Root and tuber crops for feed and industry

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Abstract

Root and tuber crops (RTC) have had a strong impact on food security of tropical regions of the world. Their bulkiness and logistic problems associated with the storage of RTC have limited their impact from ancient times to the present. In spite of these problems, however, there are increasing opportunities for the industrial uses of RTC in the tropics. The globalization of the economies has made less competitive the tropical production of maize, therefore creating an opportunity for RTC to fill the gap. There are different strategies to adapt these crops for the needs of the industry. **1)** The raw material has to have a competitive price. Therefore varieties and cultural practices should guarantee high and stable yields as well as low production costs. In most cases a key trait that has strong bearing in the value of roots or tubers for the industry is their dry matter content, which typically needs to be maximized; **2)** Costs of processing should be minimized. Certain characteristics of roots and tubers have a strong impact on processing cost. For example roots and tubers whose starch is easier to hydrolyze would be desirable for the bio-ethanol industry; **3)** The quality of the product offers additional opportunities which only recently began to be properly addressed. For the feed industry enhanced nutritional quality (i.e. higher proteins, higher vitamins or lower anti-nutritional compounds) would be a key factor. For the starch industry variation in starch chemistry and functional properties provide huge opportunities already exploited in the cereals. Amylose-free starches have a wide range of applications in the industry. High-amylose (or resistant) starches also have a positive impact for people affected with diabetes; phosphates associated to potato starch define many of its unique properties; **4)** Developing new, high-value products from RTC is also an interesting approach. For example high-quality flour could replace starches for certain uses, which offers economic as well as environmental advantages. The exploitation of foliage for animal feeding has been extensive in the case of sweet potato in China and could be extended to other RTC. To deploy these strategies RTC can now combine different technologies that gradually have been adapted such as the use of marker-assisted selection and genetic transformation. In some instances, breeding and agronomy research needs to be combined. The production of herbicide-tolerant RTC (by genetic transformation or conventional breeding) combined with direct planting practices could have huge beneficial effects by reducing costs of production, increasing yields, and reducing the environmental impact of their cultivation (i.e. reduced soil erosion, improved water use efficiency, conservation of soil fertility). The case of cassava will be used to illustrate many of the strategies highlighted above.

Introduction

Root and tuber crops (RTC) have had and still have a particular importance in tropical and subtropical regions of the world. Agriculture was invented independently in many sites of the world. One of these sites was in Polynesia where agriculture development was based on RTC. Some of the key traits of these RTC (for example, their bulkiness and short shelf life), have been used to explain why these early societies did not evolve into agriculture civilizations such as those in the Fertile Crescent, where agriculture was mainly based on grains. In spite of the typical problems of RTC, there are increasing opportunities for the industrial uses of RTC in the tropics. The globalization of the economies has made less competitive tropical production of maize, therefore creating an opportunity for RTC to fill the gap. There are different strategies to adapt these crops for the needs of the industry which are briefly discussed, using mostly cassava to illustrate these strategies.

Competitive price of the raw material

Raw material is a critical component of the production costs of any agro-industry. In the case of starch industry of sweetpotato and cassava in Asia, for example, raw material represent between 70-80% of the cost of production (Fuglie, 2004; 2005 Fuglie et al. 2005; Howeler, 2005; Nelson, 1984; Titapiwatanakun, 1994). Therefore any research that results in a reduction of the costs of production and/or increased yields of RTC would have a positive impact on the competitiveness of agro-industries based on them. Most breeding projects aim at producing cultivars with high and stable productivity. Countless articles in the literature have reported progress in this regard. There are still new alternatives for reducing costs of production that can and are currently explored. The potential of herbicide tolerance will be used as an example because of its relevance in costs of production and because it highlights an interesting case of complementation between genetic, agronomic and mechanization of field operations research.

Herbicide tolerance in crops offers several advantages. The handling of herbicides can be made in a much more efficient way, applying them at the optimal timing when weeds are most vulnerable. This implies that there is a reduction in the amount of herbicides used, reducing costs of production on one hand, and having a positive impact on the environment, on the other. Perhaps more important is the possibility that herbicide tolerance allows direct planting, which without proper technologies to handle the problem of weeds, is often unviable. Direct planting also offers several advantages: it allows the maintenance of a mulch of crop residues on the soil, therefore reducing soil erosion and maximizing the capture and conservation of water and soil nutrients. Direct planting reduces the operations of soil preparation at planting time, which offer the dual advantages of reducing costs and the negative impact on the environment. There are few alternative approaches to develop RTC tolerant to herbicides, which will be described below.

Genetic transformation

In the case of cassava the first reports on the production of transgenic somatic embryos and plants date back to 1993-1995. Since then several events ranging from herbicide tolerance, reduction of cyanogenic potential to the increase or quality of starch produced by the plant have been reported (Ihemere et al. 2006; Jørgensen et al., 2005; Sarria et al. 1993; Taylor et al., 2004). The development and exploitation of genetically modified crops faces some problems ranging from intellectual property rights, regulatory issues on human health, regulatory issues to prevent gene flow to technical issues related to the process of genetic transformation itself.

Natural occurrence of tolerance to herbicides

There are many examples reported in the literature where tolerance to different herbicides has been found in different crops (canola, cotton, lentil, lettuce, maize, rice, sugar beet, sunflower, tobacco, tomato, and wheat), which lead to the release of trade marks such as Clearfield, RoundUp Ready and Liberty Link (Sherman et al., 1996; Tan et al., 2005; 2006; Tan and Bowe, 2008). In most of these cases, tolerance to herbicides was based on recessive or partially dominant genes and self-pollinations have facilitated their identification.

Induction of mutations

Tolerance to herbicides has also been obtained through the induction of mutations using chemicals such as ethyl methanesulfonate (EMS) or radiations like gamma rays (Tan et al., 2005; 2006). It is important to highlight that the use of these natural or induced mutations can overcome some of the regulatory issues that hinder the exploitation of transgenic crops, but nonetheless would have to be used with certain caution to avoid the flow of genes from the herbicide tolerant crop to related weeds. Eco-TILLING (Guang-Xi et al., 2007; Till et al., 2003) is an interesting approach for the identification of natural or induced mutations where the actual site for the mutation is well known. For instance tolerance to imidazolinones relies on a mutation at the AHAS (acetohydoxyacid sinthase) gene. CIAT is currently growing a set of about 800 S1 genotypes in five different blocks. Each genotype is represented by two plants in each block. Each of these blocks will be sprayed with a different herbicide, using commercial doses. The aim is to identify partially inbred genotypes showing resistance or tolerance to any of these herbicides.

Minimized costs of processing

The example of bio-ethanol and cassava will be used as example for this section because of its current relevance and the significance of processing costs on the competitiveness of this industry. Bio-fuels are currently based on the production of ethanol from sugars or starch derived from vegetative biomass and grain, or bio-diesel from the more direct use of edible and non-edible plant oils and animal fats (Ortiz et al., 2006). Brazil is the shining example for carburant ethanol production and use (from sugarcane juice), either in pure form or as a blend with petrol. Billions of gallons of bio-ethanol are produced annually in Brazil from sugarcane. Recently the production of ethanol from starch-producing crops has received considerable attention. Key factors for this new development are the emerging technologies and the cost to hydrolyze the starch (originally based on two stages: liquefaction and saccharification) prior the beginning of the fermentation process (Shetty et al. 2007). Research in microbiology has led to the development of new enzymatic processes that make the hydrolysis of starch more efficient and less expensive. However, using the traditional liquefaction and saccharification process or the new enzymatic approaches, there are expenses involved in the process of conversion of roots or grain into ethanol.

One objective for the RTC research community in this regard would be the development of raw material that reduces the cost of processing. Several alternatives can be mentioned to illustrate the potential of these interventions (Reddy et al., 2008).

Modification of the roots or tubers to produce molecules simpler than starch

Carvalho and co-workers reported in 2004 a group of interesting "sugary" mutations in cassava that result in storage roots with high free sugars (mostly glucose) and a glycogen-like molecule. The roots from these genotypes have reduced levels of amylose and low dry matter content (DMC). The costs of processing this type of root into ethanol should be considerably lower compared with normal cassava roots. This mutation is widely distributed scattered in the Amazon basin. Although the cost of processing roots from this type of cassava into ethanol would be considerably reduced, a key factor for its ultimate usefulness would be its production of energy per area.

Modification of the roots or tubers to produce starches which are easier to degrade

Sharma et al., reported in 2007 studies on the enzymatic requirements for the conversion of maize into ethanol, in response to varying proportion of amylose: amylopectin in the starch. They concluded that amylose-free maize (*waxy*) would be better and more efficient for the production of ethanol. There are several reports of amylose-free RTC (described below in this article). The production of ethanol using these amylose-free RTC would be more efficient and competitive. There is an ongoing project to release commercial cassava varieties with "*waxy*" starch.

Maximized dry matter content versus production of energy per hectare

For most industries the need to reduce costs of production implies that roots or tubers from different crops and cultivars are required to have a maximum amount of DMC. A raw material with low DMC would imply higher costs of starch extraction (i.e. production of higher amount of effluents) or longer periods for drying the roots in the drying yards. Breeders frequently find that genotypes with a maximum productivity of dry matter per hectare are unacceptable because that productivity is based on high production of fresh roots, but at low levels of DMC. These genotypes have been routinely eliminated in spite of their excellent yield potential. In response to these requirements, there has been considerable progress in improving DMC of modern cassava varieties (Kawano, 2003). The bioethanol industry, however, has created a new opportunity for these genotypes with maximum productivity of dry matter per hectare but based on low dry matter contents. In the case of ethanol production it is feasible to envision that, at least in certain periods, fresh roots could be grinded directly to initiate the process of transformation into ethanol. In this case, it may be attractive for the whole process to rely on cultivars with maximum production of energy per hectare independently of the levels of DMC of the root.

Qualitative characteristics of roots and tubers

The quality of roots and tuber offer additional opportunities which only recently began to be properly addressed. For the feed industry enhanced nutritional quality would be a key factor. For the starch industry variation in starch chemistry and functional properties provide huge opportunities already exploited in the cereals.

Enhancement of the nutritional value of roots and tubers

Recently, an international initiative seeking a reduction in micronutrient malnutrition using plant breeding to develop staple food crops rich in micronutrients, including provitamin A carotenoids, was initiated. The program, known as **HarvestPlus**, involves a global alliance among research institutions and implementing agencies in developed and developing countries. The first six focal crops that comprise staple food for the majority of people in the world, who have or are at high-risk of micronutrient deficiencies, are cassava, sweet potato, maize, rice, wheat, and beans.

In the case of cassava the first step in the identification or production of cassava clones with enhanced nutritional value has been a systematic and massive screening of landraces from CIAT germplasm collection and key improved clones. The screening involved evaluations for many micronutrients but currently has been narrowed to pro-vitamin A carotenoids, minerals (Fe and Zn) and proteins. Germplasm evaluated and quantification methods were described by Chávez et al. (2005). These authors also reported wide genetic variation for levels of pro-vitamin A carotenoids. After five years of rapid-cycling recurrent selection, maximum levels of total carotenoids content has been increased almost three-fold (CIAT, 2008). β-carotene has been found to be the most important component in these measurements (typically 50-80% of total carotenoids is β-carotene). High carotene roots have a tendency for reduced or delayed post-harvest physiological deterioration (Sánchez et al., 2005, CIAT, 2009).

For Fe and Zn, in spite of the earlier promising variation (Chávez et al., 2005), it has become gradually evident that high contents for these two minerals are often the result of contamination from soil or tools used to process the roots. pH of the soil has proven to be more important than content of these elements in the soil or the genotype. Negligible effects of different types and dosages of fertilization to the cassava plant had been found on the contents of Zn and Fe (CIAT, unpublished data).

Variation in protein content of cassava roots has also been reported (Ceballos et al., 2006a). CIAT has also carried out a long-term project for higher protein content in the roots in crosses with wild relatives such as *M. esculenta* subsp. *fabellifolia* and *M. tristis* (Ceballos et al., 2006b). A total of 49 inter-specific crosses, ranging from 6.39 to 10.46% in protein content, have been selected and back-crossed into an elite *M. esculenta* clone. More than 6,000 back-crosses have been made. However, data still being processed suggest that in the case of cassava roots, the N-to-protein conversion factor is considerably lower than the standard 6.25 constant. Genetic variation is still present in these quantifications but the range of variation is drastically reduced from 1-8% (when the measurements are based on the indirect method of N quantification) to 0.5-1.8% (when soluble proteins were estimated through the Bradford method).

High-amylose starches, commonly known as resistant starches, have lead to interesting outcomes for human health in recent years. They are described in more detail in the following section but, because their advantages in human nutrition, they are also mentioned in this section.

Generation and identification of clones with novel starch types

Starch is a simple polymer of glucose units that are linked together in two forms (amyloes or amylopectin) yet, as stated by BeMiller (1997), after thousand of studies, it remains a beautifully mysterious substance. Amylose is essentially a linear chain, whereas amylopectin (which is typically the major component of starch) is a much larger molecule and is highly branched. The relative proportion of amylose and amylopectin, their degree of branching, and the length of the different branches greatly affect the properties of the starch. One of the most intriguing challenges in starch research is to explain the simultaneous synthesis of these two polymers and to understand the regulation of the several enzymes (and genes) involved (Denyer et al., 2001). RTC offer a great diversity of starches in relation to granule morphology, chemical composition, crytallinity, structure of amylose and amylopectin, swelling power and solubility, gelatinization, rheology, digestibility and retrogradation (Arachchige et al. 2009; Degbeu et al., 2008; Gunaratne and Hoover, 2002; Hoover, 2001; Peroni et al., 2006; Srichuwong and Jane, 2007). Table 1 provides a summary of the main features of starches from several RTC. Starch granule sizes vary from the very small granules of *Disocorea esculenta* (1-5 µg) to the large granules of potato (15-110 µg). Amylose content ranges from 15.9 in *Nelumbo nucifera* to 38.0% in *Canna edulis*. Cassava has very low levels of lipids (0.1%), whereas *Cucurbita foetidisima* has much higher values (around 1%). Potato starch is recognized because of its levels of phosphates associated to its starch. These phosphates confer enhanced paste clarity, high peak consistency, significant shear thinning and slow rate and extent of retrogradation. Starches belonging to the Diocorea species exhibit a higher pasting temperature and thermal stability that other RTC starches (Hoover, 2001). A characterization of starches from more than 4000 cassava genotypes has recently been published (Sánchez et al., 2009).

Cassava (*Manihot esculenta* Crantz), sweet potato and potato are among the most important sources of commercial production of starch along with maize and wheat. Cassava and sweet potato starches are particularly important in Asia. Starches from cassava and potato share many similarities: they produce relatively bland pastes, with higher viscosity, better clarity and lower retrogradation rates than starches from cereals. They also possess lower levels of proteins and lipids (Davis et al, 2003; Ellis et al., 1998). Many comparisons of the physicochemical and functional properties of starches from different crops have been published, as well as the effect of the absence of amylose in waxy starches (Peroni et al., 2006; Praznik et al., 1999; Li and Yeh, 2001; McPherson and Jane, 1999; Visser et al., 1997; Hoover and Manuel, 1996; Tetchi et al., 2007).

In spite of the wide variation in starch functional properties among different RTC, it is of utmost interest for the starch industries of each crop to have access to starches varying in their own characteristics within. The potential for new commercial starches can be even greater when biological and chemical modifications are combined (BeMiller, 1997). A key trait defining the functional properties (and therefore, potential uses for the industry) is the relative proportion of amylose and amylopectin in the starch. As a result of efforts to produce modification of starch *in planta* (via conventional breeding or genetic transformation) amylose-free as well as high-amylose starches are now available in potato (McPherson and Jane, 1999; Visser et al. 1997; Hoover, 2001), cassava (Ceballos et al., 2007; Raemakers et al., 2005), and sweet potato (Kitahara et al., 2007). These modifications in the starch main components widen the potential uses of the respective starches. Moreover, since modification is achieved *in planta* rather than *in vitro*, there are undeniable economic and environmental advantages (Davis et al, 2003; Ellis et al., 1998). High-amylose starches are frequently associated with small starch granule size. Small granule morphology has been reported in potato (Noda et al., 2005) and cassava (Ceballos et al., 2008).

The industrial applications of amylose-free starches from different crops are widely reported (Hannah, 2000; Preiss, 2004; Watson 1988). Advantages and commercial applications of high-amylose starches, on the other hand, are more recent. Increased amylose levels leads to slowly digestible and resistant starches (Jobling, 2004; Lehman and Robin, 2007), which have distinctive advantage in health, particularly in diabetes management. Slowly digestible starches may influence satiety and help control overweight problems and have also been linked to improved mental performances (Lehman and Robin, 2007). In addition, high-amylose starches in different crops offer advantages in the production of sweets, adhesives, corrugated boards and in the paper industry, and reduces the uptake of fat in certain fried products (Jobling, 2004). Very high levels of amylose result in "resistant" starches. Maize starches with more than 70% can be produced commercially. Resistant starches cannot be digested but they are rather fermented in the large intestine resulting in the production of butyrate that has been found to be beneficial to colon health (Jobling, 2004).

There are several strategies that lead to the identification of genotypes (including RTC) that modify starch properties *in planta*. The recessive nature of mutations that leads to the production of such genotypes implies certain limitations for polyploid crops because of the difficulties of recessive mutations to express themselves in polyploid genotypes.

Screening self-pollinated progenies. For many years the most common approach has been based on careful screening of self-pollinated progenies. Since most of these characteristics are due to recessive mutations, inbreeding is a key step to facilitate their expression and, therefore, identification. One of the earliest genes characterized in any organism is the waxy (*wx*) locus of maize (*Hanna, 2000*). It is the peculiar waxy texture of the endosperm of amylose-free maize that lead to the naming of the locus. Self-pollinations may possess important limitations in several RTC which have auto-incompatibility such as potato and sweet potato. Systematic self-pollinations, followed by careful screening (including special tests that will allow the identification of genotypes whose starch have special characteristics), allowed the identification of an amylose-free mutation in cassava (Ceballos et al., 2007).

Induction of mutations. Breeders have used chemical products or irradiation (i.e. gamma rays) to induce mutations and generate genetic variability with relative success, particularly in the decades of the 1950s and 1960s (Maluszynski et al., 2001; Ahloowalia et al., 2004). That was the approach taken for the induction and identification of a small granule, high-amylose mutation in cassava (Ceballos et al., 2008). In spite of this success, mutation breeding has a few drawbacks. Events are totally random, recessive in nature, and usually appear as chimeras. Therefore, thousands of genotypes need to be evaluated before a useful mutation in the desired gene can be found. With the advent of molecular biology tools, an interesting system was developed to overcome some of the limitations of mutation breeding. DNA TILLING (for *Targeted Induced Local Lesions in Genome*) has been successfully used in different plant species (McCallum et al., 2000; Perry et al. 2003; Till et al. 2003). Sexual seeds are mutagenized and, to avoid ambiguities caused by chimeras in the first generation plants ($\mathbf{M}_1$), they are self-pollinated. The resulting plants ($\mathbf{M}_2$) are then evaluated while DNA is extracted from them. For screening purposes, DNAs are pooled eightfold to maximize the efficiency of mutation detection (Till et al., 2003).

Interspecific crosse. Wild relatives are a common source of genetic variability, particularly in traits that are not commonly found in the cultivated gene pool. CIAT is actively searching for several valuable traits in *Manihot* species other than *M. esculenta*. The project for the introgression of the high-protein trait has already been mentioned. Tolerance to post-harvest physiological deterioration (PPD) in cassava roots has been identified in an inter-specific hybrid between cassava and *M. walkerae*. Accessions of *M. crassisepala* and *M. chlorosticta* are the only genotypes from the primary and secondary gene pool of the crop discovered to possess the waxy starch phenotype (Ceballos et al. 2006). For several years now molecular marker tools and a modified advanced back-cross QTL scheme have been tested for cost-effective pyramiding of useful genes from cultivated and wild gene pools through the elimination of phenotypic evaluations in each breeding cycle.

Recurrent selection. The power of recurrent selection to gradually but consistently changing the quality of crops has been well established in the now classic study on maize for altered protein and oils content. (Dudley, 1974). It is feasible, therefore, to implement recurrent selection programs to produce genotypes with altered starch quality (Ceballos et al. 2006b). However, such programs would be expensive and time consuming. Breeders, therefore, find the possibility of a discovery or induction of single mutations that have a drastic effect on starch quality traits more attractive. Recurrent selection has been used to complement the effect of high-amylose mutations in maize (*amylose extender*) for further increasing the proportion of amylose (Jobling 2004; Richardson et al., 2000).

Genetic transformation. Several of the starches with modified characteristics described above have been obtained through genetic transformation (Visser 1997, Raemakers 2005, Kitahara et al. 2007, by antinsense inhibition or RNA interference. The genetic engineering of cassava varieties to produce waxy starch via anti-sense, down-regulation of the GBSSI gene has been reported (Salehuzzaman et al., 1993; Munyikwa et al., 1997). The technology of genetic transformation has become a generalized tool in germplasm enhancement. It offers unique advantages, it is very target-specific and commercial varieties with proven adaptability and high yields can quickly be converted to produce specialty starches. However the regulatory issues related to the release of genetically modified organisms, particularly for direct human consumption, has limited the economic impact of this technology. An important contribution of genetic transformation has been the possibility of silencing different genes, thus greatly facilitating the understanding of starch biosynthesis (Denyer et al., 2001)

Developing high-value products from RTC

Considerable opportunities are also available in the area of processing RTC to develop new products that may offer competitive advantages in the market. The possibility of producing refined flours will be used as an example of the kind of products that can be developed. In many cases, RTC are characterized by low protein and/or fat contents. This has had a negative impact on the value of these crops for animal feeding. However this disadvantage can be turned into an opportunity.

The low levels of fat and protein in many RTC imply that the flour is a product that is close to pure starch, from the chemical point of view. It has been demonstrated that flours can be processed by physical methods to produce refined flour that resembles starch in many properties. The physical treatment implies separation of a considerable amount of fiber present in the flour and a further reduction in the granule size. Refined flours are very white and soft to the tact. Very much like starch, but at a considerable lower price. There are cases where these refined flours can be used to replace the more expensive starch from the respective crop. In the case of cassava, for example, the refined flours have been used successfully by the baking industry to replace up to 10% of wheat flour.. The potential of refined flours offers economic advantage because it is a product that can successfully compete with the more expensive starches from the respective crop. They also offer the advantage of a reduced impact of processing RTC on the environment. Many starch processing facilities fail to properly treat effluent water, therefore, affecting negatively the surrounding environment. Production of refined flour does not require water and does not produce effluents. Therefore the potential impact of production of refined flours from RTC on the environment is very small.

Concluding remarks

This article aimed at highlighting the diversity of approaches (mostly based on genetic enhancement) that can and are being taken to improve different TRC to better fit the needs of the industry. Below a list of key requirements for research to have a successful impact on different industries that rely on processing RTC.

- For a success in this area a fundamental requirement is a close and intimate interaction between the agricultural and industrial components of this continuum. A clear understanding of the needs of the industry is a key requisite for agriculture research to satisfy them.
- Aggressive and persistent research, frequently requiring several years to yield results, is more often than not an important requirement. A common problem faced by many research teams is the anxiety on the part of donor agencies (public or private) to produce results in an unrealistically short period of time.
- Researches must combine a clear understanding of the needs by the industry with suitable breeding and laboratory tests. For example, it took more than 40 years to identify a naturally occurring waxy-starch genotype in cassava. It was only after breeding techniques (self-pollinations) and special tests (in this case the simple iodine test) were systematically combined that such a mutation could be identified and started to be exploited.
- Researchers must also be very aggressive incorporating new technologies as they become available. Molecular markers (particularly as TILLING) and genetic transformation are becoming available technologies to many RTC. Their incorporation into the research agendas must be judicious and sensible.
- A major advantage for the industrial uses of RTC is that many technologies are crop neutral. Therefore, technologies developed for one crop can frequently be applied to other crops almost immediately. That is the case for example, of the starch hydrolyzing enzymes originally developed for maize, but equally effective on other starch crops.
- The exponential research capacity in the area of molecular markers in the past few years is astonishing. Cost and time wise the sequencing of a crop genome have become almost irrelevant issues. The availability of sequenced genomes and the increasingly efficient application of molecular tools would facilitate enormously the work to develop RTC cultivars that better fit the needs of different industries.
- A fundamental rationale behind the interest of adapting RTC to better serve the needs of the industry is that by doing it, research ultimately promotes rural development (processing of RTC because of their bulkiness is made close to production areas), strengthen and stabilize markets (one of the major drawbacks for producers or RTC) and ultimately alleviate poverty in communities that depend on RTC.

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Table 1. Descriptors of starches from different crops (adapted from Hoover, 2001)

Crop species	Starch yield (%)	Size (µg)	Amylose (%)	Lipids (%)	Org P (% dsb)	Inorg P (% dsb)
Amorphophallus paeonfolius	35	3.0-30.0	-	-	-	-
Canna edulis	60.3	13.0-57.6	38.0	0.30	-	-
Colocassia esculenta	55.1	3.0-3.5	21.4	0.39	0.021	-
Cucurbita foetidisima	-	2-24	23.2	0.92-1.14	0.01-0.06	-
Dioscorea abyssinica	-	29.2	29.7	0.05	-	-
Dioscorea alata	84.6	6-100	22.8-30.0	0.03	-	-
Dioscorea cayenesis	87.5	28.5-30.6	21.6-27.0	0.02	-	-
Disocorea dumetorum	88.0	28.5-30.6	10.0-24.6	0.04	-	-
Disocorea rotundata	86.1	10.0-70.0	22.4	0.04	-	-
Dioscorea esculenta	-	1-5	30.0	-	-	-
Ipomoea batatas	-	14.6	26	-	-	-
Lilium maximoroiczii	-	30.0	26.8	-	60 ppm	33ppm
Manihot esculenta	84.5[a]	16.3[a]	18.6-23.6	0.1	0.008	0.001
Maranta arundaceae	-	10.0-16.0	19.4	0.32	-	-
Nelumbo nucifera	-	15.0-40.0	15.9	-	48 ppm	-
Pueraria tuberosa	34.2	3.0-23.0	15.1-21.0	0.46	0.005	-
Rhizoma dioscorea	-	19.8-28.4	35	-	-	-
Solanum tuberosum	32	15-110	25.4	0.19	0.089	0.001
Xanthosoma sagitifolium	43.8	10.0-50.0	23.7	-	-	-

[a] Based on new data published by Ceballos et al., in 2008. Also see Peroni et al., 2007.