Potential of the lulo (*Solanum quitoense*) as new tropical fruit in Germany: Consumer acceptance and greenhouse cropping

DISSERTATION

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Fruit consumption and fruit trade is expected to increase rapidly in Europe; today's interest is especially rising for the exotic, lesser-known, tropical fruits which are up to now niche products in Europe. Against this background, the concept of the innovative project "Klein-Eden" in Germany to cultivate and market such tropical crops is promising for the future. By using industrial waste heat as energy source for greenhouse cropping, Klein-Eden makes it possible and environmentally acceptable to introduce novel fruits to the Central European market. One of these is the lulo (*Solanum quitoense* Lam.), as yet cultivated and consumed mainly locally and regionally in Latin America. The lulo seems to unify several promising attributes for successful marketing and cultivation, e.g. special aroma and good nutritional value of the fruits. Thus the lulo was used in this thesis as model species.

This thesis aims to assess the prospect of the lulo as an exotic tropical fruit for marketers and growers in Central Europe, with particular application in Klein-Eden, by evaluating lulo's acceptance among consumers (*Focus 1*) and suitability for local greenhouse cropping (*Focus 2*). More specifically, five major research objectives were investigated on lulo, including five manuscripts: 1) degree of familiarity among consumers and consumer sensory acceptance, 2) antioxidative capacity of the fruits, 3) influence of photoperiod on fruit supply, 4) seasonal variation in quality of fruits, and 5) pollination success by *Bombus terrestris*.

The consumer survey revealed that the lulo fruit was widely unfamiliar confirming that it is a novel, exotic fruit in Germany. The sensory acceptance among consumers was assessed to be overall high and lulo fruits are likely to be repeatedly consumed and (re)purchased. Firmness, colour, odour, juiciness, taste, sourness und sweetness were detected to be relevant attributes for consumer. Apart from sweetness, which was frequently assessed as being too low, all these attributes were liked by the majority of consumers. Furthermore, an important antioxidative capacity could be proven for lulo fruits. Taking all these findings into account, the lulo appears to be very attractive to consumers and have high commercial promise for German market.This assumption should be tested in follow-up studies. One critical factor challenging marketing could be the short shelf life of ripe lulo fruits. The sensory properties and antioxidant capacity were most favourable at fully ripeness, determined in this study to occur at fruit fall, but decreased already after four days of storage. This (currently) favours lulo as a niche product for direct marketing, as handled in Klein-Eden.

Summary

Lulo fruits for direct marketing can be gainfully produced in greenhouses in Central Europe under natural light conditions and existent cultivation practices as demonstrated for the first time in these cultivation trials. Flower initiation and fruit set occurred throughout the year under seasonal variations in day length, though harvest begin was accelerated at long-days, and only two sowing dates provided near year-round fruit supply. Furthermore, greenhouse production provided fruits with an intense fruit aroma and a similar physico-chemical quality as reported in lulo fruits harvested in Latin America, even under short-day conditions in winter. However, this study showed that seasonal effects in fruit quality, particularly a decline in dry matter, firmness and sugar level during winter season, occurred under year-round fruit production in Germany. For fruit set in lulo pollination was crucial but pollination experiments gave clear evidence that the lulo can be successfully pollinated by the Eurasian *Bombus terrestris* in greenhouse cropping. *B. terresitris* adopted lulo flowers as pollen source, visited single flowers frequently, and as long as multiple visits were ensured, fruit set and seed set were as high as those resulting from cross-pollination by hand.

The thesis gives first invaluable insights of lulo's performance in Germany, Central Europe, and indicates that lulo is overall highly attractive for marketing and cultivation in greenhouses like Klein-Eden. The obtained results can be directly implemented in Klein-Eden, transferred to similar regional projects or give motivations and implications for many other actors in the (tropical) fruit sector in future. New research issues arose from this work assumed to be relevant for contributing towards promotion and commercialization of lulo, particularly phytomedicinal issues, extending shelf life and selecting an appropriate variety or cultivar for (greenhouse) cropping. The results of this thesis and possible follow-up studies will help, in long-term, to extend knowledge of lulo in general and to promote public awareness, familiarity, scientific attention and research investment also outside the homeland of lulo. This could drive research efforts, improvements and innovations in the so far underutilized lulo in the future.

Zusammenfassung

Obstkonsum und -handel werden in Europa voraussichtlich rapide zunehmen. Vor allem exotische, tropische Früchte, die bisher noch wenig bekannt und Nischenprodukte in Europa sind, wecken das heutige Interesse. Angesichts dieses Trends, ist die Strategie von dem innovativen Projekt „Klein-Eden“, gerade solche Tropenfrüchte anzubauen und zu vermarkten, zukunftsträchtig. Klein-Eden nutzt industrielle Abwärme als Energiequelle für den Anbau tropischer Früchte unter Glas und macht es so möglich und ökologisch verträglich, gänzlich neue Früchte auf den mitteleuropäischen Markt zu bringen. Eine davon ist die Lulo (*Solanum quitoense* Lam.), die bislang primär lokal und regional in Lateinamerika kultiviert und konsumiert wird. Die Lulo hat gleich mehrere, für eine Vermarktung und Kultivierung vielversprechende Eigenschaften, hervorzuheben sind z.B. das besondere Aroma und der Nährwert der Frucht. Deshalb wurde sie als Modellart für diese Dissertation ausgewählt.

Das Ziel dieser Dissertation ist es, das Potenzial der Lulo als exotische Frucht, sowohl für Händler als auch Erzeuger in Mitteleuropa, mit speziellem Fokus auf Klein-Eden, zu beurteilen. Dafür wurde die Verbraucherakzeptanz der Lulo (*Fokus 1*), sowie deren Eignung für den lokalen Gewächshausanbau (*Fokus 2*) untersucht und umfasst im Wesentlichen folgende fünf Forschungsthemen bzw. Manuskripte: 1) Bekanntheitsgrad und Verbraucherakzeptanz, 2) antioxidative Kapazität der Früchte, 3) Einfluss der Fotoperiode auf die Fruchtproduktion, 4) saisonale Unterschiede in der Fruchtqualität, und 5) Bestäubungserfolg durch *Bombus terrestris*.

In einer Verbraucherumfrage bestätigte sich, dass die Lulo weitgehend unbekannt und damit eine neue, exotische Frucht in Deutschland ist. Die sensorische Akzeptanz bei Verbrauchern war insgesamt hoch. Relevante Fruchtattribute waren Festigkeit, Farbe, Geruch, Saftigkeit, Geschmack, Säure und Süße, die alle, abgesehen von der häufig zu gering empfundenen Süße, von der Mehrheit der Verbraucher gemocht wurden. Darüber hinaus ließ sich auch eine nennenswerte antioxidative Kapazität der Früchte nachweisen. Angesichts dieser Ergebnisse erscheint die Lulo-Frucht sehr attraktiv für Konsumenten und lukrativ für den deutschen Markt, was in Folgestudien überprüft werden sollte. Kritisch für die Vermarktung könnte jedoch die kurze Haltbarkeit reifer Früchte sein. Erst ab dem Zeitpunkt des Fruchtfalles erreichten die sensorische Qualität und die antioxidative Kapazität hohe Werte, die aber bereits nach vier Tagen Lagerung abnahmen. Das favorisiert (derzeitig) eine Direktvermarktung frischer Früchte, wie in Klein-Eden gehandhabt.

Zusammenfassung

Anbauversuche demonstrierten erstmals, dass Lulo-Früchte im Gewächshaus unter den gegebenen Lichtbedingungen und gängigen Anbaubedingungen in Mitteleuropa produziert werden können. Unabhängig von der Tageslänge blühte und fruchtete die Lulo ganzjährig, wenngleich der Erntebeginn an langen Tagen beschleunigt wurde, und nur zwei Aussaattermine ermöglichten eine nahezu ganzjährige Fruchtproduktion. Außerdem hatten im Gewächshaus produzierte Früchte, sogar im kurztägigen Winter, ein intensives Aroma und eine ähnliche physikalisch-chemische Qualität wie Lulo-Früchte, die in Lateinamerika geerntet wurde. Wie sich in der Studie zeigte, müssen jedoch saisonale Unterschiede in der Fruchtqualität, besonders eine Abnahme an Trockenmasse, Festigkeit und Zuckergehalt im Winter, beim ganzjährigen Anbau in Mitteleuropa berücksichtigt werden. Unter Gewächshausbedingungen sind für einen Fruchtansatz außerdem gezielte Maßnahmen zur Erhöhung des Bestäubungserfolges der Lulo notwendig. In Versuchen stellte sich klar heraus, dass sie im Gewächshaus erfolgreich mit der eurasischen Hummel *Bombus terrestris* bestäubt werden kann. *B. terrestris* nahm die Lulo-Blüte als Pollenquelle an, besuchte einzelne Blüten häufig, und so lange ein mehrfacher Besuch gegeben war, waren Frucht- und Samenansatz genauso hoch wie bei manueller Bestäubung.

Die Dissertation gibt erste wertvolle Einblicke in das Potenzial der Lulo in Deutschland, Mitteleuropa, und verdeutlicht, dass diese Frucht attraktiv für eine Vermarktung und einen Anbau im Gewächshaus, wie in Klein Eden, ist. Die Ergebnisse können direkt in Klein-Eden praktische Anwendung finden, auf ähnliche regionale Vorhaben übertragen werden, oder Motivationen und Erkenntnisse für eine Reihe anderer Akteure im Fruchtsektor geben. Basierend auf der Arbeit ergaben sich neue Forschungsfragen, die zur Förderung und Kommerzialisierung der Lulo notwendig sind, insbesondere zu phytomedizinischen Aspekte, zur Verlängerung der Haltbarkeit und zur Auswahl geeigneter Varietäten und Sorten. Die Ergebnisse der Studie und möglichen Folgestudien können langfristig dazu beitragen, das Wissen über die Lulo zu erweitern und die öffentliche Wahrnehmung sowie die Bekanntheit und das Forschungsinteresse an der Lulo auch außerhalb des Heimatlandes zu fördern. Dies wiederum könnte Verbesserungen und Innovationen in der Lulo vorantreiben und helfen, ihr Potenzial auszuschöpfen.

List of Abbreviations and acronyms

ACTI	Ad Hoc Panel of the Advisory Committee on Technology Innovation
ANOVA	Analysis of variance
a.s.l.	Above sea level
CAE	Citric acid equivalent
CBI	Centre for the Promotion of Imports from developing countries
d.f.	Degrees of freedom
DIN	German Institute for Standardization (Deutsches Institut für Normung e.V., Berlin)
DM	Dry matter
DW	Dry weight
EBG	Ecological-Botanical Garden of the University of Bayreuth
EFRE	European Regional Development Fund
FACT	Food Action Rating Scale
FAO	Food and Agricultural Organization of the United Nations
FAOSTAT	Statistics division of the Food and Agricultural Organization of the United Nations
FW	Fresh weight
GLM	Generalized linear model
GLMM	Generalized linear mixed model
HF	Hermaphroditic flower
LD	Long-day
LM	Linear model
LME	Linear mixed effect model
MAD	Mean absolute deviation

List of Abbreviations and acronyms

MF	Functional male flower
n	Sample size
NMR	Nuclear magnetic resonance
NTC	Norma Técnica Colombiana
n.s.	Not significant
OECD	Organisation for Economic Co-operation and Development
(H-)ORAC	(Hydrophilic) Oxygen radical absorbance capacity
PAR	Photosynthetic active radiation
PC	Principal component
PCA	Principal component analysis
R	R Development Core Team (statistics programme)
R^2	Adjusted R square
RHS	Royal Horticultural Society
SD	Short-day
Sp	Spring
sp. / spp.	Species
Su	Summer
TA	Titratable acidity
TSS	Total soluble solids
TSS/TA	Ratio of total soluble solids and titratable acidity
USD	United States Dollar
Var.	Variety
Wi	Winter

Preface

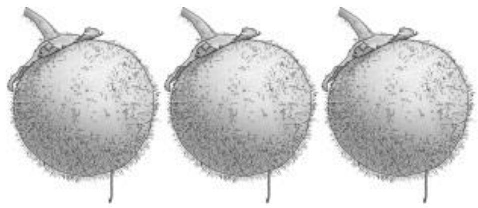
The presented doctoral study has been performed within the framework of the European project Nr. 129: "Klein-Eden" – Tropenhaus am Rennsteig. The project name stands for a tropical greenhouse that was built in 2011 in Kleintettau (Germany) and aims at producing and selling tropical food products at low environmental costs. Besides, environmental research and education are important purposes of the Klein-Eden project.

The project was funded for the period 2011 – 2014 by the European Regional Development Fund (EFRE) as part of the programme "Ziel 3 Freistaat Bayern – Tschechische Republik 2007 – 2013" (INTERREG IV A), the Bavarian State Ministry for the Environment and Health, the Upper Franconian Trust (Oberfrankenstiftung), and for the period 2014 – 2015 by the Carl-August-Heinz Stiftung and the Simon-Nüssel-Stiftung. EFRE belongs to the structural funds of the European Union and contributes to support cross-border cooperation and exchange of experiences. For this project priority was given to "*regional and environmental development*" (Priority 2); the operational target was the protection of natural resources by improvements in environmental and nature conservation.

The Ecological-Botanical Garden of the University of Bayreuth is lead partner within this project and conducts scientific research in cooperation with Klein-Eden (Tropenhaus am Rennsteig GmbH). The doctoral study forms part of the research activity which targets on investigating the cultivation of tropical crops chosen or being promising for Klein-Eden. A range of tropical crops are cultivated in Klein-Eden with focus on well-known as well as less-known or widely unfamiliar fruits. The latter one provides innovative fruit products for Klein-Eden and consumers in Central Europe, but has experienced so far less scientific awareness. Hence this study focused on obtaining insights in consumer acceptance and cultivation issues of one of these new, underutilized fruits for Central European market.

CHAPTER 1

INTRODUCTION



This chapter describes the background, motivation and aims of this doctoral study. The current and future trends in tropical fruit intake, production and trade are highlighted. An innovative and sustainable concept to produce tropical fruits in Central Europe is presented. This project, known as “Klein-Eden”, makes it possible to introduce widely unfamiliar, exotic tropical fruits in Central Europe which are of special interest in this study. Finally, the chapter presents the chosen model species, the research objectives, itemizes the hypothesis and gives an outline of this thesis.

1 Introduction

1.1 Increasing demand on exotic tropical fruits

Fruit consumption and fruit trade is expected to increase rapidly in Europe (Proctor 1990; Bartels et al. 2008). Questionnaires revealed that the increasing health awareness among consumers was one major driver of fruit consumption in the past and will also be in the future (Proctor 1990; Bartels et al. 2008; Briz et al. 2008). European consumers have clear associations between (fresh) fruits and health benefits, like disease prevention, better look and skin, overweight prevention, energy supply for sport and think of certain nutrients or ingredients, e.g. minerals, vitamins and antioxidants (Briz et al. 2008). Moreover sensory pleasure (e.g. taste or juiciness), product variation and convenience are also strong determinants for fruit intake in the future (Bartels et al. 2008; Briz et al. 2008). A further trend which is increasingly prevalent in the European market is the rising interest and demand for new fruit varieties, innovative products (e.g. juices), special and attractive fruit characteristics, novel and exotic flavours and tastes (Bartels et al. 2008; Briz et al. 2008; Sabbe et al. 2013; CBI 2015). Therefore, new varieties of the well-known, commercialized fruits but also "new" tropical fruits are expected to enter the European market (Proctor 1990; Bartels et al. 2008; CBI 2015).

According to the Food and Agricultural Organization of the United Nations (FAO) world production of tropical fruits (excluding banana which is one of the most commonly eaten fruit in the world and treated separately in statistics) was estimated to be over 82.2 million tonnes in 2009 (FAO 2011). Most of it (about 90%) was consumed in producing countries themselves; only 10% was traded internationally and half of it as fresh (5%) and processed fruit (5%), respectively (FAO 2011). However, international trade volume of fresh tropical fruit is high and reached USD 5.4 billion in 2009, similar to apples (USD 5.4 billion); additional USD 6.5 billion was traded as processed tropical fruit (FAO 2011). The highest global output was recorded for mango, pineapple, papaya and avocado representing together 79% of total tropical fruit production in 2009 (FAO 2011). They are commonly categorised as "*major tropical fruits*" (Proctor 1990; FAO 2011; Galán Saúco 2013; for more detail of fruit categories see **Box 1.1)**. For all of these major fruits an increase in production volume could be observed between 2000 and 2013 (**Figure 1.1**).

Other tropical fruits, including e.g. durian, rambutan, guavas, carambola and passion fruit (**Table 1.1**) are produced and traded in smaller volumes and represent only 22% of total tropical fruit production (FAO 2011). They are summarized in FAO statistics as "*minor tropical fruits*" but involve also some so-called "*underutilized fruits*" (**Box 1.1; Table 1.1**). Hereafter I will refer to this group as "*exotic tropical fruits"* as also the Centre for the Promotion of Imports from developing countries did in their factsheet (CBI 2015; **Table 1.1**). In this sense exotic means that these (sub)-tropical fruits "*are not produced in Europe and consumption volumes are limited making it niche products*" (CBI 2015). Correspondingly, (fresh) exotic tropical fruits could be regarded as more or less novel tropical fruits in the European market. Like for the major tropical fruits worldwide production of the exotic tropical fruits increased and raised from 14.2 million tonnes in 2000 to 22.2 million tonnes in 2013 by an average annual growth rate of 3.57% (**Figure 1.1**). Although fresh exotic tropical fruits are still considered to be "*niche products in Europe"* the import by Europe show an increasing trend since 2012 and reached over 35 thousand tonnes in 2014 which corresponds to an estimated value of nearly 94 million euro (CBI 2015). Main importers within Europe are Belgium, France, the Netherlands and Germany representing all together almost 80% of all imports (CBI 2015).

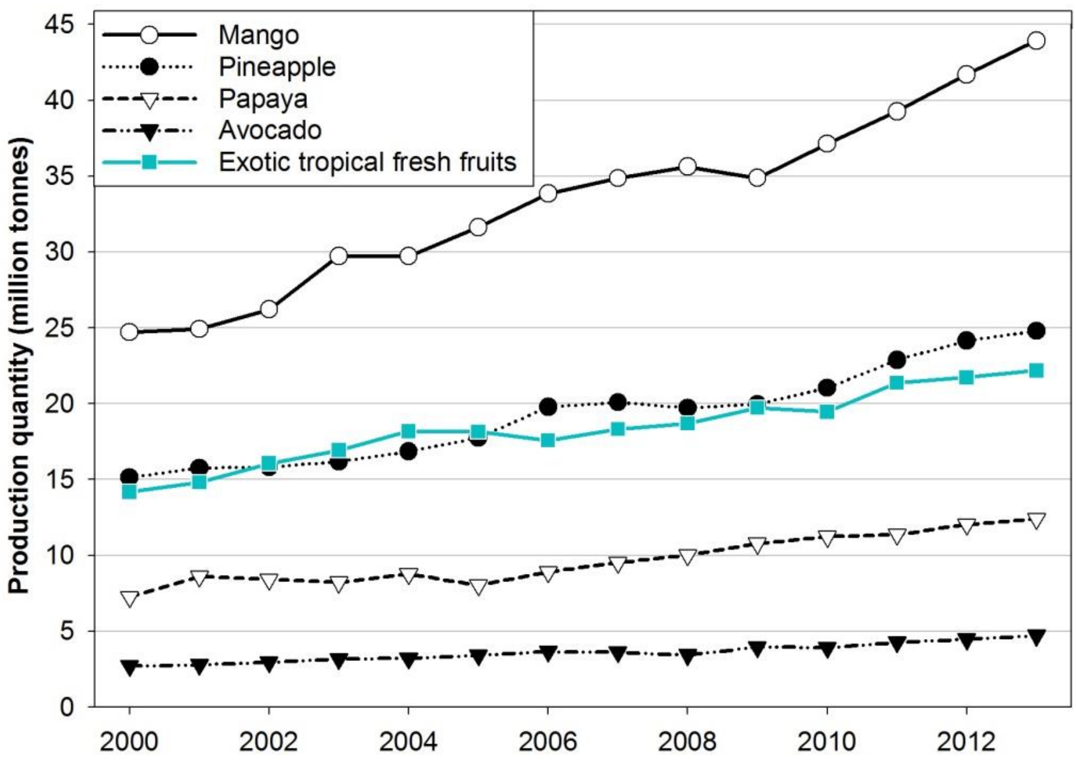


Figure 1.1: Worldwide production of mango (including guave and mangosteen), pineapple, papaya, avocado and exotic tropical fresh fruits (see classifications in **Table 1.1**) between 2000–2013 (data source: FAO 2015).

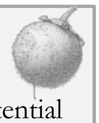
Box 1.1: Tropical fruit crop categories

In fruit industry four different fruit categories are distinguished on the basis of familiarity, spread of cultivation, level of economic establishment, production quantity and trade volumes – although definitions and classifications are not always clear (Galán Saúco 2013; overview of categories in **Box Table**).

1) The so-called **major tropical fruits** are well-known in both local and international markets and intensively cultivated in most (sub)-tropical regions (Galán Saúco 2013). They have been established in international markets for years and provide high trade volume and value (Proctor 1990). These fruit crops fulfil several properties, e.g. long shelf life, that are necessary for commercialization and hence establishment in global markets (Proctor 1990; Galán Saúco 2013), and have many registered commercial varieties (e.g. avocado over 100 varieties; Galluzzi & López Noriega 2014). Regular statistics are available for production quantity and exports (FAO 2011; Galán Saúco 2013). Banana belongs to the top 5 most commonly eaten fruit in the world and is an important food crop in agriculture (FAO 2011). Beyond mango is dominant with a global output of 31.7 million tonnes in 2009 corresponding to 39% of world tropical fruit production (excluding banana), followed by pineapple (23%), papaya (13%) and avocado (4%, FAO 2011). Import volume of fresh, major tropical fruits in 2009 was 4.2 million tonnes and was dominated by the United States (40%) and Europe Union (35%); both account for 75% of world import of mango, pineapple, papaya and avocado (FAO 2011).

2) The **minor tropical fruits** receive sometimes economic importance in their respective regional market (e.g. carambola, durian, and mangosteen in Asia) but are lesser well-known in international markets. They are less extensively cultivated and more limited geographically and quantitatively in consumption and trade than the major tropical fruits (Galán Saúco 2013). They are offered to the market irregular and produced and traded in smaller quantities (Proctor 1990; FAO 2011). Official statistic data on minor crops are rare but estimated by the FAO (2011) to reach a global output of 17.8 million tonnes accounting for 22% of total tropical fruit output in 2009 (excluding banana). Guava accounts for the largest portion of that estimated output (34%), followed by litchi (19%), longan (16%), durian (13%), rambutan (12%) and passion fruit (6%; FAO 2011). In contrast to the major tropical fruits imports were dominated in 2009 by China, Singapore and Malaysia (FAO 2011). In the last years efforts were made to establish many of these fruits in export, e.g. by overcoming pre- and post-harvest limitations, but they have not yet reached their full potential (Galán Saúco 2013).

Box 1.1 (continued)



3) The **underutilized tropical fruits** – as indicated by their denotation – have high potential to use in agriculture but lack of research, breeding and conservation efforts, commercial development or awareness of their possibilities restrict full exploitation (Vietmeyer 1986; ACTI et al. 1989; Galán Saúco 2013; Galluzzi & López Noriega 2014). A few commercial varieties are registered, growth requirements often unknown, and cultivation techniques little developed (Vietmeyer 1986; ACTI et al. 1989; Galluzzi & López Noriega 2014). The availability of agricultural statistics is limited (Galluzzi & López Noriega 2014). The crops are produced and consumed mainly locally or within production areas with no significant share on national and international trade; only few are cultivated anywhere on a large scale (Vietmeyer 1986; ACTI et al. 1989; Proctor 1990; Galán Saúco 2013). Hence they are widely virtually unknown outside their origin (Galán Saúco 2013; Sabbe et al. 2013). Examples were cherimoya, lulo, lucuma, tamarillo and camu camu (Galluzzi & López Noriega 2014).

4) The **wild tropical fruits** are currently not cultivated commercially in any country (Galán Saúco 2013). A huge number of edible fruits belong to this section; e.g. numerous species within the Solanaceae family that are recorded to be edible are semi-cultivated, tolerated as useful weeds or collected from the wild (Samuels 2015). They have great importance to be explored and conserved before they got lost (Galán Saúco 2013; Samuels 2015).

Box Table: Overview of the fruit categories, summarized from Vietmeyer (1986), ACTI et al. (1989), Proctor (1990), FAO (2011), Galán Saúco (2013), Galluzzi & López Noriega (2014) and Samuels (2015).

Criteria	Major fruits	Minor fruits	Underutilized fruits	Wild fruits
Familiarity as food crop	locally and regionally well-known well-known in international market	regionally well-known lesser-known in international market	locally well-known widely unknown in international market	not known or known only locally e.g. by indigenous groups
Cultivation area	extensive, worldwide, in most tropical countries	less extensive, mainly regional	restricted, mainly local	(currently) not cultivated commercially in any country
Economics	intensive cultivation fruit characteristics that allow commercialization available statistics of production and export	less intensive cultivation, economic importance particularly in regional market some restricting fruit characteristics (e.g. shelf life) rare official statistic data	few are cultivated on a large scale little commercial development limited/ no official statistic data	semi-cultivated, gathered in the wild lack of awareness or/and knowledge no official statistic data
Production and trade volume	high production and trade volume regular fruit supply	smaller quantities and global volume outputs irregular fruit supply	no significant share on national and international market limited fruit supply	no relevance
Examples	banana, pineapple, mango, papaya, avocado	carambola, durian, guava, litchi, passion fruit, longan	cherimoya, lulo, lucuma, tamarillo, camu camu	*Jaltomata* species
Challenges/ Future efforts	improve quality to increase trade value	effort in overcoming limiting factors (e.g. transport and storage)	breeding programmes, agronomic improvements, intensive research on marketing opportunities, storage/processing issues	need of characterization, conservation and exploration of food value, usage, agronomic value (genetic diversity/ breeding)

The current and future trends in fruit consumption and fruit trade increase the market opportunities of tropical fruits in Europe, especially those with proven health benefits and attractive sensory characteristics (Proctor 1990; Bartels et al. 2008; Sabbe et al. 2008, 2013; Galán Saúco 2013; CBI 2015). Tropical fruits are per se associated by consumers with "attractive", "special", "tasty" and "healthy" (Sabbe et al. 2008, 2009d, 2013) and could offer a range of exotic niche products for consumers and retailers (CBI 2015). While opportunities for market expansion and trade growth are great for the major, commercialized tropical fruit crops, today's interest is especially rising for the exotic tropical fruits (Proctor 1990; CBI 2015). In the recent years, contact and familiarity with tropical fruits is increasing via overseas travel, marketing and promotion strategies (e.g. attention to health benefits), extended market supply and restaurant trade that lower the barrier to taste unknown exotic tropical fruits and arouse consumer's interest (Proctor 1990; CBI 2015).

In fact, the interest in exotic tropical crops has been incessant (Proctor 1990; Prohens et al. 2003; Samuels 2015). Already in the past, e.g. after the discovery of America, mankind exchanged, introduced and grew crops in areas beyond their origin, as was the case for tomato and potato which were introduced to Europe (Prohens et al. 2003). However, as yet only a small fraction of the abundant edible fruit crops in the tropics have been fully utilized for food or received attention for their possibilities, though they can contribute to increase dietary and agricultural (genetic) diversification and food security (Prohens et al. 2003; Galán Saúco 2013; Galluzzi & López Noriega 2014; Samuels 2015). A recent survey among experts revealed that 38 fruit species are highlighted to be underutilized in Latin America; with it fruits have the largest share of underutilized crops followed by roots and tubers (Galluzzi & López Noriega 2014). Some edible crops have been neglected from scientific interest owed to their geographical restriction to the tropics or their scorn as "*poor people's plants*" (Vietmeyer 1986); others, e.g. the crops of the Incas, were forgotten over time and enjoy nowadays some revival (ACTI et al. 1989). Investment into utilization of such fruit crops can be profitable. A recent success story was e.g. the introduction of the exotic kiwi fruit to New Zealand at the beginning of the 20th century (Prohens et al. 2003). Other exotic tropical fruit crops have promising prospects to become also (more) popular and relevant to international market in near future, e.g. pitaya (Galán Saúco 2013) or passion fruit (CBI 2015).

Table 1.1: FAOSTAT classification items for production statistics of the tropical fruits referred to in this study. Source: Food and Agricultural Organization of the United Nations (FAO 2015).

Item FAO code	Item Name	Definition according to FAO	Group attribution in this doctor thesis
572	Avocados	*Persea americana*.	Major tropical fruits
486	Bananas	*Musa sapientum*; *M. cavendishii*; *M. nana*. Bananas are normally eaten raw. Trade figures may include dried bananas. Data should be reported excluding the weight of the central stalk.	Major tropical fruits but treated separately in tropical fruit statistics by FAO
603	Fruit, tropical fresh nes	Including inter alia: breadfruit (*Artocarpus incisia*); carambola (*Averrhoa carambola*); cherimoya, custard apple (*Annona* spp.); durian (*Durio zibethinus*); feijoa (*Feijoa sellowiana*); guava (*Psidium guajava*); hog plum, mombin (*Spondias* spp.); jackfruit (*Artocarpus integrifolia*); longan (*Nephelium longan*); mammee (*Mammea americana*); mangosteen (*Garcinia mangostana*); **naranjilla, lulo (*Solanum quitoense*)**; passion fruit (*Passiflora edulis*); rambutan (*Nephelium lappaceum*); sapote, mamey Colorado (*Calocarpum mammosum*); sapodilla (*Achras sapota*); star apple, cainito (*Chrysophyllum spp.*). Other tropical fresh fruit that are not identified separately because of their minor relevance at the international level. In some countries mangoes, avocados, pineapples, dates and papayas are reported under this general category.	Exotic tropical fruits, including minor and underutilized fruits
571	Mangoes, mangosteens, guavas	*Mangifera indica*. Trade figures may include dried mangoes, guaves and mangosteens, including both fresh and dried.	Mango grouped to major tropical fruits
600	Papayas	*Carica papaya*.	Major tropical fruits
574	Pineapples	*Ananas comosus*; *A. sativ*. Trade figures may include dried pineapples.	Major tropical fruits

1.2 Klein-Eden: Sustainable production and local marketing of (exotic) tropical fruits

In future, tropical fruit trade, particularly of exotic ones, is expected to increase cause of an increasing demand in Europe (see **Chapter 1.1**). In 2013 Asia was the largest producing area for exotic tropical fruits (about 2.7 million hectares), followed by Africa, Latin America (Central America, South America and the Caribbean) and Oceania (FAO 2015). Within Europe only Spain and Cyprus are reported to produce exotic tropical fruits and only in small quantities of about 60 thousand tons in Spain in 2013 (CBI 2015). So for import to Europe exotic fruits of (sub-)tropical origin have to be transported mostly over long distances, by ship or by plane. But long distance transports and cooling involve some environmental risks as emission of the greenhouse gas carbon dioxide (Öko-Institut 2007). When exported overseas via ship to Germany, about 570 g carbon dioxide per kilogram fruit is emitted, when transported via air flight even about 11,000 g. In comparison, the transport of fruits produced regionally in Germany causes about 230 g carbon dioxide per kilogram fruit (German Federal Ministry for the Environment, Nature Conservation, Building and Nuclear Safety 2012).

Challenges in future global fruit trade arises from increasing oil prices that involve losses in profit, higher prices for retailer and finally for the consumer, and stronger competition with other fruits (FAO 2011). No less important is the increasing consumer awareness of food safety and quality, and health concerns (FAO 2011; CBI 2015). Tropical fruits are linked with pleasure, good taste and health (Sabbe et al. 2008, 2009d, 2013) and an inconsistent eating quality, probably created by long transport and storage, could be more effecting consumer's purchase intention than price (Galán Saúco 2013). Tropical fruits are often shipped but many, particularly the exotic ones, are highly perishable and no adequate post-harvest techniques are established so that air flight is needed. Compared to sea shipping this increased not only product price but also product carbon footprint indicating the gas emission during transport and disposal (Galán Saúco 2013; CBI 2015). These criteria make consumers possibly more willing to buy locally or regionally produced fruits with lower transport distances (Galán Saúco 2013).

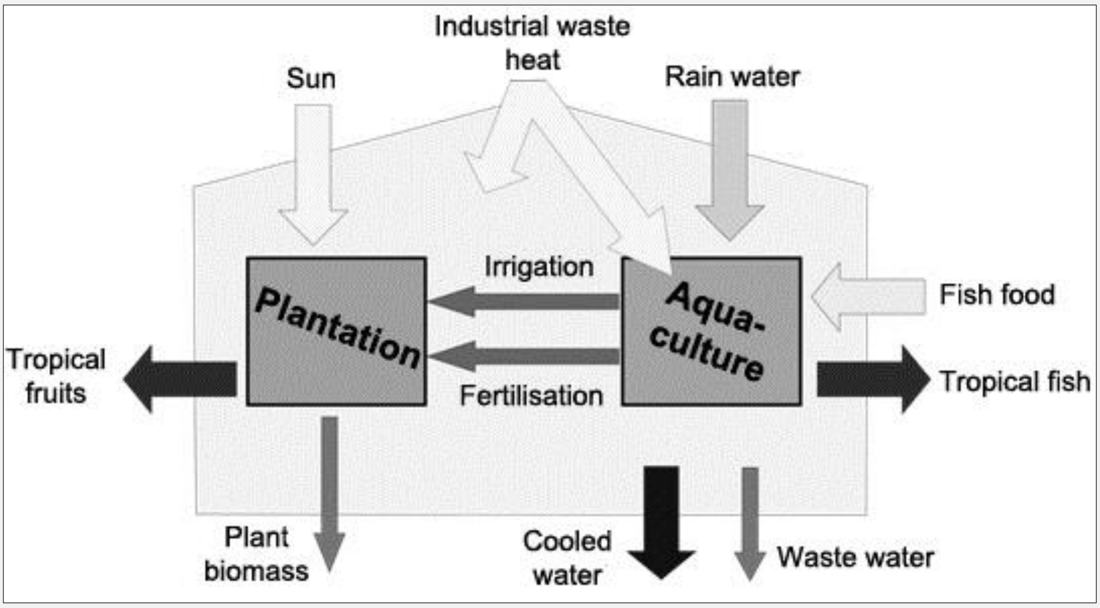
In Central Europe, tropical fruits that reach maturity late in season could only be grown in heated greenhouses. But energy costs make this production system expensive (Portas & Monteiro 1995) and would involve likewise carbon dioxide emission in spite of local production. New technologies, sustainable agricultural practices and/or sustainable use of energy are necessary to make greenhouse cultivation more profitable and environmentally acceptable (cf. Portas & Monteiro 1995). An innovative and sustainable concept that contributes to this development is the environmental project in Germany known as "Klein-Eden" (**Box 1.2**). The basic idea is to use industrial waste heat as energy resource for greenhouse production. This saves high amount of additional fuel and gas emission for heating. In 2013, an emission of 335 t carbon dioxide could be avoided in Klein-Eden compared to a conventional heating system (Schmitt 2014). Moreover, direct sales of the produced tropical fruits in Klein-Eden avoid additional energy costs and gas emission through long transports and storage (Schmitt 2014). So tropical fruits can be produced and sold in a sustainable way (**Box 1.2**) at both high quality degree and low gas emission for the first time in Germany. The Cluster of Environmental Technology Bavaria awarded Klein-Eden as *"Beacon 2012"*, an outstanding visionary project with a "*special signalling effect and an exemplary function*" (Umweltcluster Bayern 2012). This unique model project might motivate other companies and producers to replicate it.

Furthermore, such projects make it possible to introduce novel horticultural products to the Central European market. On an area of 2,600 m² 51 different crop species are currently cultivated in Klein-Eden for production and direct marketing (Schmitt 2014). Beyond the major, well-known tropical fruits such as papaya and banana, also several minor crops, e.g. carambola, passion fruit, and even underutilized fruits, e.g. tamarillo and cherimoya, are cultivated (fruit categories see **Box 1.1**). Especially the choice of the exotic tropical fruits – some kind of curiosities – would suggest special attraction for Klein-Eden. A big challenge for commercial success is the lack of knowledge and experiences at least for most minor and underutilized species. Intensive research is therefore urgently needed to study crop's properties and adaptability in order to assess the market opportunities and the suitability of the exotic tropical fruit for cultivation (see Proctor 1990; Prohens et al. 2003).

With the presented study I want to gain scientific insights into the acceptance among consumers as well as the performance of exotic tropical fruit crops under the local cultivation conditions in Central Europe in order to use it in Klein-Eden and similar facilities in future. In this study I give strong emphasis on underutilized species as they need scientific awareness and commercial development in general and provide innovative fruit products for projects like Klein-Eden and consumers in Central Europe (see **Box 1.1**).

Box 1.2: Sustainable tropical food production in Klein-Eden

In 2011 tropical greenhouses were built on an area of 3,500 m² in Kleintettau (Bavaria, Germany). Overall aim of this project is to produce and sell tropical food products at high quality level and low environmental costs (Schmitt 2014). Therefore Klein-Eden uses year-round industrial waste heat at low-temperature energy (35–38 °C) from the nearby glass factory Heinz-Glas Group Holding GmbH & Co.KGaA which was completely unexploited before. It was suggested that higher temperatures (70 °C and higher) are required for heating of tropical greenhouses (Todt 2003). But as demonstrated in Klein-Eden these "low" temperatures are sufficient to keep temperature ever above 18 °C (on average 20-24°C) and grow a wide range of tropical crops (Schmitt 2014). The integrated polyculture system plays also a significant part in sustainable agricultural production as it provides an efficient exploitation of resources (e.g. energy, water, nutrients) in more or less closed cycles (**Box Figure**). In Klein-Eden, tropical plant and fish production (tilapia, *Oreochromis* spp.) are combined in order to increase productivity without additional environmental costs. Rain water is collected in tanks to supply the water demand largely during the year; the waste water of fish production, accumulated with forage and excretion, is used as irrigation and fertilizer for the plants or can be filtered and used in aquaculture again (Schmitt 2014). Moreover, research and public education (about the diversity of tropical crops, ecological contexts, and sustainable food production) are important objectives of this project.



Box Figure: Schematic diagram of the polyculture system used in Klein-Eden.
(Schmitt 2014, translated into English)

1.3 The lulo (*Solanum quitoense*) as model species for exotic tropical fruits

For this PhD-thesis the lulo or naranjilla (*Solanum quitoense* Lam.) was chosen as model species (detailed description of lulo see **Chapter 2**) in order to study its prospects for consumer acceptance and suitability for local greenhouse cultivation. It belongs to the nightshade family (Solanaceae) and is native to the Andes of South America (ACTI et al. 1989; Villachica 1996). It produces edible fruits with an orange peel and – depending on the variety – a greenish or yellowish pulp esteemed for their unique tropical flavour (ACTI et al. 1989; Heiser & Anderson 1999; Heiser et al. 2005). Lulo plants used in this study were of the *septentrionale* variety, with spines on stem, branches, leaves, petioles and pedicels and a greenish (a* = -4.0) yellow (b* = 22.7) pulp (see Morton 1987; ACTI et al. 1989; Heiser et al. 2005, **Figure 2.1** and **2.2**). Seeds were originally collected from a lulo plantation in Santa Maria de Dola, Costa Rica, 1700 m a.s.l. in 2007, and plants have been cultivated and propagated at the Ecological-Botanical Garden of the University of Bayreuth (EBG) since this time.

Several aspects were considered for positive choice of lulo as model species (**Figure 1.2**). One crucial factor was the assumed broad novelty of lulo in European market. As yet the lulo belongs to the lesser-known exotic tropical fruits (**Box 1.1**; **Table 1.1**) cultivated and consumed mainly locally and regionally in its producing area (Vietmeyer 1986; ACTI et al. 1989; Villachica 1996; Heiser & Anderson 1999; Sabbe et al. 2013; Samuels 2015). In Central and South America it is a popular fruit nevertheless lulo's potential for becoming a major fruit product in regional market is not fully exploited, let alone in international markets (ACTI et al. 1989). In the past, the lulo receives little attention for commercial development; so difficulties in production, storage and transport, and lack of appropriate handling and processing strategies are still present (ACTI et al. 1989; Sabbe et al. 2013). As a result there are limitations to the exportation of lulo fruits or products (Sabbe et al. 2013) and they were, thus, not or hardly (mainly in big cities at high prices) available in Germany during the period of investigation (personal observation). I could therefore assume that the lulo provides a novel fruit product for most German consumers. Accordingly, the lulo belongs to the underutilized fruits with urgent research needs for successful establishment in local and export markets (**Box 1.1**).

In addition, the lulo seems to unify several promising attributes, which are necessary for successful marketing and cultivation in new regions (see Proctor 1990; Prohens et al. 2003; Galán Saúco 2013). For logistical and economic reasons relevant aspects were that the lulo is an attractive, herbaceous perennial plant, can be easily propagated by seeds, fruits already within one year (from sowing) and year-round at good conditions (Morton 1987). For both, the grower and the consumer, a long fruit supply with constant and high fruit quality is fundamental as regular exposure and access to the exotic fruit promotes repeated purchasing and so increase familiarity and acceptance among consumers (Proctor 1990). Moreover, the lulo needs no requirements for certain cultivation techniques, like use of trellis (e.g. in case of passion fruit) that involves special know how and initial monetary investment (Galán Saúco 2013). Overall, the development of an optimal cultivation management that allow for fruit production at low costs or acceptable yield would contribute towards commercial success (Proctor 1990).

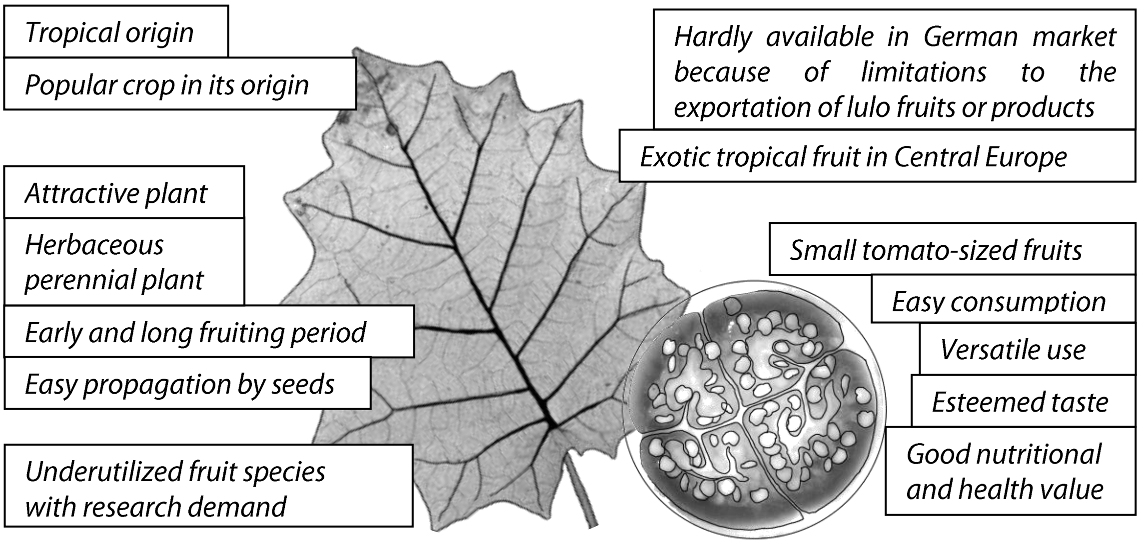


Figure 1.2: Summary of crucial aspects for choice of lulo (*Solanum quitoense*) as model species in this thesis.

With regard to the increasing demand and potential of exotic tropical fruits with outstanding sensory characteristics and healthy benefits (see **Chapter 1.1**) the lulo attaches particular attention also at consumer and market level: it offers special optic and aromatic properties and good nutritional and health related value to consumers (ACTI et al. 1989; Gancel et al. 2008; Vasco et al. 2008; Acosta et al. 2009; Mertz et al. 2009; Sabbe et al. 2013; Forero et al. 2016a). Moreover the versatile usage, small round size and easy preparation of lulo fruits are advantageous as it fulfils the demand for convenience and out-of-home consumption and make also packing and transport easier (Proctor 1990; Prohens et al. 2003; Bartels et al. 2008; Briz et al. 2008; Galán Saúco 2013). These features could favour product promotion and attract consumer's interest (Sabbe et al. 2008, 2009b, 2013; Galán Saúco 2013) provided that the sensory characteristics or organoleptic qualities are attractive to the consumer (Proctor 1990; Prohens et al. 2003; Sabbe et al. 2009c, 2013; Galán Saúco 2013).

All these characteristics made the lulo highly suitable and attractive as model species for this thesis. This crop could be interesting for projects like Klein-Eden in future. Owed to the tropical origin, the lulo is frost-sensitive (Morton 1987; ACTI et al. 1989) and cultivation in Central Europe only possible under greenhouse conditions. Together with its limited access of fruits, both fresh and processed, on European market the lulo might be an attractive rarity or speciality for greenhouse cultivation in Central Europe.

1.4 Aims and structure of this thesis

Within this doctor thesis I want to assess the prospect of the lulo (*Solanum quitoense*) as an exotic tropical fruit for Central European market and local growers. For this, I see huge advantage in regarding lulo's potential from the perspectives of both consumers and growers. By using lulo as model species I want to contribute to an extended understanding of the sensory properties, consumer acceptance and horticultural performance of the underutilized crop and to enhance awareness and opportunities for commercialization in Central Europe.

I will start with a short literature overview of the lulo (**Chapter 2**). I will describe the current crop's status and give the reader basic information of distribution, botany, fruit production and food usage to provide appropriate background of the model species used in this thesis.

A successful market launch and localized cultivation of the lulo in Central Europe requires an intensive research. A lot of factors have to be taken into account as they are strongly relevant for success or failure (see Proctor 1990; Prohens et al. 2003; Galán Saúco 2013). Consumer acceptance is the main driving force behind the success of an exotic fruit in new markets and is mainly determined by sensory characteristics or organoleptic qualities (Prohens et al. 2003; Sabbe et al. 2009b, 2009c, 2009d; Galán Saúco 2013). Disturbing characteristics (e.g. production of volatiles, a lot of seeds) or unfamiliarity with unknown, novel fruits (and their attributes) may deter consumers from purchasing them (Prohens et al. 2003; Sabbe et al. 2008, 2009c, 2013; Galán Saúco 2013). Consideration must be also given to consumer´s preference depending on geographical region (Prohens et al. 2003);

sensory characteristics that are accepted in regional markets might be unacceptable elsewhere (cf. Galán Saúco 2013; Sabbe et al. 2009a). Besides, a long shelf life per se, suitability for transport and easy handling without expensive techniques and significant loss of quality are further key factors for marketing crops over long distances (Proctor 1990; Prohens et al. 2003; Galán Saúco 2013). Optimal and, accordingly, suboptimal ripeness level for harvest and consumption should be defined as ripeness and storage can change fruit composition and sensory attributes and provide consumers with an inhomogeneous quality even in the same variety (Kader 1999; Schiele 2002; Briz et al. 2008; Proctor 1990; Prohens et al. 2003). For successful establishing in cultivation it is important that the new crop could adapt to broad environmental conditions, such as soil, photoperiod and temperature, is not vulnerable to pests and diseases, is (in case of fruit production) independent of specific pollinators, has a high yield in an early stage, has a homogenous fruit quality and easy adopts existent cultivation practices (Prohens et al. 2003; Galán Saúco 2013).

In this study, I give primary importance to gain scientific insights into the acceptance of fresh lulo fruits at the local market and the performance of this crop under greenhouse conditions and cultivation practices in Central Europe. This research is profitable as it can enhance the chance of success, reduce investment and shorten time of introduction (Proctor 1990; Prohens et al. 2003; Galán Saúco 2013) but is still missing for lulo. To the author's knowledge no data are as yet available if European consumers accept the exotic lulo fruit and only few cultivation trials were performed in Europe, e.g. England (Samuels 2013) and Spain (Prohens et al. 2004). Many recent studies focus on investigating lulo's biofunctional fruit properties (Vasco et al. 2008; Mertz et al. 2009; Cerón et al. 2010; Bagattoli et al. 2016; Forero et al. 2016a), and on finding postharvest treatments (Andrade-Cuvi et al. 2017) or processing lulo into dry fruit powder (Igual et al. 2014; Forero et al. 2015, 2016b) to overcome the perishability of fresh fruits.

The overall aim of this thesis was therefore to assess the potential of lulo as exotic tropical fruit for marketers and growers in Germany, with particular application in Klein-Eden, by evaluating lulo's

1) degree of familiarity among consumers (**Manuscript I**),
2) acceptance of consumers (**Manuscript I**),
3) fruit quality under local greenhouse production (**Manuscript II** and **IV**),
4) suitability for local, year-round cultivation under the present environmental (photoperiod) conditions (**Manuscript III** and **IV**) and
5) suitability for local, profit-yielding cultivation under greenhouse conditions and practices (**Manuscript III** and **V**).

Table 1.2 shows in detail the concrete research objectives and hypothesis being explored. The key findings of this thesis are summarized and discussed in **Chapter 3**. Finally, I assess lulo's commercial potential for marketers and growers in Central Europe, give implications of the findings and an outlook for future research.

Table 1.2: Objectives and hypothesis (H1–H5) tested in this thesis and the related manuscripts (Manuscript I–V).

Focus	Objectives and hypothesis	
Consumer acceptance	**I) Familiarity and consumer sensory evaluation of lulo fruits** H1.1: *The lulo is an unfamiliar, exotic tropical fruit in Germany.* H1.2: *Lulo fruit characteristics are attractive to German consumers.* H1.3: *People intend to consume fresh lulo fruits in Germany.*	MANUSCRIPT I
	II) Antioxidative potential of lulo fruits H2.1: *Lulo fruits have a high antioxidative potential.* H2.2: *The antioxidative potential increased until ripeness and decreased with storage time.*	MANUSCRIPT II
Suitability for local greenhouse cropping	**III) Influence of photoperiod on fruit supply** H3.1: *Changes in day length through seasons and artificial lighting affect flower and fruit phenology.* H3.2: *Seasonal changes in photoperiod impact yield.* H3.3: *Supplemental lighting during winter season enhances fruit production.*	MANUSCRIPT III
	IV) Influence of photoperiod on fruit quality H4.1: *Fruit quality of fresh lulos produced in greenhouses vary throughout the year.* H4.2: *Lulo fruits are of lower quality when ripen during winter season under low natural light conditions.* H4.3: *Seasonal differences in physico-chemical properties are sensorily perceivable by human.*	MANUSCRIPT IV
	V) Pollination of lulo by the native *Bombus terrestris* H5.1: *B. terrestris adopts lulo flowers as a source of pollen.* H5.2: *Visits of B. terrestris increase fruit set.* H5.3: *Visits of B. terrestris enhance fruit size and yield.* H5.4: *B. terrestris is less effective as a pollinator during single flower visits compared to multiple visits.*	MANUSCRIPT V

CHAPTER 2

SOLANUM QUITOENSE: BACKGROUND TO MY MODEL SPECIES

This chapter gives a short literature overview of the model species *Solanum quitoense* Lam. (lulo, naranjilla) used in this study. The exotic tropical lulo is a popular fruit crop in the region of origin but still little-known outside, like in Europe. Lulo's current status, origin, characteristics, fruit usage and production are summarized in this chapter.

2 *Solanum quitoense*: Background to my model species

2.1 Lulo is an underutilized Solanaceae crop

A recent preliminary taxonomic inventory of Samuels (2015) revealed a variety of well-known as well as lesser-known food species within the Solanaceae family. Overall, 15 genera in the subfamily *Solanoideae* provide around 180 species utilized for food; additionally there are supposed to be numerous other species that did not appear in the inventory and are gathered from the wild, particularly in tropic regions (Samuels 2015). While in the past nightshade plants became slowly accepted in Europe because of low familiarity and attribution to poison and sorcery (Prohens et al. 2003; Samuels 2009), they have nowadays high importance as food plants across the world (Samuels 2009, 2015). An economically important genus is *Solanum*, including well-known cultivated crops such as potato (*S. tuberosum*), tomato (*S. lycopersicum*), and brinjal eggplant (*S. melongena*; Samuels 2015). Beyond this, the genus still contains regionally-important domesticated solanums (Samuels 2015); some of them are valued for being promising novel fruits for the European market (e.g. Daunay et al. 1995; Heiser & Anderson 1999; Samuels 2009, 2013).

One of these promising species is the lulo or naranjilla which is native to Latin America (*Solanum quitoense* Lam., syn. *Solanum angulatum* Lam.; **Figure 2.1**; see promising attributes in **Chapter 1.3**). Already in 1986 the species was listed in *"Lesser-known plants of potential use in agriculture and forestry"* by Vietmeyer or in 1989 in "*Lost crops of the Incas: little-known plants of the Andes with promise for worldwide cultivation*" by Ad Hoc Panel of the Advisory Committee on Technology Innovation (ACTI) et al. However, the lulo is still only regionally important and little known in Europe (cf. Sabbe et al. 2013; Samuels 2009, 2015) and listed as one of the 38 underutilized fruit species among Latin American experts (Galluzzi & López Noriega 2014).

The lulo belongs to the subgenus *Leptostemonum* (Dunal), commonly called "spiny solanums", in which the majority of food species, with regard to *Solanum* species, was found (Samuels 2015). Within this subgenus the lulo is a member of the Solanaceae-section *Lasiocarpa* D'Arcy, the "woolly-fruited" solanums (Samuels 2015). Genetic analyses of Fory et al. (2010) revealed a clear separation within the *Lasiocarpa* between the Andean species, including lulo, *S. hirtum*, *S. pseudolulo*, *S. vestissimum* and *S. pectinatum*, and Amazonian species, including *S. stramonifolium* and *S. sessiliflorum*. The lulo is only known in cultivation (Samuels 2015) however it has still several biological characteristics suggesting that it is not a completely domesticated species. As summarized by Fory et al. (2010) from several literature the lulo has e.g. narrow ecological adaption of populations, allogamy, non-plastic andromonoecy, spines on whole plant, fruits with trichomes, high number of seeds and seed dormancy, leaves with ideoblasts containing calcium oxalate crystals as a defence against herbivory, and fast browning juice.

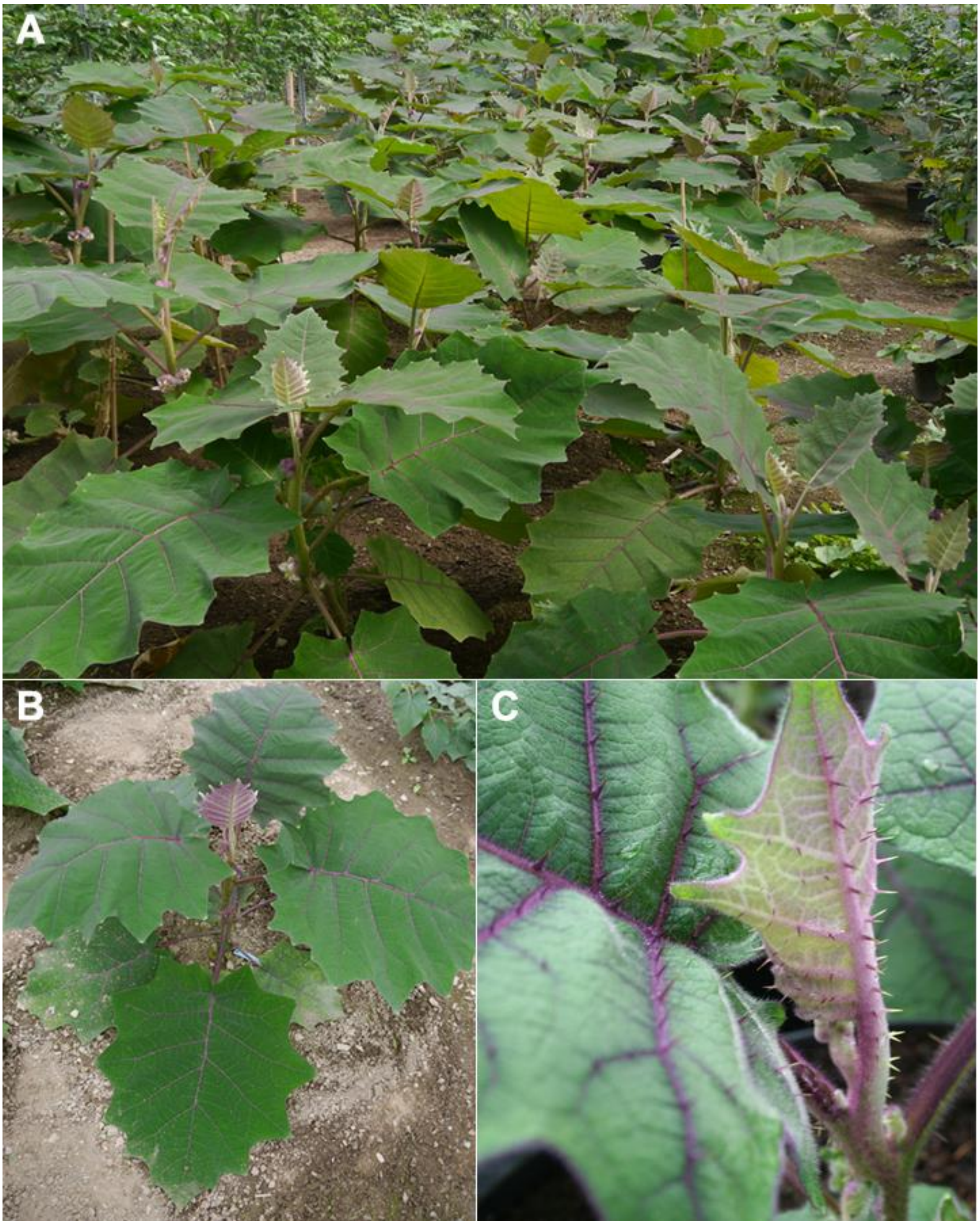


Figure 2.1: Lulo plant (*Solanum quitoense*). A: Lulo plantation in the tropical greenhouse Klein-Eden (Kleintettau, Bavaria). B: Young, 20-week-old lulo plant shortly before flowering. C: Lulo variety *septentrionale* with spines on leaf veins (upper and lower leaf surface), petioles and stem.

2.2 Description, origin, distribution and varieties of lulo

The herbaceous perennial lulo plant (**Figure 2.1**) reaches a height of 2–3 m (Morton 1987; Villachica 1996). The whole plant is densely, somewhat woolly, covered with stellate hairs (Brücher 1977; Morton 1987; Villachica 1996). The alternate, big, soft, oblong–ovate, emarginated leaves are dark green with white or frequently purple coloured petioles, midrib and lateral veins (**Figure 2.1**) making them attractive as ornamental plant in the United States (Brücher 1977; Morton 1987; ACTI et al. 1989; Villachica 1996; Heiser & Anderson 1999). The 5-fold flowers appear after 4-5 months in short leaf-opposed clusters up to 10 flowers and have white petals and prominent, dark yellow stamens (Morton 1987; **Figure 2.2**). The lulo is strongly andromonoecious and the inflorescences consist of hermaphrodite flowers with long styles and large ovaries (**Figure 2.2A**), and functionally male flowers (**Figure 2.2B**), which have short styles and never set fruit (Diggle & Miller 2004; Almanza Fandiño 2007). The pollen is enclosed in the anthers and can only be released by specialized pollinators, like *Bombus atratus*, via two apical pores (Almanza Fandiño 2007). The spherical lulo fruits (**Figure 2.2**) are 4.0–6.5 cm in diameter and resemble a tomato in external shape and internal structure (ACTI et al. 1989; Villachica 1996; Chiarini & Barboza 2007). The persistent 5-fold calyx crowns the fruit and naturally separates from it at fully ripe stage (Morton 1987). The ripe fruit has a leathery bright orange skin, densely covered with bristly hairs (**Figure 2.2E**) which can be easily rubbed off. The translucent green or yellowish pulp, depending on the variety, contained numerous small (3 mm in diameter), lenticular seeds in four locules (Morton 1987; ACTI et al. 1989; Heiser & Anderson 1999; Heiser et al. 2005; Chiarini & Barboza 2007; Gancel et al. 2008; **Figure 2.2F**).

A wild type of the lulo is unknown (Heiser 1985; Heiser & Anderson 1999). First records of cultivation are from the mid-1600s in Ecuador and Colombia where it is traditionally and mostly grown until today (ACTI et al. 1989). The epithet *"quitoense"* (acronym of Quito) or Spanish name *"naranjilla de Quito"* (English: "*Quito orange*") indicates its traditional origin in Ecuador (cf. ACTI et al. 1989). However Colombia is supposed to be possibly the primary centre of origin or diversity because of the observed higher local morphological and genetic diversity, the presence of plants with spines and the fact that the typical Colombian name *"lulo"* is of indigenous (Quechua) origin (ACTI et al. 1989; Lobo et al. 2007 and literature within; Enciso-Rodriguez et al. 2010). Nowadays the lulo can be found in the Andean highlands (1500–2800 m) from Venezuela to Peru and also in the foothill regions on the eastern side of the Andes (Villachica 1996). In the middle of the 20th century the lulo was introduced to Panama, Costa Rica and Guatemala where it became established as a small-scale crop (Morton 1987; ACTI et al. 1989; Heiser & Anderson 1999). Attempts for cultivation were also made in Florida but with slow success (Ledin 1952; Morton 1987).

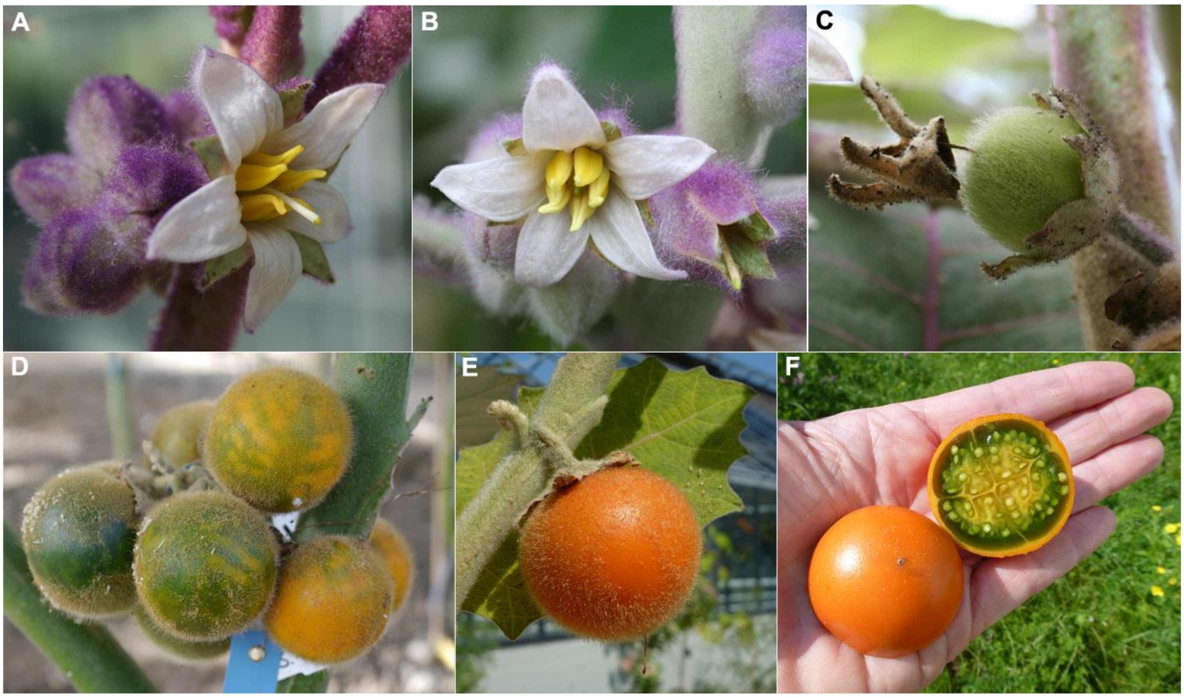


Figure 2.2: Lulo (*Solanum quitoense*) flower and fruit characteristics. A: Hermaphrodite flower with long style. B: Functional male flower with a short style. C: Fruit set after successful pollination. D: Ripening fruits (peel colour changes from green to orange-red). E: Ripening fruit on the plant. F: Ripe fruit after fallen off the plant, removed from hairs on peel and sliced into halves. © Photo E and F from M. Lauerer.

Overall, the cultivated lulo is unusually uniform (ACTI et al. 1989) but two morphologically and geographically separated varieties of the lulo are commonly distinguished: the variety *quitoense* is completely spineless and distributed in Southern Colombia, Ecuador and Peru; the variety *septentrionale* has spines on leaves, petioles and stems (**Figure 2.1C**), and is found in Central Colombia and Costa Rica (Morton 1987; ACTI et al. 1989). However, the intraspecific genetic variability appears to be low (Fory et al. 2010; Bedoya-Reina & Barrero 2010); Fory et al. (2010) even found no evident clustering pattern discriminating the lulo varieties *quitoense* and *septentrionale*. The low genetic diversity in cultivated lulo is supposed to relate, in particular, to the founder effect (Fory et al. 2010; Bedoya-Reina & Barrero 2010). In contrast to that Enciso-Rodriguez et al. (2010) showed a high genetic differentiation among populations of several Colombian regions and habitats, possibly because of the absence or restriction of genetic flow among the populations.

Interspecific hybridization with related species of the section *Lasiocarpa* could increase the genetic and morphologic variability in lulo and the possibility of obtaining vigour hybrids with agricultural desirable characteristics (Bedoya-Reina & Barrero 2010; Fory et al. 2010). The lulo is sexual compatible with close relatives of the Andes; for example, the hybridization with *Solanum hirtum* gives (after backcrossing to *S. quitoense*) the improved cultivar 'La Selva' (Heiser 1985; Heiser & Anderson 1999; Fory et al. 2010). Fory et al. (2010) also identified the Andean species *Solanum vestissimum* and *Solanum pseudolulo* to be potential compatible relatives which could be used in breeding programs for gene transfer. The sterile and spineless hybrids "Puyo" and "Polaro", differing in fruit size and pulp colour, have been obtained between lulo and *Solanum sessiliflorum*, an Amazonian species in the section *Lasiocarpa* (Fory et al. 2010), and are nowadays widely grown in Ecuador and Colombia (Heiser & Anderson 1999; Fiallos 2000; Heiser et al. 2005).

2.3 Growing conditions, fruit production and use of lulo

The lulo has narrow climatic requirements for growth and fruit production: it is susceptible to heat, full sun, dryness, and frost (Morton 1987; ACTI et al. 1989). High temperatures (above 30 °C) limit fruit set while low temperature (below 10 °C) limits plant's growth, and frost damages the plant (ACTI et al. 1989; Heiser & Anderson 1999). To that effect a successful lulo fruit production is narrowed to certain altitudes in tropical regions or frost-free subtropical sites and hampered in tropical lowlands, temperate or semiarid regions (Brücher 1977; ACTI et al. 1989; Heiser & Anderson 1999). Andean regions in Colombia and Ecuador at elevations between 1500–2400, with an annual rainfall of 1500 mm or higher (when well distributed) and a mean annual temperature of 17-19 °C provide best conditions for lulo cultivation (Morton 1987; ACTI et al. 1989).

The lulo is mainly growing by seeds but also propagated by cuttings or grafts onto rootstocks of other *Solanum* species, e.g. *Solanum macranthum*, *Solanum torvum* (Morton 1987; ACTI et al. 1989; Villachica 1996). After 2–3 months since sowing the seedlings are transplanted in the field; commonly they were planted in semi-shade, at rainy slopes, in openings in forests or interplanted with banana, tamarillo or/and other plants (Morton 1987; ACTI et al. 1989; Villachica 1996; FAO 2008). Lulo needs organic, rich and fertile soil with good drainage and balanced water supply (Morton 1987; ACTI et al. 1989). Harvest starts 6-12 months after sowing (grafted plants mature fruits at 6 months) and in areas with optimal growing conditions is continuous throughout years. In general, a plant is productive for 2–4 years, when it frequently succumbed to root-knot nematodes, and bears about 135 fruits (9 kg) per year (Morton 1987; ACTI et al. 1989; Villachica 1996). Fruits were harvested every 7–10 days in field plantations, normally between 50–75% maturity and with their pedicel and calyx still attached to guarantee good fruit characteristics, to withstand handling and transport and to extend storage period (Morton 1987; ACTI et al. 1989; Villachica 1996; Fiallos 2000; Casierra-Posada et al. 2004). For marketing, the hairs are rubbed off by man with a cloth or by machine with water and brushes (Morton 1987). Because plantation areas are often at slopes and far away from packaging stages or market places the fruits were packed in sacks or boxes and transported on trials with pack animals, causing sometimes loss of quality (Morton 1987; Villachica 1996). Most of the produced fruits is sold and consumed regionally (Villachica 1996; Sabbe et al. 2013).

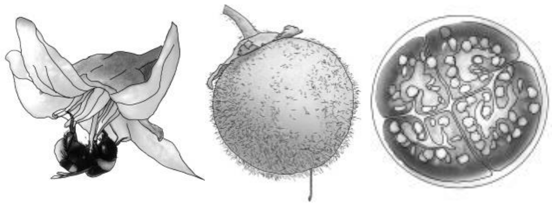
The lulo provides edible round and bright orange berries (**Figure 2.2E**), esteemed for their unique tropical flavour and described as *"the golden fruit of the Andes"* and *"the nectar of the gods"* (Morton 1987; ACTI et al. 1989). The fruit contains a juicy, slightly acid green or yellowish pulp (**Figure 2.2F**) that can be used very versatile (ACTI et al. 1989). Studies revealed a large number of volatile compounds in lulo pulp and juice (e.g. Brunke et al. 1989; Acosta et al. 2009; Forero et al. 2015). Recently, the aroma compounds (Z)-3-hexenal, ethyl butanoate, 3-sulphanylhexyl acetate, and ethyl hexanoate, were identified to be most responsible for the lulo's characteristic pulp scent (Forero et al. 2015). The pleasing flavour is likened to pineapple and lemon (Morton 1987; ACTI et al. 1989). Fresh fruits have an important antioxidant capacity and are e.g. rich in ascorbic acid, carotenoids (mainly *β*-carotene in fruit peel) and spermidine derivatives; they are thus nutritionally valuable for human diet (Gancel et al. 2008; Vasco et al. 2008; Acosta et al. 2009; Mertz et al. 2009; Cerón et al. 2010; Forero et al. 2016a).

For consumption, the ripe fruits are usually cut into halves and the pulp, without the peel (i.e. exocarp), is used (Morton 1987). It can be eaten fresh by scooping out the pulp with its seeds or it is used to make jams, jellies, ice creams, sauces or (cooked) desserts (Heiser 1985; Morton 1987; ACTI et al. 1989). Unstrained pulp is used for toppings e.g. on cakes, yoghurt, or fruit salads (ACTI et al. 1989). But most commonly it is used to prepare an aromatic juice by squeezing out the pulp into an electric blender, puréeing the pulp, straining the juice, adding sugar and serving the foamy drink with ice cubes. It is much esteemed by natives and foreigners and as "*naranjilla sorbete*" it is a national drink in Ecuador and Colombia (Heiser 1985; Morton 1987; ACTI et al. 1989). In recent times the demand and attention for lulo fruits in international markets and food technology is increasing (see e.g. Gancel et al. 2008; Sabbe et al. 2013; Samuels 2013; Igual et al. 2014; Forero et al. 2015, 2016b). Because of the functional properties lulo pulp has high international potential as basis for fruit derived-products (Gancel et al. 2008), or as an ingredient of functional food, e.g. to help in hypertension control (Forero et al. 2016a). The peel with high total carotenoid content, mainly *β*-carotene (Gancel et al. 2008) which has provitamin A activity and antioxidative properties (Bartley & Scolnik 1995; Schiele 2001) could be used as natural source of antioxidants in (processed) food, cosmetic or medicinal products (see Cerón et al. 2010).

Ripe lulo fruits are highly perishable and soften and ferment very quickly (Morton 1987; Sabbe et al. 2013). Peel browning and softening are the most prominent visual signs of deterioration in lulo fruits (Andrade-Cuvi et al. 2017). Together with the lack of advanced knowledge about transport and storage the export of fresh fruits is hampered (Sabbe et al. 2013). The juice derived from fresh fruits is often concentrated, then frozen into plastic bags or canned, sometimes also fermented to make wine (Morton 1987; ACTI et al. 1989). However, the canned juice lost much of its aromatic flavour (Heiser 1985; Heiser & Anderson 1999), and during processing (e.g. juicing or drying) an undesirable bitter taste become increasingly perceivable through an increase of bitter-active compounds (Forero et al. 2016a). But recent studies focused on analysing postharvest treatments, like short prestorage UV-C exposure that effectively delays softening in lulo (Andrade-Cuvi et al. 2017), and different drying methods preserving the sensory, nutritional and functional properties of lulo fruits (Igual et al. 2014; Forero et al. 2015, 2016b).

CHAPTER 3

SYNOPSIS



This chapter recapitulates and discusses the essentials of this thesis. I will summarize the findings for consumer acceptance (*Focus 1* including **Manuscript I** and **II**) and suitability for local greenhouse production (*Focus 2* including **Manuscript III**, **IV** and **V**) of the lulo (*Solanum quitoense*). From all these results, I assess the market prospect, commercial potential and limitation for import and local greenhouse cultivation in Germany, Central Europe, covering consumers', growers' and marketers' motivations. The results can be used in developing future market and cultivation strategies for lulo and directly applicate in the tropical greenhouse Klein-Eden or transferred to similar projects in Central Europe. Finally, an outlook for implication of the findings and future research is given.

3 Synopsis

3.1 Key results and discussion

3.1.1 Focus 1: Consumer acceptance of fresh lulo fruits in Germany

The lulo is considered to be almost less-known in Europe (Sabbe et al. 2013). By a first broad consumer survey in Germany (86% from Bavaria) with 236 voluntary respondents of balanced gender and age ratio we could verify this assumption (**Manuscript I**). The lulo fruit was widely unfamiliar by 82% of the respondents; 18% knew the fruit, but only 8% of them had already tasted it. Most respondents (n = 16) knew the lulo from educational institutions like the Ecological-Botanical Garden (EBG) or the tropical greenhouse Klein-Eden indicating public education as an important tool to promote exotic tropical fruits. Only nine respondents knew the lulo from the supermarket. Major reason for that was considered to be the low access to fresh fruits and processed products in the German market resulted from low production volume in producing countries, high perishability of ripe fruits and lack of appropriate handling and processing strategies (see ACTI et al. 1989; Sabbe et al. 2013). Hence, with this study we could definitely assume that the lulo is a novel, exotic fruit to most consumers in Germany providing a new appearance and flavour. The lulo attracts therefore great interest among the German market by fulfilling the demand for innovative exotic fruit products at retail and consumer level (see **Chapter 1**).

Manuscript I and **II** target consumer acceptance of the widely unfamiliar lulo in Germany related to sensory liking and health benefits of fresh fruits. Exotic tropical fruits are regarded by consumers as nutritious, healthy, attractive, good in taste and special (Sabbe et al. 2008, 2009d, 2013) and as shown in this study the lulo fulfilled several of these assumptions (**Manuscript I** and **II**). The lulo fruit provided bioactive compounds (**Manuscript II**), which increasingly gain scientific importance as radical catcher (antioxidant effect) for human health (Hoffmann & Staller 2004; Hoffmann 2005; Hoffmann et al. 2007). The redox potential functions as a useful and easy tool to measure the total antioxidative capacity of a fruit (Hoffmann 2005). In this study we measured for the first time (to my knowledge) the redox potential in ripe fresh lulo fruits by penetrating the electrode on the apical part of the entire hairless fruit and taking the value after 20 min measuring time. Values for lulo fruits harvested randomly from cultivated plants in the EBG ranged from 239 to 289 mV (**Manuscript II**), similar to the antioxidant capacity of tomato (232-252 mV), orange (285-349 mV), carrot (266-323 mV) or pear juice

(195-331 mV) (Hoffmann 2005). This is in accordance with other studies, where also an important antioxidative effect (measured by the H-ORAC or ORAC-value) was confirmed for lulo fruits (Gancel et al. 2008; Acosta et al. 2009). For instance, Gancel et al. (2008) measured a high total carotenoid content in peel (7450 µg of *β*-carotene equivalents per 100 g of FW) which was higher than that of guava (4298 µg/100 g FW) and papaya 'Hawaii' (4638 µg/100 g FW) and nearly as much as total carotenoid content of carrot (9508 µg/100 g FW; Mélo et al. 2006). Considering health value as an important driver for fruit intake (Proctor 1990; Bartels et al. 2008; Briz et al. 2008), we could appreciate lulo to be highly attractive for niche markets and marketing purposes. Lulo's fresh fruits, processed fruit products (e.g. juice) or processing residues have also high commercial promise as natural source for antioxidants or other functional ingredients in food and cosmetics industry (Gancel et al. 2008; Cerón et al. 2010; Sabbe et al. 2013; Forero et al. 2016a).

A more crucial aspect than health concerns for successful establishment in market is the sensory acceptance by consumers (Sabbe et al. 2009b, 2009c, 2009d) which is focused in **Manuscript I**. By a preliminary screening test (oriented after DIN) with twelve non-sensory skilled panellists characteristic and appropriate sensory attributes of fresh ripe lulo fruits could be determined. Their liking or disliking was checked by a simple consumer questionnaire with 93 volunteer participants from Germany who evaluated each of these attributes as either "liked", "neutral" (i.e. neither liked nor disliked), or "disliked". Firmness of entire fruit and pulp, peel colour, fruit and pulp odour, pulp appearance, pulp juiciness, pulp taste, pulp sourness und pulp sweetness were assessed to be relevant attributes (i.e. <50% "neutral" ratings) – only peel reflectivity, peel roughness and seeds in pulp were not and, thus, seem to be no important criterion for consumer acceptance of the lulo fruit. These tests revealed for the first time that the vast majority of consumers liked (i.e. >50% "liked" ratings) all of the relevant fruit attributes of lulo – except the lack of sweetness. In overall consideration, the lulo was liked moderately by the consumers (n = 61) in an acceptance test (median hedonic rating was 7 on the 9-point hedonic scale; Peryam & Girardot 1952, Lawless & Heymann 2010), before as well as after tasting. Hence, the sensory-based acceptability of the lulo fruit could be assessed as high forming a crucial basis for success of lulo in German market. The positive perception of the kiwi-like taste and fruity odour is particularly important as they appear to be key attribute for consumer acceptance and purchase intention (Prohens et al. 2003; Sabbe et al. 2009a, 2009c, 2013).

The “Food Action Rating Scale” (FACT) after Schutz (1965) provides a more sensitive and action-oriented measure of overall food acceptance (Schutz 1965; Lawless & Heymann 2010). We asked consumers to evaluate their intention to consume the lulo fruit (when available at an appropriate price). In accordance with the positive hedonic response in our study, the proportion (63%) of respondents who intend to consume fresh lulo fruits more or less regularly (i.e. positive attitude towards consumption) is higher than of those who indicated a negative attitude towards consumption (23%; **Manuscript I**). Based on our results we can, therefore, conclude that the lulo appears to be an attractive exotic tropical fruit for German consumers with high potential to be repeatedly consumed and (re)purchased. An increase in sugar level of fruits or fruit products could likely ensure even higher acceptance among Germans since sweet fruits usually please people in Europe (Prohens et al. 2003; Sabbe et al. 2009c). However, the findings of this study should be regarded as a first attempt to provide an overview of sensory characteristics of the exotic fruit and to assess consumer acceptance of the lulo in Germany. We highly recommend further extensive consumer and sensory studies in future to get a more detailed view of lulo’s acceptance in Germany, Central Europe.

Novelty attracts consumer’s interest but could as well act as a strong barrier to purchase and consume such fruits cause of unfamiliarity (Proctor 1990; Prohens et al. 2003; Sabbe et al. 2008, 2009c, 2013). **Manuscript I** shows that this was, to some extent, applied to lulo’s green pulp. While 56% of the consumers assessed it positively as high-contrasting to the orange peel, though 23% of the consumers perceived it negatively as unfamiliar and even described it as poisonous or unripe. But dipping into the past reveal that even the tomato (*Solanum lycopersicum*) was first likewise attributed to be poisonous being responsible for its slow acceptation as human diet after introduction to Europe (Prohens et al. 2003). To prevent such rejection for lulo, the fear of the unfamiliar characteristic should be overcome by adequate marketing and promotion. I assume that the contrasting peel-pulp colouration of lulo might even emerge as an unique, special characteristic in international markets as, e.g., it has for kiwi fruit (Galán Saúco 2013).

Manuscript II highlights that health benefits (i.e. antioxidant capacity measured by the redox potential) of fresh lulo fruits were highest at fully ripeness, determined in our study to occur not before fruit fall. A sensory test with eight sensory skilled panellists also revealed that best eating quality was likewise reached at fruit fall providing optimal properties in firmness and flavour (**Appendix A1**). So fruits should be harvested and offered to consumers as ripe as possible. But this could be problematic or even unfeasible because we found already after four days and notable after six days of storage a degradation of the bioactive substances and, thus, decreased health benefits, indicating a very short shelf life of ripe fruits (**Manuscript II**). A negative change in sensory properties (softening and development of a fermented taste) was also indicated by the sensory test (**Appendix A1**). So once a fully ripe lulo fruit is harvested it requires quick marketing. Already Morton (1987) stated that ripe lulo fruits soften and ferment very quickly and this study could support this. The high perishability is regarded as a serious weakness for export of lulo (Sabbe et al. 2013) and a lot of other exotic tropical fruits (Galán Saúco 2013). Appropriate post-ripening procedures of near-ripe fruits (defined by a certain maturity criteria), processing techniques or effective storage treatments (as e.g. short prestorage UV-C exposure; Andrade-Cuvi et al. 2017) of ripe fruits are urgently needed to provide a high quality degree and establish the lulo successfully in European markets (cf. Sabbe et al. 2013).

3.1.2 Focus 2: Lulo´s suitability for greenhouse cropping in Central Europe

A production of lulo close to markets in Central Europe could overcome the perishability (see Morton 1987; Sabbe et al. 2013; **Manuscript II**; **Appendix A1**) of the fruits by short transport distances; fresh lulo fruits could so put on the market. But the lulo has, as a novel crop in greenhouse production, to offer growers commercial promise like low-cost cultivation, year-round fruit supply and homogenous quality (see **Chapter 1.4**). In its tropical homeland the lulo is adapted to certain environmental conditions and pollination systems (see **Chapter 2**); so the **Manuscripts III**, **IV** and **V** focused on lulo's suitability for gainful greenhouse cropping.

Annual fluctuations in day length and light intensity strongly influence reproduction of some plants, also tropical ones (Borchert et al. 2005; Jackson 2009; Amasino & Michaels 2010; Nave et al. 2010). Therefore, in **Manuscript III,** we performed cultivation trials in German greenhouses and grew lulo plants sown at two dates (February and June 2012) to provide reproduction (i.e. flowering and fruiting) at natural long-day in summer and short-day in winter, respectively. Our results showed differences in flower and fruit phenology as well as in sex expression depending on photoperiod. Long-days significantly accelerated the time from flower bud to fruit set by averagely 15 days (compared to short-days) reducing total cultivation time until harvest. Moreover, in the andromonoecious lulo the portion of hermaphroditic flowers was higher under long-days (50%) compared to short-days (27%) which is in compliance with other studies on lulo and its relatives (Solomon 1985; Miller &

Diggle 2003). But the unique result of this study is that we found overall no restriction for lulo's reproduction by seasonal fluctuations in day length; therefore we could refute the assumption of J. Soria that lulo is a short-day plant (see in ACTI et al. 1989). With this study we could demonstrate quite the opposite: the lulo fructified all year long and within one year, as also indicated by cultivation experiences in United Kingdom (Samuels 2013). Moreover, the lulo provided a long-lasting fruiting period of 4–7 months and we could show that two sowing dates, one in February and one in June, are sufficient to provide a near year-round lulo fruit supply (**Manuscript III**). The results of this study could arouse growers' and marketers' interest for lulo in Europe as obviously greenhouse cropping would enable a regular income for growers and offer consumers regular access to this exotic tropical fruit.

Especially a lulo fruit supply during wintertime when other locally produced fruits are scarce seems to provide attractive marketing opportunities and might encourage growers to favour lulo. But, commonly, yield and fruit quality (e.g. sugar content, flavour, carotenoid content, amount of total phenolic compounds) are affected by season and are lower in winter with low light duration and intensity (Dorais 2003; Slimestad & Verheul 2005; Hewett 2006; Rosales et al. 2006). Supplemental lighting during winter is thus used for many greenhouse cultures, e.g. tomatoes (Dorais 2003). In **Manuscript III** we compared the yield of lulo plants grown with supplemental lighting during winter with lulo plants that did not. We could demonstrate that an artificial long-day did significantly increase fruit number by about 50% compared to short-days, but, surprisingly, not fruit yield cause of different fruit sizes. Moreover lulo plants grown in short-days in winter without supplemental light showed a second blooming period in following spring giving a longer fruiting period and, thus, higher total yield during the whole harvest period. This would save additional energy costs and make lulo cultivation financially lucrative and sustainable. Indeed these results were obtained for the specific lulo variety, light duration, light intensity and growth conditions used in this study. Variation in these parameters may lead to modified results for lulo.

Manuscript IV focuses on seasonal variation in fruit quality of fresh lulo fruits harvested in winter, spring and summer, respectively. I give special emphasis on investigating both physico-chemical and sensory properties (performed after DIN). Innovative composition analyses using NMR spectroscopy were done on lulo fruits in cooperation with the Research Center for Bio-Macromolecules (Prof. Dr. Stephan Schwarzinger, University of Bayreuth) and ALNuMed GmbH (Analyselabor für Nahrungsmittel und Medizinprodukte, Bayreuth). As expected, fruit quality varied significantly throughout the year and was lowest in winter: peel red colour value (a*) was 39.8 / 43.9 / 43.9 for winter / spring / summer, respectively, pulp dry matter (DM) was 24±5 / 31±2 / 30±2 %, pH was 3.28±0.07 / 3.46±0.06 / 3.55±0.06, total soluble solids (TSS) amounted to 9.4±0.7 / 14.9±0.8 / 14.0±0.7 °Brix, and titratable acidity (TA) was 2.48±0.16 / 1.97±0.14 / 1.76±0.13 g CAE/100 g FW. Sucrose, glucose and fructose contents were proportionally lower while citric acid concentration was 1.2 times higher in fruits harvested in winter than in spring or summer. In compliance with instrumental measurements, panellists perceived fruits in winter as much softer and less sweet, probably affecting storage suitability and consumer liking. So when growing lulo in regions with fluctuating light conditions, variations in fruit quality should be taken into account. Provided that these variations negatively affect consumer acceptance (i.e. purchase intention) or fruit storage and handling they should be overcome by horticultural (e.g. variety selection), processing or marketing strategies (e.g. adding sugar in lulo juice) in future. If no inexpensive solution can be found for producing high-quality lulo fruits or products in winter, it might be considered to restrict harvest and marketing to one period during spring until autumn.

In **Manuscript IV** we also compared our measured physico-chemical values of lulo fruits harvested during spring, summer and winter in German greenhouse with those given by recent scientific literature on lulo fruits harvested in Latin America (cf. Acosta et al. 2009; Gancel et al. 2008; Vasco et al. 2008). Quality of fruits produced in greenhouses in Central Europe was similar when harvested in winter, and even higher when harvested in spring and summer. In addition, aroma intensity (i.e. odour and taste) perceived by the panellists was very strong in lulo fruits and did not decline in winter. This was not expected since we measured significant changes in several objective parameters supposed to be positively related to flavour or liking, e.g. DM (Palmer et al. 2010), TA, TSS, or TSS/TA (Kader 1999; Harker et al. 2002). Thus this study supports the importance of using sensory studies in addition to physico-chemical measurements when addressing consumer acceptance, as also recommended by Harker et al. (2002). The results indicated that greenhouse cropping in Central Europe provides fruits of high quality degree – also in winter with low natural light duration and intensity. Hence, the lulo is overall suitable for sustainable and gainful greenhouse cropping in areas with fluctuating light conditions. Based on the observed changes in antioxidative capacity and sensory properties during ripening (see **Manuscript II**; **Appendix A1**), the level of ripeness seems to be more decisive for lulo's aroma than photoperiod. Consequently, high level of ripeness should be aimed for harvest in local production to provide the complete aroma and to be able, in an increasingly competitive fruit market, to promote this important strength for consumer's positive choice in favour of lulo.

Manuscript V addresses lulo's pollination biology and investigates different pollination treatments and their success in fruit set. The morphology of the lulo flower necessitates the involvement of specialized pollinators, like *Bombus atratus* in its homeland (Almanza Fandiño 2007). This was demonstrated in our study by bagging lulo flowers (n = 20) with a gauze mesh to prevent insect visitation throughout the whole flowering period; no fruit set occurred under the exclusion of insects and the low wind and air movement in the greenhouse. This clear result highlighted that lulo flowers have to be pollinated either by hand or by disposing insects for fruit set in greenhouses. We tested the pollination success of the Eurasian *Bombus terrestris* which is widely used in cultivation of other nightshade plants, e.g. tomatoes (Velthuis & van Doorn 2006), but has never been investigated for this purpose. *B. terrestris* adopts the lulo flower as pollen source and can buzz-pollinate it. Crucial for successful pollination of the lulo is the contact with lulo's exserted style and stigma to deposit pollen (Almanza Fandiño 2007) so that it is not self-evident that *B. terrestris* successfully pollinated the lulo. But we could clearly demonstrate that *B. terrestris* meets this requirement and both appear to be biologically compatible.

In **Manuscript V** we evaluated the pollination efficiency of *B. terrestris* by comparing fruit set, seed set, fruit size and fruit weight after a single visit and after multiple visits of *B. terrestris*, compared to the success of self- and cross-pollination by hand. Multiple visits of *B. terrestris* led to a fruit set of about 85% and were as efficient in all parameters (fruit diameter: 4.7±0.5 cm, seed number per fruit: 1335) as cross-pollination by hand. No fruit abortion (0%) was recorded, in contrast to self-pollination (20%), revealing that *B. terrestris* promotes cross-pollination in lulo to a high degree. But when *B. terrestris* visited lulo flowers only once instead of several times fruit set (50%) and fruit size (diameter: 4.1±0.7 cm) were significantly lower. We argue that this is of less importance in greenhouse cropping because we found high visitation rates of *B. terrestris* on a single lulo flower without causing huge damage like flower destruction or abortion (see e.g. on tomato: Nunes-Silva et al. 2013). Therefore these results indicated that the combination of lulo as flower source and *B. terrestris* as pollen vector is a commercially viable relationship, suitable for production of lulo fruits in greenhouse cropping systems in Central Europe. The study is helpful in preventing a failure in fruit set by a lack of pollination and demonstrates a successful and easy pollination method with *B. terrestris*. Moreover this study is a contribution to the present knowledge of lulo's pollination biology and commercial use of *B. terrestris*.

3.2 Outlook: Potential of lulo, implications of the findings and future research

This study gives first invaluable insights of lulo's performance in Central Europe. The obtained results can be directly implemented in the tropical greenhouse Klein-Eden which could emerge as pioneer in the development of commercial lulo cultivation in Germany; moreover the results can be transferred to similar projects in Central Europe. By performing both consumer tests and cultivation trials we were able to comprehensively evaluate the potential of the lulo as new tropical fruit in Germany and this might also give motivation and implications for many other actors in the (tropical) fruit sector (e.g. marketers, retailers, (processing) fruit industry, cosmetics industry, horticultural organisations). Moreover, new research issues arose from this work assumed to be relevant for contributing towards promotion and commercialization of the lulo in the future.

The mostly attractive sensory characteristics, especially odour and taste, together with the novelty and antioxidant capacity of lulo fruits would meet the high demand of European consumers for innovative, special, tasty and healthy tropical fruits (see Proctor 1990; Bartels et al. 2008; Sabbe et al. 2008, 2013; Galán Saúco 2013; CBI 2015). In overall consideration, the lulo appears to be an attractive exotic tropical fruit for German consumers with good (re)purchase rate. Producing and selling fresh lulo fruits in Klein-Eden which are up to now not or only rarely available on the German market, would be unique in the region and certainly attract consumers. In addition, the versatile use of lulo fruits (see **Chapter 2.3**) creates good possibilities to produce easy-to-handle fruit products, such as powder, marmalade and juice, offering the advantages of a better storage and taste adjustment (e.g. sugar level). Product designers, e.g., in international beverage fruit industry (cf. ACTI et al. 1989; Sabbe et al. 2013) or powder technology (cf. Igual et al. 2014; Forero et al. 2015, 2016b), can be (even more) motivated to create innovative or improved fruit products; cosmetics industry could also take advantage of lulo's antioxidative capacity (cf. Cerón et al. 2010), strong and attractive odour and colour.

The findings of this thesis should be regarded as a first attempt to assess consumer acceptance of the lulo and would clearly benefit from further extensive consumer studies with larger sample size and modified sensory methods. Consumer tests with further lulo varieties or cultivars of differing fruit characteristics are recommended here to enable a more detailed assessment of consumer preference, as well as the acceptance of the lulo against the background of consumers' age or attitudes. Until now we disregarded processed lulo fruit products in our sensory and compositional analyses but this should be also investigated in future. For successful sales of lulo fruits or lulo products I agree with Sabbe et al. (2008) that attracting promotional activities are critical, e.g. taste samples, recipe suggestions, communication about nutritional value, sensory highlights or consumption. Consumers in Germany are widely unfamiliar with the lulo that could prevent consumers from purchasing the fruit (Sabbe et al. 2008, 2009d). So in future, consumer and marketing analyses (e.g. purchase intention of fruits presented in store as whole and cut sample, hedonic response with and without nutritional information) are useful to obtain more insights into the driving factors for purchase choice of lulo (cf. Sabbe et al. 2009a, 2009b) in order to develop marketing and advertising strategies and increase the popularity of the lulo in Germany.

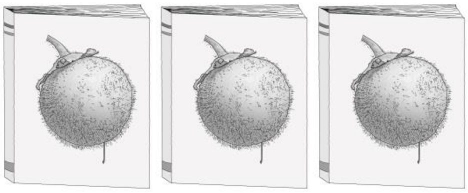
Lulo fruits for direct marketing can be produced in greenhouses in Germany, as demonstrated for the first time in our cultivation trials. Against the background of the positive market prospect, the limited access of lulo fruits (cf. ACTI et al. 1989; Sabbe et al. 2013) and the demand for sustainability and regionality in Europe (CBI 2015), lulo cultivation will be highly attractive in Klein-Eden and is recommendable to pursue in future – perhaps also in other parts of Germany or Europe. Confirmation and validation of these results with larger samples from different geographical area are desirable to substantiate lulo's promising potential. However, the quick loss in fruit quality of ripe fruits challenges handling and transport of lulo even within Germany, and (currently) favours lulo as a niche product in Klein-Eden or similar projects with direct marketing and short transport. So a main topic for future research should focus on extending the shelf life of fruits by the development of efficient and low-cost post-harvest procedures (see Galán Saúco 2013). For instance, a recent study of Andrade-Cuvi et al. (2017) showed that prestorage UV-C radiation effectively delays softening in lulo.

I argue that further research, practical experiences and educational work is necessary to increase potential user's assurance and confidence in lulo. For instance, lulo plants are still highly susceptible to some pests and pathogens known from South America (ACTI et al. 1989; Ochoa et al. 2001; Ochoa & Ellis 2005; Lozano et al. 2007; Oliva et al. 2010; Restrepo Salazar et al. 2011) and experienced also in Klein-Eden (e.g. *Fusarium oxysporum,* **Appendix A2**). Without concrete helpful preventions or methods for pest control this might deter enthusiasts from lulo production. So phytomedicinal issues seem to be one main topic especially in greenhouse production. In a preliminary experiment we grafted lulo plants on *Fusarium*-resistant rootstock and monitored grafting success and infestation rate during cultivation period (Kemper 2015). This approach should be amplified in future along with optimization of cultivation methods and selection of most appropriate lulo varieties that allow for profitable (early, high and regular yielding, high fruit quality) and easy-handling (spineless, resistant to pathogens and pests) greenhouse cropping in Germany (see Prohens et al. 2003; Galán Saúco 2013). Different lulo genotypes (varieties) may show different adaptability to environment, different resistance to pests and diseases, and different behaviour, e.g. growth traits, phenology and fruit characteristics (see e.g. Heiser & Anderson 1999; Heiser et al. 2005). Until now we studied only one variety originated from Costa Rica but first preliminary cultivation experiments gave already hints that lulo varieties can vary in morphological traits and flower number (**Appendix A3**). Thus, in a follow-up study we will test different lulo varieties or cultivars from several geographical locations and compare them in plant growth, infestation with pests and pathogens, phenology, fruit yield and quality.

Research efforts on cultivation issues in Germany will extend knowledge of lulo's requirements in general and are, thus, also of interest for growers in Latin America. Despite the popularity of the lulo in its homeland, difficulties in production still limit fruit supply (ACTI et al. 1989; Villachica 1996; Sabbe et al. 2013). Considering the positive market prospects of the lulo indicated by our studies and other authors (e.g. ACTI et al. 1989; Gancel et al. 2008; Acosta et al. 2009; Samuels 2013; Forero et al. 2016a), an increasing global demand for lulo can be expected and will of course concern current and potential producers in long-term by requiring high, regular and high-quality fruit supply (see Sabbe et al. 2013). So an improvement in cultivation is inevitably necessary in producing regions and involves much effort of horticultural organisations and research institutions, primarily at national level (see ACTI et al. 1989; Galluzzi & López Noriega 2014). In addition, (collaborative) international research efforts can help to drive that commercial development forward (see Galluzzi & López Noriega 2014). The results of this study and possible follow-up studies will help, in long-term, to promote public and scientific awareness, consumer familiarity and research dedication and investment in marketing, cultivation and processing of lulo outside of its homeland. The raising global awareness and demand would likely give the lulo also higher priority in national research and development (Galluzzi & López Noriega 2014). I guess that the more the lulo is popular and demanded internationally, the faster research, improvements and innovations in lulo can be driven. Hopefully, the high potential of the lulo could be utilized in the future.

CHAPTER 4

REFERENCES



This chapter lists the references used in the **Chapters 1–3**.

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CHAPTER 5

LIST OF INCLUDED MANUSCRIPTS AND PERSONAL CONTRIBUTION

This chapter lists the prepared and published manuscripts included within this thesis. The own contribution is given for each manuscript.

5 List of included manuscripts and personal contribution

MANUSCRIPT I

MESSINGER J, ENDREß A, SPECK S, SAMUELS J, LAUERER M.: Liked or disliked? Consumer sensory acceptance of the exotic lulo fruit in Germany. *In preparation*.

Personal contribution:

idea and experimental design	75%
field and laboratory work	30%
data analysis and figures / tables	70%
discussion and interpretation of results	80%
writing	70%
corresponding author	yes

MANUSCRIPT II

MESSINGER J, ZILLING E, HOFFMANN M, LAUERER M (2015): Reife und gesundheitlicher Wert: Redoxpotenzial-Messungen an der exotischen Lulo-Frucht. Laborpraxis Dezember 2015, 40–42.

Personal contribution:

idea and experimental design	55%
field and laboratory work	10%
data analysis and figures / tables	60%
discussion and interpretation of results	70%
writing	80%
corresponding author	yes

MANUSCRIPT III MESSINGER J, LAUERER M (2015): *Solanum quitoense*, a new greenhouse crop for Central Europe: Flowering and fruiting respond to photoperiod. Scientia Horticulturae 183, 23–30.
DOI: 10.1016/j.scienta.2014.11.015

Personal contribution:

idea and experimental design	65%
field and laboratory work	100%
data analysis and figures / tables	90%
discussion and interpretation of results	90%
writing	80%
corresponding author	yes

MANUSCRIPT IV MESSINGER J, ENDREß A, BRAUER F, SCHWARZINGER S, LAUERER M.: Physico-chemical and sensory quality of the lulo fruit is high but varies seasonally under greenhouse conditions. *In preparation*.

Personal contribution:

idea and experimental design	60%
field and laboratory work	15%
data analysis and figures / tables	80%
discussion and interpretation of results	80%
writing	70%
corresponding author	yes

MANUSCRIPT V

MESSINGER J, MARTINI M F, ROSSI G, SAMUELS J, LAUERER M (2016): Successful pollination of the Neotropical crop *Solanum quitoense* by *Bombus terrestris*: Behaviour, efficiency and yield. Journal of Applied Entomology 140, 124–134.
DOI: 10.1111/jen.12237.

Personal contribution:

idea and experimental design	65%
field and laboratory work	25%
data analysis and figures / tables	55%
discussion and interpretation of results	65%
writing	70%
corresponding author	yes

CHAPTER 6

MANUSCRIPTS

This chapter includes the prepared and published manuscripts (**Manuscripts I-V**) included within this thesis. Five major research objectives were investigated on lulo: I) degree of familiarity among consumers and consumer sensory acceptance, II) antioxidative capacity, III) flowering and fruiting respond to photoperiod, IV) seasonal variations in quality of fruits, and V) pollination success by *Bombus terrestris*.

6 Manuscripts

6.1 Manuscript I:

Liked or disliked?
Consumer sensory acceptance of the exotic lulo fruit in Germany

Jana Messinger[1], Alexander Endreß[1], Susan Speck[1], John Samuels[2], Marianne Lauerer[1]

[1]Ecological-Botanical Garden, University of Bayreuth, D-95447 Bayreuth, Germany
[2]Novel Solanaceae Crops Project, Penzance, TR208XD, United Kingdom

In preparation

Abstract

Consumer demand for novel and tasty fruits is rising in Europe, and offers possibilities for exotic fruits like the lulo (*Solanum quitoense* Lam.). The lulo is native to South America and widely unfamiliar (82%) among Germans as our questionnaire showed. Prospects for commercial success of an exotic fruit are predominantly determined by consumer acceptance of its sensory characteristics. Therefore, for the lulo fruit we investigated: 1) consumer perception of sensory fruit attributes, and 2) the overall liking and attitude towards consumption. It was shown that, apart from sweetness which was frequently assessed as being too low, the majority of consumers (>60%) liked all relevant attributes, including firmness, peel colour, odour, taste, juiciness and sourness. The green pulp, a potential unique characteristic of the lulo, was perceived negatively by some consumers (23%), but was attractive for more than half of the consumers (55%). Overall, the lulo fruit was liked moderately, both before and after tasting. 63% of the respondents would consume it, 25% even frequently, and 28% now and then. This study indicated that the lulo appears to be an attractive exotic tropical fruit for German consumers, with high potential to be repeatedly consumed and (re)purchased. But further consumer tests, e.g. on processed lulo products and on fresh fruits harvested from various lulo varieties or cultivars differing in colour and sweetness, are urgently recommended, as well as tests on acceptance of the lulo according to ripeness level and against the background of consumers' age or attitudes and product information.

Keywords

Central Europe, consumer liking, exotic tropical fruit, familiarity, hedonic response, naranjilla, likelihood of consumption, Solanaceae, *Solanum quitoense*

Introduction

In the future, fruit consumption is expected to increase rapidly in Europe because of increasing health awareness, the rising interest in special fruit characteristics, novel and exotic flavours, tastes and innovative fruit products, and the search for convenient products, e.g. attractive packaging (peeled, small portions), fresh-cut salads or juice (Bartels, Groot, Kyriakidi, & van der Lans, 2008; Briz et al., 2008; Proctor, 1990; Sabbe, Van Damme, & Verbeke, 2013). These trends increase the potential of exotic fruits in Europe, especially those with proven health benefits and attractive sensory characteristics (Bartels et al., 2008; Centre for the Promotion of Imports from developing countries [CBI], 2015; Galán Saúco, 2013; Proctor, 1990; Sabbe, Verbeke, & Van Damme, 2008; Sabbe et al., 2013). The lulo, or naranjilla (*Solanum quitoense* Lam., family Solanaceae), is native to the Andes of Ecuador and Colombia, and its flavourful fruits are supposed to have potential as a novelty for consumers in international markets all over the world (Ad Hoc Panel of the Advisory Committee on Technology Innovation [ACTI], Board on Science and Technology for International Development, & National Research Council, 1989; Sabbe et al., 2013).

The spherical lulo fruits (Chiarini & Franco, 2007) resemble a tomato in shape and size but with a bright orange peel colour (ACTI et al., 1989; Morton, 1987). The persistent 5-fold calyx crowns the fruit on the plant and naturally separates from it at the fully ripe stage (Morton, 1987). The skin of the ripe fruit is leathery and densely covered with bristly hairs which are easily rubbed off. The juicy, translucent green or yellowish pulp depending on variety, and numerous small (3 mm in diameter), lenticular seeds are contained in four locules (ACTI et al., 1989; Chiarini & Franco 2007; Gancel, Alter, Dhuique-Mayer, Ruales, & Vaillant, 2008; Heiser & Anderson 1999; Heiser et al. 2005; Morton, 1987). The lulo fruits can be eaten fresh by scooping out the slightly acid pulp, but in their native range they are commonly used for preparing aromatic juice or desserts (ACTI et al., 1989; Heiser, 1985; Morton, 1987). Moreover, the lulo fruit contains health-promoting compounds, e.g. ascorbic acid, carotenoids, flavonol glycosides and spermidine derivatives; they are thus nutritionally valuable for human diet (Acosta, Pérez, & Vaillant, 2009; Cerón, Higuita, & Cardona, 2010; Forero et al., 2016; Gancel et al., 2008; Samuels, 2013). The tropical origin (exotic, novel), the esteemed flavour and the nutritional characteristics (e.g. vitamins, spermidine) are important strengths for the current demand and attention for the lulo as a novel fresh fruit and as a raw material for processed products (e.g. exotic drinks, dried powders, ingredient of functional food) in international markets and food technology (see e.g. Forero, Orrego, Peterson, & Osorio, 2015; Forero et al., 2016; Gancel et al., 2008; Igual, Ramires, Mosquera, & Martínez-Navarrete, 2014; Sabbe et al., 2013; Samuels, 2013).

Consumer acceptance is the main driving force behind the successful introduction of an exotic fruit to new markets and is mainly determined by sensory characteristics (Galán Saúco, 2013; Prohens, Rodríguez-Burruezo, & Nuez, 2003; Sabbe, Verbeke, Deliza, Matta, & Van Damme, 2009a, 2009b; Sabbe, Verbeke, & Van Damme, 2009c; Sabbe, Verbeke, & Van Damme, 2009d). Unfamiliarity or dissatisfaction with new tropical fruits and their attributes may deter consumers from purchasing them (Prohens et al., 2003; Sabbe et al., 2008, 2009c, 2013). In this context, variation in consumer preferences according to geographical region has to be considered (Prohens et al., 2003). Sensory characteristics accepted in regional markets might be unacceptable elsewhere (cf. Galán Saúco, 2013; Sabbe et al., 2009a) as it is, e.g., assumed for the odour of durian (*Durio zibethinus;* Galán Saúco, 2013) or sweet pepino (*Solanum muricatum*; Galán Saúco, 2013). Given the increasing demand and availability of exotic fruits in Europe (CBI, 2015; Proctor, 1990) and the fact that the lulo can be grown and harvested in Central Europe under sustainable greenhouse conditions and brought freshly to the local market (Messinger & Lauerer, 2015; Messinger, Martini, Rossi, Samuels, & Lauerer, 2016) consumer perception has to be evaluated. But, as far as we know, there have been no investigations, as yet, into whether or not the sensory characteristics of the lulo fit the taste and demand of the German consumers.

This study attempts to determine the degree of familiarity with the lulo and to find out the level of acceptance for fresh lulo fruit consumption in Germany. We hypothesized that: 1) the lulo is so far unknown among Germans, because of limited imports of fresh fruits (Sabbe et al., 2013), 2) lulo fruit attributes are attractive to consumers, and 3) people intend to consume fresh lulo fruits in Germany. Our results should contribute to assess consumer acceptance of the fresh lulo fruit in Germany, Central Europe.

Materials and Methods

Degree of familiarity with lulo fruit

To evaluate the degree of familiarity of German consumers with fresh lulo fruits (Figure 1) we designed a questionnaire based primarily on the study by Sabbe et al. (2008). Volunteers had to state their residence (country), age group, gender and knowledge of the lulo fruit. We requested whether the lulo 1) is unfamiliar, 2) is familiar but has not yet been tasted or 3) is familiar and has already been tasted by the participant. In the latter two cases it was additionally requested whether the lulo is known from the supermarket, trips into the tropics or from elsewhere (additional space was available for comments). The questionnaire was held between 27 May 2016 and 15 September 2016 at four different locations in Bavaria, Germany, to sample a broad cross-section of the public: in the tropical greenhouse "Klein-Eden" in Kleintettau (27 May and 04 June 2016), at the horticultural show 2016 in Bayreuth (18 July and 15 September 2016), at the University of Bayreuth (20 July, 03, 04 and 07 August 2016), and in Eckersdorf near Bayreuth (14 August 2016). In total, 236 German residents (86% from Bavaria) filled in the questionnaire. We only recruited people who participated voluntarily, and we attempted to ensure a well-balanced gender and age ratio (Table 1). We provided participants with information on handling the questionnaire, and informed them that the fruit was called "lulo" or "naranjilla". We also showed them photographs of the whole fruit and fruit halves so that they have a visual idea of the fruit, in case participants did not know the name but remembered the fruit appearance.

Liking/disliking of characteristic lulo fruit attributes

We examined consumers' perception of lulo's sensory fruit attributes and measure consumer acceptance by a simple count of the proportion who find the given attributes of the lulo appealing or not. For that purpose, we did a preliminary screening test at the Ecological-Botanical Garden (Bayreuth, Germany) with twelve panellists of both sexes (8 females, 4 males, aged 19–51 years) from Bayreuth (Bavaria, Germany) to determine lulo's characteristic fruit attributes. These persons were not sensory skilled (i.e. naive assessor; see DIN 10950-1: 1999-04) and were assumed to provide a subjective opinion of the lulo fruit. Each panellist received a lulo fruit and was allowed to select the attributes freely with its own vocabulary covering visual, haptic and olfactory-gustatory impressions of the entire fruit, peel and pulp (oriented on DIN 10964:1996-02, DIN 10967-1: 1999-10). The descriptions were collected from all panellists and afterwards pooled, limited to the characteristic or frequently listed ones and sorted according to their sensory perception within the panel (see DIN 10967-1: 1999-10). Appropriate attributes (Table 2) were then used to design a simple consumer test where participants evaluated each attribute (first for entire fruit and peel, then for pulp) as either "liked", "neutral" (i.e. neither liked nor disliked) or "disliked". In order to know why they like or dislike the attributes we used open-ended questions (Lawless & Heymann, 2010) with no given answers or checklists where the participants had to comment on their decision (additional space was available). They are easy to write and should uncover participants' subjective opinion and give new insights of the lulo fruit (see Lawless & Heymann, 2010).

Figure 1. Fresh fruits of *Solanum quitoense*. A: Ripening fruit, shortly before fruit fall at the Ecological-Botanical Garden (EBG) of the University of Bayreuth, with bristly short hairs on the red-orange peel and the persistent 5-fold calyx. B: Fully ripe fruit (from plants at the EBG), as used in consumer test to evaluate the liking/disliking of lulo fruit attributes, with hairs removed and sliced crossways into halves. C: Ripe lulo fruit as used in consumer test to evaluate the overall liking and attitude towards consumption, sliced lengthways into halves. Fruits were bought from a local hypermarket (imported by plane from Ecuador).

Each participant received a fresh, fully ripe and physically undamaged lulo fruit, picked randomly during February 2013 to May 2014 from *Solanum quitoense* plants grown in a greenhouse at the Ecological-Botanical Garden (EBG) of the University of Bayreuth, Bavaria, Germany. Lulo fruits used in this study had an orange peel and greenish pulp (Figure 1B). The bristly hairs (Figure 1A) had previously been removed from the peel, as commonly done prior to marketing (Morton, 1987). The criteria for full ripeness were the orange peel colour (Figure 1) determined by colour chart (Orange Group 28A, 28B, 25A according to Royal Horticultural Society, RHS, Woking, United Kingdom), that the fruit detaches of its own from the calyx (Morton, 1987), and a slightly soft feeling when pressing the fruit between the fingers (ACTI et al., 1989). In total, 93 German volunteers participated in the test; they were recruited mainly at the University of Bayreuth and were local residents and students of Southern Germany. They were picked from both sexes and different age groups (Table 1) to represent a broad range of potential consumers. We informed participants shortly about the background of the study, about handling the questionnaire and that the sample is a tropical fruit called "lulo" or "naranjilla" native to Latin America.

Table 1. Gender and age distribution among the participants of the questionnaire and consumer tests in Germany.

	Questionnaire: Familiarity (Section 2.1)		**Test: Liking of attributes (Section 2.2)**		**Test: Attitude towards consumption (Section 2.3)**	
	n	%	n	%	n	%
Total	236	100	93	100	61	100
Age groups						
18-30 years	65	28	45	48	33	54
31-40 years	30	13			6	10
41-50 years	38	16	37	40	5	8
51-60 years	55	23			8	13
>60 years	48	20	11	12	9	15
Gender						
Female	134	57	55	59	28	47
Male	102	43	38	41	32	53

Overall liking and attitude towards lulo consumption

During this consumer test we examined consumers' degree of overall liking as well as attitudes and behaviour towards consumption of fresh lulo fruits. Therefore, fresh lulo fruits were purchased from the hypermarket in Nürnberg (Bavaria, Germany) on 11 December 2015. Fruits were imported by plane from Ecuador (FLP del Ecuador S.A., premium quality). They arrived free of peel-hairs, had an average fresh weight of 98 g and a 50–75% ripeness stage (personal rating based on peel colour). The fruits were firstly stored for five days in a refrigerator at 10 °C, and then kept for further two to six days in the dark at room temperature for ripening. Ripeness was defined subjectively when peel colour was completely (100%) orange, fruits were becoming slightly soft and odoriferous. Ripe fruits resembled those used in the first consumer test in appearance (see Section 2.2; Figure 1C).

Table 2. *Solanum quitoense* fruit attributes used in the consumer test to evaluate consumers' hedonic response (liking/disliking of attributes; see Chapter 2.2). Attributes were determined and described through a preliminary screening test with twelve sensory unskilled panellists.

	Fruit attribute		Sensory perception
Entire fruit	Firmness	Resistance when pressing the fruit between the fingers	By hand
	Odour	Fruity odour with notes of fruit gum, strawberry, citrus and seabuckthorn fruits	Sniffing
Peel	Colour	Orange shade	Visual
	Reflectivity	Reflection of light on surface, degree of gloss	Visual
	Roughness	Unevenness of the surface	Feeling with fingertips
Pulp	Appearance	Structure, green colour	Visual
	Firmness	Force required for spooning the pulp out and chewing	By hand & feeling in mouth
	Odour	Fruity, fresh odour with notes of kiwi fruit	Sniffing
	Seeds	Appearance and crispy feeling in the mouth	Visual & feeling in mouth
	Juiciness	Moisture, watery juice released when eating	Feeling in mouth
	Taste	Fruity aroma with notes of kiwi, gooseberry and citrus fruits	Tasting
	Sourness	Acid, refreshing aroma	Tasting
	Sweetness	Sugary aroma	Tasting

In total, 61 persons attended this consumer test (Table 1). They were mainly visitors of the EBG and residents/students of Bavaria (95%) and were selected first by a screening test. Only volunteers older than 18 years, having no medical related dietary restrictions (e.g. diabetes), were not allergic or sensitive to any fruits, have not yet tasted lulo fruits (i.e. unfamiliar taste) and consume fresh fruits at least once a week (user group) were chosen to attend the test. On 17, 18 and 21 December 2015 consumer tests were performed at the EBG. We prevented distraction and arranged the tables in room so that the panellists could not face each other (see Lawless & Heymann, 2010). Mean room temperature was controlled at 22.7 (±0.2) °C, 22.6 (±0.1) °C and 21.8 (±0.2) °C for the three sampling dates. Samples were prepared in a separate room where the panellists had no visual or physical access. Fresh lulo fruits were cut and one eighth of one whole fruit was served to each panellist within a maximum of 30 minutes after preparation. The lulo peel was not eaten; the pulp had to be spooned out before consumption (instruction on both was given to consumers). Participants had to taste at least one half of the sample to evaluate the lulo.

We provided participants before the test with information on handling the questionnaire and that the sample is a tropical fruit called "lulo" or "naranjilla" native to Latin America.

For evaluation we designed a questionnaire with preset answers. Panellists had to assess first overall liking of lulo fruit samples before (i.e. visual and olfactory perception) and after tasting (i.e. visual, haptic and olfactory-gustatory perception) and second given attribtes (colour, firmness, taste, sourness and sweetness) by the 9-point hedonic scale after Peryam & Girardot (1952) ranging from 1 ("dislike extremely") over 5 ("neither like nor dislike") to 9 ("like extremely") (Peryam & Girardot, 1952; Lawless & Heymann, 2010). Finally, consumers evaluated their intention to consume the lulo fruits (when available at an appropriate price) by using the "Food Action Rating Scale" (FACT) after Schutz (1965) which provides a more sensitive and action-oriented index of overall food acceptance (Schutz, 1965; Lawless & Heymann, 2010).

Data analysis

Statistics were performed with R (version 3.4.2, R Development Core Team, 2017) and Rstudio (version 1.1.383, RStudio Inc. 2009-2017) and significance level was defined as $p < 0.05$. Illustrations were created with SigmaPlot (version 10.0, Systat Software Inc. 2006). The percentage frequency of the degree of familiarity with fresh lulo fruits was calculated. The frequencies of respondends who are unfamiliar and familiar (i.e. familiar but not tasted/ familiar and tasted) with lulo fruits were compared by a binomial test. The binomial probability was tested against the expected value of 0.5 (equal proportions) assuming that the probability of unfamiliarity was greater than 0.5 (one-sided alternative hypothesis).

Data on participants' sensory evaluation on fruit attributes was likewise analysed: the percentage frequency of "like", "neutral" and "dislike" assessments for each fruit attribute was calculated. Sensory attributes were assessed as irrelevant or neutral (i.e. value-free) for consumers and, thus, negligible for consumers' acceptance of the lulo fruit when neutral ratings were ≥50% and as relevant when they were <50%. Each attribute was checked whether it was liked by the majority of consumers (>50% "liked" ratings) or not (≤50%). Consumers' comments on attributes were listed considering their hedonic responses. Total number of mentions (no frequencies because of non-responses) were counted per attribute according to consumers' evaluation of each fruit attribute as "liked" or "disliked", respectively. The comments were subjectively coded and combined; multiple responses of the same person with different meanings were used separately. Hedonic terms (e.g. appealing, appetizing, good), vague terms (e.g. sour for description of odour) were eliminated from descriptive terms, intensities (e.g. too much, low) were only accepted for the attributes sourness and sweetness. Statements with similar perception (e.g. tropical/exotic, stable/firm, watery/liquid) were subjectively pooled and only those descriptions that were mentioned by at least five consumers were considered.

The hedonic rating scores of overall liking were averaged (median values) and the mean absolute deviation (MAD) was calculated as amount of variation. For comparison of hedonic scores between overall liking before and after tasting was tested by a paired Wilcoxon signed rank test (R-package stats, basic setting was changed in "paired=true"). The consumption behaviour was analysed in frequencies across the food action rating scale. Responses were grouped into "positive attitude towards consumption" (above mid-point) and "negative attitude towards consumption" (below midpoint). The frequencies of both ratings were compared by a binomial test while ignoring the mid-point votings. The binomial probability was tested against the expected value of 0.5 (equal proportions) assuming that the probability of a positive attitude towards consumption was greater than 0.5 (one-sided alternative hypothesis).

Results and discussion

Lulo is highly unfamiliar among German consumers

The questionnaire demonstrated that the lulo fruit is unfamiliar by 82% of the respondents; 18% knew the fruit, but only 8% of them had already tasted the lulo (Figure 2). Thus, as expected, the proportion of respondents who did not know the fruit was higher than of those who knew it ($p<0.001$; $n=236$; binomial test, one-sided). Interestingly, only nine persons stated they knew the lulo from supermarkets (Figure 2), supporting our assumption of restricted access to lulo fruits for consumers in Germany. This might be even the main reason for its high unfamiliarity among German consumers. Six respondents knew the lulo from travel to the tropics, and 16 knew it from educational institutions (Figure 2) such as the EBG, or the tropical greenhouse Klein-Eden in Kleintettau. This indicates public education as an important tool in promoting exotic fruits. In comparison to other tropical fruits, tested by Sabbe et al. (2008) in a similar study in Belgium in 2007, the lulo was less familiar than guava (*Psidium* sp.: not known by about 75%), dragon fruit (*Hylocereus* sp.: 73%) and tree tomato (*Solanum betaceum*: 68%). Sabbe et al. (2008) named these fruits unknown by more than 60% of the respondents as "*exotic tropical fruit*" and, accordingly, our study shows that in Germany the lulo belongs to this group. Hence, the lulo has high promise of a novel exotic appearance and taste to most consumers and fulfilling the demand for innovative exotic fruit products (see Proctor, 1990; CBI, 2015).

However unfamiliarity could prevent consumers from purchasing exotic fruits (Sabbe et al. 2008, 2009d). In accordance with Sabbe et al. (2008), we suggest that information (e.g. on nutritional value, sensory highlights concerning the fruit, or consumption instructions), promotional activities (e.g. taste samples) and recipe suggestions (e.g. preparing juice or desserts) are essential for promoting exotic fruits in a new market. Also cooperation with local restaurants and/or public educational institutions might be useful tools to increase familiarity with the lulo in the future.

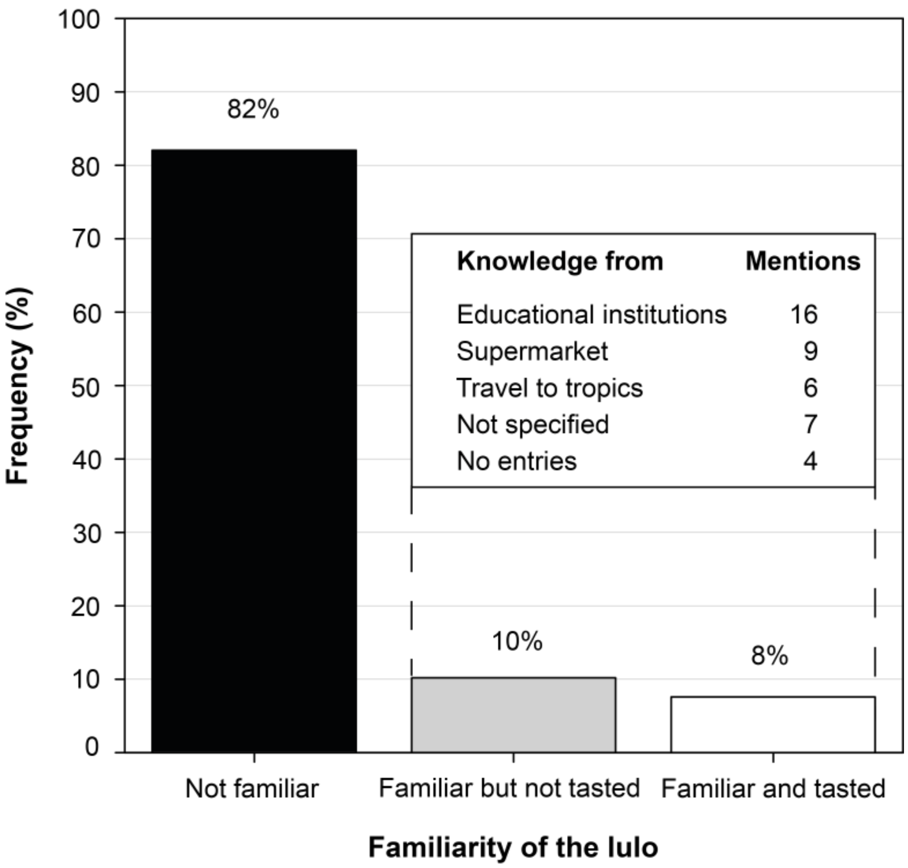

Figure 2. Degree of familiarity of German consumers (n = 236) with the tropical lulo fruit (*Solanum quitoense*). In case of knowledge ("familiar"), the respondents had to specify the source of their knowledge (inbox table). The gender and age distribution among the participants of the consumer questionnaire can be seen in table 1.

Consumers like most of lulo fruit attributes

Most of the 13 sensory fruit attributes of the lulo tested were assessed as relevant for consumers - only peel reflectivity, peel roughness and seeds in the pulp were not (Table 3). One of the most attractive fruit attributes was the peel colour (liked by 86% of all consumers) which was predominantly described as orange, bold and luminous (Table 3; Figure 1). Because of the similarity to an orange the lulo has its Spanish name "naranjilla" ("little orange"; Morton, 1987). This positive perception is quite important because it is known that external appearance determines initial consumer purchase and consumption (Briz et al., 2008; Kader, 1999) and might act as an indicator of taste, juiciness, healthiness and food safety (Briz et al., 2008). So the appealing colour might therefore motivate the consumer to buy and taste this exotic fruit. This might be further enhanced by the pleasant odour of the entire fruit, rated also positively by 86% of the consumers (Table 3). It was mainly perceived as fruity, tropical and frequently attributed to strawberry (Table 3). In contrast, the roughness of the peel was perceived as unpleasant by 30% of the consumers. But the slight majority evaluated this attribute as "neutral" (Table 3) and nine consumers even stated that this attribute is "not relevant" for them; it therefore does not seem to be an important criterion for a purchase decision.

Odour and juiciness were the most attractive attributes of the fruit pulp and rated positively by 80% and 78%, respectively (Table 3). Odour was perceived as fruity and fresh/refreshing and associated mainly with that of kiwi fruits (Table 3). Some studies have revealed a large number of volatile compounds in lulo pulp and juice (e.g. Acosta et al., 2009; Brunke, Mair, & Hammerschmidt, 1989; Forero et al., 2015). Recently, the aroma compounds (Z)-3-hexenal, ethyl butanoate, 3-sulphanylhexyl acetate, and ethyl hexanoate, were identified to be most responsible for the lulo's characteristic pulp scent (Forero et al., 2015). Furthermore, fruit and pulp firmness, pulp taste and pulp sourness were rated positively (more than 60% of the consumers, Table 3). Consumers obviously favoured firm lulo fruits with a pulp easy to spoon out and eating (Table 3). In confirmation with the pulp odour, the pulp taste resembled that of a kiwi fruit and was described positively as sour, fresh/refreshing and fruity (Table 3). In combination with the slight, balanced sourness and juiciness the lulo is likely to be refreshing, especially in the summer (see Briz et al., 2008; Sabbe et al., 2009d).

Consumer satisfaction with taste is a major challenge to the successful introduction of exotic fruits to new markets (see Prohens et al., 2003; Sabbe et al., 2009a, 2009c, 2013);

association with known fruit flavours is advantageous because fruits with unfamiliar tastes are more likely to be rejected, as observed for açaí and baobab juice (Sabbe et al., 2009a, 2009c). The kiwi-like taste of the lulo was pleasant; however consumers frequently complained that the pulp was too sour and not sweet enough (Table 3). Indeed sweetness was not liked by the majority of consumers (Table 3). It is known that in Europe, people usually favour sweet fruits, while e.g. in the Far East more acidic flavours are preferred (Prohens et al., 2003). This is in accordance with findings in Belgium in which sweeter fruits (e.g. cherimoya) fulfilled consumer expectations of taste, and fruits with higher acidity (e.g. mangosteen, tree tomato) did not (Sabbe et al., 2009c). Thus, lulo cultivars with higher fruit sugar levels or, alternatively, sweetened lulo fruit products (e.g. juice, jam and ice cream) would be likely to ensure higher acceptance among German consumers.

Assessments on the appearance, including the prominent green pulp colour (Figure 1) were ambiguous. On one hand, half of the consumers rated it positively (56%) and assessed it as attractive cause of the colour contrast to the orange peel but others disliked (23%) the green pulp (Table 3). Frequently, a green pulp (in combination with the contrasting orange peel) was not expected by the consumers (seven total mentions) and was unfamiliar for overall 15 consumers; in some cases the pulp appeared unripe (three total mentions) or even poisonous (five total mentions) to consumers. In this context it is interesting that there is a lulo hybrid named "Palora", which has orange instead of green pulp, and this cultivar is believed to be better received in international markets (Centre for Underutilised Crops, retrieved online in 2012). However, in South America the lulo cultivars with greenish pulp (e.g. common lulo and hybrid "Puyo", Heiser et al. 2005) are preferred (Centre for Underutilised Crops, retrieved online in 2012; Heiser & Anderson, 1999). We suggest that possible unfamiliarity could be overcome in Europe by marketing strategies of this exotic fruit (cf. Sabbe et al. 2008, 2009d). The contrasting peel-pulp-colouration might even emerge as an unique characteristic for this fruit as, e.g., it has for kiwi fruit (Galán Saúco, 2013).

With regard to the demand for easy-to-eat fruits with less preparation, the presence of seeds can be inconvenient for consumers (Briz et al., 2008). The lulo contains numerous small seeds (Figure 1; Morton, 1987) in the pulp (ca. 1400 seeds per fruit; Chiarini & Franco, 2007), more than in many other species in the subgenus *Leptostemonum*, to which it belongs (Chiarini & Franco, 2007). The high number of seeds was also perceived by the consumers as negative (Table 3), but was overall a neutral attribute, und thus negligible for broad consumer acceptance (Table 3).

Table 3. Consumer (n = 93) perception and description of *Solanum quitoense* sensory fruit attributes (pulp sweetness: n = 92, seeds: n = 90; because of non-responses or no clear assignment by one and three consumers, respectively). An attribute was assessed as relevant for consumers (yes) when <50% of consumers scored it as "neutral", otherwise it was not relevant (no). When the majority of consumers (>50%) evaluated the fruit attribute as "liked" it was rated as majority-liked (yes), otherwise it was not (no). Comments on attributes were listed by ignoring the neutral ratings. Total number of mentions were counted per attribute and indicated in brackets. Only those descriptions that were mentioned by at least five consumers were considered and assigned according to consumers' perception of the respective attribute as liked or disliked. The gender and age distribution among the participants of the consumer test can be seen in table 1.

	Fruit attribute	Consumer perception (%)			Assessment		Consumer description / assessment	
		Neutral	Liked	Disliked	Relevant	Majority-liked	Liked	Disliked
Entire fruit	Odour	12	86	2	yes	yes	fruity (19), tropical (7), strawberry (7), aromatic (5)	
	Firmness	21	68	11	yes	yes	balanced (6), firm (7), not pulpy (5)	soft (7)
Peel	Reflectivity	53	47	0	no		–	–
	Roughness	51	19	30	no		–	rough (6)
	Colour	13	86	1	yes	yes	orange (19), bold (10), luminous (6)	–
Pulp	Seeds	51	29	20	no		–	high number (12)
	Odour	16	80	4	yes	yes	kiwi (16), fruity (11), fresh/refreshing (8)	–
	Juiciness	18	78	4	yes	yes	juicy (17), nonliquid/not dripping (12), balanced (9), not dry/floury (6)	–
	Firmness	24	73	3	yes	yes	easy to spoon out and eating (18)	–
	Taste	21	70	9	yes	yes	sour (14), kiwi (13), fresh/refreshing (9), fruity (7), aromatic (5)	–
	Sourness	16	65	19	yes	yes	slight/not too much (16), refreshing (7), balanced (5)	(too) much (10)
	Appearance	21	56	23	yes	yes	green (10), contrasting the peel (7)	green (8)
	Sweetness	36	49	15	yes	no	slight/not too much (15), balanced (6)	low (8)

Lulo fruits are very likely to be consumed

Overall, the lulo fruit was liked moderately by the consumers, both before (7 ± 1.48 MAD) and after tasting (7 ± 1.48 MAD; Figure 3), indicating, first, that external appearance of the fruit is positive and, second, that taste and texture is satisfying and meet consumers' expectation. This might stimulate initial and repeated purchase of the exotic fruit. Studies on other exotic tropical fruits by Sabbe et al. (2009c) demonstrated that repeated purchase and consumption are highly dependent on a good, satisfying taste. For example, a positive purchase intention was found by the authors for persimmon (*Diospyros kaki*) and cherimoya (*Annona cherimola*) with good taste ratings, but not for dragon fruit (*Hylocereus* sp), mangosteen (*Garcinia mangostana*) or tree tomato (*Solanum betaceum*) because of disconfirmation of prior taste expectations (Sabbe et al. 2009c). Similarly, consumer studies by Tuorila and Cardello (2002) revealed that dislike of taste can have a negative impact upon the likelihood of consuming a fruit juice repeatedly or over an extended period of time. Indeed, the taste of the lulo fruit was appealing to the consumers (7 ±.1.48 MAD, Annex 1) what might explain the high overall liking.

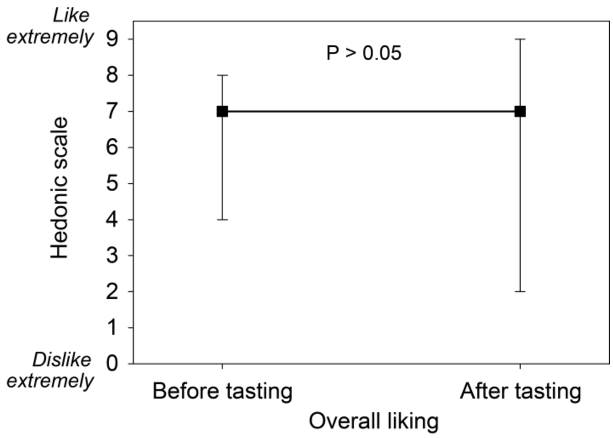

Figure 3: Hedonic scores (median values, maximum and minimum values, n = 61) for overall liking before and after tasting lulo fruit were not significantly different (paired Wilcoxon signed-rank test; p = 0.57; V = 519). The gender and age distribution among the participants of the consumer test can be seen in table 1.

In accordance with the positive hedonic response in our study, the proportion of respondents who intend to consume fresh lulo fruits more or less regularly (i.e. positive attitude towards consumption) is higher than of those who indicated a negative attitude towards consumption (p<0.001; n=52; binomial test, one-sided). In particular, 63% of the respondents would consume the fruit, of whom 25% frequently and 28% now and then; only 23% indicated a low intention to consume the fruit (Table 4). Due to our results we can, therefore, conclude that the lulo appears to be overall an attractive exotic tropical fruit for German consumers with high potential to be repeatedly consumed and (re)purchased. Maybe an increase in sugar level could promote consumption as sweetness was valued on average one score lower than taste (6 ± 1.48 MAD, Annex 1).

It has to be mentioned that the fruits used for the evaluation of the attitude and behaviour towards consumption were harvested prematurely and imported from overseas. But it is known that best eating quality for lulo fruit is achieved when harvested fully ripe (Messinger et al. 2015, Morton 1987). As noted by Kader (1999), fruit quality, especially flavour, suffers under pre-ripe conditions. So taste satisfaction can be expected to be even higher for lulo fruits harvested fully ripe. Recent trial studies revealed that the lulo can be grown in protected cropping systems in Europe, e.g. United Kingdom (Samuels, 2013) and Germany (Messinger & Lauerer, 2015; Messinger et al., 2016). Such localised production and consumption allow harvest of fruits at a more advanced stage of ripeness, because of reduced need for transport, and might enhance consumer acceptance. In addition, consumption of the lulo would be also interesting against the background of consumers' age and attitudes (e.g. health interest) as the findings presented relate mostly (54%) to a sample test of younger age group (between 18-30 years, Table 1). Further research should also evaluate the effect of product information, e.g. nutritional value, on sensory perception and consumption (cf. Sabbe et al., 2009a, 2009b, Tuorila & Cardello, 2002) because it is known that the lulo is rich in antioxidants (Acosta et al., 2009; Gancel et al., 2008; Messinger et al., 2015). However, as noted by Tuorila and Cardello (2002), the consumer's personal prediction of future behaviour (as also requested from participants in our study), may not reflect reality and long-term behaviour; thus studies on actual fruit usage are also recommended for lulo in the future.

Table 4: Respondents' (n = 60) attitude and action towards consumption of fresh lulo fruits (*Solanum quitoense*). The gender and age distribution among the participants of the consumer test can be seen in table 1.

FACT[a] after Schutz (1965)	**Attitude towards consumption**	**Consumer evaluation**	
		Number (n)	**Percentage (%)**
I would eat this food every opportunity I had	Positive (n = 38)	1	2
I would eat this very often		5	8
I would frequently eat this		15	25
I like this and would eat it now and then		17	28
I would eat this if available but would not go out of my way		8	13
I do not like it but would eat it on an occasion	Negative (n = 14)	4	7
I would hardly ever eat this		5	8
I would eat this only if there were no other food choices		5	8
I would eat this only if I were forced to		0	0

[a]FACT: Food Action Rating Scale

Conclusion

In the study presented it was shown for the first time that the lulo is a novel, exotic fruit and is broadly accepted and very likely to be consumed by the majority of people in Germany. Thus the lulo has high commercial promise in the German market. But the findings of this study should be regarded as a first attempt to assess consumer acceptance of the lulo and would surely benefit from further extensive consumer studies (e.g. larger consumer samples, repetition of tests with modified sensory methods or in different regions). We highlighted relevant and (un-) pleasant attributes which could be used as basis for further consumer or sensory studies on lulo; other attributes could be also determined in descriptive analysis e.g. with sensory skilled panellists. The importance of the attributes on overall liking and attitude towards consumption should be investigated. Moreover, the attractive sensory properties, e.g. the odour, taste, juiciness and colouration, could be gainfully exploited in the marketing of the lulo. Consumer tests with further lulo varieties or cultivars of differing pulp colour and sweetness are recommended here to enable a more detailed assessment of consumer preference, as well as the acceptance of the lulo according to ripeness level, and against the background of consumers' age or attitudes and product information. Besides fresh consumption, processing the refreshing, fruity pulp for juice production in Germany could be lucrative and also worthy of investigation, as colour and sweetness could be adjusted.

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Annex 1: The hedonic rating scores of sensory fruit attributes of lulo

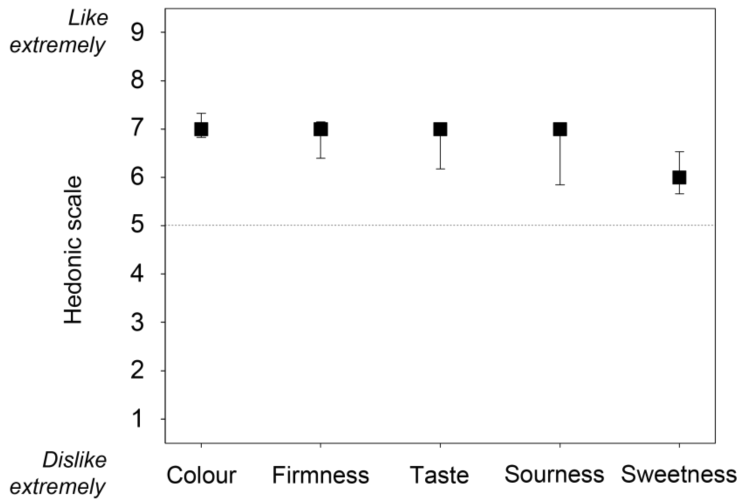

Fig. A1: Hedonic scores (median values, 95% confidence interval, n = 61) for sensory attributes of cut lulo fruit samples used in the consumer test to evaluate the attitude towards consumption. The dotted line marked the neutral value ("neither like nor dislike"). The gender and age distribution among the participants of the consumer test can be seen in table 1.

6.2 Manuscript II:

Reife und gesundheitlicher Wert:
Redoxpotenzial-Messungen an der exotischen Lulo-Frucht

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Zusammenfassung

Die Nachfrage der Verbraucher nach gesunden Nahrungsmitteln steigt zunehmend. Insbesondere die Sekundären Pflanzenstoffe haben hier aufgrund ihrer Eigenschaft als Radikalfänger großes Interesse erlangt. Ihre Wirkung kann relativ einfach über das Redoxpotenzial gemessen werden – so auch in der Lulo-Frucht.

Einleitung

Die Nachfrage der Verbraucher nach einer gesunden Ernährung steigt zunehmend und gerade Obst wird mit „Gesundheit und Frische" assoziiert [1, 2]. Die Lulo (*Solanum quitoense*) ist eine in Deutschland noch weitgehend unbekannte Frucht aus den Anden Sudamerikas, der aber aufgrund ihres exotischen Geschmacks und ihrer Inhaltsstoffe (z.B. Beta-Carotin) ein großes Potenzial für den internationalen Markt zugetraut wird [z.B. 4, 5, 6, 8]. Im Hinblick auf die gesundheitliche Bedeutung gewannen die Sekundären Pflanzenstoffe, wie die Carotinoide, in den letzten Jahren großes wissenschaftliches Interesse [9, 10]. Sie sind vor allem in ihrer Eigenschaft als Radikalfänger (antioxidative Wirkung) für die menschliche Gesundheit von Bedeutung [3, 9, 10]. Als einfache Alternative zur chemoanalytischen Quantifizierung der Sekundären Pflanzenstoffe kann die antioxidative Kapazität eines Lebensmittels über das so genannte Redoxpotenzial gemessen werden [9]. Die Sekundären Pflanzenstoffe fungieren als Elektronenspender und je elektronenreicher das Nahrungsmittel ist (d.h. je niedriger das Redoxpotenzial), umso mehr Elektronen können an unseren Körper abgegeben werden, wo sie als Radikalfänger wirken [3, 9, 10]. Die Fähigkeit, Elektronen abzugeben ist u.a. abhängig von den Anbaubedingungen, der Reife und der Lagerung [3, 9]. In der vorliegenden Studie wurde mittels des Redoxpotenzials der gesundheitliche Wert der Lulo-Frucht als Radikalfänger in Abhängigkeit vom Reifegrad und der Lagerung ermittelt.

Abb. 1: Vollreife, gerade heruntergefallene und quer aufgeschnittene Lulo-Frucht.

Material und Methoden der Experimente

Lulo-Pflanzen wurden am 15.02.2013 ausgesät und in einem Gewächshaus des Ökologisch-Botanischen Gartens der Universität Bayreuth kultiviert. Vom 17.04 bis 21.05.2014 wurden unbeschädigte Lulo-Früchte (s. Abb. 1) mit einem Durchmesser von 4 bis 5 cm und zu 6 verschiedenen Reifestadien (jeweils 6 bis 8 Früchte) zufällig von 20 Individuen ausgewählt und vermessen (s. Tab. 1, beim Redoxpotenzial zusätzlich zwei 6 Tage gelagerte Früchte).

Tab. 1: Untersuchte Reifestadien der Lulo-Frucht.

	Reifestadien		Bestimmung	Beschreibung
Reifung an der Pflanze	1	gelbgrün	visuell	75% Gelbanteil und 25% Grünanteil
	2	orange	visuell (Farbtafel)	einheitlich orange gefärbt (Farbton 25A)
	3	rotorange	visuell (Farbtafel)	einheitlich rotorange gefärbt (Farbton 28A)
	4	Fruchtfall	visuell	Frucht löste sich selbstständig vom Blütenkelch und wurde noch am selben Tag gemessen
Lagerung (21°C, 54%)	5	2 Tage	zeitliche Skala	abgefallene Frucht wurde 2 Tage gelagert
	6	4 Tage	zeitliche Skala	abgefallene Frucht wurde 4 Tage gelagert

Das Redoxpotenzial wurde am apikalen Pol der ganzen enthaarten Frucht mit einer Platin-Einstich-Elektrode gemessen (SI-Analytics, Mainz, s. Abb. 2). Der jeweilige Messwert wurde nach 20 min, wenn das Fließgleichgewicht für eine reproduzierbare Messung erreicht war (Vorversuch), genommen. Das Redoxpotenzial wurde als E_H-Wert angegeben und ist das auf die Normalwasserstoffelektrode bezogene gemessene Potenzial. Anschließend wurde das Fruchtfleisch inkl. der Samen der zuvor beprobten Früchte homogenisiert, zentrifugiert und im Überstand Leitfähigkeit, Säuregehalt und pH-Wert mittels eines Titrators (Mettler Toledo, Gießen) sowie Zuckergehalt mit einem digitalen Refraktometer (Mettler Toledo, Gießen) gemessen. Das Zucker/Säure-Verhältnis [11] und die elektrische Leistungsgröße P (P-Wert als integrierte Praxis-Qualitätsgröße aus pH, Leitfähigkeit, Redox) [3] wurden berechnet.

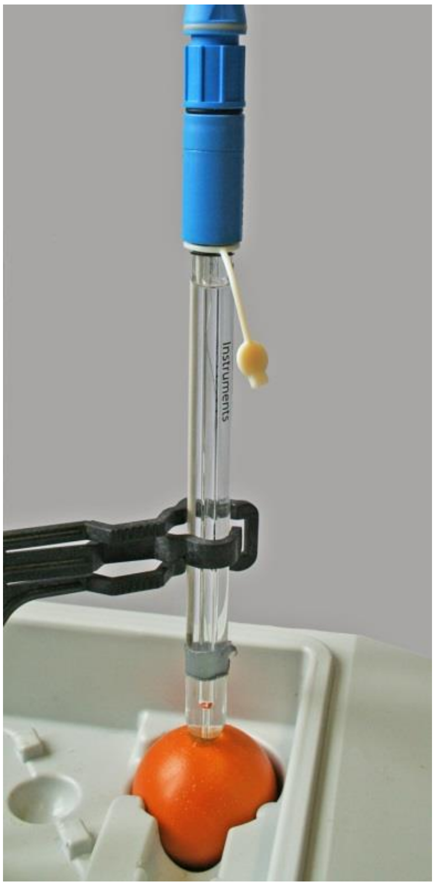

Abb. 2: Messung des Redoxpotenzials der Lulo-Frucht.

Zur Feststellung des Einflusses (Signifikanzniveau < 0,05) der Fruchtreife und Lagerung auf die Messparameter wurde ein lineares gemischtes Modell [12] mit anschließendem post-hoc-Test mittels „glht"-Funktion [13] berechnet. Für das Redoxpotenzial und Zucker/Säure-Verhältnis wurde anhand der jeweiligen Einzelwerte eine Trendkurve über alle Reifestadien mit Sigmaplot (Version 10.0, Systat Software Inc.) gefittet. Der statistische Zusammenhang zwischen dem Redoxwert und dem Zucker/Säure-Verhältnis wurde mit einer Pearson-Korrelation berechnet. Für die statistische Auswertung wurde das Statistikprogramm R (Version 3.1.1, R Development Core Team), sowie R Studio (R Studio, Inc.) verwendet.

Elektrochemische Ergebnisse und Zucker/Säure-Verhältnis

Das Redoxpotenzial lag bei den untersuchten Lulo-Früchten zwischen 271 und 333 mV und war höchst signifikant von Reife und Lagerung abhängig (s. Tab. 2, s. Abb. 3). Mit der Reife, von gelbgrünen Früchten bis zum natürlichen Fruchtfall, nahm das Redoxpotenzial kontinuierlich ab, war bei den 2 Tage gelagerten Früchten am niedrigsten und stieg mit dem 4. Lagerungstag wieder leicht an (s. Abb. 3). Werden die zwei Lulo-Früchte, die nach 6-tagiger Lagerung gemessen wurden, in diesem Verlauf berücksichtigt, wird der Trend der Zunahme des Redoxpotenzials mit der Lagerungsdauer noch deutlicher (s. Abb. 3). Statistische Unterschiede (ohne 6-tagig gelagerte Früchte) konnten zwischen dem rotorangen Stadium und der 4-tagigen Lagerung jedoch nicht festgestellt werden (s. Tab. 2). Das Zucker/Säure-Verhältnis korrelierte negativ mit dem Redoxpotenzial (Signifikanz-wert = 0,017, cor = -0,38) und stieg an, wenn das Redoxpotenzial sank (s. Abb. 3). Für den P-Wert zeigte sich ein ähnlicher Trend wie beim Redoxpotenzial (s. Tab. 2). Die Leitfähigkeit und der pH-Wert waren nicht signifikant vom Reifegrad abhängig (s. Tab. 2). Die niedrigsten Redox-Werte in Lulo-Früchten lagen zwischen 239 und 289 mV. Ihre antioxidative Wirkung ist damit ähnlich wie bei Saft von Tomaten (232–252 mV), Orangen (285–349 mV), Möhren (266–323 mV) oder Birnen (195–331 mV) (9, allerdings unterschiedliche Probenform und Messperiode). Auch in anderen Studien wurde eine hohe antioxidative Wirkung der Lulo-Frucht (z.B. höher als bei Bananen, Kiwis, Nektarinen, Ananas und ähnlich hoch wie bei Grapefruit, Orange, Pfirsich, Birne) über die Messung des H-ORAC bzw. ORAC-Wertes nachgewiesen (5, 8 und darin zitierte Literatur). Zusammen mit den hervorragenden geschmacklichen Eigenschaften ist der Lulo damit ein hohes Potenzial auf dem europäischen Markt zuzutrauen, sowohl als Frischobst als auch für mögliche Zubereitungen, z.B. als Getränk [vgl. 5, 6]. Zudem wäre eine Nutzung von Lulo-Früchten oder deren Verarbeitungsrückstände als natürliche Quelle für Antioxidantien in der Nahrungsmittel- und Kosmetikindustrie oder in der Pharmazie denkbar [14].

Tab. 2: Mittelwerte (± Standardabweichung) der elektrochemischen Messwerte in Abhängigkeit von den Reifestadien. Unterschiedliche Kleinbuchstaben innerhalb einer Spalte geben signifikante Unterschiede zwischen den Reifestadien an.

Reifestadien	pH	Leitfähigkeit (mS/cm)	Widerstand ρ (Ω)	Redox E_H (mV)		P-Wert (µW)	
gelbgrün	3.15 (±0.29)	8.3 (±0.8)	121.1 (±10.9)	333.3 (±35.0)	a	930.5 (±209.9)	a
orange	3.21 (±0.15)	8.6 (±0.8)	117.5 (±11.3)	313.8 (±8.7)	ab	843.7 (±79.2)	ab
rotorange	3.20 (±0.32)	8.1 (±0.6)	124.0 (±8.9)	297.5 (±14.5)	bc	717.8 (±79.2)	bc
Fruchtfall	3.37 (±0.69)	7.8 (±0.7)	129.8 (±11.4)	295.9 (±28.0)	bc	688.7 (±181.6)	cd
2 Tage Lagerung	3.19 (±0.10)	7.6 (±0.7)	132.7 (±11.8)	271.2 (±19.3)	c	558.5 (±77.0)	d
4 Tage Lagerung	3.18 (±0.13)	7.8 (±0.3)	128.4 (±4.6)	283.7 (±15.8)	bc	643.2 (±66.5)	cd
Signifikanzwert	*0.96*	*0.086*	*0.086*	*0.0003*		*0.0001*	

Höchster gesundheitlicher Wert zur Vollreife

Die Ergebnisse deuten darauf hin, dass die Lulo erst ab dem Zeitpunkt des Fruchtfalles die so genannte Genussreife mit dem höchsten Gesundheitswert (d.h. höchste antioxidative Kapazität) erreicht [vgl. 3, 9]. Dies wurde auch durch das ansteigende Zucker/Säure-Verhältnis, welches im Obstbau häufig als Reifeindex herangezogen wird, bestätigt [11, 15]. Damit zeigte sich in dieser Studie, wie auch in der an Äpfeln [3], dass niedrige Redox-Werte mit der Genussreife korrelieren und damit als Reifeindikator herangezogen werden können. Tendenziell (aber nicht signifikant) stieg das antioxidative Potenzial während einer 2-tagigen Lagerung sogar weiter an. Eine längere Lagerungsdauer lässt allerdings einen voranschreitenden Abbau der Sekundären Pflanzenstoffe und damit sinkenden Gesundheitswert vermuten, was sich bereits nach 4 und insbesondere nach 6 Tagen Lagerung durch ansteigende Redox-Werte andeutete [vgl. 3, 9]. In der Tat ist bekannt, dass reife Lulo-Früchte nicht lange lagerfähig sind und daher angestrebt werden sollte, die Ernte bzw. die Lagerungsbedingungen für diese Frucht zu optimieren [6, 7]. Eine weitere Möglichkeit wäre es, die vollreifen Früchte sofort nach der Ernte zu verarbeiten. Neue schonende Aufbereitungs- und Konservierungsmaßnahmen (z.B. Frostung, Trocknung) könnten dabei helfen, einen optimalen Gesundheitswert zu garantieren.

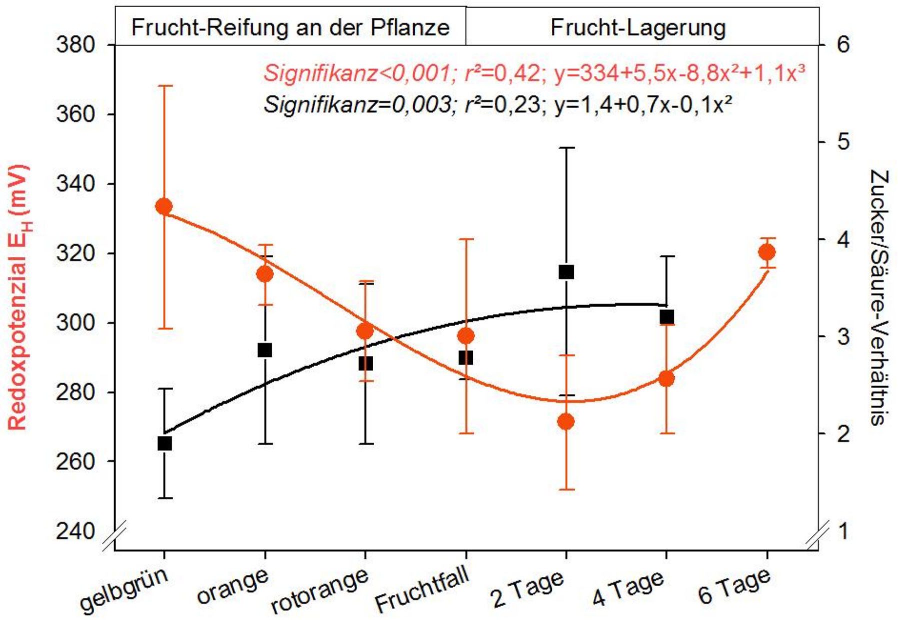

Abb. 3: Mittleres Redoxpotenzial (rote Kreise ± Standardabweichung) und mittleres Zucker/Säure-Verhältnis (schwarze Quadrate ± Standardabweichung) von Lulo-Früchten für die jeweiligen Reifestadien. Der Berechnung der Trendlinien lagen jeweils die Einzelwerte von Redoxpotenzial (rote Linie, inkl. Werte von zwei 6 Tage gelagerten Früchten) sowie des Zucker/Säure-Verhältnisses (schwarze Linie) zugrunde.

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LP- Info zur Lulo Frucht

Lulo, Naranjilla (*Solanum quitoense,* Solanaceae)

- Heimat: Bergregionen Ecuadors und Kolumbiens [4]
- Früchte essbar, tomatengroß mit rotoranger Schale und grünem saftigen Fruchtfleisch, welches geschmacklich an Kiwi, Erdbeere und Stachelbeere erinnert
- Frischverzehr (Fruchtfleisch inkl. der Samen wird ausgelöffelt) und Herstellung von Saft, Desserts und Soßen [7]
- Früchte sind reich an Vitamin C und Beta-Carotin [5, 8]

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6.3 Manuscript III:

Solanum quitoense, a new greenhouse crop for Central Europe: Flowering and fruiting respond to photoperiod

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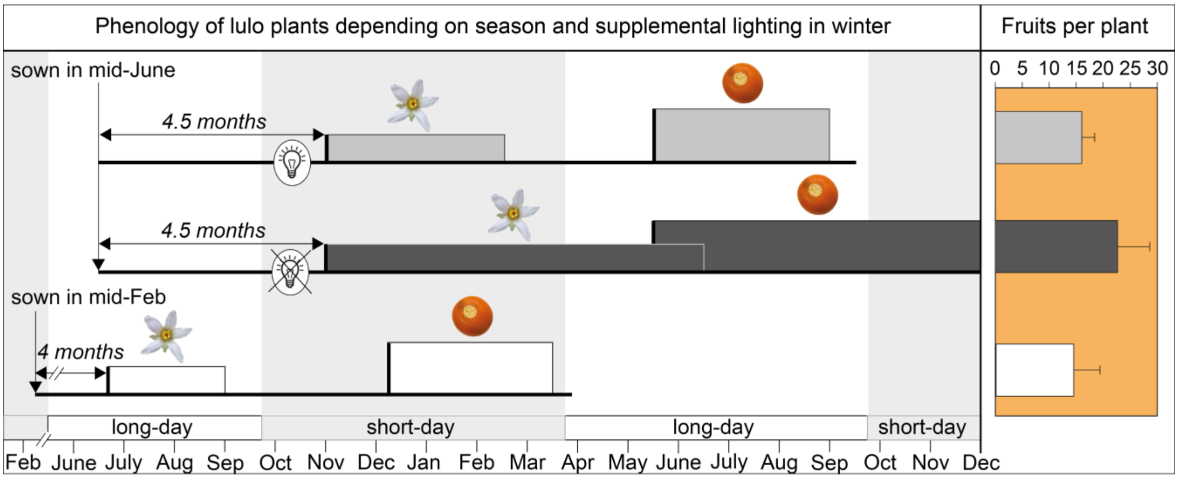
Highlights

- Lulo flowered and fructified throughout the year at long-days and at short-days.
- Long-days accelerated harvest and increased fruit number but not yield.
- Artificial lighting in winter does not enhance yield compared to ambient light.
- Without lighting in winter harvest duration was longer and yield even higher.
- Sowing only twice a year ensures a year-round lulo fruit supply.

Abstract

The lulo (*Solanum quitoense* Lam.), an underutilized fruit crop originally from the Andes, is still widely unknown in Europe. Because of its delicious taste and high nutrition values it has high potential as greenhouse crop in Central Europe. But production of tropical crops in temperate regions might be limited by seasonal fluctuations in day length. Thus we studied lulo's reproductive development and yield in regard to seasonal photoperiod and supplemental lighting in winter. Therefore, we sow lulo seeds twice a year on 15 February and 20 June 2012 and grew them under natural light conditions so that bloom started in summer (natural long-day) and winter (natural short-day), respectively. Further lulos sown in June were exposed to an artificial long-day photoperiod as of 26 October 2012 (16 h day, ~150 μmol m^{-2} s^{-1} photosynthetic active radiation). We confirmed that in lulo flower initiation and fruit set occurs throughout the year and timing is not significantly different between plants grown under long-day (natural, artificial) and those grown under short-day conditions. However, flower development is affected by photoperiod as first time from bud to fruit set and therefore harvest begin was accelerated at long-days. Second, portion of hermaphroditic flowers increased in andromonoecious lulo in natural, not artificial long-days probably due to higher light intensity. Summer blooming plants bore more fruits (15 fruits per plant) than winter blooming ones (10 fruits). Supplemental lighting in winter only increased fruit number to a comparable amount as in summer but not yield. Surprisingly, blooming and fruiting period was conspicuously longer when flowering started under natural conditions in winter and therefore lasted until spring. So regarding this whole blooming period total yield was even higher when plants were grown during winter without supplemental lighting. In conclusion, reproduction of lulo plants is not restricted to a certain seasonal day length indicating that this crop is suitable for year-round fruit production under greenhouse conditions in Central Europe.

Graphical abstract



Abbreviations

LD, long-day; SD, short-day; Wi, winter; Su, summer; Sp, spring; HF, hermaphroditic flower; MF, functional male flower; PAR, photosynthetic active radiation

Keywords

Lulo; Underutilized crop; Nightshade; Day length; Supplemental lighting; Yield

Introduction

Consumer's demand for varieties in diet, nutritive and healthy compounds is rising, and people are increasingly interested in novel tastes and flavours from different countries and regions of the world (Aitken and McCaffrey, 2012, Babb, 1990, Bartels et al., 2008 and Briz et al., 2008). In fact, there are several underutilized edible crops in the subtropics and tropics which are still unknown in Central Europe but commercially cultivated and marketed in their countries of origin (Prohens et al., 2003). Especially the nightshades, particularly potato (*Solanum tuberosum*), tomato (*Solanum lycopersicum*), sweet and hot pepper (*Capsicum annuum*), are of high economic relevance, and 33 million hectares of nightshade crops were cultivated worldwide in 2007 (Samuels, 2009). However there are many more crops within this family with a high potential for the European market (e.g. Brücher, 1977, Daunay et al., 1995, Heiser and Anderson, 1999, Samuels, 2013 and Samuels, 2009).

One of these novel nightshade crops is lulo or naranjilla (*Solanum quitoense* Lam.), originated in the Andean of Ecuador and Colombia where it is a very popular fruit (ACTI et al., 1989, Brücher, 1977 and Dennis et al., 1985). The annual to herbaceous plant produces tomato-sized, orange fruits (ACTI et al., 1989, Heiser and Anderson, 1999 and Morton, 1987) resembling in taste a mixture of strawberry, pineapple and banana (Daunay et al., 1995). They are eaten fresh or used for ice creams, sauces and most frequently for a delicious drink which is much valued in Andean countries (e.g. ACTI et al., 1989, Brücher, 1977, Heiser, 1985, Heiser and Anderson, 1999 and Morton, 1987). Despite its popularity, products of lulo are still not or hardly available in Germany because little effort in commercial development (e.g. increase productivity or develop processing methods for export) had been done in the past (ACTI et al., 1989, Dennis et al., 1985 and Heiser and Anderson, 1999). In addition, the fruits have to be harvested nearly ripe for their typical aroma (cp. 75% maturation for *Solanum vestissimum*: Suárez and Duque, 1992) and moreover soften and ferment quickly when stored, whereas canned juice loses much of its taste (Dennis et al., 1985, Heiser and Anderson, 1999 and Morton, 1987).

The lulo with its exotic taste and high nutrition values appears to be a potential species for global markets (e.g. ACTI et al., 1989, Gancel et al., 2008 and Mertz et al., 2009). Indeed, cultivation spread out in South and Central America, in Africa (Brücher, 1977, Dennis et al., 1985 and Morton, 1987) and first experiences were also conducted in Europe, e.g. Spain (Prohens et al., 2004) and United Kingdom (Samuels, 2013). In Central Europe, cultivation of lulo is limited mainly because of climatic terms (Dennis et al., 1985, Daunay et al., 1995 and Prohens et al., 2004). The crop requires a mean temperature of 14–22 °C and is susceptible to frost, temperatures above 29.4 °C and full sun (ACTI et al., 1989, Daunay et al., 1995, Morton, 1987 and Villachica, 1996). Furthermore, fruits are slow to develop, and period from germination to harvest takes up to 10 months in Germany and 12 months in United Kingdom (Samuels, 2013). Thus growing season in Central Europe is too short to grow lulo in open fields, making cultivation only possible under greenhouse conditions.

Due to technical, energy and labour costs (Portas and Monteiro, 1995) greenhouse cultivation is very expensive. Nevertheless, regarding the cultivation of other nightshades, e.g. tomato and sweet pepper, greenhouses are common in Europe (Portas and Monteiro, 1995). In addition, new technologies, novel systems (Portas and Monteiro, 1995) and sustainable uses of energy, e.g. using industrial waste heat to warm up a greenhouse for tropical crop production like it is demonstrated within the EU-project "Klein-Eden" ("Little-Eden", running since 2011, Germany), could make such a practice more profitable and environmentally acceptable.

In temperate regions, seasonal fluctuations in day length (Jackson, 2009) may also limit cultivation of tropical crops throughout the year. It is known, e.g. that flower development in passion fruit (*Passiflora edulis*) requires a long photoperiod (Nave et al., 2010) and long-days promote amount of flowers in potato (Turner and Ewing, 1988). For pepino (*Solanum muricatum*) a delayed development of flower clusters and a lower fruit set is recorded under short-day conditions (Kowalczyk and Kobryń, 2003) but for physalis (*Physalis peruviana*), another fruit originating at the Andean region (ACTI et al., 1989), anthesis was accelerated under short-day conditions (Heinze and Midasch, 1991).

In case of lulo's flowering and fruiting respond to photoperiod, there is a lack of advanced knowledge (see also ACTI et al., 1989 and Dennis et al., 1985). It is supposed that lulo requires a short-day (Soria from ACTI et al., 1989), indeed flowering and fruit set occurred also under long photoperiod in United Kingdom (Samuels, 2013). To gain insights of lulo's development under greenhouse conditions in Central Europe and to evaluate the opportunity for cultivation, we investigated phenology, flower and fruit production of lulo according to seasonal fluctuations in day length and supplemental lighting in winter. We hypothesize that (1) changes in day length through seasons and artificial lighting affect flower and fruit phenology, (2) seasonal changes in photoperiod impact yield and (3) supplemental lighting during winter season enhances fruit production.

Materials and methods

Plant material and growth design

Seed material was obtained from plants cultivated since 2007 at the Ecological-Botanical Garden of the University of Bayreuth (EBG), Germany, and primarily derived from Costa Rica (Santa Maria de Dola, 1700 m a.s.l.). In Costa Rica, *S. quitoense* was introduced as an important crop in the middle of the twentieth century (Heiser and Anderson, 1999) and widely cultivated for fruit production (Gargiullo, 2008). On 15 February 2012 seeds were gained, cleaned and stored at 3 °C until sowing.

Experiments were conducted in greenhouses at the EBG. To study the reproductive development of *S. quitoense* under long-day (LD) conditions in summer (Su) and short-day (SD) conditions in winter (Wi), lulo seeds were sown on 15 February 2012 and on 20 June 2012, respectively, and in each case 12 plants were grown under natural light conditions (Fig. 1A). Further 11 lulo plants sown on 20 June 2012 were exposed to an artificial long-day (LD*) photoperiod in winter by supplemental lighting from 26 October 2012 until the end of harvest (end of the experiments) in a separate greenhouse (16 h day, ~150 µmol m^{-2} s^{-1} photosynthetic active radiation on 1 m height). Assimilation lamps (Poot-Leuchten PL 90 N 400, Poot Lichtenergie B.V., Schipluiden, Netherlands) were installed 2 m above ground floor. All plants were cultivated at a day/night temperature regime of 24 °C (±3.5)/20 °C (±1.5) in plastic pots (up to 10 L at a plant's age of about 9 weeks). Despite shading and ventilation temperature increased above 30 °C on several days during summer months (June: up to 18 d, July: up to 25 d, August: up to 10 d). The commercial potting mixture contained white peat (39%), black peat (11%), coconut fibre (20%), lava (15%) and bark compost (15%) and for nutritional supply 25 g fertilizer/10 L was added (20-10-15+6, N-P-K+MgO, PlantoSan, Germany). During whole growth the plants were regularly manured with liquid fertilizer following guidelines of 'Hoagland's Nutrient Solution' (Hoagland and Arnon, 1950) so that obviously no nutrient limitation occurred. To provide similar growth conditions for all individuals, the plants of each treatment were rotated weekly and all flowers were cross-pollinated by hand.

Reproductive biology: phenology, flower number, fruit set and yield

Dates of bloom and harvest were recorded. Individuals were checked daily for bloom initiation defined as the petals of the first flower of a plant were fully opened. During bloom flowers were counted every 7 d and bloom duration was calculated as the number of days between first and last open flower (cp. Haggerty and Galloway, 2011). Lulo flower is strongly andromonoecious (Miller and Diggle, 2003) carrying hermaphroditic flowers (HF) with a long style and fruit set after successful pollination and functional male flowers (MF) with a short style and without setting fruits (Almanza Fandiño, 2007; Fig. 1B and C). Both flower types were documented separately and HF:MF-ratio was calculated. Furthermore, the time span from bud to fully ripe fruits was documented by tagging closed HFs randomly distributed over all individuals of each treatment (21 flowers of lulos developed in summer and 30 of each winter-treatment). Flowers were checked daily and the duration of four stages was documented: (1) opening flower, when petals are already visible in the bud, (2) open flower, when all petals are fully unfolded (1 and 2 cp. Almanza Fandiño, 2007), (3) fruit set, when diameter of ovary reached 1.5 cm and (4) duration of fruit maturation (fruit growing and colouring) from fruit set until harvest. A fruit was regarded as ripe when the skin was completely coloured orange with a shade of 28 A and B referred to RHS colour chart (The Royal Horticultural Society, Woking, United Kingdom), the calyx naturally separated from the fruit (Morton, 1987) and the fruit became soft (fruit firmness $<578{,}592.35\ m^{-1}\ kg\ s^{-2}$). The following fruit parameters were recorded per plant: (1) harvest begin, determined when the first fruit ripened, (2) harvest duration as the period from first until last ripe fruit, (3) fruit number and (4) percentage of fruit set of total HFs. Fruits (Fig. 1D) were cleaned from spiny hairs and weight, height and diameter was measured. Yield was specified as total fruit fresh weight per plant. Fruit volume (V_{fruit}) was, due to their flattened form, calculated by following equation: $V_{fruit} = 4/3\pi a^2 b$ (a = diameter/2, b = height/2).

Data analysis

The effect ($P < 0.05$) of photoperiod on reproductive phenology parameters including time until bloom initiation, bloom duration, harvest begin, harvest duration and stages of single flower development (bud, flower, fruit set) was tested with Kruskal–Wallis Test. Differences between the light treatments were analysed using post hoc Mann–Whitney *U*-Test with sequential Bonferroni (Holm, 1979). Duration of fruit maturation and total length from bud to fruit set of single flower were compared by analysis of variance (ANOVA) with a post hoc Tukey HSD-Test (R-package 'multcomp' version 1.2-3, Hothorn et al., 2008).

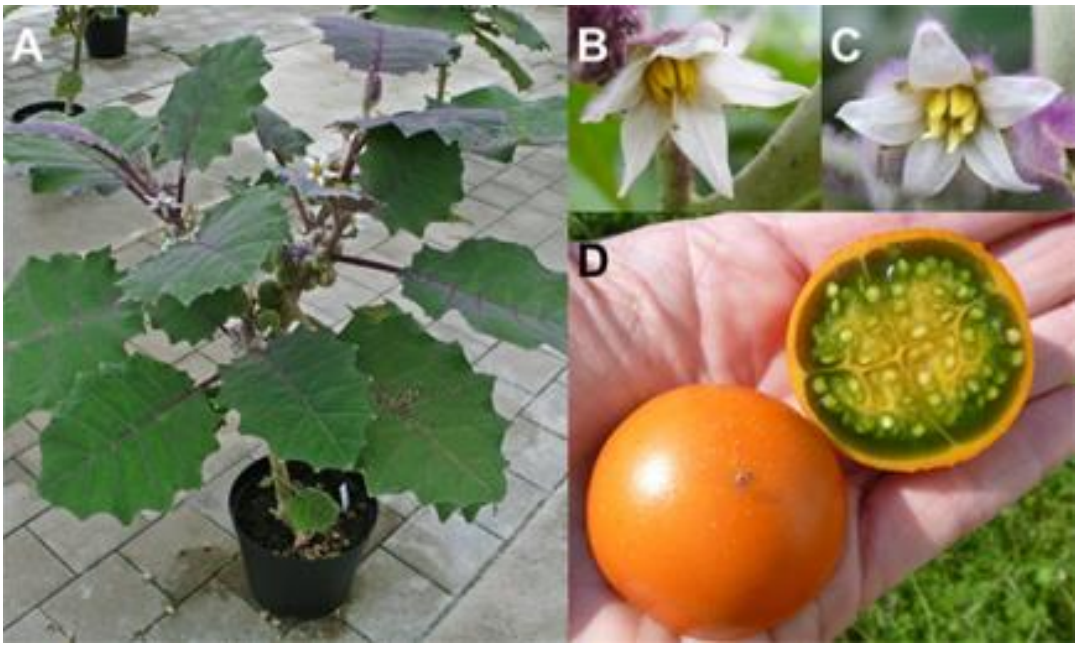


Fig. 1. *Solanum quitoense*: adult plant grown in a 10 L pot (A), hermaphroditic flower (HF) with a long style (B), functional male flower (MF) with a short style (C), and ripe fruits cut into halves (D).

To assess the influence of the different light conditions on flower number and yield we combined all blooming seasons to one analysis by using a linear mixed effect model (R'package 'nlme' version 3.1-96; Pinheiro et al., 2009). For lulos grown in winter, the first (natural SDs in winter) and second blooming period (natural LDs in spring) as well as the sum of both periods were regarded as discrete treatments. Individual was defined as random factor. In addition, we did a post hoc comparison for general linear hypotheses (Tukey, R package 'multcomp' version 1.2-3, Hothorn et al., 2008) to test the significant differences between the light treatments. In case of percentage (portion of HFs and rate of fruit set) and ratio between HFs and MFs we applied a generalized linear mixed model (R'package 'MASS' version 7.3-3, Venables and Ripley, 2002) with a binomial family error and a gamma family error, respectively. Again, we did a post hoc comparison for general linear hypotheses (Tukey, R package 'multcomp' version 1.2-3, Hothorn et al., 2008).

All statistical analyses were performed with R version 2.10.0 (R Development Core Team, 2009). Illustrations were provided with ADOBE Illustrator CS5 version 15.1.0 (Adobe Systems Incorporated, 1987–2011) and graphs with R and Sigma Plot version 10.0 (Systat Software, Inc., 2006).

Results

Flower and fruit biology

Lulo flowered and fructified year-round at long-days in summer (LD) as well as at short-days in winter (SD). But reproductive development depended on sowing season and light regime during growth (Fig. 2). Plants sown in February flowered after 4 months in summer (LD) and fruits were ripe in winter, 9.5 months after sowing so that whole life span of these plants was about 13 months (treatment LD_{Su}). Plants sown in June flowered in winter after 4.5 months, both at artificial long-day (treatment LD^*_{Wi}) and natural light conditions (treatment $SD_{Wi}\rightarrow LD_{Sp}$). In this latter case the plants developed two blooming periods (Fig. 2) where the first fell into natural short-days in winter (SD_{Wi}) and the second one arose in natural long-days during spring (LD_{Sp}, Fig. 2). Fruiting period of both June-sown-treatments started spring to summer, 11 months after sowing so that plant life span was 15 months (LD^*_{Wi}) and 18 months ($SD_{Wi}\rightarrow LD_{Sp}$), respectively (Fig. 2).

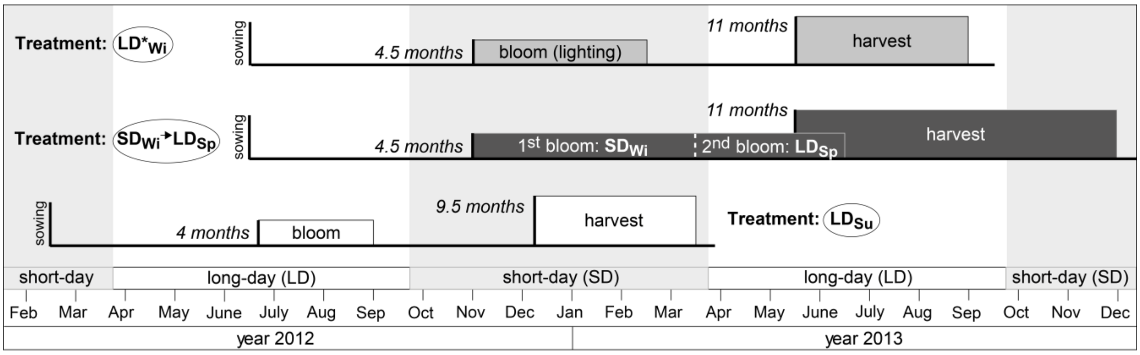


Fig. 2. Sequence of developmental stages of *Solanum quitoense* for the three treatments depending on the light conditions. Seeds were sown in February 2012 so that bloom occurred in summer (Su) at long-days (treatment: LD_{Su}) and June 2012 with winter bloom. Plants sown in June were grown in winter (Wi) with supplemental light, inducing artificial long-day conditions (treatment: LD^*_{Wi}) and under natural light conditions (treatment: $SD_{Wi}\rightarrow LD_{Sp}$). In this latter case the plants developed two flower periods (see also Fig. 4) where the first fell into natural short-day (SD_{Wi}) from November 2012 to mid-March 2013 and the second one arose in a natural long-day (LD_{Sp}, marked with a slashed line) during spring (Sp) from mid-March 2013 to June 2013.

Photoperiod had a slight impact on bloom begin ($\chi^2 = 7.2$, df = 2, $P = 0.03$*). However, the difference was not significant between plants grown under long-day conditions (LD_{Su}: 137 d, LD^*_{Wi}: 147 d) and under short-day conditions in winter (SD_{Wi}: 150 d, Fig. 3A). But obviously bloom initiation was more uniformly synchronized in long-days (Median Deviation: 2 d/16.5 d/0 d, respectively for LD_{Su}/SD_{Wi}/LD^*_{Wi}, Fig. 3A). But then bloom duration depended highly on the treatment ($\chi^2 = 29.6$, df = 2, $P < 0.001$***) and was 230 d and therefore considerably longer under natural conditions during winter and spring ($SD_{Wi} \rightarrow LD_{Sp}$) compared to both long-day-treatments (LD_{Su}: 59 d and LD^*_{Wi}: 99 d, Fig. 3B). As well, developmental time of hermaphroditic flowers (HF) from bud to fruit set was significantly influenced by photoperiod ($F = 68.6$, df = 2, $P < 0.001$***) and was shortest under long-days in summer (LD_{Su}: 21 d) and longest under short-days in winter (SD_{Wi}: 36 d). Supplemental light in winter (LD^*_{Wi}) reduced this period by 5 d though not reaches the level of LD_{Su} (Table 1).

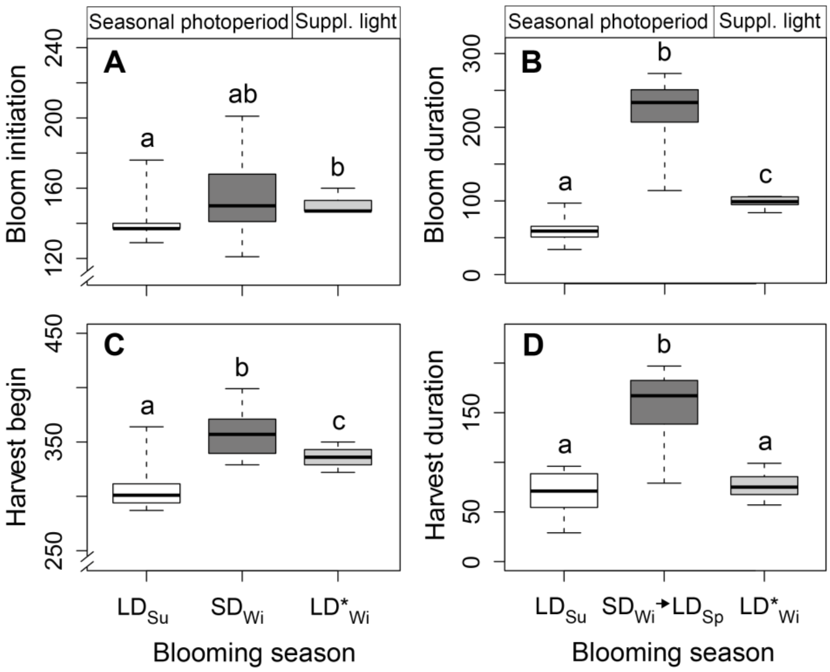


Fig. 3. Flower and fruit phenology parameters for *Solanum quitoense* sown in February 2012 with bloom at natural long-days in summer (LD_{Su}, $n = 12$) and June 2012 flowering from natural short-days in winter (SD_{Wi}, $n = 12$) to natural long-days in spring ($SD_{Wi} \rightarrow LD_{Sp}$, $n = 12$) or at artificial long-day photoperiod (LD*) in winter by supplemental (suppl.) lighting (LD^*_{Wi}, $n = 11$). Phenology parameters include plant's age at bloom initiation (A), bloom duration (B), plant's age at begin of harvest (first ripe fruit, C) and duration of harvest (D). All values are given in days and boxplots with whiskers extending to the data extremes. Lowercase letters indicate significant differences ($P < 0.05$, Mann–Whitney *U*-Test with sequential Bonferroni).

Time for fruit maturation was independent of photoperiod ($F = 1.4$, df = 2, $P = 0.25$) and was in all treatments about 175 d (Table 1). Nevertheless, total cultivation time until first fruits were ready for harvest was significantly depending on season and light treatment (Fig. 3C). It was shortest when sown in February and grown during summer (300 d after sowing for LD_{Su}) and longest when sown in June and grown through short-days in winter (SD_{Wi}: 350 d). Supplemental lighting in winter (LD^*_{Wi}) accelerated this period by about 14 d (336 d) but nevertheless was 36 d longer than at natural long-days in summer (LD_{Su}, Fig. 3C). According to bloom duration, harvest period was longest for plants flowering from winter to spring under natural light conditions (SD_{Wi}→LD_{Sp}: 167 d) and less than half as long in both other long-day-treatments (LD_{Su}: 71 d and LD^*_{Wi}: 75 d, Fig. 3D).

Table 1. Length of developmental stages (mean ± standard deviation or median values) of single hermaphroditic flowers from bud to ripe fruit of lulos (*Solanum quitoense*) at natural long-days in summer (LD_{Su}), artificial long-days in winter (LD^*_{Wi}) and natural short-days in winter (SD_{Wi}).

Blooming period		n	Duration (days) of developing stages				
Day length	Season		Flower bud	Mature flower	Fruit set	Bud to fruit set	Fruit maturation
LD	Su	21	6 a	4 a	10 a	21 a (± 2)	176 a (± 26)
SD	Wi	32	9 b	6 b	19 b	36 b (± 4)	178 a (± 12)
LD*	Wi	32	8 b	6 b	16 c	31 c (± 5)	171 a (± 9)

Different lowercase letters indicate significant differences within columns ($P < 0.05$, Mann–Whitney *U*-Test with sequential Bonferroni for median values, Tukey HSD for mean values). *n* = number of flowers investigated.

Flower number, fruit set and yield

Regarding the quantitative development of hermaphroditic flowers (HF) within the experimental lifetime of all three treatments, there was an obvious difference between plants grown in a short-day (SD_{Wi}→LD_{Sp}) and those grown in long-days (LD_{Su} and LD^*_{Wi}). While the latter ones had only one blooming period finished between 33 and 36 weeks of plant's age, in short-day grown plants (SD_{Wi}→LD_{Sp}) started a second blooming period on 25 March 2013 (week 41) and lasted to a plant's age of 60 weeks (Fig. 4).

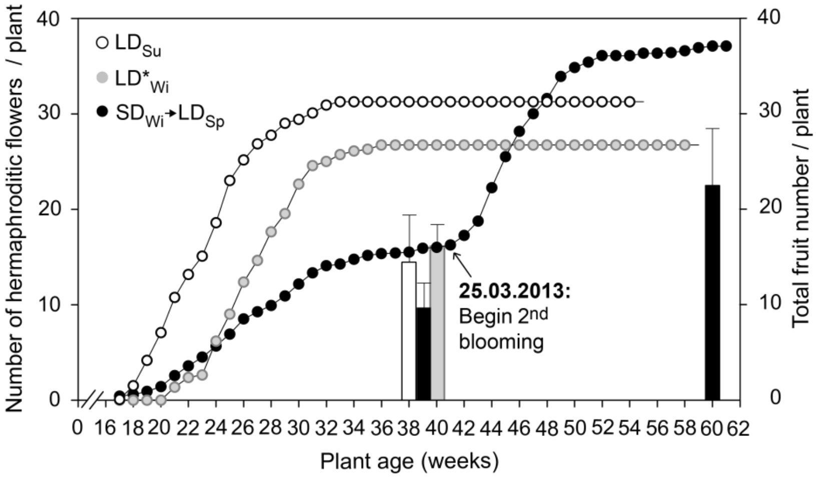


Fig. 4. Quantitative development of hermaphroditic flowers (dots) and fruits (bars) of *Solanum quitoense*. Plants were sown in February 2012 (summer bloom LD_{Su}, *n* = 12) and June 2012 flowering from winter to spring under natural light conditions (SD_{Wi}→LD_{Sp}, *n* = 12) or at artificial long-day photoperiod in winter by supplemental lighting (LD^*_{Wi}, *n* = 11), respectively. Hermaphroditic flowers were counted weekly per individual plant and average flower number of each treatment was summed up for the experimental lifetime. Fruit number (mean + standard deviation) is given for all three treatments after 39 and for the SD_{Wi}→LD_{Sp}-treatment also after 60 weeks of plant's age.

Regarding total number of flowers, lulos grown in winter with supplemental light (LD^*_{Wi}) had after the first flower period 85 flowers significantly more than in both other treatments (Table 2). But as mentioned above, plants grown in winter without supplemental light (SD_{Wi}→LD_{Sp}) initiated a second blooming period which started in spring 2013 and revealing a natural long-day-treatment (LD_{Sp}). In this period 42 additional flowers developed so that in total (sum of both blooming periods) these plants built averagely 100 flowers during their 60 weeks of plant lifetime and reaching a similar value as plants grown in winter with supplemental light (LD^*_{Wi}, Table 2). The portion of HFs was highest when anthesis was at natural long-day conditions (LD_{Su} and LD_{Sp}). In this case half of the flowers were hermaphroditic, whereas in winter blooming plants, independently of supplemental light or not (SD_{Wi}, LD^*_{Wi}), the portion was about 30% (Table 2).

Plants flowered in winter under short-day conditions (SD_{Wi}) built 10 fruits per plant which is significantly less than in those flowered at long-days in summer (LD_{Su}: 15 fruits) and during winter with supplemental light (LD^*_{Wi}: 16 fruits). The rate of fruit set was 48% and therefore lowest in summer blooming plants (LD_{Su}) whereas in all other treatments fruit set was about 60% independently of light conditions or blooming period (Table 2). However, fruits developed from winter blooming plants were significantly bigger than the other ones (Table 2, Fig. 5A). Thus there was no difference in yield between winter (SD_{Wi}) and summer (LD_{Su}) flowering plants, and supplemental light in winter (LD^*_{Wi}) did not enhance yield per plant (Fig. 5B). But regarding the whole plant lifetime, the treatment with two flowering and fruiting periods (SD_{Wi}→LD_{Sp}) had finally the highest amounts of fruits (23 fruits) and highest yield per plant during the 60-week growth period (Table 2, Fig. 5B).

Table 2. Flower and fruit parameters (mean values ± standard deviation) of *Solanum quitoense* sown in February 2012 (summer bloom from June until September 2012: LD_{Su}) and June 2012 with (winter bloom from November 2012 until February 2013: LD^*_{Wi}) and without supplemental lighting (winter–spring bloom: SD_{Wi}→LD_{Sp}). Flower and fruit parameters for plants sown in June and flowering from November 2012 until June 2013 (SD_{Wi}→LD_{Sp}) were given after mid-March 2013 revealing a natural short-day treatment (SD_{Wi}), from mid-March until June 2013 revealing a natural long-day treatment (LD_{Sp}) and as the sum of both blooming periods (SD_{Wi}→LD_{Sp}).

Sowing date	Blooming period			n	Flower					Fruit		
	Day length	Season	Date		Total	Hermaphroditic (HF)		Functional male (MF)	HF : MF ratio	No	Volume (cm³)	Fruit set (%)
					No	No	%	No				
Feb 2012	LD	Su	June – Sep	12	64 a (± 22)	31 ac (± 12)	50 a (± 13)	32 ab (± 15)	1.14 a (± 0.6)	15 a (± 5)	31 a (± 4)	48 a (± 10)
	SD	Wi	Nov – Mar	12	58 a (± 13)	16 b (± 3)	27 b (± 6)	42 a (± 12)	0.41 b (± 0.1)	10 b (± 3)	44 b (± 5)	62 b (± 14)
June 2012	LD	Sp	Mar – June	12	42 b (± 17)	21 b (± 12)	47 a (± 15)	21 b (± 7)	1.01 a (± 0.52)	13 ab (± 6)	30 a (± 11)	61 b (± 16)
	SD→LD	Wi→Sp	Nov – June	12	100 c (± 27)	37 a (± 13)	37 c (± 4)	63 c (± 16)	0.58 b (± 0.1)	23 c (± 6)	37 c (± 4)	63 b (± 8)
June 2012	LD*	Wi	Nov – Feb	11	85 c (± 8)	26 bc (± 3)	31 bc (± 5)	59 c (± 8)	0.45 b (± 0.1)	16 a (± 2)	34 ac (± 3)	62 b (± 12)

Different lowercase letters indicate significant differences within columns ($P < 0.05$, Tukey). *n* = number of plants respectively flowers and fruits investigated.

Fruit supply throughout the year varied regarding the three treatments (Fig. 6). Lulo plants sown in February and flowered during summer (LD_{Su}) had a constant high yield for 4 months (December to March). Lulos sown in June and grown without supplemental light during wintertime (SD_{Wi}→LD_{Sp}) supplied fruits from May to November for 7 months (Fig. 6). Both treatments together would provide a nearly year-round fruit supply (Fig. 6). Plants grown with supplemental light in winter (LD^*_{Wi}) had a fruit supply during 4 months from May to August with a conspicuous maximum in June. This harvest time overlapped with the one of the first fruiting period of plants grown without supplemental light (Fig. 6).

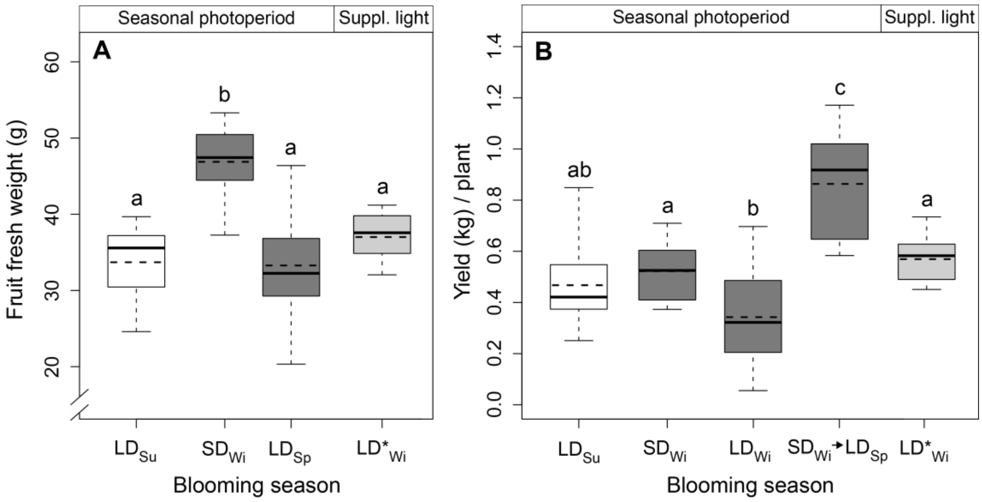


Fig. 5. Boxplots show fruit fresh weight (A) and yield per plant (B) for *Solanum quitoense* sown in February 2012 with bloom at natural long-days in summer (LD_{Su}, $n = 12$) and June 2012 flowering from natural short-days in winter from November 2012 until March 2013 (SD_{Wi}, $n = 12$) to natural long-days in spring since March 2013 (LD_{Sp}, $n = 12$). Values of the June sown treatment were given for both blooming periods separately (SD_{Wi}, LD_{Sp}) and in case of yield also as the sum (SD_{Wi}→LD_{Sp}). Light grey boxplots depict plants exposed to artificial long-day photoperiod in winter by supplemental (suppl.) lighting (LD^*_{Wi}, $n = 11$). Whiskers extend to the data extremes and mean values are illustrated as slashed lines within the boxplots. Lowercase letters indicate significant differences ($P < 0.05$, Tukey).

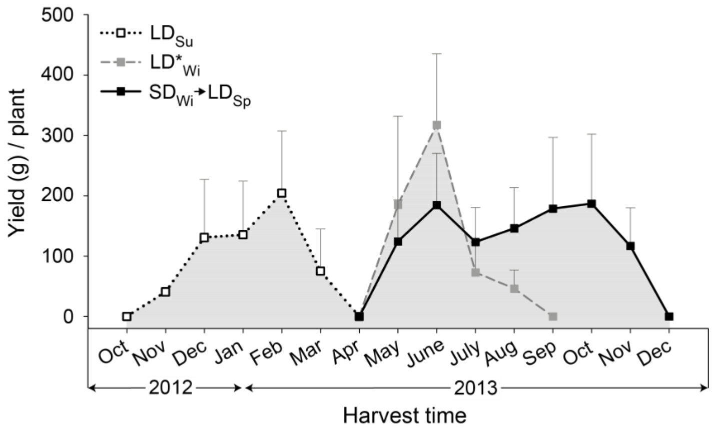


Fig. 6. Time course of fruit supply of *Solanum quitoense* sown in February 2012 with bloom at natural long-days in summer (LD_{Su}, $n = 12$) and June 2012 flowering from winter to spring under natural light conditions (SD_{Wi}→LD_{Sp}, $n = 12$) or at artificial long-day photoperiod in winter by supplemental lighting (LD^*_{Wi}, $n = 11$), respectively. Yield is given as mean fruit fresh weight per plant and month (+standard deviation).

Discussion

Lulos fructify all year long in Central Europe

Annual fluctuations in day length are a reliable environmental cue for many plants, also tropical ones, to produce flowers at a certain season when optimal reproductive conditions are prevailed (Amasino and Michaels, 2010, Borchert et al., 2005 and Jackson, 2009). Already in 1920, Garner and Allard discussed the effect of photoperiod on growth and reproduction in plants and remarked that some plants flower and fructify only at a certain day length. Lulo is thought to require a short-day for fruiting (Soria from ACTI et al., 1989). However, our results revealed that lulo's reproduction is not restricted to a certain season of the year, indeed this tropical crop performed well under seasonal fluctuations in day length.

In general, lulo plants offer a long period of fruit supply to consumers. In our experiments harvest period was 4 (December to March) and 7 months (May to November) when sown in February and June, respectively. So if lulos were sown twice a year, fruits would be available in Central Europe nearly year-round without supplemental lighting which is of commercial interest and a good base to market new crops (see Prohens et al., 2003). This year-round fruit production is in accordance to cultivation experiences in its native countries (ACTI et al., 1989 and Morton, 1987). Furthermore, it should be of great consumer interest when fresh fruits, regionally cultivated and harvested, are available especially during wintertime in Central Europe when other fruits are rare or have to be transported over long distances. It is known that lulo fruits are rich in healthy compounds, e.g. vitamin C and carotenoids (Acosta et al., 2009, Mertz et al., 2009 and Samuels, 2013) supporting health in winter and improving the opportunity for successful marketing (see Bartels et al., 2008 and Prohens et al., 2003).

Long-days promote flower and fruit biology in lulo

In detail however, our results indicated differences in flower and fruit phenology depending on photoperiod. For several plant species it is known that special light conditions promote flowering, e.g. in *Arabidopsis thaliana* (Amasino and Michaels, 2010 and Jackson, 2009) and tomato (Kinet, 1977), or influence flowering period, e.g. in *Cyclamen persicum* (Heo et al., 2003). In case of lulo, two aspects are of considerable interest under long-day conditions (summer, winter with supplemental lighting). First, the time from flower bud to fruit set is shorter at long-days, finally reducing total cultivation time of lulos until harvest. Conspicuously, natural long-days in summer accelerated this period more effective than artificial long-days in winter. Likely, high light intensity in summer increased accumulation of assimilates and assimilate supply for flower production (see Aloni et al., 1996) and thus promote development to fruit set. Second, flowering period and therefore fruiting period are shorter when flowering started at long-days. Consequently, harvest time and lulo fruit supply for the market is more compact.

Lulo is strongly andromonoecious and in general bears about 40% hermaphroditic flowers per inflorescence (Miller and Diggle, 2007 and Miller and Diggle, 2003). But sex expression could be changed by resource availability, like water and nutrient supply, as well as light conditions (Solomon, 1985). Our experiments confirmed that light conditions influence sex expression. Under natural long-day conditions the portion of hermaphroditic flowers was 50% and under short-day conditions only 40%. Miller and Diggle (2003) also found that in lulo, *Solanum candidum*, *Solanum ferox* and *Solanum pseudolulo* percentage of male flowers is higher under shaded conditions (159 compared to 264 μmol m^{-2} s^{-1}). Interestingly, shade increased only the portion of male flowers not total flower number in *Solanum carolinense* (Solomon, 1985). A possible explanation for this issue is that flower development depends on resource supply and high light intensity improve the photosynthetic rate and therefore the carbohydrate supply probably also for fruit production. Thus development of hermaphroditic flowers increased (see Aloni et al., 1996, Marcelis et al., 2004, Miller and Diggle, 2003 and Stephenson, 1981). This would also plausibly explain why plants in our experiments only at natural long-days developed a higher portion of hermaphroditic flowers and not under artificial long-day conditions in winter where only about 150 μmol m^{-2} s^{-1} (PAR) were adjusted.

Surprisingly, fruit set in summer blooming lulo plants (48%) was lower than in all other treatments (about 60%). Usually, fruit set increased with high light intensities as it is reported for pepper plants (Aloni et al., 1996 and Marcelis et al., 2004). But reproductive responses also interact, e.g. with temperature, fertilization, water supply and fruiting status (Dorais, 2003, Jackson, 2009 and Marcelis et al., 2004). For tomato, a decreasing fruit set was reported by Peet et al. (1997) as mean temperatures rises from 25 °C to 29 °C. As well, high temperatures (33 °C) induce the abortion of fruits in sweet pepper (Marcelis et al., 2004). ACTI et al. (1989) stated that also lulo grows poorly at high temperatures above 30 °C and fruit set does not occur at high night temperatures. In our experiments day temperature rose above 30 °C on several days during summer which might cause the lower fruit set. Thus temperature control in summer seems to be important for lulo's greenhouse production.

But nevertheless fruit number per plant was higher in long-days compared to short-days. This is probably due to the higher number of hermaphroditic flowers. But interestingly, these less predetermined fruits in winter were finally bigger probably due to a lower demand for assimilates (surplus) that could support fruit growth (see Marcelis, 1996). So despite lower fruit number, yield of winter blooming plants was as high as of summer blooming plants supporting a year-round production.

Supplemental lighting did not enhance yield for lulo

In temperate regions of the world, the low light availability during winter is often a main limitation for a profitable cultivation (Papadopoulos and Demers, 2002). Modification of photoperiod by supplemental lighting in winter (Marcelis et al., 2002 and Papadopoulos and Demers, 2002) increases yield of many greenhouse crops, e.g. tomato (Dorais, 2003 and Dorais et al., 1991) and sweet pepper (Demers and Gosselin, 1998). This improvement of light conditions promotes photosynthesis and secures a high flowering and thus high fruit number in winter (Dorais, 2003) and it is widely used to ensure a year-round production (Dorais and Gosselin, 2002).

As suggested, flower number increased in lulo plants when exposed to longer photoperiod which is also known for potato (Turner and Ewing, 1988). Lulo plants produced even more flowers in artificial (winter) compared to natural long-days (summer) although light intensity was lower and a reduced flower production in winter was expected (see Aloni et al., 1996). Likely, heat stress in summer increased abscission rate of flowers (Aloni et al., 1991). Fruit number was enhanced through lighting by about 50% compared to short-day conditions in winter and was nearly as high as in summer. As in summer these fruits were smaller than the ones developed in winter without supplemental light. And so against our assumption supplemental lighting in winter did not enhance yield in lulo, and potential technical and energy costs for lighting could be saved.

But it has to be considered that additional lighting in winter might improve fruit quality, e.g. increase sugar content or decrease acidity (Dorais, 2003) and therefore would guarantee a high fruit quality for consumers. And possibly, further variation in day length, light intensity, cultivation conditions or the used cultivars may lead to modified results for lulo in a so called light experiment (see e.g. Aloni et al., 1996, Demers et al., 1998, Dorais, 2003, Dorais et al., 1991, Heo et al., 2003 and Turner and Ewing, 1988).

Total yield was higher when plants bloom during winter without supplemental light

When lulos were sown in early summer and grown without supplemental light in winter first fruits could be harvested in summer the following year. Surprisingly, these lulos flowering at short-days in winter developed a second blooming period in spring (mid-March) of the following year when natural long-days arose. This photoperiod fluctuation from a less favourable short-day (less fruits) to a natural long-day with optimal light conditions for high photosynthesis rate could initiate the second blooming period. Kinet (1977) demonstrated that transferring tomatoes from adverse to favourable conditions at a time of macroscopic appearance of the inflorescences promotes flowering. On the contrary, flowers were aborted when exposing them inversely (Kinet, 1977). This confirms the more favourable status of high light conditions. Fruit production would be advantageous under such conditions related to a higher assimilation supply. A second flowering period could be also promoted by a lower assimilate demand (less competing fruits), so that the plants were able to support subsequent flower and fruit development in contrast to the other treatments (see Marcelis et al., 2004 and Stephenson, 1981). Finally, these plants grown in winter without supplemental lighting had in our experiments at the end highest yield and longest harvest period and could therefore be of special commercial interest. But beyond continuous fruit supply consumers expect a homogenous sensory quality (Briz et al., 2008) which could vary with day length and light availability (see Hewett, 2006 and Slimestad and Verheul, 2005). Thus additional studies on fruit quality are desirable to determine optimal harvest season or to optimize production for the local market.

Conclusion

Flower and fruit production of lulo is not restricted to seasonal photoperiod indicating that this crop is suitable for year-round greenhouse cultivation in Central Europe. Nevertheless, long-days in general (natural and artificial) during bloom accelerated harvest begin, let to an abbreviated harvest period and to more fruits per plant while only natural long-days increased portion of hermaphroditic flowers in lulo. Supplemental lighting in winter increased flower and fruit number but not yield. Actually, when lulos grew at natural light conditions since winter they developed a second blooming period in spring of the following year. Finally, these plants had the longest harvest period as well as the highest yield and thus are of special commercial interest. Moreover, lulo's fruit supply in winter, when fruits of temperate region are rare, may expect high market potential. Further investigations in year-round fruit quality should be performed because beside a continuous fruit supply a homogenous quality is important for successful marketing.

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6.4 Manuscript IV:

Physico-chemical and sensory quality of the lulo fruit is high but varies seasonally under greenhouse conditions

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In preparation

Abstract

The lulo (*Solanum quitoense* Lam.) has high promise as a novel fruit for European market and greenhouse cropping. The guarantee of a high and homogenous fruit quality to consumers is relevant for successful marketing which might be challenging in Europe because of seasonal variation in light conditions. In this study, physico-chemical and sensory characteristics of fresh lulo fruits produced in greenhouses in Germany and sampled in winter, spring and summer, respectively, were investigated. We confirmed that fruit quality in lulo varies with season and is lowest in winter: peel red colour (a*) was 39.8 / 43.9 / 43.9 for winter / spring / summer, respectively, pulp dry matter was 24±5 / 31±2 / 30±2 %, pH was 3.28±0.07 / 3.46±0.06 / 3.55±0.06, total soluble solids amounted to 9.4±0.7 / 14.9±0.8 / 14.0±0.7 °Brix, and titratable acidity was 2.48±0.16 / 1.97±0.14 / 1.76±0.13 g CAE/100 g FW. In compliance, panellists perceived fruits in winter as much softer and less sweet, probably affecting consumer liking. However, the physico-chemical values obtained in winter samples were in the range of that given by recent literature on lulo fruits harvested in Latin America. Fruit aroma of lulos in our study was very intensive throughout the year. These results indicated that greenhouse production in Germany provides high-quality fruits, even under short-day conditions in winters, suggesting promising opportunities for marketing the lulo. In future, studies on determination of thresholds for sensory perception, and development of cultivation and marketing strategies for lulo are recommended to overcome seasonal variations and provide homogenous quality to consumers.

Abbreviations

CAE: citric acid equivalent; DM: dry matter; EBG: Ecological-Botanical Garden of the University of Bayreuth; FW: fresh weight; NMR: nuclear magnetic resonance; PCA: principal component analysis; TA: titratable acidity; TSS: total soluble solids

Keywords

aroma, dry matter, light, naranjilla, novel fruit crop, nuclear magnetic resonance, sensory analysis, Solanaceae, *Solanum quitoense*

Introduction

The interest in new or exotic tropical fruits has been incessant; today the so-called "*minor*" and "*underutilized*" fruits enjoy increasing attention (see e.g. CBI 2015; Galán Saúco 2013; Galluzzi and Noriega 2014; Proctor 1990; Prohens et al. 2003; Sabbe et al. 2013; Samuels 2009; Samuels 2015). Already in the past, e.g. after the discovery of America, mankind exchanged, introduced and grew crops in areas beyond their origin, as was, e.g., the case for tomato and potato (Prohens et al. 2003). A more recent success story was the introduction of the kiwifruit to New Zealand at the beginning of the 20^{th} century (Prohens et al. 2003). There are still further crops with promising prospects which deserve closer scientific attention and dedication in order to become (more) popular in near future (see e.g. CBI 2015; Galán Saúco 2013; Galluzzi and Noriega 2014; Prohens et al. 2003; Sabbe et al. 2013). One of these crops is the lulo (*Solanum quitoense* Lam., Solanaceae) because of the attractive sensory characteristics, particularly the intense fruit aroma, and the good nutritional value of the fruits (Acosta et al. 2009; ACTI et al. 1989; Forero et al. 2016; Gancel et al. 2008; Messinger et al., in prep.).

The lulo is a perennial shrubby species originated from the Andes of South America (ACTI et al. 1989). It provides edible round and bright orange berries (Spanish name "*naranjilla*" means "*little orange*"; Morton 1987), esteemed for their unique tropical flavour and described as "*the golden fruit of the Andes*" and "*the nectar of the gods*" (ACTI et al. 1989). The ripe fruit contains a translucent, juicy, slightly acid green or yellowish pulp that can be eaten fresh or more commonly used for preparing aromatic juice or desserts (ACTI et al. 1989; Heiser 1985; Morton 1987). First cultivation trials in Germany revealed that the lulo is suitable for cultivation and year-round fruit production in greenhouses in Central Europe (Messinger and Lauerer 2015; Messinger et al. 2016).

Several other factors (besides fruit yield) are relevant for success or failure of lulo cultivation and marketing outside its native range (see Galán Saúco 2013; Proctor 1990; Prohens et al. 2003). In this regard a high and homogenous fruit quality related to sensory properties and nutritional value is important and allows for market promotion and repurchases by consumers (Briz et al. 2008; Proctor 1990; Prohens et al. 2003; Sabbe et al. 2013). Seasonal variations in light could influence plant growth and fruit ripening, e.g. carbohydrate assimilation, distribution and accumulation as well as biosynthesis of pigments and bioactive substances like ascorbic acid, β-carotene and phenolic compounds (Hewett 2006; Rosales et al. 2006; Slimestad and Verheul 2005). It is known for some solanaceous crops, that low light conditions and linked low temperatures in European autumn and winter reduced fruit quality, e.g. of tomato (decline in soluble solids) and pepper (fruit colour spots damage), in greenhouse culture (Rylski et al. 1994). Since physico-chemical characteristics inherently control sensory characteristics, variations in fruit quality depending on the season could affect consumer perception, and hence acceptability and repurchase intention (Taub and Singh 1998).

Consequently, a challenge for successful cultivation and sales of the lulo in Europe is the ability to guarantee a high and homogenous fruit quality (Briz et al. 2008; Prohens et al. 2003; Sabbe et al. 2013). It is unsure if quality of lulo fruits produced in greenhouses in Central Europe is similar to those produced in their native tropical range, especially during winter season with low natural light conditions. This study aims at investigating physical, chemical and sensory fruit characteristics of lulo grown during different seasons in Germany, Central Europe. We hypothesized that 1) fruit quality of fresh lulos produced in greenhouses in Germany varies throughout the year, 2) and lulo fruits are of lower quality when ripened during winter season under low natural light conditions. 3) These seasonal differences in physico-chemical properties are sensory perceivable by humans.

Materials and Methods

Plant material and growth conditions

Fruits of *Solanum quitoense* were harvested from plants cultivated in greenhouses at the Ecological-Botanical Garden (EBG) of the University of Bayreuth (Bavaria, Germany). The lulo studied in this work belonged to the variety *septentrionale* (Morton 1987, ACTI et al. 1989) by having spines on leaves, petioles and stem, and a greenish yellow fruit pulp (green value: a* = -4.0, yellow value: b* = 22.7 for L*a*b* colour space). It originates from a plantation in Santa Maria de Dola, Costa Rica (elevation: about 1700 m a.s.l., harvested in 2007) and has been grown for several generations at the EBG. Seeds for this study were collected on 15 February 2012 in the EBG, cleaned and stored at 3 °C until sowing on 15 February 2012 and on 20 June 2012, respectively. In each case 12 individuals were randomly chosen from a larger number of homogeneously vigorous plants and grown under natural light conditions. All plants were cultivated at a day/night temperature regime of 24 °C (±3.5)/20 °C (±1.5) in plastic pots (10 L) and randomly placed within the greenhouse with regular spacing. The commercial potting mixture contained white peat (39%), black peat (11%), coconut fiber (20%), lava gravel (15%) and bark compost (15%), and was enriched with 25 g fertilizer (20-10-15+6, N-P-K+MgO, PlantoSan®, Germany) per 10 L soil. The plants of each treatment were rotated weekly and all flowers were cross-pollinated by hand.

Plants sown in February produced fruits during winter season under natural short-day conditions and were sampled from December 2012 until February 2013 ("winter" harvest). Harvest duration of the second sowing date in June 2012 was from May until late November 2013 under natural long-day conditions. Due to their prolonged fruiting period (167 d), these plants were sampled twice: first from May until June 2013 ("spring" harvest) and second from July until August 2013 ("summer" harvest). Only fully ripe (Morton 1987; Messinger et al. 2015) fruits without damages were used for analysis. Fruits were usually checked daily or within a maximum of three days for ripeness.

Instrumental measurements: physical, chemical and NMR analyses

In total, 16 ripe and intact fruits per winter (07.12.2012–20.02.2013) and spring harvest date (25.05–05.06.2013), respectively, and 14 ripe fruits in summer (25.07.–08.08.2013) were randomly sampled over all individuals. The fresh fruits were removed from spiny hairs with a cloth, weighed in fruit fresh mass with a digital analytical scale, accurate to 0.1 mg (Mettler Toledo PM4600 Delta Range, Gießen, Germany) and measured in height (i.e. length from apical to basal pol) and diameter (i.e. length of equator, widest diameter). The ratio of height to diameter (*height/diameter*) was calculated and used as an indicator for fruit shape (elongation; Smith et al. 1994; van der Knaap & Tanksley 2003). Afterwards peel colour was determined by colour charts (RHS Colour Chart, The Royal Horticultural Society, London). In total three different orange shades (Table 1) of the colour charts (Orange Group "25A", "28B", "28A" of Fan1) were appropriate for lulo peel of which the corresponding L*-value (brightness value), a*-value (green-red-value) and b*-value (yellow-blue-value) was measured with a Chroma meter CR-400/410 (Konica Minolta, Marunouchi, Japan). In case peel colour was between two successive grades and, thus, could not be clearly assigned to the given ones, transitional colour grades were allowed and expressed as means. Table 1 shows the 6 colour grades with the corresponding L*-value, a*-value and b*-value.

Table 1: Defined colour grades employed for determination of *Solanum quitoense* peel colour. Transitional colour grades were expressed as means.

Defined Colour Grade	Colour Chart according to RHS	L*a*b* colour space measured by Chroma Meter L* (brightness)	a* (green-red)	b* (blue-yellow)
1	25A	72.0	35.7	66.0
2	25A-28B	71.2	38.0	64.8
3	28B	70.5	40.3	63.6
4	25A-28A	68.4	39.8	63.1
5	28B-28A	67.7	42.1	61.9
6	28A	64.8	43.9	60.2

For compositional analyses the pulp including the seeds (edible part) of each half per fruit was extracted separately using one half for physico-chemical analyses and the other for nuclear magnetic resonance (NMR) analyses. The extracted pulp mass was frozen by liquid nitrogen cooling, grinded up in a ball mill (Retsch MM400, Haan, Germany) and kept at -24 °C until analyses.

For pH, total soluble solids (TSS) and titratable acidity (TA) measurements, one part of the frozen and grinded pulp of the first fruit half was separated in a Heraeus Pico17 centrifuge (Thermo Scientific, Langenselbold, Germany). The clear supernatant was transferred into an Eppendorf vial. pH-value was determined with a SevenCompact pH-meter (Mettler Toledo, Gießen, Germany). TSS were measured with a portable refractometer (STEP Systems GmbH, Nürnberg, Germany) and indicated in °Brix. TA was measured with a T50 Titrator (Mettler Toledo, Gießen, Germany) and controlled by LabX titration software (Mettler Toledo). 0.1 M NaOH was used as titrant and endpoint of titration was pH 8.3. Values were expressed as grams of citric acid equivalent (predominant acid in lulo pulp, Gancel et al. 2008) of 100 grams fresh weight (FW, calculation see OECD 2005). The ratio of TSS and TA (°Brix / % citric acid) was calculated (OECD 2005). Water content was determined by Karl-Fischer titration. Therefore, the other part of the frozen pulp samples was extracted with water-free Methanol (Roti®Hydroquant D, Carl Roth, Karlsruhe, Germany). The solution was separated (Heraeus Pico17 centrifuge, Thermo Scientific, Langenselbold, Germany) and the clear supernatant was drawn into a syringe for sample injection. Karl-Fischer titration was made with a T50 Titrator and a Karl-Fischer Kit DV704 (Mettler Toledo) and pyridin-free Hydranal Composite 5 (Sigma Aldrich, Taufkirchen, Germany) served as one-component-reagent. Titration was repeated three times and water content was calculated by using formula 1. Water content was expressed as the mean of three titrations; dry matter (DM) content was calculated as the reciprocal relative to water content.

$$\text{Water content} = \frac{(P_{\text{Total}} - P_{\text{MeOH}}) \times V_{\text{MeOH}} \times D_{\text{MeOH}}}{M_{\text{Lulo}}} \qquad \text{(Formula 1)}$$

P_{Total} = Percent water in sample

P_{MeOH} = Percent water in MeOH

V_{MeOH} = Volume of MeOH in sample (= 5 ml)

D_{MeOH} = Density of MeOH (=0.79 g/ml)

M_{Lulo} = Mass lulo in sample (= 0.5 g)

NMR analyses were done with the pulp of the second fruit half. Therefore, the frozen samples thawed at room temperature. The pulp was taken out using a spatula and centrifuged at 1920 g for 15 minutes. Supernatant was centrifuged for 10 more minutes at 17.200 g. 900 µl of the supernatant were transferred to a new reaction vessel. Using a BTpH unit (Bruker Biospin, Rheinstetten) 100 µL of NMR buffer containing potassium phosphate in deuteriumoxide and trimethylsilylpropionate as a chemical shift standard (ALNuMed, Bayreuth) were added to the sample and the pH was adjusted to 3.12 using 1N HCl and 1N NaOH, respectively. 600 µL were transferred to a 5 mm NMR tube. Spectra were measured on a Bruker Ascend™ 400 Avance III equipped with 60-fold BACS-sample changer and 5 mm PABBI 1H/D-BB Z-GRD probe using the following parameters: pulse program: noesygppr1d, time domain: 65536, spectral width (ppm): 20.5524, acquisition time: 3.984 s, relaxation delay: 4 s, receiver gain: 16, number of scans: 16, dummie scans: 4, frequency offset: 1882.10 Hz, temperature: 301.8 K. The excitation pulse was calibrated individually for each measurement using the "pulsecal" routine. FIDs were Fourier transformed using a line broadening of 0.3 Hz. Phase adjustment and baseline correction were calculated automatically by Topspin (Bruker Biospin).

Sensory evaluation

The sensory characteristics of fresh lulo fruits sampled randomly at winter, spring and summer were evaluated by a sensory unskilled panel. Characteristic attributes (Table 2) of lulo fruits for consumers, identified through prior consumer tests in Germany (Messinger et al., in prep.), were chosen for sensory profiling and ordered according to visual, haptic and olfactory-gustatory impressions. Profile tests (for definition see DIN 10950-1; 10950-2; implementation and directives in DIN 10967-1) were conducted by a panel of 10 members (6 females and 4 males, aged 19–51 years, resident in Bayreuth, Germany) to detect potential variations in lulo fruit attributes depending on harvest season. These panellists were staff members of the EBG and students of the University of Bayreuth and chosen by availability over one year and interest in tropical fruits. Within the panel an intensity scale (references for lowest and highest expression) for each attribute was defined. Before evaluation, the participants were made familiar with lulo fruits; during four meetings they have to perceive and rate each attribute on fresh fruits for testing purposes. On 22 and 25 February 2013 ("winter"), from 18 to 28 June 2013 ("spring") and 14 to 30 August 2013 ("summer") each panellist received one entire and intact fruit of the respective sampling date coded with an identification number. In the first step fruit and peel characteristics were assessed; afterwards the fruit was cut into halves and pulp characteristics were evaluated on an intensity scale from "1" (lowest expression) to "5" (highest expression).

Data analysis

Statistics were performed with R (version 3.4.2, R Development Core Team 2017) and Rstudio version 1.1.383 (RStudio Inc. 2009-2017). If not otherwise noted, all used tests and models were available in R package "stats". The influence ($p < 0.05$) of the harvest season on fruit characteristics of entire fruit (diameter, height, shape, fresh weight) and pulp (water content, DM, pH, TSS, TA, TSS/TA) was tested using a mixed-effects model (LME, package "nlme"; version 3.1-105, Pinheiro et al. 2009) with individual as random factor (repeated measurements on same plant). Model assumptions were not met for diameter and height. Models were thus repeated with transformed data but no qualitative differences in results were found. In the following we reported the results of the untransformed data. Peel colour grades indicated by L*a*b*-values between harvest seasons were compared by Kruskal-Wallis Rank Sum Test and pairwise Wilcoxon Rank Sum Test. Because peel colour was not affected by plant individual ($P > 0.05$), we disregarded it as random effect.

NMR spectra were evaluated quantitatively using the Multi Integration tool included in the AMIX software package (Bruker Biospin). Peaks corresponding to glucose, fructose, sucrose and citric acid were assigned by comparison with reference spectra. For glucose, peaks of the anomeric protons of alpha and beta form were integrated from 5.25 to 5.20 ppm and 4.66 to 4.62 ppm, respectively, and the integral values were added. Fructose was quantified from 4.12 to 4.08 ppm, sucrose from 5.47 to 5.33 ppm and citric acid from 2.95 to 2.91 ppm (Fig. 1).

Table 2: *Solanum quitoense* fruit attributes used in sensory profile tests with ten panellists. The sensory attributes were evaluated by an intensity scale from 1 (lowest) to 5 (highest expression).

Sensory attributes			**Sensory perception**
Entire fruit			
	Firmness	(Resistance when pressing the fruit between the fingers)	By hand
	Odour	(Fruit odour)	Sniffing
Peel			
	Colour	(Orange shade)	Visual
Pulp			
	Firmness	(Force required for spooning the pulp out and chewing)	By hand and feeling in mouth
	Odour	(Fruit odour)	Sniffing
	Juiciness	(Amount of moisture, watery juice released when eating)	Feeling in mouth
	Taste	(Fruit aroma)	Tasting
	Sourness	(Acid aroma)	Tasting
	Sweetness	(Sugary aroma)	Tasting

The effect ($P < 0.05$) of the harvest seasons on sensory attributes was tested with a Friedmann-Test, as the assessment was based on an intensity scale. Harvest seasons were defined as groups and panellist as random factor. Differences ($P < 0.05$) between the ripening stages were assessed by using a pairwise Mann-Whitney-U Test with Bonferroni adjustment. The results were graphically presented in a spider's web diagram (cp. DIN 10967-1) using Microsoft Excel 2010 (Microsoft Corporation). To illustrate the sensory profiles for all harvest seasons including all fruit attributes principal component analysis (PCA for sensory analysis: see DIN 10967) was performed using the package "vegan" (R Development Core Team 2012; Oksanen et al. 2013). The principal components that explained highest amount of variation were retained and chosen visually by using a scree plot (Costello and Osborne 2005). Correlations between fruit attributes were calculated but limited to the 10 most highly correlated ones. Illustrations were created with R and SigmaPlot (version 10.0, Systat Software Inc. 2006).

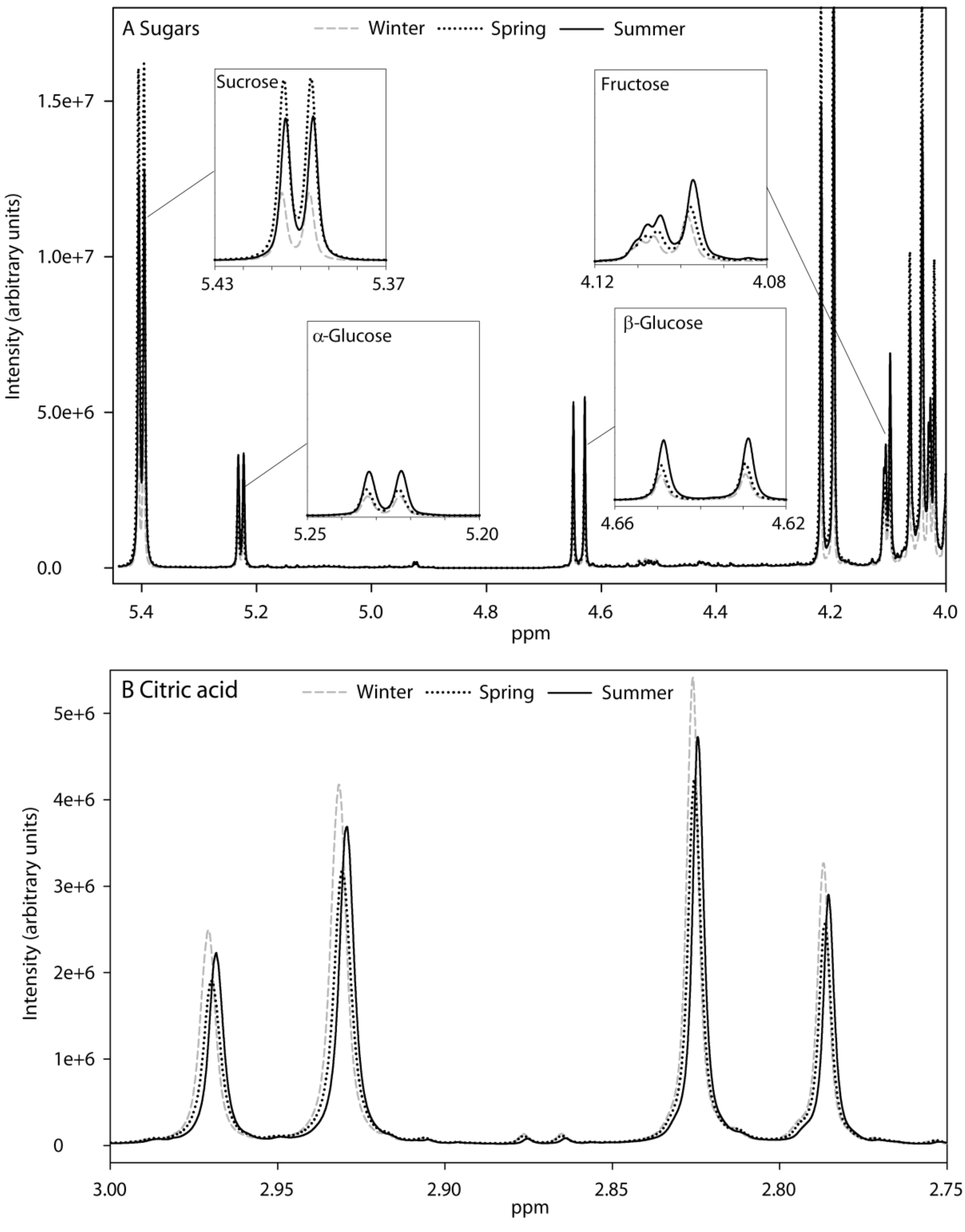

Figure 1: NMR-spectra of lulo fruits harvested during winter (December until February, n = 16), spring (May and June, n = 16) and summer (July and August, n = 13). A: Sugars, B. Citric acid. Spectra (lines) are given as mean per harvest season.

Results and discussion

Characterization of whole lulo fruits

Lulo fruits var. *septentrionale,* investigated in the study presented, were 3.7–4.3 cm in height and 4.3–4.6 cm in diameter (Table 3). Mean diameter was similar throughout the growing seasons ($F = 1.28$, d.f. = 2,22; $P = 0.30$) as also reported for tomato (Slimestad and Verheul 2005) and was in the range of other reports for lulo (e.g. Chiarini and Barboza 2007; Heiser et al. 2005; Vasco et al. 2008). Bigger fruits were recorded for the lulo F_1-hybrids "Palora" (Heiser et al. 2005) and "Puyo" (Gancel et al. 2008), although the large size of "Puyo" is likely reached by spraying the fruits with a dilute solution of 2,4-D (see Heiser et al. 2005). Our fruits fulfilled the criteria of commercial fruit class 2 (diameter: 4–5 cm, NTC 1979). It would be recommendable to test different varieties or different cultivation methods (e.g. removal of competing fruits, Marcelis 1996) to produce fruits with higher fruit diameter that conform to commercial class 1 (diameter > 5 cm, NTC 1979). As also reported by Chiarini and Barboza (2007) and Gancel et al. (2008) the lulo fruit was almost round by being only slightly wider than high (Table 3). Fruits in summer were higher (4.3±0.3 cm) and hence more round than in winter (3.7±0.3 cm) and spring (3.8±0.5 cm). Nevertheless, mean fruit fresh weight was similar throughout the year (39–47 g), probably because of the high variation within harvest seasons ($F = 1.87$; d.f. = 2,22; $P = 0.18$; Table 3) and corresponded to the lower range values of Ecuadorian samples (40–120 g; Vasco et al. 2008).

At the time of purchasing firmness and appearance (colour) are important attributes for consumer's judgment of fruit quality (Kader 1999, Briz et al. 2008). Our sensory results revealed strong variations in firmness between harvest seasons and that fruits in winter are perceived as softer than those in spring and summer, i.e. less force was required by the panellist to press the entire fruit (Figs. 2–3). Low assimilation rates in winter might cause the softness since fewer carbohydrates are so available for the synthesis of cellulose, pectin and other cell wall material or structural substances that contribute to the firmness (see Lieberei and Reisdorff 2012).

Characterization of lulo peel

Peel colour of ripe fruits in our study was orange (b*>0 and a*>0) and shaded more reddish (a* = 40–44) than those of the Puyo hybrid (a* = 16.7, Table 3). Gancel et al. (2008) identified flavonol glycosides in lulo peel, e.g. of quercetin which is a yellow plant pigment common in tree rind, fruit peel, leaves and flowers (Schiele 2001, 2002; see e.g. in onion: Slimestad et al. 2007). But the colouration of fruits from yellow to red is particularly caused by carotenoids, a large group of plant pigments that can accumulate within chromoplasts of fruits and is supposed to serve as coloured attraction for pollinators and seed disperser, act as precursors to a range of scents and as photoprotective compounds (Bartley and Scolnik 1995; Howitt and Pogson 2006; Schiele 2001). In lulo, Acosta et al. (2009) and Gancel et al. (2008) measured a high carotenoid content, especially in fruit peel, and identified β-carotene (*all-trans-*β-carotene) as the main carotenoid. B-carotene exhibits provitamin A activity and antioxidative properties making it an essential and valuable component of human's diet (Bartley and Scolnik 1995; Schiele 2001).

Colour of fruit peel and hence pigment accumulation in lulo varied throughout the year (χ^2 = 11; d.f. = 2; P = 0.004). Fruits harvested in spring and summer were more red (a* = 43.9) and less yellow (b* = 60.2) than in winter (a* = 39.8, b* = 63.4; Table 3). In compliance with our instrumental measurements (Fig. 4A) sensory analysis also showed that fruits harvested in spring and summer tended (although not significantly) to be perceived as more reddish by the panellists than those in winter (Figs. 2–3). Therefore we suggest higher carotenoid accumulation in spring/summer than in winter induced by enhanced rate of biosynthesis or rather higher enzyme level in response to higher light availability (see Howitt and Pogson 2006). A seasonal variation of β-carotene related positively to photosynthetic photon flux density was, e.g., found in cherry tomatoes (Slimestad and Verheul 2005). In further studies our assumption should be confirmed by quantifying changes in β-carotene content in lulo peel. In order to offer consumers fruits with maximal health benefits and best visual properties research on lulo varieties and growth environment (e.g. UV-B-enriched or UV-B-free greenhouses) is recommended (see Giuntini et al. 2005).

Table 3: Physico-chemical characterisation of ripe *Solanum quitoense* fruits cultivated and harvested in Germany under greenhouse conditions, and values given by literature and gained from fresh lulo fruits harvested in Latin America. In total, 16 fruits were sampled in German greenhouse during winter (December–February) and spring (May–June), respectively, and 14 fruits during summer season (July–August). For water content 10 (winter, summer) and 12 (spring) fruits, for TA and TSS/TA 12 fruits per harvest date, respectively, were analysed. Values are given as mean (with standard deviation) or median. Colour was derived from RHS Colour Charts and the corresponding L*a*b*-values are given. Different lowercase letters indicated significant differences within rows for harvest seasons ($P < 0.05$, LME and Tukey, except colour: Kruskal-Wallis multiple comparison). n.d. = no data given by the authors.

Fruit parameters	Unit	Greenhouse Germany			Field plantations Latin America		
		Winter	Spring	Summer	Costa Rica[1]	Ecuador[2]	Ecuador[3]
Whole fruit							
Diameter	cm	4.3 (0.3) a	4.4 (0.5) a	4.6 (0.3) a	n.d.	5.4 (0.1)	4–6.5
Height	cm	3.7 (0.3) a	3.8 (0.5) a	4.3 (0.3) b	n.d.	4.7 (0.1)	3–5.5
Shape[4]		0.87 (0.03) a	0.88 (0.03) a	0.94 (0.03) b	n.d.	*0.87* [5]	n.d.
Fresh weight	g	39 (9) a	44 (12) a	47 (9) a	n.d.	65.7 (5.9)	40–120
Peel colour							
L*		69.5 a	64.8 b	64.8 b	n.d.	47.2 (2.1)	n.d.
a*		39.8 a	43.9 b	43.9 b	n.d.	16.7 (1.9)	n.d.
b*		63.4 a	60.2 b	60.2 b	n.d.	46.1 (4.0)	n.d.
Pulp							
Water content	%	76 (5) a	69 (2) b	70 (2) b	90.6 (0.3)	91.5	82–92
Dry matter (DM)	%	24 (5) a	31 (2) b	30 (2) b	*9.4* [5]	*8.5* [5]	*8–18* [5]
pH		3.28 (0.07) a	3.46 (0.06) b	3.55 (0.06) c	3.20 (0.04)	3.24 (0.06)	n.d.
Soluble solids (TSS)	°Brix	9.4 (0.7) a	14.9 (0.8) b	14.0 (0.7) c	9.1 (0.5)	7.3 (0.4)	7.3–10.2
Titratable acidity (TA)	g CAE[6]/ 100 g FW[7]	2.48 (0.16) a	1.97 (0.14) b	1.76 (0.13) c	2.63 (0.07)	2.86 (0.16)	n.d.
TSS/TA		3.82 (0.49) a	7.60 (0.82) b	7.97 (0.96) b	*3.46* [5]	*2.55* [5]	n.d.

[1] Acosta et al. (2009). [2] Gancel et al. (2008). [3] Vasco et al. (2008). [4] Elongation (*height/diameter*). [5] Calculated from mean values and not given directly by the authors. [6] Citric acid equivalent. [7] Fresh weight.

Characterization of lulo pulp

Water content and firmness

Lulo fruits were more than 70% water but water content depended on harvest season ($F = 16.34$; d.f. = 2,10; $P < 0.001$; Table 3). Lulo fruits harvested in winter contained on average 76% water in pulp and had therefore significantly more water and less dry matter (DM) than fruits during spring and summer (both about 70% water content; Table 3). Light is required for DM accumulation (Hewett 2006). In European winter the low light intensity and short day length reduce assimilation and, hence, DM accumulation and content (see Marcelis 1996). The DM content is increasingly discussed as a new holistic quality index for fruits (e.g. wine grapes: Hewett 2006; apples: Palmer et al. 2010; kiwifruits: Crisosto et al. 2012). Based on this we suggest lulo fruits in winter to be of lower quality than fruits harvested in spring or summer but, nevertheless, of high quality when compared to lulo fruits harvested and analysed in Latin America (water content: 82–92%; Table 3).

Palmer et al. (2010) hypothesised that high DM content in fruits would suggest high flesh firmness due to more cell wall material. Our sensory results would support this assumption as lulo fruits in winter, having less DM, shared also lower fruit and pulp firmness (Figs. 2–4B). In accordance with firmness of the whole fruit pulp firmness was higher in fruits during spring ($P = 0.007$) and tended also to be higher ($P = 0.094$) during summer due to a strong positive correlation (PC1, Fig. 2). In apples, firmness also correlated with other texture attributes like juiciness or mealiness (Harker et al. 2002a). We found a seasonal impact on juiciness perception ($\chi^2 = 7.44$, $P = 0.024$) but in contrast to the results of our instrumental measurements (Fig. 4C), the panellists could not significantly distinguish fruit samples based on juiciness (Fig. 3). Although juiciness was defined as the amount of watery juice that escapes the fruit pulp during chewing, the difference in moisture of about 6% between fruits in winter and spring/summer might be too low to be directly perceivable by humans (see Harker et al. 2002b). In addition an altered perception of juiciness due to seasonality cannot be ruled out.

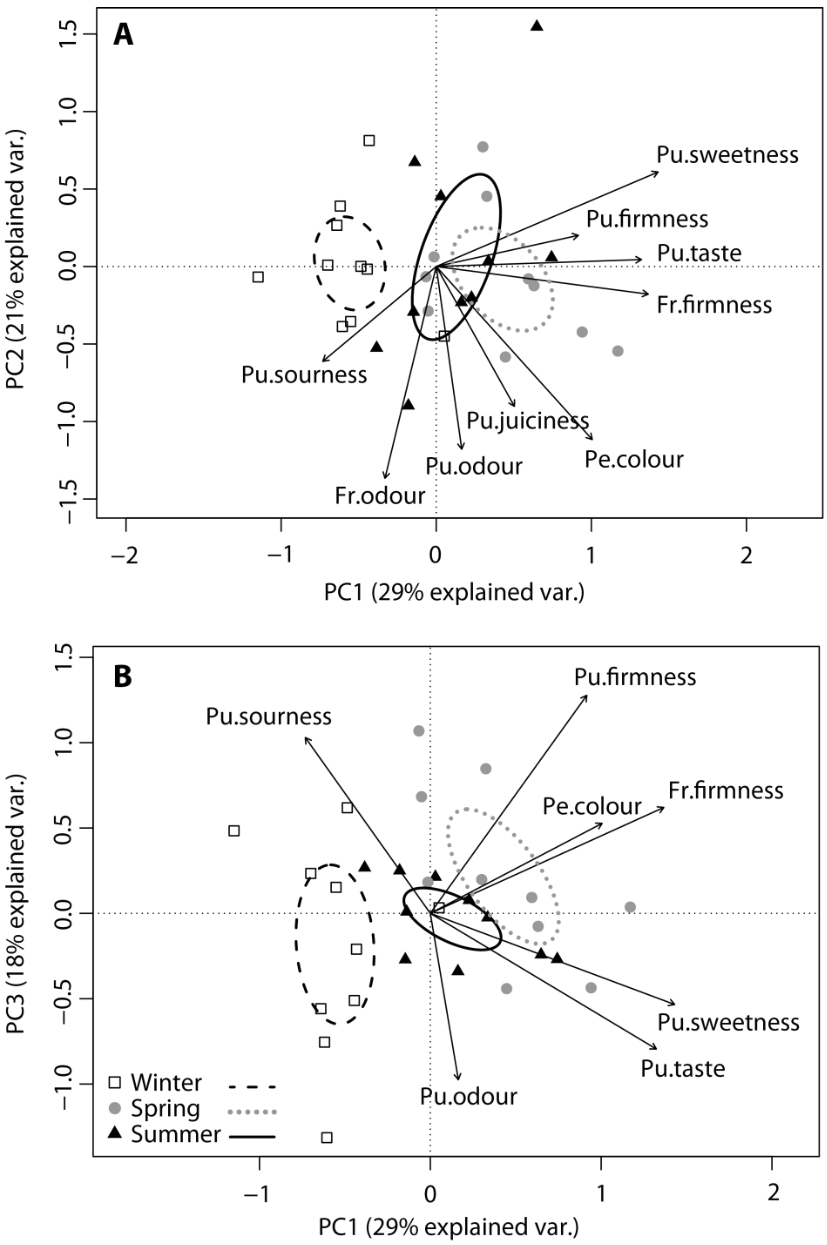

Figure 2: PCA plot of sensory profile for lulo (*Solanum quitoense*) fruits samples harvested in winter (February), spring (June) and summer (August). PCs were A): PC1 and PC2 and B): PC1 and PC3. Values (symbols) of each panellist per harvest season (n = 10), sensory attributes (arrows) and 95% confidence interval of averaged value per harvest season (lines) are given (scale factor = 3). Fr. = fruit, Pe. = peel, Pu. = pulp.

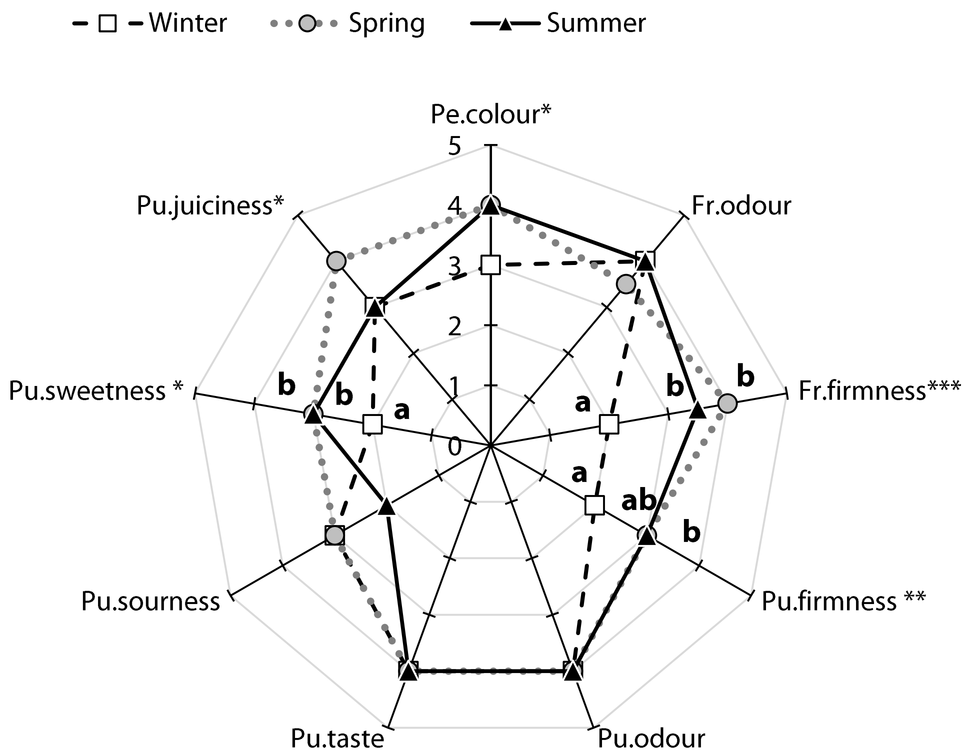

Figure 3: Evaluation of lulo (*Solanum quitoense*) fruits in terms of whole fruit (Fr.), peel (Pe.) and pulp (Pu.) characteristics by a panel. Fruits were harvested in winter (January), spring (June) and summer (August), respectively. Median values of 10 panellists are given per sensory attribute. Symbols indicated significant impact of harvest date on fruit attribute (Friedman-Test, *P < 0.05, **P < 0.01, ***P<0.001); different lowercase letters within the spider web indicated significant differences (P < 0.05) between harvest seasons per fruit attribute (pairwise Mann-Whitney-U Test with Bonferroni adjustment).

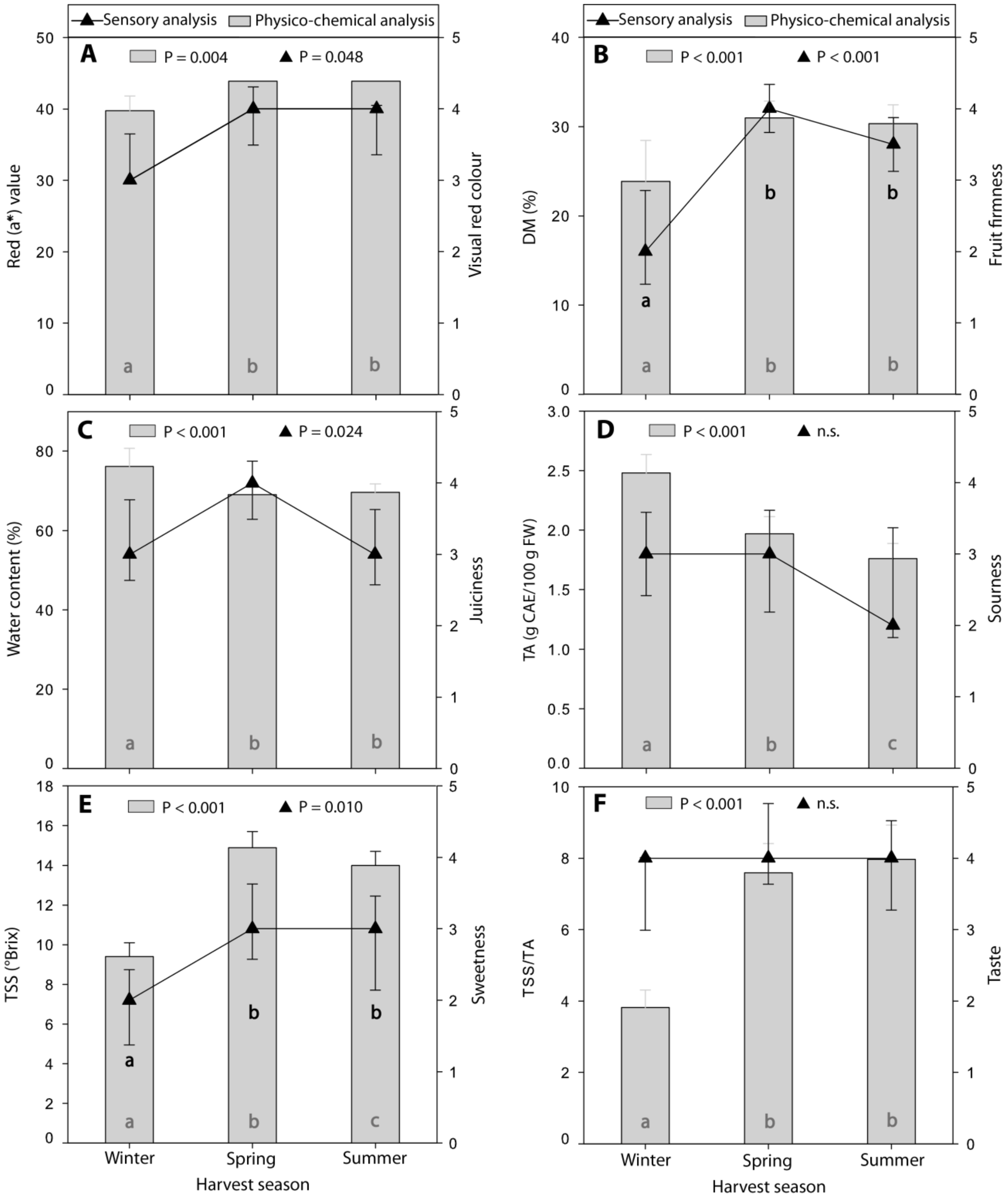

Figure 4: Comparison between results obtained from physico-chemical and sensory measurements during harvest period in winter (December until January), spring (May and June) and summer (July and August). Mean values and standard deviation were given for physico-chemical attributes (except median and 95% confidence interval for a*-value), median values and 95% confidence interval for sensory attributes. Different lowercase letters indicate significant differences between harvest seasons per fruit attribute respectively measured by physico-chemical (grey letters at the bottom of the bars) and sensory analysis (black letters within the bars).

pH, sugar content and acidity

pH of lulo pulp was affected by harvest season (F = 73.98; d.f. = 2,22; P < 0.001). Mean pH in winter was 3.28 (±0.07) and therefore similar to values given by recent scientific literature on lulo fruits harvested in Latin America, but increased significantly to 3.55 (±0.06) in our study in summer (Table 3).

Mean total soluble solids (TSS) content ranged between 9.4–14.9 °Brix and was similar to that of kiwi fruits (10.4–13.1 °Brix, Crisosto et al. 2012). TSS depended on harvest season (F = 244.13; d.f. = 2,22; P < 0.001) and, in compliance with the low DM content, was lowest in fruits harvested in winter (Table 3). Sugars contribute to about one third of DM in lulo fruits (32%: Acosta et al. 2008; 39%: Gancel et al. 2009) and Palmer et al. (2010) determined a positive relationship between DM and TSS. In analogy to the DM content, seasonal variations in TSS could be explained by enhanced photosynthesis rate and hence higher carbohydrate availability in spring and summer. It is known, e.g. also for tomato, that TSS content tends to increase with increasing light intensity and vice versa (Dorais 2003; Rylski et al. 1994; Slimestad and Verheul 2005). Our data also indicated seasonal variations in content and ratio of glucose, sucrose and fructose (Figs. 1 and 5). In winter, glucose, sucrose and fructose contents were proportionally lower; e.g. sucrose was only about half of the level reached in spring and summer (Fig. 5). Fruits harvested in spring were characterized by 1.3 times higher sucrose content compared to fruits in summer, but contained only 60% and 70% of glucose and fructose, respectively (Fig. 5).

In compliance with the instrumental measurements, panellists perceived fruits in winter with lower levels of TSS and sugars as less sweet compared to those in spring and summer (Figs. 2–4E). Sweet taste is regarded as being crucial for consumer acceptance of tropical fruits in Europe (Prohens et al. 2003; Sabbe et al. 2009b). Thus the decrease in sweetness level in winter might have negative effects on consumer acceptance of fresh lulo fruits. In contrast to our instrumental measurements, panellists did not perceive fruits in spring (having higher levels of TSS; Table 3) as sweeter (Figs. 2–4E). Harker et al. (2002b) found TSS to be the most convenient predictor for sweetness in apple fruits but only when differences exceed a certain threshold. Maybe fruits in spring (14.9±0.8 °Brix) and summer (14.0±0.7 °Brix) did not differ enough in TSS to induce significant differences in sweetness perception (Fig. 3).

Mean titratable acidity (TA) during the year was in the range of 1.76–2.48 g CAE/100 g FW being e.g. much higher than of kiwi fruits (TA: 0.4%–1.1%, Crisosto et al. 2012). TA content was affected by harvest season ($F = 81.44$; d.f. = 2,13; $P < 0.001$) and highest values were measured in winter, lowest values in summer harvested fruits (Table 3). The predominant acid in lulo pulp is citric acid representing 97% of total organic acids (Gancel et al. 2008). We found 1.2 times higher concentration of citric acid in winter than in both other harvest seasons (Figs. 1 and 5). TA is associated with sourness taste (Harker et al. 2002b), and the high TA content in lulo contributed generally to a typical sourness flavour (Fig. 3) which is sometimes associated with lemon or kiwi flavour (e.g. ACTI et al. 1989; Gancel et al. 2008; Messinger et al., in prep.; Morton 1987). Fruits in winter were evaluated slightly, but not significantly sourer than fruits in summer (Fig. 3), hence neither TA nor citric acid was a significant predictor of sourness taste in this study (Fig. 4D). Maybe differences in TA between seasons were below the threshold for perception of sourness (see Harker et al. 2002b). Sometimes it is difficult for consumers, i.e. untrained panel, to distinguish between sweet and sour taste because the sourness of acids could be partially masked or balanced by sweetness from sugars (Crisosto et al. 2012; Lawless and Heymann 2010) and as it can be seen in our study they were strongly and negatively correlated (Fig. 2). This would explain why fruits in spring with higher TA (and higher TSS) values were not perceived sourer than fruits in summer with lower TA.

In comparison to Latin American lulo fruit samples, we had similar TA and TSS values in fruits in winter but, obviously, lower TA and higher TSS values (up to 1.5–2.0 times) during spring and summer harvest (Table 3). TSS and its ratio to TA is often related to fruit quality and consumer acceptance (Kader 1999) and therefore fruits from greenhouse production in Germany could be considered to be of high eating quality, even in winter (Table 3). Maybe this was an effect of ripeness level as sugar content increased with ripening (e.g. Mejía et al. 2012; Messinger et al. 2015). In commercial production, lulo fruits are harvested before full ripeness to withstand handling and packaging (Casierra-Posada et al. 2004; Morton 1987). Acosta et al. (2009) analysed lulo fruit samples that fulfilled 75–100% orange colour in peel whereas in our study we analysed the fruits at full ripeness (Messinger et al. 2015; Morton 1987). This would (currently) support a local production and consumption in Germany with short transport.

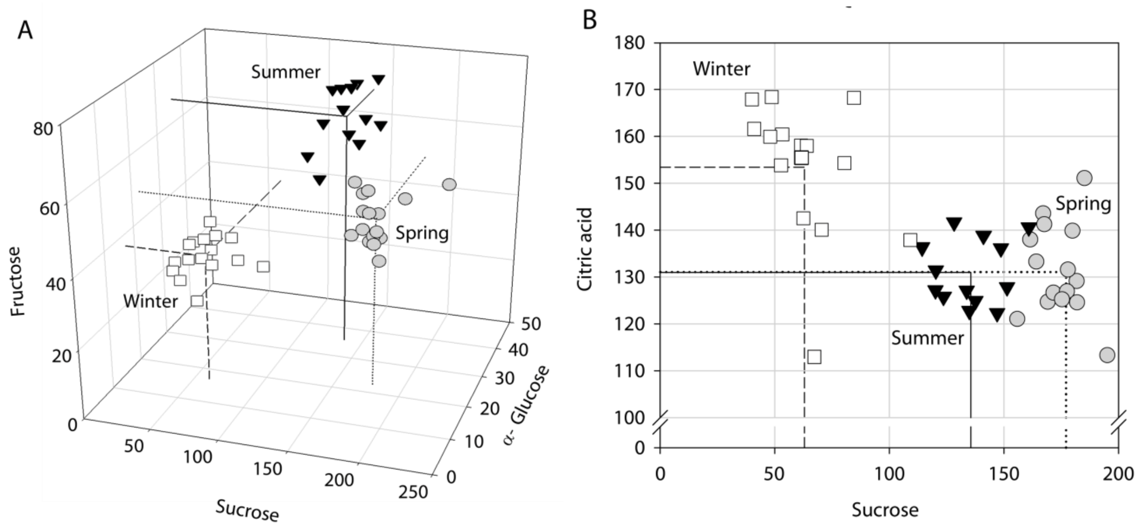

Figure 5: NMR signal intensities proportional to content of sugars and citric acid of lulo fruits (*Solanum quitoense*) harvested in spring (May and June, n = 16), summer (July and August, n = 13) and winter (December until January, n = 16). The drop lines of mean values per harvest season are given. A: α-glucose, fructose and sucrose. B: sucrose and citric acid. Components were analysed by integration of the corresponding peaks in the NMR spectrum and shown in arbitrary units (integral surfaces / 1000000). The integration limits (i.e. regions from left to right on the spectra) were from 2.95 to 2.91 ppm for citric acid, from 5.47 to 5.33 ppm for sucrose, 5.25 to 5.20 ppm for α-glucose, 4.12 to 4.08 for fructose.

Aroma intensity

Satisfaction with taste is a major challenge for consumer acceptance of exotic fruits (Prohens et al. 2003; Sabbe et al. 2009a, 2009b, 2013). TA, TSS and TSS/TA were discussed to be positively related to flavour (Harker et al. 2002b; Kader 1999). Palmer et al. (2010) provided evidence of a good and positive relationship between DM content at harvest and consumer liking of apples. In our study we observed differences in all these parameters, e.g. TSS/TA was about 50% less in fruits in winter than in spring/summer (Table 3). But panellists could not significantly distinguish fruit samples based on olfactory perception (fruit odour: $\chi^2 = 0.7$, $P = 0.70$; pulp odour: $\chi^2 = 0.08$, $P = 0.96$; Fig. 3), and although taste correlated positively with sweetness and negatively with sourness, no differences in taste intensity were perceived (Figs. 2A and 3). Thus our results of instrumental measurements could not provide proof by sensory analysis (Fig. 4F). In our study, lulo fruits were strong in aroma throughout the year (ranking 4 of 5 for pulp odour and taste, Fig. 3). Maybe lulo's aroma profile is more related to ripeness level. In the close relatives (Heiser 1985) *S. sessiliflorum* and *S. vestissimum* an intensive fruity odour developed only at full ripeness by reaching highest concentrations in aromatic compounds such as esters (Quijano & Pino 2006; Suárez & Duque 1992). Given full ripeness (as in our study) greenhouse production would allow a supply of aromatic lulo fruits year-round and possibly provide positive taste experiences and good market prospects. Nevertheless we did not measure overall liking of aroma (including flavour, sweetness and sourness) and we suggest that the low sweetness level of fruits in winter will meet disappointments among consumers. Additional consumer tests should be performed to test that assumption. For logistical reasons, our profile tests could not be performed on the same session. The long-time lack between the tests could make it difficult for the sensory unskilled panellists to compare between the samples. On the other hand this would meet realistic purchase conditions.

Implications for greenhouse production and marketing in Germany

Lulo fruits produced under greenhouse cropping in Germany, Central Europe, were of high quality, even in winter under short-day conditions. Particularly the intensive year-round fruit aroma, i.e. odour and taste, would assume promising prospects for marketing lulo fruits in Germany (see e.g. Briz et al. 2008; Galán Saúco 2013; Sabbe et al. 2013). Hence, the lulo is highly suitable for sustainable and gainful cultivation in areas with fluctuating light conditions.

However, seasonal effects and, as hypothesized, a reduction in fruit quality have to be expected in winter. We suggest that the low sweetness and firmness in fruits harvested in winter will reduce consumer liking; the low firmness would also assume shorter storage suitability and difficulties with transport and handling for the already perishable lulo (Sabbe et al. 2013). In follow-up studies it should be evaluated which upper and lower thresholds of the sensory and physico-chemical attributes are acceptable to consumers and marketers and if fruits harvested in winter are within this range. With this regard, DM seems particularly promising to be tested as a reliable predictor for fruit quality and consumer liking of lulo, as is the case for apple (Palmer et al. 2010) or kiwi fruit (Crisosto et al. 2012). When assessing fruit quality, like in our case, it should be considered that sensory perception need not necessarily be in accordance with physico-chemical measurements. This was revealed in our study, e.g. for juiciness and aroma. Therefore we recommend sensory studies in addition to instrumental measurements, as also Harker et al. (2002a, 2002b) did.

Provided that the seasonal variation in fruit quality affects consumer acceptance or fruit storage and handling negatively, cultivation and marketing should be adapted. Most of all a high level of ripeness should be favoured in local production since fruit quality, notably aroma, is apparently more influenced by ripening than by photoperiod. In case no inexpensive solution can be found for producing fresh high-quality lulo fruits in winter, it might be considered to restrict harvest and marketing of fresh fruits to one period during spring until autumn in Germany. As an alternative, fruits in winter could be processed to juice or other products which would allow addition of sugar and would prevent the loss of fresh fruits through softening during transport or handling. In the future, strategies for providing a homogenous eating quality to consumers should be developed to successfully market the lulo in Germany, Central Europe.

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6.5 Manuscript V:

Successful pollination of the Neotropical crop Solanum quitoense by Bombus terrestris: behaviour, efficiency and yield

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Abstract

The South American lulo (*Solanum quitoense* Lam.) is a crop plant of the Andes of Ecuador and Colombia, pollinated by South American bumblebees, such as, *Bombus atratus* Franklin. The cultivation of lulo outside of its native range, for example in European glasshouses, requires the presence of efficient pollinators to enable high fruit set and yield. Until now, the suitability of *Bombus terrestris* L., native to Europe and commonly used in agriculture, has been untested for this purpose. In this study, the pollen-collecting behaviour of *B. terrestris* when visiting lulo flowers was investigated. It was shown that *B. terrestris* adopted the lulo as a pollen source, and on average visited three flowers per minute, had five buzzing events per stay and foraged for 15 s on a single flower, independently of the previous number of visits and level of bruising to the anthers. The pollination efficiency of five different treatments was evaluated: (i) exclusion of bees, (ii) single and (iii) multiple visits of *B. terrestris*, (iv) self- and (v) cross-pollination by hand. The results clearly demonstrated that, for fruit set, pollination is crucial. It was also found that lulo flowers can be successfully self-pollinated, but give 25% fewer fruit set compared with pollination via multiple bumblebee visits, or cross-pollination by hand. Fruit set, seed set and fruit size were as high with pollination by *B. terrestris* as with crosspollination by hand, indicating that this bumblebee is an appropriate pollinator for lulo. However, *B. terrestris* was conspicuously less effective when a flower was visited only once. Therefore, when growing lulos commercially, multiple bumblebee visits should be encouraged, but it is likely that the behaviour of *B. terrestris* would ensure this anyway. Our results indicate that *B. terrestris* is a suitable and efficient pollinator for the production of lulo fruits

Keywords

bruising level, bumblebees, fruit set, glasshouse culture, lulo, multiple visits

Introduction

The lulo or naranjilla (*Solanum quitoense* Lam., Solanaceae) originating from the Andes of Ecuador and Colombia is a popular fruit crop in Latin America but still cultivated and consumed mainly locally (ACTI et al. 1989; Heiser and Anderson 1999; Sabbe et al. 2013; Vietmeyer 1986). Because of the characteristic flavour and high nutritional value of the tomato-sized fruits, the lulo is believed to have high potential on the international market (e.g. Acosta et al. 2009; ACTI et al. 1989; Gancel et al. 2008; Mertz et al. 2009; Sabbe et al. 2013; Samuels 2009). Cultivation best suits cool but frost-free, moist sites, and it has been introduced, for example into Costa Rica, Panama, Guatemala, tropical Africa and New Zealand (ACTI et al. 1989; Endt 1990; Morton 1987). The lulo is also suitable for humid and cloudy subtropical regions (ACTI et al. 1989; Prohens et al. 2004), protected cropping in the United Kingdom (Samuels 2013) and year-round glasshouse cultivation in Central Europe, particularly Germany (Messinger and Lauerer 2015).

The morphology of the lulo flower necessitates the involvement of specialized pollinators to ensure sufficient fruit set (Almanza Fandiño 2007). Flowers appear in short clusters (Morton 1987) and are of the typical 'Solanum type' (Buchmann 1983; Buchmann and Cane 1989) with five white petals and five prominent, dark yellow stamens (Morton 1987). The lulo is strongly andromonoecious (Miller and Diggle 2003); the inflorescences consist of hermaphrodite flowers with long styles and large ovaries, and functionally male flowers, which have short styles and never set fruit (Diggle and Miller 2004; Almanza Fandiño 2007). The lulo produces no floral nectar, but instead provides a protein-rich pollen source as a food reward for pollinators, as in most solanums (Buchmann 1983; Roulston et al. 2000; Almanza Fandiño 2007). The pollen is enclosed in the anthers and can only be released via two apical pores per anther. As in many *Solanum* species, this is facilitated in *S. quitoense* by rapid bumblebee-produced vibrations during so-called 'buzz pollination' (Buchmann 1983; Almanza Fandiño 2007) or 'sonication' (Buchmann and Cane 1989). In pollination experiments in Colombia, fruit set was doubled (76%) and fruit quality was improved when native bumblebees (*Bombus atratus* Franklin; Hymenoptera: Apidae) were allowed to visit flowers, compared with flowers excluded from bumblebee visits (Almanza Fandiño 2007). Hence, efficient pollinators are of high economic value when growing lulo commercially, especially outside of its region of origin where native pollinators are absent. The Eurasian *Bombus terrestris* L. (buff-tailed bumblebee) is widely used in agriculture (Velthuis and van Doorn 2006). As an effective buzz pollinator, it increases yield in many cultivated solanaceous plants, for example sweet pepper (*Capsicum annuum*: Serrano and

Guerra-Sanz 2006), eggplant (*Solanum melongena*: Abak et al. 1995) and tomato (*Solanum lycopersicum*: Velthuis and van Doorn 2006). Given that lulo flower architecture is similar to that of tomato and that, in its native Neotropical range, it is pollinated by *B. atratus* (Almanza Fandiño 2007), it can be assumed that *B. terrestris* could also be used for lulo pollination. The characteristics of lulo, for example its pollen chemistry (Buchmann 1983), pollen availability, floral scent and flower morphology, may influence the preference and behaviour of bumblebees (see e.g. Lefebvre and Pierre 2006; Morse et al. 2012; Nunes-Silva et al. 2013). Although it could be essential for profitable production of this new crop, it is not known how effective *B. terrestris* would be as a lulo pollinator.

Therefore, we designed an experiment to study the behaviour of *B. terrestris* and its effects on fruit set and yield of *S. quitoense*. We hypothesized that: (i) *B. terrestris* adopts lulo flowers as a source of pollen, (ii) its visits increase fruit set and (iii) enhance fruit size and yield. Further, we postulated that: (iv) *B. terrestris* is less effective as a pollinator during single flower visits compared to multiple visits because of lower pollen deposition (cf. Kawai and Kudo 2009).

Materials and Methods

Plant material and bumblebee colony

Experiments were performed in glasshouses (121 m²) at the Ecological-Botanical Garden of the University of Bayreuth (EBG), Germany. Lulo (*S. quitoense*) seed material was obtained from plants cultivated since 2007 at the EBG; seed was originally obtained from a plantation in Costa Rica (Santa Maria de Dola, 1700 m a.s.l.). Seeds were sown on 15 February 2013, and 20 individuals randomly chosen from homogeneously vigorous plants were grown for the pollination experiments in 10-l plastic pots and randomly placed within the glasshouse with regular spacing. The commercial potting mixture contained white peat (39%), black peat (11%), coconut fibre (20%), lava gravel (15%) and bark compost (15%), and was enriched with 25 g fertilizer (20-10-15 + 6, N-P-K+ MgO, PlantoSan; Hermann Meyer KG, Rellingen, Germany) per 10 l soil. During growth, the plants were regularly watered and provided with Hakaphos (Düngerexperte, Attenzell, Germany) liquid fertilizer (growth and blooming period: 15-10-15 + 2 / fruiting period: 8-12-24 + 2). Mean glasshouse temperature during experiments (June 2013 to July 2014) was 20 ± 5°C.

During lulo blooming, a hive containing a colony with 30–50 foraging workers and brood (eggs, larvae and pupae) of *B. terrestris* and additional sugar solution was placed into the glasshouse on its north side. Introduction and management followed the recommendations of the manufacturers (Sautter and Stepper, Ammerbuch, Germany). In total, three bumblebee colonies were used for the pollination experiments, the first from 19 July to 14 August 2013 (mean temperature: 24°C), the second from 14 August to 23 September 2013 (20°C) and the third from 12 July 2014 to 22 July 2014 (26°C). Temperature of the colony was controlled (shadowing, air conditioning and moistening the surrounding area) and monitored with a Six's (maximum–minimum) thermometer.

Behaviour of *Bombus terrestris* on *Solanum quitoense*

Behaviour of *B. terrestris* was observed during the blooming period of 20 lulo plants in 2013 (30 July to 11 September) on several days between 7.00 a.m. and 4.00 p.m. Behaviour of individual bumblebee workers (foraging, buzzing, stigma contact) was qualitatively documented (based on observations of Almanza Fandiño 2007), and the time they spent on a single flower from landing until leaving it (visit duration) was recorded for functionally male (n = 250) and hermaphrodite flowers (n = 404) separately. On 4 days in the time period mentioned above, the number of flowers an individual bumblebee settled on within 5 min was counted on 21 different occasions. To evaluate whether the amount of previous visits have an impact on bumblebee worker behaviour, visit rate and anther manipulation during multiple visits on 10 mature hermaphrodite flowers randomly selected over 10 different plant individuals (one flower per plant) were documented on 14 July 2014. Unopened hermaphrodite flowers were enclosed in fine mesh bags, which were then removed for 1 day as soon as they were fully open (fig. 1a). Number of bumblebee visits on each flower with at least one buzzing event (bumblebee vibrating the androecium) was counted from 9.00 a.m. to 4.00 p.m. until a maximum of 75 visits was achieved. The duration of every first, third, fifth and each further fifth visit was measured. Concurrently, the number of buzzing events per visit was counted. After each recorded visit, bruising intensity (degree of discolouration of the anthers as a result of biting; see fig. 1b), was classified and recorded according to the categories of Morandin et al. (2001), employed for their study of tomatoes. They distinguished between five bruising levels (0–4) where 0 referred to 'no bruising' and 4 referred to 'entire anther cone bruised and anthers coming apart' (Morandin et al. 2001).

Fig. 1 A) Mature, fully open hermaphrodite flower of *Solanum quitoense* with five prominent anthers and a long style (black arrow) exceeding the anthers. This flower was not exposed to previous bumblebee visits (bruising level 0). B) Bruising marks (dark discolouration) of *S. quitoense* anthers due to biting by *Bombus terrestris* during multiple buzzing (bruising level 4; according to Morandin et al. 2001).

Pollination treatment and yield

To investigate pollination efficiency, each plant (n = 20) was subjected to five different pollination treatments between 19 July and 23 September 2013. On each plant, four hermaphrodite flowers were enclosed in a fine mesh bag before they opened (bud stage when petals are already visible). The first of the five treatments was (i) flowers remained bagged throughout the whole flowering period to prevent bumblebee visitation. In the next three treatments, randomly selected flower buds had their mesh bags removed on the first day of anthesis, then flowers were either (ii) self-pollinated by hand dipping the stigma in pollen released from its own anthers, (iii) emasculated (anthers of the flower were removed before any pollen had escaped) and cross-pollinated by hand with the pollen of another randomly chosen plant or (iv) exposed to one visit of *B. terrestris* with at least one buzzing event. Subsequently, these treated flowers were bagged again. Treatment (v) involved one single, unbagged and open-pollinated (at least five bumblebee visits) flower of each plant. Fruit development was monitored daily. Fruit set (recorded when ovary width reached 1.5 cm), number of fruits aborted during maturation, and number of ripe fruits (fully orange and the calyx naturally detached from the fruit, see Morton 1987) per plant were counted. Bristly hairs were removed, and the fresh ripe fruits weighed (fruit fresh mass) with a digital analytical scale, accurate to 0.1 mg (Mettler Toledo AE 240, Gießen, Germany), and fruit diameter was measured. Fruits were graded by diameter into two commercial lulo fruit quality classes, as specified by NTC (1979). Additionally, fresh mass of fruit peel was measured to calculate fruit pulp weight. Seeds were extracted from fruit pulp, weighed and their proportional weight of the fruit pulp (fresh wt%) calculated. Then, seeds were dried for 4 h at 30°C, and total dry seed mass per fruit was measured. Seed number per fruit was calculated from the specific thousand-grain weight per treatment. The thousand-grain weight was measured from three (for the single bumblebee visit treatment) or six (remaining treatments) randomly chosen fruits and averaged for each treatment.

Data analysis

Significant differences ($P < 0.05$) in pollination behaviour according to flower type were investigated using a generalized linear model (GLM) and defining a log-distribution with gamma family error. Similarly, to determine whether the number of earlier visits had an impact on bumblebee worker's visit duration and number of buzzing events on single flowers, a generalized linear mixed model (GLMM, R'package 'MASS' version 7.3-3, Venables and Ripley 2002) with gamma family error and flower number as random factor was applied. The influence of the visit number per flower on bruising level was tested with a Spearman's rank correlation test. A fitted curve with R^2 as an indicator for 'goodness-of-fit' was derived from values of 10 different and consequent observed hermaphroditic flowers.

The effect ($P < 0.05$) of pollination methods on fruit set and number of ripe fruits was tested with a GLM. Because the data were of binary structure, a binomial family error was used. The *post hoc* comparison for general linear hypotheses (Tukey, R package 'multcomp', version 1.2-3, Hothorn et al. 2008) did not work properly for this data set (0% fruit set of bagged flowers), so we performed a pairwise comparison with GLM (binomial family error) between all treatments separately to test the significant differences between the pollination treatments. Fresh fruit weight and seed number were compared by a mixed-effect ANOVA with a *post hoc* TukeyHSD-Test (R-package 'multcomp' version 1.2-3, Hothorn et al. 2008). Fruit diameter was squared (^2-transformed) to fulfil the normal distribution and model assumption and analysed in the same way. For comparison of seed content of fruit pulp between pollination treatments, we applied a GLM with a binomial family error. Seed number and fruit fresh weight were correlated and whether or not this correlation was pollination-specific was checked with a linear model (LM, seed number x pollination treatments). Because correlations were not different for the pollination treatments ($F = 0.47$; d.f. $= 3, 47$; $P = 0.70$), linear regression was calculated for values of all four treatments.

All statistical analyses were performed with R version 2.10.0 (R Development Core Team 2009) and RStudio version 0.97.551 (RStudio Inc. 2009–2012). Unless otherwise noted, all used models and tests were available in R package 'stats', version 2.10.0 (R Development Core Team 2009). Graphs were provided with R (R-package 'plotrix': Lemon 2006; R-package 'stats': R Development Core Team 2009) and SigmaPlot version 10.0 (Systat Software Inc. 2006).

Results

Behaviour of *Bombus terrestris* on *Solanum quitoense*

Bombus terrestris adopted lulo flowers as a source of pollen by foraging on them regularly and showing typical buzzing behaviour. After landing on a flower (Fig. 2A), workers usually rotated around the anthers (Fig. 2B) and started "buzzing". For this process the bumblebees grasped the anthers with their mandibles and flapped their wings with high frequencies so that their bodies vibrated, facilitating pollen release from the anthers (Fig. 2C). During foraging on the flower, as well as grooming, workers came into contact with the style and stigma (Fig. 2D). The total time spent on a single flower averaged 15 s (±12 s; n = 813) but depended on flower type (F = 8.65; d.f. = 1; P = 0.004). On hermaphrodite flowers mean visit duration was 14 s (±11 s; n = 404) whereas on functionally male flowers it was significantly longer (17±13 s; n = 250). But on both flower types very short (around 1 s) as well as much extended visits (74 s on hermaphrodite and 96 s on male flower) could be observed-thus the duration of visits varied greatly. Individual workers foraged on 3 (±1) different flowers per minute on average. During buzz-pollination the anthers were damaged and, as the number of bumblebee visits increased, the degree of anther discolouration intensified from bright yellow to dark orange (bruising marks, Figs. 1B and 3; $r_s = 0.89$; $P < 0.001$). These bruising marks increased non-linearly with number of visits (Fig. 3). On average, the first bruising level was recorded in flowers which had been visited 10 times by *B. terrestris*, and level 4 (cf. Fig. 1B) after 60 visits. Although flowers were damaged by bumblebees during each visit, neither the length of stay (t = -0.23; d.f. = 142; P = 0.81) nor the number of buzzing events (on average five per visit; t = 1.13; d.f. = 142; P = 0.26) changed with increasing number of visits (between 0 and a maximum of 75 visits).

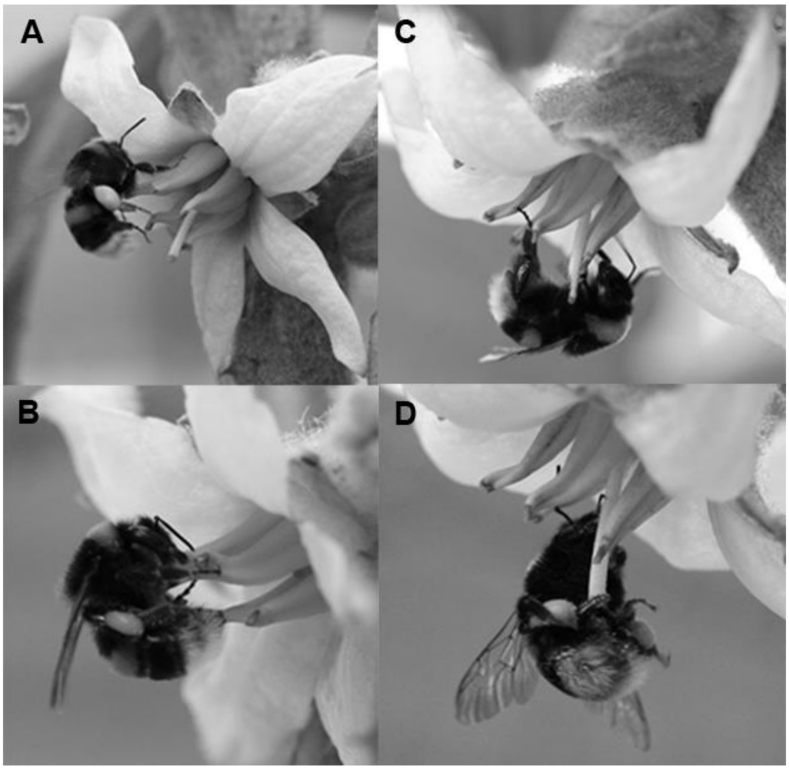

Fig. 2 Patterns of *Bombus terrestris* behaviour during a flower visit on *Solanum quitoense*: A) landing, B) rotation on the flower, C) "buzzing" by grasping the anther with the mandibles and vibrating the body rapidly through flapping its wings, D) contact with the style of hermaphrodite flower.

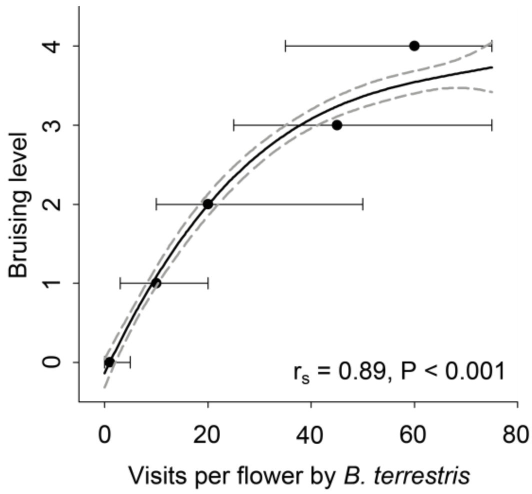

Fig. 3 Bruising level of anthers (classified by the degree of discolouration of the anthers after Morandin et al. 2001) according to *Bombus terrestris* visits to hermaphrodite *Solanum quitoense* flowers. Data were obtained from continuous observations of one virgin flower per plant (n = 10). Median, maximum and minimum values as well as fitted curve ($y = 8.6*10^{-06}x^3 - 0.002x^2 + 0.139x – 0.138$) with 95% confidence level (dotted lines) are given.

Fruit set

Pollination treatment had a highly significant impact on fruit set of *S. quitoense* (n = 20; $\chi^2 = 51.34$; d.f. = 4, 95; $P < 0.001$). Without pollination (i.e. bagged flowers) there was no fruit set at all (0%, Fig. 4). Cross-pollination by hand was as successful as multiple visitations by bumblebees; both treatments led to fruit set of about 85% and no fruit abortion during ripening (Fig. 4). In comparison, 75% of the self-pollinated flowers set fruits, but 20% (three fruits) of them dropped from the plant at an early stage of development, so that a total of 60% of all pollinated flowers developed fruits which ripened fully. There was a trend ($P = 0.07$) of 25% less ripe fruits than obtained through cross-pollination or multiple bumblebee visits. Fruit set was 50% when the flowers were visited only once by *B. terrestris,* with one fruit abortion during ripening (10% fruit loss of set fruits), giving 45% final fruit set for this treatment. This was not statistically different to the self-pollination treatment but significantly less than that obtained through multiple bumblebee visits. Hence, *B. terrestris* was as efficient in pollination of lulo flowers as cross-pollination by hand, as long as multiple visits occurred.

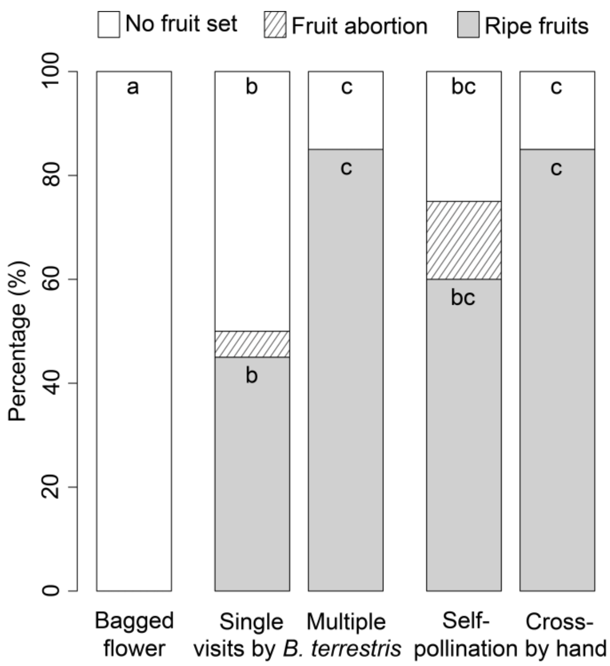

Fig. 4 Percentage of fruit set (sum of grey and shaded parts of the bars), fruit abortion during ripening (shaded bars) and ripe fruits (grey bars) for the five pollination treatments (n = 20). Fruit set was recorded when ovary width reached 1.5 cm. Lower case letters indicate significant difference between treatments ($P < 0.05$, pairwise GLM) for fruit set (denoted within white bars) and ripe fruits (denoted within grey bars).

Fruit characteristics: size, weight and seed set

Fruit diameter ($F = 6.36$; d.f. = 3, 51; $P < 0.001$) and fruit fresh weight ($F = 6.53$; d.f. = 3, 51; $P < 0.001$) depended on pollination treatment and were distinctly less in fruits developed after a single visit by *B. terrestris* (Figs. 5A-B). Mean fruit diameter of this treatment was 4.1 cm (±0.7 cm) and significantly less than in all other treatments (Fig. 5A). Therefore, none of these fruits fulfilled the criteria of commercial fruit class 1, only 56% reached class 2, and 44% of these fruits were too small to be classified (Table 1). Multiple bumblebee visits resulted in bigger fruits. In this case, fruit diameter was 4.7±0.5 cm and was not significantly different to those fruits gained via self- or cross-pollination by hand (Fig. 5A). After multiple bumblebee visits, a higher percentage of fruits fulfilled commercial fruit class 1 (23%) or class 2 (65%), so nearly all fruits conformed to a commercial class (Table 1). Self- and cross-pollination by hand led to only a slightly higher proportion of fruit reaching class 1 (33 and 35%, respectively; Table 1). Similar results were obtained with fresh fruit weight. This was lowest when bumblebees visited the flowers only once (36 g) and significantly higher in self- and cross-pollinated flowers (62 and 60 g, respectively; Fig. 5B). There was also a trend ($P = 0.08$) that fruits were heavier (51 g) when bumblebees visited flowers several times instead of once. Due to dissimilar fruit set and fruit weight between the treatments, highest yield (total fruit fresh weight) per treatment was obtained when flowers were cross-pollinated by hand (1016 g) and when multiple pollination by bumblebees occurred (864 g). In the self-pollination treatment the yield was 741 g; when bumblebees visited the flower only once it was 322 g.

Table 1 Commercial fruit classes of *Solanum quitoense* (NTC 1979) depending on the pollination treatment. The proportion of total fruit yield in each fruit class is given per treatment.

Pollination treatment		Sample number (n)	Quality class by fruit diameter		
			class 1 (> 5 cm)	class 2 (4 - 5 cm)	no class (< 4 cm)
Pollination by *B. terrestris*	Single	9	0%	56%	44%
	Multiple	17	23%	65%	12%
Pollination by hand	Self	12	33%	67%	0%
	Cross	17	35%	65%	0%

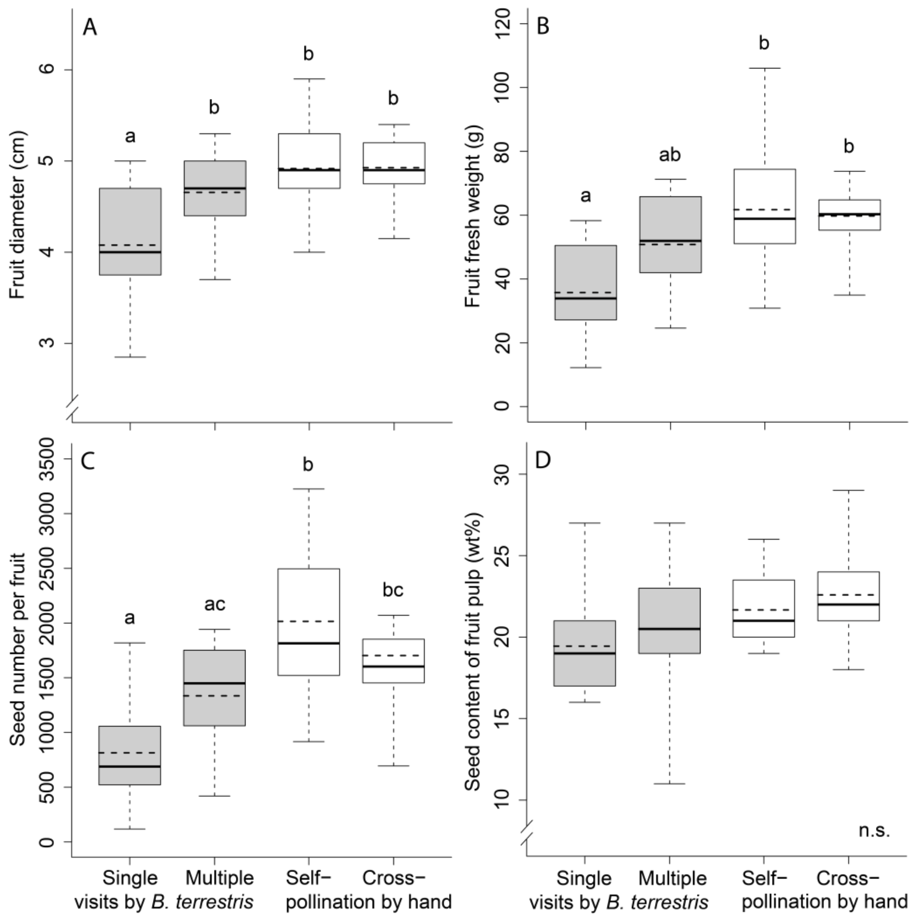

Fig. 5 Fruit and seed characteristics of ripe *Solanum quitoense* fruits depending on the pollination treatments. Flowers were exposed to exactly one visit (n = 9) or multiple visits by *Bombus terrestris* (n = 17) and were self- (n = 12) or cross-pollinated by hand (n = 17). Measured characteristics were fruit diameter (A), total fruit fresh weight (B), seed number per fruit (C) and seed content (D). Seed number was calculated by the specific thousand-grain weight per treatment and seed content of fruit pulp was calculated by the total fresh seed weight per fruit as a percentage of fresh pulp weight. Whiskers extend to the data extremes and mean values are illustrated as dashed lines within the boxplots. Lower case letters indicate significant differences between treatments ($P < 0.05$, TukeyHSD); no significant differences between the treatments were indicated by "n.s." (= not significant).

Pollination treatment also had a significant impact on seed number ($F = 9.11$; d.f. = 3, 51; $P < 0.001$; Fig. 5C). After multiple bumblebee pollination, the number of seeds per fruit (1335) was similar to cross-pollination by hand (1597, Fig. 5C). Seed number per fruit tended to decrease to an average of 814 seeds when flowers were visited only once by *B. terrestris* ($P = 0.10$). Despite these differences in seed number per fruit, seed content per edible fruit pulp weight was on average about 20wt%, independently of the pollination treatment ($\chi^2 = 0.64$; d.f. = 3, 51; P = 0.89; Fig. 5D). This was because of high positive linear correlation of fruit fresh weight and seed number for all pollination treatments ($R^2 = 0.81$; d.f. = 1, 53; $P < 0.001$; Fig. 6). Accordingly, big fruits contained more seeds than smaller ones.

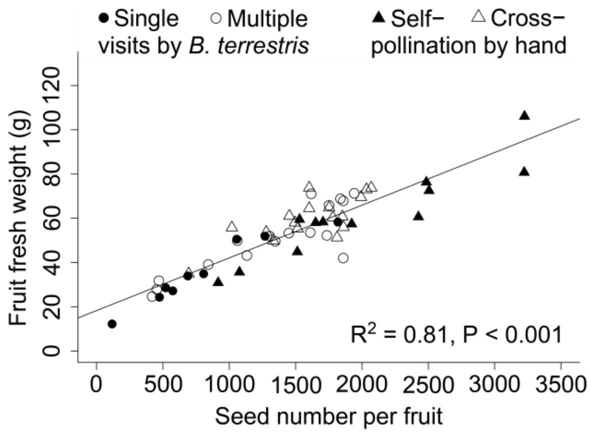

Fig. 6 Correlation of fruit fresh weight with seed number per fruit of *Solanum quitoense* for the four pollination treatments. Flowers were visited by *Bombus terrestris* exactly once (n = 9), or several times (n = 17), or were self- (n = 12) or cross-pollinated by hand (n = 17). Because correlations were not different for the treatments (F = 0.47; d.f. = 3, 47; P = 0.70) linear regression (solid line, y = 18.27 + 0.024x) was calculated for values of all four treatments.

Discussion

Lulo has to be (cross-) pollinated for high fruit set in glasshouse production

When lulo flowers were bagged with a gauze mesh (excluding insects, but not air movements) no fruits were set, even though our results and those of Almanza Fandiño (2007) confirm self-fertility in the lulo. Nevertheless, self-pollinated fruits aborted more frequently prior to maturity (20% loss of initial fruit set) compared to cross-pollinated ones (0%), which was also observed in *Shorea siamensis* (Ghazoul et al. 1998). This presumably could reduce the impact of inbreeding, so-called inbreeding depression (see e.g. *Campanula rapunculoides*: Vogler et al. 1999; *Solanum carolinense*: Mena-Ali et al. 2008) and would reinforce the use of pollinators, which promote exogamy via cross-pollination.

Nonetheless, wind and air currents can facilitate pollination of lulo flowers, as noted by Almanza Fandiño (2007) who observed a fruit set of 38% for bagged flowers in an open field experiment. Our experiment was performed in a glasshouse with low level of wind and air currents (cf. Abak et al. 1995), and this might plausibly explain why no fruits were set in bagged flowers. A similar situation exists in tomatoes and eggplants, which are also self-fertile and not exclusively dependent on insects for pollen transfer and high fruit set in the open field, but clearly benefit from pollinators when grown in the glasshouse (Abak et al. 1995). Whereas bagged tomato flowers still set fruits in glasshouses (cf. Abak et al. 1995; Dogterom et al. 1998), we obtained no fruits at all in lulo under these conditions. Hence, lulo depends on pollination by insects or by hand when cultivated in glasshouse in Central Europe.

Bombus terrestris is well adapted to lulo flowers and visits them frequently

As expected, *B. terrestris* buzz-pollinated lulo flowers effectively, as is the case for the Neotropical *B. atratus* (Almanza Fandiño 2007). The suitability of *B. terrestris* as a pollinator is probably due to the similar flower architecture of lulo to other *Solanum* species and plants with poricidal dehiscence, likewise adapted to buzz pollination (Buchmann 1983; Buchmann and Cane 1989). Almanza Fandiño (2007) highlighted that large pollinator body size is crucial for contact with the exserted style and stigma of the lulo, to deposit pollen. *B. terrestris* is similar in body length (11–17 mm: Bellmann 2005) to *B. atratus* (12–15 mm: Franklin 1913) and, indeed, we observed stigmatal contact when bumblebees foraged on lulo flowers. So in the study in hand, it is shown for the first time that *B. terrestris* is well adapted to pollination of the lulo and meets the requirements for its efficient pollination.

Bombus terrestris visited an average of three lulo flowers per minute and individual flowers on multiple occasions. In their study of tomato and eggplant flowers, Abak et al. (1995) observed five *B. terrestris* visits per minute on clear days and three on cloudy days. Thus, *B. terrestris* seems to visit lulo flowers with a comparable rate to other *Solanum* crops (Abak et al. 1995), where bumblebee pollination is already established for commercial purposes. The average visit duration of *B. terrestris* on lulo flowers (15 s) is in accordance with the behaviour of the native *B. atratus* on lulo in Colombia (18 s, Almanza Fandiño 2007) and also of native *Bombus sonorus* foraging on a southeast Arizona *Solanum elaeagnifolium* population (17 s, Buchmann and Cane 1989). Interestingly, *B. terrestris* workers foraged 20% longer on male than on hermaphrodite lulo flowers. We expect no appreciable differences in the amount of pollen between the two types of flowers as is the case for *S.*

carolinense, another andromonoecious species (Vallejo-Marín and Rausher 2007). According to Diggle and Miller (2004), the shorter style of male flowers does not interfere with pollen collection and could increase efficiency of pollen removal. This might make foraging easier and more rewarding for bumblebees and would explain the longer visit duration on male flowers (see Buchmann and Cane 1989; Wanigasekara and Karunaratne 2012; Nunes-Silva et al. 2013).

Bombus terrestris ensures high fruit set, fruit size and seed set

In the present study, open pollination (i.e. multiple visits) by *B. terrestris* was as efficient as cross-pollination by hand in terms of fruit set, fruit size and seed set, revealing that behaviour of *B. terrestris* promotes crosspollination in lulo. Pollination efficiency of *B. terrestris* (85%) even exceeded the fruit set reached by the native *B. atratus* in an open field experiment in Colombia (76%: Almanza Fandiño 2007). A slightly higher fruit set has been recorded for other *Solanum* species, for example glasshouse tomato pollinated by *Bombus impatiens* (90–100% fruit set: Nunes-Silva et al. 2013) and glasshouse hot pepper pollinated by *B. terrestris* (95–100%: Kwon and Saeed 2003). In contrast to lulo (Almanza Fandiño 2007), pollination of the tomato flower is independent of bee size, probably because of its floral morphology that allows self-pollination (Nunes-Silva et al. 2013). This might facilitate successful pollination in tomato. During pollination experiments, the mean glasshouse temperature was between 20 and 24°C, meaning that fruit abortion was unlikely to be induced by heat stress (see Peet et al. 1997; Marcelis et al. 2004).

Seed number is regarded as an indicator of successful pollination (see Stephenson 1981; Dogterom et al. 1998; Almanza Fandiño 2007), and accordingly *B. terrestris* was an effective lulo pollinator. In contrast to the findings of Almanza Fandiño (2007), we found no increase in seed content by bumblebee pollination compared to pollination by hand. Seed formation stimulates hormonal activity that is believed to play an important role in fruit growth by mobilizing resources into the developing fruit. As a consequence, a high level of seed production increases fruit size (Stephenson 1981). This was confirmed in our study, as well as in that of Almanza Fandiño (2007) in lulo, and of Kwon and Saeed (2003) in hot pepper. This explains plausibly why the seed content of lulo fruit pulp was independent of fruit size and therefore should not have any effect on pulp texture for human consumers when in the mouth. In addition, larger fruits achieve higher market prices. In this study, commercial fruit quality was mostly (88%) ensured in lulo by open bumblebee pollination. For tomato, Kevan et al. (1991) also found out that bumblebee pollination led to the same average fruit weight as pollination by hand. In conclusion, open pollination by *B. terrestris* produced lulo fruits of marketable quality. Furthermore, potentially expensive manual pollination by humans, as well as the use of hormones which artificially encourage fruit set and growth (Stephenson 1981; Heiser and Anderson 1999; Velthuis and van Doorn 2006), would not be necessary.

Behaviour of *Bombus terrestris* ensures necessary multiple flower visits

When lulo flowers were visited only once instead of several times by *B. terrestris*, fruit set and fruit quality were clearly reduced and the risk of fruit abortion increased. These results are in contrast to those obtained with tomato pollinated by *B. impatiens* (Nunes-Silva et al. 2013) and lulo pollinated by *B. atratus* (Almanza Fandiño 2007), where fruit set and fruit quality were high after a sole visit. The lower pollination efficiency in our study is most likely due to insufficient pollen deposition on the stigma at a single visit (see tomato: Morandin et al. 2001; sweet pepper: Serrano and Guerra-Sanz 2006; *Pedicularis chamissonis*: Kawai and Kudo 2009). This might be explained by the lack of contact with the stigma during each visit, low levels of pollen transfer, or differences in behavior between *B. terrestris*, on the one hand, and *B. atratus* and *B. impatiens* on the other (e.g. pollen removal and transfer, see Kawai and Kudo 2009). Maia-Silva et al. (2014) observed differences in number of pollen grains deposited after a single visit by two native stingless bees (*Melipona bicolor* and *Melipona marginata*) on the wild *Solanum variabile* in Brazil. However, a single visit of both species was enough to transfer sufficient pollen and fertilize all ovules in *S. variabile* (Maia-Silva et al. 2014). Hence, for a detailed explanation, additional studies on bumblebee behaviour, pollen release and deposition should be pursued. Further, it should be evaluated how much pollen has to be deposited on the stigma for high seed set in lulo.

Our results indicated that, for the viable use of *B. terrestris* for commercial cultivation of lulo, multiple flower visits have to be guaranteed. However, the behaviour of *B. terrestris* should facilitate multiple visits and should ensure high yield. In contrast to observations on tomato where visit duration of *B. impatiens* generally decreased after the first visit (Nunes-Silva et al. 2013), we found no decline after previous bumblebee visitation, even when 75 visits in a single day occurred. Therefore, long-standing attractants, for example floral scent, colour, apparently pollen-filled anthers (Buchmann 1983), or a substantial pollen 'reward', must be maintained during multiple visits (cf. Buchmann and Cane 1989; Nunes-Silva et al. 2013). Lulo anthers are longer (about 10–11 mm: Diggle and Miller 2004) than those of the tomato (e.g. cultivar 'Beefsteak': 8.8 mm; Lefebvre and Pierre 2006) and might therefore appear (to bees) to provide larger amounts of pollen. This suggestion is supported by the findings of Lefebvre and Pierre (2006) in two tomato cultivars with different anther size.

It is known that frequent buzzing could cause flower destruction and abortion (e.g. tomato: Nunes-Silva et al. 2013) or malformations of the fruits (Velthuis and van Doorn 2006). Lulo flowers tolerated high visit rates and duration of *B. terrestris*, and sustained relatively less damage, compared with tomato pollinated by *B. impatiens* (Morandin et al. 2001; Nunes-Silva et al. 2013). This difference could be explained primarily by differences in the pollinator's behaviour. Mean visit duration of *B. impatiens* on its first visit on tomato flowers was much longer (89 ± 71 s: Nunes-Silva et al. 2013) than those measured for *B. terrestris* on lulo flowers (15 ± 12 s), thus causing potentially higher levels of damage at a single visit. In addition, the lulo anther is apparently more robust than that of the tomato and less likely to be damaged by biting. This may help maintain the attraction of bumblebees, as the anthers appear to be virgin and pollen-filled. This is an ideal precondition for multiple visits facilitating cross-pollination (see Kawai and Kudo 2009; Wanigasekara and Karunaratne 2012), and high yield.

In overall conclusion, the bumblebee, *B. terrestris*, and the lulo, *S. quitoense*, seem to be biologically compatible as pollen vector and pollen source, respectively. As long as multiple visits were ensured, fruit set, seed set and fruit size were as high as those resulting from cross-pollination. In general, workers visited flowers frequently and the floral characteristics of the lulo facilitated multiple visits. The combination of the two indicates that this is a commercially viable interrelationship, suitable for the production of lulo fruits in glasshouse cropping systems in Central Europe.

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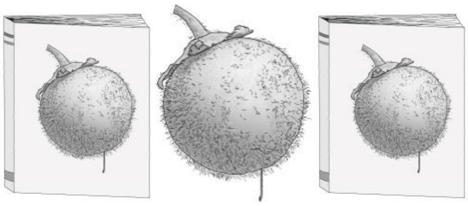
CHAPTER 7

LIST OF PUBLICATIONS



This chapter lists further articles not included within this thesis, conferences, posters and other publications.

7 List of further, not included publications

Articles published in international peer-reviewed journals

IRL S, STEINBAUER M, BABEL W, BEIERKUHNLEIN C, BLUME-WERRY G, MESSINGER J, PALOMARES-MARTÍNEZ A, STROHMEIER S, JENTSCH A (2012): An 11-yr exclosure experiment in a high-elevation island ecosystem: introduced herbivore impact on shrub species richness, seedling recruitment and population dynamics. Journal of Vegetation Science 23 (6), 1114 –1125.

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IRL S, STEINBAUER M, MESSINGER J, BLUME-WERRY G, PALOMARES-MARTÍNEZ A, BEIERKUHNLEIN C, JENTSCH A (2014): Burned and devoured - Introduced herbivores, fire and the endemic flora of the high-elevation ecosystem on La Palma, Canary Islands. Arctic, Antarctic, and Alpine Research 46(4), 859–869.

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MESSINGER J, GÜNEY A, ZIMMERMANN R, GANSER B, BACHMANN M, REMMELE S, AAS G (2015): *Cedrus libani*: A promising tree species for Central European forestry facing climate change? European Journal of Forest Research 134, 1005–1017.

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Conferences and Seminars

MESSINGER J, AAS G, KONNERT M, ROMMEL D, SCHMIEDINGER A, STIMM B, BACHMANN M (2012): Neue Gastbaumarten braucht das Land: Anspruch und Realität am Beispiel dreier Pinaceae. Oral presentation at the FowiTa (Forstwissenschaftliche Tagung), München, Germany, 21.09.2012.

MESSINGER J, LAUERER M, AAS G (2014): Forschungsergebnisse 2012-2014: Optimierung des Anbaus tropischer Nutzpflanzen unter Glas in Mitteleuropa. Oral presentation at the Projektbeiratstreffen, Bayreuth, Germany, 11.03.2014.

MESSINGER J, LAUERER M (2015): Ausgerechnet Bananen! Exotische Früchte aus nachhaltigem Anbau in Klein-Eden im Frankenwald. Oral presentation at the Naturforschende Gesellschaft Bamberg e.V. Bamberg, Germany, 30.10.2015.

Posters

MESSINGER J, ENDREß A, LAUERER M (2013): Greenhouse cultivation of Lulo in Central Europe: a suitable new crop considering seasonal fluctuations? Presented at the 2nd Int. Symposium on Organic Greenhouse Horticulture, Avignon, France.

MESSINGER J, LAUERER M (2013): Phenology and yield of the new greenhouse crop Lulo in Europe. Poster presented at the Bayceer-Workshop, Bayreuth, Germany.

ENDREß A, MESSINGER J, LAUERER M (2013): New crop in testing phase: Do pinching and post-harvest ripening influence yield and fruit quality of Lulo? Poster presented at the Bayceer-Workshop, Bayreuth, Germany.

MESSINGER J, ENDREß A, BRAUER F, SCHWARZINGER S, LAUERER M (2017): Physico-chemical and sensory quality of the lulo fruit is high but varies seasonally. Presented at the Symposium by Lebensmittelchemische Gesellschaft LChG, Kulmbach/Bayreuth, Germany.

Other publications and reports

MESSINGER J, LAUERER M, AAS G (2014): Optimierung des Anbaus tropischer Nutzpflanzen unter Glas in Mitteleuropa – Untersuchungen an Lulo (*Solanum quitoense*). EU-Forschungsbericht Projekt „Klein-Eden: Tropenhaus am Rennsteig".

LAUERER M, MESSINGER J, AAS G (2012): Tropische Früchte aus Franken: Das Umweltprojekt „Klein Eden" ist „Leuchtturm-Projekt 2012". Medienmitteilung der Universität Bayreuth Nr. 327

CHAPTER 8

APPENDIX

This chapter lists results and observations of further studies on lulo (*Solanum quitoense*) conducted in this thesis but not prepared in the manuscripts.

8 Appendix

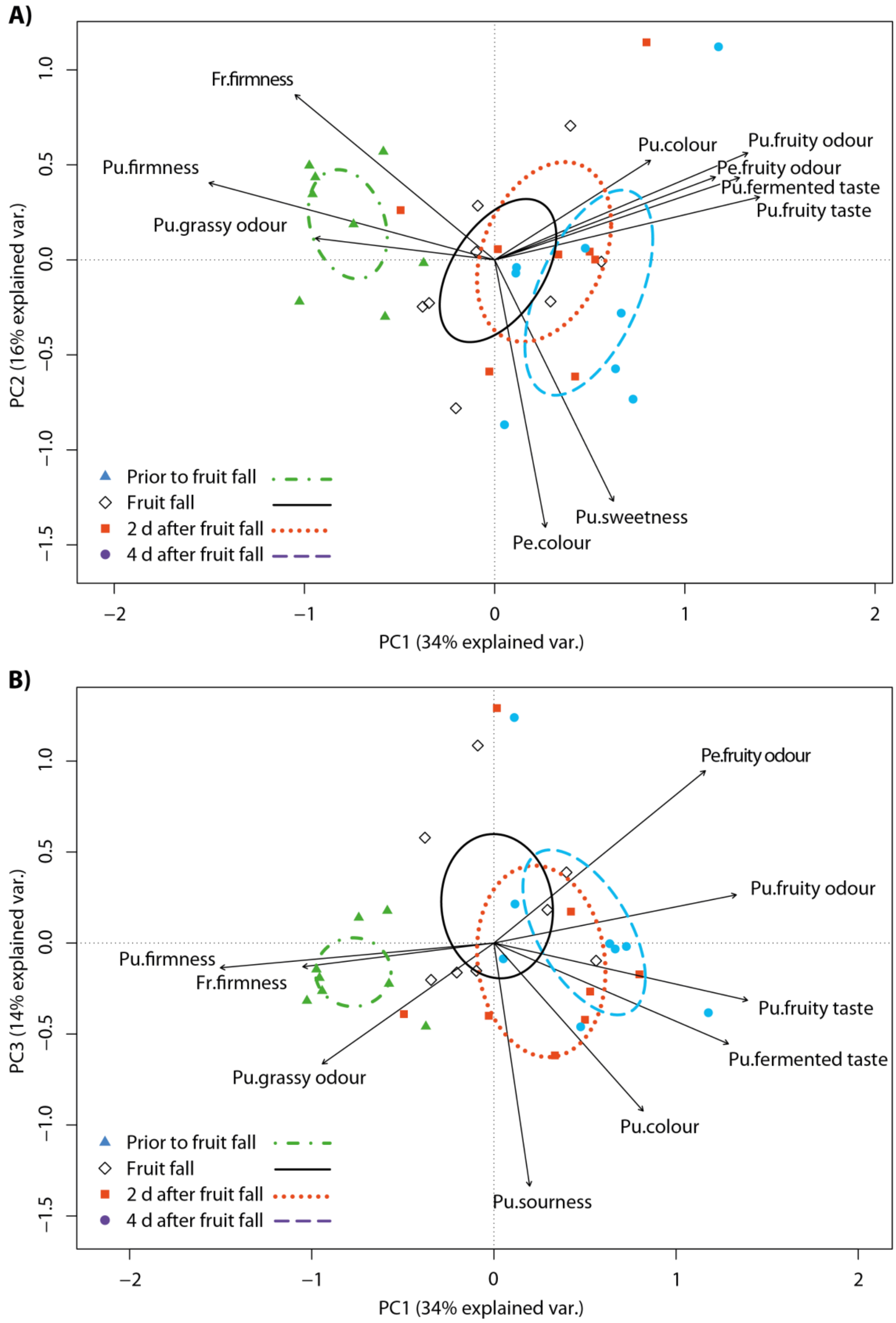
8.1 Appendix A1: Study of impact of ripeness/storage on sensory profile

Appendix A1.1: Ripeness stages and storage periods of lulo fruits (*Solanum quitoense*) investigated. Lulo fruits were checked daily for colour changes and fruit fall. Physically undamaged and medium-sized fruits with a diameter between 4 and 5 cm were randomly chosen from 20 lulo plants grown at the EBG.

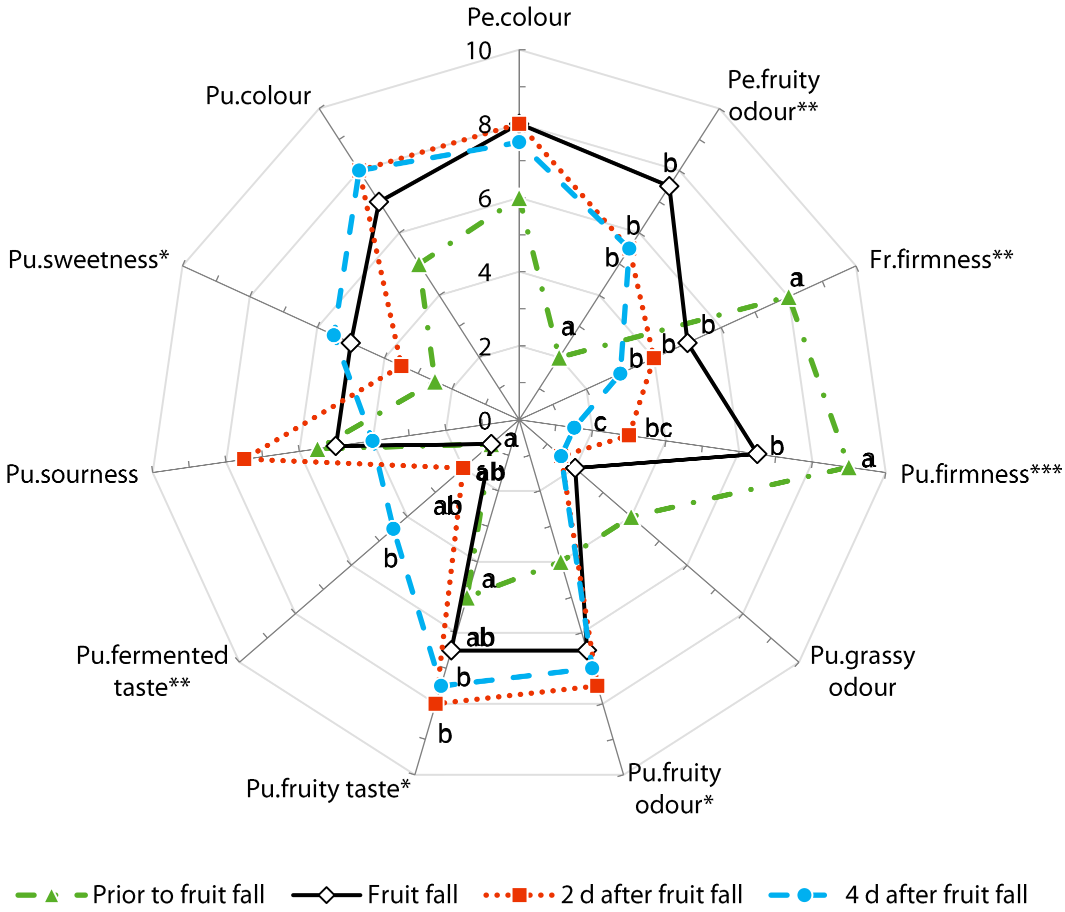
Ripeness stage / Storage period	Description	Method
Prior to fruit fall	Fruits were on the plant and picked when peel colour changed to overall (100%) red-orange (shade 28A)	Visual on plant by RHS Colour Chart, (Royal Horticultural Society, London)
Fruit fall	Fruits were taken as close to fruit fall as possible (fruits were checked daily for fruit fall)	Fruit detached from the plant
2 d after fruit fall	Fruits fallen off the plant were stored subsequently for 2 d and stored before analyses in the dark at a mean temperature of 21 °C and mean relative humidity of 54%.	Time scale
4 d after fruit fall	Fruits fallen off the plant were stored subsequently for 4 d and stored before analyses in the dark at a mean temperature of 21 °C and mean relative humidity of 54%.	Time scale

Appendix A1.2: *Solanum quitoense* fruit attributes used in sensory profile test (after DIN-standard) from 24 May 2014 to 20 July 2014 by a sensory skilled panel of 8 members (5 females and 3 males, aged 20–50 years, resident in Bayreuth and Kulmbach, Bavaria, Germany) to detect variation in lulo fruit attributes according to ripening stage and storage time. The panellists were asked to describe the characteristic value of each fruit attribute by using an intensity scale from "0" (lowest intensity of characteristic value) to "10" (highest intensity of characteristic value) as a basis for assessment. Before analysis the panellists were introduced to this intensity scale for each fruit attribute (references for lowest and highest expression). An entire fresh fruit of each treatment was offered to one panellist on one day, or (when not all ripening stages were available on the same day) successively within a maximum of seven days in a room. The samples were encoded by a randomly selected triple-digit code and offered to each panellist in a random sequence. Primarily, entire fruit and peel characteristics were assessed; the fruit was then cut into halves and pulp characteristics were evaluated. Still water was offered to panellists to neutralize the taste between samples.

Fruit attribute		Description	Method	Scaling
Entire fruit	Firmness	Resistance when pressing the fruit between the fingers	By hand	Soft to firm
	Fruity odour	Overall fruity, strawberry-like odour	Sniffing	Low to high intensity
	Grassy odour	Green, herbal odour, attributed to grass	Sniffing	Low to high intensity
Peel	Colour	Orange shade	Visual	Yellowish to reddish
Pulp	Colour	Green brightness	Visual	Bright to dark
	Firmness	Force required for spooning the pulp out and chewing	By hand & feeling in mouth	Soft to firm
	Fruity odour	Overall fruity, kiwi-like odour	Sniffing	Low to high intensity
	Grassy odour	Green, herbal odour, attributed to grass	Sniffing	Low to high intensity
	Fruity taste	Overall fruity, kiwi-like taste	Tasting	Low to high intensity
	Sourness	Sour, acid taste	Tasting	Low to high intensity
	Sweetness	Sweet, sugary taste	Tasting	Low to high intensity
	Fermented taste	Over-ripe, unpleasant taste with a slightly bitter note	Tasting	Low to high intensity



Appendix A1.3: PCA plot of sensory profile for *Solanum quitoense* fruit samples picked (▲) prior to fruit fall, (◇) at fruit fall, and stored for (■) 2 d or (●) 4 d after fruit fall. Values (symbols) of each panellist per ripening stage (n = 8), sensory fruit attributes (arrows, for description of attributes see **Appendix A1.2**) and 95% confidence interval of averaged value per ripening stage (lines) are given (scale factor = 3). Fr. = entire fruit, Pe. = peel, Pu. = pulp.



Appendix A1.4: Sensory evaluation of *Solanum quitoense* fruit attributes (Fr. = entire fruit, Pe. = peel, Pu. = pulp, for description of attributes see **Appendix A1.2**) by a skilled panel (n = 8). Each panellist tested four different ripening stages: (▲) prior to fruit fall, (◇) fruit fall, (■) 2 d and (●) 4 d storage after fruit fall. Median values are given. The numbers 0-10 signify panels' assessment on the intensity scale from "0" (lowest intensity of characteristic value) to "10" (highest intensity of characteristic value) used in the profile test. Significant impact of ripening stage on each fruit attribute is indicated by asterisks (Friedman, *P < 0.05, **P < 0.01, ***P < 0.001). Lowercase letters within the spider web indicated the significant differences for each attribute (P < 0.05, pairwise Mann-Whitney-U) and in case of "Pu.fruity taste" the trend (P < 0.1, pairwise Mann-Whitney-U) between the ripening stages per fruit attribute is given.

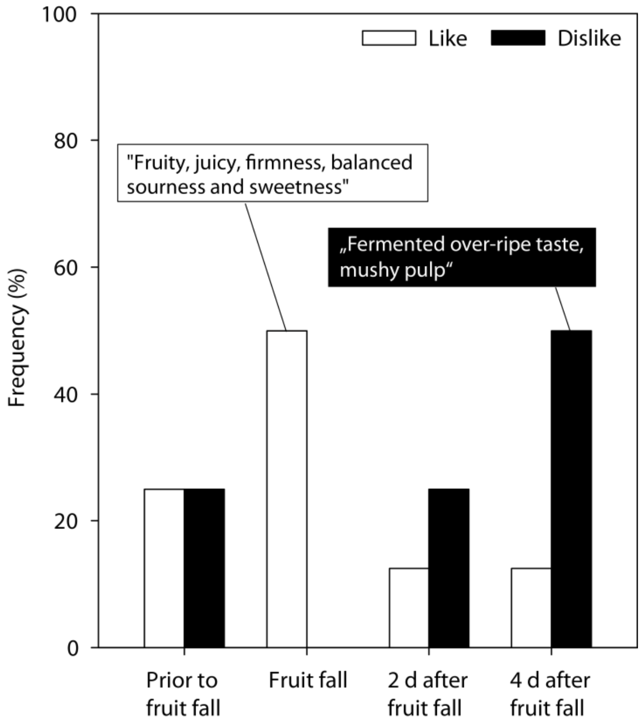
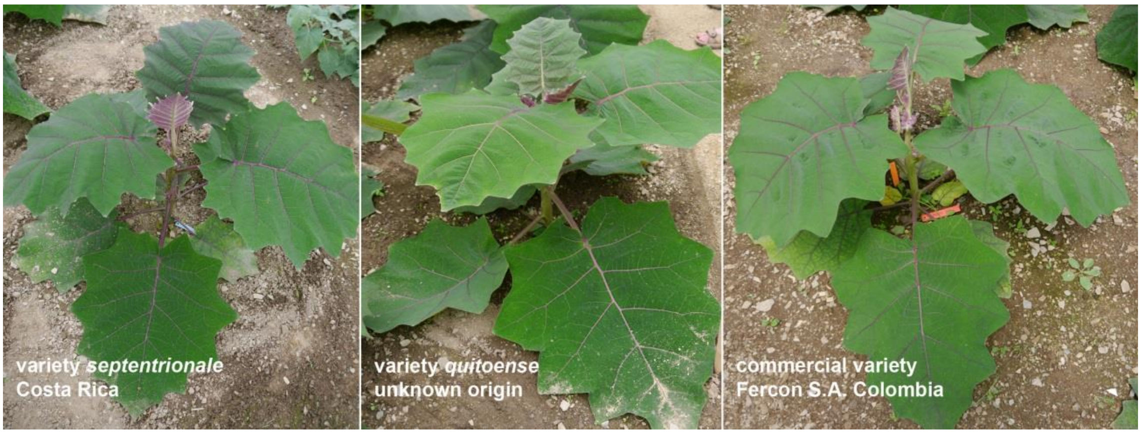


Figure A1.5: Overall perception of *Solanum quitoense* fruits by a skilled panel (n = 8). Each panellist stated the most liked (white bars) and disliked (black bars) fruit sample. The comments of their decision are given for the most liked and most disliked sample. Fruits were sampled at four different ripening stages: prior to fruit fall, at fruit fall, 2 d and 4 d storage after fruit fall (see **Appendix A2.1**).

8.2 Appendix A2: *Fusarium*-infestation of lulo plants

Appendix A2: *Fusarium*-infestation of *Solanum quitoense* plants in the tropical greenhouse Klein-Eden (Kleintettau, Germany) in 2014. Typical symptoms were leaf necrosis (A), apex wilting (B), browning and wilting of the fruits before fruit drop (C). In cooperation with Mathias Krauss (Pflanzenschutzdienst, Amt für Ernährung, Landwirtschaft und Forsten, AELF, Bayreuth) *Fusarium oxysporum* was laboratory-confirmed in lulo plant samples (cross section of stem). The pathogen caused crop failure and finally plant death.

8.3 Appendix A3: Preliminary growing trial of different lulo varieties



Appendix A3.1: Different *Solanum quitoense* varieties and origins cultivated in a preliminary experiment from February 2013 until January 2014. The plants were about four months old. The variety *septentrionale* (left) and *quitoense* (middle) were differentiated by presence/absence of spines on the plant: the variety *septentrionale* had spines on leaves, petioles and stems, the variety *quitoense* was completely spineless (see Morton 1987; ACTI et al. 1989). The variety from a commercial source (Fercon S.A., Colombia, "commercial variety") was spineless and had a yellowish pulp (personal observation).

Appendix A3.2: Flower parameters (mean values) of different *Solanum quitoense* varieties / origins during investigation period from 03 July 2013 until 02 December 2013. Plants were cultivated in Klein-Eden (Kleintettau, Germany) and flowers were counted weekly of each individual per variety (n = 9). The varieties *septentrionale* and *quitoense* were differentiated by presence/absence of spines on the plant (see Morton 1987; ACTI et al. 1989).

Varieties / Origin of *Solanum quitoense*	Total flower	Hermaphroditic flower (HF)		Functional male flower (MF)		HF:MF ratio
	n	*n*	%	*n*	%	
var. *septentrionale* / Costa Rica	236	81	34	155	66	0.53
commercial variety[1] / Colombia	323	174	54	149	46	1.35
var. *quitoense* / unknown origin	212	53	25	159	75	0.32

[1]Commercial source from Fercon calidad que crece, Fercon S.A, Colombia. These plants were completely spineless and had a yellowish fruit pulp (in contrast to the other varieties with greenish pulp).

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Finally I thank my family for the permanent and never ending support during my whole life. I am deeply grateful to my husband Ronny Messinger for the love and energy he gave me for this step of my career. I appreciate his support with my ideas and during all circumstances in life.

Declarations

(§ 8 Satz 2 Nr. 3 PromO Fakultät)

Hiermit versichere ich eidesstattlich, dass ich die Arbeit selbständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe (vgl. Art. 64 Abs. 1 Satz 6 BayHSchG).

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