The Sweetpotato (Ipomoea batatas) from Early Migration to Future Conservation

"The Worlds Most Under-Rated Crop"

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Introduction:

Described by Villareal (1982), as the worlds most under-rated crop and the best kept secret in Agriculture, the sweetpotato (*Ipomoea batatas*) ranks as the world's seventh largest food crop (FOA) and one of the two most important tuber crops in Asia, the Pacific and Oceania (APO) region (Nissila et al, 1999). Despite its importance it has received less attention than some garden ornamentals! Of the 50 genera and more than 1,200 species of the *Convolvulaceae* family the sweetpotato is the only member that is grown as a food crop with other members; *Convolvulus sepium* (Hedge bindweed), *Convolvulus arvensis* (Field bindweed) and *Ipomoea pandurata* (Man of the earth) being economically important due to their role as noxious weeds (Edmond 1971.p.1).

Nutritionally the sweetpotato is a good source for easily digestible carbohydrate. Having a high vitamin A content with some varieties containing sufficient concentrations to provide the recommended daily allowance (RDA) with a daily intake of only 13g. Consumption of only 113g per day can further be relied upon to provide reasonable amounts of vitamin C (25% RDA), B complex (5-7% RDA of niacin, riboflavin and thiamine respectively) , iron (10.2% RDA), potassium (10.8% RDA), sodium (2.3% RDA) and calcium (1.6% RDA). With fibre and protein content as high as 23% the sweetpotato can provide an extremely valuable component to poor diets. Even the tops of the plant can be eaten and have been shown to contain nutrient levels equal to pork or beef (Collins et al., 1982.p355-363).

One of the highest yielding crops the sweetpotato has a higher food value and exceeds the total food production per unit are than rice(Villareal 1982). In relative obscurity in scientific literature the sweetpotato has one of the greatest potentials for development of superior varieties. In Asia it is considered to have a greater potential for yield improvement than any other crop (Bohac et al. 1995), whilst in North America and Japan the large potential of sweetpotato for use in industrial processes has led to specific programmes targeted to developing improved strains (Komaki 1996). Furthermore sweetpotato is extremely tolerant of limited water and nutrient availability being able to produce acceptable yields from the residual fertilizer following a rice crop (Villareal 1982 p.v). In the Southern Highlands of Papua New Guinea, where the sweetpotato forms the staple crop, continuous monocropping for ten years or more without the addition of fertilizer produces consistently acceptable yields despite the decrease in nutrient availability (Sillitoe et al. 1999).

Historical Perspectives on the Origin and Spread of The Sweetpo tato

The existence of sweetpotato germplasm throughout Polynesia, New Zealand, Australia and the Indonesian / New Guinea archipelago in pre-Columbus times, and the lack of evidence to account for this distribution, has led to controversy over the origin of the sweetpotato. However since the development of greater taxonomical and cytological studies it is rarely questioned that the sweetpotato originates from the America's (Yen 1982. p2). Its migration and distribution out of the Americas however is less certain and with, in 1947, the Kon-Tiki expedition establishing the possibility of successful drift voyages across the Pacific the possibility of extremely early migration is not discounted. In anthropology , Heyerdahl (1952) citesthe distribution of the sw eet potato as one of the primary foci of plant evidence tosupport the thesis of very early Pacific contact by American Indians. In essence, a reaffirmation of a contention long held that the plant was of American origin (de Candolle 1886). had assembled the conflicting views of his time in arriving at this probability. The controversy on the origin and movement of the sweet potato forms part of the wider problem of the movement of peoples into and within the Pacific" (Yen 1974. p1).The main hypotheses which are at variance with one another are summarized by Yen (1974 p2 -39) as:

The Prehistoric Hypotheses

The spread of the sweetpotato from west-to-east originating from an Asianic point or, in a modified theory, from an African species which spread to the APO region in one direction and then to America in the other. The former hypothesis however does not stand up to scrutiny whilst the latter is presented as "a plausible explanation of the pantropic distribution of the plant in a number of places by Merrill (1954) in his review of the botany of the voyages of James Cook."

The other prehistoric hypotheses also include the more widely held view of the spread of the sweetpotato in an east to west direction effected either by the early Polynesian seafarers, who reached the continental west coast and returned with the sweetpotato, or alternatively by early American Indian sailors who were in contact with the Polynesians. The degree to which these two peoples traded, if at all, is highly controversial. Other authors, such as Purseglove (1963) overcame the problem of germplasm transfer by promoting the multiple origin hypothesis however later modifying his ideas to support earlier claims that the plant distributed itself by flotation of the dried capsule or fruit on ocean currents (Purseglove 1965).

The Historic Hypotheses

Maintains that the sweetpotato was unknown outside the America's prior to the discovery and subsequent exploitation by the European explorers of the 16th and 17th centuries. That two of these early European explorers, Alvaro de Mendana and Pedro Fernandez de Quiros carried the plant and introduced it to the islands of the Marquesas, the Solomons and the New Hebrides. The implication of this hypotheses is that the plant was diffused and spread throughout the Pacific islands by Oceanic voyagers within a period of less than two centuries before the discovery and recording of the sweetpotato in these areas by later European explorers. Dixon (1932) however strongly opposed this theory on the grounds of the lack of evidence of planting of sweetpotato by early Europeans, the doubtful identification skills of these early voyagers and most importantly the strong indications of antiquity in Polynesia.

A more recent historical hypothesis put forward by Brand (1971) argues that the plant was transferred to India between 1498 and 1505 and then subsequently carried to Indonesia and then New Guinea by Persian and Hindu traders before being spread to Polynesia by sporadic one-way drift voyages. However since the publication of Yen's book Indonesia and New Guinea have become recognized as the areas of Asia most rich in genetic diversity (Nissila et al. 1999) so it is unlikely that the sweetpotato was first introduced into India prior to it's introduction into these areas.

The Combination Hypothesis

Maintains the American origin but identifies separate introductions into the western Pacific and Polynesia. Of the many proposed routes Barrau (1957) ameliorated the possibilities and proposed a tripartite hypothesis whereby sweetpotato underwent three separate introductions. The first or earliest being the prehistoric or Kumara line from Peru to Polynesia and from Polynesia the spread of germplasm to New Zealand, New Guinea, Australia and Hawaii. The arrival of Europeans in the 15th Century saw the introduction of the sweetpotato, this time from the Caribbean, into Europe and Africa, the Batata line; later continuing on, during the 15th and 16th centuries, from Africa to India and then into Indonesia and New Guinea . The last main introduction occurring in the 16th Century when sweetpotato travelled from Mexico to the Philippines before spreading into India, Japan and China. This hypothesis would account for the conflicting evidence and hypotheses. The high diversity of germplasm in Indonesia and New Guinea could well be a phenomena resulting from the convergence of these introductions on the area.

Whilst the tripartite hypothesis accounts well for the migration of sweetpotato out of America it does not explain the spread of the plant within the America's nor whether the plant originates from Central or South America. The early records of the Spanish explorers and missionaries in Mexico and Peru and the Portuguese in Brazil indicate that the sweetpotato was widely spread throughout Southern and Central America long before the arrival of Europeans (Yen 1982 p.20). The plant is believed to be Central America or NW South America with the ancient

Peruvian and Mayan civilizations undertaking extensive cultivation some 5000 years B.P and responsible for the spreading of the plant throughout the region (O'Brien 1972). With the demise of these civilizations long before the arrival of Europeans the likelihood of identifying a specific point of origin is now very remote.

The Taxonomy, Incompatibility and Adaptations of the Sweetpotato

Whilst the historical spread and distribution of the sweetpotato is largely accounted for by the hypothesis of Barrau (1957) the same is not true however of the genealogy where considerable difference of opinion in the nature of the relationship between the various Ipomoea genera exist (Yen 1982). The sweet potato was among the earliest of the American plants to be introduced to Europe being known in England and the Mediterranean before the Irish potato (Solanum tuberosum). Early reference to the sweetpotato can be found in both Shakespeare's The Merry Wives of Windsor [act 5, sc.4] and Troilus and Cressida [act 5, sc.2] (Salaman 1949). With such early recognition tt is not surprising that the first attempt to classify the sweetpotato within the morning glory family was by John Ray in his Historia Generalis Plantarum (1686) where he named it *Convolvulus indicus*. Linnaeus (1753) also placed the plant within the genus *Convolvulus* but retained it's species differentiation using the common vernacular of the period, *batatas*, whilst Lamarck (1791) placed the sweet potato into the genus *Ipomoea* rather than *Convolvulus* and it is from this that the name *Ipomoea batatas* has been derived (Yen 1974).

A reviewed the taxonomy of Convolvulaceae (van Oostroom and Hoogland, 1954) resulted in the family being divided into two major divisions, the Cuscutoideae (parasitic leafless plants) and the Convolvuloideae (non-parasitic green leaved plants). This latter group being further divided into the two groups on the basis of their pollen: the Convolvuleae (smooth or spineless pollen) and Ipomoeeae (spinulose pollen). The genus Convolvulus falls into the former whilst the Ipomoea genus falls into the latter with a further five other genera differentiated by corolla and fruit characteristics. In total the Ipomoea genus accounts for over 500 species distributed throughout the tropical and subtropical regions (Yen 1974 p.161).

In the study of the origin of crop plants it is generally necessary to possess knowledge of how, when and where the prehistoric plant first occurred. Our knowledge so far suggests that the cultivated plant and it's ancestor(s) usually have the same or nearly the same genome constitution. However the phylogenic relationship between I*. batatas* and other *Ipomoea* species has proved to be a difficult question to answer with *I. batatas* being the sole hexaploid, prior to the discovery of a new hexaploid form of *I. Trifida* (K123) in Mexico (Nishiyama, 1955). However it has become clear that *I. batatas* (L) Lam (2n = 90) is distinct from other species (2n = 30, 60) in chromosome number, cross-compatibility and domestic characters (Nishiyama 1982. p263-264). Several hypothetical evolutionary routes have been proposed for the sweetpotato however no firm hypothesis for the origin, in which the ancestral species are defined, has been made. Furthermore the ordering of taxonomical relationships of the *Ipomoea* has done little to suggest derivative descent of the *batatas* species (Yen 1974 p.162). Prior to the work carried out by Kehr et al. (1953) no phylogenic relationship between *I. batatas* and other *Ipomoea* species was found. However this work indicated that the sweetpotato was descended from two ancestral lines and led to the formulation of the hypothesis that the sweetpotato originated from the hybridization of two related but different species; one a diploid (2n = 30) and the other a tetraploid (2n = 60). This then resulted in a sterile hybrid (2n = 45) which underwent doubling to produce a fertile hybrid (2n = 90) and it is from this final plant that all modern sweetpotato varieties are descended. This allopoidal origin however is disputed by Nishiyama (1982) who proposed that sweetpotato is an autohexaploid derived from hexaploid wild plants by gene mutation and increase of gene dosage. Nishiyama supports this contention through cytogenetic investigations into the sweetpotato and it's relatives and proposes that the sweetpotato originated through two evolutionary events; [1] the occurrence of *I. trifida* (6x) by duplication of a single chromosome set B from *I. trifida* (2x) or it's close relative *I. leucantha* and [2] the domestication of wild type characteristics of *I. trifida* (6x) into cultivated types. Nishiyama also states that "it seems likely that harmony has been acquired by genetic differentiation or heterozygosity in hexaploids or in it's diploid and tetraploid progenitors."

Attempts to study the phylogeny of the sweetpotato and it's related species are further complicated due to a complex self-incompatibility mechanism. This mechanism operates between most of the sweetpotato clones which, according to the classification developed in Japan (Nakanishi and Kobayashi 1979), divides into 17 groups with clones in each group being incompatible with each other whilst clones in different groups are compatible. The compatibility can be further complicated as some clones exhibit imperfect cross-compatibility with seed setting only possible in one direction. Rarely can a pair of sweetpotatoes be found that can be said to be fully cross-fertile and it is often the case that when cross-pollination does occur very few seeds are set (Martin 1982 p275). In studying the incompatibility of the sweet potato Martin (1982) compared the incompatibility of the diploid relative *I. setifera* which is free from the sterility problems of the sweetpotato and concluded that "the system of incompatibility in the family Convolvulaceae appeared to be of the multi-allelic, sporophytic type found in the families Compositae and Cruciferae. This is the only system extent capable of explaining the particular results of the study. With the sweetpotato being a hexaploid the incompatibility locus must have been duplicated or even triplicated during it's evolution." One peculiarity of the sweetpotato flower is the incomplete polymorphism. Normally polymorphic flowers encourage out-crossing however with the sweetpotato only the pin form of the flower is complete, the thrum does not develop where all the stamens exceed the combined length of the style and stigma (Yen 1974. p182). Martin (1982) makes no reference as to whether the diploid relative *I. setifera* exhibits polymorphism, incomplete or otherwise but such behaviour could help to explain the behaviour of pollen with incompatible plants. In the diploid species incompatibility resulted in pollen failing to germinate on the stigma, however in sweetpotato pollen would often germinate but fail to fertilize the ovules or the resulting seed would be malformed, empty, fail to germinate or produce week seedlings that died. What role the polymorphic traits of the sweetpotato play in this is not known. In his paper and the session discussion Martin concludes that incompatibility and sterility in sweetpotato is expressed at many stages due to genetic unbalance accompanying hexaploidy and it is likely that some sterility is always present.

As agricultural plants go the sweetpotato exhibits one of the greatest abilities to adapt to harsh environments and can contribute greatly to alleviation of food problems in the developing world (Villareal. 1977). The ability of the sweetpotato to adapt to a wide range of edaphic and climatic conditions is amply demonstrated in Oceania (Yen. 1982. p24) where it shows the greatest adaptability of any Pacific plant and it is unlikely that [a plant collector] will come away without the sweetpotato from any of the environments if they are occupied by humans (Yen. 1974. p48). Whilst the sweetpotato suffers from incompatibility and sterility problems it would not appear to have hindered the development of a large number of accessions with over 16,000 currently being maintained in field genebanks in national programmes across the APO region (Nissila et al. 1999). Considerable variation of leaf and tuber morphology exists in the sweetpotato with leaves that are typically cordate, single lobed to leaves which are heavily divided and palmate like with seven lobes or more. Equally tuber size, shape, colour and arrangement vary greatly and it is normal practice to initially distinguish accessions first by tuber quality; dividing it into three groups based on cooking qualities: those that are sweet and gelatinous, those that are firm and mealy and those that are coarse and suitable only as animal feed or industrial uses. Skin colour can vary from white, brown, yellow or purple and flesh from white through to orange. Since the sweetpotato is a root crop that is propagated asexually the majority of this variation is likely to have arisen from spontaneous mutation rather than sexual outcrossing. In Taiwan, mutations in the sweetpotato roots are very often observed (Wang 1964) and in the early 20th century before flowering induction techniques were perfected, the selection of mutant types of sweetpotato was the only method which could be used for changing the genetic makeup (Miller 1939). However most mutations in sweetpotato were reported to be retrogressive (Hernandez et al 1964).

Although the sweetpotato has adapted to growing in tropical to temperate regions it is not hardy and requires a minimum frost free period of 4-6 months and even where this is possible the plant growth is severely restricted at temperatures below 100 C. Sweetpotato is also a short day plant requiring 11 hours or less of light to promote flowering and is the main reason why little or no flowering occurs in temperate regions at latitudes higher than 300 N or S (Onwueme. 1978 p.169). However since the main form of propagation is by stem cutting or tuber saving maintenance of the stock is not reliant on seed setting.

Breeding and Conservation Programmes for the Sweetpotato

Given the large number of sweetpotato accessions that currently exist in the Pacific many writers have suggested this as evidence for antiquity. The premise being that all the "varieties" have been derived through asexual reproduction and somatic mutation from a few ancestral plants (Yen 1974. p223). Yen (1974. p 331) argues though that " The alternate sexual reproductive mode, however, is seen as the explanation for the large number of varieties in many Pacific areas. Genetic recombination is regarded as the major source of "new" varieties, with mutation and the effects of random genetic drift as secondary contributors."

How much of a conscious influence the native populations in the Pacific have had on the development of the sweetpotato in their area is unknown. Yen (1974 p231) states that "the arising of new varieties is a common claim, but in no recorded case is there a spontaneous account that could be attributed to conscious selection that would show that the agriculturist was aware that such change occurs within the plant. Thus within the contexts of native agricultures, the selection of new forms of familiar plants may be regarded as accidental, rather than the purposive exploitation of a well-observed natural phenomenon" and that "Generally there was ignorance of the presence of natural seed as a consequence of sexual reproduction." These observations whilst valid may not be representative of the historical inhabitants of these Islands, many of whom would have been displaced as a consequence of Colonialism. In the Philippines, where 16th Century Spanish similar patterns to that in America, and in 19th Century Fiji the establishment of sugar plantations under British Colonialism displaced indigenous populations in favour of imported bond workers (Instituto del Tercer Mundo. 1995). It is therefore possible that Yen erroneously interviewed the descendents of immigrants rather than the true indigenous inhabitants. The history of the Pacific and the influence of the inhabitants on the evolution of the sweetpotato is, like many issues surrounding the sweetpotato, yet to be fully investigated.

Whilst a fuller understanding of the history of the sweetpotato is essential in determining it's phylogeny, a greater understanding of the genetic diversity needs first to be acquired. The first International Symposium in 1982 set out to both acknowledge the importance that the sweetpotato has played in human evolution and to set in motion international co-operation on developing and improving the crop so that it may can continue to play a role in world food production. To achieve this comprehensive programmes in both conserving the existing gene pool and developing new cultivars which are resistant to pest and disease and have higher nutritional value must be the main aim for the future.

In world production of food, fodder and industrial products, particularly in areas where the environmental conditions prohibit the production of other crops such as cereals, the sweetpotato has a tripartite role to play. It is not surprising that in the APO region, where over 90% of world production now takes place, the plant has acquired an important role (FAO 1999). With over 16,000 accessions maintained within field genebanks in national programmes across Asia and the Pacific the potential for these collections to succumb to pest and disease and the heavy burden that such programmes place on financial and labour resources necessitates the development of alternative complimentary strategies and rationalization of the existing collections (Nissila et al. 1999). Within this framework a comprehensive strategy would normally include the development of seed banks owing to the relative low cost of establishment and maintenance. However the sexual incompatibility between sweetpotato varieties and the complex hexaploid genome tends towards quantitative rather than qualitative inheritance traits (Jones 1967). It has been proposed that it is a unique combination of genes rather than unique genes that lead to superior clones. Te heterozygosity and consequent dominance effects are high with epistasis also observed to be a very important variance component (Martin 1988). Other workers too have reported that the quantitative characters of inheritance are complex with transgressive segregation occurring with some F2 progenies being superior to the superior grandparent whilst others were inferior to the inferior grandparent (Hammett, 1965). This situation makes the potential for maintaining varietal integrity via seed banks an unlikely option, however this should not distract from the potential that seed collections offer in storing a large amount of germplasm in a small area at relatively low cost. The production of seed will always be important and despite the advances in bio-technology it is still the most important route for genetic recombination.

As the situation currently stands preservation of specific varietal types in field genebanks is currently the main method available, however advancements in *in vitro* techniques have great potential for collecting, exchange and conservation of plant germplasm (Engelmann 1991). In order to rationalize costs of *in vitro* storage, reducing the growth rate and thereby extending the subculture interval would be advantageous. Among the methods available for induction of slow growth in *in vitro* cultures is the use of low, non-freezing temperatures however not only does this demand costly cooling facilities but can induce injury in tropical plants (Staritsky et al. 1986). Alternative methods include the modification of culture media so as to increase osmotic stress. The addition of mannitol at concentrations of 15 or 20g l-1 or the reduction of sucrose from 30 to 25g l-1 is effective at extending subculture intervals from four to twelve months at cultural temperatures of 250C + 20C with more than 65% survival (Mandal and Chandel. 1996). Cryopreservation, the storage of material at ultra low temperatures (-1960C) resulting in the cessation of all metabolic process may enable indefinite storage of material with techniques for numerous crops having now been developed (Engelmann 1997). Currently large sweetpotato germplasm collections are maintained under slow growth in vitro in various national, regional and international genetic resources centres (Lawrence et al. 1996).

Despite the development of in vitro and seed collections the majority of sweetpotato germplasm in the APO region is still maintained through ex situ field genebanks (Nissila et al. 1999). Owing to the high cost of maintenance and the potential for disaster (disease, pest, extreme weather) field genebanks need to be rationalized so as to make the most effective use of resources. One of the many problems identified by Nissila et al. (1999) is the incidence of duplication within collections and the tendency for favouring accessions that are currently popular at the expense of unfashionable varieties. This can quickly lead to genetic erosion as selection processes discriminate in favour of popular types. It is therefore necessary to realize the linkage between conservation, use and improvement. In dealing with these issues Nissila et al. (1999) identifies structuring as the key to reducing the number of accessions. By structuring, field genebanks can be categorized into three basic groups: Use-based (UBS), Type of material based (TBS) and Genetic diversity structuring (GDS).

Accessions held in UBS field banks would be those currently important in sweetpotato production. Within these collections accessions would be divided into three sub-groups; (1) Frequently used. (2) Less frequently used, and (3) Hardly ever used. In TBS collections the accessions held are more important in conservation and providing potential UBS material; again TBS is to be divided into three groups; (1) Local landraces or farmers' varieties, (2) Breeding lines, and (3) Foreign introductions. These two divisions provide the distinction between working and conservation collections. GDS collections are yet to be created but would be derived out of analysis of existing germplasm within current collections with the intention of creating a core collection. The core collection consists of a limited number of accessions which represent the genetic spectrum of the species in the whole collection but not in all it's possible combinations. In theory it should be possible to recreate a variety from the material within the core. Nissila et al. (1999) proposed the following linear model for rationalization of collections and stratification of the use of complimentary conservation methods:

Type of material based > Genetic diversity structuring > Use-based
TBS -> characterization -> **GDS** -> evaluation -> **UBS** -> GDS*UBS

With this model, the rationalization of a sweetpotato collection and stratification of the use of complimentary methods can be carried out in the following steps.

TBS
Classify accessions in field genebank to groups of local landraces or farmers' varieties, breeding lines and foreign introductions. Rearrange foreign introductions from field genebank to breeding collection.

Characterization
Characterize local landraces/farmers' varieties and breeding lines using standardized descriptors. Identify morphological duplicates within the group of local landraces/farmers' varieties. Verify, if possible, duplicate identification with RAPDs. Convert morphological duplicates to botanical seeds using cross block targeted, depending on the characteristics of the clone in question, to geographical or niche specific or trait specific diversity.

GDS
Carry out GDS using passport and characterization data. Identify the core (Yonezawa et al. 1995).

Evaluation
Evaluate the core in replicated trials in all different agro-ecological sites. Score the expressions of adaptive traits, i.e. yield performance and resistance to different biotic and abiotic stresses, and quality. Evaluate all accessions (if this is not possible, evaluate the promising part of them) in different GD-clusters (GD-cluster is the set of accessions clustering together in a dendogram revealed with hierarchical cluster analysis in GDS) focusing on traits found to be important for the core entries drawn from that GD cluster.

UBS
Identify the importance in use, taking into account both evaluation results and experiences in breeding programmes, and classify accessions into groups of frequently used, less frequently used and hardly ever used.

GDS*UBS
Clonally maintained accessions: With focus on only the UBS groups 'frequently used' and 'less frequently used', merge the results of GDS and UBS: (1) reveal the possible redundancy, i.e. clones expressing very similar genetic performance in GDS and closely related phenotypic performance of UBS, (2) reduce possible redundancy by sampling in proportion to the amount of genetic diversity in the GD-clusters, i.e. use the G-strategy (Yonezawa et al. 1995). From (1) + (2) identify (3): the germplasm which include both a representative set of the genetic spectrum in a whole collection plus accessions important in use (3) is the germplasm which should be conserved in the field and, if possible, the in vitro genebank. If this germplasm consists of a larger number of breeding lines, consider - based on GDS - which part of them (genetically closely related) can be rearranged into the breeding collection. The number of accessions conserved in field / in vitro depends on the resources available.

Dynamic seed populations
Establish dynamic seed populations with accessions (4) expressing fairly similar performance, based on GDS and UBS, with accessions to be maintained in field / in vitro, and (5) clones in UBS group 'hardly ever used'. With accessions of (4), establish the crossing blocks and define the target diversity, i.e. geographical or niche-specific or trait specific populations, based on evaluation results of the clone + core entries + other accessions in the same GD-cluster which the clone in question represents. With (5) accessions, establish crossing blocks targeting geographical diversity. A particular clone, as well as clones which are to be maintained in field /*in vitro* genebanks, can be used in establishment of several dynamic populations. After successful seed conversion, the redundancy in field collection (clones very similar to those to be maintained in field /*in vitro* genebanks) can be reduced by eliminating these clones from the field genebank to be conserved using dynamic seed populations and, if sufficient resources are available, *in vitro*.

Summary: Introductions and Adaptations, The Unsolved Puzzle.

The sweetpotato's distribution adaptation and evolution within the Pacific, where it has achieved global importance, continues to perplex the scientific community. No one current theory adequately accounts for the phylogenic origin or extent of distribution. Like so many cultigens the antiquity of the human relationship and the influence of such has led to the plant evolving so far beyond its ancestral relatives as to make it difficult, some would aver impossible, to unravel the genealogy.

With the increasing global population and the possible adverse effects of global warming the adaptability of the sweetpotato to unforgiving environments may yet prove to be an asset in global food security. Our quest for improvement has so far concentrated on the tuber however, as referred to in the introduction, the plant tops have nutrient levels equivalent to pork or beef (Collins et al. 1982) and the breeding of varieties which have high leaf production may prove as advantageous as improving the tuber. In seeking the origin of the sweetpotato we have perhaps erroneously ignored the role and importance of the tops to the prehistoric agriculturist. In none of the literature reviewed was it suggested that cultivation may have originally begun for the "greens" and that the tuber was a secondary development. It is not too improbable that tuber development may have been a consequence of cultivation or propagation requirements that ultimately succeeded the tops in importance.

Perhaps the "new" science of biotechnology and the increasing ease of genetic mapping may ultimately solve this and other plant riddles; or it may simply add a new dimension to the complex and fascinating subject of Evolution.

“Your misfortune really lies, not in knowing too little and in not having arranged things enough, but in ever having embarked on researches which were obviously doomed to be incomplete. . . .”

THE IGUANA to THE ZOOLOGIST, In the Galopagos, by Edmund Wilson, 1925.

(from Yen, The Sweet Potato and Oceania, 1974)

References

Barrau, J. (1957). L'Enigme de la patate douce en Oceanie. Etudes d'Outre-Mer. 40: 83- 87.[cited in Yen, D.E. (1974). The Sweet Potato and Oceania, An Essay in Ethnobotany. Bishop Museum Press, Honolulu, Hawaii.]

Bohac, J.R., Dukes, P.D., Austin, D.F. (1995). Sweetpotato. Pp. 57-62 in Evolution of Crop Plants (J. Smartt and N.W. Simmonds, eds). Longman Scientific and Technical, London, UK. [cited in Nissila, E.A.J., Rao, R.V., Engelmann, F., Riley, K.W. 1999. Ex situ strategies for complementary conservation of Asian sweet potatoes. Plant Genetic Resources Newsletter. No 117, 1-11.]

Brand, D.D. (1971). The sweetpotato: an exercise in methodology. In Man across the sea, Pp.343-365 (C. J. Riley et al. eds). Austin Univ. Texas Press.[cited in Yen, D.E. (1974). The Sweet Potato and Oceania, An Essay in Ethnobotany. Bishop Museum Press, Honolulu, Hawaii.]

Candolle, A. de. (1886) Origin of cultivated plants. Hafner. (1959 reprint of 2nd edition) New York, USA.[cited in Yen, D.E. (1974). The Sweet Potato and Oceania, An Essay in Ethnobotany. Bishop Museum Press, Honolulu, Hawaii.]

Collins, W.W and Walter, W.M. (1982). Pp. 355-369. Potential for Increasing Nutritional Value of Sweet Potato. in Proceedings of the first international symposium. Asian Vegetable Research and Development Center (Villareal, R.L., Griggs, T.D, eds)., Shanhua, Tainan, Taiwan, China. Publication No 82-172.

Dixon, R.B. (1932). The problem of the sweetpotato in Polynesia. American Anthropologist 34: 40-66.[cited in Yen, D.E. (1974). The Sweet Potato and Oceania, An Essay in Ethnobotany. Bishop Museum Press, Honolulu, Hawaii.]

Edmond, J.B. (1971). Sweet Potatoes: Production, Processing, Marketing. The AVI publishing Co; Westport, Conneticut.

Englemann, F. (1991). In vitro conservation of tropical germplasm- a review. Euphytica 57: 227-243. [cited in Nissila, E.A.J., Rao, R.V., Engelmann, F., Riley, K.W. 1999. Ex situ strategies for complementary conservation of Asian sweet potatoes. Plant Genetic Resources Newsletter. No 117, 1-11.]

Englemann, F. (1997). In vitro conservation methods. Pp. 119-162. In Biotechnology and Plant Genetic Resources: Conservation and use (Ford-Lloyd, B.V., Newburry, J.H., and Callow, J.A. eds). CABI, Wellingford, UK. [cited in Nissila, E.A.J., Rao, R.V., Engelmann, F., Riley, K.W. 1999. Ex situ strategies for complementary conservation of Asian sweet potatoes. Plant Genetic Resources Newsletter. No 117, 1-11.]

FAO. (1999). Faostat, Statistical Database < http: / / apps.fao.org / >

Hammett, H.L. (1965). A study of the inheritance of root shape, skin colour, total carotenoid pigments, dry matter, fiber and baking quality in the sweetpotato. Ph.D. Thesis, Louisiana State Univ., Baton Rouge. [cited in Edmond, J.B. (1971). Sweet Potatoes: Production, Processing, Marketing. The AVI publishing Co; Westport, Conneticut.]

Hernandez, T.P., Hernandez, Travis P. and Miller, J.C. (1964). Frequency of somatic mutations in several sweetpotato varieties. Proc. Amer. Soc. Hort.Sci. 85: 430-433. [cited in Yen, D.E. (1974). The Sweet Potato and Oceania, An Essay in Ethnobotany. Bishop Museum Press, Honolulu, Hawaii.]

Heyerdahl, T. (1952) American Indians in the Pacific. Allen and Unwin, London, UK. [cited in Yen, D.E. (1974). The Sweet Potato and Oceania, An Essay in Ethnobotany. Bishop Museum Press, Honolulu, Hawaii.]

Instituto del Tercer Mundo. (1995). The world . A third world guide 1995/96. Instituto del Tercer Mundo, Montevideo, Uruguay.

Jones, A. (1967). Theoretical segregation ratios of qualitively inherited characters for hexaploid sweetpotato. Technical bulletin No. 1368. USDA. [cited in Nissila, E.A.J., Rao, R.V., Engelmann, F., Riley, K.W. 1999. Ex situ strategies for complementary conservation of Asian sweet potatoes. Plant Genetic Resources Newsletter. No 117, 1-11.]

Komaki, K. (1996). Conservation and use of genetic resources in Japan. Pp 61-65 in Proceedings of the workshop on the formation of a network for the conservation of sweet potato biodiversity in Asia, Bogor, Indonesia, 1-5 May 1996 (V. Ramanatha Rao, ed.). IPGRI. [cited in Nissila, E.A.J., Rao, R.V., Engelmann, F., Riley, K.W. 1999. Ex situ strategies for complementary conservation of Asian sweet potatoes. Plant Genetic Resources Newsletter. No 117, 1-11.]

Lamarck, J.B.P.A. de M. de. (1791). Tableau Encyclopedique Methodiquede Trois Regnes de la Nature. Botanique 1. Paris: Agasse.[cited in Yen, D.E. (1974). The Sweet Potato and Oceania, An Essay in Ethnobotany. Bishop Museum Press, Honolulu, Hawaii.]

Lawrence, T., Toll, J. and van Sloten, D. (1996). Directory of Germplasm collections. 2. Root and tuber crops. Revised edition. IBPGR, Rome, Italy. [cited in Nissila, E.A.J., Rao, R.V., Engelmann, F., Riley, K.W. 1999. Ex situ strategies for complementary conservation of Asian sweet potatoes. Plant Genetic Resources Newsletter. No 117, 1-11.]

Linnaeus, C. (1753). Species Plantarum. Ray Soc.(reprint 1957) London. UK. [cited in Yen, D.E. (1974). The Sweet Potato and Oceania, An Essay in Ethnobotany. Bishop Museum Press, Honolulu, Hawaii.]

Mandal, B.B, and Chandel, K.P.S. (1996). Conservation of Genetic Diversity in sweetpotato and yams using In vitro strategies. In Tropical tuber crops; problems, prospects and strategies (Kurup, G.T., Palaniswami, M.s., Potty, V.P., Padmaja, G., Kabeerathumma, S. and Pillai, Santha V. eds). Science Publis. New Hampshire. USA.

Martin, F.W. (1982). Analysis of the Incompatibility and sterility of sweetpotato. Pp275- 283. in Proceedings of the first international symposium. Asian Vegetable Research and Development Center (Villareal, R.L., Griggs, T.D, eds)., Shanhua, Tainan, Taiwan, China. Publication No 82-172.

Martin, F.W. (1988). Preservation of sweetpotato germplasm as population. Pp. 159-167 in Exploration, maintenance and utilization of sweetpotato genetic resources. Report of the first sweetpotato planning conference, 1987. CIP, Lima, Peru. [cited in Nissila, E.A.J., Rao, R.V., Engelmann, F., Riley, K.W. 1999. Ex situ strategies for complementary conservation of Asian sweet potatoes. Plant Genetic Resources Newsletter. No 117, 1-11.]

Merrill, E.D. (1954). The botany of Cook's voyages and it's unexpected significance in relation to anthropology, biogeography and history. Chronica Botanica 14 (5/6). Cambridge. .[cited in Yen, D.E. (1974). The Sweet Potato and Oceania, An Essay in Ethnobotany. Bishop Museum Press, Honolulu, Hawaii.]

Miller, J.C. (1939). Further studies and technic used in sweetpotato breeding in Louisiana. J. Hered. 30: 485-492. [cited in Edmond, J.B. (1971). Sweet Potatoes: Production, Processing, Marketing. The AVI publishing Co; Westport, Conneticut.]

Nakanishi, T. and Kobayashi, M. (1979) Geographical distribution of cross incompatibility group in sweetpotato. Incompatibility Newsl. 11:72-75. [cited in Nissila, E.A.J., Rao, R.V., Engelmann, F., Riley, K.W. 1999. Ex situ strategies for complementary conservation of Asian sweet potatoes. Plant Genetic Resources Newsletter. No 117, 1-11.]

Nishiyama, I. (1982). Autoploid Evolution of the Sweetpotato. Pp. 263-274 in Proceedings of the first international symposium. Asian Vegetable Research and Development Center (Villareal, R.L., Griggs, T.D, eds)., Shanhua, Tainan, Taiwan, China. Publication No 82-172.

Nissila, E.A.J., Rao, R.V., Engelmann, F., Riley, K.W. 1999. Ex situ strategies for complementary conservation of Asian sweet potatoes. Plant Genetic Resources Newsletter. No 117, 1-11.

O'Brien, P.J. (1972). The Sweet Potato; it's origin and dispersal. Am Anthropologist, 74: 342-365.

Onwueme, I.C. (1978). The tropical tuber crops. John Wiley & Sons Ltd. New York, USA.

Ooststroom, S.J. van and Hoogland, R.D. (1954). "Convolvulaceae". In Flora Malesiana. (Steenis, C.G.G.J. van. ed.). Ser.6, No. 4. Noordoff-Kolff, Djakarta, Indonesia.[cited in Yen, D.E. (1974). The Sweet Potato and Oceania, An Essay in Ethnobotany. Bishop Museum Press, Honolulu, Hawaii.]

Purseglove, J.W. (1963). Some problems of the origin and distribution of tropical crops. Genetica Agraria 17: 105-122. [cited in Yen, D.E. (1974). The Sweet Potato and Oceania, An Essay in Ethnobotany. Bishop Museum Press, Honolulu, Hawaii.]

Purseglove, J.W. (1965). The spread of tropical crops. in Genetics of Colonizing Species (Baker, H.G. and Stebbins G.L., eds). pp375-389. New York: Academic Press. [cited in Yen, D.E. (1974). The Sweet Potato and Oceania, An Essay in Ethnobotany. Bishop Museum Press, Honolulu, Hawaii.]

Salaman, R.N. (1949) The history and social influences of the potato. Cambridge: Cambridge Univ. Press. [cited in Yen, D.E. (1974). The Sweet Potato and Oceania, An Essay in Ethnobotany. Bishop Museum Press, Honolulu, Hawaii.]

Sillitoe, P. and Shiel, R.S. (1999). Soil fertility under shifting cultivation and semi- continuos cultivation in the Southern Highlands of Papua New Guinea. Soil Use and Management 13, 230-244.

Staritsky, G., Dekkers, A.J., Loowaars, N.P., and Zandvoort, E.A., (1986). In Vitro conservation of aroid germplasm at reduced temperatures and under osmotic stress. In Plant tissue culture and it's agricultural applications (Withers, L.A and Alderson, P.G. eds). Butterworths, London. pp277-283. [cited in Mandal, B.B, and Chandel, K.P.S. (1996). Conservation of Genetic Diversity in sweetpotato and yams using In vitro strategies. In Tropical tuber crops; problems, prospects and strategies (Kurup, G.T., Palaniswami, M.S., Potty, V.P., Padmaja, G., Kabeerathumma, S. and Pillai, Santha V. eds). Science Publis. New Hampshire. USA.]

Villareal, R.L. (1977). Sweet potato: it's present and potential role in the food production of developing countries. South Pacific Commission Tech. paper 174: 170- 182. [cited in Villareal, R.L. (1982)]

Villareal, R.L. (1982). Sweet Potato in the tropics - progress and problems. in Proceedings of the first international symposium. Asian Vegetable Research and Development Center (Villareal, R.L., Griggs, T.D, eds)., Shanhua, Tainan, Taiwan, China. Publication No 82-172.

Wang, H. (1964). The mutations of sweetpotatoes. (in Chinese). Dept. of Agric. and Forestry, upland crop inprov. Conference. Upland Crop Newsletter 13.

Yen, D.E. (1982). Sweet Potato in Historical Perspective. in Proceedings of the first international symposium. Asian Vegetable Research and Development Center (Villareal, R.L., Griggs, T.D, eds)., Shanhua, Tainan, Taiwan, China. Publication No 82-172.

Yen, D.E. (1974). The Sweet Potato and Oceania, An Essay in Ethnobotany. Bishop Museum Press, Honolulu, Hawaii.

Yonezawa, K., Nomura, T. and Morishima, H. (1995). Sampling strategies for use in stratified germplasm collections. Pp. 35-54. In Core collections of plant genetic resources (Hodgkin, T., Brown, A.H.D., van Hintum, Th. J.L. and Morales, E.A.V., eds). IPGRI / John Wiley and Sons. [cited in Nissila, E.A.J., Rao, R.V., Engelmann, F., Riley, K.W. 1999. Ex situ strategies for complementary conservation of Asian sweet potatoes. Plant Genetic Resources Newsletter. No 117, 1-11.]