exhibits excellent freeze-
thaw stability (Jobling et al., 2002). This example reveals that genetic modification of starch crops have a great potential to engineer starches of industrial interest.

I designed transgenic cassava lines with the intention of increasing starch-bound phosphate. As described in ‘Chapter 5’ a key gene involved in phosphorylating starch is GWD. Cassava starch has only little starch bound phosphate (0.05%) – one tenth that of potato (0.5%). It was already reported that the expression of StGWDC could increases total starch bound phosphate content in barley (Carciofi et al., 2011). Moreover StGWDC is redox regulated, being inactive when oxidised, but can be rendered constitutively active with an amino acid substitution in the redox-motif (from a cysteine to serine; StGWDC1084). Many positive, individual transformants with variation in StGWDC and StGWDC1084 expression levels were analysed. Preliminary analysis of the starch-bound phosphate of one plant per transgenic line revealed that expression of the redox-insensitive StGWDC1084 appears to double phosphorylation levels compared to the wild type. This was seen for 31P-NMR signal as well as in a Malachite Green assays (not in this thesis). This finding is very promising; the transformation was successful and more importantly, the overexpressed protein is functional. However, not everything is clear. It is surprising that the C3:C6 phosphorylation ratio was the same as for wild type, given that StGWDC phosphorylates C6 position of the glucose residues (Ritte et al., 2006). However it is possible that the endogenous PWD, which phosphorylates at the C3 position, responds to the increase in prephosphorylated starch, and is more active as a consequence.

As discussed in Chapter 5, starch-bound phosphate potentially solubilizes amyllopectin chains. Indications for an increased accessibility to hydrolytic enzymes were given by SEM pictures of starch granules in StGWDC overexpressing lines of barley, showing more pores and irregularities (Carciofi et al., 2011). The iodine stained leaves of my transgenic cassava StGWDC/StGWDC1084 showed that for most lines less starch was observed at the end of the night compared to wild-type leaves. Although very preliminary, this may suggests that starch mobilization is increased by StGWDC. Alternatively, starch synthesis may be impaired or disturbed. To test this, it will be crucial to analyse the starch content of leaves at the end of day and end of night.

The preliminary data showing that starch-bound phosphate can be increased leads to further questions. The first results revealed that the one transgenic line had doubled starch-bound phosphate compared to wild type. This is still less than was reported for StGWDC overexpression in barley endosperm, and less than for normal potato starch. This is
surprising as starch from different potato varieties are even more highly phosphorylated (8.33 nMol G6P mg⁻¹ starch, Carciofi et al., 2011). There are several reasons why phosphorylation activity of potato StGWD might be less efficient in another species. Firstly, the storage roots of transgenic lines were still small and not developed to the same extent as the wild-type control (Figure 5.7). This might be caused either by the transgenic event (a secondary effect of StGWD/StGWD₁₁₁₇₈₄₅ overexpression) or simply because plants from this first generation (coming from culture media) develop their storage root more slowly than wild-type plants. However, it is likely that starch accumulation and storage capacity is not yet fully developed. Thus, it is possible that the degree of phosphorylation could change. Starch is phosphorylated during its synthesis (Nielsen et al., 1994). This can explain the phosphate residues within the starch granules. However, it was recently shown that the majority of starch-bound phosphate sits on the granule surface (Buleon et al., 2014), and could be subject to constant turnover (see below). The development of storage roots in the next generation is needed to rule out some of the more trivial explanations above.

Another reason for the lower phosphate content compared to potato starch might be that StGWD has a preference for a certain molecular architecture common in potato, but rare in cassava. This is not an unreasonable suggestion; it was reported that down-regulation of SBE in potato tubers change both the degree of polymerisation of linear glucan chains and, in addition, increased the degree of phosphorylation (Jobling, 1999; Blennow et al., 2000). In this respect, cassava starch has C-type architecture of the crystalline lamellae whereas potato has a B-type and barley A-type (reviewed in Damager et al., 2010). This means that the helices formed by the side chains of amylpectin are arranged in different patterns. Even minimal differences in granule surface could potentially affect the affinity and activity of the protein. This could be tested for instance in vitro with heterologous expressed StGWD protein - both wild type and redox-insensitive forms - using native starches isolated from different biological origins with different packing types (A-, B-, and C-type). This would show how efficiently StGWD phosphorylates different starch types.

Another reasonable explanation would be that increased phosphorylation of the cassava starch by StGWD occurs but is only transient and that a high proportion is again released by SEX4 and LSF2 before the phosphate can be buried and protected inside the starch granule. My other attempts to increase total starch bound phosphate should address this. As described in ‘Chapter 5’ I generated RNAi constructs against the two active glucan phosphatases SEX4 and LSF2. Once the transgenic lines are growing in the greenhouse, one
could try to generate double or multiple transgenic crosses in order to generate cassava plants combining \textit{StGWD/}StGWD\textsubscript{C10845} with the silencing constructs RNAi-SEX4 and RNAi-LSF2. The combination of high kinase activity and decreased phosphatase activity could potentially increase the phosphate content much more. Furthermore, Arabidopsis sex4 mutants were shown to accumulate phosphooligosaccharides, released in part by AMY3 (Kotting et al., 2009). Hence, the double mutant lines RNAi-AMY3 and RNAi-SEX4 could also potentially lead to increased starch yield in combination with increased phosphate content. These generation and analyses of these combinations will need to be undertaken by a future PhD student or researcher.

Taking together all the results I gathered during my PhD, I believe that I could significantly contribute towards knowledge in cassava starch metabolism. Furthermore, I believe that the isolated transgenic lines have potential for valuable future research and maybe also for industrial applications.
7. References


7. References


7. References


7. References


7. References


7. References


7. References


8. Curriculum vitae

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8. Curriculum vitae

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PUBLICATIONS


LANGUAGE SKILLS

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English: proficient (C1), written and spoken

French: independent (B1) written and spoken

Spanish: basic (A2) written and spoken
Supplemental Table 4.1. Quantitative proteome map of cassava roots during pruning. Root proteins were extracted by phenol/methanol precipitation (Saravanand and Rose, 2004) and equivalent amounts of protein were separated by SDS-PAGE followed by in-gel tryptic digestion. Peptides were analyzed by mass spectrometry (MS) using an Orbitrap mass spectrometer. Three biological replicates including sample collection, protein extraction and separation were analyzed by MS for each time point. Measured spectra were analyzed by Mascot using the cassava genomic database Mesculenta_147_peptide.fa (download from ftp://ftp.jgi-psf.org/pub/IGI_data/phytotome/v7.0/Mesculenta/) and quantitative information for each identified peptide and protein was obtained by data analysis using the software Progenesis LC-MS (www.nonlinear.com). Information about Arabidopsis AGI-homologues and protein descriptions were downloaded from ftp://ftp.jgi-psf.org/pub/IGI_data/phytotome/v7.0/Mesculenta. SUB-cellular protein localization was based on the database SUBA (Heazlewood et al., 2007; http://suba.plantenergy.uwa.edu.au). DAP: days after pruning.

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Biodegradation of Xenobiotics

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Supplemental Table 4.2. Significantly differentially regulated proteins during pruning. Proteins significantly more abundant zero or ten days after pruning (DAP) were defined as having an ANOVA p-value of less than 0.05 and a Max fold change of greater than 1.2 or less than 0.8. The highest condition mean is defined as the mean of the highest mean condition for each protein in the conditions associated with pruning and the mean of the highest condition mean for each protein in the conditions associated with pruning and the condition with the highest mean condition.}

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