# BIO 235 – Plants & People – Evolution and Domestication of Crops
## Lecture 1 – Introduction – Plants that Changed the World

This course is entitled *Plants & People* because it is about the relationships, interactions and dependencies between plants and humans, about how people have altered plants, but equally about how plants have played their part in shaping and determining the course of human history, how those relationships have changed through time and influenced the rise of human civilizations and the state of the planet as we know it today.

At the heart of this story will be the most dramatic change of all – the evolution and domestication of crops and the origins of agriculture, when, where, how, how many times and ultimately why those developments came about. In addition, the course will examine the revolutionary impacts that agriculture has had on human civilizations - the transformation of the planet from one with a small human population in which nature predominated and where plants grew largely undisturbed in pristine vegetation, to one which is dominated and controlled by a burgeoning human population in which what plants grow where, is largely determined by people; a world in which people are perhaps in charge.

### The Anthropocene

Human alteration of the Earth's environments has been pervasive prompting Crutzen & Stoermer (2000) to suggest that we live in the Anthropocene – an epoch in which humans have replaced nature as the dominant environmental force on Earth. They suggested the Anthropocene started in the 1700s with the industrial revolution, while Zalasiewicz et al (2015) suggested 1945 as a better start date because the isotopic by-products of the first atomic bomb tests would provide a 'golden spike' readily detectable in the stratigraphic (geological) record. What is relevant here is that the origins of agriculture and the domestication of crops and livestock are among the most prominent key defining markers of human impacts on the environment that permitted and precipitated far-reaching environmental change including large scale forest clearance and soil erosion. Arguably it was these changes that heralded the start of the Anthropocene, without which there would have been no industrial revolution and no atomic bomb….

### Domestication of Crops – the biggest plant-human interaction of them all

By far the biggest change in plants brought about by humans is the domestication of crops. We can define plant domestication as genetic modification of a wild species to create a new form of plant altered to meet human needs, such that fully domesticated crops are completely dependent on humans and unable to self-propagate in the wild (e.g. maize, cauliflower). It is this change that will be the central focus of the course – What is domestication? How did domestication happen? What were the outcomes of domestication, and especially the transformation from foraging to farming.

### De Candolle & Darwin

Alphonse Pyramus de Candolle (1882). *Origin of Cultivated Plants* – 'This shows how the history of cultivated plants is allied to the most important problems of general history of organized beings.' Charles Darwin (1883). *The Variation of Animals and Plants under Domestication* – 'Although Man does not cause variability and cannot prevent it, he can select, preserve, and accumulate the variations given to him by the hand of Nature almost in any way he chooses; and thus he can certainly produce a great result.'

Plants & Humans: it is impossible to exaggerate the importance of their interactions through history. When human desires collide with the diversity of nature, the result can be great indeed. It is those collisions and their outcomes that are the focus of this course.

## Crops in Plant Science

Domestication of crops is an exciting area in plant biology. Because agriculture is one of the largest global industries and food security one of the greatest challenges to humans, this means that research on crop plants dominates plant sciences and it is work on crop plants that has often been at the forefront of many of the most significant revolutions, innovations and scientific developments and discoveries in plant biology.

- Charles Darwin's studies of variation of plants under domestication and the insights that crops provided into selection 1883 - *The Variation of Animals and Plants under Domestication.* For Darwin, the observation of what happened to plants and animals when subjected to selection by humans was instrumental in providing insights into natural selection and the theory of evolution. So, here we have one of the earliest and most potent examples of how crops, and their evolution and domestication have been instrumental in providing critical biological insights that, in this case have fundamentally altered how we view the evolution of diversity.
- Gregor Mendel's (1822-1884) experiments on the garden pea and the insights they provided into the mechanisms and laws of inheritance. Mendel was an Augustinian monk who gained posthumous fame as the figurehead of the new science of genetics even though the significance of his work was not recognized until the turn of the 20th century. The independent rediscovery of Mendel's laws formed the foundation of the modern science of genetics.
- Barbara McClintock's discovery of transposable elements in maize in the 1940s and 1950s for which she won a Nobel Prize in 1983. Transposable elements were long dismissed as useless junk, but since emerging as major players in evolution. Their interactions with the genome and the environment affect how genes are translated into physical traits.
- Jun Yu and the rice genome in 2002 – the first crop plant to be sequenced and the second plant species after *Arabidopsis* to have its entire genome sequenced. The rice genome contains 466 million base pairs - 3.7 times larger than the only other sequenced plant genome, the mustard plant, *Arabidopsis*, but 6.7 times smaller than the human genome. The rice genome sequence of course just the precursor of the current proliferation of genome sequencing much of it focused on crop plants, which lie at the heart of comparative plant genomics.

Thus, research on crop plants occupies centre stage in plant science. This is likely to continue for the foreseeable future. For example an international group of scientists funded by money from the Bill Gates Foundation has recently embarked on a quest to change the photosynthetic pathway in rice from C3 to C4, i.e. to transform a complex physiological trait in the world's most important crop. All this means that understanding the diversity and origins of crops, is of central importance in plant biology and beyond. It also means that we know far more about crop plants than we do about almost all other plant species.

## Food Security

Food security remains an on-going and massive world challenge, which has returned to the top of the mainstream agenda in the last few years as prices of staple food crops have soared. Global food security is dominating development debates. Some 800 million people can't afford the food they need and are under-nourished. At the same time an equal or greater number of people, estimated by some to be as many as 1 billion, are obese and suffering from unbalanced diets. The green revolution and industrial agriculture has been remarkably successful over the last 6 decades, but yield gains have slowed in the last decade and there are major questions about food security as we race towards and past landmarks of 'peak oil', 'peak water', 'peak soil' well before we reach 'peak population' or 'peak consumerism'. How close are we to 'peak food'? What are the limits to food production? How sustainable is modern food production? Have increased crop yields been achieved at the cost of decreased resilience and sustainability and loss of cultural heritage? Are there on-going technical developments and innovations that can continue to increase food production for the next 50 years? Towards the end of the course we will examine some of these questions and how they are challenging the relationships between plants and people in new ways.

The central dependence of humans (and other animals as well) on plants is well known and hopefully widely appreciated. Plants are nature's alchemists – perfectionists at organic chemistry and experts at transforming water, soil and sunlight into an array of useful substances, and of course most crucially they are able to convert sunlight into food via the astonishing trick of photosynthesis. A quick glance at the everyday items that we eat and use illustrates the central importance of plants and plant products to provide basic necessities. Without plants many of the things that we take for granted in every day life would not be there. Gone are not just the grass the cows eat, the cows themselves and the milk they produce, the flowers we admire, much of the food we eat, but also the tobacco that some of us smoke, many of the fibers and cloth we wear and use, much of the furniture we use, the paper we write on to make the books and magazines we read, some of the fuel we burn, the materials we use to build our houses and many of the medicines we use to heal and cure our ailments….. Without plants the world would not be a happy place for us humans, or for cats….

### Sweetness, Desire & Intoxication

Of course, plants are not just about food, human nutrition, medicines and other basic utilitarian products, but also satisfy many other human desires and pleasures – taste, sweetness, beauty, and intoxication. As we shall see, flowers underpin the very foundations of human appreciation of beauty. It is the flower that most likely first ushered in the idea of beauty into the world. Intoxication is a human desire we might never have cultivated had it not been for a number of plants that manage to manufacture chemicals with the precise molecular keys needed to unlock the mechanisms in our brains governing pleasure, memory and maybe even transcendence. It is plants that produce the wide range of intoxicating substances - alcohol, tobacco, marijuana, cocaine, coffee, tea, and other herbs that humans use to wake themselves up, put themselves to sleep, calm themselves, and intoxicate, excite and hallucinate themselves for pleasure or even perhaps to transcend human consciousness.

### Economic Botany

There are a number of books that tell some of the often strange and wondrous stories about plants and their complex and intricate connections and relationships with people, society as a whole and the course of human history.

- *The Botany of Desire – a Plant's-eye view of the World* by Michael Pollan, the human desires that connect us to plants – taste or sweetness, beauty, intoxication, illustrated by the apple, tulip, cannabis and the potato.
- *Seeds of Change – Six Plants that Transformed the World* by Henry Hobhouse – quinine, sugar, tea, cotton, potato, coca.
- *Seeds of Wealth – Five Plants that Made Men Rich* also by Henry Hobhouse – focused on cash crops have had, for the past three centuries, a profound effect on our world.
- *What Have Plants Ever Done for Us? Western Civilisation in Fifty Plants.*
- *Dinner with Darwin* – Jonathan Silvertown – explores how humans have altered what they eat and how that has happened…
- *Feeding the Market – South American Farmers, Trade and Globalisation* by Jon Hellin & Sophie Higman – explores the debate about globalization and its interface with resource-poor farmers in South America focusing on bananas, coffee, potatoes, coca, grapes, timber trees and the Andean grain quinoa.
- *Flora Mirabilis – how plants have shaped world knowledge, health, wealth and beauty* by Catherine Howell provides an illustrated timeline of how plants have shaped the course of human history.

In this first lecture, I will introduce some of these links that intertwine plants and people via four plant portraits in an attempt to assemble a panorama of these often complex, unforeseen, and far-reaching relationships and interdependencies of plants and people.

**Potato**

We shall start with the potato, *Solanum tuberosum*, a small unassuming stem tuber from the Andes, that can be toxic in the wild, but which has been transformed over the last 8,000 years into a fat nourishing staple crop, that is now consumed on a vast scale throughout the world, and which has had dramatic impacts on human history at different times in different places.

Potatoes were domesticated in the Andes by the pre-Inca farmers of southern Peru and Bolivia about 8,000 years ago. Domestication involved selection for underground characters of shorter stolons, larger tubers, (often) coloured and variously shaped tubers, reduction of bitter tuber glycoalkaloids, and greater vigour.

Landrace potato cultivars are highly diverse. In the Andes, this complexity translates into a cornucopia of potato races developed by pre-Inca farmers – the Peruvian blue potato, reds, pinks, yellows and oranges, all manner of thin and fat ones, smooth-skinneds and rough, short-season and long, drought-tolerant and water-loving, sweet tubers and bitter ones, starchy potatoes and others almost buttery in texture – some 3,000 different land races in all. This extravagant harnessing of wild diversity in the Andes, owes partly to the early Andean farmer's desire for variety, partly due to their flair for experimentation, and partly the complexity of their agriculture, the most sophisticated in the world at the time of the Spanish conquest. The Incas had figured out how to grow impressive yields of potatoes under often harsh, extremely variable, and uncertain conditions encompassing different altitudes and orientations that demand diversity – a different tuber for every environment. A polyculture.

The potato was introduced to Europe in the late 16th century, almost by accident and with little intent. For example in Switzerland, Konrad Gesner, a polymath who lived in Zurich in the first half of the 17th century, set up an embryonic botanic garden in which both potatoes and tobacco were cultivated. Interestingly, the uses of both these plants were unknown – what were tobacco leaves useful for? Which part of the potato is useful? Initially viewed skeptically – staple food of an uncivilized and conquered race; member of the nightshade family; thought to cause leprosy and immorality – new, unknown, unappealing.

## Ireland, population growth and famine

Nowhere was the potato more widely adopted than Ireland, a country where grains like wheat grew poorly, but where the potato thrived and could be easily grown to feed a family on water soaked impoverished soils in so-called 'lazy beds'. The cool wet climate was ideal for potato growing and allowed the population to grow from c.0.5million in 1660 to 1.25 million in 1688 and c. 9 million by 1840. This spectacular population explosion was in large part dependent on and attributable to the potato as the staple food crop for this burgeoning population.

The arrival of potato blight in Ireland in 1845 was announced by the stench of rotting potatoes caused by the fungus *Phytopthera infestans*. The spores of the fungus are carried by the wind and appear initially as a black-spotting on the leaves, a gangrenous stain spreading down the stem, then the blackened tubers turning to an evil-smelling slime. In Ireland the potato blight caused catastrophe in the form of starvation and famine, as a result of which one in every 8 Irishmen - > 1 million people died and millions more emigrated to America. Within a decade, Ireland's population was halved, c. 5.5 million people had emigrated by 1900, and the composition of America's population was permanently altered. This was the result of perhaps the biggest experiment in monoculture and surely the most convincing proof of its folly. Potatoes are propagated vegetatively, so fields are clones and thus genetically identical. In Ireland a single variety Lumper was planted, all of them descended from a single plant.

With c. 100,000 Irish arriving in America per year in the 19th Century, Irish came to form up to 30% of the population of major cities like Boston and New York. These were destitute people, but they had a vote and the Irish influence has been a notable part of American political life ever since. The fact that U.S. president Bill Clinton was able to play a key role in bringing peace to northern Ireland, stems from the power and influence of the Irish vote in the U.S.A., a result of the Irish potato famine, itself the result of the introduction of the potato from the Andes. The influences of the potato on human history continue to reverberate around the globe today.

Introduction and large scale cultivation of potatoes has been implicated in sustaining population growth in many other diverse areas, such as in the middle hills of Nepal in the Himalayas and even here in Switzerland as well.

## Modern Potato Growing

Growing potatoes, perhaps more than any other crop, is dominated by pests and epitomizes the dilemmas and conflicts surrounding different approaches to modern agriculture – high inputs, genetic modification, monocultures - large quantities of chemical fertilizers, pesticides, machinery and fuel that are expensive and questionably sustainable.

So much of what modern agriculture is all about - the clean potato fields and computer-controlled crop circles of Idaho – comes down to the perfection and uniformity demanded by consumers. McDonald's French fries provide the classic example. The perfect slender golden rectangles, long enough to overshoot their trim red containers like a bouquet. The image and the food rolled into one, and an expectation that McDonalds has successfully planted in the heads of a few billion people around the world. The same in Tokyo, Zurich, Beijing, Moscow, Azerbaijan, Cape Town, and even Lima and La Paz. It is perhaps a sobering revelation that McDonald's in Lima and La Paz, with the heartlands of the potato and its treasure house of diversity nurtured and engineered over millennia by Andean farmers on the doorstep, import Monsanto's NewLeaf genetically modified *Roundup-Ready* potatoes from the USA to make French fries in Bolivia and Peru….Such perfection can only be produced by a few varieties, and concentrating on a single variety like NewLeaf for global production of perfect French fries is the ideal option for McDonalds – the ultimate uniformity and control in global food production. The current global desire for perfect French fries needs a global monoculture that depends on technologies like genetic engineering. NewLeaf might never have been developed without support from McDonalds and the massive and uniform market that they represent.

The history of the potato encapsulates the central feature of crop domestication – drastic reduction of diversity from the hugely rich treasure house of diversity selected, nurtured and driven by Andean farmers over millennia to the single clones that led to the Irish famine and the genetically engineered varieties that dominate modern potato production today…. That story is far from complete. As increasing numbers of crop genomes are sequenced, the genomics era is just starting and we can anticipate many new developments in crops as genes and their actions are understood….

The potato also encapsulates the often far-reaching impacts of cultivation and domestication in a story that started in the high Andes of Peru and Bolivia, moved to Europe, prompted population growth and precipitated mass famine and emigration in Ireland, altered the demography of the U.S.A. for ever, and has gone on to spawn one of the largest industrial agricultural crops and globalization of fast food.

## Tulip

(This section derived in large part with thanks to Michael Pollan's *'The Botany of Desire'*)

Flowers underpin the very foundations of human appreciation of beauty. It is the flower that most likely first ushered in the idea of beauty into the world. Our second plant portrait the tulip is the story of hard, glamorous, scentless beauty and how it transfixed the rulers of the Ottoman Empire, generated a speculative frenzy in Holland in the early 17th Century that would be the ruin of many Dutch citizens, and later formed the basis for a global bulb industry that supplies the municipal flower borders of Europe and North America, and which is a ubiquitous element of modern municipal flower beds and ultimately linked with the Netherlands.

### Swiss tulips

There are a few doubtfully native species of tulip in Switzerland – Tulipa grengiolens from Grengiols in Wallis and there is a Fete de la Tulipe in Morges on Lac Leman.

There are c. 75 wild species of tulip, most of them from central Asia and notably Persia and Iran, a few from south-central Europe and most of them short, pretty, cheerful, frank, open, unprepossessing 6-petaled star flowers, which were transformed into coveted flowers of great beauty in Turkey and later Holland, and which now form the basis for a huge bulb industry that supplies the municipal flower borders of Europe and North America. Via selection and propagation, tulips have been reinvented every century or so to reflect shifting ideas of beauty across time and in different societies and to suit every change in the aesthetic weather.

Tulips in Persia

Tulips in Iran
Symbol of the revolution and martyrdom

Ottoman tulips – absurdly long pointed petals – elongated like daggers, usually pure in colour, the petals smooth-edged, the flowers elegant, sharp, masculine

Introduced to Europe – Conrad Gesner in 1559 – lived in Zurich

Introduced to the Netherlands in 1593

1634-1637 – new to Western Europe and surrounded by an aura of intoxicating Oriental allure, the tulip unleashed a madness, a speculative frenzy that shook a whole nation and nearly brought its economy to ruin during an episode in history when a flower took a star turn on the stage of history – the episode of Dutch *tulipomania*. The pinnacle of the Dutch mania was perhaps the Semper Augustus tulip, an intricately feathered red-and-white masterpiece of a tulip, a bulb of which changed hands for 10,000 Guilders at the height of the mania, a sum that would have bought one of the grandest canal homes in Amsterdam, part of a wildly escalating mania during which values were turned on their head, thrift, patience, value for money were cast aside as speculators sold their businesses, mortgaged their homes, invested their life savings in tulips, scarcity and speculation driving prices ever higher until 1637 when the bubble burst and many had been lured to their ruin.

Queen of the Night - Black tulips – cool, scentless, somewhat aloof – as close to black as a flower gets and which draws more light into itself than it reflects – a floral black hole, also appealed to the Dutch and the quest for a truly black tulip became part of tulipomania.

20th century – rise and triumph of municipal flower borders – a sort of mass-produced eye candy, flowers for kids, providing a straightforward spectrum of pure colours – black, red, purple, pink, yellow, orange, white in early Spring, these are accessible, cheap and uncomplicated and now ubiquitous Spring companions.

Tulips are on the surface of it conspicuously useless plants – a thing of beauty – no more no less, yet have become at different times one of the most beloved and coveted of flowers

## Coca

Mention *Coca* and most people probably think either of *Coca Cola*, or more likely cocaine, Colombia, drug barons, narco-terrorists, and drug addiction with all its associated violence, corruption, crime and disorder in both the supplier countries in Latin America and in the cities of the U.S.A. and Europe – the outcomes of the long-running war on drugs. Few will realize that Coca leaves have been traditionally chewed and used to make tea by indigenous people in the Andes for the last two millennia. Chewing Coca leaves and drinking Coca tea have a very different effect from using the refined powder. Coca leaves are harvested from an Andean shrub, *Erythroxylon coca*, that is indigenous and now widely cultivated on the eastern slopes of the Andes from Colombia to Argentina. The leaves are harvested and dried like tea, and marketed widely in countries like Bolivia. The leaves act as a mild stimulant, promoting a sense of warmth, well-being and comfort, alleviating altitude sickness, tiredness and hunger (suppressing appetite), and enabling people to walk long distances and work long hours. In fact Andean travelers would often measure the length of a journey not by distance, but by time periods called *cocadas* – the time taken to chew a given quantity of coca leaves or around 45 minutes and a long day might amount to 16 cocadas, often with packs of 45-50kg the workload and hunger alleviated by constant coca chewing which maintains blood sugar levels despite poor diets. Coca chewing has been and still is ubiquitous throughout the Andes and the cultivation and use of Coca have been an integral and apparently harmless and potentially beneficial part of Andean life and culture for centuries, especially at higher altitudes where cold was ever-present and temporary shortages of food were an important incentive to chew Coca leaves.

By comparison, cocaine, an alkaloid ($C_{17}H_{21}NO_4$) isolated, refined and concentrated from Coca leaves and the most potent stimulant or psychoactive drug of natural origin, is a relatively recent and much less benign development. It was first isolated by Niemann and Lossen in 1860, but has become widely snorted and injected in Western urban societies causing euphoria, soared to command astronomical prices, spawning problems of drug addiction, associated crime, a massive Coca growing eradication programme - the war on drugs in Latin America, sponsored and in large part executed by the U.S. military – associated violence, corruption and disorder, and ultimately posing a threat to aspects of western urban life and civilisation. It is concentration and refining that increases the danger and risk of addiction and harm – the purer the substance, the more addictive it becomes (opium, coffee, cocaine, tobacco, alcohol are all the same in this regard). It is this purification, the concentration of active agents, that has caused these plant products to become addictive, and addiction to cocaine is generally a one-way street.

Cocaine is the second most commonly used illicit drug (following marijuana) in the United States. According to the 2003 National Survey on Drug Use and Health, more than 34 million Americans (14.7%) age 12 or older had used cocaine at least once in their lifetime. There are no drugs approved for replacement-pharmacotherapy (drugs taken on a chronic basis as a substitute for the abused drug, like methadone for heroin addiction). Cocaine addiction treatment relies heavily on psychotherapy and drugs like antidepressants to relieve some of the effects of cocaine abuse.

Yields of c.2 tonnes of leaves per ha translate into about 15kg of pure cocaine powder with a street value of >$0.5 million in 2002. This value is mainly dependent on addicts and illegality – the legal price would be more like $15,000…. It is arguable that in Bolivia, Peru, Ecuador and Colombia activity generated by growing and purifying coca leaves plus the efforts at suppressing the trade constitute the single most important economic national activity, generating as much as one third of GDP in these countries.

The main tactic deployed in the drugs war has been to stop the supply rather than addressing the demand. This has been attempted by border control measures and by eradication programmes. Coca eradication in the Andes, initially voluntary and linked to alternative development opportunities for Andean farmers (growing bananas, oranges, pineapple, palm heart and other crops), has proved difficult, not least because of the much lower prices these crops command cf. Coca, market saturation for many of these alternative crops, and the sacred esteem in which Coca is held in some Andean societies, and the difficulties of separating legal from illicit production.

No eradication or interdiction programme in the past 35 years has had any serious impact on the supply of illegal drugs to the U.S.A. and Europe. Military intervention cannot repeal the laws of supply and demand. Supply suppression in one area leads to Coca production and drug refining activities being moved elsewhere – the balloon effect – squeeze it in one place and the bubble transfers elsewhere e.g. 1995-1999 Coca production in Bolivia and Peru fell by 55% and 66%, but increased in Colombia by 141%. With the subsequent Plan Colombia focusing on eradication there, production in remote parts of Peru is once again on the rise. The rules of supply and demand and pricing dictate that the temptation to cultivate Coca will remain whilst the demand for cocaine exists and the alternatives are not seen as viable. Despite controls and eradication, the successful northward export of millions of $ worth of cocaine goes on.

Elements of hypocrisy. Unbeknown to the millions of daily users, coca leaves are still used in the manufacture of the world's favourite drink with 50-70 tonnes of coca leaves legally exported to the USA for extraction of the decocainized flavour essence from the coca leaves that is an ingredient in Coca Cola. While there had been other 'pick-you-up' drinks that had cocaine as an ingredient, Coca Cola was the only commercially successful one longterm. Mixing essence of Coca leaves with sugar, caramel, caffeine, phosphoric acid, cinnamon, nutmeg, vanilla, glycerin and ground Cola nut from west Africa – a potent mix of stimulants was formed to invent the world's favourite drink, which went on to become a global company and the largest corporation in the world. It is all a long way from the Andean bush called *The Devine Plant of the Incas*.

All about markets, supply and demand, and prices, the clash between indigenous and external economic forces, epitomized perhaps by one of the most successful drinks in the Andes, Inca Kola that to me perhaps symbolizes this clash.

Rarely have the leaves of such an innocuous and unprepossessing looking shrub commanded such a value as Coca, nor come to dominate the economies of a set of Andean countries, nor spawned such widespread and disruptive violence and social problems.

### Sugarcane

In a world saturated with sweetness in many foods and drinks, it is hard to imagine a world without sugar. However, sugar, at least in the Western diet, is a recent introduction and innovation that has happened just in the last few centuries. Before the 16th century, the whole of Europe had managed virtually without sugar with honey as the only available sweetner. Sugar was, and is, an unnecessary 'food' yet Europe imports > 1 billion tones each year, a symptom of our addiction to it.

Sugarcane prehistory spans a vast area of south and south-east Asia from India to Polynesia, but few archaeological remains with which to track its origins, spread and domestication. As a result, most theories about its domestication come from living wild and cultivated plants. The earliest evidence for making sugar from sugarcane comes from India and was not known from Melanesia and Polynesia, but sugarcane is abundant in villages throughout these regions and is simply consumed by chewing.

The primary domestication of sugarcane probably occurred in New Guinea from the wild species S. robustum and resulted in a series of sweet clones known to botanists as S. officinarum. These cultivars were transported by humans to continental Asia where they hybridized with a wild species, S. spontaneum, giving rise to a new series of cultivars better adapted to subtropical environments and to sugar manufacture. These are identified as S. barberi for those from India and S. sinense for cultivars from China. It is a complex story involving several species, human movement, spontaneous hybrids, and one that we will return to again later in the course.

Sugar and slavery are intimately tied together and sugar remains one of the great moral mysteries, responsible for the Africanization of the Caribbean – a region that until 1800 was responsible for >80% of both sugar production and the trade in slaves on islands like Barbados, Jamaica and Cuba. As a result, the Caribbean was responsible for nearly half of all the seagoing effort, naval and civil of western Europe.  The planting and harvesting of sugarcane was labour intensive and it was this, along with rising demand and higher prices that made slavery inevitable – it was a job for blacks, not whites, slaves, not free men, a relationship whose hallmark was the brutalization of slave and master alike. The scale of slavery in the Americas is staggering – estimated that 10-12 million slaves were imported from Africa into the New World between 1450 and 1900. Sugar is a substance which we know that we can well do without, even today when it is cheap and freely available. Why, when it caused so much death, cruelty and misery, did sugar move from a luxury afforded and used by just a few in 1600, to a necessity for many just 200 years later, a demand that drove the slave trade to such excesses, where in 1700 every ton represented one slave’s life a ratio that increased to 2 tonnes by 1800.

Of course, the slave trade altered the makeup of the population Caribbean forever. The native Amerindians have disappeared almost without trace.

Nowadays, sugarcane is an important industrial crop grown on around 20 million ha throughout the tropics and subtropics for its sucrose rich stalks, most of which is refined into sugar, but more recently refined to make ethanol, as a renewable substitute for fossil fuels. The modern crop is based around a series of artificial interspecific hybrids generated at the end of the 19th century in Java and India.

So, a plant with a long and complex prehistory of domestication in SE Asia, that produces an unnecessary food, but one to which westerners have become accustomed and possibly addicted, led to the shipping of millions of human slaves from Africa to the Caribbean.

**Conclusions – Plants that Changed the World**

Equally interesting stories could be told about other plants such as the Cinchona tree and quinine, rubber, cotton, opium poppies, cannabis, tea, coffee, oil palm, mahogany, tobacco, chicle, and many many others. How timber deficiency sparked an industrial revolution, tobacco lead to a wealthy and young nation – the USA, the rubber tree created nations - Malaysia, and wine provided the head, heart, and pocketbook with wealth. These are all plants whose attributes satisfy multifarious human desires that ultimately link their destinies to our own.

The outcomes and impacts of these plants on people, societies, and civilizations that were often unexpected, often happened in places far distant from the home of the plants involved (potatoes from the Andes in Ireland; tulips from Anatolia in Holland; Coca from the Andes in the U.S.A; Sugarcane from SE Asia in the Caribbean), reverberating around the globe. The ancient marriage between plants and people is often far stranger, more marvelous and all embracing that we realize.

**Lecture 1 Background Materials & Sources**

Harris, S.A. 2015. *What Have Plants Ever Done For Us? Western Civilisation in Fifty Plants.* University of Chicago Press.
Hellin, J. & Higman, S. 2003. Chapter 6, Coca eradication and alternative development. In: *Feeding the Market: South American Farmers, Trade and Globalisation*. ITDG, London.
Hobhouse, H. 2002. Sugar and the slave Trade. Chapter 2 in: *Seeds of Change. Six Plants that Transformed Mankind*. Pan Books, London.
Howell, C. 2009. Flora Mirabilis: how plants have shaped world knowledge, health, wealth and beauty. National Geographic Society, Washington D.C., U.S.A.
Pavord, A. 1999. The Tulip: The Story of a Flower that has Made Men Mad. Bloomsbury, London.
Pollan, M. 2001. *The Botany of Desire. A Plant's-Eye View of the World.* Random House, New York.
Reader, J. 2008. *Propitious Esculent: The Potato in World History*. William Heinemann.

Ruddiman, W.F. et al. 2015. Defining the epoch in which we live. Is a formally designated "Anthropocene" a good idea? *Science* **348**: 38-39.

Colin Hughes, Sept 2018

## BIO 235 – Plants & People – Evolution and Domestication of Crops
## Lecture 2 – The Origins of Agriculture

Today's lecture focuses on the most momentous of all the plant-people interactions, the most dramatic story of them all, the evolution and domestication of crops and the origins of agriculture, the transition from foraging to farming, from the last hunters to the first farmers.

### Summary

- Archaic foraging to first farmers
- Where, when, how many times, and using which crops, did agriculture arise?
- Alphonse De Candolle & Nikolai Vavilov
- Documenting domestication – archaeology & genetics
- The first domesticated plant – the bottle gourd
- Two independent origins or one? – eastern North America and the origins of the sunflower

### Foraging to Farming

For more than a million years, and almost throughout the 200,000 years since the emergence of modern humans, our ancestors were hunter-gatherers, relying exclusively on the gathering of wild plants and the hunting of wild animals for their food. Then virtually simultaneously between 10,000 and 5,000 years ago, a number of plants and animals were domesticated, and agriculture arose in a number of different regions of the world. The questions are where, when, how many times independently, and perhaps most puzzling of all why did this happen?

Indeed, domestication was without doubt amongst the most significant events in human history and a major turning point in the earth's history – the lever by which humans transformed the earth and its terrestrial ecosystems. That was when there was a changeover from the natural environment in control of humans to humans in control of the natural environment.

Whatever the causes of the change from foraging to farming, food production created enormous demographic, technological, political and military advantages. As we shall see, the first farmers got the first metal tools, first invented writing, and generated professional armies and empires. Remarkably enough agriculture also spawned many of our deadliest infectious diseases which require dense human populations to thrive and which often involved switches from domesticated livestock to humans (measles and tb from cattle, influenza from pigs and chickens). These advantages were the agents of conquest and were set to change the course of history. So, there is no doubt that the switch from foraging to farming was a turning point in human and planetary history, and for these reasons sometimes referred to as the *Neolithic Revolution*

### Archaic Foraging Diet

Here we can see a typical set of foods that we might have found ourselves eating in Europe 12,000 years ago:

- Acorns – *Quercus robur* & Sweet Chestnuts – *Castanea sativa* - staples, boiled or roasted to reduce bitterness, sometimes a flour or porridge and easily stored. Large parts of northern Europe used to be covered in oak forests; chestnuts occurred further south.
- Pignuts – *Chonopodium majus* (Apiaceae) small, but delicious edible nutty tuber
- Seaweed – Carrageen – *Chondrus crispus* – a member of the red Algae – 55% of the mucilaginous body comprises the polysaccharide carrageenan, which forms a jelly when boiled, 10% protein, 15% minerals – a useful food if you lived beside the sea and especially important in western Europe
- Wild boar – *Sus scrofa* – the wild ancestor of the domesticated pig, native across much of Eurasia, albeit extinct in some areas by the 17th century.

Alongside other elements like charlock (*Sinapsis arvensis*, Apiaceae) seeds used to make a bread, Corn Surrey (*Spergula arvensis*) seeds rich in oils, plants that are now common arable weeds.

Some such items are indeed still foraged today – fungi, berries, nuts etc – '*Food for Free*'. So, even today there is a mix of foraging and farming, even if the vast majority of the world's food is farmed, not foraged. It would be an eye-opener to try for a week or two to forage for food and see how much time it takes and how hungry you get. Set out to the forest, with no modern equipment and see what happens. Would you know what to eat? Would you know where to find it? Would you survive? Probably not; most modern humans are decoupled from the knowledge and skills required for hunting and gathering.

Certainly this could indeed be a very nutritious breakfast, and arguably more nutritious than some modern-day supermarket options, as suggested in the interesting book *The Hunter Gatherer Within*, but it would have taken pretty much all your available time to gather, hunt & prepare meals of this sort.

- Reliant on MUSCLES - Extremely labour intensive – all available time & whole human population taken up with hunting & gathering. High demand for calories.
- Highly seasonal.
- Entirely local. In our globalised world it is remarkable to consider that the prehistoric peoples of the world would have consumed quite different sets of plants and animals – whatever was available locally.
- Dependent on comprehensive and sophisticated knowledge of plants, knowledge manifest in complex systems of 'folk taxonomy' and common names that are the focus of ethnobtany.
- Very little choice, especially at certain times of year
- Main concern would have been - Will harvest be large enough to hold off starvation for another year?

Contrast that with the supermarket

- Reliant on MACHINES – a very small fraction of people directly involved in food production (<2% in the U.S.A. and that fraction still declining). Reduced need for calories as most of population > sedentary.
- seasonality has all but gone
- global production
- loss of knowledge of local plants
- endless consumer choice – are we simply spoilt rotten?

- Concerns shifted away from famine to 'Am I getting too fat?' Too much food and its associated impacts. The advent of obesity as a larger health problem than lack of food across most of the world
- most of the products in the supermarket basket are the products of intensive crop breeding

**Origins of Agriculture**

At the beginning of the 19th century, the origins of most of our cultivated species were unknown, as documented by Alexander von Humboldt (1807) in his *Essai sur la Géographie des Plantes*.
"The origin, the first home of the plants most useful to man, and which have accompanied him from the remotest epochs, is a secret as impenetrable as the dwelling of all our domestic animals.... We do not know what regions produced spontaneously wheat, barley, oats, and rye. The plants which constitute the natural riches of the tropics, the banana, the pawpaw, the manioc, and maize, have never been found in the wild state. The potato presents the same phenomenon." Essentially, even the most basic documentation of crop origins had hardly started.

**De Candolle**

In 1882, Alphonse Pyramus De Candolle (1806-1893), a French Swiss botanist who worked in Geneva, put forward hypotheses determining centres of origin for various crop species based on evidence from botany, geography, history, linguistics and archaeology – an impressive multi-disciplinary synthesis of the available evidence. De Candolle's 1882 book, *Origin of Cultivated Plants*, aimed to document where the c.250 most important plants found in cultivation came from originally. It was de Candolle who first clarified the idea of independent origins. "It is clear that, owing to their well-known qualities.... it was at an early period found easy to cultivate rice and several leguminous plants in southern Asia, barley and wheat in Mesopotamia and in Egypt, several species of Panicum in Africa, maize, the potato, sweet potato and manioc in America." His book provides the first worldwide Encyclopedia of 250 of the world's most important cultivated plants, with their temporal and geographic origins. He noted that:
- no species was common to the two hemispheres before cultivation, and no evidence of pre-Columbian communication between the New and Old Worlds – i.e. there is a remarkable distinctiveness of domesticated crops in different parts of the world.
- 199 species came from the Old World and 45 from the Americas.
- A relatively small number of species of Gramineae, Leguminosae and Brassicaceae dominated.
- the absence of cultivated plants in some areas, e.g. The Cape, Australia.
- some plants seemed to have been cultivated well before others.
- annuals dominate and came before perennials
- some 27 species remained unknown in the wild

A series of potent observations which lay the foundations for much of what we know about the origins of crops today.

**Vavilov**

Russian scientist Nikolai I. Vavilov, who worked at the Bureau of Applied Botany, now the Vavilov Institute, in Leningrad from 1921 to 1940, greatly expanded de Candolle's ideas through field research and breeding experiments. Vavilov traveled over five continents, collecting hundreds of thousands of seeds in an effort to outline the ancient centers of agricultural diversity and guard against widespread hunger by establishing a collection of 1000s of crop varieties from their areas of greatest diversity around the world. He proposed that the seven regions containing the greatest genetic diversity of crop species and their wild relatives corresponded to 7 broad centres of crop domestication. These became known as Vavilov's centres. However, perhaps his greatest contribution was his idea to collect the wild relatives of crop plants which were incorporated into the Vavilov Institute of Plant Industry germplasm collections – the second largest germplasm collection in the world with 320,00 accessions, about which we will hear more in a subsequent lecture.

Vavilov repeatedly criticised the non-Mendelian concepts of Trofim Lysenko who was favoured by the Stalin regime and who replaced Vavilov as director. As a result, Vavilov was arrested for espionage on August 6, 1940 while conducting fieldwork in Ukraine and died, ironically for a man who had devoted his life to the elimination of hunger in the world, of malnutrition, in a Soviet prison in 1943. If you are interested in reading more about Vavilov, there is a book by Peter Pringle – *The Murder of Nikolai Vavilov – The story of Stalin's persecution of one of the twentieth century's greatest scientists*, and a book by Nabhan called '*Where does our food comes from'* in which Nabhan retraces Vavilov's footsteps.

These broad centres provide a framework for studying the origins of crop plants and these have been progressively refined and extended ever since, notably by Harlan, with at least two additional independent centres in eastern North America and New Guinea, ideas of subcentres, or secondary centres where crops were initially introduced from other areas and only subsequently were local plants domesticated and added to the overall crop system. Here we can see a more refined view suggesting 10-11 independent origins of agriculture and some of the crop origins linked to each one, and perhaps even more independent origins of agriculture, but as we shall see later in the lecture, the independence of some of these centres even now, remains the focus of debate.

### Different Crops in Different Centres

We will examine in detail the origins of domestication in terms of when, where, how many times and from what progenitors sets of major crops were domesticated in later lectures. For now it is worth highlighting sets of crops and animals that were domesticated in four areas: Mesoamerica, the Andes, The Fertile Crescent and New Guinea.

Very often a combination of cereals and pulses in each regional centre of domestication:

- Maize and *Phaseolus* beans in Mesoamerica
- Rice and soya beans in China
- Wheat/ barley and lentils / peas / faba beans in the Fertile Crescent
- Millet and mung beans in India

The idea of a balanced diet was in place from the very beginnings of agriculture.

### The independent domestication of plants and animals in c.10 regions of the world

- Independent origins - striking that different plants were domesticated as crops in different parts of the world, reinforcing the idea that these origins of agriculture were indeed independent.

- More or less simultaneous - in terms of the evolutionary history of humans, this transition from foraging to farming apparently took place more or less simultaneously (within a period of 5,000 years).
- Within that short period, domestication and agriculture started earlier in some areas than others

Here we can see some of the details in terms of where, when, and which crops. We can see that different crops appear in different areas. There is virtually no overlap (see below for one notable exception), providing powerful evidence that agriculture did indeed arise independently in different areas.

This all sounds very straightforward, but deciding whether agriculture arose independently in two closely adjacent areas is not necessarily straightforward. As we delve deeper, the developmental histories of each of these independent centres are turning out to be far more complex and nuanced than previously thought. For example, the range of crops involved is much greater than indicated by the handful of crops that have emerged into global prominence.

## Documenting Domestication

Modern approaches use two main sources of evidence to provide increasing precision about the central questions – *when? Where? how many times?* and *from what progenitors?* crops were domesticated

<u>Archaeological data</u> – identification and dating of plant remains.

- Direct accelerator mass spectrometer (AMS) radiocarbon age determinations now allow unequivocal temporal placement of early domesticates using very small samples.
- Increasingly sophisticated microscale morphology and anatomy to distinguish wild from domesticated plant remains in archaeological contexts

<u>Biological data</u> – taxonomy, morphology and genetics.

- DNA sequence data and other markers provide comprehensive genetic comparisons to reveal the identity and geographical ranges of present-day wild progenitors.
- Comparison of wild progenitor(s) and domesticates to pinpoint and quantify the morphological changes associated with domestication.

Cross-illumination and consilience of these linked but independent sources of evidence has seen powerful recent advances in our understanding of the origins of domestication for major crops. Both types of data provide geographical placements for domestication. The aim to seek congruence between the geographical location of the oldest remains of a domesticated crop and the geographical location of the genetically closest wild relatives / progenitors of a crop. Where gaps are apparent between the archaeological and genetic data, this points to where new evidence should be sought.

## The Earliest Plant Domesticate

The first example I want to talk about is the bottle gourd, *Lagenaria siceraria*, an Old World plant from tropical Africa. We have seen that distinct suites of food crops were used and domesticated from local native floras independently in different regions of the world. The bottle gourd is a notable exception – it has been used and grown by diverse early human cultures worldwide (across Eurasia, the Pacific islands and the New World since pre-Colombian times, usually not as a food source, but for its strong, lightweight, hard-shelled, buoyant fruits which have long been prized as containers – especially before the advent of pottery and settled village life – the ultimate 'container crop'. It is this variety of non-food uses that probably explains why bottle gourds are so globally pervasive. Choosing to focus on this non-food crop may seem an odd choice, but it is interesting because as we shall see, it is likely to be the earliest domesticated plant, and it also illustrates this reciprocal illumination of genetic and archaeological data.

### Bottle Gourd Archaeological Data

One of the puzzles surrounding the bottle gourd has been its consistent occurrence in close association with the earliest New World domesticates. The discovery of bottle gourds at disparate archaeological sites across the Americas – raised questions about the timing, routes and mechanisms of the plant's global diffusion to include the Americas.
Interdisciplinary approach to examine bottle gourd rind fragments recovered from early archaeological sites in South America involving:

- accelerator mass spectrometer (AMS) radiocarbon dating
- morphological analysis
- ancient DNA sequencing

These analyses show:

- earliest occurrences of bottle gourd in the Americas from 9,000-10,000 years in Mexico, 8,400 years in Peru and 8,000 years in Florida
- a distinctive cross-sectional cellular structure diagnostic of bottle gourd and thick rinds associated with domestication
- bottle gourd remains found amongst the earliest New World cucurbits used for food and in Florida preceding the first evidence of locally domesticated food crops by several millennia.

One of the features of the archaeological evidence is that there are few sample points – there are simply not that many places where plant remains have been preserved more or less intact for 10,000 years – mostly dry caves and they are very sparsely distributed – a very fragmentary record.

The central question about bottle gourd domestication that has been the focus of on-going controversy and debate is how did the bottle gourd arrive in the Americas. Were already domesticated bottle gourds transported by Paleoindian settlers moving from Asia across the Bering strait when humans colonized the Americas, or did wild bottle gourds arrive in the New World by long distance dispersal of gourds drifting across the Atlantic Ocean, establishing in the Neotropics and then being domesticated there independently?

### Bottle Gourd Genetic Data I

Scientists have attempted to address this question by generating DNA sequence data for a wide sample of African wild and Asian / African & New World domesticated accessions, including samples taken from ancient archaeological bottle gourd remains dating back to c.8,000 years from sites across the Americas. An initial study screening of ITS and 10kb chunk of mtDNA revealed no DNA sequence differences amongst Asian and African material. Three plastid DNA markers showed variation, and two of these indels which avoid problems associated with post-depositional mutations that plague interpretations of ancient material based in SNPs. Ancient

DNA extracted from New World rind fragments showed that all the fragments predating the arrival of Europeans were identical to the modern Asian land races. A single fragment post-dating European arrival (1660) from Mexico is the same as the African type and hence attributable to one of many European introductions. Using this small set of structural mutations in ancient DNA it was suggested that this provided powerful evidence that New World bottle gourds were derived from Asian domesticates and most likely transported by humans.

**Bottle Gourd Genetic Data II**

Later, a much more comprehensive study sampling many more accessions and using much more sophisticated laboratory techniques (hybrid capture of >80,000 bp of plastid DNA sequence), came to very different conclusions. The relationships of the ancient bottle gourd samples are shown in red. We can see that, the two domesticated subspecies are sister to each other; a wild gourd from Zimbabwe (one of only two known wild populations) forms an outgroup to the rest. The asiatica lineage is subtended by a domestic Ethiopian landrace, whereas a wild Kenyan accession is sister to the siceraria lineage, suggesting east Africa as the likele ancestral area of bottle gourd diversity. These results strongly support an African origin of New World bottle gourds, suggesting that wild bottle gourds likely drifted across the Atlantic ocean and became established in the New World and were subsequently domesticated there. The deep intermingling of African and New World accessions points towards multiple long distance dispersal events across the Atlantic and a scenario of diffuse domestication multiple times independently in different regions in the Americas. One intriguing result is the appearance of an Argentinian accession within the asiatica lineage – this could represent an historic introduction to South America, or more interestingly indicate a possible prehistoric contact, material cultural exchange and domesticated germplasm transmission between Polynesia and South America. One of the most impressive examples of use of ancient DNA.

**Bottle Gourd Conclusions**

American bottle gourd came directly from Africa, likely via long distance dispersal across the Atlantic – known that bottle gourds can float for up to a year in sea water and maintain seed viability and ocean current modeling shows probability of crossings in < 1 year.
Grown as a domesticated plant in the New World as early as 10,000BP
Likely that bottle gourd was the earliest plant domesticate, coinciding with initial domestication of the dog somewhere in Eurasia.
Two utilitarian species, the bottle gourd and the dog brought under domestication long before any food crop or animal domesticates.
This perhaps not surprising given the great value of bottle gourds (for carrying water) and dogs (for hunting) to hunter-gatherer communities…

**Eastern North America and Mesoamerica – one independent origin or two?**

Before we delve deeper into the detailed developmental trajectories of domestication and agriculture, I want to return to this question of how we know whether these centres are truly independent or not.

There are two hypotheses regarding the origin of agriculture in eastern North America. One hypothesis holds that agriculture arose independently in this region with domestication of four to seven indigenous species. The alternative states that most major cultigens originated in Mesoamerica and were dispersed northwards to the eastern woodlands of North America, triggering domestication of minor indigenous crops secondarily, i.e. that it formed a secondary centre of domestication and that agriculture arose here non-independently of Mesoamerica.

The primary evidence that agriculture arose independently in eastern North America derives from morphological changes in the archaeobotanical record of three important crops – squash, goosefoot and sunflower, as well as an extinct minor cultigen, sumpweed. However, the geographic origins of two of these – squash and goosefoot are debated, and until recently sunflower has been considered the only undisputed eastern North American domesticate. The sunflower, *Helianthus annua*, a member of the Asteraceae, or Compositae, is a well known oil crop, cultivated across many areas, including here in Switzerland of course, where fields of nodding sunflowers are a common sight in summer.

The discovery of a 4,000 year-old domesticated sunflower seed in plant remains from an archaeological site at San Andres, Tabasco, southern Mexico (Lentz et al., 2001) (within the Mesoamerica centre of crop domestication and early agriculture), implies an earlier and possibly independent origin of domestication in Mexico and has stimulated re-examination of the geographical origin of domesticated sunflower. Determining the geographic origin(s) of sunflower impinges directly on the question of an independent eastern North American origin of agriculture.

**Origins of domestication of the sunflower Harter et al (2004)**

Harter et al (2004) examined the relationships among 21 populations of wild Helianthus annua and eight native American landraces from the USA and Mexico, as well as two modern cultivars using 18 microsatellite loci distributed across the sunflower genome. Here we can see the sampling locations for these accessions and the archaeological sites, where A is the San Andres site in Tabasco, Mexico dating to 4,130 radiocarbon years BP, B is Tennessee at 2,850BP, C is also in Tennessee at 4,265BP and D is in Arkansas at 2,843 BP.

In the phylogram, colours correspond to local area model source clusters, while domesticated strains are shown in black, including the two modern cultivars Mammoth and USDA, line lengths correspond to genetic distances, numbers on terminal branches are measures of genetic drift. Results show that all domesticated strains form a monophyletic group, suggesting a single origin of domestication with a sister group in the central USA, and with Mexican strains more distantly related / less genetically similar, thus supporting a central USA origin for domesticated sunflower. We can also see that measures of genetic drift are much higher for the domesticated strains, the likely result of genetic bottlenecks associated with domestication.

Subsequent re-examination of the Lentz et al. (2001) archaeological remains casts doubt over the identities of these seeds and suggests that they were mis-identified (Smith 2006). All this confirms that eastern North America could indeed have been an area where agriculture arose independently.

This illustrates very well the interplay between genetic and archaeological evidence. When there is congruence, this provides powerful evidence to pinpoint the time and place of domestication; when they disagree as here, this prompts re-examination of the evidence. It is a process of reciprocal illumination.

### Chenopodium berlandieri

Ancient DNA confirms a local origin of domesticated chenopod in eastern North America. Chenopod (Chenopodium berlandieri) is a weedy relative of quinoa and spinach, and was an important starchy seed crop in eastern North America from c. 3800BP until c. 1100BP or later, when maize-based agricultural intensification arrived from the south. Just as for the sunflower, it has been unclear whether chenopod was domesticated locally in the woodlands of eastern North America, or introduced from Mesoamerica where morphologically identical chenopods are cultivated today – locally referred to as huazontle.

Samples from across North America, from Mexican cultivated populations and from Archaeological remains in eastern North America, were sequenced for a series of chloroplast intergenic spacers. Modern samples cluster into three clades with little variation in each clade. The domesticated Mexican samples and most wild eastern North American samples fall into two clades sparated by 4 SNPs. All the ancient archaeological samples carry the eastern North American haplotype.

These results demonstrate that chenopod was domesticated in eastern North America from native wild populations independent of the cultivated Mexican lineage. Taken together with sunflower, these results provide compelling support for development of an entirely indigenous agricultural complex in eastern North America.

### The lost crops of eastern North America

In addition to the sunflower and goosefoot, four other crops are thought to have been cultivated in eastern North America:
a. Goosefoot – *Chenopodium berlandieri*
b. Sumpweed / Marsh Elder – *Iva annua*
c. Little Barley – *Hordeum pusillum*
d. Erect Knotweed – *Polygonum erectum*
e. Maygrass – *Phalaris carolinum*
These are now so called ‘lost crops’ which we shall return to in Lecture 7.

### The Origins of Agriculture – Questions

So this is the current picture. Virtually simultaneously a number of plants and animals were domesticated in 8-?13 regions – or maybe even more - of the world independently within the last 5,000-10,000 years. Crop and livestock domestication heralded the transition from archaic foraging to agriculture, with:

- important biological impacts and the rapid evolution of crop plant genomes
- far reaching consequences for the development of human societies and civilization as we know it
- ecological impacts on natural environments.

Independent centres appear to offer a promising comparative set of developmental trajectories for investigation that may gradually reveal more general underlying principles and processes. For example, the Fertile Crescent presents a remarkable array of plant and animal domesticates that were domesticated relatively quickly resulting in a powerful and expansive agricultural economy. In contrast, in eastern N. America no animals were domesticated and just four crops, only two of which survived as modern crops. These contrasting scenarios offer a rich worldwide mosaic of diverse agricultural systems.

Many significant questions still remain:

- Why did agriculture arise more or less simultaneously in 10-13 independent areas?
- Why in these areas and not others?
- Why did domestication operate on so few species – 350,000 higher plants but only c.100 serious domesticates?
- Also notable that some areas had no early agriculture or domesticated crops. These include several of the areas of the world where modern agriculture is most productive – e.g. southern Africa and Australia where despite a rich biota and vibrant modern-day agricultural economies, the aborigines and African bushmen did not develop agriculture but persisted as hunter gatherers until the arrival of Europeans. Why did agriculture arise in these areas and not others? Why do these areas not overlap significantly with area of most productive modern agriculture?

**For Next Week:**

Why did agriculture arise?
Why did it arise more or less simultaneously and independently in different places?
Is there a global explanation?

## Lecture 2 The Origins of Agriculture - Source Materials

Balter, M. 2007. Seeking agriculture's ancient roots. *Science* **316**: 1830-1835.

Brock, K.G. & Diggs, G.M. 2013. *The Hunter Gatherer Within: Health and the Natural Diet.*

Brown, T.A., Jones, M.K., Powell, W. & Allaby, R.G. 2009. The complex origins of domesticated crops in the Fertile Crescent. *Trends in Ecology & Evolution* **24**: 103-109.

De Candolle, A.P. 1886. *The Origin of crop Plants.* (reprinted 1959, Hafner Publ. Co. New York).

Diamond, J. 2002. Evolution, consequences and future of plant and animal domestication. *Nature* **418**: 700-707.

Erickson, D.L. et al. 2005. An Asian origin for a 10,000-year-old domesticated plant in the Americas. *Proceedings National Academy of Sciences* **102**: 18315-18320.

Harter, A.V., K.A. Gardner, D. Falush, D.L. Lentz, R.A. Bye, L.H. Rieseberg. 2004. Origin of extant domesticated sunflowers in eastern North America. *Nature* **430**: 201-205.

Kistler, L. & Shapiro, B. 2011. Ancient DNA confirms a local origin of domesticated chenopod in eastern North America. *J. Archaeological Science* **38**: 3549-3554.

Kistler, L. et al. 2014. Transoceanic drift and the domestication of African bottle gourds in the Americas. *Proceedings National Academy of Sciences* **111**: 2937-2941.

Larson, G. et al. 2014. Current perspectives and the future of domestication studies. *Proceedings National Academy of Sciences* **111**: 6139-6146.

Lentz, D.L. M.E.D. Pohl, K.O. Pope, A.R. Wyatt. (2001). Prehistoric sunflower (*Helianthus annuus* L.) domestication in Mexico. *Economic Botany* **55**: 370-376.

Mueller, N.G., Fritz, G.J., Patton, P., Carmody, S. & Horton, E.T. 2017. Growing the lost crops of eastern North America's original agricultural system. *Nature Plants* **31**.

Nabhan, G. 2008. *Where Our Food Comes From. Retracing Nikolai Vavilov's Quest to End Famine.* Island Press.

Pringle, P. 2009. *The Murder of Nikolai Vavilov. The Story of Stalin's Persecution of One of the Twentieth Century's Greatest Scientists.* MPG Books, UK.

Purugganan, M.D. & Fuller, D.Q. 2009. The nature of selection during plant domestication. *Nature* 457: 843-848.

Rieseberg, L.H., A.V. Harter. (2006). Molecular evidence and the evolutionary history of the domesticated sunflower. In Motley, T. N. Zerega, H. Cross (eds.) *Darwin's Harvest: New Approaches to the Origins, Evolution, and Conservation of Crops*. Columbia Univ. Press.

Smith, B.D. 2001. Documenting plant domestication: the consilience of biological and archaeological approaches. *Proceedings National Academy of Sciences* **98**: 1324-1326.

Smith, B.D. 2006. Eastern North America as an independent center of plant domestication. *Proceedings National Academy of Sciences* **103**: 12223-12228.

Zeder, M.A., et al. 2006. Documenting domestication: the inter-section of genetics and archaeology. *Trends in Genetics* **22**: 139-155.

Online Case studies in Crop Domestication
http://www.botany.wisc.edu/courses/botany_940/06CropEvol/CropEvol.html

Colin Hughes
Sept 2018

## BIO 235 – Plants & People – Evolution and Domestication of Crops
## Lecture 3 Crop Origins – Maize, wheat & rice – the three most important crops

Genetics & Archaeology
As I mentioned in the last lecture, the combination of evidence from genetics of modern crops and their wild relatives and candidate progenitors and from archaeology is providing powerful new insights into crop origins in terms of where, when, how many times and from what progenitors our crops were domesticated.

Archaeological data – identification and dating of plant remains.

- Direct accelerator mass spectrometer (AMS) radiocarbon age determinations now allow unequivocal temporal placement of early domesticates using very small samples.
- Increasingly sophisticated microscale morphology and anatomy (SEM) to distinguish wild from domesticated plant remains in archaeological contexts to determine the location of the earliest domesticated remains.

Biological data – taxonomy, morphology and genetics.

- DNA sequence data and other markers provide comprehensive genetic comparisons to reveal the identity and geographical ranges of present-day wild progenitors. This ever-expanding as genome sequencing gathers momentum.
- Comparison of wild progenitor(s) and domesticates to pinpoint and quantify the morphological changes associated with domestication.
- Cloning and molecular evolutionary analysis of key domestication genes is providing additional insights into crop origins.
- This also extended to ancient DNA extracted from archaeological remains.

Monophyly
The principle of monophyly is central to inferring how many times a crop was domesticated. Using DNA sequence data to build a phylogenetic tree, a hypothesis of sister group relationships between wild and domesticated forms can be established. If the domesticated accessions form a monophyletic group, i.e. a group that contains all of the descendants of a common ancestor, then a single origin of domestication can be inferred. Furthermore, by looking at which wild accessions are most closely related to the domesticate, the geographic origin of domestication can also be inferred.

Archaeology
Archaeology = the excavation and study of past site of human activity/ occupation
Archaeobotany = recovery and study of plant remains preserved on those sites

Oswald Heer 1809–1883; 1865 *Die Pflanzen der Pfahlbauten* [Plants of the pile-dwellings]
Summary translation in English, 1866; also, summaries by Darwin & Lubbock
One of the earliest archaeobotanists was Oswald Heer, a Swiss who excavated and documented plant remains from Neolithic lake settlement sites in Switzerland e.g. 6,000 BP from Bielersee, Lac de Neuchatel, published in 1865. Indeed, Heer is generally considered the world's first archaeobotanist.
"Altogether 115 species of plants have been determined…Dr. Heer, from whose very interesting memoir the above facts are borrowed, calls particular attention to the fact that, while the remains Of wild species found in the Pfahlbauten. Agree in the most minute particulars with those still Living in Switzerland, the cultivated plants, on the contrary, differ from all the existing varieties, and invariably have smaller seeds and fruits. Man has evidently in the course of time effected considerable improvements" (Lubbock *Pre-Historic Times,* 3rd ed, 1872, pp. 212-214)

## Archaeobotany

For the most part, archaeology has focused on intact remains of seeds or fruits – so called macrobotanical remains retrieved from well-preserved chronologies that span the transition from archaic foraging to farming and the domestication of crops. Key traits indicating domestication, such as characteristic abscission layers of non-shattering grass spikelets, can be used to distinguish wild and domesticated remains. Here we can see the earliest domesticated >6,000 year-old maize cobs from southern Mexico and a set of rice seeds from the lower Yangtze river in China dating to 4,000 BP with distinctive wild and domesticated abscission layers.

## Flotation

A key technique for recovering plant remains from archaeological sites is flotation, whereby seeds and other plant remains are mixed with water and the floating remains can be screened out using a 250 micron mesh. Although it is a simple innovation, this technique did not become widely used until the 1960s. This provided the first way to really obtain quantitative data on domestication traits from archaeological sites. For example, flotation means that it has been possible to recover very large numbers (1000s) of rice spikelets to estimate the proportions of shattering vs non-shattering spikelets through time….

## AMS radio carbon dating

The advent of accelerator mass spectrometer radio carbon dating has transformed the scope to establish accurate ages for small pieces of plant materials excavated from archaeological sites. Radio carbon dating relies on measurement of the ratio of the radioactive isotope carbon-14 $^{14}C$ to carbon-12 $^{12}C$ atoms which provides an age estimate as radioactive $^{14}C$ decays at a known rate with a half-life of 5730 years. Conventional radiocarbon dating measures the $^{14}C$ decay events over a period of hours, but required large amounts of material – much larger than the quantities available in seeds or many other plant remains. This sample size problem meant that until the 1980s the age of materials could only be determined indirectly, by dating larger samples of organic material, usually charcoal, thought to be contemporary (inferred by adjacency in the stratigraphic layer in an excavation) with the plant remains in question. Such indirect estimates are unreliable. New AMS dating counts actual $^{14}C$ atoms directly rather than measuring decay events, thus enabling measurements on samples 1000 times smaller than before, and as small as a few hundredths of a gram, and heralding a new era of accuracy in dating archaeobotanical remains.

## Small is big – microbotanical remains

The biggest problem with conventional macrobotanical archaeological data is that very few sites with well-preserved chronologies of plant remains have been found, which means that there is only a very sparse and scattered geographic sample available. Indeed plant remains are only well-preserved in very dry or waterlogged (anaerobic) conditions. The truism that absence of evidence is not evidence of absence holds particular force in archaeology, and nowhere more so than in the prehistory of human-plant interactions. To get around the coarse sampling problem, archaeologists need to develop every possible source of useful information.

## Invisible clues to plant domestication

Within the last few decades, use of microbotanical evidence from phytoliths (plant crystals) and starch grains has contributed potent new evidence, especially for root crops (tubers) that leave few macro remains and in lowland tropical wet sites not suited to preservation of plant remains. Here we can see a sample of stone tools from 7,800 years ago in Panama from which maize, arrowroot, manioc and yam starch grains and phytoliths have been recovered indicating the movement and adoption of these crops in lowland tropical agriculture almost 8,000 years ago. Hence the title ‘small is big’ – big discoveries from tiny ‘micro’ remains. It is even possible to estimate the ages of microbotanical remains using AMS radiocarbon dating (below).

## Biomolecular Archaeology

High performance liquid chromoatography & chemical ionization mass spectrometry can provide highly sensitive techniques to identify ancient foods and beverages from residues on cooking pots, pottery and other ancient vessels.

For example, detection of theobromine, a chemical distinctive to cacao from spouted vessels from Central America used to infer the earliest use of chocolate (Teobroma cacao) by PreClassic Maya 2,600 BP. Theobroma cacao is the only Mesoamerican plant that contains theobromine as the primary methylxanthine and hence can be used as a marker for the presence of cacao. This evidence pushed the date of cacao use back by 1,000 years and suggests a continuous consumption of chocolate by the Mayans from 2,600 BP to the present day.

## Ancient DNA

Increasingly possible to extract usable DNA from plant and animal specimens preserved in museums or extracted from archaeological excavations or other deposits. However, yields of DNA are usually low and the quality of DNA is often also low - highly degraded and fragmented. The upper age limit for DNA extraction so far has been about 1 million years, and that from frozen or dry remains only. However, next generation sequencing technologies using relatively short sequence reads can deal with partially degraded DNA better than traditional PCR-based Sanger sequencing. Other challenges surrounding use of ancient DNA are post-mortem mutations and contamination, such that special dedicated labs and protection are essential. The most spectacular use of ancient DNA has been the successful assembly of a draft genome sequence for Neandertal man, while in plants we saw the example of successful use of 10,000 year-old DNA to place the Peruvian archaeological remains of bottle gourd rinds.

## The archaeological revolution

These new techniques, including SEM, AMS radiocarbon dating and an ever wider spectrum of ever more variable DNA markers, genome scale DNA data, cloning and molecular evolutionary analysis of key domestication genes, and analysis of ancient DNA from archaeological remains, developed over the last few decades have revolutionized the accuracy and precision with which we can assess these two sources of evidence, allowing us to home in on exactly where and when crops first appeared with surprising precision, say to within a few 100km and a few 100 years, something that seems quite remarkable for an event that happened as much as 10,000 years ago.

## Grasses

11,000 species
Global distribution in all biomes
Grasslands: tropical savannas; temperate prairies, alpine meadows
Fostered the evolution of large herbivores
Natural grasslands dominate the planet
Man-made grasslands dominate the planet: fields of food crops, fields of livestock, lawns, sports fields
Grasses form the granaries of the world and the cradle of agrculture
- The biggest crops – maize, wheat, rice and sugar cane are all grasses

Excellent book entitled ‘Grasses’ by Stephen Harris – a book that encapsulates the essence of this course in documenting the complex and far-reaching interactions between plants and people, for the most important family of plants for humans.

## Cereals

The domestication of grasses has been of unique importance in the history of human civilisations and today cereals provide the staple foods for the vast majority of the world’s population. Maize, *Zea* *mays*, from Mesomaerica; wheat *Triticum spp*., from the Fertile Crescent; and rice, *Oryza sativa* from SE Asia, are the world's three top crops.

Global consumption of 10 major vegetal foods
Just how these three crops dominate human food consumption is illustrated here, with rice and wheat each accounting for 31% of all plant food, dwarfing all other crops including potatoes, oil palm, soya and others.

Global grain consumption map
The regional domains of the three major cereal crops, reflecting their origins, spread and dominance in modern agriculture.

Grass phylogeny
Grasses can be divided into two major groups, the so-called PACMAD clade of tropical grasses which includes all the grasses with C4 photosynthesis, and the BEP clade with the temperate grasses, which all have the C3 photosynthetic pathway.The major cereal crops occur in distantly related grass lineages, as seen in the outline phylogeny of the Poaceae, with maize, sugar and sorghum, the main tropical grass crops in the Panicoid clade, and wheat, barley, rye and oats in the mainly temperate Pooid clade, subtended by the rice and bamboo clades.

Phenotype of wild vs domesticated cereals and relevant terminology
The morphological differences that distinguish wild from domesticated cereals are crucial for understanding the origins of domestication. A common combination of three basic characters underlies the transition from wild to domesticated in all cereals – here illustrated for einkorn wheat with spikelets, or ears with two rows of seeds:

- Seed size increase in domesticated forms
- Non-shattering spiklets due to a tough rachis that holds the seeds together in a harvestable and threshable ear
- Leaf-like structures that protect the seed – called glumes – are attached tightly to the seed or fused to it in wild forms whereas they release the seed in the more advanced domesticated forms, which are therefore termed 'free-threshing' or naked.

Maize: The most widely grown crop in the Americas; 332 million metric tonnes /yr in the U.S.A., 800 worldwide; transgenic maize comprised 85% of maize planted in the U.S.A. in 2009; a greater weight of maize is produced each year than any other grain; > 150 million ha worldwide.

The Mystery of Maize
The large maize cob with its naked seed kernels is unique amongst grasses and finds no morphological counterpart in Mexico or Mesoamerica and for a long time it was thought that the progenitor of domesticated maize must be extinct. Nothing resembling maize had been found amongst wild species of maize in Mexico.

George Beadle
The first steps to solving this mystery were taken be George Beadle who came up with the radical suggestion that teosinte was the progenitor of maize. Despite the stark morphological differences between domesticated maize (size, shattering vs non-shattering, seed case vs naked grains), Beadle suggested teosinte based on two pieces of evidence: (i) he showed that the chromosome complements of maize and teosinte are almost identical; (ii) he showed that maize and teosinte can be readily crossed and that the hybrid between them is fertile. Taken together these results suggested that maize and teosinte are very closely related.

Maize Genetic Data

In a comprehensive phylogenetic analysis of maize and teosinte involving 264 maize and 64 teosinte accessions from across the Americas, showed that:

- all domesticated maize accessions were placed in a single monophyletic lineage derived from within teosinte – providing strong evidence for a single domestication event with teosinte as the progenitor.
- the region harbouring the teosinte populations phylogenetically most closely allied is the Balsas Depression (marked with asterisks on the phylogeny) – can be considered a candidate region for domestication.
- Progressive geographic diversification independently into North and South America, with the earliest branching lineage of domesticated maize found in Oaxaca.

## Maize *tb1* gene

A single domestication of maize is also supported by the cloning and molecular evolutionary analysis of a key domestication gene, *teosinte branched 1, tb1*, which also provides evidence for the single origin of maize.

- *tb1* is a key domestication gene in maize
- It encodes a TCP protein (TCPs are growth regulators)
- It is expressed in the axillary meristems of maize but not teosinte
- Maize shows strong evidence of selection in the tb1 gene promoter region
- Presence of maize tb1 gene in teosinte suppresses outgrowth of axillary branches
- Identical *tb1* genes in different domesticated maize accessions support single origin

## Maize – Archaeological Data I – Guila Naquitz Cave, Oaxaca

The evidence for the earliest clearly domesticated maize cobs comes from the Guila Naquitz Cave near Oaxaca in southern Mexico. The cave was excavated in 1966 and revealed a continuous chronology of plant remains from 10,650 BP to 1,260 BP – a remarkable 9,000 years spanning the transition from archaic foraging to agriculture and the first maize cobs date to 6,250BP. These remains look more like vertebrae from a spinal column than maize cobs, but that is what they look like after sitting for >6,000 years amongst the accumulated debris in the floor of a cave. We can see that Guila Naquitz is not very far away from the Balsas depression where wild populations of teosinte, the progenitor of domesticated maize suggested by genetic data, grow.

## Maize – Archaeological Data I – Xihuatoxtla Rock Shelter, Guerrero

Based on the genetic data which pointed to the Balsas Depression as the likely location for the teosinte populations that gave rise to domesticated maize, subsequent archaeological excavations were focused in that area. The most notable of these was the Xihuatoxtla Rock Shelter in Guerrero where a chronology spanning 1200 to 8990 BP was excavated and where a number of grinding stones and stone tools were analyzed for phytoliths and starch grains. These yielded starch grains characteristic of domesticated maize from as early as 8,700BP.

## Teosinte becomes popcorn

Another question surrounding the domestication of maize and teosinte as the likely progenitor, is how was teosinte used, given that the grains are surrounded by a hard seed case. Beadle showed that teosinte seeds can be soaked and ground, and even popped, like popcorn.

## Teosinte – the progenitor of Maize

Maize provides an excellent example of this sort of new precision. Maize was domesticated as a major cereal crop in Mexico, in the Mesoamerican centre of crop domestication and early agriculture. While there has been considerable controversy about the origin and early history of maize, there is an emerging consensus that an annual species of teosinte (*Z. mays* ssp. *parviglumis*) is the ancestor of domesticated maize. Teosinte is currently found in the Balsas Depression in Mexico. The differences between the spiklets of teosinte and maize are dramatic and there are also marked differences in plant habit – teosinte being a highly branched plant and maize single-stemmed with strong apical dominance. It is remarkable to observe the diversity of forms of domesticated maize that have been derived from this seemingly innocuous Mexican grass teosinte – an illustration of the impressive outcomes of the process of domestication, and the ways that humans have been able to alter plants, beyond all recognition. Perhaps one of the most striking features of this diversity of form amongst land races and cultivars of maize, is that it transcends what might be considered conventional limits of species in terms of natural diversity. This shows just how potent the changes in plant form brought about by humans have been. It also proves that selection is a powerful tool when applied to natural diversity, an insight that was critically important to Charles Darwin when he formulated his theory of evolution on the basis of natural selection more than 150 years ago.

### Maize conclusions

There is thus an exciting correspondence between the archaeological and genetic evidence. However, there is also a gap of some 400-500km from the populations of teosinte in the Balsas and the Guila Naquitz cave. Could suggest that:

- either teosinte was once more widespread, i.e. that key teosinte populations of relevance to domestication are now extinct, or maybe teosinte has still to be found closer to Oaxaca.
- the archaeological sampling has so far missed the key moment of initial domestication.
- Finally, entirely possible that maize was domesticated nearer, or in the Balsas before 6,300BP and subsequently introduced into Oaxaca and Tehuacan.
- Scope for further botanical and archaeological exploration.
- The later study of Piperno et al (2009) brings an exact geographical congruence between the genetic and archaeological data.

### A short history of the exploration and discovery of maize species – Rafael Guzman & Hugh Iltis

1979 – Maize as we know it, that is *Zea mays*, is an annual plant. In 1910 a perennial maize, arising from rhizomes, was discovered in western Mexico and named *Zea perennis*. Subsequently it was thought that this species was extinct in the wild until two populations were rediscovered in 1978 by Rafael Guzman, an undergraduate student from Guadalajara. Closer examination of these revealed that one of these populations, growing at 2200-2400m in the Sierra de Manantlán was actually a distinct species of perennial maize. This was described as *Zea diploperennis* by Hugh Iltis, Doebley and Guzman. This was a truly remarkable discovery – a close relative of one of our most important cereal crops, and interfertile with that crop, discovered just 30 years ago, and it was so newsworthy that the authors succeeded in publishing their new species in the high impact journal *Science*, something unheard of in plant taxonomy in general.
2000 – A wild teosinte, *Zea luxurians*, has long been known to occur further south in Guatemala. However, in 2000 a related but distinct species, *Zea nicaraguensis* was discovered and described from a handful of small, very local populations on seasonally flooded coastal plains in NW Nicaragua, again led by Hugh Iltis. This species grows under seasonal inundation at sea level.

2011 – Three new teosintes informally described from west-central Mexico – a perennial diploid variant related to *Z. diploperennis*, a perennial tetraploid close to *Z. perennis*, and an annual diploid with affinities to *Z. luxurians* and *Z. nicaraguensis*.

Still uncovering new species and infraspecific variants that are closely related to one of the world's most important crops. Some of these could be key 'missing links' in unlocking the secrets surrounding the origins of domestication. They also harbor genes and variation that could be crucial for future maize breeding efforts with e.g. perenniality, tolerance of waterlogging and adaptation to montane (*Z. diploperennis*) and lowland tropical (*Z. nicaraguensis*) environments. These spectacular discoveries emphasize the key on-going importance of botanical field exploration – a time-consuming and painstaking task to locate and document the sum total of biological diversity, including crop diversity, on the planet.

### Popped Secret – the Mysterious Origin of Corn

Video describing the quest for the progenitor of maize with interviews of two of the main scientific protagonists involved, Doebley the geneticist and Piperno the archaeologist.
https://www.youtube.com/watch?v=mBuYUb_mFXA

Wheat: Like rice, also supplies 20% of all calories consumed by humans; in 2007 world production of 607 million tonnes; second only to rice as main human food crop and ahead of maize, after allowing for use in animal feeds. Globally, wheat is the leading source of vegetable protein in human food, with a higher protein content than maize or rice.

The Fertile Crescent
Definition of the Fertile Crescent, centred on the valleys of the Tigris and Euphrates in Iraq and across the mountains of northern Iraq, SE Turkey and N Syria. The core fertile crescent area defined by the overlapping areas of distribution of the multiple Fertile Cresecent crop domesticates – wheat, barley, peas, faba beans, lentils, etc.

Wheat
There are several distinct kinds of wheat which have involved ploidy changes. The earliest cultivated wheat, Einkorn, is a diploid, *Triticum monococcum*, with a series of tetraploids – known as Emmer and Durum wheat, the latter used for pasta, and finally bread wheat, sometimes as here termed common wheat, which is a hexaploid. We shall examine this interesting polyploid series in more detail later in the course, but for now we will look just at the origin of the diploid Einkorn – a crop that was important for Neolithic agriculture, but which was subsequently superceded and is now redundant – a relic crop.

Origins of Einkorn wheat – genetic data
Einkorn wheat provides another excellent example of the use of genetic and archaeological data to reveal the exact place and time when wheat was first domesticated. Wild einkorn wheat – *Triticum monococcum* subsp. *boeoticum* is the wild ancestor of domesticated einkorn wheat, T. monococcum subsp. monococcum and is found in primary habitats in the northeast part of the Fertile Crescent in SE Turkey and northern Iran/Iraq. Heun et al attempted to pinpoint the precise location of domestication by screening a large set of wild *boeoticum* and domesticated *monococcum* lines from known locations across this region. They found that domesticated lines form a single monophyletic lineage and that lines from the Karacadag Mountains of SE Turkey are most similar to domesticated lines and suggested this area as the site of domestication for einkorn wheat. A good example of use of monophyly to infer a single domestication event and geography of the region harbouring the phylogenetically most closely related allied populations to infer crop origins.

Origins of Einkorn wheat – archaeological data
It is notable that this location is just 200km from the archaeological site of Abu Hureyra in NE Syria where the earliest evidence of farming domesticated einkorn around 9,500 BP has been found. Furthermore, several archaeological sites in the Karacadag area have yielded wild and cultivated einkorn seed dating back to around 9,000BP. Here we have a rather dramatic example of independent genetic and archaeological data being used to home in on the location of domestication with increasing precision – potentially to within 200km – the ability to pinpoint where something that happened 10,000 years ago actually took place.

Rice: The world's most important staple food crop; feeds >50% of the world's population and > people than any other crop since the time of its domestication; 20% of all calories consumed by humans; 408,661 million metric tonnes produced per year.

## Polyphyletic Crop Origins – Rice *Oryza sativa*?

Despite its place as the world's most important staple food crop, the history of rice domestication from its wild ancestor *Oryza rufipogon* has remained a mystery. Although it is now well established and that *O. rufipogon* is the wild ancestor of domesticated rice, the number of domestication events and their precise location have been, and still are, the focus of debate. We can see the key changes brought about by domestication of rice – the switch from prostrate to erect growth habit, and of course from shattering to non-shattering spikelets – changes that we will look at in more detail in the next lecture.

## Rice – one domestication or two?

The genus *Oryza* comprises 21 wild species. There are two cultivated species, *O. sativa* (which is grown worldwide) and *O. glaberrima* (which is restricted to west Africa). Within *O. sativa* there is huge diversity in ecology, physiology and morphology, encompassing some 120,000 different named cultivars, ranging from traditional varieties preserved by local indigenous farmers to commercially bred 'elite' cultivars developed during the green revolution. These varieties fall into two major groups or races: *japonica* which are concentrated in the hills of south China bordering the Yangtze river, SE Asia and Indonesia, and *indica* which predominates in the lowlands of tropical Asia, plus a number of other types such as the drought tolerant *Aus* varieties from India and Bangladesh, the deep water *Ashinas* varieties from Bangladesh and the aromatic *Basmati* varieties from India. Cultivation and domestication are thought to have started c.9,000BP across a broad area from eastern India to south China. The wild ancestor, *O. rufipogon*, is found across this entire range.

The question is whether all this diversity arose from a single domestication event, with first japonica domestication in south China and subsequent development of indica varieties in India, or whether there were geographically independent origins of indica and japonica. This domestication history is complicated by large scale movement associated with trading of cultivated rice varieties and movement of people across Asia.

## Origins of rice – archaeological data

The most convincing archaeological evidence for the domestication of rice comes from the spectacular Tianluoshan site in the lower Yangtze river in China, where strata spanning 6,000 years containing rice seeds have been recovered, a chronology once again spanning the transition from foraging to farming in that region. This record clearly documents initial cultivation of rice c.7,000 years ago and domestication c. 4,000 years ago, based on detailed examination of the the abscission layers from a large sample of 2,641 rice spikelets.

## Origins of rice – genetic data

Londo et al (2005) studied spatial variation in wild haplotypes to identify geographic regions from which cultivated rice arose. They had two different hapolotype networks for plastid and nuclear loci that show variation between rufipogon and sativa. They showed that:

- Cultivated rice contains just 22-28% of total haplotype diversity (lower than average of 65% found in wheat and maize) suggesting that rice experienced an intense genetic bottleneck during its domestication.
- Land race varieties (indigenous cultivars) contain more diversity suggesting that they may represent intermediate stages in domestication between wild and cultivated varieties and an important reservoir of rice genetic diversity.
- nuclear genes place *rufipogon* at the centre (labeled A in the haplotype network) of an unrooted network as expected. Haplotypes B & C = *japonica*; haplotypes D &E = *indica*; these are strongly separated and occupy distinct geographic regions strongly supporting the hypothesis of multiple independent origins of domestication in rice – *indica* in the S and SW Himalaya and *japonica* in S China – from separate ancestral *rufipogon* genepools.

So for rice, in contrast to maize and einkorn wheat, we have an example where there is at least some rather convincing evidence that a crop has potentially arisen more than once from the same ancestor. Multiple independent origins of crops offer fascinating comparative study systems for investigating processes of domestication and of course the genes involved in domestication. However, that is not the end of the rice story. Far from it!

## The non-shattering *sh4* rice allele

You will recall that cloning and molecular evolutionary analysis of the *tb1* gene in maize supported the idea of a single origin of that crop. Recent cloning of the rice shattering gene *sh4* which is required for the development of the abscission zone and which is thus a key domestication gene in development of non-shattering domesticated rice varieties. However, this gene does not support the idea of two independent domestications of rice. The idea is that early farmers selected a mutation that changed the way seed dispersal occurs that made it easier to harvest rice. A survey of 17 divergent domesticated rice cultivars covering *indica* and *japonica*, showed that all the cultivars invariably carry the same functional mutation in the *sh4* gene. In contrast all wild species had the wild-type *sh4* gene. This evidence supports a single origin of the non-shattering *sh4* allele in cultivated rice. This brings the multiple origins of rice hypothesis under renewed scrutiny. Does the single origin of the non-shattering *sh4* allele and its fixation in all diverse domesticated rice cultivars surveyed so far mean a single origin of cultivated rice?

## Two scenarios for the domestication of rice

Two scenarios still seem possible that might explain these inconsistent results. In both models, crossing between early cultivars and between early cultivars and wild species would have been important (conventions in Sang & Ge (2007) Fig. 1 where this is presented: squares = wild populations; hexagons = earliest domesticated rice cultivars; circles = contemporary rice cultivars; shading indicates genomic divergence; shapes inside = critical domestication alleles that are fixed in contemporary cultivars; double arrows = hybridization; single arrows = progress of domestication):

1. Single origin of rice, domestication started from a relatively small wild population and continued over a relatively long period of time. The earliest domesticated cultivars would have fixed alleles for the majority of the critical domestication traits, including the non-shattering *sh4* allele. This cultivar was then more widely introduced across Asia where it exchanged genes with local populations of *O. rufipogon* under primitive agricultural management via hybridization and introgression and *japonica* and *indica* emerged as divergent hybrid lines selected for different climatic conditions and agricultural practices. Under this scenario, the core domestication alleles once fixed in the first domesticate were maintained through hybridization and introgression.
2. Multiple origins starting from divergent wild populations with different alleles fixed for the same trait in different cultivars. Subsequent crosses between these semi-domesticated cultivars at an early stage of rice cultivation allowed farmers to select the best alleles for critical domestication traits which became rapidly and widely fixed in both of the independently derived initial domesticates.

## Accumulating DNA sequence data and new analysis methods

The sequencing of the rice genome has opened the way for much larger scale DNA comparisons of wild, indica and japonica lines, as well as identification of additional domestication genes and loci. These burgeoning data alongside new analysis methods are pointing back in the direction of a single origin:

- Persistence of ancestral polymorphisms through incomplete lineage sorting resulting in sequence similarities that do not necessarily reflect species and population relationships, and incongruent gene trees when multiple loci are analysed independently. Re-analysis of data using the multi-species coalescent can detect signals of species differentiation even before gene trees are reciprocally monophyletic. These all point to a single origin where japonica is sister to indica.

- Key domestication genes *Sh4* – non-shattering and *prog1* have nearly identical sequences in all indica and japonica lines. 4 selective sweeps that are shared across *japonica* and *indica* lines all correspond to known domestication loci. The remaining sweeps are not shared and correspond to neutral (diversification) loci. Further evidence that there was a single origin of domesticated rice.

It is important to recognize that the two models are not mutually exclusive. It is possible to envisage a case where most of the critical domestication alleles had the same origin, whereas the rest were derived from diverged wild populations via crossing, a view slightly different from either a single or multiple independent domestications, but rather something in between!

The rice paradox: multiple origins but single origin of Asian rice

More recent analyses of genome assemblies from domesticated rice and its wild progenitors suggest multiple origins, where each domesticated rice subpopulation (japonica, indica, aus) arose separately from progenitor O. rufipogon. Coalescence analysis of demographic parameters indicates that the first domesticated rice population split off from O. rufipogon was O. sativa ssp. Japonica around 13-24Kyr, an order of magnitude older than the earliest archaeological date of domestication. These analyses also show that there was significant geneflow from japonica to both indica and aus which led to the transfer of domestication alleles from early-domesticated japonica to proto-indica and proto-aus populations. This suggests that the different rice subspecies had separate origins, but that de-novo domestication occurred only once, in O. sativa ssp. Japonica, and introgressive hybridization from early japonica to proto-indica and proto-aus led to domesticated indica and aus rice.

Rice Conclusions

- Much initial evidence to suggest that the genomes of the major cultivar groups came from different wild populations that diverged considerably earlier than the time of rice domestication.
- However, the non-shattering allele of sh4, primarily responsible for the reduction of grain shattering from wild to cultivated rice, as well as other domestication genes, originated only once during domestication.
- Re-analyses of DNA sequence data using the multi-species coalescent to account for ancestral polymorphism and incomplete lineage sorting all point towards a single origin.
- Thus, despite the remarkable rapid accumulation of molecular and phylogenetic data for rice, including the first genome sequence for a crop plant, over recent years, it is remarkable how difficult it remains to reconcile the conflicting evidence between a single vs multiple origins.
- This suggests that rice domestication is indeed a very complex puzzle, due to human activities that may have eroded the genetic signatures that might reveal the evolutionary histories of these lineages and which have almost certainly prompted continuous geneflow and introgression between cultivars. This is supported by the occurrence of the non-shattering sh4 allele in three accessions of supposedly wild rice.
- Possible misidentification of accessions in germplasm collections…

African Rice

An intriguing additional dimension in the story of rice domestication is that a separate species of Oryza was independently domesticated in Africa. In this case a quite different species, Oryza barthii was brought into cultivation around 3,000 years ago in the Niger river delta in west Africa, leading to the evolution of Oryza glaberrima, a second species of domesticated rice.

Parallel domestications on two different continents provide opportunities to gain insights into the trajectory and process of domestication. The genome of O. glaberrima was sequenced this year, and as we shall see in a subsequent lecture, this has provided the opportunity to examine the genetics of domestication in a powerful comparative framework.

It is clear from historical accounts of early colonists from Portugal that African rice was cultivated on a large scale in the 15th century. Latterly, O. glaberrima has been displaced by the higher yielding O. sativa. Artificial hybrids between O. sativa and O. glaberrima have been generated.

## Neotropical Rice I

Wild rice, based on one or more of four species of Oryza native to the Americas, has provided a seasonal staple in indigenous subsistence diets in several seasonally flooded parts of South America for several millennia and continues to do so today in a few places on a small scale. It is known as Arroz de pato (duck rice) or Arroz de brejo (swamp rice). Neotropical Oryza includes four species: diploid annual/biannual/perennial O. glumaepatula and three perennial tetraploids: O. alta, O. grandiglumis and O. latifolia. Grain has traditionally been harvested by canoe & flail methods, i.e. beating rice grains into a canoe with a stick. This means that there has been no selection for non-shattering spikelets.

## Neotropical Rice II

Recent archaeological excavations have provided tentative evidence that rice was domesticated in the SW Amazon. The Monte Castelo anthropogenic shell mound in SW Amazonia (Rondonia, Brazil) is 160m in diameter and 6.3m high and contains a 7m deep chronology of plant remains from 9,400 to 667BP. Phytoliths diagnostic of Oryza provide evidence of rice use throughout this time and evidence of human manipulation from c. 5,000BP. From 4,000BP there is a significant increase in the size of the rice phytoliths indicative of domestication and in line with evidence from elsewhere in Asia that phytoliths increase in size with plant size and with domestication. The wild progenitor is probably O. glumaepatula, but the domesticated form apparently disappeared after the Spanish conquest in 1492.

It is though that cassava, peanut and chili peppers were also domesticated in this part of the Neotropics and were cultivated alongside maize and squash from 5,000 BP.

Third independent parallel domestication of rice, one each in Asia, Africa and South America, each from different local wild progenitors, presenting an unusual comparative framework to gain insights into domestication processes.

## Chili pepper

Chili is the world’s most widely grown spice and comes from Capsicum annuum in the family Solanaceae. All 30 or so species of Capsicum are native to the Americas, and five different species have been domesticated. As we have seen, inferences about the where, when and how many times questions about the origins of domestication have been based primarily on archaeological and genetic data, often with great success. However, for many crops, especially those lacking a strong archaeological record or phylogenetic pattern, it can be difficult to answer the question about time and place of origin. Here two additional sources of evidence are added:

- Species distribution modeling to predict areas that are environmentally suitable for a species using species occurrence data and bioclimatic niche modeling
- Paleobiolinguistics which is a comparative method of historical linguistics used to reconstruct the biodiversity known to human groups in the remote past, based on centres of ancestral name diversity.

## Modelling Origins of Crop Domestication

By converting each of the four lines of evidence into spatially explicit units the evidence can be integrated into a single framework and models of the likelihood that chili pepper originated in an area can be constructed.

These four independent lines of evidence can then be integrated in to a single likelihood predictor, providing an approach that is truly multidisciplinary.

## For Next week

Draw a phylogenetic tree that shows multiple independent origins of a crop

## Lecture 3. Crop Origins – Maize, wheat & rice – the three most important crops

### Source Materials

Bryant, V.M. 2003. Invisible clues to New World plant domestication. *Science* **299**: 1029-1030.

Doebley, J. 2004. The genetics of maize evolution. *Annual Review of Genetics*. **38**: 37-59.

Choi, J.Y. et al. 2017. The rice paradox: multiple origins but single domestication on Asian rice. Molecular Biology & Evolution **34**: 969-979.

Fuller, D.Q., Qin, L., Zheng, Y., Zhao, Z., Chen, X., Hosoya, L.A. & Sun, G.-P. 2009. The domestication process and domestication rate in rice: spikelet bases from the lower Yangtze. *Science* **323**: 1617-1610.

Gross, B. & Zhao, Z. 2014. Archaeological and genetic insights into the origins of domesticated rice. *Proceedings National Academy of Sciences, USA* **111**: 6190-6197.

Harris, S.A. 2014. Grasses. Reaktion Press, London.

Heun, M. et al. 1997. Site of Einkorn wheat domestication identified by DNA fingerprinting. *Science* **278**: 1312-1314.

Hilbert, L. et al. 2017. Evidence for mid-Holocene rice domestication in the Americas. *Nature Ecology & Evolution* **1**: 1693-1698.

Iltis, H.H., Doebley, J.F., Guzman, R. & Pazy, B. 1979. *Zea diploperennis* (Gramineae): a new teosinte from Mexico. *Science* **203**: 186-188.

Iltis, H.H. & Benz, B.F. 2000. *Zea nicaraguensis* (Poaceae), a new teosinte from Pacific coastal Nicaragua. *Novon* **10**: 382-390.

Kraft, K.H., Brown, C.H. et al. 2014. Multiple lines of evidence for the origin of domesticated chili pepper, *Capsicum annuum*, in Mexico. *Proceedings National Academy of Sciences* **111**: 6165-6170.

Londo, J.P. et al. 2006. Phylogeography of Asian wild rice, *Oryza rufipogon*, reveals multiple independent domestications of cultivated rice, *Oryza sativa*. *Proceedings National Academy of Sciences* **103**: 9578-9583.

Li, C., Zhou, A. & Sang, T. 2006. Rice domestication by reducing shattering. *Science* **311**: 1936-1939.

Linares, O.F. 2002. African rice (Oryza glaberrima): history and future potential. *Proceedings of the National Academy of Sciences* **99**: 16360-16365.

Matsuoka, Y. et al. 2002. A single domestication for maize shown by multilocus microsattelite genotyping. *Proceedings National Academy of Sciences* **99**: 6080-6084.

Molina, J. et al. 2011. Molecular evidence for a single evolutionary origin of domesticated rice. *Proceedings National Academy of Sciences, USA* **108**: 8351-8356.

Morrell, P.L. & Clegg, M.T. 2007. Genetic evidence for a second domestication of barley (Hordeum vulgare) east of the Fertile Crescent. *Proceedings National Academy of Sciences, USA* **104**: 3289-3294.

Piperno, D.R. et al. 2000. Starch grains reveal early root crop horticulture in the Panamanian tropical forest. *Nature* **407**: 894-897.

Piperno, D.R. & Flannery, K.V. 2001. The earliest archaeological maize (*Zea mays* L.) from highland Mexico: new accelerator mass spectrometry dates and their implications. *Proceedings National Academy of Sciences, USA* **98**: 2101-2103.

Piperno, D.R., Ranere, A.J., Holst, I., Iriarte, J. & Dickau, R. 2009. Starch grain and phytolith evidence for early ninth millennium B.P. maize from the Central Balsas River Valley, Mexico. *Proceedings National Academy of Sciences, USA* **106**: 5019-5024.

Purugganan, M.D. 2014. An evolutionary genomic tale of two rice species. *Nature Genetics* **46**: 931-932.

Ranere, A.J., Piperno, D.J., Holst, I., Dickau, R. & Iriarte, J. 2009. The cultural and chronological context of early Holocene maize and squash domestication in the Central Balsas River Valley, Mexico. *Proceedings National Academy of Sciences, USA* **106**: 5014-5018.

Salamini, F., Ozkan, H., Brandolini A., Schafer-Pregl, R., & Martin, W. 2002. Genetics and geography of wild cereal domestication in the near East. *Nature Reviews Genetics* **3**: 429-441.

Sanchez, J.J. et al. 2011. Three new teosintes (*Zea spp.*, Poaceae) from Mexico. *American Journal of Botany* **98**: 1537-1548.

Sandweiss, D.H. 2007. Small is big: the microfossil perspective on human-plant interactions. *Proceedings National Academy of Sciences*, USA **104**: 3021-3022.

Sang, T. & Ge, S. 2007. The puzzle of rice domestication. *Journal of Integrative Biology* **49**: 760-768.

Shapiro, B. & Hofreiter, M. 2014. A paleogenomic perspective on evolution and gene function: new insights from ancient DNA. *Science* 343: 1236573.

Wang, M. et al. 2014. The genome sequence of African rice (Oryza glaberrima) and evidence for independent domestication. *Nature Genetics* **46**: 982-988.

Online Case studies in Crop Domestication
http://www.botany.wisc.edu/courses/botany_940/06CropEvol/CropEvol.html

Video about the domestication of Maize
Popped Secret – the Mysterious Origin of Corn
https://www.youtube.com/watch?v=mBuYUb_mFXA

Colin Hughes
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## BIO 235 Plants & People – Evolution & Domestication of Crops

### Lecture 4 - How Were Crops Domesticated?

Two independent origins of common bean, *Phaseolus vulgaris*

Common bean, *Phaseolus vulgaris*, in the legume family, comes in a wide variety of fresh and dried forms including French beans, kidney beans, string/runner beans and pinto beans. In many parts of Africa and the Americas common bean is the largest source of dietary protein. While it has long been clear that Phaseolus was domesticated in the Americas, there has been on-going debate as to whether it was domesticated twice – once in Mesoamerica and once in the Andes. The genome sequence of common bean was published in 2014, along with low coverage sequencing of 160 wild and cultivated land accessions across the Americas, were used with demographic modeling to show that wild populations in the Andes are derived from an ancestral Mesoamerican population around 165,000 years ago, well before humans were in the New World, with two subsequent domestication events around 8,000 years ago in the Andes and western Mexico. This is perhaps one of the best documented examples of multiple independent origins of domestication of a major crop.

Two independent origins of the Cocount, *Cocos nucifera*

The Coconut, *Cocos nucifera*, in the palm family (Palmae or Araceae) has provided a source of food and water for several millennia across the tropics. A study of 1,322 coconut accessions from across the tropics revealed two highly genetically differentiated subpopulations corresponding to the Pacific and Indo-Atlantic basins. This pattern suggests independent origins of coconut cultivation in these two regions, with persistent population structure on a global scale despite long-term human cultivation and dispersal. On Madagascar, the E coast of Africa and the Comores islands we see admixture reflecting later trading along this route, but not in the Seychelles which were only colonized very late. The distribution of coconut diversity in the New World is very striking and reflects later human introductions of Pacific coconuts to the W coast (probably pre-Columbus to S. America and by Spanish to Mexico), and the Caribbean by early Spanish conquistadors.

Outline

- Crop domestication syndromes
- Indigenous knowledge and incipient domestication
- Darwin's variation under domestication; methodical and unconscious selection
- Molecular genetics of early crop domestication
- Definition of domestication

Crop domestication and phenotypic change

Another feature of crops in plant science is the special nature of the crop progenitor – domesticate relationship. Unlike when we study the relationships among wild species to establish sister group relationships and pairs of sister species where ancestors and ancestral character state reconstructions are hypothetical, for crops, we know the ancestors and can infer precisely what phenotypic changes have taken place. This opens the way for elegant experiments to understand the nature and genetic basis of phenotypic change. For example John Doebley's work on understanding the genes controlling domestication in maize and the specific mutations within those genes or their regulatory regions that generate the phenotypic changes associated with domestication have provided some of the best systems and early insights into the developmental genetics of plant form, as well as novel opportunities for genetic modification. Such insights depend on inferring an ancestor-descendent relationship and a progenitor-domesticate system is ideal for that.

Crop domestication and phenotypic change

Most members of modern agricultural societies have never seen and would not recognize the unpromising wild plants that are the progenitors of our remarkably productive crops. Very few would survive if all they had were a field of wild grain and herbs and their own wits to sustain them. So, what do wild crop progenitors actually look like? Here we can see a few examples of the sorts of phenotypic changes brought about by domestication, what plant traits were affected and how?

Phenotypic Changes from progenitor to crop.

- Tomato – the massive cultivated fruit compared to the wild progenitor.
- Sunflower – a wild sunflower has many small heads borne on multiple slender stalks, whereas the domesticated sunflower has a single large head borne on a thick stalk.
- Maize – teosinte multi-stemmed with long branches and 5-10 kernels protected by a tough case; maize single-stemmed with 500+ naked kernels
- Rice – wild rice has a panicle that shatters, whereas domesticated rice has a solid panicle of grain.
- Wheat – cultivated wheat has a condensed and tough spike compared to the slender fragile spike of wild wheat.

## Crop Domestication Syndromes

- **Gigantism** – larger fruits or grains (often fewer fruits or grains)
- **Suppression or loss of natural seed dispersal** - seeds remain attached to the plant for easy harvest by humans
- **Secondary metabolites** - biochemical changes – decrease in bitter substances in edible structures

- Changed growth form – more robust plants
- Changed life form - > determinate growth; increased apical dominance – robust growth of the central stem at the expense of side shoots; shift from perennial to annual, or near-annual habit.
- Changed breeding system
- Physiological changes
  - Loss of seed dormancy
  - Changes in photoperiod sensitivity
  - Synchronized flowering
- Changed ploidy level

## Phenotype of wild vs domesticated cereals

- Seed size increase in domesticated forms – an early adaptive response to cultivation and strongly correlated with seedling vigour. Such changes are well documented in the fossil record e.g. comparisons of wild einkorn wheat from 9,300 yr BP with domesticated einkorn from 8,000 yr BP.
- Non-shattering spikelets due to a tough rachis that holds the seeds together in a harvestable and threshable ear
- Leaf-like structures that protect the seed – called glumes – are attached tightly to the seed or fused to it in wild forms whereas they release the seed in the more advanced domesticated forms, which are therefore termed ‘free-threshing’ or naked.

## Rice changes during domestication

- Perennial to annual
- Shattering to non-shattering seeds, critical for effective harvesting, and the hallmark of domestication
- Disparate to synchronized seed maturation
- Awns to lack of awns
- Prostrate habit to erect habit providing improved plant architecture and increased yields
- Many to fewer tillers
- Low yield to high yield
- Seed dormancy to reduced seed dormancy

## Maize changes during domestication

Maize and its progenitor teosinte present extreme differences in their adult morphologies, such that it is hard to imagine that these differences are the result of human selection during domestication. Although maize and teosinte share a similarly robust growth form, their female inflorescences or ears are strikingly different. The teosinte ear has just 5-12 kernels, each sealed tightly in a stony casing, the kernel plus casing known as the fruitcase. At maturity the teosinte ear disarticulates such that the individual fruitcases are the dispersal units, enabling seed dispersal and survival after passage through an animal gut. By comparison, the massive maize cob can bear 500 or more kernels, each of which is attached to the central axis, and are non-shattering. Furthermore they are naked and lack the protection of the fruit case.

## Gigantism in Maize

Dramatic increase in cob size over the course of just under 6,000 years. Also illustrating that half way through this period, the maize still does not resemble modern maize.

## Brassicas

Here we can see a rather different scenario where a whole set of different crops have been derived from a single wild progenitor Brassica oleracea via selection for different plant parts – the inflorescence in broccoli and cauliflower, the stem in kole rabi, the lateral buds in Brussels sprouts and the leaves in cabbage and kale. At first sight it is inconceivable that these vegetables, with their dramatically divergent morphologies, are all members of the same species. It turns out that they share an almost identical genome save for a few tiny changes caused by a small number of mutations in key genes regulating plant development, and principally homeotic mutations in genes determining floral or meristem development:

- Kale, only the leaf shape is altered – habit of plant and inflorescence development unaltered.
- Cabbage – leaves packed into a congested head
- Kohl Rabi – the leaf-producing stem is grossly swollen
- Sprouts – secondary shoots with densely congested heads of tightly packed leaves
- Broccoli – hundreds of tiny unopened flower buds, the inflorescence with arrested development

## Cauliflower

Perhaps the most unusual mutant of all is the cauliflower, where the phenotype is due to arrested development of the floral meristem that maintains it in a permanent vegetative state instead of differentiating into normal flower structures. This means that the inflorescence meristem continuously generates replicas of itself in a spiral on its flanks, with each meristem producing up to 10th order branching and beyond. It is this that accounts for the novel form and texture of the cauliflower. An Arabidopsis mutant with miniature cauliflowers was discovered in 1993 and since then it has been shown that a mutation in a single gene, the Cal gene, is enough to convert Arabidopsis into a plant that resembles a miniature cauliflower.

## Pulses

A whole other category of crops that we haven't talked much about so far are the legumes, often called pulse crops that include phaseolus beans, faba beans, soya beans, lentils, chick peas, peas and numerous other lesser known legume crops, all of which follow a broad legume domestication syndrome. These are highly nutritious foods, generally with high protein contents and, as we saw before, which often complement cereals with legume-cereal pairs in different regions where agriculture arose.

The typical legume domestication syndrome traits are: indehiscent pods, large seeds, water permeable seed coats, reduced seed pigmentation, rapid and uniform germination and growth, and nearly annual life history, and reductions in levels of seed alkaloids. We can see immediate similarities with cereals. For example, just as for cereals, domestication of legumes generally involved suppression of seed dispersal via indehiscent or non-shattering pods, i.e. pods that don't open, facilitating harvest of the crop. This is a case of a similar function (non-shattering) brought about by very different morphological changes in grasses (suppression of development of abscission layer in spikelet) and legumes (suppression of fruit dehiscence). Another similarity between grasses and legumes is increase in seed size and here we can see comparisons of seeds from archaeological sites and modern domesticated varieties of pea, lentil, faba bean, bitter vetch and chickpea, the suite of pulse crops domesticated in the Fertile Crescent and adjacent regions of the Mediterranean.

Tarwi – *Lupinus mutabilis*

An important but little-known indigenous pulse crop in the Andes, domesticated in pre-Inca times and one of a cohort of little known Andean crops sometimes referred to as the *Lost Crops of the Incas*. This provides another classic example of the legume domestication syndrome of indehiscent pods, large seeds, water permeable seed coats, reduced seed pigmentation, rapid and uniform germination and growth, and nearly annual life history, although in this case seed alkaloid levels remain elevated, and consumers rely on various de-bittering techniques to wash and leach alkaloids out of the seeds. In this case the increase in seed size from wild to domesticated appears to have been as dramatic as for any pulse crop.

Oca – *Oxalis tuberosa*

Oca, *Oxalis tuberosa* is another little-known Andean crop, grown for its nutritious tuber, which can be eaten raw or cooked, and which, just like the potato, tolerates the cool wet conditions found at high elevations in the Andes. The where, when, how many times and from what progenitors and the origin of Oca are still not clear, with several candidate progenitors, each from different parts of the Andes. Oca shows that gigantism is also a feature of the domestication of tuber crops – a dramatic increase in tuber size compared to the candidate wild progenitor species

Domestication Syndrome

Meyer et al (2012) attempted to summarize the types of plants domesticated (annuals, perennials, trees), the plant parts involved (fruits, seeds, tubers etc), and the domestication traits involved for 203 crops, On average they found that 2.8 traits per crop were involved in the domestication process, in other words that for almost all crops multiple traits were involved. They found that annuals preceeded trees, being easier to domesticate due to short generation times. Biochemical changes involving loss or reduction in toxic or bitter plant secondary metabolites were the most common change brought about by domestication. Fruits and seeds (gigantism) were more common targets of domestication than roots.

Definition of domestication = genetic modification of a wild species to create a new form of a plant altered to meet human needs.

Fully Domesticated = for some, but not all crops, domesticated forms are completely dependent on humans and unable of propagating in the wild.

For some crops domestication means they are rendered no longer capable of reproducing themselves naturally any more – maize, cauliflower and bananas are examples of highly modified crops that depend on man for their continued propagation and survival. Cultivated bananas are sterile plants that set no seed. Cauliflower is the same. In maize, as we saw earlier, the kernels are naked, without adequate protection from predation, and are easily digested by any animal that consumes them. The kernels are also firmly attached to the cob, so the whole cob falls to the ground intact. Should such a cob survive intact to germinate - which as a nutritious food source is highly unlikely - the resultant thicket of seedlings are too closely packed to survive. Maize, like cauliflower and bananas, is dependent on humans for its survival. This might be viewed as the ultimate and rather extreme manifestation of the sorts of changes that people have brought about in plants, i.e.

the complete control of plants by humans. Other crops are less drastically modified and can revert to the wild and become self-propagating weeds.

These examples - cereals, tomato, brassica, oca, and legumes - provide a panorama of the phenotypic changes associated with crop domestication. But how did these changes actually come about and what is known about the genetic basis of these changes. To look at this we need to return to Charles Darwin and his insights into selection.

### Darwin's Pigeons and Intentional & Unintentional Selection

Alongside the potent insights that Darwin gained from observing groups of closely related species, such as his famous finches in the Galapagos, Darwin also spent a huge amount of time observing variation in domesticated animals and plants. This work formed the basis for his book published in 1868 entitled *The Variation in Animals and Plants under Domestication*.

Darwin used plant domestication as a proxy for evolution under selection, as evidenced by this quote from the 1875 Origin of Species: *'I often asked myself how these many preculiar animals and plants had been produced: the simplest answer seemed to be that the inhabitants of the several islands had descended from each other, under on-going modification in the course of their descent...... But it long remained to me an inexplicable problem how the necessary degree of modification could have been affected, and it would have remained thus forever, had I not studied domestic productions and thus acquired a just idea of the power of selection.'*

Darwin's book about domesticated plants and animals is a phenomenal achievement. It has chapters on dogs, horses and asses, chickens, rabbits and perhaps most famously pigeons. His chapter on pigeons is a hugely detailed 110 page monograph documenting the variation amongst >150 named breeds of pigeons – *English Poulter, Dutch Poulter, Lille Poulter, Grosses Gorges, English Carrier, Tronfo, Runts, Barbs, Fantails, Tumblers, Indian Frill Back, Trumpeter, Dovecotte pigeon* – it is hard to believe that there could be so many breeds and so many people interested in what is not the most useful animal, the pigeon! In 1855 Darwin constructed a pigeon breeding loft at his house to rear and breed pigeons, building up a collection of around 90 birds, he collected pigeons from far and wide from friends and correspondents who sent him skins and skeletons from across India the near-East, India, and China, he was admitted into the pigeon clubs in London, where he met amateur pigeon fanciers who were breeding, crossing and keeping collections of pigeon breeds, and he read historical accounts of the origins of these different breeds. In short, Darwin was a pigeon aficionado. He measured and assessed variation to assemble an encyclopedic dossier on variation in size, plumage, beak morphology, behaviour and other traits of pigeons, the outcomes of crossing, modes of inheritance of traits and inbreeding depression, and showed that such variation was inherited and generated from natural variation via selection. What fascinated Darwin was the idea that all these breeds were derived from one ancestor, the wild rock pigeon, *Columba livia*, and observing the impacts of selection on phenotype and the sheer diversity that could be rapidly generated by such human selection – a sort of rapid evolution - acting on external, i.e. visible traits. This quote from the start of his pigeon chapter sums this up: '*I have been led to study domestic pigeons with particular care, because the evidence that all domestic races are descended from one known source is far clearer than with any other anciently domesticated animal. Secondly, because many treatises in several languages, some of them old, have been written on the pigeon, so that we are enabled to trace the history of several breeds. And lastly, because, from causes which we can partly understand, the amount of variation has been extraordinarily great. The details will often be tediously minute; but no one who really wants to understand the progress of change in domestic animals, and especially no one who has kept pigeons and has marked the great difference between the breeds and the trueness with which most of them propagate their kind, will doubt that this minuteness is worthwhile. Notwithstanding the clear evidence that all breeds are the descendants of a single species, I could not persuade myself until some years had passed that the whole amount of difference between them, had arisen since man first domesticated the wild rock-pigeon.'* And later: *'While man does not cause* *variability, he can select, preserve and accumulate the variations provide by nature in almost any way he chooses, and thus he can certainly produce a great result'*.

Domestication of Pigeons

Here we can see a modern depiction of the domestic breeds of pigeons, as reconstructed from genome-scale SNP data (1.48 million variable loci) and illustrating the diversity of phenotpyes that arose almost simultaneously via conscious selection, and including:

- Racing homers – can navigate home across 100s km
- Tippler – can fly continuously for > 20 hours
- Tumblers & Rollers – perform backwards somersaults in flight
- Beak types, feather ornaments, head crests and an order of magnitude range in body mass.

A set of phenotypes that is of a similar order of magnitude to that normally observed among distinct species or even genera), but which are crossable and selected within a single species.

Chickens & dogs – methodical and unconscious selection

Darwin observed similar variation under domestication from single progenitors in the chicken and the dog. He noticed that selection could be ***methodical*** and intentional focused on specific traits to attain a perceived goal, or ***unconscious*** and unintentional, whereby simply retaining prized individuals and destroying worthless ones, allowed pigeons and other domesticated animals to be modified for the benefit of man. Darwin's excitement was that via the accumulation of small differences could often produce exaggerated forms that transcend variation observed in wild populations and species. Darwin observed that breeds differ from each other as much or more than wild species in external characters to the extent that such variation, if observed in wild populations would definitely have been ranked as species, in any conventional taxonomic work.

Through all this, Darwin gained insights into how selection works. His big leap of course to infer that natural selection could be equally effective in the accumulation of differences and diversification of one species from another that underpinned his Theory of Evolution and the *Origin of Species*. Even now, 150 years after the publication of Darwin's most influential work, domesticated species are some of the best-studied examples of evolutionary diversification, and archaeological and genetic investigations of this unique case of plant–animal co-evolution have provided some of the most comprehensive views of species diversification. The case Darwin made in *On the Origin of Species* remains true: the study of domestication is central to understanding the nature of what Darwin referred to as "the obscure problem" of natural selection. For us, Darwin's work is equally insightful for how domestication came about in demonstrating the dramatic effects of human selection, conscious or unintentional on variation and the spectacular diversity of varieties and breeds that we see amongst our crops and livestock today.

How were these changes brought about?

People were 'messing around' with plants for a very long time – Neolithic genetic tinkering that involved a series of steps:

- sophisticated plant knowledge systems – just like the modern crop breeder who has vast experience and knowledge about particular crops and finely tuned abilities to observe variation in crop traits, early proto-agriculturalists were tuned into plant diversity in a similar way. They often knew up to 500 species of useful plants in any one area and for food plants, they were aware of and able to name and classify variation within species. If you look at folk taxonomies, they tend to become increasingly finely differentiated for the more important plant groups and especially for important food plants, and reach their peak of sophistication and complexity for crop plants, e.g. Sorghum in Ethiopia. Sophisticated knowledge systems of this kind are essential for selection to happen – people with such detailed knowledge would immediately spot interesting mutants and variants and be intrigued by them – individual plants with larger fruits, plants that fruit earlier or later, individuals with sweeter fruits, grasses with non-shattering spikelets, legumes with non-shattering pods. This knowledge provided the basis for selection, just as it does in modern crop breeding; crop breeders have exceptionally detailed knowledge about variation in the crop they work with and survey variation across very large numbers of lines.

Most researchers believe that agriculture began as an attempt to modify the landscape and thereby encourage the growth of edible wild plants at the expense of less useful ones.
- manipulation of natural vegetation – burning to favour grasses
- protection of favoured species and prized individuals, culling of others
- unintentional and deliberate selection, as envisaged by Darwin, could have an impact even at this early stage, before cultivation had started and when people were essentially still foraging and definitely not farming.

From such modification it was but a small step to sowing favoured species gathered from nearby locations. Once sowing starts, selection and crop improvement could begin in earnest.
- accidental sowing – middens, camp followers
- pre-domestication cultivation, backyards, dump-heaps, disturbed middens and seasonal camp grounds provided fertile ground for the sort of colonizing plants that were the progenitors of crops and seeds discarded with kitchen trash, and which would grow the next year – the 'Treasure in the Trash' syndrome.
- gradual selection of favoured phenotypes and eventually seed from the wild no longer sown. Selection might focus on just a few individual plants, a drastic winnowing of the genetic diversity and a substantial genetic bottleneck with consequent reduction in genetic diversity across the genome.

Methodical & Unconscious selection
Intentional selection e.g. for visible traits such as palatability, colour, cooking qualities, of the sort observed by Darwin amongst pigeons.

Darwin & the 19th Century Gooseberry Fairs
A good example of intentional selection would be the gooseberry which was very popular in the 19th century in U.K. and was again observed in great detail by Darwin. He visited the Gooseberry Fairs, where people exhibited their gooseberries each year. There were prizes for the biggest gooseberries and this provided an incentive for selection that transformed the wild gooseberry from 7g to a 10x bigger fruit at 70g, once again an example of gigantism brought about by intentional selection.

Unconscious selection
In addition, it is thought that unconscious (unintentional, inadvertent, automatic) selection – the by-product of planting and harvesting – was also important in crop domestication. Unconscious selection refers to selection resulting from human activities not involving a deliberate attempt to change the organism. In that sense it is akin to natural selection, albeit in human-modified environments.

A number of crop traits are thought to be associated with inadvertent selection due to broadcasting and harvesting of grain crops – *"automatic"* changes that occurred because they increase the likelihood of the seed of a genotype being collected and planted (Harlan et al. 1973).

| Selection Pressure | Response | Adaptation |
|---|---|---|
| Harvesting | Increase in % seed recovered | Non-shattering spikelets<br>> determinate growth |
|  | Increase in seed production | Increased seed set<br>Larger inflorescence<br>> inflorescences |
| Seedling competition | Increase in seedling vigour<br>> rapid germination | Increased seed size<br>Loss of or reduction in germination inhibitors |

Reduction in glumes or
other inhibitors

A key element here could have been harvesting methods. In a classic experiment Hillman & David (1990) tracked domestication experimentally using different harvesting techniques and showed that the innovation of harvesting using primitive sickles was critical to impose the selection pressure to induce non-shattering spikelets.

So, we can see that cultivation itself, as a new technique, a strategic shift in human behavior, had unintended consequences in terms of favouring genetic innovations in cultivated plant populations. Some changes in genes can be attributed to changes in habitats which in turn are the result of innovations in human practice, with the initiation of cultivation as perhaps the key behavioural change in humans. Subsequent progressive forms of pre-domestication cultivation require behavioural shifts that constitute intensification and may include innovations in soil preparation (tillage, irrigation, manuring), while shifts in harvesting and crop-processing will have necessary responses to changes in morphology of incipiently domesticated plants. Many of these changes were unintended consequences of interactions between humans and plants. Domestication can thus be seen as an 'entangled process of behavioural and genetic innovation, response, and further response' (Fuller et al., 2010: 14).

Plant domestication through an ecological lens

Humans have modulated almost every ecological process occurring in the habitats where populations of early domesticates thrived. These changes included supplying nutrients and water, protecting crops from herbivory and weed competition, and regularly harvesting biomass, thereby affecting soil fertility, the mode, frequency and intensity of disturbances, the presence, abundance, and dynamics of organisms other than crops.

Genes Controlling Domestication Traits

In recent years, major crops such as rice, maize, wheat and tomato have been the focus of major research programmes in molecular genetics that have been providing remarkable new insights into how the genetic control of phenotypic traits is effected. This is an extremely rapidly moving field, and as the number of genome sequences increases, new insights into the molecular basis of domestication-related changes are accumulating rapidly. DNA analysis and manipulation combined with crop genome research (genome maps, QTL analysis, fine resolution gene mapping, genome sequencing, candidate gene analysis, gene cloning) is revolutionizing our understanding the underlying genetic control of phenotypic traits. Cloning and evolutionary analysis of domestication-related genes to unravel the molecular basis of domestication-related changes – such as loss of seed shattering, increase in organ size, branchy to erect habit. This is relevant also to transferring genes between species and how to control the expression of the genes once they are transferred.

Genes & Domestication – one gene/one enzyme – maize *Sugary1*

- One gene one enzyme hypothesis – each gene controls a single enzyme, governing a single step in a metabolic pathway
- *Sugary1* in maize is one of the genes that produces sweet corn, encodes an enzyme converting sugar to the amylopectin fraction of starch. If this gene is inactivated, sugar accumulates in the kernels.
- In N American sweet corn, a single nucleotide substitution in the coding region of the gene causes a single amino acid change that inactivates the enzyme

Genes & Domestication – Maize *tb1*

- *tb1* is a key domestication gene in maize
- It encodes a TCP protein (TCPs are growth regulators)
- It is expressed in the axillary meristems of maize but not teosinte

- Tb1 mutant has pleiotropic effects on apical dominance, length of lateral branches and development of spikelets
- Presence of maize *tb1* gene in teosinte suppresses outgrowth of axillary branches
- Lack of any fixed amino acid differences between maize and teosinte in the *tb1* protein
- Differences in tb1 expression patterns between maize and teosinte indicate that human selection was targetted at regulatory differences that produced a higher level or tb1 message in maize.
- Identical *tb1* genes in different maize accessions support single origin

Genes & Domestication – Rice shattering sh4

- Sh4 is the key shattering gene that distinguishes cultivated from wild rice
- *Sh4* is a transcription regulator responsible for reduced shattering via activation or not of the abscision process.
- A single amino acid substitution differentiates the shattering and non-shattering alleles

Genes & Domestication – Rice growth habit *prog1* gene

- Transition from prostrate to erect growth habit critical in rice domestication to generate improved plant architecture and increased grain yield via increased plant density and enhanced photosynthetic efficiency
- Prostrate growth is controlled by a semi-dominant gene prostrate growth (*prog1*)
- *Prog1* variants in domesticated rice disrupt *prog1* function and inactivate *prog1* expression
- All domesticated cultivars tested carry identical mutations in the *prog1* coding region (15SNPs and 6 indels invoking 20 amino acid changes)
- Mutations in a single gene can alter and improve plant architecture and yield. This potentially the product of artificial selection against undesirable prostrate architecture

Genes & Domestication – Tomato Fruitweight 2.2

- Fruitweight 2.2 (*fw2.2*) identified as a large effect QTL controlling 30% of the difference in fruit mass between wild and cultivated tomato
- No differences in protein sequence between the large and small-fruited alleles
- Supports the model that changes in gene regulation underlie the evolution of tomato fruit size, as controlled by *fw2.2*

Genes & Domestication – Conclusions

- General finding that domestication largely involved filtering out of the best alleles from standing allelic variation in crop ancestors, although new mutations in key developmental pathways may have been instrumental in some traits.
- Role of human selection has been modification rather than elimination of gene function across diverse developmental pathways, reflecting the short time span of domestication.
- High speed evolution represented by crop domestication the result of strong selection pressures on pre-existing variation.
- Up and down regulating of transcription factors has played a central role in domestication, as found more widely in plant developmental genetics.
- Genes controlling cell division (like fw2.2) also likely to be over represented among major domestication genes.
- Changes often involve just single or a few amino acids

Comparative genomics of crop domestication

Within the last year, a new era of comparative genomics of crops has started to be explored for the first time. With the publication of a much larger set of crop plant genomes, it is now for the first time possible to compare gene content and levels of gene conservation across the genomes of our major crops. Good examples are the recent sequencing of the African rice genome (Oryza glaberrima) allowing comparison with the Asian rice genomes. Similarly, having many sequences of common bean from across the Americas facilitates comparison of the putatively independent domestication events in Mexico and the Andes, and to further compare the common bean genome with the soya bean genome. For example, 91% of Phaseolus bean genes are found in the soya bean genome. We can also compare levels of genetic diversity, genetic bottlenecks and divergence, e.g. the Andean domesticated bean genome shows 4.5 times less sequence divergence than the Mesoamerican domesticated bean. Similarly we can ask, how many genes were involved in domestication, and to what extent are these shared across crops?

- the *shattering1* gene (*sh1*) which controls seed shattering in sorghum, was under parallel during the domestication of sorghum, rice and maize.
- three shattering-related genes in Asian rice, *Oryza sativa* also show changes in the domesticated African rice, *Oryza glaberrima*, suggesting that African and Asian farmers unwittingly selected for mutations in all three genes that prevent seed shattering. However, it is notable that the mutation profiles of each orthologous pair of genes are completely different. This means that the control of seed shattering in a African and Asian rice is the result of independent, parallel domestication with different genetic changes resulting in convergent phenotypes.
- 59 candidate domestication genes shared between Mexican and Andean bean domesticates.

Selection after domestication & crop diversification

Selection after domestication has led to the immense diversity of varieties that characterizes many domesticated plant and animal species, which, as Darwin pointed out, can exceed the range of phenotypic variation in their wild ancestors. We will return to the diversity of crop genetic resources in Lecture 9.

Domestication as a large scale experiment in evolutionary genetics

Domestication provides us with in a sense a large scale experiment into the impacts of intensive directional selection for particular phenotypes spanning several millennia, and useful models for investigating evolutionary genetics. Again, pigeons provide a salient example. Many of the traits that vary among pigeon breeds also vary among many natural species of birds, such that pigeons provide a model for understanding the genetic mechanisms that control diversity of wild birds. By looking at the genomes corresponding to distinct phenotypes that arose just in the last few millennia (and are thus genetically very close) it is possible to home in on genes controlling these phenotypes. A good example is that all breeds with crests, which are an important trait in mate selection in many avian species) share the same mutation in the Ephrin receptor B2 gene (EphB2), and that crests evolved just once within the domesticated pigeon.

# BIO235 – Lecture 4 How were crops domesticated? – Source Materials

Brown, T.A. et al. 2009. The complex origins of domesticated crops in the Fertile Crescent. *Cell* **24**: 103-109.

Darwin, C. 1868. *The Variation in Animals and Plants under Domestication*.

Doebley, J. 2004. The genetics of maize evolution. *Annual Review of Genetics* **38**: 37-59.

Doebley, J.F., Gaut, B.S. & Smith, B.D. 2006. The molecular genetics of crop domestication. *Cell* **127**: 1309-1321.

Driscoll, C.A., Macdonald, D.W. & O'Brien, S.J. 2009. From wild animals to domestic pets, an evolutionary view of domestication. *Proc. National Academy of Sciences* **106**: 9971-9978.

Emshwiller, E. et al. 2009. Origins of polyploidy and domestication in Oca (Oxalis tuberosa) 3. AFLP data of Oca and four wild, tuber-bearing taxa. *American Journal of Botany* **96**: 1839-1848.

Fuller, D.Q., Allaby, R.G. & Stevens, C. 2010. Domestication as innovation: the entanglement of techniques, technology and chance in the domestication of cereal crops. *World Archaeology* **42**:13-28.

Fuller, D.Q. & Allaby, R. 2009. Seed dispersal and crop domestication: shattering, germination and seasonality in evolution under cultivation. *Annual Plant Reviews* **38**: 238-295.

Gaut, B.S. 2014. The complex domestication history of the common bean. *Nature Genetics* **46**: 663-664.

Gunn, B.F., Baudouin, L. & Olsen, K.M. 2011. Independent origins of cultivated coconut (Cocos nucifera L.) in the Old World Tropics. *PLoS One* **6**: e21143.

Hancock, J.F. 2004. *Plant Evolution and the Origin of Crop Species*. CABI.

Harlan, J.R., de Wet, J.M.J. & Price, E.G. 1973. Comparative evolution of cereals. *Evolution* **27**: 311-325.

Hillman, G. C. & Davies, M. S. 1990. Measured domestication rates in wild wheats and barley under primitive cultivation, and their archaeological implications. *Journal of World Prehistory*, **4**: 157–222.

Jin, J. et al. 2008. Genetic control of rice plant architecture under domestication. *Nature Genetics* **40**: 1365-1369.

Li, C., Zhou, A. & Sang, T. 2006. Rice domestication by reducing shattering. *Science* **311**: 1936-1939.

Lv, S. et al. 2018. Genetic control of seed shattering during African rice domestication. *Nature Plants* **4**: 331-337.

Mekbib, F. 2007. Infra-specific folk taxonomy in sorghum in Ethiopia: folk nomenclature, classification and criteria. *Journal of Ethnobiology and Ethnomedicine* 3:38.

Meyer, R.S., DuVal, A.E. & Jensen, H.R. 2012. Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops. *New Phytologist* **196**: 29-48.

Milla, R., Osborne, C.P., Turcotte, M.M. & Violle, C. 2015. Plant domestication through an ecological lens. *Trends in Ecology & Evolution* **30**: 463-469.

Pickersgill, B. 2009. Domestication of plants revisited – Darwin to the present day. *Botanical Journal of the Linnean Society* **161**: 203-212.

Purugganan, M.D. 2014. An evolutionary tale of two rice species. *Nature Genetics* **46**: 931-932.

Purugganan, M.D. & Fuller, D.Q. 2009. The nature of selection during plant domestication. *Nature* **457**: 843-848.

Salamini, F., Ozkan, H., Brandolini A., Schafer-Pregl, R., & Martin, W. 2002. Genetics and geography of wild cereal domestication in the near East. *Nature Reviews Genetics* **3**: 429-441.

Schmutz, J. et al. 2014. A reference genome for common bean and genome-wide analysis of dual domestications. *Nature Genetics* **46**: 707-713.

Shapiro, M.D. & Domyan, E.T. 2013. Domestic pigeons. Current Biology 23: R302-R303.

Shapiro, M.D. et al. 2013. Genomic diversity and evolution of the head crest in the rock pigeon. *Science* **339**: 1063-1067.

Tan, L. et al. 2008. Control of a key transition from prostrate to erect growth in rice domestication. *Nature Genetics* **40**: 1360-1364.

Tanksley, S.D. 2004. The genetic, developmental, and molecular bases of fruit size and shape variation in tomato. *The Plant Cell* **16**: S181-S189.

Vaughan, D.A., Balzas, E. & Heslop-Harrison, J.S. 2007. From crop domestication to super-domestication. *Annals of Botany* **100**: 893-901.

Wang, M. et al. 2014. The genome sequence of African rice (Oryza glaberrima) and evidence for independent domestication. *Nature Genetics* **46**: 982-988.

Wang, R.L., Stec, A., Hey, J., Lukens, L. & Doebley, J. 1999. The limits of selection during maize domestication. *Nature* **398**: 236-239.

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## BIO 235 Plants & People – Evolution & Domestication of Crops
### Lecture 6 – Hybrids, Polyploidy & Crop Domestication II

Introduction

In lecture 5 we surveyed the extent of serendipitous backyard hybridization for the incipiently domesticated perennial crops *Leucaena*, *Opuntia* and *Agave* in Mesoamerica. We saw that:

- Disturbed sites such as backyards, kitchen middens, and informal orchards are important sites for spontaneous hybridisation, where otherwise isolated plant species were brought into sympatry following cultivation.
- For Guajes, Nopales & Maguey – three of the dominant perennial plants cultivated in south-central Mexico - predomestication cultivation has resulted in extensive artificial sympatry, and a complex series of geographically dispersed hybrids and polyploids.
- In each case, there is evidence to suggest that the most prominent species in cultivation – *Leucaena leucocephala*, *Opuntia ficus-indica*, and *Agave tequilana*, have had hybrid origins most likely following cultivation.
- The simple step of bringing species together, casually or consciously in dump heaps and informal orchards has played a key role in domestication of these crops.
- Incipient or semi-domesticates like these can provide powerful insights into the early stages of domestication

Today, we will look at a set of more mainstream polyploid crops – strawberry, wheat, banana, potato, sugarcane and oil-seed rape – to see, where, when and how these polyploids arose, and the extent to which they follow this pattern of pre-domestication cultivation spawning hybrids that can trigger domestication.

Strawberry

The strawberry is a member of the genus *Fragaria* (Rosaceae), the main cultivated species being *Fragaria ×ananassa*, an octoploid ($2n=8x=56$) derived from an interspecific hybrid. This hybrid originally appeared spontaneously or accidentally in a European garden in about 1750, when plants of the beach strawberry *F. chiloensis* from Chile and western North America were planted adjacent to the Virginian strawberry *F. virginiana* from the Atlantic coast of North America. In this case, there is historical documentation that F. *×ananassa* arose as a spontaneous hybrid in cultivation. Both these wild species are also octoploids. The history of these polyploids is not fully known. In Europe there are diploid, tetraploid and hexaploid species, but the octoploids are restricted to the New World, where the only diploid is *F. vesca*, which is a likely early progenitor of the octoploids.

This spontaneous hybrid is a late episode in the history of cultivation and domestication of strawberries. *Fragaria vesca* was cultivated in Roman and Greek times and by the 1300s *F. vesca*, *F. viridis* and *F. moschata* were being grown all across Europe. Strawberries can reproduce asexually by stolons and can thus be easily transplanted from the wild to gardens. Many strawberry species are dioecious, i.e. they have separate genders, although *F.* ×*ananassa* is largely hermaphrodite, having been selected as such during domestication. *F. chiloensis* was domesticated at least 1000 years ago by the Mapuche Indians in Chile and arrived in France in 1714 via French army officer Frezier who had been sent to Chile to spy on the Spanish. He noticed large-fruited *F. chiloensis* being cultivated by the native peoples at Concepcion in Chile. Imported *F. virginiana* had found its way to Europe in the 1600s and rose in importance during the 1700s in Europe. At first the introductions of *F. chiloensis* and *F. virginiana* were grown separately. The *F. chiloensis* introductions were a great disappointment because Frezier had unwittingly brought back only female plants and no males to fertilize them. It was not until *F. virginiana* was identified as a successful pollinator of *F. chiloensis* that this species began to show its potential. A strong industry developed in France around 1750, where Frezier's female plants of *F. chiloensis* were interplanted with males of *F. virginiana*, and the first F. ×ananassa hybrids arose, these ultimately replacing the parent species in cultivation in the late 1700s. This long history of use and cultivation means that it is no surprise that the spontaneous *F.* ×*ananassa* would have been noted and propagated immediately when it arose.

### Wheat

In lecture 3 we looked very briefly at the origin of one type of domesticated wheat, einkorn wheat. We can remind ourselves that wheat is one of the big three cereal crops alongside maize and rice – in 2007 world production of 607 million tonnes; second only to rice as main human food crop and ahead of maize, after allowing for use in animal feeds. Globally, wheat is the leading source of vegetable protein in human food, with a higher protein content than maize or rice.

### The origins of bread

Bread is one of the most important foods in the modern world. Uses flour + water to make dough or batter +- fermentation then baking, frying or steaming. Most early finds of bread remains in the archaeological record are from Neolithic sites in Europe and SW Asia have been linked to fully-fledged agricultural communities that exploited domesticated species. However, recent excavations from the Shubayqa 1 site in NE Jordan have revealed  a huge treasure trove of plant remains from 14.6-11.6Kyr assembled by Natufian hunter-gatherers and especially: club-rush tubers, crucifers, small-seeded legumes, wild einkorn wheat, barley, oat and rye. Amongst all these are 24 bread-like remains. These verified via detailed SEM analyses – pore sizes and cereal tissues and 2-celled aleurone layers typical of wheat and rye as well as vascular tissue from club-rush. Clear evidence of bread combining cereal flour and starch from club-rush tubers. Probably at this time around 14.4Kyr bread was only produced for special occasions (travelling or feasting) and only later, after 9Kyr and after the advent of wheat domestication and cultivation, did bread become a daily staple food.

### Wheat polyploids

I mentioned in that lecture that the different types of wheat form a polyploid series.

### Origin of Einkorn wheat

We also saw that the very first domesticated wheat – einkorn wheat, a diploid that was domesticated c. 9,500 BP in the Fertile Crescent – in fact in NE Syria / SE Turkey – formed a primitive, or relic crop that was abandoned in the Bronze Age and is no longer used, having been superceded by the more recent and superior polyploid wheats, with their superior adaptation to warm climates and favourable harvesting properties conferred by naked seeds and soft glumes. Although Einkorn wheat is a relic crop it was an important progenitor of the subsequent tetraploid and hexaploid wheats.

So how did these polyploids arise?

### Ploidy in wheat

The ploidy levels of domesticated wheat species range from diploid, $2n=14$, to hexaploid, $6n=42$. Wheats of all ploidy levels have been domesticated:

- Diploid einkorn – the earliest primitive, but now relic wheat, *T. monococcum* derived from wild *T. boeticum*
- Tetraploid emmer – the durum wheats used to make pasta, *T. durum* & *T. turgidum* derived from *T. dicoccoides*
- Hexaploid bread wheats, *T. vulgare*, including spelt, *T. spelta*.

The wild tetraploid emmer wheats, T. dicoccoides, resulted from crosses between einkorn wheat and another wild diploid goat grass, T. urartu or T. speltoides. Domesticated emmer varieties derive from this single wild tetraploid progenitor T. dicoccoides. Soon after domestication of this tetraploid, free-threshing forms evolved, including T. turgidum and T. durum. Emmer wheat was the most important crop in the Fertile Crescent until the early Bronze Age, was spread cultivated early, e.g. in ancient Egypt, and the free-threshing T. durum forms (hard wheat) are still widely cultivated, e.g. across the Mediterranean today.

## The core Fertile Crescent

We saw the evidence for a single origin of domesticated Einkorn wheat in the Karacadag mountains of NE Syria. There is also evidence to suggest that domesticated tetraploid Emmer wheat is most closely related to wild emmer populations from SE Turkey, suggesting that Emmer was domesticated in the same area as Einkorn. Furthermore, the ranges of several wild progenitors of other legumes, such as pea, chickpea and lentils, intersect a small region of SE Turkey and NE Syria encompassing the Karacadag Mountains, leading some to suggest this as the 'core' area of the Fertile Crescent – the true cradle of agriculture.

## Hexaploid bread wheat

Subsequently, these tetraploid emmer wheats, T. turgidum (AABB), were involved in a fateful experiment – accidental crosses with another wild diploid species *Aegilops tauschii* (DD), gave rise to hexaploid wheats (AABBDD). It is worth noting that the taxonomy of these grasses remains in a state of flux. At first sight it may seem surprising to have hybrids between species in different genera, but it has been shown that neither Triticum, nor Aegilops, nor the two genera together are monophyletic. These hexaploids comprise T. spelta (a hard, hulled wheat called spelt) and T. aestivum (T. vulgare), a free-threshing form, the bread wheat, which are most suitable for baking. Bread wheat has no wild hexaploid progenitor in nature; it is, therefore, a farming-associated natural or spontaneous hybrid that has since become one of the world's leading crops. So, at some unknown time and place in the past, tetraploids hybridized with the diploid species and generated spelt-like hulled hexaploid wheats. This cross probably involved domesticated emmer T. turgidum, because the distribution range of Aegilops tauschii doesn't overlap with wild tetraploid T. dicoccoides. The AABBDD genome therefore probably stems from the anthropogenic expansion of tetraploid domesticated species into the distribution area of A. tauschii. A possible venue for this hybridization event is the southern Caspian basin, because the likely parental forms of A. tauschii still grow in that area, but there is still considerable uncertainty surrounding this. It remains unclear whether there were in fact one or more independent hybridizations involving tetraploid T. turgidum and A. tauschii giving rise independently to spelt and bread wheat, or a single origin followed by modification of spelt to produce bread wheat. It is also possible that A. tauschii was more widespread in the Neolithic than it is now, possibly even occurring as a weed in fields of domesticated tetraploids. If this was the case, then spelt could have arisen via introgression of a non-free-threshing emmer into stands of T. vulgare. Thus the precise details of the origin or origins of the hexaploid wheats are as yet unresolved. What is clear is that once included in the agricultural package, free-threshing bread wheats followed a Mediterranean route to Europe and by c.6,000 BP were growing on the northern foothills of the Alps.

## Banana

Banana, in the genus *Musa*, is a monocot in the order Zingiberales. These are giant herbs to 3m ht that grow on the margins of rainforests in S.E. Asia, with a likely centre of origin in New Guinea, Malaysia and Indonesia. Nowadays, both sweet bananas and green cooking plantains are important crops throughout the tropics, both as a staple crop (plantains) in many tropical countries, but also as a massive export crop to feed the taste that we have developed for bananas in Europe and the U.S.A. –soft palatable flesh, an excellent nourishing source of carbohydrates, snack-sized portions, the easy peel covering that conveniently changes colour to indicate ripeness seem almost purpose-designed for efficient human consumption and distribution. However, wild bananas are very different – they have seedy fruit with little starch and very little fleshy pith and have no value as crops. Banana is now the fourth most important crop in developing countries, and >85% of bananas are grown for local consumption in tropical / subtropical countries – a crucial staple food in these regions. Bananas are eaten cooked, roasted or even brewed, or eaten raw as for the yellow Cavendish variety sold in supermarkets globally. Bananas are readily propagated by suckers. There are 100s of varieties which are the products of centuries, or even in some cases millennia of clonal (vegetative) reproduction.

## Wild bananas

The majority of cultivated bananas are diploid or triploid crosses of *M. acuminata* 2n=2x=22 AA genome, and *M. balbisiana* 2n=2x=22 BB genome. Domestication involved seed suppression and the development of parthenocarpy (i.e. the fruit develops without seed development or pollination / fertilization), and cultivated bananas are seedless, sterile and parthenocarpic. Most cultivars are wild collections made by farmers of spontaneously occurring diploid inter-subspecific M. acuminata hybrids or sterile triploid hybrids between M. acuminata and M. balbisiana which have unexpectedly tasty, seedless, parthenocarpic and yellow fruits which were brought into cultivation and then multiplied and distributed by suckers. So, like maize and cauliflower, we can see that banana is a true domesticate, unable to survive and reproduce without the help of humans.

## Musa acuminata

Wild M. acuminata is diverse and differentiated into several subspecies across Island South East Asia. These geographical and morphologically defined subspecies are supported by molecular markers. It is known that subsp. banksii from the highlands of New Guinea played an important role on banana domestication. Musa balbisiana occupies a more northerly distribution and although not domesticated, it has been widely translocated thereby founding small free-growing populations from New Guinea to Sri Lanka. Edible diploid AA varieties derive from hybrids between different subspecies of M. acuminata which could only have been brought into contact with each other by human movement and propagation during the Holocene (11,700 years). Chromosomal re-arrangements between the parental subspecies led to gametic sterility. In association with human selection for greater pulp this led to parthenocarpic fruits and edibility.

## Archaeological evidence

Leaf phytoliths from key archaeological sites anchor the time thresholds of prehistoric Musa domestication. Firstly the occurrences of ancient banana phytoliths from archaeological excavations at Kuk Swamp, in the highlands of Papua New Guinea demonstrate that bananas were in cultivation 6,950-6,440 BP. These match subsp. banksii, the only naturally occurring subspecies of M. acuminata in New Guinea. Musa leaf phytoliths have also been confirmed from pottery remains in Nigeria in west Africa 2,790-2,300 BP, providing evidence for cultivation of exotic plantains in west Africa > 2,000 years ago.

## Linguistic evidence

A cultivated plant often migrates with its name, and when this plant is culturally innovative, its name is often retained in the receiving language. Successive dispersals accumulate terminological changes from the original forms that enable the historical pathways of successive transformations to be reconstructed. In the case of the banana the genotype associated with a name is relatively fixed by vegetative propagation enabling a geographical reading of the linguistic paths that illustrates movements of these terms and genotypes.

There are > 1,100 names for banana varieties, belonging to 4 groups: muku – a clear example of a name that survived incorporation into new languages – strongly resistant to change in the face of radical language shifts; punti – poorly resolved representing a relatively recent and rapid spread and multiple processes of local differentiation; qu-Rutay – Philippines with later westward ripples to mainland Asia; baRat – Philippines and later Borneo.

## Hybridization, polyploidy and banana domestication

Occasional diploid (unreduced) gametes plus normal haploid gametes generated spontaneous sterile triploid genomes 2n=3x=33, which were also subject to human selection and vegetative propagation generating the diversity of modern cultivated hybrids including pure AAA – sweet desert bananas. For example banksii x zebrina resulted in the AAA highland bananas of East Africa. Interspecific AAB or ABB – starchy plantains – for example the AAB plantains of west Africa and the Pacific. There are also some seedless cultivated AA and AB diploids and various tetraploids: 2n=4x=44, AAAA, AAAB, AABB, ABBB.

Triploid hybrids

It is thought that this triploidization occurred independently in various contact zones and is still on-going. Again, these have been collected from multiple independent sources in the wild, so the hybridization events and mutations giving rise to the seedless parthenocarpic characters have occurred many 100s of times and spontaneous hybridization continues to produce new diversity. In order to generate these hybrids, numerous long-distance movements of either one of the parents need to be invoked, making banana domestication one of the most spectacular examples of serendipitous backyard hybridization following human translocation and cultivation.

The combined archaeological, genetic and linguistic evidence suggests:

- Pre-domestication cultivation and translocation of AA subspecies used for food, fibre, fodder and construction materials – so-called 'CULTWILD' in reference to pre-domestication cultivation
- Three contact zones – NG/Java; NG/Philippines; Philippines/Borneo/mainland SEA - where hybrids led to domesticated seedless parthenocarpic diploids. The earliest involving subsp. banksii from New Guinea, where bananas were in cultivation nearly 7,000 years ago.
- These contact zones correspond to key areas of linguistic origin and diversification.
- Subsequent triploids AAA and AAB – three of which are remarkable because they are largely cultivated far from their region of generation – African sweet AAA; African AAB plantains; Pacific AAB plantains, new wonderfruit to Africa which were carried by African traders to Africa, and later by Spanish conquistadors relayed them onwards to the Americas, where it forms the basis for industrial-scale plantations across the tropics.

Diversity of bananas & plantains in south India

Genome compostitions:

- a = cultivar Red = AAA, a prized sweet desert banana cultivar
- b = Palayam Codan = AAB
- c = Njalipoovan = AB (unripe and ripe green and yellow) sweet desert banana with small fingers, thin skin and delicate flavour, but poor storage
- d = Robusta (Cavendish group) = AAA (these green bananas ripen without turning yellow when above 22C
- e = Nendran = AAB, plantain used for cooking and making chips
- f = Peyan = ABB, used as a vegetable for curries and cooked snacks
- g = Poovan = AAB

Modern banana production

The bananas we find in supermarkets and which we use to make our banana splits, are just one of numerous varieties found in the tropics – the Cavendish cultivar – all of them genetically identical, highly uniform, possessing the same predictable pleasant taste and texture, and inevitably, just like the monocultures we saw of potato, susceptible to diseases. But this has not always been the case. Until the mid twentieth century, most bananas sold in the developed world belonged to the Gros Michel cultivar, another sweet and tasty variety that didn't spoil too quickly making them suitable for commercial export. However, this cultivar was decimated by a wilt fungus called Panama disease. Stuck with vegetative reproduction, disease and pest problems are especially problematic for bananas, and the Cavdenish monoculture that dominates cultivation today is no exception and is sustained mainly via enthusiastic applications of pesticides.

Potato

Solanaceae – many domesticated species including several economically important crops. *Solanum* (c.1500 species) includes three major food crops:

- potato (*S. tuberosum*)
- tomato (*S. lycopersicum*)
- eggplant (*S. melongena*)

Wild relatives (*Solanum* section Petota) are all tuber bearing and include 190 wild species widely distributed in the Americas from sw U.S.A. to southern Chile, spanning all ploidy levels known amongst the cultivars (below), as well as hexaploids. Wild progenitors of Andean landraces have long been in dispute, but all hypotheses centre on a group of 20 morphologically very similar wild species referred to as the *Solanum brevicaule* complex, distributed from central Peru to Argentina, and most notably *S. candolleanum*. The members of the *S. brevicaule* complex are so similar that their identities have frequently changed. Many members grow as weeds in or adjacent to cultivated potato fields and form crop-weed complexes. All hypotheses have suggested complex hybrid or multiple origins.

Potatoes were domesticated in the Andes of southern Peru about 8,000-10,000 years ago. Domestication involved selection for underground characters of shorter stolons, larger tubers, (often) coloured and variously shaped tubers, reduction of bitter tuber glycoalkaloids, and greater vigour.

Landrace potato cultivars are highly diverse, containing diploids ($2n = 2x = 24$), triploids ($2n = 3x = 36$), tetraploids ($2n = 4x = 48$), and pentaploids ($2n = 5x = 60$).

The taxonomy of cultivated potatoes is controversial with anywhere from one to 20 morphologically similar species recognized, but all from a common gene pool. Wild species of section Petota of Solanum show high rates of unreduced (2n) gametes reducing the barriers to interploidy geneflow.

(i) Autopolyploidization of early diploid land races (sections Stenotomum and Phureja) via unreduced gametes resulted in the cultivated Andean tetraploids, S. tuberosum group Andigena, $2n=4x=48$, the initial Andean domesticated potatoes.
(ii) Migration south to coastal Chile resulted in long-day-adapted S. tuberosum group Chilotanum, $2n=4x=48$, which provided the genetic background for commercial cultivars across the world.
(iii) A large number of the over 100 tuber-bearing wild relatives (Solanum section Petota) which ranges from the SW U.S.A. to S. Chile have contributed to the genomes of commercial potato cultivars via introgression. Including: (a) diploid Peruvian land races of S. candolleanum, S. medians, and S. raphanifolium; (b) Bolivian tetraploids, S. brevicaule, S. leptophyes, and S. microdontum; (c) Argentinian tetrploids, S. bethaultii, S. chacoense, S. gourlayi, S. kuntzianum, S. spegazzinnii and S. vernei.

The margins and hedgerows of the Andean farm were, and still are, populated by weedy wild potatoes and cultivated potatoes have regularly crossed with their wild relatives, producing new hybrids, some of which if noted as worthy, have been promoted and adopted from the field margins to the fields, and then to neighbours fields as well. Artificial selection is thus a continual local process, each new potato the product of an on-going back-and-forth between the land and the cultivators, mediated by the universe of all possible potatoes – the gene pool.

Recent genome sequencing of wild diploids, S. American land races and N. American commercial cultivars has shown that the potato genepool has greater sequence diversity than any other crop resequencing study to date, in large part due to expanded wild introgressions following polyploidy.

In an era of genomics-enabled crop breeding, this spectacular diversity is critically valuable, an extraordinary cultural achievement and a gift of incalculable value for the world, a free and unencumbered gift. Pizarro and the conquistadors from Spain were of course not looking for plants, but gold, so little did they imagine that the funny looking tubers they encountered high in the Andes would prove to be the single most important treasure they would bring back from the New World.

Modern cultivars are all tetraploid cytotypes – these are the highest yielding. These are known from two areas: (i) highland Andes, from Venezuela to Argentina (Andean landraces); (ii) lowland south-central Chile in Chiloé Island, including the immediately adjacent Chilean lowlands and other islands of the Chonos archipelago. Despite these altitudinal differences, tuberization response is related to day length, not altitude. As a result the Andean landraces tuberize poorly in the latitudes of much of Europe, but the Chilean landraces tuberize well there.

Origin of European potato has been the subject of long controversy:

- from tetraploid landraces in Chile
- initially from the Andes until the potato late blight epidemics in the UK starting in 1845, after which it was replaced with Chilean germplasm through introductions and breeding efforts.
- initially introduced from the Andes, later evolving towards a Chilean type potato (including long-day tuberization) through selection following import into Europe.

Ames & Spooner (2008) examined this question by screening DNA from 64 historical (1700-1910) herbarium specimens for a 241bp plastid deletion in the trnV-UAC/ndhC intergenic region, which is absent in 95% of Andean tetraploid landraces and present in 81-86% of tetraploid Chilean landraces. Amplified in all but 15 of the 64 samples, i.e. 49. 21 of these were collected before 1850, and 28 from 1850-1910. Sequenced the spacer region to check that the deletion is the same as that previously reported. Results show that the Andean potato, lacking the DNA plastid deletion, first appeared in Europe around 1700 and persisted until 1892, long after the late blight epidemics, while the Chilean potato (possessing the deletion) first appeared in Europe in 1811, long before the late blight epidemics and persisted to the present day. Suggests:

- original introductions from the Andes
- Chilean potatoes became dominant by at least 1811, 34 years before the late blight epidemics, refuting the idea that late blight epidemics beginning in Europe in 1845 stimulated introductions of Chilean germplasm as breeding stock to combat the disease, or eliminated the Andean potato which persisted up to 1892.
- Refutes the idea that Andean potatoes were mass selected for long day length adaptation.

Utility of herbarium specimens (ancient DNA) for investigating the historical origins of crop plants, here providing the first direct evidence about the long-held controversy of an extra-Andean origin of this major food plant.

## Sugarcane

In a world saturated with sweetness in many foods and drinks, it is hard to imagine a world without sugar. However, sugar, at least in the Western diet, is a recent introduction and innovation that has happened just in the last few centuries. Before the 16th century, the whole of Europe had managed virtually without sugar with honey as the only available sweetner. Sugar was, and is, an unnecessary 'food' yet Europe imports > 1 billion tones each year, a symptom of our addiction to it.

## Sugarcane prehistory

Sugarcane prehistory spans a vast area of south and south-east Asia spanning India to Polynesia, but few archaeological remains with which to track its origins, spread and domestication. As a result, most theories about its domestication come from living wild and cultivated plants. The earliest evidence for making sugar from sugarcane comes from India and was not known from Melanesia and Polynesia, but sugarcane is abundant in villages in these regions and is simply consumed by chewing.

## Sugarcane – hybridization and domestication

The primary domestication of sugarcane probably occurred in New Guinea from the wild species S. robustum and resulted in a series of sweet clones known to botanists as S. officinarum. These cultivars were transported by humans to continental Asia where they hybridized with a wild species, S. spontaneum, giving rise to a new series of cultivars better adapted to subtropical environments and to sugar manufacture. These are identified as S. barberi for those from India and S. sinense for cultivars from China. It is a complex story involving several species, human movement, spontaneous hybrids.

Nowadays, sugarcane is an important industrial crop grown on c.20 million ha throughout the tropics and subtropics for its sucrose rich stalks, most of which is refined into sugar, but more recently refined to make ethanol, as a renewable substitute for fossil fuels. The modern crop is based around a series of artificial interspecific hybrids generated at the end of the 19th century in Java and India.

## Brassicas

We saw before the many different brassicas that are grown as vegetable crops, all of which are mutated forms of a single species, Brassica oleracea: kale, broccoli, cauliflower, cabbage, kohl rabi and cabbage. At first sight it is inconceivable that these vegetables, with their dramatically divergent morphologies, are all members of the same species. It turns out that they share an almost identical genome save for a few tiny changes caused by a small number of mutations in key genes regulating plant development, and principally homeotic mutations in genes determining floral or meristem development:

- Kale, only the leaf shape is altered – habit of plant and inflorescence development unaltered.
- Cabbage – leaves packed into a congested head
- Kohl Rabi – the leaf-producing stem is grossly swollen
- Sprouts – secondary shoots with densely congested heads of tightly packed leaves
- Broccoli – hundreds of tiny unopened flower buds, the inflorescence with arrested development

## Turnip

Another important brassica, and probably the earliest domesticate was the turnip, B. campestris or B. rapa. This species is a ruderal plant, i.e. a weedy species that can colonize disturbed sites and it is often found as a weed in arable fields and this is almost certainly how it was first noticed and used as a seed oil and was apparently domesticated repeatedly across wide areas of Eurasia and the Mediterranean as early as 4,000BP.

## Domestication of Brassica olearcea

*Brassica oleracea subsp. oleracea* – native along coasts of Europe from Greece to England
Leafy kales – recorded in cultivation in Greece at least 2500 years ago
Early cabbage in Germany c.1000 years ago
Cauliflower - northern Europe c. 500 years
Broccoli – eastern Mediterranean c. 500 years
Brussels Sprouts – spontaneous mutation in France in 1750

As each new Brassica type emerged, it spread quickly across Europe, and hybridization with wild congeners undoubtedly played an important role in the domestication of these crops. For example, B. cretica contributed to the development of cauliflower. There is also evidence for introgressive hybridization between B. oleracea, B. campestris, and B. napus. Many of these crops probably first appeared as weeds in wheat fields and other crops.

## Brassica & the triangle of U (1935)

Some of these hybrids and the resulting polyploids were elegantly summarized by the Japanese geneticist Naga-Hara U in his now famous ‘triangle of U’. This shows that the genetic history of brassicas is every bit as complicated as that of wheat or potatoes. U proposed that three diploids, B. rapa / B. campestris, B. oleracea and B. nigra had spontaneously hybridized with each other yielding three new tetraploids, B. napus, B. juncea and B. carinata. These allotetraploids probably arose well after people had begun to cultivate diploid brassicas as crops, with e.g. B. napus probably arising in the last 2,000 years.

Oil Seed Rape / Canola

*Brassica napus* is a polyploid: 2n=38 derived from a hybrid between:

- Kale – *B. oleracea*: 2n=18 domesticated at least 2500 years ago in Europe
- Turnip – *B. campestris*: 2n=20 – domesticated c.4000 years ago in Mediterranean
- The genome of B. napus still contains the fully intact and essentially unre-arranged genomes of its two recent parent species.
- Although oil seed rape is a major crop, its relatively recent domestication is evident from its many persistent wild and weedy traits. For example, fruits of B. napus still tend to lose seeds before harvest due to premature fruit shattering, a trait in rape that has proved difficult to control. This incomplete non-shattering trait is indicative of incomplete domestication and probably a result of both recency and a more complex multi-gene control than for the non-shattering cereals and legumes.
- Oil seed rape is often found naturalized and weedy alongside cultivated or wild populations of its progenitors, B. oleracea and B. campestris, which themselves intercross freely and which show evidence for recent introgressive hybridization between these two species and oil seed rape.

The genome of the recent allopolyploid (neopolyploid) *Brassica napus*

- Oilseed rape (*Brassica napus* L.) was formed ~7500 years ago by hybridization between *B. rapa* and *B. oleracea*, followed by chromosome doubling, a process known as allopolyploidy.
- Together with more ancient polyploidizations, this conferred an aggregate 72× genome multiplication since the origin of angiosperms and high gene content.
- In the *B. napus* genome the constituent $A_n$ and $C_n$ subgenomes are engaged in subtle structural, functional, and epigenetic cross-talk, with abundant homeologous exchanges.
- Incipient gene loss and expression divergence have begun.
- Selection in *B. napus* oilseed types has accelerated the loss of glucosinolate genes, while preserving expansion of oil biosynthesis genes.
- These processes provide insights into allopolyploid evolution and its relationship with crop domestication and improvement

Similarly the Ethiopian mustard is thought to have arisen spontaneously in Ethiopia where the ranges of its parents – weedy B. nigra and cultivated B. oleracea overlapped, providing yet another example of serendipitous hybridization and the origin of crops.

This crossability in brassicas means that breeders can recreate new versions of these alloptetraploid crops by artificially constructing new diploid hybrids, for example a re-synthesized B. napus oil seed rape with scope to introduce useful traits from wild relatives.

Hybridization, Polyploidy & Crop Domestication – Conclusions

- Many of our most important crops are polyploids
- The origins in terms of where, when, how many times and from what progenitors, of several of these are highly complex, involving multiple sequential cycles of hybridization and multiple sets of wild species and early domesticates, and as yet incompletely understood – e.g. potato, banana, sugarcane

- For at least two of these – strawberry and bread wheat – there is evidence to suggest anthropogenic origins in cultivation
- For the others – potato, banana, sugarcane & canola - there is abundant circumstantial evidence that serendipitous hybridization following early cultivation, translocation and incipient domestication played an important part in generating the diversity that we see today amongst the set of important crops.
- There are many other hybrid / polyploid crops – citrus, tobacco, peanut, oca, kiwi fruit.......

Hybridizing the Planet

'We bring strangers together to make strange bedfellows, and we remake the beds they lie in all at once..... Thus, our disturbances hybridize both the environment and the species. are hybridizing the planet'  Jonathan Weiner, The Beak of the Finch

# BIO235 – Lecture 6 Hybridization, Polyploidy & Crop Domestication II

## Source Materials

Ames, M. & Spooner, D.M. 2008. DNA from herbarium specimens settles a controversy about origins of the European potato. *American Journal of Botany* **95**: 252-257.

Arranz-Otaegui, A. et al. 2018. Archaeobotanical evidence reveals the origins of bread 14,400 years ago in north-eastern Jordan. *Proceedings National Academy of Sciences* **115**: 7925-7930.

Chalhoub, B. et al. 2014. Early allopolyploid evolution in the post-Neolithic *Brassica napus* oilseed genome. *Science* **345**: 950-953.

Grivet, L., Glassman, J.-C. & D'Hont, A. 2006. Molecular evidence of sugarcane evolution and domestication. Pp. 49-66, in: Motley et al. (Eds.) *Darwin's Harvest - New Approaches to the Origins, Evolution, and Conservation of Crops*. Columbia University Press.

Hancock, J.F. 2004. *Plant Evolution and the Origin of Crop Species*. CABI.

Hancock, J.F. & Luby, J.J. 1993. Genetic resources at our doorstep: the wild strawberries. *BioScience* **43**: 141-147.

Hardigan, M.A. et al. 2017. Genome diversity of tuber-bearing *Solanum* uncovers complex evolutionary history and targets of domestication in cultivated potatoes. *Proceedings National Academy of Sciences* **114**: E9999-E10008.

Heslop-Harrison, J.S. & Schwarzacher, T. 2007. Domestication, genomics and the future for banana. *Annals of Botany* 100: 1073-1084.

Hilu, K.W. 1993. Polyploidy and the evolution of domesticated plants. *American Journal of Botany* **80**: 1494-1499.

Kilian, B. et al. 2006. Independent wheat B and G genome origins in outcrossing Aegilops progenitor haplotypes. *Molecular Biology & Evolution* **24**: 217-227.

Lev-Yadun, S., Gopher, A., & Abbo, S. 2000. The cradle of agriculture. *Science* **288**: 1602-1603.

Liston, A., Cronn, R. & Ashman, T.-L. 2014. *Fragaria*: a genus with deep historical roots and ripe for evolutionary and ecological insights. *American Journal of Botany* **101**: 1686-1699.

Matsuoka, Y. 2011. Evolution of polyploidy *Triticum* wheats under cultivation: the role of domestication, natural hybridization and allopolyploid speciation in their domestication. *Plant Cell Physiology* **52**: 750-764.

Murphy, D.J. 2007. *People, Plants & Genes*. OUP.

Perrier, X. Et al. 2011. Multidisciplinary perspectives on banana (Musa spp.) domestication. *Proceedings National Academy of Sciences* **108**: 11311-11318.

Petersen, G., Seberg, O., Yde, M. & Berthelsen, K. 2006. Phylogenetic relationships of *Triticum* and *Aegilops* and evidence for the origin of the A, B and D genomes of common wheat, *Ttriticum aestivum*. *Molecular Phylogenetics & Evolution* **39**: 70-82.

Renny-Belfield, S. & Wendel, J.F. 2014. Doubling down on genomes: polyploidy and crop plants. *American Journal of Botany* **101**: 1711-1725.

Salamini, F., Ozkan, H., Brandolini A., Schafer-Pregl, R., & Martin, W. 2002. Genetics and geography of wild cereal domestication in the near East. *Nature Reviews Genetics* **3**: 429-441.

Smith, D.R. 1995. Origin of the cauliflower. *Current Biology* **5**: 361-363.

Spooner, D.M., McLean, K., Ramsay, G., Waugh, R. & Bryan, G.L. 2005. A single domestication for potato based on multilocus amplified fragment length polymorphism genotyping. *Proceedings National Academy of Sciences* **102**: 14694-14699.

U, N. 1935. Genome analysis of *Brassica* with special reference to experimental formation of *B. napus*. *Journal of Heredity* **73**: 335-339.

Weiner, J.S. 1994. *The Beak of the Finch. Evolution in Real Time.* Jonathan Cape, London

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## BIO 235 Plants & People – Evolution & Domestication of Crops
## Lecture 7 – Minor Crops – Lost crops of the Incas: quinoa, tarwi, mashua, oca, ulluco (llama, alpaca & guinea pig)

### Minor Crops

Minor crops are underutilized or non-commercial crop species that are important components of regional or national agricultural biodiversity, which were potentially more important in the past, but which are today mainly used locally. These minor, displaced and underutilized crops nevertheless continue to play an important role in food security of rural communities in many parts of the world, and have the potential to be improved for use elsewhere in the world and become mainstream crops in their own right. This lecture will examine what we know about such 'lost crops' in one region of the world, the Andes.

### Lost Crops of the Incas

Potato – an ancient staple unknown outside the Andes until the time of the Spanish conquest and more or less inadvertently introduced to Spain from where it spread to the rest of Europe, and in spite of its unpromising start it went on to eventually become the 4th largest crop in the world. So, in a sense the potato was also a 'lost crop' until it started being cultivated in Europe in the 18th century. Another well-known crop from the Andes is the tomato.

Alongside these mainstream domesticates that have gone on to become globally important crops, there are a wide range of other minor, little-known crops in the Andes, that are essentially known there and not much elsewhere. These are in general not crops that you find in supermarkets in Switzerland.
Ulluco – Ullucus tuberosa, Basselaceae
Mashua – Tropaeolum tuberosum, Tropaeoleaceae
Amaranth – Amaranthus caudatus, Amaranthaceae.
Grain amaranth was perhaps a more famous crop of the Aztecs in Mexico, but a separate independent domestication occurred in the Andes and this plant is still found widely in cultivation in the Andes today.
Quinoa – Chenopodium quinoa, Chenopodiaceae

### The Andes

We know that the Andes form one of the most important hotspots of plant species diversity. In fact some have suggested that the tropical Andes may be the hottest hotspot of plant species diversity on the planet. So we have in the Andes a remarkable concentration of 10,000s of plant species. At the same time we know that much of this diversity has arisen relatively recently, in the last 2-5 Myr following recent and very rapid mountain uplift, and we know that this diversity has probably arisen in part due to the very steep and extended environmental gradients that we find in the Andes. Unlike in Europe or North America where plants grow from sea-level up to a little over 3,000m, in the Andes, the upper limit for plant growth is over 5,000m. We also know that there were a series of sophisticated civilizations in the Andes stretching back over several millennia and that by 600 A.D. these societies were sophisticated, with large sedentary populations living in fortified citadels like this one at Kuelap in northern Peru, indicative of highly differentiated societies dependent on agriculture for food production. Without money, iron, the wheel or work animals for ploughing, the Andean civilizations were able to transform the Andes into an advanced agricultural society with extensive terracing and irrigation that was able to feed 15 million people or more. Of course they were well behind European societies as was starkly apparent at the time of the Spanish Conquest when small numbers of Spanish soldiers with iron swords and horses were able to easily defeat the very large Inca armies. In fact the title *Lost Crops of the Incas*, is a misnomer, because it was not the Incas themselves who started plant domestication, but earlier pre-Inca groups, although at the peak of the Inca empire in 1400 A.D., Andean agriculture was at its peak, had spread throughout the Andean region and involved a vast infrastructure of terracing, irrigation, roads and footpaths and rock-walled silos for crop storage. The Incas really were master agriculturalists, and it is the crops that they used that are being lost today.

Range of Andean environments

Pacific coast – after the uplift of the Andes – isolated from Amazonian moisture and barricaded against the cold Pacific Humboldt current, the coast became a hyper-arid desert – the Atacama. However dissected by perennial rivers from the mountains above with fertile valleys, with extensive and sophisticated irrigation. These valleys provided some of the earliest sites for Andean towns – with access to fish, irrigated crops and manure from sea bird guano. Mid elevations – now highly developed agricultural systems where we find most of the Andean crops in cultivation today. In contrast, the fertile plains around Lake Titicaca formed another major centre for early agricultural development – with extensive evidence of early pre-Inca terracing. This area today is home again to diverse and complex crop mixtures. Hard to imagine when you see this massive lake that it lies at 3,800m or 12,500 feet above sea level. Agriculture and crops in the Andes are vertically diversified.

*Inga edulis* & *Erythrina edulis* – two legume trees, incipiently domesticated in the Andes. Note the specific epithet edulis – edible, i.e. these two species have long been known to be edible, one for the sweet white fleshy aril or sarcotesta that surrounds the seed, and which is sometimes used to make ice cream, hence the name Ice cream Bean, and I'd really recommend Inga Ice Cream on a hot day on the eastern flanks of the Andes. The second is known for its large and highly nutritious seeds – and these really are large seeds for legumes. Both these trees are cultivated in hedgerows and traditional agroforestry systems across the Andes.

Quinoa

Chenopodium quinoa is perhaps the most important indigenous grain crop domesticated in the Andes – the equivalent of wheat / rice / maize in other early centres of agriculture, and sometimes because of this termed a *pseudocereal*. It thrives in the cold dry climates and sometimes saline soils of the Bolivian and southern Peruvian altiplano, where it remains an important subsistence crop today, and from where commercial quinoa for export is mainly grown.

Quinoa – nutrition

Highly nutritious pseudocereal – the 'mother grain' of the Incan empire
Gluten-free, low glycaemic index, excellent balance of essential amino acids, fibre, lipids, carbohydrates, vitamins & minerals.
Adapted to harsh abiotic conditions – aridity (highly drought tolerant), cold, high elevations (up to 4500m), salinity

Three different forms of quinoa have been cultivated in the Andes:

- Quinoa – Chenopodium quinoa

- Its weedy counterpart – quinoa negra or ajara – Chenopodium quinoa var. melanospermum
- Chenopodium pallidicaule – kañawa – a second poorly known and understood Andean domesticate.

Quinoa - archaeology
Domestication is thought to have involved dramatic reductions in testa thickness to much thinner seed coats alongside changes in fruit shape. In the S-C Andes around the Lake Titicaca basin there is archaeological evidence to suggest that domesticated thin seed coat forms were being used by 3600 BP and also further north around the same time or possibly slightly earlier (based on seeds from the Panaulauca Cave in the Junin Basin in Peru). Initially both quinoa and quinoa negra were apparently grown and harvested together, but from ca. 2800 BP, quinoa was dominating indicating a shift around this time to more careful cultivation, weeding out quinoa negra, careful seed selection and field construction. This proposed S-C Andean heartland is contiguous with the western edge of the range of C. hircinum, a widely distributed chenopod and the potential wild ancestor of quinua.

Chenopodium domestication
Five separate domestications
*C. pallidicaule* - Peru/Bolivia altiplano – diploid
*C. giganteum* - Asia – hexaploid
*C. quinoa* – Andes - tetraploid
*C. berlandieri* subsp. *nuttalliae* – Mexico – tetraploid
*C. berlandieri* subsp. *jonesianum* – S.E. U.S.A. – tetraploid
Single New World polyploidy event, but too poorly resolved to ascertain parentage beyond *C. standleyanum* as one putative diploid parent.

*Chenopodium quinoa* genome
Further insights into the evolutionary history of quinoa have come with the sequencing of the *Chenopodium quinoa* genome in 2017. Estimated that the allotetraploid arose in North America 3-6 Myr. Multiple interfertile tetraploid species have arisen from the ancestral tetraploid, including *C. berlandieri*, *C. hircinum* and *C. quinoa.* It is suggested that there was a long distance dispersal even from N to America and that *C. quinoa* was domesticated from tetraploid *C. hircinum* and this new analyses highlights the possibility that quinoa was domesticated independently in the highland and coastal environments.

Llama & Alpaca
It has often been suggested that quinoa and llamas go together in the sense that quinoa is a highly favoured forage for llamas, and that the llamas disperse seeds with their dung, such that new stands of quinoa would become readily established around alpaca and llama corrals. Once again this harks back to the backyard venue for early domestication.

This idea is potentially in line with archaeological evidence for shifts in age profiles and abundance of llama bones that show a dramatic increase from 26-42% of animal bones prior to 7,000BP to 82-98% by 4,000BP. Similarly there is evidence of herding of llama by 4,000BP in Ayacucho and 3,000BP from Lake Titicaca. Data from the 8,200 year sequence from the Telermachay rockshelter in southern Peru (which included a metric tonne of animal bones…) suggested a shift from hunting guanaco and vicuna to herding domesticated camelids by 5,500

BP, indicated by high mortality of young camelids thought to the result of disease problems that are associated with corrals and which are absent in the wild.

Four S American camelids
Alpaca – *Lama pacos*
Llama – *Lama glama*
Vicuña - *Vicugna vicugna*
Guanaco – *Lama guanicae*

While there has been debate about the origins of the two domesticated species, there is general consensus that the llama, Lama glama was domesticated from the guanaco = Lama guanicae and the alpaca, Lama pacos was domesticated from the vicuna = Lama vicugna
Llama – pack animals; llama and alpaca – meat and wool

Both the vicuna and the guanaco are pre-adapted to domestication in the sense that they are gregarious, strongly social animals that form herds with strong dominance hierarchies that leave them open to control by humans who can step in at the top of the pecking order and take advantage of pre-existing social structure to manage and manipulate herds. So there is compelling evidence that by 4,500BP humans had begun to exert control over camelid herds.

Guinea Pig
The only other 'livestock' domesticated in the Andes is perhaps more surprising, and that is the guinea pig, Cavia porcellus. Wild guinea pigs are native from Venezuela to Argentina and have been an important food source for hunter gatherers from as early as 12,000 B.P. They are not related to pigs but show some attributes that make then attractive for domestication – a high reproductive rate, feed on household refuse, easily raised in confined spaces, drawn to the warmth, protection and food scraps of human habitation sites and thus susceptible to domestication. The significant increase in guinea pig bones around 4,500BP thought to be indicative of domestication.

Potato
There are at least four species of tubers domesticated in the Andes. Three of them are still important crops today in Andean farming communities.
Oca – Oxalis tuberosa
Mashua – Tropaeolum tuberosum
Ulluco - Ullucus tuberosus
Potato – Solanum tuberosum

The most likely origin of domestication of the potato also lies in the S-C Andes in southern peru and northern Bolivia. However, the timeframe for domestication of potatoes is much less certain, simply because potatoes are very rarely preserved intact in archaeobotanical remains. In fact there are very few potato remains, but in some of the coastal desert sites, such as Casma on the coast of Peru, a few 100 km north of Lima, 20 well-preserved potatoes have been found dating to between 4,000 and 3,200BP. The starch grains of domesticated potatoes are significantly larger than wild potatoes and, based on this evidence, it suggests that these Casma potatoes were indeed domesticated.

Andean Domestication – the early consensus

The general consensus that has been accepted for some time is that the S-C Andes of southern Peru and Bolivia in southern Peru and adjoining Bolivia, focused especially on the Lake Titicaca basin, was the area of initial crop and livestock domestication in the Andes – a sort of 'core Andes' analogous to the 'core Fertile Crescent'. It has been thought that this cohort of crops centred on quinoa and potatoes and accompanied by domestication of llama, alpaca and guinea pigs, were all domesticated in this region between 7,000 and 4,000BP and that by the end of this period agriculture was firmly established in this region, reflected in the present day traditional agricultural systems found for example around Lake Titicaca. This was essentially a highland agriculture – based on high altitude crops and animals, but with clear links to coastal settlements, where remains of many of these crops were also found by 4,500BP.

### Nanchoc – early crop adoption in northern Peru

However, this idea is essentially based on very sparse evidence from just a few archaeological sites and a handful of rather incomplete molecular studies, and there have been some recent studies that cast doubt on the timing and geography of agriculture in the Andes.

New archaeological excavations from Nanchoc, a dry valley in NW coastal Peru has revealed much earlier dates for a suite of crops indicating their adoption and cultivation in that area:

- Squash – 9240-7660BP – match to Cucurbita moschata, probably representing an early cultigens, probably introduced from Colombia
- Peanut – 7840BP – this one of the more surprising finds because peanut has always been considered to be among the later cultivated plants, and because the peanut originated on the east side of the Andes in Bolivia / NW Argentina. There are no records of any wild Arachis from the W side of the Andes. The remains here represent an early stage domesticate – probably an early cultigen dispersed at an earlier date from a long way S and E.
- Quinua – 8,000-7,000BP – a single specimen of a large-seeded Chenopod resembling C. quinoa, also a long way from the highlands of Junin where this species is thought to have been domesticated.

There is no evidence to suggest that the Nanchoc Valley was a domestication centre for any of these crops. These findings suggest that:

- All of these crops were cultivated elsewhere before their appearance in Nanchoc and were brought to this valley.
- Presence of mixed horticultural / gathering communities, using combined suites of resources and technologies indicative of > advanced communities by 9,000-7,000BP.
- Significant exchange of ideas and products with horticulturalists living in distant coastal, highland and tropical forest areas.
- Agriculture and managing water via irrigation played a more important and earlier role in the development of Andean civilizations than previously understood.
- The timing of Andean agriculture, extending back to nearly as early as many parts of the Old World.

These new finds  suggest a more diffuse, complex regional mosaic may be a better model that a simple Lake Titicaca basin centric view. Recent research on two other Lost Crops of the Incas confirms this idea of a more diffuse regional mosaic of crop origins.

### Oca

*Oxalis tuberosa*, commonly known as Oca, is an indigenous crop of the Andes. Like many other 'underutilized', minor or displaced crops, it plays an important role in food security of rural communities. It arose from within a clade informally known as the *Oxalis tuberosa* alliance, a group of several dozen morphologically similar species found throughout the central and northern Andes. Cultivated Oca is an octoploid, but most species in this alliance are diploids, with only a few wild polyploids. The majority of the species of this alliance do not form tubers, but wild, tuber-bearing populations have been found in four geographic areas from central Peru to northwest Argentina, and these seem to comprise four distinct species and likely candidate progenitors of domesticated oca. However, only two of these four species have been described – *O. picchensis* from southern Peru and *O. chicligastensis* from NW Argentina, both of which are probably tetraploids, the other two are as yet un-named and are designated simply as Lima W/T for wild tuber-bearing populations from the western slopes of the Andes in Lima Dept, Peru, which is probably hexaploid, and BolW/T for the wild tuber-bearing *Oxalis* populations found on the east side of the Andes in Bolivia, almost certainly a polyploid, but of uncertain ploidy.

Some evidence to suggest that *O. tuberosa* may comprise two distinct groups. This is based on both molecular data and ethnobotanical evidence from Cusco in Peru, where Quechua-speaking farmers in that area distinguish two use categories of Oca: (i) the sweeter folk cultivars wayk'u which are usually cooked fresh after a few days to sweeten in the sun; (ii) the sour khaya or P'osqo cultivar which is cultivated separately and used for processing into dried tubers that can be preserved for years. AFLP data show that these two cultivar types form separate genetic clusters, suggesting that they may have different evolutionary histories, perhaps in their origins of polyploidy and or origins of domestication.

Chloroplast-expressed glutamine synthetase ncpGS and ITS gene sequences identified O. picchensis and BolW/T as progenitor candidates, leading to the hypothesis that these two Oxalis taxa may have hybridized to form cultivated Oca. However, the *O. picchensis*-like ncpGS sequence was absent from one of the nine *O. tuberosa* plants sampled and AFLP data of O. picchensis show few markers shared with all oca samples. This suggests that oca's origins maybe more complex than the simple hybridization scenario. In addition, the two wild tuber-bearing species LimaW/T and *O. chicligastensis* were unknown at the time of the first study.

AFLP data used to: (i) determine whether the wild tuber-bearing Oxalis populations form four geographically distinct species, and whether the two use-categories are molecularly distinct groups; (ii) assess the evidence that each of the wild taxa might have been a genome donor of octoploid oca.

Results suggest:

(i) That each of the wild tuber-bearing populations represent potentially distinct species

(ii) The two cultivated oca use categories are molecularly distinct, suggesting some as yet unknown difference in their evolutionary histories – possibly separate polyploidy events and/or separate origins of domestication. This provides a good example of how ethnobotanical information can reveal evolutionary differences that might otherwise have been overlooked.

(iii) That the BolW/T and *O. chiclisgastensis* are possible genome donors of domesticated oca, but great uncertainty about the polyploid origins and domestication of this crop remain

(iv) Complex origins of polyploids

(v) Comparisons among closely related and recently diverged species where little variation in DNA sequences.
(vi) Incomplete taxonomy poses problems for these sorts of studies e.g. the unrecognized wild tuber-bearing populations of *Oxalis* may well represent distinct species.

## Mashua

Tuberous Nasturtium *Tropaeolum tuberosum* Tropaeoleaceae

Alongside Potatoes, Quinua, Oca and Ulluco, Mashu was an important food plant and is cultivated in the high Andes from Venezuela to central Bolivia.
In this case the putative wild progenitor apparently lacks tubers altogether
subsp silvestre – wild form without tubers
subsp tuberosum – domesticated form with subterranean tubers

The wild and domesticated subspecies occupy similarly extensive distributions, and there are no data about where it was domesticated. Thus although the south-Peru Titicaca region is thought of as a possible core area for early domestication in the Andes, the lack of data for several of the lesser-known Andean crops, means that there is much still to be investigated and much still to learn, and no real consensus on the regional development trajectory of agriculture in this region.

## Tarwi

Research to discover when, where, how many times and from what progenitors tarwi was domesticated has faced similar problems to Oca – namely confused taxonomy and lack of DNA sequence variation. Lupinus mutabilis shows the classic legume domestication syndrome of indehiscent pods, large seeds, water permeable seed coats, reduced seed pigmentation, rapid and uniform germination and growth, and nearly annual life history, but the seeds retain high alkaloid levels unlike modern lupin domesticated varieties that are based on sweet low alkaloid mutants. This means that lupin seed need to be treated by rinsing in flowing water to remove the alkaloids.

Tarwi is grown throughout the Andes (Venezuela to Bolivia) and the seeds are sold in markets. However, no wild populations of tarwi have been discovered. Attempts to reconstruct relationships among the Andean species of Lupinus have encountered difficulties due to lack of resolution, attributable to low levels of DNA sequence variation among the Andean species. This has been attributed to the recency and rapidity of the Andean Lupinus radiation and means that using conventional DNA sequence loci provides essentially no information about the relationships / likely progenitors of tarwi.

## Tarwi Archaeology

Limited archaeological remains. Earliest domesticated tarwi seeds date from 1800BP from the Mantaro Valley in central Peru. No remains found further south from the putative Lago Titicaca centre of early Andean agriculture.

## Tarwi Origin

Recent work using larger next generation DNA sequencing data provided strong support to suggest that L. piurensis is the most likely progenitor of tarwi. This fits with morphology and would suggest that tarwi was domesticated in N Peru or southern Ecuador.

## Tarwi Demography

Demographic analysis suggests that tarwi was domesticated c. 2500BP and experienced a genetic bottleneck after its initial domestication. This is broadly congruent with the archaeological data from 1800BP in the Mantaro valley, well to the north of the putative S-C Andean centre of agriculture in the Lago Titicaca basin. This suggests that tarwi was a late stage domesticate, added into the exiting crop assemblage of potatoes, quinoa etc as agriculture spread north with the expansion of the pre-Inca empires, which by 1,000BP spawned sophisticated fortified cities in northern Peru.

## Lost Crops of the Incas

Several of these minor Andean crops are being progressively displaced by introduced European crops. For example faba bean, Vicia faba, is increasing cultivated in place of tarwi, wheat in place of quinoa. Similar erosion of diversity can be seen in some Andean crops such as potatoes due to increasing cultivation of more productive and uniform bred varieties from outside.

## Other Lost Crops – African vegetables

The rise of Africa's super vegetables – see Cernansky (2015).

## Other Lost Crops – Eastern North America

Thousands of years before maize-based agriculture practiced by Native American societies in eastern North America at the time of contact with Europeans, there existed a unique crop system only known from archaeological evidence. In this case, these really are lost crops – no longer used, relictual and under threat from modern agriculture, habitat loss and invasive introduced weeds. See Mueller et al (2017)
Goosefoot – *Chenopodium berlandieri*
Sumpweed / Marsh Elder – *Iva annua*
Little Barley – *Hordeum pusillum*
Erect Knotweed – *Polygonum erectum*
Maygrass – *Phalaris carolinum*

## Neglected & Under-utilized Crops to Improve Food Security

Indigenous ancient crops often still used locally & regionally – wider use offers scope to help poorer subsistence farmers
Reduce risks of over-reliance on a small number of major crops – strength in diversity
Environmental benefits: Increases sustainability of agriculture using crops with wider environmental tolerances requiring lower inputs of fertilizers, pesticides, water and energy
Nutritional benefits: Contribute to food quality and nutritional value
Preserve, promote and celebrate cultural and dietary diversity

# BIO235 Lecture 7 – Minor Crops – Lost Crops of the Incas – Source Materials

Anon 1989. *Lost Crops of the Incas. Little-Known Plants of the Andes with Promise for Worldwide Cultivation*. National Academies Press.

Atchison, G.W. et al. 2016. Lost crops of the Incas: Origins of domestication of the Andean pulse crop tarwi, *Lupinus mutabilis*. *American Journal of Botany* **103**: 1592-1606.

Bradbury, E.J. & Emshwiller, E. 2010. The role of organic acids in the domestication of Oxalis tuberose: a new model for studying domestication resulting in opposing crop phenotypes. *Economic Botany* **65**: 76-84.

Cernansky, R. 2015. Super vegetables: Long overlooked in parts of Africa, indigenous greens are now capturing attention for their nutritional and environmental benefits. *Nature* **522**: 146-148.

Dillehay, T.D., Rossen, J., Andres, T.C. & Williams, D.E. 2007. Preceramic adoption of peanut, squash and cotton in northern Peru. *Science* **316**: 1890-1893.

Emshwiller, E. & Doyle, J.J. 2002. Origins of domestication and polyploidy in oca (*Oxalis tuberosa*, Oxalidaceae). 2. Chloroplast-expressed glutamine synthetase data. *American Journal of Botany* **89**: 1042-1056.

Emshwiller, E., Thiem, T., Grau, A., Nina, V. & Terazas, F. 2009. Origins of domestication in Oca (*Oxalis tuberosa*; Oxalidaceae). 3. AFLP data of Oca and four wild tuber-bearing taxa. *American Journal of Botany* **96**: 1839-1848.

Hickmott, S. *Growing Unusual Vegetables – Weird and Wonderful Vegetables and how to Grow Them*.

Jarvis, D.E. et al. 2017. The genome of *Chenopodium quinoa*. *Nature* 542: 307-312.

Mueller, N.G. et al. 2017. Growing the lost crops of eastern North America's original agricultural system. *Nature Plants* **3**: 17029.

Pastor, S., Fuentealba, B. & Manuel, R. 2008. Under-utilized species policies and strategies – under-utilized crops in Peru. Global Facilitation Unit Underutilized Species (GFU), Italy. http://www.underutilizedspecies.org/Documents/PUBLICATIONS/underutilized_species_policies_and_strategies_peru_lr.pdf

Walsh, B.M. et al. 2015. *Chenopodium* polyploidy inferences from *SALT Overly Sensitive 1* (*SOS1*) data. *American Journal of Botany* **102**: 533-543.

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**BIO 235 Plants & People – Evolution & Domestication of Crops**
**Lecture 8 – Revolution or Evolution - The tempo of domestication and the evolution of agriculture**

In lecture 4 we discussed the phenotypic changes associated with domestication – crop domestication syndromes. We also started to think about how these changes were brought about via a combination of methodical and unconscious selection. We saw that Charles Darwin used domestication as an analogy to evolution by natural selection, and how ever since there has been a debate as to whether this process of recent rapid species evolution in domesticated taxa, brought about by human association, is a valid paradigm for evolutionary study.

What this lecture aims to do is examine this paradigm and come to some sort of conclusions about the tempo of domestication.

## Genes & Domestication – Conclusions

- General finding that domestication largely involved filtering out of the best alleles from standing allelic variation in crop ancestors, although new mutations in key developmental pathways may have been instrumental in some traits.
- Role of human selection has been modification rather than elimination of gene function across diverse developmental pathways, reflecting the short time span of domestication.
- *High speed evolution* represented by crop domestication the result of strong selection pressures on pre-existing variation.
- Up and down regulating of transcription factors has played a central role in domestication, as found more widely in plant developmental genetics.
- Changes often involve just single or a few amino acids

## Revolution vs Evolution

Some of the simple underlying genetic changes associated with domestication, alongside early genetic work, might suggest sudden, almost instantaneous domestication. This might be even more likely in the case of sudden changes brought about by serendipitous hybridization and polyploidy which involve the instantaneous emergence of novel traits and adaptations. This rapid domestication transition model prevailed for several decades through the 1970s to 1990s, prompting ideas that the transition from foraging to farming could also have happened rapidly, potentially over the space of just a few centuries.

Idea of rapid species evolution in domesticated taxa

- cultivation exerts selection pressures for recurrent adaptations
- presumption that selection under domestication is strong
- rapid or very rapid evolution of cultivated species
- timespan of domestication of a few 100 years

Domestication as a form of animal / plant coevolution

- conceptually similar to evolutionary diversification driven by other multispecies interactions
- similar levels and patterns of evolutionary change to those observed in wild species
- timespan of domestication several 1000 years

Illustrated by Fuller et al's. (2010) schematic diagram showing domestication as a rapid transition under strong selection pressures on a scale spanning 200 years, vs a much more protracted transition under weak selection spanning up to 5,000 years. Thus, even recent viewpoints differ by a factor of 10-20 in terms of how fast people think domestication happened.

## How fast was domestication?

Here we can see a similar portrayal of these contrasting timescales considered rapid or more gradual for domestication and the transition from foraging to farming. The time scale is in 1000s of years from the Pleistocene and late glacial to the Holocene and the present day. Two short cool dry spells are indicated the Older and Younger Dryas periods, which have been implicated by some in the shift from foraging to farming. We can see the prevailing view of domestication as a rapid transition spanning just a few centuries, vs an alternative model whereby domestication was preceded by a long period of pre-domestication cultivation and was itself a long and gradual process, spanning several millennia. One might argue that rates of domestication don't really matter, that this is not a very interesting question, but it is one that we need to investigate if we are going to understand the central questions about why and how farming arose.

## Measuring the rate of domestication: experimental approaches

One way to investigate how quickly domestication happened is to attempt to repeat this process experimentally using populations of wild einkorn wheat, and measure the selection pressure for non-shattering spikelets brought about by cultivation and harvesting. George Hillman attempted to do this via a set of experiments in SE Turkey in wild populations of einkorn wheat. His experiments showed that several factors are key to domestication:

- cultivation of wild wheat is essential; selection is not effective in the absence of cultivation
- cultivation needs to move onto new ground, rather than stay on the same field indefinitely
- harvesting methods are critical. Simple beating which was the early method used to harvest grain from wild (non-cultivated) populations of wheat doesn't work, but instead either sickle harvesting or uprooting are needed to invoke selection.
- Even with just unconscious selection at the lowest selection coefficients, domestication can occur within 20-200 years.
- With some element of conscious selection (as the frequency of non-shattering phenotypes increased and would have been noticed) it could go even faster.

This work was highly influential in promoting the idea that domestication could have happened very quickly, within the space of 100-200 years. However, just because it could have happened that way, it doesn't mean it did happen that way and we also need to carefully examine the archaeological record to see what rates can be measured there.

## Measuring phenotypic rates of evolution during the domestication process

Archaeology – track phenotypes through time to estimate rates of evolution and strengths of selection under domestication

Two particular traits – rachis non-shattering in cereal crops & grain / seed size in seed crops – two key traits of the domestication syndrome - can provide quantitative information on phenotypic evolution during domestication. As we saw before, the seed non-shattering trait is considered the key phenotypic indicator of domestication, especially for cereals and legumes. The evolution of non-shattering is regarded as the hallmark of domestication because the fixation of this trait reduces the ability for natural seed dispersal and is thus deleterious in wild populations and makes the cultivated species dependent on human intervention for continued reproduction. Non-shattering evolves due to changes in harvesting methods, such as the advent of sickle harvesting which selects for retention of seed after harvesting. Previous work has suggested that this trait can become fixed in <100 generations, via spread of non-shattering alleles within c. 100 years. In the archaeological record, non-shattering is readily identified by the remains of the infructescence rachis segments or spikelet bases with non-dehiscent attachment scars.

## Flotation: a key technique in archaeobotany

In order to conduct quantitative analyses of the trajectories of domestication using archaeological remains, large numbers of samples need to be assessed and measured. Prior to the 1960s, this was rarely attempted and archaeological surveys produced mainly lists of the first appearances of species and domesticated forms. The introduction of flotation techniques allowed much larger numbers of small plant remains to be recovered from archaeological deposits through time – for example cereal grains to measure changes in grain size through time, and most importantly large numbers of spikelet bases to assess the proportions of shattering vs non-shattering spikelets through time, and hence facilitating statistically valid quantitative analyses of the temporal and spatial trajectories of domestication. As we shall see, the expanding data from many sites and across different crops is revealing a very different picture of the tempo of domestication than that suggested by Hillman and Davies based on their experimental measurements of selection coefficients.

### Rice domestication in the lower Yangtze

Non-shattering rice spikelet & the sh4 gene

Increasing proportion of non-shattering (domesticated) rice spikelets from 27% to 39% over a 300-year period between 6,900BP and 6,600BP.

This period thus corresponds to an intermediate stage between first cultivation and full domestication. It suggests that domestication of rice was incomplete at this time. It also points to the idea that domestication was a protracted process spanning more than just a few 100 (in this case 300) years, and we can see that only 2,000 years later the proportion of non-shattering rice had reached 95%, i.e. nearly fully domesticated.

### Proportions of wild and domesticated barley and einkorn wheat remains in the Near East

The proportions of wild and domesticated barley and einkorn wheat remains in the Near East are arranged chronologically. A = barley; B = einkorn wheat, showing again that, although theoretically the evolution of non-shattering could have happened very quickly, it was actually gradual.

### Domestication rates for barley and wheat

These data can be transformed to produce a regression of domestication rate over time. Once again the trend from wild dominance to domesticated dominance is clear, but fairly gradual and slow, spanning c.2000 years. A=barely; B=einkorn wheat.

### Frequency of non-shattering, domesticated forms of barley wheat and rice in the archaeological record

We know that fixation of some of these domestication alleles took a long time from data that document the frequency of non-shattering, domesticated forms of barley, wheat and rice in the archaeological record. For example, fixation of non-shattering rachises in wheat and barley (yellow & blue in the graphs) took about 2,000 years with non-shattering forms increasing at a rate of 0.03-0.04% per year. For rice (red in graph), fixation of non-shattering was surprisingly late in China, with only around 50% of the rice from the lower Yangtze having non-shattering rachises as late as 7,500-6,500 years.

### Purugganan & Fuller (2010)

Data on non-shattering and grain/seed size from 60 archaeological sites in five regions in Africa, Asia and North America, that date from the Neolithic (12,000BP) to historical times (800BP), encompassing 11 crop species:

- Five cereals – Hordeum vulgare, barley; Triticum monococcum, einkorn wheat; Triticum dicoccum, emmer wheat; Pennisetum glaucum, pearl millet; Oryza sativa, rice
- Three legumes – Vigna radiata, mung bean; Pisum sativa, pea; Lens culinaris, lentil
- Cucmis melo, melon; Helianthus annuus, sunflower; Iva annua, sumpweed, a relic crop from eastern North America.

Compare rates of phenotypic change in these two traits with evolutionary rates in wild species, to address the question of whether domestication is indeed a case of rapid evolutionary diversification or has similar tempo to cases of natural selection.

Non-shattering
8189 spiklets from 12 sites

- Einkorn wheat - > 3,000 years to go from 22% at 11,725BP to 95% by 8675BP
- Rice: increase in % non-shattering from 27% to 39% between 6,900BP & 6,660BP, giveing a fixation time span of >2,500 years
- Barley: <4% at 11,075BP to >90% by 8350BP

Indicates that non-shattering, and hence domestication, did not occur rapidly, but may have taken several 1000 years to rise to fixation in these crop species

What these data show is that in domesticated grasses, changes in grain size and shape evolved prior to non-shattering ears. Initial grain size increases may have evolved during the first centuries of cultivation, within perhaps 500-1000 years. Non-shattering infructescences were much slower, becoming fixed about 1000 to 2000 years later. Pulses by contrast, do not show evidence for seed size increase in relation to earliest cultivation, and seed size increase may be delayed 2000 to 4000 years. This implies conditions that were sufficient to select for larger seed size in Poaceae were not sufficient in Leguminosae, and different thresholds of selective pressure, for example in relation to different seed ontogenies and underlying genetic architecture in these families.

Archaeological evidence for protracted domestication
Bringing all the data on Old World cereals together into one place, we can see that domestication, as measured by fixation of the non-shattering trait, took at least 2,000 to 2,500 years, and increases in grain size are more gradual over the same period. After domestication, grain size becomes variable, fluctuating both up and down, suggesting processes of varietal differentiation and local adaptation.

Comparison of Evolutionary Rate Estimates
The 'darwin' = one logarithmic increase in the phenotypic value of a trait for each million years of evolution
The 'haldane' = the change of one standard deviation of a trait value per generation

A- in darwins; B – in haldanes
DOM = domestication; DOM* = domestication under a shortened (2,000 yr) domestication period
Wild PLAN = plants; AN = animals anthopogenic; NAT = animals natural

The range of rate estimates for evolution under domestication are lower than those observed for plants and animals under natural or anthropogenic conditions.

Comparison of Selection Coefficients
DOM = domestication; DOM* = domestication under a shortened (2,000 yr) domestication period
WILD = Wild; LH = life history traits; MO = morphological traits

Perhaps not surprisingly, given the lower rates of evolutionary observed under domestication, selection coefficients are also at the lower end of the range for wild species.

These data suggest that rates of phenotypic change under domestication are lower than under natural selection / evolution of wild species, a result that is perhaps surprising, but one that is indicative of domestication as an evolutionary process that proceeds over 1000s of years, not 100s.

Rates of change in domestication traits
Here we can see summaries of rates of change in domestication traits across different crops. A – graph comparing frequency of rates in terms of percentage change in a trait per year; B – Scatter of Haldane rate estimates, indicating trait/crop type; C – Frequency of estimated selection coefficients in the dataset. This shows that evolutionary change in non-shattering is generally faster than grain

size change, and that rates of phenotypic evolution under domestication are generally similar to rates in wild animal and plant studies.

### Early allelic selection in maize as revealed by ancient DNA

As you will recall, maize was first domesticated from teosinte, a wild grass, by 6,300BP in south-central Mexico. After initial domestication, early farmers continued to select for advantageous morphological and biochemical traits in this important crop. Jaenicke-Després et al (2003) characterized three genes involved in the control of plant architecture (*tb1*), storage protein synthesis (p*bf*) and starch production (*su1*) from five archaeological maize samples from the Ocampo caves in NE Mexico and six cobs from the Tularosa Cave in the SW U.S.A. The results showed that the alleles typical of contemporary maize were present in Mexican maize by 4,400 BP. This shows that plant morphology as well as biochemical properties of the protein and starch were selected early in the history of maize, and before maize was introduced into the SW U.S.A. However, as recently as 2,000 BP, allelic selection at one of the genes may not yet have been complete, as revealed by the presence of a su1 allele which today occurs in teosinte, but is very rare or absent in maize in a 2,000 year-old cob from the U.S.A.

This study represents provides a spectacular example of the integration of archaeological data in the form of a time series of maize cobs from 4,300 to 650 years, dated using accelerator mass spectrometry with genetic data for three domestication genes, characterized from the archaeological remains using ancient DNA – a tour de force in terms of the consilience of archaeological and genetic data, and the application of modern archaeological and molecular technologies and techniques.

It also fits with a model of gradual progression from initial to full domestication over a period of several millennia.

### The trajectory of barley domestication

The domestication of barley also apparently involved a c.2,000 year period for the establishment of key traits of the domestication syndrome.

### Meta-stable semi-domestication

Episodes of both gradual and more rapid change, and the possibility of a potentially lengthy phase of semi-domestication. In this model, the initiation of cultivation and/or new harvesting methods should allow adaptations to emerge in the crop population and perhaps rapidly increase, but to a fairly stable minority balanced against persistence of wild populations – in adjacent fallow fields, e.g. shifting cultivation or volunteers in subsequent years. It is possible that ‘intermediate’ early cultivars of this sort could have persisted for some time. This of course raises the question as to the tipping point and what finally pushes an intermediate equilibrium towards full domestication? Possible triggers might be changing cultivation and processing methods – so-called tipping points of intensification. Alternatively, grain exchanges might transfer mutations between regions, in a merging of domestication pathways that began separately.

### Weed evolution by de-domestication

Crop progenitors are often weeds of disturbed, ruderal sites, pre-adapted to growing in open habitats, and hence to cultivation. *Oryza rufipogon*, the progenitor of rice is a good example

### Weed evolution by de-domestication: rice

Invasive weeds that colonize agricultural fields cost millions of dollars in crop losses and weed control measures every year. Many of these agricultural weeds share similar fitness-related traits that make them highly competitive with crop species. For example, rapid growth, deep roots, high seed production and increased seed dispersal allow weeds to acquire more resources, as well as to produce more offspring. Efficient seed dispersal, in particular, may be a trait crucial to weed fitness. By increasing seed dispersal via ‘shattering’ or scattering their seeds, weeds can increase their presence in the seed bank and spread into new areas. Plants that shatter their seeds within agricultural fields can often avoid collection by farmers, and subsequent seed consumption / destruction, thus persisting within fields.

Zhang et al (2012) in China: weedy rice in China shown to be more closely related to domesticated rice in fields than other cultivated rice or common wild rice varieties, suggesting a process of de-domestication, whereby weedy rice probably originated from local cultivated rice.

Thurber et al (2010) in the USA: Cultivated rice fields worldwide are plagued with weedy rice, a conspecific weed of cultivated rice (*Oryza sativa*). The persistence of weedy rice has been attributed, in part, to its ability to shatter (disperse) seed prior to crop harvesting. In the United States, separately evolved weedy rice groups have been shown to share genomic identity with exotic domesticated cultivars. Thurber et al (2010) found that all U.S. weedy rice groups shatter seeds easily in contrast to the decrease in shattering ability seen in cultivated groups. Allelic identity and diversity at the major shattering locus, *sh4*, in weedy rice showed that all cultivated and weedy rice, regardless of population, share similar haplotypes at *sh4*, and all contain a single derived mutation associated with decreased seed shattering. These data constitute the strongest evidence to date of an evolution of weeds from domesticated backgrounds. The combination of a shared cultivar *sh4* allele and a highly shattering phenotype, suggests that U.S. weedy rice have re-acquired the shattering trait after divergence from their progenitors through alternative genetic mechanisms.

These crop-derived weedy rices show re-aquisition of the shattering trait, but in ways where the abscission layer which leads to shattering breaks down sooner leading to earlier shattering than in wild rice – a potentially useful adaptation for beating the farmer to it and getting into the seedbank before the rice harvest.

Genetic characterization found that these weedy rices all possessed the *sh4* mutation that characterizes domesticated non-shattering rices, suggesting the acquisition of a different novel mutation in the *sh4* gene that allows shattering.

This apparently rapid process de-domestication provides an interesting and instructive counterpoint to understanding the complex selection pressures operating within cultivated fields of agricultural landscapes.

<u>Weed evolution by de-domestication: rye</u>
Rye: bread of the poor in northern & eastern Europe

19th century immigrants introduced rye to the U.S.A. and grown widely there until the 1960s, then demand dropped and less and less rye grown

Late 1900s rye began appearing as a weed in other crops

By early 2000s weedy rye infested 1 million ha of cropland in western U.S.A.

A change in a single gene had restored seed shattering; seeds had become smaller and feral rye now phenotypically distinct and reproductively isolated (via phenological shifts) from domesticated cereal rye.

Rapid evolution away from domesticated ancestor in < 120 yr since its introduction.

<u>Rates of crop domestication - summary</u>

- Available quantitative archaeobotanical data on domestication traits, and especially seed size and loss of seed dispersal mechanism, can be used to explore changes during domestication and how quickly those changes occurred.
- These data show that in domesticated grasses, changes in grain size and shape evolved prior to non-shattering ears. Initial grain size increases may have evolved during the first centuries of cultivation, within perhaps 500-1000 years. Non-shattering infructescences were much slower, becoming fixed about 1000 to 2000 years later.
- Pulses by contrast, do not show evidence for seed size increase in relation to earliest cultivation, and seed size increase may be delayed 2000 to 4000 years.
- Rates of phenotypic evolution in multiple crop species appear to be significantly slower than rates observed in wild species.
- Selection coefficients associated with domestication are at the lower end of the distribution for wild species.
- Rates are comparable for non-shattering and seed size traits and across crops and locations
- These findings require a reassessment of the nature of selection during domestication.

## Rates of crop domestication & the nature of selection during domestication - summary

- The domestication process appears to have been driven largely by unconscious selection, i.e. as a byproduct of cultivating plants in agricultural environments
- Unconscious selection is similar to natural selection in novel environments established by human agriculture
- Domestication genes may have pleiotropic effects, such that deleterious mutations may segregate at higher frequencies in population bottlenecks associated with crop origins leading to decreased selection efficiency
- Farmers continued to cultivate and gather wild plants alongside proto-domesticates during the initial phases of domestication, possibly resulting in gene flow that hampered fixation of selected alleles
- Other domestication traits may evolve at higher rates

There is now also plenty of molecular and archaeobotanical evidence that sudden change is not the rule, but rather that domestication spanned both an early and relatively rapid incipient domestication phase and a later and slower stage to reach fixation of full domestication, the complete transition in the suite of traits that changed wild populations into domesticated crops spanning many centuries or millennia. While the dramatic phenotypic changes brought about by domestication within just 1,000 years may indeed appear ‘revolutionary’, these evolutionary changes were far from instantaneous, and comparable to, or somewhat lower than, rates of evolution in wild species.

## Building up Regional Pictures

By studying suites of crops and understanding the geotemporal facets of their origins in any one of the 10 or more regions where agriculture arose independently, it is possible to start to build up more complete regional pictures of the origins of agriculture and geotemporal agricultural development trajectories in that area.

## The Fertile Crescent

We saw before that the Fertile Crescent – this horse shoe area spanning SE Turkey, NE Syria, northern Iraq and south down the fertile valleys of the Tigris and Euphrates rivers – was the area of domestication for a series of cereal and pulse crops, wheat, barley, rye, lentil, pea, faba bean, as well as the four most important livestock domesticates, the goat, sheep, pig and cattle.

## The Core Fertile Crescent – The Cradle of Agriculture & the Dawn of Civilization

When we come to look at the geotemporal progression of the development of agriculture in this area, we see that there is not only remarkable congruence between the archaeological and genetic evidence that allows crop origins to be pinpointed with surprising precision, but also congruence between the geographic origins of most of these crops and livestock.

The geographical distributions of seven Neolithic so called founder crops - lentil, chickpea, bitter vetch, einkorn and emmer wheat, and barley all overlap in one part of the Fertile Crescent and are found together only in this core area. The distribution of chickpea is particularly interesting because it is narrowly restricted to a small part of the Fertile Crescent and it is unlikely that such a globally rare species would have been domesticated so early, c.10,000 BP, had farming originated outside this area. You can see that the putative point of domestication of einkorn wheat lies within the distribution of chickpea. Furthermore, the wealth of archaeological data strongly suggests farming-based Neolithic societies in this core area were the earliest settlements of this type in the Fertile Crescent. In regions beyond the core area, there is no evidence for domesticated forms of cereals and pulses earlier than 7300 to 7000 BP. The idea of a single core area of plant domestication is further supported by the limited genetic variability of crops and by genetic evidence suggesting these crops were domesticated only once (except perhaps barley). This suggests that there was a small core area within the Fertile Crescent, near the upper reaches of the Tigris and Euphrates rivers in present-day SE Turkey and N Syria that formed the so called *Cradle of Agriculture*, and sometimes also labeled as the area of the *Dawn of Modern Civilization*, in reference to the reverberations that this first development of agriculture would have on the subsequent history of the world.

### The origin & dispersal of domestic livestock species in the Fertile Crescent

When we come to look at domestication of livestock, we can see similar geotemporal patterns for the four major Near East livestock species, sheep, goats, cattle and pigs. Domestication followed a prolonged period of human interaction with the ancestors of these livestock species that unfolded across a broad area of the Fertile Crescent. Over time hunting strategies aimed at maximizing local availability of wild ungulates developed into active management with all four species coming under management c.11,000-10,000 BP in an area centred on SE Anatolia. The geographical and temporal congruence with crop plant domestication in the core Fertile Crescent is striking.

### The Evolution of Agriculture in the Fertile Crescent

So, we can see clear evidence for the first domestications of crops and livestock 11,000-10,000 BP in the upper Euphrates and the subsequent establishment and initial spread of farming during the early Holocene across a wider region spanning the full Fertile Crescent, parts of central and western Turkey and the Nile Valley in Egypt over the subsequent three millennia. Fully fledged agricultural economies reliant on a mix of domesticated crops and livestock apparently do not fully crystallize in the region until c.9,500-9,000 BP.

### Post-8,000BP agricultural expansion from the Fertile Crescent across the Mediterranean and Europe

The post-8,000BP era marks a rich period of rapid agricultural expansion, intensification and innovation. Pottery was developed; irrigation allowed intensification of arable farming; new varieties of wheat and barley were selected; larger villages and small towns sprung up and by 6,000BP metal working had developed and settlements of c.4,000 inhabitants, with more complex social stratification, beaurocracy, writing and empires emerged. During this period, farming also spread and expanded across Europe, initially across the Mediterranean, reaching Iberia before 7,000BP and north into central and western Europe by 6,000BP, all based on the Fertile Crescent farming package of cereals, pulses and livestock, via the transfer of knowledge and the trading of seed as much as via migration or conquest. The exact mix of colonization, diffusion and possible independent domestication that underpins the mechanisms of this expansion, is undoubtedly complex and hard to discern, perhaps involving colonist farming enclaves initially restricted to coastal areas around the Mediterranean, and subsequent diffusion inland. Evidence suggests transport of the entire Fertile Crescent crop / livestock package, albeit with the possible exception of pigs for which there is evidence for independent domestication from European wild boar.

### The Evolution of Agriculture in the Fertile Crescent

A series of continuous human activities have led to an equally continuous series of changes to crop plants. The human activities began with a variety of human interventions in the growth of wild plants, probably beginning over 13 000 cal BP and. These interventions prompted the gradual emergence of domestication traits in the crop plants, the first indications of these traits being seen in the archaeobotanical record around 12 500 cal BP. Eventual fixation of the domestication syndrome by ∼9000 cal BP enabled agriculture to spread beyond its area of origin to other parts of southwest Asia and throughout Europe, north Africa and south-central regions of Asia and. The spread of agriculture exposed crops to new environments to which they adapted by further evolutionary change, an example being the alteration in flowering time that enables barley to undergo a longer period of growth and resource storage before setting seed during the cool, wet summers of northern Europe. The nutritional and culinary properties of locally adapted landraces also underwent change as agriculture gradually intensified, ancient DNA analysis suggesting that glutenin alleles associated with good breadmaking were present in wheat being grown during the Greek Bronze Age at 3000 cal BP. The series of human activities continues today with the application of directed breeding programmes which have resulted in the elite varieties of cereals that support our modern society.

### Mesoamerica I - *Phaseolus vulgaris* domestication

26 microsatellite markers in a representative sample of 155 wild and domesticated common bean accessions from its Mesoamerican gene pool showed: (i) monophyly of most domesticated accessions from Mesoamerica, suggesting a single origin; (ii) the most closely related wild beans to the domesticated clade originated from a restricted region in the Rio Lerma – Rio Grande de Santiago basin in west-central Mexico, suggesting that beans were domesticated in a region separate from Maize and that they were only later united in a single cropping system.

### Mesoamerica II

We saw earlier in the course the detailed study of maize domestication from the Balsas Depression, and the remarkable precision that has been achieved to ascertain where, when and from what progenitors maize was first domesticated in southern Mexico. Maize was the pre-eminent cereal in the New World and widely grown in North and South America when Europeans arrived in the New World. Other mainstream Mesoamerican crops include the common bean, *Phaseolus vulgaris* and squash, *Cucurbita pepo*. Much bigger gaps between genetic and archaeological data for these two crops. Beans – closest wild relatives from western Mexico, but earliest remains from >700km away in Tehuacan 2,300BP. Squash – wild progenitor remains unknown, very early remains from 10,000BP Guila Naquitz.

### Mesoamerica III

Much still to do both to find and map wild relatives and expand archaeological sampling. In fact, most of what is known comes from a handful of caves from 3 localities – Tamaulipas, Tehuacan and Guila Naquitz. However, even with this sparse 3-crop geo-temporal matrix we can still infer some interesting trends:

- maize and squash first in S, then moving sequentially N
- beans first in W, simultaneously appearing later in N and S
- Different rates of diffusion – maize fastest
- Different crops appear at different times

Tentative scenario:

- squash 10,000 – domesticated by hunter-gatherer groups
- maize 7,000 – domesticated by low-level food producing societies already growing squash for > 1,000 years – the *Era of Incipient Cultivation*
- 4,000 – first appearance of village-based farming societies
- Beans – 2,500 – added into already well-established farming economies

Again, we can see that the overall pattern is one of gradual, rather than instantaneous development of agriculture, and of a diffuse rather than a single geographic origin.

China

Although China includes clearly one, and possibly two of the independent original centres of intensive agriculture, until recently, much less was known about its origin and development compared to the Fertile Crescent. What is known suggests:

- Modern humans arrived in central Asia c.50,000 BP as hunter gatherers, ebbing and flowing as ice came and went in certain areas.
- Farming based mainly on millet (Setaria italica and Panicum miliaceum) emerged independently in at least two areas of north China within a few millennia of wheat-based farming in the Near East. Initial domestication of millet c. 6,000 BP and widely farmed across much of the Yellow River basin (grey area on map) by 5,000 BP. Rice from further south was added to farming in this area as late as 3,000 BP
- Further south in the warmer and damper climates of the Yangtse basin wetlands, rice cultivation probably started around 5,400 BP

Representative early rice finds in China

Earliest fully domesticated rice comes from 3,000-4,000BP in bays south of the lower Yangtze estuary, and notably from a small number of archaeological sites including Tianluoshan, with subsequent spread north and west into the Yellow River basin.

Tianluoshan I

- Discovered and excavated from 2004 onwards
- Impressive waterlogged preservation of abundant plant remains, spanning the tipping point at which non-shattering rice spikelets become more frequent than shattering ones, i.e. the transition from foraging to a mix of foraging and farming and farming including domesticated rice, i.e. the shift from low intensity rice cultivation to more modern paddy field systems.
- This site is characterized by numerous waterlogged posts forming remains of settlements, and is now protected under a dome-shaped roof as an open-air museum.
- These photos also show the location of this site at the edge of coastal plains which formed extensive wetlands and marshy meadows, next to hilly country where warm temperate broadleaved woodlands dominated by oak prevailed.

Tianluoshan II - Water Chestnut, Acorns and Fox Nuts

At the start of this period, around 6,900BP there was heavy reliance on wild gathered resources and notably aquatic nuts, acorns and fish. These included:

- The water caltrop, water chestnut, buffalo nut, species: *Trapa natans* and *T. bicornis* are floating annuals growing in slow-moving water up to 5 meters deep. They bear ornately shaped fruits, which in the case of *T. bicornis* resemble the head of a bull, each fruit containing a single very large starchy seed.
- Fox nut - *Euryale ferox* in the water lily family, Nymphaeaceae, is another aquatic annual that produces starchy white edible seeds which may be eaten raw or cooked.
- Acorns (Quercus spp), which just as in Europe were widely harvested and eaten.
- Deer, wild boar and fish widely hunted
- Rice also favours wetland areas

Thus Trapa, Euryale, rice, and fish go easily together. This all suggests an extensive resource base spanning both the wetlands and surrounding hills. Estimates suggest a catchment area of 4-6 hours walk for staple foods and up to 12 hours for all wild food gathering, which is much greater than the 1-3km radius typical for early agriculturalists in other areas.

Tianluoshan III

Here we can see the shift in nearly complete reliance on wild gathered resources to an increasing proportion of rice in the plant assemblage as a whole with an implied decline in the consumption of aquatic nuts and acorns, across a 300 year period spanning the start of agriculture, prior to full domestication of rice.

## Tianluoshan IV

Expanding this to include with wider context of rice domestication indicators, we can see even more clearly these quantitative trends in rice grain size and away from wild wetland foods. As in the Fertile Crescent in the Near East, early Chinese farmers of East Asia gradually shifted from growing semi-domesticates to fully domesticated crops.

## Evolution of Agriculture – Conclusions

Sometimes crop domestication and the origins of agriculture have been dubbed the *Neolithic Revolution*, but in fact, now clearer that the transition from foraging to farming was a much more gradual, protracted and complex *evolutionary* process – spanning several millennia rather than a few centuries, even if the impacts and outcomes of that process were indeed *revolutionary*.

Episodes of domestication were protracted processes in which human practices, local ecologies and plant adaptations became entangled.

Some of the simple underlying genetic changes associated with domestication might suggest sudden, almost instantaneous domestication. However, we know that fixation of some of these alleles took much longer from data that document the frequency of non-shattering, domesticated forms of barley, wheat and rice in the archaeological record. For example, fixation of non-shattering rachises in wheat and barley took about 2,000 years with non-shattering forms increasing at a rate of 0.03-0.04% per year. For rice, fixation of non-shattering was surprisingly late in China, with only around 50% of the rice from the lower Yangtze having non-shattering rachises as late as 7,500-6,500 years.

Data from all three regions – the Fertile Crescent, Mesoamerica, and China indicate that:
- early active resource management / ecosystem engineering aimed at encouraging plant production and manipulation of herd structure to promote a secure and predictable yield of animal products preceding any manifestation of traditional markers of domestication by 100s if not 1000s of years.
- initial domestication and the gradual emergence of domestication traits followed by a long period of low-level food production with continued hunting and gathering, suggestive of a continuum between wild and domesticated, between foraging and farming, between hunting and herding.
- cultivation that included a mix of wild and domesticated species with wild varieties only gradually replaced by domesticated species
- wild and domesticated plants frequently intermixed with opportunities for geneflow
- initial domesticates still not like modern ones; domestication as a process of gradual frequency change, with an earlier, more rapid semi-domestication, and a later, slower fixation of full domestication.
- crops added sequentially over several millennia, not all at once.
- even today, although we are overwhelmingly dependent on farming domesticated crops and livestock, the transition from hunting and gathering to farming is not 100% complete. Even in some of the most agriculturally intensive parts of the world, foraging for berries, nuts, and fungi, and hunting and trapping of animals still continue today.

Domestication was a more protracted and complex process than had been thought and the transition to agriculture was a more protracted and long drawn out process that spanned multiple episodes.

The evolutionary model of the transition from foraging to farming is a model of co-evolution between plants and people.

# Bio235 – Lecture 8 – Revolution vs Evolution: The tempo of domestication and evolution of agriculture – Source Materials

Balter, M. 2007. Seeking agriculture's ancient roots. *Science* **316**: 1830-1835.

Balter, M. 2009. Recipe for rice domestication required millennia. *Science* **323**: 1550.

Brown, T.A., Jones, M.K., Powell, W. & Allaby, R.G. 2008. The complex origins of domesticated crops in the Fertile Crescent. *Trends in Ecology & Evolution* **24**: 103-109.

Burger, J.C., Holt, J.M. & Ellstrand, N.C. 2017. Rapid phenotypic divergence of feral rye from domesticated cereal rye. *Weed Science* **55**: 204-211.

Doebley, J. 2004. The genetics of maize evolution. *Annual Review of Genetics* **38**: 37-59.

Doebley, J.F., Gaut, B.S. & Smith, B.D. 2006. The molecular genetics of crop domestication. *Cell* **127**: 1309-1321.

Fuller, D.Q. 2007. Contrasting patterns in crop domestication and domestication rates: recent archaeological insights from the Old World. *Annals of Botany* **100**: 903-924.

Fuller, D.Q. et al. 2009. The domestication process and domestication rate in rice: spikelet bases from the lower Yangtze. *Science* **323**: 1607-1609.

Fuller, D.Q. & Qin L. 2010. Declining oaks, increasing artistry, and cultivating rice: the environmental and social context of the emergence of farming in the lower Yangtze region. *Environmental Archaeology* **15**: 139-159.

Fuller, D.Q., Allaby, R.G. & Stevens, C. 2010. Domestication as innovation: the entanglement of techniques, technology and chance in domestication of cereal crops. *World Archaeology* **42**: 13-28.

Fuller, D.Q., Denham, T., Arroyo-Kalin, M. Lucas, L., Stevens, C.J. Qin, L., Allaby, R.G. & Purugganan, M.D. 2014. Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record. *Proceedings of the National Academy of Sciences, U.S.A.* **111**: 6147-6152.

Hillman, G.C. & Davies, M.S. 1990. Measured domestication rates in wild wheats and barley under primitive cultivation, and their archaeological implications. *Journal of World Prehistory* **4**: 157-222.

Jaenicke-Després, V., Buckler, E.S., Smith, B.D., Gilbert, M.T., Cooper, A., Doebley, J. & Pääbo, S. 2003. Early allelic selection in maize as revealed by ancient DNA. *Science* **302**: 1206-1208.

Jin, J. et al. 2008. Genetic control of rice plant architecture under domestication. *Nature Genetics* **40**: 1365-1369.

Jones, M.K. & Liu, X. 2009. Origins of agriculture in East Asia. *Science* **324**: 730-731.

Kwak, M., Kami, J.A. & Gepts, P. 2009. The putative Mesoamerican domestication center of *Phaseolus vulgaris* is located in the Lerma-Santiago basin of Mexico. *Crop Science* **49**: 554-563.

Lev-Yadun, S., Gopher, A. & Abbo, S. 2000. The cradle of agriculture. *Science* **288**: 1602-1603.

Li, C., Zhou, A. & Sang, T. 2006. Rice domestication by reducing shattering. *Science* **311**: 1936-1939.

Murphy, D.J. 2007. *People, Plants and Genes. The Story of Crops and Humanity.* Oxford Univ. Press.

Purugganan, M.D. & Fuller, D.Q. 2009. The nature of selection during plant domestication. *Nature* **457**: 843-848.

Purugganan, M.D. & Fuller, D.Q. 2010. Archaeological data reveal slow rates of evolution during plant domestication. *Evolution* **65**: 171-183.

Smith, B.D. 2001. Documenting plant domestication: the consilience of biological and archaeological approaches. *Proceedings National Academy of Sciences* **98**: 1324-1326.

Tan, L. et al. 2008. Control of a key transition from prostrate to erect growth in rice domestication. *Nature Genetics* **40**: 1360-1364.

Tanksley, S.D. 2004. The genetic, developmental, and molecular bases of fruit size and shape variation in tomato. *The Plant Cell* **16**: S181-S189.

Thurber, C.A., Reagon, M., Gross, B.L., Olsen, K.M., Jia, Y. & Caicedo, A.L. 2010. Molecular evolution of shattering loci in U.S. weedy rice. *Molecular Ecology* **19**: 3271-3284.

Wang, R.L., Stec, A., Hey, J., Lukens, L. & Doebley, J. 1999. The limits of selection during maize domestication. *Nature* **398**: 236-239.

Zeder, M.A. 2008. Domestication and early agriculture in the Mediterranean Basin: origins, diffusion and impact. *Proceedings National Academy of Sciences* **105**: 11597-11604.

Zhang, L., Dai, W., Wu, C., Song, X. & Qiang, S. 2012. Genetic diversity and origin of Japonica and Indica-like rice biotypes of weedy rice in the Guangdong and Liaoning provinces of China. *Genetic Resources & Crop Evolution* **59**: 399-410.

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## BIO235 People & Plants – Evolution & Domestication of Crops
## Lecture 9 - Cattle, pigs & goats – similarities and differences between crop and livestock domestication

### Introduction

If we are going to understand the origins of agriculture, we need to also think about domestication of animals as well as plants. This lecture aims to do that by providing an overview of the domestication of livestock. The aim is to look for similarities and differences between crop and livestock domestication across some of the areas we have been looking at for crop plants, namely:

- The dog – the earliest animal domesticate
- Centres of agricultural origins and livestock domestication
- Diversity of domestic livestock
- Domestication syndrome of livestock – herd-living herbivores
- Morphological markers of domestication
- Where, when, how many times and from what progenitors were domestic livestock domesticated?
- The Fertile Crescent
- Goats, pigs, cats, chickens & donkeys
- Complex origins of domestication of livestock
- Hybrids & polyploids
- Diversification after domestication
- Conclusions

### How many species of animals have been domesticated? Diversity of Livestock species

We saw in the course assignment that only a rather small fraction of flowering plants have been domesticated. For animals the fraction and the absolute number of domesticated species is even smaller. If you were to tally up how many species of animals you had eaten during a week, the task would be much smaller than for plants – beef, pork, lamb, chicken would be the main ones, plus possibly turkey, duck, goat, and horse, maybe 3-4 species, 8 at the most for truly dedicated carnivores perhaps. In total there are only around 35 species of domestic animals.

### Domestication of the Dog

The dog is thought to have been the first animal to be domesticated. There is no doubt that dogs have been selected to be compatible with humans and that selection has worked in terms of dogs being adapted to their role as human companions, developing sophisticated social skills not seen in most domesticated livestock. There are few if any other animals that form such close relationships with humans – Man's best friend. It is also the only animal that accompanied humans to every continent in ancient times and therefore has a central place in human history.

There has been a lot of controversy surrounding and interest in the where, when, how many times and from what progenitor questions for the dog. Generally accepted that dogs evolved from wolves, but doubts about where and how many times with suggestions that an origin from several different wolf populations could help to explain the extreme morphological variation among dog breeds.

There are also doubts about how the wolf was domesticated to become the dog – was it that early humans raised wolf puppies and tamed wolves as pets, selecting for ever more docile animals? Or was it that wolves became less fearful of humans as they adapted to scavenging food from them, such that wolves born with greater boldness around humans thrived, eventually parting company with their more wary wild companions. This is referred to as the commensal domestication pathway (below).

Recent studies, based on analyses of mtDNA sequences (Savolainen et al., 2002; Leonard et al., 2002; Pang et al., 2009) suggest: The current consensus suggests that:

- It is clear that dogs were domesticated from wolves, *Canis lupus*
- Interpretation of the archaeological record is problematic because of the difficulties in distinguishing between small wolves and domestic dogs. The earliest firm archaeological evidence for domesticated dogs comes from an assemblage of canids from c 12,000 BP from Israel, suggesting an origin in SW Asia and the Fertile Crescent, with subsequent evidence from 10,000 in Europe, 8,100 in N. America and 7,100 in China. However, there are also particular similarities between dogs and wolves from China.
- In the mtDNA analysis [coy=coyote; dog=unlabelled; wolf=filled square], wolf sequences are interspersed with dog sequences across 6 clades, suggesting possible multiple independent origins in different parts of Eurasia, but wolves are extremely mobile and there is very little mtDNA variation among wolves upon which to base firm conclusions.
- The sharing of haplotypes across clades A, B and C [14 universally occurring haplotypes indicated by bold outlines; blue=haplotypes shared with other regions; orange=haplotypes unique to regions] suggests a common origin (or very effective gene flow). Furthermore, the lack of any obvious correlation between dog breeds and these clades suggests that the extreme morphological variation does not relate to different wolf origins.
- The genetic data are thus extremely complex, complicated by subsequent post-domestication geneflow between wolves and commensal dogs and human transport, making it difficult to come up with a definitive origin.
- Hapoltype frequencies are greatest in East Asia and decline progressively northwards and westwards. The current consensus is for a common origin from a single gene pool, involving multiple maternal wolf lines, in East Asia, 15,000-16,000BP.
- American dogs originated from multiple Old World lineages of dogs that accompanied Pleistocene humans across the Bering Strait.

### Village dogs & domestication

Pictured is a village dog in Tengboche, Nepal. Village dogs are members of free-breeding populations adapted to living amongst humans, and their genetic and geographic diversity makes them useful for tracing the evolutionary history of domestic dogs. Shannon et al. (2015) analyzed genomic data from more than 5,000 dogs, including more than 500 village dogs from 38 countries, and found that dog populations in the Neotropics and South Pacific were almost completely derived from European dogs, whereas dogs from East Asia, India, and Southwest Asia showed minimal evidence of European interbreeding. The global patterns of genetic diversity in village dogs suggest a Central Asian origin for dog domestication.

### Dog Diversification after Domestication

Although domestication happened c 15,000 BP, the spectacular phenotypic diversity exhibited among breeds is thought to have originated much more recently, largely through artificial selection and strict breeding practices to perpetuate desired characteristics. Thus, the canine genome, shaped by centuries of strong selection, likely contains many important lessons about the genetic architecture of phenotypic variation and the basis of short-term evolution. A genome-wide scan for selection in 275 dogs from 10 diverse breeds identified 155 genomic regions that possess strong signatures of recent selection and contain candidate genes for size, coat colour and texture, behaviour, skeletal morphology & physiology. A first-generation map of selection in the dog and a framework for understanding the mechanistic basis of how artificial selection promotes rapid and pronounced phenotypic evolution

### Studies of crop and animal domestication show some obvious similarities

Even just thinking about the domestication of the dog, we can immediately see some obvious similarities between crop and livestock domestication:

- Similar techniques have been used (ancient DNA, AMS radiocarbon dating), and the same weighing up of complementary evidence from genetics and archaeology, to answer the when, where and how many times questions.
- The earliest plant domesticate, the bottle gourd, like the dog was not used for food, but rather to support hunting and gathering activities – a container plant to carry water and a hunting companion / sentry were the first organisms to be domesticated by humans. Both were apparently domesticated in the Old World and taken very early on to the New World by humans.
- Selection and massive diversification after domestication – divergent behaviours for different uses, divergent morphologies – all the different dog breeds that we are familiar with today from Great St. Bernard's to poodles, Great Danes to Chihuahuas, wolfhounds, terriers, greyhounds & Mexican hairless dogs – who would guess them all to belong to the same species?
- Genomic data are revealing the genetic architecture of phenotypic diversity and the genes associated with phenotypic change brought about by domestication.

## Markers of Animal Domestication

The comparative lack and subtlety of morphological changes associated with animal domestication creates special challenges to finding markers of animal domestication. Here we can see some examples of the rather modest and subtle changes thought to be associated with animal domestication:

- Horns of goats
- Toe bones of cattle are smaller. In fact there is a general idea that domesticated livestock tend to be smaller than their wild ancestors, but this is often misleading
- Teeth in domesticated pigs are shorter and fewer than in their wild boar ancestors

Other markers, such as overall size and bone micro-structure, once thought to be useful, have since proven to be misleading. This means that other more sophisticated and complex markers need to be used, based on patterns of change in large assemblages of bones, representing whole herds or flocks assessed through time to look for herd age profiles or sex ratios indicative of increasing captivity and human control of breeding. For example, infections caused by corralling alpacca at night lead to higher juvenile mortality.

## Animal Domestication syndromes

Plants generally show marked morphological changes associated with domestication. However, for animals, morphological changes are often much more subtle, because the central selection pressures and changes on animals undergoing domestication are behavioural (elements affecting mood, emotion, agnostic and affiliative behaviour, social communications), and sometimes physiological, rather than morphological.

Behavioural predisposition:

Tolerance of proximity to and lack of fear of people – a prerequisite for domestication. Domestic animals are selected to be less aggressive and tamer – biddable by humans.

- Tolerance of penning and close living quarters
- Social structure based on dominance hierarchies
- Sexual precocity, freely breeding in the presence of people
- Weak alarm systems
- Reduced awareness and aggression

Selection has led to:

- General reduction in responsiveness to environmental stimuli
- Reduced activity levels
- Increased social compatability

- Intensified sexual behavior

Domestication syndrome of animals

Morphological traits shared across unrelated domestic animals – phenotypic convergence

- Variations on coat colour and texture
- Docility
- Shifts in reproductive timing
- Alterations in skull shape and tooth crowding
- Dwarf and giant varieties
- Floppy ears

Similar debate about the relative importance of deliberate intentional domestication vs unconscious / unintentional domestication.

Domestication syndrome of animals

This syndrome is shared across many different domesticated animals, suggesting some underlying genetic cause linking all these traits, such that artificial selection on a trait like docility influences the whole suite of domesticated traits.

Experimental domestication of the silver fox

As we saw with the experimental domestication of einkorn wheat by George Hillman, similar experiments have been carried out to experimentally domesticate animals. The most famous one carried out by Dmitry Belyaev, a Russian animal breeder, which started in the 1950s. He domesticated the silver fox, Vulpes vulpes in a massive experiment involving 10,500 individual foxes as parents and c.50,000 offsrping. At the start of the experiment, nearly all of the foxes showed typical aggressive behaviour of wild foxes when approached by humans to feed them. Selecting the <10% least aggressive / fearful / most docile animals each generation over many decades, Belyaev was able to domesticate the fox. Very quickly aggressive behaviour was reduced and almost eliminated after just 3 generations. After 8 generations of selection for docility patterns coats, floppy ears and curly tails began to appear and after >30 generations the entire group was fully domesticated, showing the full domestication syndrome phenotype. In other words, Belyaev showed that the full suite of traits constituting the domestication syndrome can arise relatively quickly under selection for tameness alone in a species having no prior history of domestication. This strongly suggests that this is indeed a package (syndrome) of traits that develop semi-concurrently, rather than an assemblage of independently or sequentially acquired ones…

The Neural Crest and animal domestication

This apparently tightly linked set of domestication traits demands an explanation. This has recently been provided by Richard Wrangham and colleagues who suggested that the link is that all these traits share a common step in embryonic development in that all these traits depend on the supply of cells from a single source, the neural crest which runs along the spine of animals and contains stem cells that supply material for construction of the brain, the adrenal glands, skin pigments and other cells. Because the adrenal glands are what controls aggression, this is controlled by the number of cells in the neural crest. Selection for tameness effectively selects for fewer cells in the neural crest, such that > docile animals inherit a deficiency in the number of neural crest cells which links to all these other domestication traits, as by-products of the main target of selection for docile behavior.

Animal domestication pathways

1. Commensal – no intentional action by humans; wild animals attracted to elements of the human niche (food waste, smaller prey animals); habituation leading to adaptations and divergence of tamer, less aggressive individuals and populations / ecotypes, i.e.

commensalism and partnership – a reciprocal co-evolutionary relationship between humans and animals which provided the foundation for domestication and eventually captivity, human-controlled breeding, and later deliberate human selection. Dog, cat, pigeon, guinea pig, possibly pigs & chickens all probably followed this pathway. So we can imagine one or more wolf populations diverged into ecotypes suited to the human niches created by hunter-gatherers. Even with occasional interbreeding this ecotype could have adapted, diverged and maintained its genetic integrity despite significant geneflow, leading eventually to domestication of the dog – a classical commensal domesticate.

2. Prey – under this scenario the primary human motive was not domestication but altered hunting strategies to increase the efficiency of hunting large herbivores targeted as prey (e.g. killing young males and allowing females to produce > offspring) and herd management (perhaps driven by over-hunting) to maximise the availability of prey. Archaeological data on size, sex-ratios and mortaility profiles show changes in management strategies of herded sheep, goats, pigs and cows in the Fertile Crescent starting in the early Holocene ca. 11-10kyr. This would have led to divergence of more docile herded populations; eventually domestication and direct breeding. Sheep, goat, cow, reindeer, llama, alpacca & turkey.

Under both these scenarios animal domestication was brought about by the unintentional entanglement of humans and animals that were evolving in response to human innovations, and mirrors what happened with plant domestication. As human interference in the lives of animals intensified, the evolutionary pressures for a lack of aggression would have led to acquisition of the same domestication syndrome traits found in both prey and commensal domestication pathways despite having entered the human niche through completely separate trajectories.

3. Directed – deliberate objective to domesticate; only after humans were already reliant on domestic plants and animals; often in regions outside those where early animal domestication started, and often aimed at more efficient transport / traction that were needed with the expansion of trade and agriculture into new areas. Donkey, horse, Eurasian camels, honey bee, silk worm, rabbit, geese

Herd-living herbivores

The most important of today's domestic livestock began as animals that were already hunted for food before domestication. The successful domesticates were those most behaviourally pre-adapted to domestication – generally herd-living herbivores whose ancestors followed a dominant individual through territory shared with other herds. Neolithic peoples exploited this dominance hierarchy by, in effect, supplanting the alpha individual and thereby gaining control of the herd.

Usually these behavioural changes lead to a significant dependence on humans for food and shelter. However, domestication should not be confused or conflated with taming. Taming is conditioned behavioural modification of an individual; domestication is a permanent genetic modification of a bred lineage that leads to a heritable predisposition toward human association. Domestic animals need not be 'tame' in the behavioural sense (e.g. Spanish bull fighting) and , conversely, wild animals can be quite tame (e.g. a hand-raised cheetah or tiger). A domestic animal is one whose mate choice is influenced by humans and whose tameness and tolerance of humans is genetically determined, Controlled breeding amounts to pre-zygotic selection, a critical element in domestication because captive breeding allows for the strongest and most direct artificial selection.

Why were so few wild species domesticated?

There are 148 species of large terrestrial mammalian herbivores and omnivores weighing > 45kg, yet only 14 of these were actually domesticated. This raises the question as to why were so few wild species domesticated and especially why was it that close relatives of our farm animals were not domesticated? For example why were horses and donkeys domesticated while zebras were not. Other comparisons of domesticated species and their never-domesticated close relatives are equally intriguing. There is abundant evidence to suggest that the obstacles to domestication lie with the animal species themselves:

- Eurasian domesticates were very rapidly accepted in other parts of the world
- Rapid and more or less simultaneous domestication of the most valuable species
- The failure of even modern European animal breeders to add significantly to this short list
- Many highly valued species that were never domesticated
- Subtle, but often potent reasons. For example, European horse breeders who tried to domesticate the zebra found that it is an incurably vicious animal with a habit of biting handlers and not letting go until the handler is dead. Zebras also have much better peripheral vision than horses making them impossible even for professional rodeo cowboys to lasso.

Specific obstacles to animal domestication:

- Diet not easily supplied by humans, e.g. anteater
- Slow growth rates and long birth spacing, e.g. elephants, gorillas
- Nasty disposition, e.g. grizzly bears, rhinoceroses
- Reluctance to breed in captivity, e.g. pandas, cheetahs
- Lack of follow-the-leader dominance hierarchies, e.g. bighorn sheep and antelope
- Tendency to panic in enclosures, e.g. deer and gazelles

## Selection

Like plants, many animals had early commensal relationships to humans having begun their associations with humans as camp-follower scavengers. Artificial selection has both weak and a strong form. In weak artificial selection, selection pressure is applied postzygotically (e.g. selectively culling a herd of deer) and natural selection proceeds from this modified genetic baseline. In strong artificial selection, selection is prezygotic, as well as post-zygotic (e.g. mating male offspring of high yielding dairy cows to high yielding cows). This will result in a dramatic acceleration of evolutionary processes and entailing a much greater level of control over the selected organism.

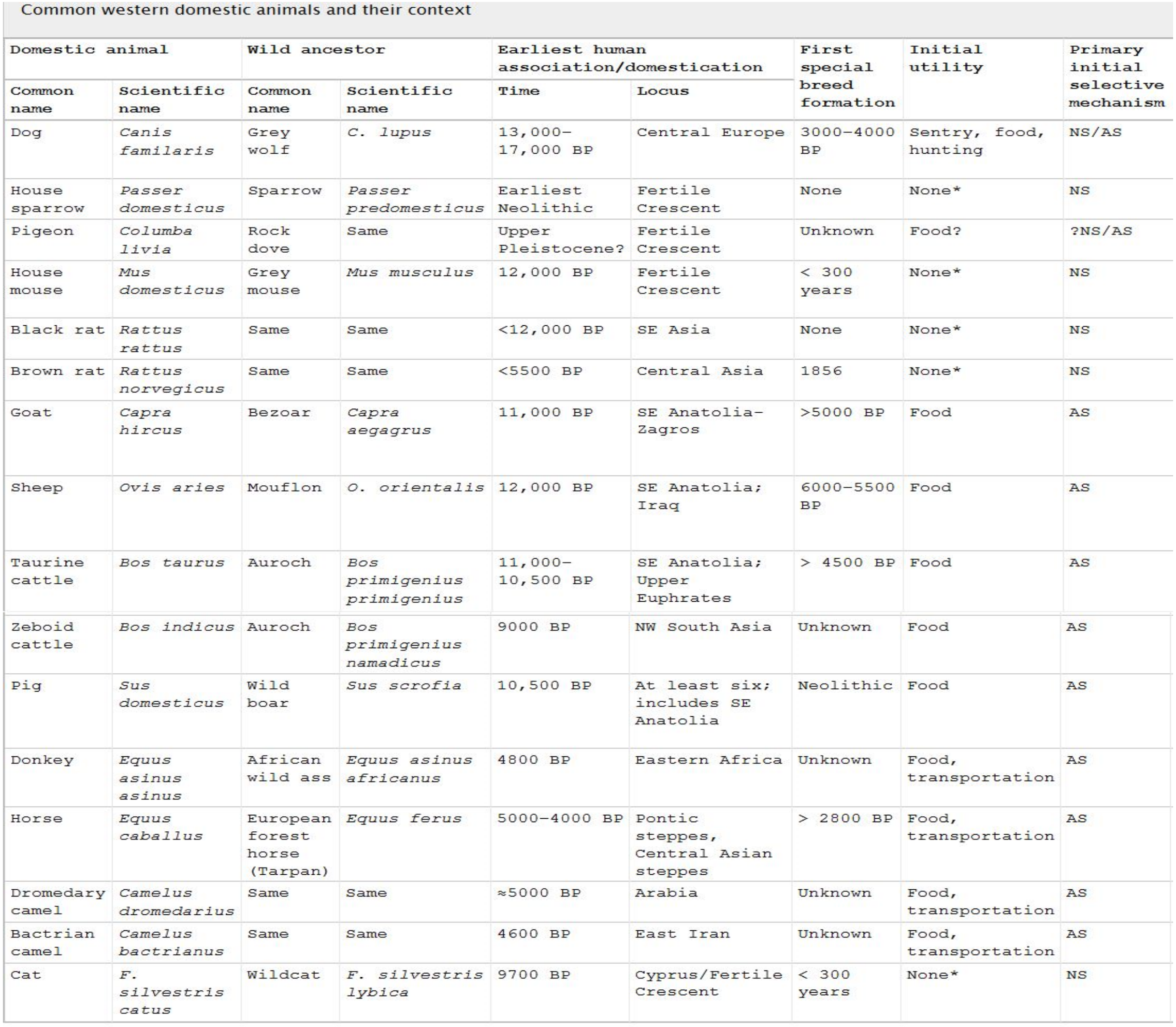
## Independent centres of Agriculture & livestock domestic origins

Here we can see a selection of the important animal domesticates or farm animals and the broad areas where they are thought to have originated in relation to the centres of crop domestication and regions where agriculture is thought to have arisen independently. We can see:

- Overall few species of animals have been domesticated.
- Most originate in Eurasia with at least one origin of domestication in the Fertile Crescent – these include the four most important farm animals the cow, pig, sheep and goat.
- Very few animals were domesticated in the New World – just the two camelids the alpaca and llama plus the guinea pig in the Andes, and the turkey in North America.
- The chicken and dog are two of the most important east Asian animal domesticates.
- Several areas where agriculture is thought to have arisen independently that lack domesticated livestock – eastern North America, New Guinea
- Several areas that have domesticated livestock where there was no independent origin of agriculture – Lapland, the Himalaya.

## Draught animal power and the origins of agriculture

Although the primary use of domesticated livestock today is for food, in historical and pre-historical times, equally or potentially even more important would have been use of animals as a source of draught power for land clearance, ploughing, harvesting, threshing and transport. Without animal power, and with sole reliance on human power, agricultural development would undoubtedly have been limited. For example in the highlands of New Guinea, which lacked domesticated livestock of any kind, agriculture never progressed beyond basic, relatively small scale crop subsistence, and was still functioning in that same primitive fashion 50 years ago, when these indigenous agriculturalists were first encountered by outsiders.



Common western domestic animals and their context

| Domestic animal | | Wild ancestor | | Earliest human association/domestication | | First special breed formation | Initial utility | Primary initial selective mechanism |
|---|---|---|---|---|---|---|---|---|
| Common name | Scientific name | Common name | Scientific name | Time | Locus | | | |
| Dog | *Canis familaris* | Grey wolf | *C. lupus* | 13,000–17,000 BP | Central Europe | 3000–4000 BP | Sentry, food, hunting | NS/AS |
| House sparrow | *Passer domesticus* | Sparrow | *Passer predomesticus* | Earliest Neolithic | Fertile Crescent | None | None* | NS |
| Pigeon | *Columba livia* | Rock dove | Same | Upper Pleistocene? | Fertile Crescent | Unknown | Food? | ?NS/AS |
| House mouse | *Mus domesticus* | Grey mouse | *Mus musculus* | 12,000 BP | Fertile Crescent | < 300 years | None* | NS |
| Black rat | *Rattus rattus* | Same | Same | <12,000 BP | SE Asia | None | None* | NS |
| Brown rat | *Rattus norvegicus* | Same | Same | <5500 BP | Central Asia | 1856 | None* | NS |
| Goat | *Capra hircus* | Bezoar | *Capra aegagrus* | 11,000 BP | SE Anatolia–Zagros | >5000 BP | Food | AS |
| Sheep | *Ovis aries* | Mouflon | *O. orientalis* | 12,000 BP | SE Anatolia; Iraq | 6000–5500 BP | Food | AS |
| Taurine cattle | *Bos taurus* | Auroch | *Bos primigenius primigenius* | 11,000–10,500 BP | SE Anatolia; Upper Euphrates | > 4500 BP | Food | AS |
| Zeboid cattle | *Bos indicus* | Auroch | *Bos primigenius namadicus* | 9000 BP | NW South Asia | Unknown | Food | AS |
| Pig | *Sus domesticus* | Wild boar | *Sus scrofia* | 10,500 BP | At least six; includes SE Anatolia | Neolithic | Food | AS |
| Donkey | *Equus asinus asinus* | African wild ass | *Equus asinus africanus* | 4800 BP | Eastern Africa | Unknown | Food, transportation | AS |
| Horse | *Equus caballus* | European forest horse (Tarpan) | *Equus ferus* | 5000–4000 BP | Pontic steppes, Central Asian steppes | > 2800 BP | Food, transportation | AS |
| Dromedary camel | *Camelus dromedarius* | Same | Same | ≈5000 BP | Arabia | Unknown | Food, transportation | AS |
| Bactrian camel | *Camelus bactrianus* | Same | Same | 4600 BP | East Iran | Unknown | Food, transportation | AS |
| Cat | *F. silvestris catus* | Wildcat | *F. silvestris lybica* | 9700 BP | Cyprus/Fertile Crescent | < 300 years | None* | NS |

From Driscoll et al (2009) * - these species were commensals that seized advantage of anthropogenic habitats

## Behavioural pre-adaptations for animal domestication

| Favourable | | Unfavourable |
|---|---|---|
| | Social structure | |
| Dominance hierarchy | | Territoriality |
| Large gregarious groups | | Family groups or solitary |
| Male social group affiliation | | Males in separate groups |
| Persistent groups | | Open membership |
| | Food preferences | |
| Generalist herbivores or omnivores | | Dietary specialist or carnivore |
| | Captive breeding | |
| Polygamous / promiscuous mating | | Pair bonding prior to mating |
| Males dominant over females | | Females dominant or males appease females |
| Movement or posture mating cues | | Colour or morphological mating cues |

| | | |
|---|---|---|
| Easy divestiture of young | | Difficult divestiture of young |
| High meat yield per food/time | | Low meat yield |
| | Intra- or inter-species aggressiveness | |
| Non-aggressive | | Naturally aggressive |
| Tameable / readily habituated | | Difficult to tame |
| Readily controlled | | Difficult to control |
| Solicits attention | | Avoids attention / independent |
| | Captive temperament | |
| Low sensitivity to environmental change | | High sensitivity to environmental change |
| Limited agility | | Highly agile / difficult to contain |
| Small home range | | Large home range |
| Wide environmental tolerance | | Narrow environmental tolerance |
| Non-shelter seeking | | Shelter seeking |
| Implosive herd reaction to threat | | Explosive herd reaction to threat |
| | Commensal initiative | |
| Exploits anthropic environments | | Avoids anthropic environments |

Driscoll et al (2009)

## The Fertile Crescent

So what about the central questions - Where, when, how many times and from what progenitors were livestock domesticated? Once again we will see many examples where the consilience of archaeological and genetic data and increasing data from genomics, have shed light on these questions for our main farm animals. Complicated by the fact that the wild progenitors of some domestic livestock are extinct. For example, the auroch, thought to be the ancestor of cattle; and the wild horse.

There is compelling evidence from archaeology and genetics that all four of our major livestock domesticates had origins of domestication in the Fertile Crescent, in parallel to the suite of important crops that we have discussed from that region. This concentration of both plant and animal domesticates in one region is thought to have been particularly important in the early emergence of agriculture in that region. However, as we shall see in the following examples, there are also indications that the Fertile Crescent was not the only origin of domestication for most of our farm animals.

## Domestication of the Goat I

The domestic goat, *Capra hircus*, is often known as the poor man's cow, implying a somewhat inferior animal, but in practice the goat is the most adaptable and geographically widespread livestock species ranging from Siberia across the mountains of central Asia to the deserts of Africa. Goats are a critically important resource across many developing countries and elsewhere and it is thought that there are 700 million goats worldwide providing meat, milk and skins. It is clear that the goat also played a central role in early agriculture, with extensive early archaeological remains across the Near East from 8,000 to 10,000BC as well as remains found further east in Pakistan. The origins of the goat have remained very uncertain and controversial. There seems little doubt that the goat was domesticated in the Fertile Crescent, but there have also been suggestions that the goat might also have been domesticated independently in Pakistan and that independent domestications of the goat might have involved different wild species of *Capra*, an idea in part prompted by the great diversity of goats, with more than 300 breeds and significant morphological diversity. The question as to whether this diversity arose as a result of diverse origins or as a result of diversification after domestication has remained controversial.

## Domestication of the Goat II

Analysis of mtDNA sequences of 406 goats shows there to be three divergent lineages of goats, providing possible evidence of three independent origins from different lineages, with the most closely related wild species the bezoar, *Caprus aegagrus*. However, given that these three lineages from a monophyletic group, with no intermingling of different wild goat exemplars, the alternative explanation of a single origin from one very large and diverse population remains a possibility. This is further complicated by the fact that several wild goat lineages are extinct. When we look at the geography of the three lineages of domestic goats, clade C is present only in E and S Asia (Pakistan and further east), supporting the idea of at least two independent origins, one in the Fertile Crescent and one further east.

## Domestication of the Goat III

There is little or no geographic structure amongst goat populations, indicative of extensive human mediated transport of goats in commercial trade or during migratory or exploratory movements of humans. Goats appear to have been especially mobile perhaps due to their versatility and hardiness.

## Domestication of the pig

- Wild boar were, and to some extent still are, important prey animals for hunter-gatherers across Eurasia.
- Archaeological evidence of domestic pigs from 9,000 BP in the Near East, suggesting original domestication in the Fertile Crescent, but much debate about whether one or multiple domestications. The availability of extant wild boar across the whole of Eurasia (unlike other progenitors such as the auroch, wild horse which now extinct), offers an opportunity to investigate this.
- The phylogeny of wild and domestic pigs shows strong geographic structure with the first branching lineages in SE Asia and European boar in a more recently derived clade.
- Domestic pigs are found in 6 different lineages, suggesting multiple centres of domestication across Eurasia.
- European domestic pigs are within the European cluster and lack any affinity with wild boar lineages from the Near East, suggesting independent domestication, probably at least twice within Europe

## Domestication of the cat

- Each wildcat group represents a genetically & geographically distinct subspecies.
- Wildcats are improbable candidates for domestication – obligate carnivores, solitary, defend exclusive territories (more attached to places than people), utility is debatable. Nevertheless the domestic cat is overwhelmingly tolerant of people.
- Cats were domesticated in the Near East, probably starting as a comensal feeding on rodent pests in grain stores of the first farmers coincident with agricultural village development in the Fertile Crescent c 3,600BP. Likely that tolerated and over time and space gradually diverged from their wild ancestors.
- Domestic cats derive from a single protracted domestication episode involving at least five probably sympatric founders from across this region and differ in behaviour, tameness and coat colours.
- Descendants of these first domestic cats were transported across the world by humans in some areas interbreeding with wild cats and blurring the boundaries between subspecies in some areas. Now c 1 billion domestic / feral cats on the planet – the world's most numerous pet.

## Domestication of the Chicken

Earliest chicken remains in archaeological sites c 7,400 BP from the Indus valley and Hebei Province in China. Gallus gallus domesticus is thought to have been domesticated from wild red jungle fowls

Gallus gallus, a species with several subspecies: gallus in Thailand, spadiceus in Burma and Yunnan Province in China, jabouillei in southern China and Vietnam, murghi in India and bankiva in Java.

- 542 mtDNA sequences for domesticated chickens and 38 for red jungle fowls from China and Myanmar.
- Clade H – only wild red jungle fowls
- Clade C – only domesticated chickens
- The other 7 clades include samples of both domesticated chickens and red jungle fowl
- All 7 clades include samples from Yunnan Province, China
- Domestication of chickens replicated in several places from several lineages of red jungle fowl across different areas of S & SE Asia
- Patterns potentially complicated by gene flow due to human movement and hybridization

### Arrival of the chicken in the New World

The only widespread domestic livestock that apparently didn't have its origins in the Near or Middle East. There has been some debate about when and how the chicken arrived in the New World. While the accepted wisdom has been that the chicken was introduced to the New World by the Spanish when they arrived on the east coast of South America around 1500 AD, the presence of chickens in Peru when Pizzaro arrived in 1532 and its integration into Inca culture would have required not only very rapid dispersal across the continent, but the almost immediate incorporation of chickens into the economy, a highly unlikely combination of events. Recent evidence has dated chicken bones from coastal Chile to c1400 AD. In addition ancient DNA from these bones is most similar to DNA from Polynesian chickens providing evidence that chickens were introduced to South America from Polynesia prior to the arrival of Europeans in the New World.

### Kon-Tiki and Thor Heyerdahl

***Kon-Tiki*** was the raft used by Norwegian explorer and writer Thor Heyerdahl in his 1947 expedition across the Pacific Ocean from South America to the Polynesian islands. It was named after the Inca sun god, Viracocha for whom "Kon-Tiki" was said to be an old name. Heyerdahl believed that people from South America could have settled Polynesia in pre-Columbian times, although most anthropologists now believe they did not. His aim in mounting the *Kon-Tiki* expedition was to show, by using only the materials and technologies available to those people at the time, that there were no technical reasons to prevent them from having done so. With the help of dockyard facilities provided by the Peruvian authorities, they constructed the raft out of balsa logs and other native materials in an indigenous style as recorded in illustrations by Spanish conquistadores. The trip began on April 28, 1947. Heyerdahl and five companions sailed the raft for 101 days over 6,880 km across the Pacific Ocean before smashing into a reef at in the Tuamotu Islands on August 7, 1947. The crew made successful landfall and all returned safely.

### Domestication of the donkey

The history and origins of the donkey are especially interesting because, along with the horse, the donkey (Equus asinus) has been used for transportation of people, possessions, and produce in many cultures. This domestication thus marked a shift away from sedentary, agrarian lifestyles to more extensive movement and trade. African wild asses are likely progenitors. The only ungulate domesticated in Africa. Data suggest two independent maternal origins of the domestic donkey from two distinct wild populations, one from E. asinus africanus and one from E. asinus somaliensis, both in NE Africa, but once again potentially complicated by movement and geneflow.

### Domestication of cattle

Widely accepted that cattle were domesticated twice independently from the Auroch (*Bos primigenius*), once from aurochs in the Fertile Crescent giving rise to taurine cattle (*Bos tauris*) and once in SW Asia giving rise to zebuine cattle (*Bos indicus*). Wild auroch were very large and aggressive animals, but by the 13th century they were very rare and only in eastern Europe, with the last recorded aurochs dying in Poland in 1627. There is also evidence that European aurochs contributed to modern European *Bos tauris* via sporadic interbreeding events with domestic herds grazing in the wild.

Complex Multiple Independent Origins of Domestication of Livestock

- Original view of sole Fertile Crescent origins questioned and now largely superceded by evidence for multiple independent origins of domesticated livestock
- Bicentric clade patterns for cattle, sheep, & water buffalo.
- Pig, goat & horse have even more complex patterns suggestive that Eurasian domestication was not so constrained in time and space.
- Patterns complicated by extensive human-assisted transport.
- Possibility remains that apparently genetically independent domestication events are not necessarily culturally, or even biologically independent, but are rather the result of movement of a few domestic animals into an area, with the genetic signature of the founders subsequently submerged in recruitment of local wild animals.

Hybrids & Polyploids I

Here we can see one of few examples of an artificial or man-made hybrid animal – the mule which is an F1 hybrid between a male donkey and a female horse, i.e. an interspecific hybrid between distinct species, in this case species with different chromosome numbers. As we shall see, many hybrids have reduced fertility due to problems arising from bringing together unlike genomes, even those with different numbers of chromosomes in terms of abnormal chromosome behaviour are meiosis. The mule is a good example of a hybrid that is sterile, i.e. all mules represent de novo F1 hybrids. So why should a sterile hybrid be useful? In the case of the mule, it combines useful traits of the two parent species – mules are characteristically more sure-footed, hardy and long-lived than horses, but < stubborn, faster and > intelligent than horses.

Hybrids & Polyploids II

- **Yak bovid hybrids -** The **yak**, ***Bos grunniens***, is a long-haired Himalayan domesticated bovine. In the Nepal, Tibet & Mongolia domestic cattle are crossed with yaks. This gives rise to the infertile male dzo as well as fertile females known as *dzomo* or *zhom*, which may be crossed again with cattle.
  Crosses between yaks and domestic cattle have been recorded in Chinese literature for at least 3,000 years. Crossbred females are an important source of milk and dairy products. Since males cannot be used for breeding, they are used as draught animals or are slaughtered for meat. These hybrids are very suitable for work as they are easily tamed and have better heat tolerance than pure yak.
- An experimental cross between yak and American bison is called a yakalo.
- **Limits to Hybridization** Poor reproductive performance in yak hybrids severely limits opportunties for crossbreeding. In practice, it has been found best to produce the F1 generation and then slaughter the F2 generation for meat. Since the males are sterile, only the F1 females can be backcrossed to yak or cattle bulls. However, reduced productivity (relative to the F1) makes the backcross generations commercially unattractive.

Overall, these sterility and reduced productivity problems mean that hybrids have played only a minor role in domestication compared to crops.

Common domestic animals, their contexts, timing & geography

Here we can see a global summary of domestic animals: pink=commensals; pale green=prey; yellow= directed; it also shows the timing and geographic locations of domestication.

Diversification after domestication

Spectacular morphological diversification.
Dogs: 1.5m+ high Great Danes to 10cm or less Chihuahuas; 2kg poodles to 90kg mastiffs; slender greyhounds to squat bulldogs, for a single species, dogs come in a vast array of shapes and sizes, and apparently, they all come from the same single domestication event, when wolves were taken and made into 'man's best friend, the earliest animal domesticate. Spectacular example of diversification after domestication. The same applied to other farm animals, such as sheep, where again numerous breeds have been selected for different products and environments.

## Rare breeds and erosion of livestock genetic diversity

As for traditional varieties of crops, there are many breeds of all the major livestock domesticates. Some of these are disappearing, and again, the main cause is displacement by modern highly bred breeds. It has been estimated that one breed of farm animal becomes extinct every month. Again, just as for crops, the world has both high level formal mechanisms and organizations like the CGIAR, International Livestock Research Institute, ILRI in Nairobi, Kenya, AND non-government, grassroots organizations and associations of farmers who are attempting to keep some of these rare breeds going, and example here the Rare Breeds Survival Trust in the UK and some rare / extinct breeds. For example, the Lincolnshire Curly-coated pig is now extinct, while the Jacob's and Teeswater sheep breeds are the focus of conservation efforts. These are generally being pursued in similar ways to crops, by garnering the support and participation of farmers who keep and maintain small herds or flocks of rare breeds alongside mainstream herds, just as we saw for Fructus for traditional fruit varieties in Switzerland.

## Conclusions

- Similar approaches using archaeological and genetic evidence.
- But, morphological markers of domestication are much more elusive for livestock animals than crop plants.
- Origins of domesticated livestock are much more controversial in terms of when, where and how many times, but >evidence of multiple independent domestications than for crops. In fact multiple domestications may be the norm for livestock – pigs, goats, cattle, chickens, donkeys & horses.
- Evidence of extensive movement of livestock, and especially goats across Eurasia, this complicating inferences about the origins of domestication.
- Diversity of domesticated animal species is much lower than domesticated crops – just 4 major livestock species used as food plus a few minor ones.
- Hybrids and polyploidy of very limited importance in livestock compared to their central and pivotal importance in crops.
- Diversification after domestication has been equally important for livestock and crops, and there are similar concerns about erosion of rare livestock breeds as for traditional crop varieties – several wild progenitors are known to already be extinct…..

## BIO235 – Lecture 9 – Cattle, pigs and goats – similarities and differences between crop and livestock domestication

## Source Materials

Achilli, A. et al. 2009. The multifaceted origin of taurine cattle reflected by the mitochondrial genome. *PLoS ONE* **6**: e5753.

Achilli, A. et al. 2014. Mitochondrial genomes of extinct aurochs survive in domestic cattle. *Current Biology* **18**: R157-158.

Akey, J.M. et al. 2010. Tracking the footprints of artificial selection in the dog genome. *Proceedings National Academy of Sciences* **107**: 1160-1165.

Beja-Pereira, A. et al. 2004. African origins of the domestic donkey. *Science* **304**: 1781.

Driscoll, C.A. et al. 2007. The Near Eastern origin of cat domestication. *Science* **317**: 519-523.

Driscoll, C.A., Macdonald, D.W. & O'Brien, S.J. 2009. From wild animals to domestic pets, an evolutionary view of domestication. *Proceedings National Academy of Sciences* **106**: 9971-9978.

Larson, G. et al. 2005. Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. *Science* **307**: 1618-1621.

Larson, G. & Fuller, D.Q. 2014. The evolution of animal domestication. *Annual Reviews of Ecology, Evolution & Systematics* **45**: 115-136.

Leonard, J.A. et al. 2002. Ancient DNA evidence for Old World origin of New World dogs. *Science* **298**: 1613-1616.

Liu, Y-P. et al. 2005. Multiple maternal origins of chickens: out of the Asian jungles. *Molecular Phylogenetics & Evolution* **38**: 12-19.

Luikart, G. et al. 2001. Multiple maternal origins and weak phylogeographic structure in domestic goats. *Proceedings National Academy of Sciences* **98**: 5972-5932.

MacHugh, D.E. & Bradley, D.G. 2001. Livestock genetic origins: goats buck the trend. *Proceedings National Academy of Sciences* **98**: 5382-5384.

Pang, J-F. et al. 2009. mtDNA data indicate a single origin for dogs south of the Yangtze River, less that 16,300 years ago, from numerous wolves. *Molecular Biology & Evolution* **26**: 2849-2864.

Pennisi, E. 2002. A shaggy dog story. *Science* **298**: 1540-1542.

Savolainen, P. et al. 2002. Genetic evidence for an East Asian origin of domestic dogs. *Science* **298**: 1610-1613.

Shannon, L.M. et al. 2015. Genetic structure in village dogs reveals a Central Asian domestication origin. *Proceedings National Academy of Sciences* **112**: 13639-13644.

Smith, B.D. 1998. *The Emergence of Agriculture*. Scientific American Library, New York.

Storey, A.A. et al. 2007. Radiocarbon and DNA evidence for a pre-Columbian introduction of Polynesian chickens to Chile. *Proceedings National Academy of Sciences* **104**: 10335-10339.

Trut, L., Oskina, I. & Kharlamova, A. 2009. Animal evolution during domestication: the domesticated fox as a model. *BioEssays* **31**: 349-360.

Wilkins, A.S., Wrangham, R.W. & Fitch, W.T. 2014. The domestication syndrome in mammals: a unified explanation based on neural crest cell behaviour and genetics. *Genetics* **197**: 795-808.

Zeder, M.A. 2006. Central questions in the domestication of plants and animals. *Evolutionary Anthropology* **15**: 105-117.

Zeder, M.A. 2008. Domestication and early agriculture in the Mediterranean basin: origins, diffusion and impact. *Proceedings National Academy of Sciences* **105**: 11597-11604.

Zeder, M.A. 2012. The domestication of animals. *Journal of Anthropological Research* **68**: 161-190.

Zeder, M.A., Emshwiller, E., Smith, B.D. & Bradley, D.G. 2006. Documenting domestication: the intersection of genetics and archaeology. *Trends in Genetics* **22**: 139-155.

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## BIO 235 Plants & People – Evolution & Domestication of Crops
## Lecture 10 - Genes in the Field - Crop Genetic Diversity and Conservation

### Why Does Crop Diversity Matter?

- ‘Crop diversity is a life insurance for crops (and the people who eat them)‘
- ‘The susceptibility of monocultures is the Achilles tendon of global food production‘
- ‘Crop diversity replaces boredom with delight‘
- ‘Our world would taste very different without diversity‘
- ‘Sameness leads to monotony and limits (culinary) creativity‘
- ‘The focus on diversity is a luxury‘
- ‘To monopolize diversity is hard, if not impossible‘
- ‘Why fight a war for the crop when it is best fought for itself‘
- ‘Nature can be understood as an immense pool of information with unprecedented benefits for our economy‘

### Why Does Crop Diversity Matter?

Diversity as a luxury or a necessity? Different strategies for subsistence smallholder farmers vs intensive large scale industrial agriculture? – uniformity achieved via high inputs of fertilizer / pesticide / breeding / energy

- Insurance against pests and diseases & climate change – bananas, potatoes, either directly or for future crop breeding – economic value for crop breeding
- Local adaptation, site matching, crop rotation, soil maintenance, sustainability, risk reduction
- Extend season of production (early / late ripening) in relation to markets, processing, storage
- Associated biodiversity, > diverse ecosystems = > sustainable?
- Health & nutrition
- Aesthetics – taste, shape, colour, texture, culinary richness of human experience
- Cultural as well as biological heritage of our ancestors – knowledge, history, cultural diversity, sense of place, sense of community
- Ethical responsibility, ownership issues, monopolies and control

### The Genetic Bottleneck & Domestication

Reduction in levels of genetic diversity is a recurrent, indeed universal theme in domestication and crop breeding. Domestication and subsequent crop breeding have largely involved filtering out the best alleles from standing allelic variation in crop ancestors. Such bottlenecks apply equally to neutral genes as well as genes under selection.

This has been quantified for crops like rice, wheat, maize. For example, Londo et al (2006) compared levels of genetic diversity between wild and domesticated rice indicate that cultivated rice has a reduced subset of the total genetic variation of *Oryza rufipogon*. These results are consistent with other studies on rice diversity. *Oryza sativa* cultivars, whether elite or landrace, share only a subset of haplotypes with *O. rufipogon*. As in many domesticated species, the domestication history of rice appears to involve an intense genetic bottleneck. Using haplotype number as a proxy for genetic diversity, cultivated rice contains 22-28% of the total haplotype diversity and wild rice comprises 82-88% of the total haplotype diversity. This level of diversity is much lower than the approximately 66% level of diversity preserved in wheat or maize when compared to their wild relatives (Buckler et al., 2001). However, these species are outcrossing species, whereas rice is primarily a selfing species, potentially creating a stronger genetic bottleneck during domestication of rice.

### Reduced crop genetic diversity

And of course it is not just initial domestication that causes genetic bottlenecks. Further reductions in genetic diversity are also associated with modern crop breeding – as the result of further intensive selection. In many cases the narrowness of the genetic base in advanced crop breeding programmes is quite staggering. This is understandable given the challenges of introducing new diversity into elite lines. Striving for uniformity is a prerequisite in high input modern industrial agriculture. Soya bean: *Glycine max* provides a good example:

- 220 million metric tonnes on 92 million hectares
- >86% of genes present in modern-day N. American cultivars traced to just 17 lines used in initial breeding programme
- 19,000 accessions in USDA germplasm collections
- A single variety, Roundup Ready Genetically-Modified soybean accounts for 91% USA, 98% Argentina, 53% Brazilian production, indicating even greater reductions in diversity in recent years.

### Selection after domestication & crop diversification

In apparent contradiction to this narrowing of genetic diversity, crop domestication has also involved spectacular phenotypic diversification via selection after domestication, generating the large numbers of traditional cultivars and land races that are known for most crops today. Here is one example for maize showing the initial domestication from teosinte and a subsequent blossoming of cultivars and land races that can be found scattered across south-central Mexico today – colours, cooking qualities, popcorns, corns for tortillas, corns for eating directly, and modern sweet corns, a pale shadow of this diversity.

### Selection after domestication & crop diversification

Selection after domestication has led to the immense diversity in varieties that characterizes many domesticated plant species, which, as Darwin pointed out, can exceed the range of phenotypic variation in their wild ancestors. Selection for crop diversification leads to local adaptation, driven by human groups developing varieties with:

- preferred cooking, processing and storage qualities
- the ability to grow in new environments
- different growing periods and seasons of production – early & late varieties
- desirable visual or gustatory features

This process happens as a result of selection. Unlike key domestication traits such as non-shattering spikelets, however, selection for crop diversification may involve a greater level of conscious selection, as human cultures deliberately chose varieties with the desired characteristics. However, it is also a potentially self-adapting process. The belief that a named recognizable population is adapted to a particular soil or disease regime, leads to particular actions by farmers based on that belief. This is likely to set up a powerful selection routine that will work to improve that population for the farmers preferred trait, leading to diversification and a self-adapting system. As humans began to save seeds and plant the same field every year, local adaptations would gradually have increased over time as the highest proportion of seeds were gathered from the most vigourous individuals. This was accompanied by increases in adaptedness to the local environment and also by striking ecogenetic differentiation among local populations that occupy unlike habitats, including differentiation between cultivated plants and their wild progenitors.

This means that there is often a massive disparity between the handful of lines in modern crop breeding programmes and the huge number of accessions from wild land races held in germplasm banks and in situ in farmers fields in traditional indigenous farming systems.

Other examples: potatoes, chiles, bananas, apples, squashes, tomatoes. You will also remember Darwin's pigeons, dogs & chickens.

### Potato

In the Andes, this complexity translates into a cornucopia of potato races developed by the per-Inca farmers – the Peruvian blue potato, reds, pinks, yellows and oranges, all manner of skinnies and fatties, smooth-skinneds and russets, short-season and long, drought-tolerant and water-loving, sweet tubers and bitter ones, starchy potatoes and others almost buttery in texture – some 4,000 different land races in all. This extravagant harnessing of wild diversity in the Andes, owes partly to the early Andean farmer's desire for variety, partly due to their flair for experimentation, and partly the complexity of their agriculture, the most sophisticated in the world at the time of the Spanish conquest. The Incas had figured out how to grow impressive yields of potatoes under often harsh, extremely variable, and uncertain conditions encompassing different altitudes, orientations that demand diversity – a different tuber for every environment. A polyculture.

## Growing Diversity

Small scale subsistence and resource-poor farmers often use diversity to avoid and spread risks more thinly. Diversity is an important element in farmers livelihood strategies. Risks can be environmental (drought, frost, storms, floods), or in the form of pests and diseases, or in the form of unstable and fickle markets and prices. Diversity can buffer against risk. Resource-poor farmers also use diversity to maximise yields in highly variable environments by employing a mixture of crops and crop varieties, rather than a few 'modern' ones. Uniform varieties will only reach their potential if the environment is also uniform, i.e. when variation has been evened out using high levels of inputs (energy, irrigation, fertilizers and pesticides) not available to resource-poor farmers

## Local adaptation and productivity

As humans began to save seeds and plant the same field every year, local adaptations would gradually have increased over time as the highest proportion of seeds were gathered from the most vigourous individuals. Experimental verification of this using a synthetic population of 28 barley varieties, initially sown in a large plot in 1929 and subsequently allowed to reproduce by natural crossing without artificial selection, with a random sample of seeds collected and sown annually. Over the ensuing decades, they documented dramatic changes in gene frequency, resulting in higher and more stable grain yields with more compact, heavier spikes with larger numbers of seeds. These results suggest changes in adaptedness via incorporation of increasing numbers of favorably interacting alleles into large synergistic complexes. In inbreeding populations this was accompanied by increases in adaptedness to the local environment and also by striking ecogenetic differentiation among local populations that occupy unlike habitats, including differentiation between cultivated plants and their wild progenitors.

## Local adaptation & traditional maize seed systems

- 80% of maize in Mexico is planted with recycled seed, i.e. seed selected from the previous harvest by farmers
- > 90% of seed obtained within <10km and < 50m elevation
- Seed saving is motivated by trust of one's own seed which is well known and has the desired characteristics and performance; strong genotype environment interactions, close matching to sites and markets generating a demand for diversity as one part of managing risk (one size doesn't fit all; security; saving money; social norm of a good farmer with losing seed = humiliation; elements of inheritance and seed held in trust and a link to ancestors with seed saving as a way of conserving and honouring important ties.
- Seed system is fundamentally a moral system based on trust and social responsibility for mutual assistance, rather than commerce and maximising profits
- >1 seedlot per farmer; communities maintain 5x diversity of individuals
- role of improved varieties and formal seed system is minimal
- stable and consistent selection pressures on maize populations both from farmers and environment and hence strong selection for local adaptation. On-farm diversity is manifest

by phenotypic traits under selection. Lack of population structure in neutral markers indicative of geneflow.

- not closed / static - >25% of farmers experiment, but retention is low. Motivations for obtaining seed from outside, i.e. seed flows include: lack of sufficient saved seed and experimentation – curiosity, but small scale and on the periphery of the seed system. Use of outside seed is usually based on knowledge and observation of crops grown by neighbours, family and friends (compadres) – strong element of trust
- maintenance of a revolving portfolio of varieties
- Fundamentally conservative with elements of innovation, generating overall resilience
- Each farmer is essentially creating and maintaining their own almost unique maize varieties.
- Maintenance of diversity depends on maintenance of the integrity of the seed system and continued reliance of farmers on saved seed, and this in turn on a large population of farmers and maintenance of the social and cultural fabric of farming communities.

Rice in the Cordillera region of the Philippines
400-2,000 year-old terrace system; UNESCO World Heritage site;
Cultivated by smallholder farmers who use at least 40 different varieties of rice – with a profusion of colours, nutritional qualities, flavours, aromas and market potentials.
Stable systems spanning generations of farmers

Very similar traditional seed systems for other crops in other parts of the world – potatoes in the Andes, durum wheat in Ethiopia, millet in India.

Nutritional value of crops & micronutrient malnutrition
Green Revolution – strong emphasis on yield and taste at the expense of nutritional value such that major crops such as the most widely cultivated and highly bred varieties of rice, wheat and maize have significant nutritional deficiencies

The importance of traditional / heirloom varieties and crop wild relatives for making crops more nutritious

Rice – huge reliance on rice for calory intake while heralded as one of the major success of the Green Revolution, masks a hidden hunger of micronutrient malnutrition – iron, zinc, vitamin A, vitamin B.

Utility of wild crop relatives
However, traditional diversity is not just an important component of farmers' livelihood strategies and immediately valuable in that sense. Crop diversity and wild relatives of crops can also be an important reservoir of genes for potential use in crop breeding with in some cases dramatic effects on yields. Here we can see some data on releases of cultivars containing genes from crop wild relatives. These are dominated by genes conferring pest and disease resistance that have been introgressed into crops such as tomato, potato, rice and wheat, and it is abundantly clear just how important these genes from the wild have been for maintaining agricultural productivity of these mainstream crops. Of course the ways to do this have changed dramatically from the old paradigm of looking for phenotypes vs the new paradigm of looking for the gene, via marker-assisted selection, genomics etc.

Crop Wild relatives
Hugh Iltis (1988) – Serendipity in the exploration of biodiversity – what good are weedy tomatoes?

Crop Wild relatives
Maize wild relatives – 2000 - Hugh Iltis & the discovery of *Zea nicaraguensis*, 0-20m, Pacific coastal Nicaragua, Iltis & Benz (2000) *Novon*

### Crop Wild relatives

Seven new species of Phaseolus

### Erosion and loss of crop genetic diversity

So there appear to be several very good reasons to believe that crop diversity is important in underpinning many agricultural systems directly, and also indirectly in ensuring future genetic gains from crop breeding, even if most of that diversity remains largely untapped and crop breeding and modern agriculture are still reliant on a very narrow genetic base.

We, and indeed most people in the western world, know what is happening to biodiversity of rainforests and coral reefs, but not all of us realize that the same thing has been happening for crop varieties, or agrobiodiversity. Recent decades have seen the rapid loss of crop genetic diversity as well as the detailed knowledge of the meaning, utility and maintenance of that diversity among farmers and other growers. FAO has estimated that 75% of crop diversity has been lost and one animal breed is lost every month. This erosion of crop diversity is largely as a result of displacement of traditional indigenous crops and varieties by improved varieties, i.e. the advances of modern industrial agriculture are destroying the very resources upon which future crop breeding depends.

### Lost Crops of the Incas

Several regionally important Andean crops are being progressively displaced by introduced European crops. For example faba bean, *Vicia faba*, is increasing cultivated in place of tarwi, Lupinus mutabilis, and wheat in place of quinoa.

### How people domesticated Amazonian forests: 4,500 years of polyculture agroforestry

Most people think of the Amazon basin as a vast tract of pristine tropical rain forest with a sparse and very scattered human population of lost tribes following a hunter gatherer way of life that is largely unchanged over the last several millennia. However, this is far from the case. There is growing evidence from archaeology, paleoecology and floristic data that significant parts of the Amazon were transformed into large-scale polyculture agroforestry systems that involved management, incipient domestication and cultivation of up to 85 tree species as well as cultivation of a set of agricultural crops. The evidence for this comes from:

(i) Hyper-dominance of Amazonian forests by small numbers of tree species (accounts for 50% of trees) with domesticated tree species more than 5x more likely to be hyper-dominant than non-domesticated species. These include species such as the brazil nut - *Bertholletia excelsa*, *Pouteria caimito*, cacao - *Theobroma cacao*, the ice cream bean - *Inga spp*, and various palms including the peach palm - *Bactris gasipaes*.

(ii) Anthropogenic soils – Amazon dark earth soils that were modified and indicative of pre-Colombian cultivation and sedentary occupation.

(iii) Archaeological data that suggest a millennial scale polyculture with enrichment of edible plants, limited forest clearance for cultivation of crops, low severity fore management.

All these data show that Amazonian forests are far from untouched by humans, but were instead shaped by extensive human domestication of useful species over several millennia.

### 1492 and the Loss of Amazonian Crop Genetic Resources

These extensive agroforestry systems are likely to have supported a population of 4-5 million people in Amazonia at the time of European contact. These people cultivated and managed at least 138 plant species at that time. Many of these species were domesticated to a level where they required human intervention for their maintenance. After European contact, the Amazonian Amerindian population declined dramatically – a massive demographic collapse, with as many as 90-95% of the people killed by European diseases or resisting attempts to enslave them, dropping to around 0.5 million. This rapid decline in human population led to a concomitant decline in Amazonian crop genetic diversity, precipitating an order of magnitude loss of crop genetic resources that is continuing today.

## Widespread Adoption of Modern Crop Varieties

Similar erosion of diversity can be seen in some Andean crops such as potatoes due to increasing cultivation of more productive and uniform bred varieties from outside. Modern agriculture is characterized by simplification, specialization, mechanization, uniformity, high inputs, risk management via pesticides, irrigation and fertilizers, globalization and monocultures. In contrast, traditional farming systems are generally more complex, more diverse, often involve polyculture of crops and crop varieties, this in part a strategy of risk avoidance and in part an 'adaptive mosaic' that is resilient in the face of turbulent markets, economics and extreme climatic events when high inputs of water, fertilizers and pesticides are too expensive.

## Lost Crops of eastern North America

An entirely unknown agricultural system has been revealed in eastern North America, dating to around 5,000BP. Evidence for this came initially from sunflower, as we saw in Lecture 2. In addition to sunflower and squash, at least five other crops were used:

a. Goosefoot – *Chenopodium berlandieri*
b. Sumpweed / Marsh Elder – *Iva annua*
c. Little Barley – *Hordeum pusillum*
d. Erect Knotweed – *Polygonum erectum*
e. Maygrass – *Phalaris carolinum*

These five crops exist now only in an archaeological context – no longer grown, relicts.

At least three of these five lost crops are now rare in the wild:
*Polygonum erectum* – largely replaced by invasive Eurasian *P. aviculare*
*Phalaris carolina* – under threat from expanded herbicide use and elimination of field margins
*Chenopodium berlandieri* threatened by herbicides used to target goosefoot in agricultural fields and spread of herbicide-resistant Eurasian *C. album*

## Lost Crops of eastern North America II

These species are disappearing from increasingly homogeneous and intensively cultivated agricultural landscapes where they were once common, due to:

- Competition from their invasive cousins
- Shrinking field margins
- Increased herbicide use

These three crop examples are symptomatic of global loss of biodiversity in and around agroecosystems related to agricultural intensification

## Intensive Farming Fades Your Genes – Diversity Doesn't

## Genetic Conservation - in situ, circa-situm, ex situ

There are two main ways to conserve species and genetic resources – in situ conservation in natural habitats and ex situ in germplasm collections, both so called living collections like gardens, and seedbanks. A third category, circa situm, has been coined for conservation of native diversity in disturbed and human managed landscapes, sometimes referred to as on-farm conservation, farmer-based conservation, conservation *in hortus*, or simply 'Growing Diversity'.

Most of the diversity of crop plants lies outside natural vegetation in farmers fields, so the contribution of strict in situ conservation, via biological reserves is limited for crop genetic diversity and crop genetic resources. Much more important are the other two categories, ex-situ and circa-situm.

## The 'Vavilov' Institute

You will recall from lecture 2 that one of the pioneers in the discovery and collection of crop genetic diversity was Nikolai Vavilov. While developing his theory on the centres of origin of cultivated plants, Vavilov organized a series of botanical-agronomic expeditions, collected seeds from every corner of the globe, which formed the foundations for one of the world's largest collection of plant seeds in Leningrad, or what is now St. Petersburg in Russia. This seedbank was diligently preserved and survived through some desperate trials, the most notable being the deaths of 9 of the curatorial staff who died of starvation whilst guarding the collections throughout the 28-month siege of Leningrad during the Second World War. Vavilov had accumulated a collection of 200,000 plant seeds from the Soviet Union and from abroad. As I mentioned before, Vavilov himself, the only man who had collected seeds of food crops on all five continents and who had organized 115 research collection expeditions to 64 countries, was also dying of hunger in 1943 in a Soviet prison. The seeds had survived while their proponents had not. Today, the N.I. Vavilov Institute of Plant Industry still maintains one of the world's largest collections of plant genetic material - >380,000 samples of seeds, roots and fruits of c.2,000 species. The Institute began as the Bureau of Applied Botany in 1894, and was reorganized in 1924 into the All-Union Research Institute of Applied Botany and New Crops, and in 1930 into the Research Institute of Plant Industry. Vavilov was the head of the institute from 1921 to 1940. In 1968 the institute was renamed after him in time for its 75th anniversary. One might imagine that such a valuable collection would be securely protected and maintained without question today, but that is not the case. Just this year the collections have come under threat.

These threats to one of the world's largest crop gene banks illustrate the potential vulnerability of ex situ collections and the need for replication.

Fortunately, the Vavilov Institute is not the only crop gene bank in the world and nowadays, these collections are indeed replicated in different locations around the globe. Here we can see recent publicity for another massive plant ex situ conservation project, the Millennium Seed Bank at Kew Gardens in London, which now houses 10% of the world's plant species as seeds.

## CGIAR

Consultative Group on International Agricultural Research of FAO, The Food & Agriculture Organisation of the United Nations. The various CGIAR Gene Banks alone store > 1 million samples of crop, forage and agroforestry genetic resources in the public domain.

## Bioversity International

Formerly known as the International Plant Genetic Resources Institute, IPGRI.

## Doomsday Global Seed Vault, Svalbard

The Svalbard GSV is currently the world's largest secure seed storage facility, established in 2008 by the Royal Norwegian Ministry of Agriculture and Food; the Global Crop Diversity Trust (now known as the "Crop Trust"), an independent international organization based in Germany (established as a partnership between the United Nations Food and Agriculture Organization (FAO) and the Consultative Group on International Agricultural Research); and the Nordic Genetic Resource Centre (NordGen). At a cost of US$9 million to the Norwegian government. Situated on the remote island of Spitsbergen in the Norwegian Svalbard archipelago, high in the Arctic north, it received its first deposits of seeds in 2008. NordGen is responsible for the day-to-day operations of the facility and maintains a publicly accessible database documenting its samples. SGSV holds in its frozen repository approximately 850 thousand accessions and 54.7 million seeds, provided by 233 countries and 69 depositor institutions. Each accession represents a sample taken of a specific living crop population from a specific geographic location at a specific point in time, and is usually made up of approximately 500 individual seeds. Depositing institutions first dry the seed accessions to limit their moisture content to 5-6%, and then seal them inside an individual airtight aluminum bag which are refrigerated to maintain a constant temperature of −18°C. These vaults have been excavated approximately 120 meters into the side of a sandstone mountain at a height of 130 meters above sea level; entry to the vaults is via a 100-meter entrance tunnel. Equal parts bunker and frozen "ark," the dramatic façade includes a commissioned artwork, *Perpetual Repercussion* by Dyveke Sanne, which "renders the building visible from far off both day and night, using highly reflective stainless steel triangles of various sizes". The cold climate and permafrost ensure that even if power is lost, the storage vaults would remain frozen for a significant period of time, even taking into account the possible effects of climate and sea level changes. "Designed for [a] virtually infinite lifetime," it is perceived to be "robustly secured against external hazards and climate change effects".

### The Frozen Ark

The Frozen Ark is a UK-based, international biobanking initiative which aims to preserve the DNA of endangered animal species – a cryogenic or technoscientific ark to save cells and DNA of endangered species. The apopcalyptic message conveyed by the project's logo – a stylized ark on a stormy sea is both strong and urgent. Such initiatives to freeze genetic material of non-human animals have shifted from a sort of 'heroic' narrative that cast such biobanks as a static, isolated and dormant 'arks' to carry endangered DNA into an uncertain future, to a more active foundation which acknowledges their potential for reanimation of genetic material in future de-extinction programmes, along the lines of the at the time improbable idea in Stephen Spielberg's 1993 Jurassic Park whereby long-extinct species could be regenerated from ancient DNA. Could be viewed as speculative investments where genetic materials could be actively reworked and revived to build new futures – active experimental conservation including use of cryopreserved gametes in artificial hybrids to save extinct species by crossing them with close relatives and allowing the possibility of breaking down species into a range of components at the biomolecular level which allow for almost endless recombination.

### Ex-situ conservation of crop wild relatives

1,076 plant species identified as important wild relatives of 81 important crops
313 (29%) species associated with 63 crops not represented in existing germplasm collections
257 (24%) represented by fewer than 10 accessions

### On-Farm Conservation of Crop Genetic Diversity – 'Growing Diversity' – 'Genes in the Field'

As we have seen, during the second half of the 20th Century, considerable efforts have been devoted to collecting, characterizing and conserving crop diversity in gene banks – ex situ conservation – via a worldwide network of national and international gene banks. However, these cannot accommodate the full range of diversity of economically useful plant species, nor can they conserve the dynamic processes of crop evolution and farmers' knowledge of crop selection and management inherent in the evolution and development of local cultivars. Gene banks = frozen in time and literally and otherwise disconnected from farmers knowledge…. To address these potential inadequacies, attention in addition to on-farm conservation of crop genetic diversity and resources. In many parts of the world, traditional crop varieties (sometimes referred to as land races) are still grown in traditional farming systems and form important elements of production systems and farmers' livelihood strategies.

Circa situm conservation strategies also present some interesting advantages over ex situ gene banks. As living systems, farmer management of diversity is itself part of a self-adapting system, e.g. The belief that a named recognizable population is adapted to a particular soil or disease regime, leads to particular actions by farmers based on that belief. This is likely to set up a powerful selection routine that will work to improve that population for the farmers preferred trait, leading to diversification and a self-adapting system.

'*Use it or lose it*'

Global assessment of traditional crop-variety diversity maintained by farming communities

10 year, coordinated global partnership measured the amount and distribution of genetic diversity present among 27 crop species in farmers fields

- Traditional varieties dominate planting at most sites, except for rice
- On average farmers grow 1.38-4.25 traditional varieties
- There are larger numbers of varieties at the community level – 8x individual level - ranging from 4 (durum wheat) to 60 (cassava), suggesting that different farmers grow different mixes of traditional varieties reflecting different choices of diversity. This underscores the importance of divergence between farms within a community.
- Results underscore the importance of large numbers of small farms adopting distinctive varietal strategies as a major force in retaining crop genetic diversity on farm.
- Well-intentioned interventions that unify landscapes genetically may threaten such diversity in the longterm.

Formal Ex situ vs informal Farmer-based Conservation

| Technology | Farmer-based | Formal Crop breeding |
|---|---|---|
| Taxonomy | Folk | Scientific |
| Circa-situm conservation | Yes | Virtually none |
| Ex situ conservation | Some community seed banks | Gene banks, long and short-term |
| Germplasm acquisition | Neighbour exchange / informal | Global / commercial |
| Interspecific introgression | Limited to natural crosses | Expanded via species techniques |
| Introgression of weedy races | Common | Sometimes used |
| Gene technology | No | Yes |
| Screening germplasm | For local, not wide adaptation | For wide, not local adaptation |

Fructus/Prospecierara/Retropomme

Local templates for farmer-based conservation of crop genetic diversity in Switzerland.

Lost Crops Garden Network

http://lostcrops.org/

# BIO235 – Lecture 10 – Genes in the field: crop genetic diversity and conservation – Source Materials

Altieri, M.A. & Merrick, L.C. 1987. In situ conservation of crop genetic resources through maintenenace of traditional farming systems. *Economic Botany* **41**: 86-96.

Badstue, L.B. et al. 2003. The dynamics of seed flow among small-scale maize farmers in the central valleys of Oaxaca. CAPRi-IPGRI Workshop.

Bartha-Pilcher, B. et al. 2005. *Rosenapfel und Goldparmane. 365 Apfelsorten – Botanik, Geschichte und Verwendung*. ProSpecieRara & Fructus.

Bellon, M.R., Hodson, D. & Hellin, J. 2011. Assessing the vulnerability of traditional maize seed systems in Mexico to climate change. *Proceedings National Academy of Sciences* **108**: 13432-13437.

Breithoff, E. & Harrison, R. 2018. From ark to bank: extinction, proxies and biocaptials in ex-situ biodiversity conservation practices. *International Journal of Heritage Studies* DOI: 10.1080/13527258.2018.1512146.

Brush, S.B. (Ed.) 1999. *Genes in the Field. On-Farm Conservation of Crop Diversity*. Lewis Publishers.

Buckler, E.D. et al. 2001. *Genetics Research* **77**: 213-218.

Castaneda-Alvarez, N.P. et al. 2016. Global conservation priorities for crop wild relatives. *Nature Plants* **2**: 16022.

Chang, S.H. et al. 2007. Progress in research and development in hybrid rice: a super-domesticate in China. *Annals of Botany* **100**: 959-966.

Clement, C.R. 1999. 1492 and the loss of Amazonian crop genetic resources. I. The relation between domestication and human population decline. *Economic Botany* **53**: 188-202.

Cooper, D., Vellve, R. & Hobbelink, H. 1992. *Growing Diversity. Genetic Resources and Local Food Security*. Intermediate Technology Publications.

Delgado-Salinas, A. 2000. New species of Mexican *Phaseolus*. *Systematic Botany* **25**: 414-436.

Doebley, J.F., Gaut, B.S. & Smith, B.D. 2006. The molecular genetics of crop domestication. *Cell* **127**: 1309-1321.

Dyer, G.A. & Taylor, J.E. 2008. A crop population perspective on maize seed systems in Mexico. *Proceedings National Academy of Sciences* **105**: 470-475.

Gruber, K. 2016. Re-igniting the green revolution with wild crops. *Nature Plants* **2**: 1-4.

Hajjar, R. & Hodgkin, T. 2007. The use of wild relatives in crop improvement: a survey of developments over the last 20 years. *Euphytica* **156**: 1-13.

Harrison, R. 2017. Freezing seeds and making futures: endangerment, hope, security and time in agrobiodiversity conservation practices. *Culture, Agriculture, Food and Environment* **39**: 80-89.

Iltis, H. 1998. Serendipity in the exploration of biodiversity. What good are weedy tomatoes? Pp. in Wilson, E.O. Biodiversity. Island Press.

Jarvis, D.I. et al. 2008. A global perspective of the richness and evenness of traditional crop-variety diversity maintained by farming communities. *Proceedings National Academy of Sciences* **105**: 5326-5331.

Levis, C. et al. 2017. Persistent effects of pre-Colombian plant domestication on Amazonian forest composition. *Science* **355**: 925-931.

Levis, C. et al. 2018. How people domesticated Amazonian forests. *Frontiers in Ecology & Evolution* **5**: 171.

Londo, J.P. et al. 2006. Phylogeography of Asian wild rice, *Oryza rufipogon*, reveals multiple independent domestications of cultivated rice, *Oryza sativa*. *Proceedings National Academy of Sciences* **103**: 9578-9583.

Maezumi, S.Y. et al. 2018. The legacy of 4,500 years of polyculture agroforestry in the eastern Amazon. *Nature Plants* **4**: 540-547.

Massawe, F., Mayes, S. & Cheng, A. 2016. Crop diversity: an unexploited treasure trove for food security. *Trends in Plant Science* **21**: 365-368.
Mueller, N.G. et al. 2017. Growing the lost crops of eastern North America's original agricultural system. *Nature Plants* **3**: 17092.
Tanksley, S.D. & McCouch S.R. 1997. Seed banks and molecular maps: unlocking genetic potential from the wild. *Science* **277**: 1063-1066.
Zimmerer, K. 1991. Managing diversity in potato and maize fields of the Peruvian Andes. *Journal of Ethnobiology* **11**: 23-49.

*Fructus* – the Swiss Association for the Protection of Fruit Diversity: http://www.fructus.ch/
*ProSpecieRara* - http://www.prospecierara.ch/Generator.aspx?tabindex=0&tabid=128&palias=fr
*Retropomme* – Asociation et fondation pour la sauveguarde de le patrimoine frutier du Suisse Romande - http://www.retropomme.ch/

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## BIO 235 Plants & People – Evolution & Domestication of Crops
## Lecture 12 – Guns, Germs & Steel - The causes and consequences of domestication.

### Non-human agriculture

### The evolution of agriculture in insects
An additional perspective on the origins of agriculture is available from non-human agriculture. Farming mutualisms, whereby an organism promotes the growth of another on which it depends for food, i.e. agriculture, have evolved independently in three different insect orders: once in ants, once in termites and seven times in ambrosia beetles. Although these insect farmers are in some ways quite different from each other, in many more ways they are remarkably similar, suggesting convergent evolution. All these groups farm fungi – termed insect fungiculture – fungivores.

### Ant Fungiculture
A - Sections of leaves are cut from vegetation around the nest by specialised workers.
B - The leaf sections are carried away along trails.
C - The leaf sections are taken back into the ant nest, where they are given to another group of specialised workers that process the leaves.
D - The processing workers reduce the leaf fragments to a mulch which is used to feed the ant colony's fungus garden. The fungus feeds on the mulch and uses the nutrients to grow. It also produces special structures called gongylidia which are fed on by the ants.
E - The queen sits among the fungus garden laying her eggs. When the eggs hatch, the larvae that emerge will eat the gongylidia while they are being cared for by specialised nurse workers.
F - When the nutrients have been removed from the leaf material, the waste is transported to special dump chambers, where dead ants and dead fungus are also placed.
Fungus-growing ants are a monophyletic group of c.200 species in the New World. They are obligate agriculturalists and their cultivated fungi are an important food source for larvae and adults. Different ant lineages use different substrates, the best known being freshly cut leaves of the leaf-cutting ant genera Atta and Acromyrmex. Involves four symbionts: Fungus-growing ants; Fungal cultivars; Mutualistic antibiotic-producing actinomycete bacteria; Garden parasites in the fungal genus Escovopsis.

### Obligate plant farming by a specialized ant
Despite the diversity of ant-plant mutualisms and even though plants are obvious 'crops', no faming mutualisms involving ants and plants had been described until 2017. Most ant-plant symbioses involve plants with preformed cavities (domatia) that house ants in return for protection or extra nutrients. Typically these symbioses need to be re-established each generation. Different from ground-dwelling ant-plant symbioses that are mostly defence mutualisms, epiphytic ant-plants usually are nutritional mutualisms. In Fiji one ant species actively and exclusively plants the seeds and fertilizes the seedlings of six species of the epiphytic plant genus *Squamellaria*. This farming plays a key role in mitigating the re-establishment step. In this case, the ant species creates large monocultures of *Squamellaria* consisting of plant siblings, a feature found in most complex farming systems. Thus *Squamellaria* plants are obligately farmed by the ant species *Philidris nagasau*, which actively plants and fertilizes its hosts.

### Non-human agriculture – ants, termites, ambrosia beetles, damselfish and amoebae
Alongside ants, a small number of other non-human animals, and notably fungus-growing termites and ambrosia beetles, have advanced agriculture that involves dispersal and seeding of food propagules, cultivation of a crop, and sustainable harvesting of food.

Rather than building fungal gardens underground like the ants, ambrosia beetles bring fungi to their host trees, often carrying them via a striking array of glandular structures that serve to maintain fungal spores and mycelia in pure cultures for inoculation into the galleries the ovipositing beetles dig into wood. Like the fungi used by ants, some of the ambrosia beetle fungi have become obligately associated, vertically transmitted, polyphagous asexual domesticates and serve as the primary food source of their beetle farmers.

More primitive forms of agriculture, which we might label as husbandry because they involve fewer adaptations, include marine snails farming intertidal fungi and damselfish farming algae. Recent work as even shown that a species of amoeba has a primitive farming symbiosis that also involves dispersal and prudent harvesting of a crop, in this case bacteria, another micro-organism.

Inesct fungiculture and human farming share the defining features of agriculture:

- *Habitual planting* (or inoculation) of sessile cultivars in particular habitats or on particular substrates, including the seeding of new gardens with crop propagules (seeds, cuttings, or inocula) that are selected by the farmers from mature (ripe) gardens and transferred to novel gardens
- *Cultivation* – aimed at improving growth conditions for the crop or protection of the crop from herbivores
- *Harvesting* the crop for food
- *Nutritional dependency* – obligate dependency for food

It is notable that this definition of agriculture does not require conscious intent in planting and harvesting – conscious planning, learning and teaching have clearly accelerated the development of complex agricultural in humans, but not insects.

Agricultural behaviour of farming ants, termites, ambrosia beetles and humans

| Agricultural behaviour | Ants | Termites | Ambrosia beetles | Humans |
|---|---|---|---|---|
| Dependency on crop for food | Obligate | Obligate | Obligate | Facultative |
| Engineering optimal growth conditions | YES | YES | YES | YES |
| Planting crop on improved substrate | YES | YES | YES | YES |
| Intensive continuous monitoring of growth and disease status of crop | YES | YES | YES | NO |
| Sustainable harvesting of crop for food | YES | YES | YES | YES |
| Protection of crop from diseases and consumers | YES | YES | YES | YES |
| Weeding of alien organisms invading the garden | YES | YES | ??? | YES |
| Use of chemical herbicides to combat pests | YES | ??? | ??? | YES |
| Use of microbial symbionts for nutrient procurement for crop | YES | ??? | ??? | YES |
| Use of disease-suppresant microbes for biological pest control | YES | ??? | ??? | NO |
| Sociality | Strictly social | Strictly social | Subsocial /communal | Social |
| Task partitioning in agricultural processes | YES | ??? | YES | YES |
| Artificial selection for crop improvement | ??? | ??? | ??? | YES |
| Learning and cultural transmission of agricultural innovations | NO | NO | NO | YES |

From Mueller et al. (2005)

Phylogenetic origins of insect agriculture

- Ants – single origin 45-65 Mya in the Amazon
- Termites – single origin 24-34 Mya in Africa

- Ambrosia beetles – 7 independent origins 20-60 Mya
- Termites & beetles – single specific cultivar clade to which descendants have adhered
- Ants – multiple independently domesticated cultivar lineages
- No known cases of reversals from agricultural to non-agricultural life in any of the 9 agricultural insect lineages
- cf. Humans - 10-??13 independent origins, all of them in the last 10,000 years....

Non-human agriculture – a broader comparative framework to investigate the origins of agriculture
So, we can add ants, termites, ambrosia beetles and snails farming fungi, damselfish farming algae, and amoebae farming bacteria to humans as agriculturalists. This provides an intriguing and much more expansive comparative framework for thinking about and gaining insights into the central question of *'Why did agriculture arise?'*

We have seen that agriculture has been a large part of the ecological success of humans, and sustainable high-yield agriculture has become critical for the survival of modern human societies. We have also seen how multiple independent origins of agriculture offer opportunities to gain insights into the underlying causes of agriculture and the ultimate question of why did agriculture arise. However, an even broader evolutionary perspective is available if we also consider the very intriguing and biologically fascinating set of non-human agricultural systems that have evolved in other groups of organisms. In subsequent lectures, we will look briefly at some of these systems in order that we can think about:
- what common ground there might be between fungus-growing ant, wheat-growing human and algae farming damsel fish agricultural systems?
- what insights we might gain into why agriculture arose by adopting this much broader evolutionary perspective on agriculture?
- what lessons non-human agriculture might have, for example to improve disease and pest control strategies, in modern agriculture, if any?

The title for this lecture is taken from Jared Diamond's book, *Guns, Germs and Steel* in which he explores the consequences of the origins of agriculture in terms of the fates of human societies, painting an ambitious global panorama. It is a book that is well worth reading and as a reminder there is a version of Diamond's treatise available on YouTube – see list of sources at the end.

Causes of Domestication
There are only a handful of major events in human history that compare in significance to the emergence of agriculture. These might include the origins of our earliest ancestors, the appearance of modern humans, and the rise of hierarchical society, and later on the industrial revolution. Of all of these, the emergence of agriculture is perhaps the most remarkable because it represents a major turning point in human history. It is no wonder that people have sought to understand the causes of domestication and explanations for why agriculture arose when and where it did.

For more than a million years our ancestors were hunter-gatherers, relying exclusively on the gathering of wild plants and the hunting of wild animals for their food. Then virtually simultaneously a number of plants and animals were domesticated in a number of different regions of the world. Crop and livestock domestication heralded the transition from archaic foraging to agriculture, with:

- important biological impacts and the rapid evolution of crop plant genomes
- far reaching consequences for the development of human societies and civilization as we know it
- ecological impacts on natural environments.

Indeed, domestication was without doubt amongst the most significant events in human history and the lever by which humans transformed the earth and its terrestrial ecosystems. That was when there was a changeover from the natural environment in control of humans to humans in control of the natural environment, and for these reasons sometimes referred to as the *Neolithic Revolution*.

Origins of Agriculture: established paradigm vs new evidence

- Early dogma that agriculture arose just a few times in parallel
- Rapid – the Neolithic revolution
- Largely as a result of unintended consequences that allowed revolutionary changes in the economy
- Idea of rapid change lent itself to identification of single big universal causes of agricultural origins
- Most often the origin of agriculture has been attributed to *climate change* in combination with *population growth*
- Emergence of sedentary hunter-gatherers with social hierarchy and competitive feasting as an alternative cause

10, 13 or more independent origins of agriculture?

Vavilov - 7
Harlan (1971) -3
1990s – 6-8
Diamond (2002) – at most 9
Balter (2007) – 11
Purugganan & Fuller (2009) – 13
Fuller (2010) – at least 13 and maybe up to 24, with possible additions in Central America, the Amazon, west Africa, India & eastern Tibet – areas not yet subject to systematic, intensive and quantitative archaeology and archaeobotany.

So there is clear evidence for several centres of independent agricultural origins, probably at least 20. Within each, these processes were often a mosaic with several local foci in parallel and interaction.

Evolution not revolution of agriculture

It is now clearer that the transition from foraging to farming was a much more gradual, protracted and complex process – spanning several millennia rather than a few centuries.

Data from all three regions – the Fertile Crescent, Mesoamerica, and China indicate that:
- early active resource management / ecosystem engineering aimed at encouraging plant production and manipulation of herd structure to promote a secure and predictable yield of animal products preceded any manifestation of traditional markers of domestication by 100s if not 1000s of years.
- initial domestication and the gradual emergence of domestication traits followed by a long period of low-level food production with continued hunting and gathering, suggestive of a continuum between wild and domesticated, between foraging and farming, between hunting and herding.
- cultivation that included a mix of wild and domesticated species with wild varieties only gradually replaced by domesticated species
- wild and domesticated plants frequently intermixed with opportunities for geneflow
    - initial domesticates still not like modern ones, domestication as a process of gradual frequency change, with an earlier, more rapid semi-domestication, and a later, slower fixation of full domestication.
    - Fixation of non-shattering (=time frame of domestication) = 1000s, (3,000) not 100s of years
    - crops added sequentially over several millennia, not all at once.
    - domestication was a protracted, multi-stage and complex process spanning perhaps 150 human generations

Comparing Pathways to agriculture I

Although the multiple independent origins of agriculture all happened within a short time frame of a few thousand years, these origins were not precisely synchronous. Here we can see a chronological chart listing the regions where, and the time frames over which key plants and animals were domesticated. Grey dashed lines indicate documented exploitation before domestication or suggested as necessary lead-time to domestication. Blue lines indicate either management of plants or animals including translocation and/or predomestication cultivation of plants, but without phenotypic indications of domestication. Red bars frame the period over which morphological changes associated with domestication are first documented and a short red bar the latest time by which domestication occurred. We can see that: early Holocene plant domestication took place independently in both the New and Old Worlds, early Holocene animal domestication was restricted to the Near East. In addition, few domestications began with the Holocene transition (11,000-10,000 years ago); the majority of plants and animals were domesticated in the middle Holocene (6,000-3,000 years ago). Despite the non-synchronicity the rates of domestication were apparently very similar for different crops in different regions. The big question is whether the causes were also similar?

### Why then but not earlier?

The human lineage diverged from chimpanzees around 6myr and modern humans emerged at least 55,000-80,000 years ago. Throughout 99% of our independent evolutionary history, and 85% of our modern history, there was no agriculture, until it emerged independently in 9-13 (or more) areas on four continents in the short span of 6,000 years between 10,500 and 4,500 BP. So many nearly simultaneous independent origins seem to be too much of a coincidence. What triggered agriculture repeatedly then, and why had it never arisen during the previous 55,000 years?

### Why there and not elsewhere?

Why did humans become farmers? Why more or less simultaneous origin of agriculture independently in different places? Is there a global explanation? Why did agriculture arise in these areas and not others? Why do these areas not overlap more significantly with areas of most productive modern agriculture? Why did domestication involve so few species? – 350,000 flowering plant species, but only c.100 important domesticated crops?

### Explanations & Theories

Much of this course has been devoted to describing and understanding the origins of particular crops and the processes of crop domestication – where, when, how many times, from what progenitors and how hunter gatherers actually transformed wild species into domesticated crops. Each of these individual discoveries does not in itself provide an overall explanation as to *why*, agriculture started. However, they do provide the building blocks for reconstructing geotemporal regional agricultural development scenarios and hence the foundations for constructing deeper explanations for why human societies made the transition from hunting and gathering to an agricultural way of life. What were the ultimate causes and human motivations behind this transition? What were the factors and circumstances that prompted the shift from hunting and gathering to farming? Any theories need to match with this growing body of evidence.

### Theories about why agriculture arose

Some theories refer to specific regions, like the Fertile Crescent, while others are universal. Regional explanations are much more firmly anchored in the detailed evidence about the emergence of agriculture in specific areas and recognize differences in timing and environmental factors in different areas. However, local explanations ignore the striking, albeit not precise, coincidence of agricultural origins independently in different areas at different times, and absence of agriculture in other areas as features that perhaps suggest that a common set of contributing factors might offer more universal explanations. Some focus on a single cause, others invoke multiple causes, and combinations of preconditions and contributing factors. Some see the causes as lying in nature and hence external to human societies, others focus on cultural changes within hunter-gatherer societies.

Did human societies first domesticate plants and animals as an adaptive response to some external pressure like climate change, or did domestication take place in the absence of outside stress, as a result of changes in the organization and integration of the societies themselves? Did agriculture arise out of need or opportunity?

## Climate or Environmental Change – the Oasis Theory

One potentially universal trigger of domestication that has been suggested is climate change and especially colder and dryer periods prior to the origin of agriculture. The idea is that such periods would have restricted and reduced the availability of wild food resources prompting, crowding near to water sources and attempts to increase food production in other ways. However, while there are indeed suggestions that cooler dryer periods preceded domestication in different parts of the world, the likelihood that this alone prompted the transition to agriculture is low, not least because under such circumstances in many areas, time and other resources are likely to have been at a minimum and people likely to have been more mobile, rather than more sedentary and it is widely accepted that sedentary communities are a pre-requisite for agriculture to emerge.

## Population Pressure

It is absolutely clear that growth of human population has been one of the most dramatic consequences of domestication of crops and animals, something that we will return to later in the lecture. Population growth has also been proposed as perhaps the most credible global cause of domestication that provided the impetus that spurred hunter-gatherer societies to develop agriculture. Under this theory, human societies were forced to turn to agriculture as a solution to problems of overpopulation on a global scale. More recently, this has been seen as just one of a wider set of possible factors.

## Implications of protracted gradual domestication trajectories

- Over the course of 3,000 years, social and environmental circumstances are likely to have changed
- Domestication would have involved extra work in e.g. soil preparation, threshing
- Need to dispense with the idea of an agricultural revolution
- Unlikely that transitions in different areas followed identical trajectories driven by common causes
- There may be little that is predictable about the relationship between early plant cultivation and animal husbandry – animals only important in some areas.
- Cultivation, animal management and labour demands were entangled in different ways

## Factors contributing to the emergence of agriculture common to different regions

In several, and potentially most of the areas of independent agricultural origins, a number of common factors seem to emerge:

- *Familiarity with wild plants and animals*. Agriculture is very much the endpoint of a long period of use of wild ancestors of domesticate crops and animals, i.e. it is the same species that had been the focus of hunting and gathering that were domesticated.
- *Harvesting, processing and storage technologies*. The first species brought under domestication were seed plants rather than root crops or animals. In all areas, the wild ancestors of these domesticates appear to have been important food sources prior to domestication and the human societies involved had already developed efficient technologies for harvesting, processing and storing wild seeds and other foods.
- *Sedentism*. People who domesticated these seed plants already lived in relatively large, permanent communities occupied throughout most of the year, i.e. they were relatively affluent sedentary communities rather than small nomadic bands of hunter-gatherers living in temporary camps at different seasons.
- *High Resource Diversity & the Importance of Aquatic Environments*. These societies enjoyed a relatively broad spectrum of wild plants and animals because they had access to relatively

rich aquatic resources – i.e. the large permanent settlements were tied to permanent, year-round water resources (rivers, river flood plains, lake margins) and their associated plant and animal life, which provided both abundant animal protein in the form of fish and waterfowl such as ducks and geese, but also well-watered soils for secure harvests. Examples would be the Tigris and Euphrates Rivers of the Fertile Crescent; similar permanent river valleys in the heartlands of agricultural development in the Tehuacan and Oaxaca valleys in Mexico; the Yangtze Valley corridor, with its vast landscape of lakes and marshes which formed the heartland of rice domestication; the Yellow River valley further north in China where millet was domesticated is similar; somewhat surprisingly, the central Andes may also fit this picture, even though it is primarily a high elevation centre of domestication where a distinctive mixed agricultural economy emerged based on both root and seed crops and animals, it is anchored at both ends by river and lake environments, and notably the large upland Lake Junin and Lake Titicaca basins. Initial cultivation was near these lake-margin and river-valley fields with their predictable water supplies ensured reliable harvests. Flood plain weeds of eastern North America and China (e.g. rice) were ideal for cultivation in such environments.

- *Changes in climate & vegetation*. Although these societies enjoyed the benefits of lakeside or riverside environments offering plentiful resources, their communities were also bounded both in time and space by far less secure environments. Domestication coincides with climate changes that could have significantly curtailed food resources from wild plants and animals in these surrounding less secure environments. For example the Younger Dryas climate downturn 11,000-10,000 BP brought cooler temperatures for 200-300 years, not long before the domestication of cereals. Similar changes in eastern North America 8,000-4,000 BP, the Sahara 5,000 BP, and the Andes 7,000 – 4,000 BP. These climate downturns would have accentuated the contrasts between the rich lakeside, riverside and marshland habitats and the outlying savannas, steppes and shrublands, i.e. a steepening of the environmental gradients between rich waterside habitats and outlying dryer zones, making these outlying zones less able to sustain hunter-gatherer societies, especially sedentary ones with larger populations and rendering the waterside communities relatively ‘boxed in’.
- *Population Density*. These more favourable waterside locations may also have been relatively densely populated, suggesting that population growth in such an environmental context could as previously suggested have been an important factor contributing to the initial experiments with cultivation and domestication. By heightening the ever-present fear of resource shortfall, even in times of abundance, pushing societies to increase the yield and reliability of some food resources and pointing the way towards domestication. The expectation of lean years would have provided the motivation to experiment with ways of increasing storable food supplies.
- *Competition, ownership & social stratification*. Newly sedentary societies living in larger settlements would need new forms of social integration and interaction and new rules of ownership and control of land and its resources. Such changes may have encouraged the production of greater harvest surplus, if such surplus could have been used to establish and maintain contracts between families or larger kinship groups via e.g. lending resources in times of need, offering up resources for ceremonial and celebratory occasions. Such societies are often referred to as complex hunter-gatherer communities.
- *Good potential domesticates*. Of key importance was the presence of promising wild species that had star-quality pre-adaptations or pre-dispositions to domestication

## Biogeographic Luck

One possible explanation for the why there and not elsewhere question, is simply that agriculture arose in areas to which the most numerous and most valuable domesticable plants and animals were native. This is an idea favoured and championed by Jared Diamond, and for which there is indeed some evidence from domesticated animals and grasses. As we have seen, The Fertile Crescent is home to, not only a suite of the world’s most important crops, but was also one of the origins of domestication of the world’s four most important farm animals. It is a remarkable fact that 33 of the world’s 56 heaviest-seeded grasses are native in the Fertile Crescent and that wheat and barley are amongst the heaviest. It is equally remarkable that four of the very few easily domesticable herd-living herbivores are native in that same region. Arguably the areas where agriculture arose and the fact that it arose first in the Fertile Crescent were no more than biogeographic luck – a function of the biogeography of plants and animals and little to do with the make-up of the hunter-gatherer societies who lived in the different regions of the world.

World Distribution of the 56 Heaviest-Seeded Grasses

| **Area** | **Number of species** | |
|---|---|---|
| **West Asia, Europe, North Africa** | | 33 |
| **Mediterranean zone** | 32 | |
| **England** | 1 | |
| **East Asia** | | 6 |
| **Sub-Saharan Africa** | | 4 |
| **Americas** | | 11 |
| **North America** | 4 | |
| **Mesoamerica** | 5 | |
| **South America** | 2 | |
| **Northern Australia** | | 2 |
| **Total** | | 56 |

Thus, there does indeed seem to be some evidence that biogeographic luck could have been important, at least in determining why perhaps agriculture started first in the Fertile Crescent. However, it seems a poor explanation for lack of agriculture in areas of spectacular plant diversity, such as South Africa, Australia or California, where it seems unlikely that given the right circumstances, hunter-gatherers could not have found domesticable plants.

### Comparing Pathways to agriculture II

The Comparative Pathways to Agriculture project, ComPAg – aims to produce the first global comparative synthesis of the convergent evolution of domesticated plants and early agricultural systems based primarily on archaeobotanical data. This allows the establishment of comparative timelines for different locations. Clear that non-synchronous, but similar rates and that domestication and the establishment of agriculture were protracted evolutionary episodes, rather than rapid events – typically 2,000-3,000 years. The emerging model is one of protracted parallel trajectories from multiple starting points, but also with important differences that impinge on the bigger questions surrounding why agriculture arose:

- the role of Holocene climate change in some regions – north China, the Fertile Crescent, the Neotropics
- sedentism - the Fertile Crescent, the Yangtze in China
- seasonal mobility – north China and the Americas
- livestock farming – west Africa, south India

### The Causes of Domestication - Conclusions

Domestication and the origins of agriculture followed slow, complex, protracted and entangled processes and trajectories.

There may indeed have been a common set of conditions prompting agricultural origins, which involved both need and opportunity as contributory factors. In all cases we see: hunter-gatherer communities living in lakeside or river valley habitats so rich in wild food resources that they could establish larger sedentary communities where early experiments in cultivation and domestication would have been possible and where well-watered soils ensured reliable harvests. External triggers of climate change that accentuated the boundaries between these rich areas and surrounding hinterlands and pressures of growing human population are likely to have been important spurs prompting investigation and experimentation in ways to increase food resources, while intrinsic factors related to new opportunities for social integration in newly sedentary societies could also have played a key role.

Once started, process was autocatalytic – a one-way ticket.

## Unanswered questions

While these scenarios provide compelling ideas about why agriculture arose, many questions are still left without answers. Firstly, why did food production eventually outcompete hunting and gathering over almost the whole world, at the particular times and places that did, but not at earlier times and other places? Furthermore, why were there so few (13 to maybe 24) independent origins of agriculture? This seems even more puzzling because of the almost complete mismatch between the areas of independent agricultural origins (Fertile Crescent, E N America, Mesoamerica, Andes, China, New Guinea etc), and modern bread baskets of the world (California, North America’s Great Plains, Europe, the pampas of Argentina, Australia’s wheat belt, the cape of Southern Africa. Because these areas are so well suited to farming today, why were they not good areas to start farming in the past? One might expect that these would coincide, but they don’t.

## Consequences of Domestication – Agriculture in New Guinea

To understand the outcomes and consequences of domestication and the origin of agriculture, we can start by looking at agriculture in the highlands of Papua New Guinea, an area that we have talked rather little about up to now on the course.

For more than 50 years after outsiders arrived in New Guinea, it was thought that the highlands of Papua New Guinea were uninhabited, yet in fact this was the most densely populated part of the island, and was an area where agriculture had developed independently in isolation more than 6,000 years ago. However, in New Guinea, agriculture was based on just a handful of essentially starch crops and most notably banana and taro – an edible root crop, Colocasia esculentum in the family Araceae. These were the most important food staples in New Guinea and were not very productive or nutritious, with little protein. This implied a continued reliance on foraging and especially hunting in parallel with agriculture right up to the present day. No animals were domesticated (the pig was introduced much later), meaning there was no animal draught power and that agriculture was entirely dependent on human muscle power with all the limitations that entails. Advanced technologies were never developed, even in the 1960s people were still working with stone tools, no metal working specialists, no metal tools, no food surpluses and no development of sophisticated or advanced societies or expansionist civilizations. For 6,500 years agriculture in the highlands of PNG ticked along essentially unchanged.

## The First Farmers

Of course the asynchrony in the timing of the origins of agriculture also strongly influenced the consequences for human societies and cvilisations. As we saw, some areas had agriculture before others, and most notably the Fertile Crescent.

This all stands in stark contrast to other areas like the Fertile Crescent, Mesoamerica and the Andes, where rapid development of increasingly sophisticated societies followed the origins of agriculture within 3-4,000 years, and especially in the Fertile Crescent, blessed with its extraordinary biogeographic luck in terms of large-seeded grasses and docile herding animals predisposed for domestication, and where the early Babylonian empire grew with its massive temples 4,000 years ago. An early start and the vagaries of biogeography had propelled rapid rise of civilizations on an unprecedented scale that were set to change the course of human history.

## Consequences of Domestication I

- Investment in infrastructure, architecture and more permanent material culture
- Crop processing technology and labour requirements
- Larger community sizes
- Specialization of roles such as craft production
- Land ownership and the development of differential wealth accumulation
- Stratification in societies
- Population growth

## Consequences of Domestication II

Once domestication began, the changes of plants and animals that followed automatically under domestication, and the competitive advantages that domestication conveyed upon the first farmers, made the transition from the hunter-gatherer lifestyle to food production autocatalytic. However, the timing and speed of that transition varied considerably across regions.

The immediate consequences of the transition to agriculture were sedentism, investment in infrastructure, architecture and more permanent material culture, which in turn prompted larger community sizes and more specialization of roles such as craft production, land ownership and the development of differential wealth accumulation and stratification in societies. Whatever the causes of domestication, food production created enormous demographic, technological, political and military advantages – the first farmers got the first metal tools, writing, empires and professional armies. Remarkably enough agriculture also spawned many of our deadliest infectious diseases which require dense human populations to thrive and which often involved switches from domesticated livestock to humans (measles and tb from cattle, influenza from pigs and chickens). These advantages, guns, germs and steel, were the agents of conquest and were set to change the course of history. Food production bestowed on farmers enormous demographic, technological, political and military advantages over neighbouring hunter-gatherers. This means that the history of the last 10,000 years consists of tales of hunter-gatherer societies being driven out, infected, conquered or exterminated by farming societies in every area of the world suitable for farming.

## Consequences of Domestication III

Because agriculture arose in only a few areas of the world, and in certain of those areas earlier than in others, the peoples who through biogeographic luck first acquired domesticates acquired enormous advantages over other peoples, and expanded. As a result of these expansions and replacements, about 88% of all humans alive today speak a language belonging to one of a mere seven language families confined in the early Holocene to two small areas of Eurasia, that happened to become the two earliest areas of domestication, the Fertile Crescent and parts of China. Through that head start, the inhabitants of these two areas spread their languages and genes over much of the rest of the world.

Expansions of crops, livestock, people and technologies tended to occur more rapidly and earlier along east-west axes than along north-south axes, simply because the environments tend to be more similar in terms of climates, day length and habitats. This is evident in the rapid east-west movements and expansions of crops and especially livestock across Eurasia, and the rapid enrichment of societies in each part of Eurasia by crops and technologies from other parts of Eurasia. This contrasts with the rather slow spread and lack of connectivity between North America / Mesoamerica and South America, where Mexican wheels and writing never reached the Andes and vice versa, llamas ad potatoes never made it to Mexico.

## Consequences of Domestication IV – Impacts on Human Societies

Ultimately, these differences in biogeographic 'luck' and continental orientation / isolation became one of the main reasons why Eurasian peoples conquered Native American peoples, rather than the other way round. From c. 10,500 BP, the advent of food production was accompanied by human population explosion that has continued unabated to the present day. Food could be produced much more densely and productively. Food production also led to an explosion of technology, because storable food surpluses resulting from agriculture could be used to feed full time craftspeople and inventors, kings, beaurocrats, and soldiers prompting social stratification, political centralization and standing armies. All these advantages are what enabled farmers to eventually displace hunter-gatherers.

Rapid demographic expansions after origins of agriculture

The invention of agriculture is widely assumed to have driven human population growth. Here estimated population sized through time from a set of globally distributed whole mitochondrial genomes, after separating lineages associated with agricultural populations (Holocene) and hunter gatherer communities (Paleolithic) to test whether adoption of agriculture affect human population size.

Europe – very rapid population expansion coincident and following agriculture
Asia – same
These expansions were 3 to 6 times faster than earlier population expansions.
Africa – later, and more modest, but still detectable.

Although initial stimuli for the origins of early agriculture appear to be complex, changing modes of food production facilitated a novel capacity for exceptional human population growth.

Consequences of Domestication V - The Evolution of Epidemic Infectious Diseases

The main killers of human beings since the advent of agriculture have been acute, highly infectious, epidemic diseases that are confined to humans and that either kill the victim quickly or, if the victim recovers, immunize him/her for life. Such diseases could not have existed before the origins of agriculture, because they can sustain themselves only in large dense populations that did not exist before agriculture – often called crowd diseases. The mystery of the origins of many of these diseases has been solved by molecular biology which has revealed that they evolved from similar epidemic diseases of our herd domestic animals with which we began to come into close contact with 10,000 BP. For example, measles and tuberculosis arose from diseases of cattle; influenza from disease of pigs and ducks; smallpox from either cattle or camels.

These crowd diseases paradoxically became agents of conquest, because exposed individuals acquired some immune resistance and populations gradually acquired genetic resistance, but unexposed populations lacked any immunity. Because all but one of our large domestic mammals were Eurasian species, evolution of crowd diseases was concentrated in Eurasia, and these diseases became some of the most important agents by which Eurasian colonists expanding overseas killed indigenous peoples of the Americas, Australia, the Pacific and southern Africa.

Collision at Cajamarca

The uneven pace of agricultural development and of some societies getting ahead of others is epitomized in Jared Diamond's book *Guns Germs and Steel* in his chapter 'Collision at Cajamarca', the greatest collision of empires in human history. It was here that the Spanish conquistador arrived in 1532 and encountered the Inca emperor Atahuallpa, the monarch of the largest and most advanced state in the New World. Pizarro was leading a ragtag group of just 62 Spanish soldiers mounted on horses and 106 foot soldiers, was in unfamiliar mountainous terrain, ignorant of the local inhabitants, and completely out of touch with the nearest Spanish reinforcements 1500km to the north in Panama. Atahuallpa was in the heart of his own empire of millions of subjects, immediately surrounded by an army of 80,000 soldiers. Nevertheless Pizarro captured Atahuallpa within a few minutes of arriving in Cajamarca, held him prisoner for 8 months, and extracted history’s largest ransom of enough gold to fill a room 7 x 5 m to a height of 2m. Atahuallpa’s capture was enough to secure the conquest of the Incan empire by the invading Spanish. So, how did 168 Spanish soldiers overcome an army of 80,000? – the odds seem long, but the technological disparities were stark – European maritime technology, horses, guns and steel to make swords and knives and impenetrable armour – strong sharp weapons that slaughtered 1000s of thinly armoured Indians. The transformation of warfare had been transformed 5,500 years earlier by the domestication of horses on the Eurasian steppes. Pizarro of course arrived in the New World by sea, using European maritime technology, something lacking to Atahuallpa. Another factor in the Spaniards favour was writing, something that the Incan empire lacked, and which ultimately left Atahuallpa ignorant of the earlier Spanish conquests further north in Mexico.

## Conclusions

Domestication and the emergence of agriculture occurred in areas where hunter-gatherers, long familiar with the wild progenitors of crops and domestic animals, had reached a level of complexity and security that included sedentary settlements and accomplished harvesting, processing and storage technologies, in areas of high resource diversity generally located close to aquatic environments, such that farming was initially a supplement to a diverse and rich diet. Changes in climate that accentuated boundaries between these resource rich habitats and surrounding marginal hinterlands and associated increases in population density are likely to have spurred experimentation in food production. These circumstances coincide with more complex social organisation including competition, ownership & social stratification – larger and more complex hunter-gatherer societies. Finally, the availability of good potential domesticates – species that are pre-adapted or pre-disposed to domestication - biogeographic luck – is likely to have played a role in dictating where agriculture emerged first. Plant and animal domestication is the most important development in the past 13,000 years of human history, and one of the most important in the whole history of modern humans. It was the prerequisite to the rise of civilization and it transformed global demography. The timing of agriculture was a major factor in determining the outcomes of human history and explaining why some societies got ahead of others.

# BIO235 Lecture 12 – Guns, Germs & Steel – Source Materials

Denham, T.P., Haberle, S.G., Lentfer, C., Fullager, R., Field, J., Therin, M., Porch, N. & Winsborough, B. 2003. Origins of agriculture at Kuk Swamp in the highlands of New Guinea. *Science* **301**: 189-193.

Diamond, J. 1997. *Guns, Germs & Steel. The Fates of Human Societies*. W.W. Norton. A version of Jared Diamond's *Guns Germs & Steel* is available free on topdocumentaryfilms.com: http://topdocumentaryfilms.com/guns-germs-and-steel/

Diamond, J. Evolution, consequences and future of plant and animal domestication. *Nature* **418**: 700-707.

Fuller, D.Q. 2010. An emerging paradigm shift in the origins of agriculture. *General Anthropology* **17**: 8-12.

Fuller, D.Q., Allaby, R.G. & Stevens, C. 2010. Domestication as innovation: the entanglement of techniques, technology and chance in the domestication of cereals. *World Archaeology* **42**: 13-28.

Fuller, D.Q. et al. 2015. Comparing pathways to agriculture. *Archaeology International* **18**: 61-66.

Gignoux, C.R., Henn, B.M. & Mountain, J.L. 2011. Rapid global demographic expansions after the origins of agriculture. *Proceedings National Academy of Sciences, U.S.A.* **108**: 6044-6049.

Larson, G. et al. 2014. Current perspectives and the future of domestication studies. *Proceedings National Academy of Sciences, U.S.A.* **111**: 6139-6146.

Preece, C. et al. 2015. Were Fertile Crescent crop progenitors higher yielding than other wild species that were never domesticated? *New Phytologist* **207**: 905-913.

Price, T.D. & Gebauer, A.B. 1995. *Last Hunters First Farmers. New Perspectives on the Prehistoric Transition to Agriculture.* School of American Research Press.

Smith, B.D. 1998. Epilogue. *The Emergence of Agriculture*. Scientific American Library, New York.

## Non-human agriculture

Aanen, D.K. et al. 2002. The evolution of fungus-growing termites and their mutualistic fungal symbionts. *Proceedings National Academy of Sciences, U.S.A.* **99**: 14887-14892.

Brock, D.A., Douglas, T.E., Queller, D.C. & Strassmann, J.E. 2011. Primitive agriculture in a social amoeba. *Nature* **469**: 393-396.

Chomicki, G. & Renner, S.S. 2016. Obligate plant farming by a specialized ant. *Nature Plants* **2**: 1-4.

Farrell, B.D. et al. 2001. The evolution of agriculture in beetles (Curculionidae: Scolytinae and Platypodinae). *Evolution* **55**: 2011-2027.

Hata, H. & Kato, M. 2006. A novel obligate cultivation mutualism between damselfish and Polysiphonia algae. *Biology Letters* **2**: 593-596.

Mueller, U.G., Gerardo, N.M., Aanen, D.K., Six, D.L. & Schultz, T.R. 2005. The evolution of agriculture in insects. *Annual Review of Ecology, Evolution & Systematics* **36**: 563-595.

Silliman, B.R. & Newell, S.Y. 2003. Fungal farming in a snail. *Proceedings National Academy of Sciences, U.S.A.* **100**: 15643-15648.

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## BIO235 Plants & People – Evolution & Domestication of Crops
## Lecture 13 –Crop Breeding, the Green Revolution, Modern Food Production & Super-Domestication

### Introduction

Gaining an understanding of the relationships between plants and people, has been a central theme throughout the course. We have seen how people have changed plants, most notably via domestication of crops – the story of the harnessing of plant diversity to meet human needs. Similarly we have seen how plants have changed the world, and specifically how domestication has altered the course of human history.

- Plants are important for people
- Plants that changed the world
- The history of plant discovery
- The transition from foraging to farming
- The multiple independent origins of agriculture
- Domestication of crops and the phenotypic changes associated with domestication
- The movement and globalisation of crops and plants more generally
- Bioinvasion in a borderless world – moving whole genomes inter-continentally
- Polyploidy and crops – spontaneous hybrids following human movement and artificial sympatry
- Artificial hybrids to combine genomes of two species into one = genetic modification??
- Selection after domestication driven by farmer seed saving
- Does crop diversity matter? Prospecierara, Frutus & Retropomme

To bring the course to some sort of conclusion, I want to turn our attention to modern agriculture, modern crop breeding and some of the new technologies, such as genetic modification, that are involved in so-called super domestication. The question that we might want to think about is whether these technologies and their consequences are fundamentally changing the relationships between plants and people.

### Population Growth, Income Growth & Food security

Agricultural food production, including animal husbandry, has allowed the human population to grow from an estimated 10 million in the Neolithic to 6.9 billion today, and still expanding towards an expected peak of >9 billion by 2050. As we saw last week, the consequences for the planet (as well as for humanity and its domesticates) have been profound, and have included the complete transformation of almost every natural ecosystem on Earth. This staggering growth in human population combined with rising incomes and wealth are relentlessly pushing up global demand for food. Only 29% of the Earth's surface is land and only a little over a third of it is suitable for agriculture. In other words, only 10% of the surface of the Earth is suitable in terms of topography and climate for food production. Today, 75% of the world's 6.6. billion people live in the developing world where most of the world's poverty is concentrated. Currently c. 1 billion people live on < $1 / day and spend half their income on food. 60% of the world's population lives in Asia, where each hectare of land provides food for 27 people. By 2050 that land will have to support at least 43 people, even without factoring in the impacts of climate change, loss of land to biofuel production, loss of land to urbanization etc. 4.93 billion hectares are used for agricultural purposes, which also account for 70% of all fresh water consumed.

All this is happening at a time when crop production has slowed as efficient farmers have approached yield limits and yield gains from crop breeding are tailing off. Current evidence suggests that maximum crop yields, e.g. of rice, are close to fundamental yield barriers shaped by the efficiency of solar energy conversion.

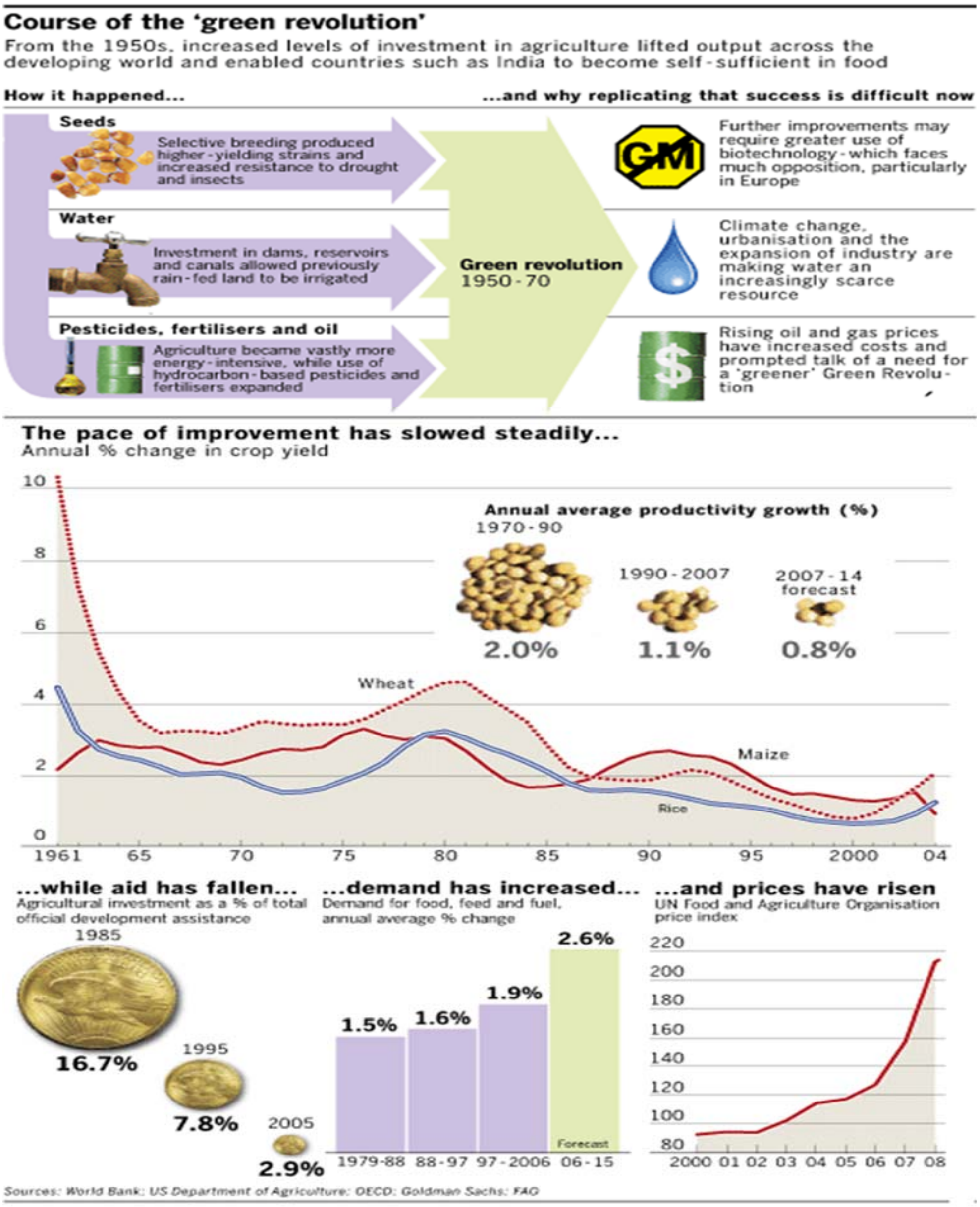
### Biofuels

Biofuels are competing for agricultural land and for crops like maize and oil palm. This is pushing the prices of food crops higher and reducing available land for food production.

Traditional Crop Breeding and the Green Revolution

Before the beginning of the 20th century almost all increases in crop production were achieved by expanding the area cultivated. Farmer selection had led to the development of landraces suited to particular environments, but grain yields, even in favourable environments, rarely averaged > 2.0 metric tonnes per ha. From the 1930s, yield gains via conventional crop breeding, i.e. selection and backcrossing to generate elite high yielding varieties have pushed up yields steadily over the last 70 years or so, initially in the USA, Japan and Europe. Since the early 1970s, dramatic yield increases, heralded as the Green Revolution, have occurred also in many developing countries, especially in Asia and Latin America. In some respects crop breeding has been remarkably successful in continuing to push crop and food production ever higher. However, yield gains have tailed off and many believe that the physiological limits to conventional crop breeding have been reached.

This raises questions as to how the required increases in yields will be achieved?



## Modern Agriculture

Growing potatoes, perhaps more than any other crop, has underpinned human population growth. We heard about this in Ireland. The same was true in Switzerland and the same has happened in more recent years in other countries, for example in the last few decades in Nepal in the Himalaya. Also, perhaps more than any other crop, potato growing is dominated by pests and epitomizes the dilemmas and conflicts surrounding different approaches to modern agriculture – high inputs, centralization, monoculture, uniformity, an industrial food chain

Idaho – the American Midwest. 100ha circles formed by irrigation pivots. Doused with so much pesticide that leaves have a dull white chemical bloom, the fields and soil cleansed of all life except the potato plant – a triumph of human control.

- Early Spring before sowing - soil fumigant to control nematodes and soil diseases – enough to kill every trace of microbial life in the soil.
- Herbicide Lexan, Sencor or Eptam – to eradicate weeds
- Systemic insecticide such as Thimet to the soil to be absorbed by seedlings and kill any insects that eat the leaves.
- Young plants - Second herbicide to control weeds
- 10 weekly sprays of chemical fertilizer
- As rows close, a fungicide, Bravo applied to control late blight, the same fungus that caused the Irish potato famine
- Dust crop with an organophosphate insecticide against aphids which transmit the leaf roll virus with causes necrosis a brown-spotting of the potato's flesh

Large quantities of chemical fertilizers, pesticides, machinery and fuel. Expensive and energy hungry inputs.

## Control and uniformity

So much of what modern agriculture is all about - the clean potato fields and computer-controlled crop circles of Idaho – comes down to the perfection and uniformity demanded by consumers. McDonald's French fries provide the classic example. The perfect slender golden rectangles, long enough to overshoot their trim red containers like a bouquet. The image and the food rolled into one, and an expectation that McDonalds has successfully planted in the heads of a few billion people around the world. The same in Tokyo, Zurich, Beijing, Moscow, Azerbaijan, Cape Town, and even Lima and La Paz. It is perhaps a sobering revelation that McDonald's in Lima and La Paz, with the heartlands of the potato and its treasure house of diversity nurtured and engineered over millennia by Andean farmers on the doorstep, import Monsanto's NewLeaf potatoes from the USA to make French fries in Bolivia and Peru….Such perfection can only be produced by a few varieties, and concentrating on a single variety like NewLeaf for global production of perfect French fries is the ideal option for McDonalds – the ultimate uniformity and control in global food production. A global desire for perfect French fries needs a global monoculture that depends on technologies like genetic engineering. NewLeaf might never have been developed without support from McDonalds and the massive and uniform market that they represent.

The history of the potato encapsulates the central feature of crop domestication – drastic reduction of diversity from the hugely rich treasure house of diversity selected, nurtured and driven by Andean farmers over millennia to the single clones that led to the Irish famine and the genetically engineered varieties that dominate modern potato production today….

## The Backlash against Modern Agriculture

One of the biggest changes brought about by domestication is the globalization of food. The idea that we can eat foods that originate from anywhere in the world, and which may have been produced anywhere in the world. We saw this when we tallied up what we eat today. Much of this is still a one-way transfer to richer countries in the north, but increasingly this globalization is operating truly globally. As developing countries become wealthier, many of them have developed a taste for fast food. The globalization of food is nearly complete and many would argue has brought us abundant food at low prices. Of course, not everyone is happy and the last decade has seen growing awareness of environmental, health, and quality of life issues associated with modern food production – a backlash in the form of a whole suite of movements favouring a return to more local production, to more seasonal foods, of tallying up food miles, of devoting more attention to the quality of food which lies are the heart of the slow food movement, of worrying about the environmental and health impacts of high pesticide use and the advent and rise of organic food, and finally, of thinking about the wider equity issues associated with globalization and the advent of Fair Trade Food. In short, in wealthier countries, where there is a general adequacy of food, consumers and the food market have become more complex.

Organic Farming
Long complex crop rotations
Strips of flowers on field margins
Biocontrol
Diversity - Mix of crops and crop varieties
Green manures, manure
> labour; fewer inputs

Feeding 9 billion people
Projections and analyses reveal a number of key features about future food production and how the world is going to feed a population of 9 billion people:

- Nearly all new food production in the next 25 years will have to come from existing agricultural land
- Only 55% of food crop calories directly nourish people – meat, dairy products and eggs from animals raised on plant food, supply another 4%
- Reducing food waste – 30-40% of food is lost to waste
- Closing the yield gap: improving nutrient and water supplies where yields are lowest could result in a 58% increase in global food production

Here the emphasis is on *sustainable intensification*

Beyond that the emphasis will be on increasing production limits through superdomestication – the harnessing of plant genomes in ever more sophisticated ways.

Nature Outlook on Food Security

- The Living Library
- Space to Grow
- Solar Upgrade
- A Meaty Issue
- The Future of Agriculture

Nature (2017)

Technology I - Robobees
Pollinators around the world are in trouble: A recent report puts 40% of the smallest ones—like butterflies and bees—at risk of extinction. Could miniature drones fill the gap? To find out, researchers ordered a small drone online and souped it up with a strip of fuzz made from a horsehair paintbrush covered in a sticky gel. The device is about the size of a hummingbird, and has four spinning blades to keep it soaring. With enough practice, the scientists were able to maneuver the remote-controlled bot so that only the bristles, and not the bulky body or blades, **brushed gently against a flower's stamen to collect pollen**—in this case, a wild lily (*Lilium japonicum*), they report today in *Chem*. To ensure the hairs collect pollen efficiently, the researchers covered them with ionic

liquid gel (ILG), a sticky substance with a long-lasting “lift-and-stick-again” adhesive quality—perfect for taking pollen from one flower to the next. What’s more, the ILG mixture has another quality: When light hits it, it blends in with the color of its surroundings, potentially camouflaging the bot from would-be predators. But don’t expect fields filled with buzzing bots just yet. Because the pollinator bot is remote controlled, it would need a human pilot to guide it from plant to plant, impractical for guiding large swarms. However, it’s possible that the drones could one day learn to fly on their own, using GPS and artificial intelligence, the scientists say. The one thing they still won’t be able to do? Make honey. But with their pollination workload lightened, maybe we could leave that one to the bees.

### Technology II – Robots on the Farm

Autonomous machines to solve shortage of agricultural labourers.
Vertical agriculture - verticrop

### Technology III – Electric Food

This sounds like science fiction, but it is already approaching commercialisation. For the past year, a group of Finnish researchers has been producing food without either animals or plants. Their only ingredients are hydrogen-oxidising bacteria, electricity from solar panels, a small amount of water, carbon dioxide drawn from the air, nitrogen and trace quantities of minerals such as calcium, sodium, potassium and zinc. The food they have produced is 50% to 60% protein; the rest is carbohydrate and fat. They have started a company (Solar Foods) that seeks to open its first factory in 2021. This week it was selected as an incubation project by the European Space Agency. They use electricity from solar panels to electrolyse water, producing hydrogen, which feeds bacteria that turn it back into water. Unlike other forms of microbial protein (such as Quorn), it requires no carbohydrate feedstock – in other words, no plants.

### Neglecting legumes has compromised human health and sustainable food production

- A shift in land use towards grain legumes and away from livestock will reduce carbon footprint for production of protein
- Legumes lag far behind cereals
- Health and nutritional benefits of legumes
- Symbiotic nitrogen fixation contributes to sustainable cropping systems – crop rotations, inter-planting

### Urban Agriculture

Detroit, Havanna, Zurich and Honk Kong – the growing interest in growing food close to people (locavores) and for city people to get more involved in food production.

### Super-Domestication

We are entering a new era in relation to human understanding of an influence on the genetics of crop domestication. Future advances in crop improvement will come via understanding the genome and its genes. This new era has been dubbed ‘super-domestication’ in reference to using new ways to enhance yields that go beyond selection from naturally occurring genetic variation using techniques not available to traditional plant breeders. As an array of genome manipulation technologies are developed, new ways to overcome barriers to gene exchange are possible. These will be the way to generate super domesticates with increased yields, resistance to biotic and abiotic stress and new traits for new markets. The extent to which plant development can be modified to meet human needs has certainly not reached its limits. In fact there is every reason to expect that by using the full range of available tools, modern breeders can further modify crops to improve their productivity and nutrition, and to reduce the impacts of humans on the environment.

### New Breeding Techniques

New phase of exponential discovery and innovation

New genes with large beneficial effects
Construction and deployment of complex blocks of useful genes
which can be easily inserted into elite germplasm
New Breeding techniques:

- Genome editing
- Oligonucleotide directed mutagenesis
- Cisgenesis & transgenesis

## Rapid improvement of domestication traits in an orphan crop by genome editing

Genome editing holds great promise for increasing crop productivity, and especially advancing breeding in minor crops which may be burdened by undesirable characteristics resembling wild relatives. The CRISPR (clustered regularly interspersed short palindromic repeats) approach to mutate orthologues of a mainstream crop and target genes that control plant architecture, flower production and fruit size, i.e. translating knowledge from model crops to rapidly create targeted allelic diversity and novel breeding germplasm in distantly related minor crops.

The example here is the ground cherry, Physalis pruinosa a wild Solanaceae grown for its sweet berries in C and S America and distantly related to the tomato and the potato. This species shows many traits that look just like the wild progenitor of the tomato. The CRISPR allows orthologues of select domestication and improvement genes in domesticated tomato to be used to modify the ground cherry via genome editing. For example, engineering the coding sequence and regulatory mutations in orthologues of the tomato fruit abscission gene or tomato fruit size QTLs

## Biotechnology & Genetically Modified Crops

GM foods or GMOs (genetically modified organisms) involving transfer of specific genes from one organism to another. This, of course, involves not just the transfer of genes from wild relatives of crops into mainstream crops, but across all plants and also from non-plant organisms as well. The best-known example is use of Bt genes in maize and other crops. Bacillus thuringensis is a naturally occurring bacterium that produces crystal proteins that are lethal to insect larvae. By transferring Bt crystal protein genes into maize, enables it to produce its own pesticides against insects, such as the European corn borer. This ability to extend the frontiers over which genes can be transferred is what is new about GM technology.

USA - > 50 million acres planted to genetically modified crops – most of it maize, soybeans, cotton and potatoes that have been engineered to produce their own pesticides or to withstand herbicides. Examples are:

- Herbicide Tolerance. Monsanto has produced a strain of soybeans that is genetically modified not to be affected by their herbicide product Roundup – so-called Roundup-Ready Soya. Use of this strain means that farmers require only one application of weed-killer, reducing the amounts of herbicides used.
- Pest Resistance. Monsanto's 'Newleaf' Potato – genetically engineered to produce its own insecticide via a gene borrowed from one strain of the common soil bacterium *Bacillus thuringiensis*, or Bt, which gives the potato cells the information they need to manufacture a toxin lethal to the Colorado potato beetle, but which is harmless to humans. This insecticide is produced in every cell of every leaf, stem, flower, root, and potato. The promise of genetic engineering is to replace expensive and toxic chemicals with expensive and apparently more benign genetic information.
- Attempts have been made to enhance cold tolerance by introducing antifreeze genes from cold water fish into crops such as tobacco and potato.
- 'Golden Rice' – researchers at the Swiss Federal Institute of Technology Institute of Plant Sciences, funded by the Rockefeller Foundation, have created a strain of golden rice containing unusually high content of beta-carotene (Vitamin A). However, deployment of this

nutritionally-enhanced rice has not happened, perhaps because of vigourous anti-GM food protests in Europe.

We are promised that crops will soon be genetically modified to bring us potatoes that absorb less fat when fried, maize that can withstand drought, grass lawns that don't need to be mowed, bananas that deliver vaccines, tomatoes enhanced with flounder genes to withstand frost, wheat, barley and rye 'on the cob' using the maize tga1 gene which regulates cob development, cotton that grows in every colour of the rainbow, hay-fever free grass, a no-tears onion, caffeine-free coffee plants, and rice with the C4 photosynthetic pathway.

Genetic modification overrides and extends genetics beyond the limits imposed by crossability in natural systems. Now Man can add new and unexpected variability using genes transported across whole phyla into the genome of a plant – frost tolerance from flounder genes, disease resistance from viruses, insecticides from soil bacteria, luminescence from fireflies, the possibilities are virtually endless… For the first time the genome itself is being domesticated.

### How prevalent are GM crops?

In the USA, there has been very rapid growth in the % cultivated area devoted to GM varieties for a many mainstream crops, and especially cotton, oil seed rape (canola), soybean and maize. This means that most processed foods in the USA are likely to contain at least a % of GM ingredients, especially given the ubiquity of soybean derivatives as food additives in the modern American diet. Thus, virtually all US consumers have been exposed to GM food products. GM crops are also being grown in Argentina, Canada, China, Mexico, South Africa, and Australia.

### Criticisms of GM foods – Frankenstein Food, Jumping genes and Super Weeds

In sharp contrast to this mainstream adoption of GM varieties in the USA, Europe has been extremely slow to release GM varieties for commercial use, due to widespread public opposition. Anti-GM food protestors have been especially active in Europe, perhaps because of recent food scares that have undermined confidence in food safety. In response, Europe entered an unofficial moratorium on the growth and import of GM crops, that led to a trade dispute with the USA, and a requirement for mandatory labeling of GM foods. GM crops are today very rare in Europe, and public opinion remains largely negative.

Criticisms of GM fall into three main categories: environmental hazards, human health risks and economic concerns.

- Environmental hazards. These include:
    - Unintended harm to other, non-target organisms. The example that has captured most publicity is a study suggesting that Monarch butterflies have been killed by being exposed to pollen from Bt corn, but the results of this study are contentious.
    - Reduced effectiveness of pesticides – i.e. that insects will become resistant to B.t.
    - Gene transfer to non-target species, e.g. of herbicide tolerance genes into weeds, that will become 'superweeds'. The idea of GM gene transfer has been the focus of several legal cases brought by Monsanto against farmers who had GM genes detected in their crops and were accused of not paying royalties, but who claimed that their crops had been cross-pollinated by neighbours GM crops. This hazard has prompted development of male sterile lines, or lines in which the pollen does not contain the transgene.
    - Gene transfer of ecologically relevant traits to traditional crop varieties and land races and other crop wild relatives with potential impacts on the genetic diversity and crop genetic resources. The reality of this sort of gene transfer was dramatically demonstrated for maize where the presence of a common element in the transgenic constructs – the 35S promoter – used in Yieldguard Bt maize and Roundup-Ready maize GM varieties - was detected in 'criollo' land races in the remote mountains of

    Oaxaca, the centre of origin and diversification of maize. It is thought that the occurrence of numerous introgression events of these transgenic DNA constructs happened via pollination, suggesting a high level of gene flow from industrially produced GM maize towards populations of progenitor land races. The frequency of these transgenic constructs suggests that they are probably maintained in land race populations from one generation to the next. The diversity of introgressed DNA in land races is particularly striking given the existence in Mexico, of a moratorium on the planting of transgenic maize since 1998. The presence of these constructs must either have happened before the moratorium, or loose implementation of the moratorium.

- Human health risks include possible:
    - Allergenicity – new allergins caused e.g. by transferring a gene from peanut into soybean.
    - On the whole, health scares (Frankenstein Foods), have been prompted by controversial studies that suggested that a few strains of GM potatoes might be toxic to laboratory rats in the mid 1990s. These concerns have largely proved to be groundless and scientists believe that GM foods do not present any risks to human health.
- Economic concerns: bringing GM varieties to commercial use is long and costly and Agri-Biotech companies want to protect these investments via patents. Consumer advocates are concerned that patenting plant varieties will raise the price of seeds so high that small farmers in developing countries will not be able to afford seeds for GM crops. So-called Terminator Technology is a way to introduce Suicide genes into GM plants to ensure that patents cannot be infringed and royalties have to be paid. These concerns are heightened by the idea that the agricultural biotech industry is encouraging reliance on own-brand herbicide resistant plants (e.g. Roundup-ready), which could create monopolies.

Implications of GMOs: Who owns plant genetic resources?
Until the 1970s, biodiversity was considered to be part of the 'common heritage of humankind'. Under this regime, biological resources are treated as belonging to the public domain and are not owned by any individual, group, or state. This principle of common heritage has guided diffusion of crop genetic resources, their exchange among farmers and their introduction to new countries via international and national genebanks, which still operate by that principle. There have been exceptions to the rule of open access:

- Restrictions on export of e.g. Cinchona by Peru and Bolivia in the 19th Century, coffee by Ethiopia.
- Attempts by colonial powers to monopolize certain resources, e.g. Myristica fragrans, the nutmeg by England the Netherlands and Portugal in the 17th Century.

Nevertheless, the overarching principle of open and free access dominated.

The last three decades have seen a significant change from this common heritage principle to a resource under sovereignty of nation states and intellectual property rights (IPRs), including:

- Utility patents for life forms
- Plant Variety Protection or Rights
- CBD and MTAs.
- Genes are now the intellectual property of companies like Monsanto – proprietary genetic 'operating systems' to run this new generation of crop plants.

Terminator Technology
In March 1998, patent number 5,723,765, describing a novel method for the 'control of plant gene expression' was granted jointly to USDA and a cottonseed company Delta and Pine Land, the bland language obscuring a radical new genetic technology that causes the seeds that a plant makes to become sterile. This new technique quickly became known as the Terminator, designed to ensure

that seed can only come from companies. It is only in the last few decades, with the introduction of modern hybrids, that farmers began to buy their seeds from big companies. Even today many farmers save some seed to replant the following year. It has been estimated that 1.4 billion people depend on saved seed for growing food. This has allowed farmers to select strains adapted to local conditions. It is this process that has produced most of our major crops over the millennia.

Terminator technology spawned an international barrage of criticism and companies such as Monsanto have given up such approaches, but there are other 'genetic use restriction technologies' that are used to protect crop variety patents.

### Rice (again...)

- The world's most important staple food crop
- Feeds >50% of the world's population, 700 million people in Asia alone depend on rice, and > people than any other crop since the time of its domestication
- The world's population is expected to reach 10 billion by 2050.
- 20% of all calories consumed by humans
- 408,661 million metric tonnes produced per year
- During the next 40 years, rice production needs to increase by 50%, whilst adapting to adverse changes in climate and water availability
- Rice yields are approaching a theoretical limit set by the crop's efficiency to harvest sunlight and using its energy to make carbohydrates

### How can rice production keep pace with population growth?

In Asia, for the last few decades, rice production has tracked human population growth. The big question is how to keep on increasing rice production in line with human population growth?

### The C4 Rice Project

The realization that genetic gains in terms of increased yields from crop breeding are declining against a backdrop of progressively increasing demand for food and limited resources of land and water, suggest that perhaps the only way to increase world rice production to the levels foreseen for 2050 is to change the fundamental biophysical structure and biochemical pathways of the rice plant from C3 to a C4 photosynthesis to make it a more efficient user of energy from the sun. Rice has a C3 photosynthetic pathway, which is less efficient than that of e.g. maize which has a C4 pathway. This is the aim of the C4 Rice Project – *'Using the sun to end hunger'*. The aims of this project are to discover the genes that are responsible for C4 photosynthesis and generate a model rice plant with increased photosynthetic efficiency by installing this suite of genes in elite rice lines. Once the genes controlling C4 photosynthesis are discovered, it should be possible to introduce and activate them in wheat and legume crops as well.

### C4 photosynthesis

Rice has a C3 photosynthetic pathway, which is less efficient than that of e.g. maize which has a C4 pathway. In terms of water use efficiency, photosynthetic nitrogen use efficiency and radiation use efficiency, C4 (maize) is 1.5-2.8 times more efficient than maize. C4 crops have higher yields, reduced water loss and increased nitrogen use efficiency, especially when grown in hot and dry environments. This raises the prospect of significantly increasing the productivity of rice if it could be changed into a C4 plant.

In the majority of plants, including rice, C02 is fixed into carbohydrate by the photosynthetic enzyme rubisco. Rubisco is inherently inefficient because it also catalyzes a reaction with oxygen from the air as photorespiration. Above 20C, there is increasing competition by oxygen and a dramatic reduction in CO2 fixation and photosynthetic efficiency. While all this is happening, water is escaping from the leaves while CO2 is diffusing in. Thus in the tropics, where most rice is grown, photosynthesis becomes very inefficient. C4 plants are more efficient in CO2 concentration that results in increased efficiency in water and nitrogen use and improved adaptation to hotter and drier environments.

## C4 photosynthesis

C4 photosynthesis is a complex trait that involves BOTH important leaf anatomical differences AND significant biochemical pathway changes. The anatomy of leaves of C4 plants such as maize is modified (Kranz anatomy) such that different photosynthetic pathways take place in bundle sheath cells and mesophyll cells, a distinction not seen in C3 plants. In C3 plants atmospheric CO2 reacts with ribulose 1.5-biphosphate catalysed by the rubisco enzyme, to produce an organic molecule with a backbone of three carbon atoms which is then used to build sugars and more complex hydrocarbons. In C4 plants, CO2 is assimilated using a different enzyme, phosphoenolpyruvate carboxylase – PEPC – which attaches CO2 to the three carbon compound PEP to produce oxaloacetate, a molecule that contains four carbon atoms, which is in turm converted to a series of other four-carbon products, which are finally broken back down into three-carbon compounds and CO2, which is then fed to Rubisco. This two-stage process is more efficient because it allows plants to boost levels of CO2 reaching Rubisco. PEPC has a stronger affinity for CO2 than Rubisco and so can work better a low concentrations of CO2, and it is thought that the evolution and rise to ecological dominance of C4 grasses was triggered and driven by falling atmospheric C02 levels in the Miocene. Given that it would involve major changes in both biochemistry and anatomy, turning rice into a typical C4 plant is no trivial matter. A large number of genes are clearly involved. In that sense the C4 rice project is extremely ambitious.

## Convergent evolution of the C4 pathway

The fact that in nature the shift from C3 to C4 photosynthesis has occurred at least 45 times, indicating that despite the leaf structural and biosynthetic complexity of the C4 trait, it is a relatively easy pathway to evolve. The C4 Rice consortium, formed in 2008 and coordinated by IRRI and funded by the Gates Foundation, believes that this is feasible and will increase rice yields by 50%, double water use efficiency, and use less fertilizer.

Genetic transformation of rice to C4 photosynthesis would represent a different league of genetic modification in terms of the scale and complexity of the changes required. It is also being approached by a consortium of scientists working entirely in the public domain, with potential benefits this could ensure for the free availability of the technology to farmers in the future.

## Nitrogen Fixation

Another ‘big’ complex trait that is being worked on in similar ways is nitrogen fixation, the symbiotic association of N-fixing bacteria Rhizobium through formation of root nodules, that is common in legumes and legume crops such as beans, soya bean, lentils, peas etc. $N_2$ constitutes 80% of the atmosphere providing a virtually unlimited supply yet very few plants, and no animals can assimilate nitrogen in its free form. Furthermore, synthetic nitrogen fertilizers used in agriculture have high economic, energy and environmental costs. The genes involved in the signalling pathways between the bacteria and the plant are now well understood and, just as for C4 rice, scientists are working to transform cereal crops into nitrogen fixing plants.

## A New Era in the Relationship between Plants & People?

New classes of crop plants is transforming the long and complex and by now largely invisible food chain that links every one of us to the land and to plants. Some have suggested that this represents a new era in the relationship between plants and people. Has genetic modification fundamentally changed the relationship between plants and people?

Some have argued that the new technology of genetic modification represents the biggest change in terms of our relationship with plants since people first learned how to cross one plant with another.

Human control of nature is taking a giant step forward. The kind of reordering of nature represented by rows in a farmer’s field can now take place at a whole new level: within the genomes of the plants themselves. Arguably we have stepped out onto new ground.

# BIO 235 – Lecture 13 Source Materials

Abraham, B. et al. 2014. The system of crop intensification: reports from the field on improving agricultural production, food security, and resilience to climate change for multiple crops. *Agriculture & Food Security* **3**:4.

Boivin, N.L. et al. 2016. Ecological consequences of human niche construction: examining long-term anthropogenic shaping of global species distributions. *Proceedings National Academy of Sciences, U.S.A.* 113: 6388-6396.

Cassman, K.G. & Liska, A.J. 2007. Food and fuel for all: realistic or foolish? *Biofuels, Bioproducts and Biorefining* **1**: 18-23.

Christin et al., 2007. $C_4$ photosynthesis evolved in Grasses via parallel Adaptive Genetic changes. *Current Biology* 17: 1241-1247. (See commentary by E.H. Roalson, same issue).

Ellis, E.C. et al. 2013. Used planet: a global history. *Proceedings National Academy of Sciences, U.S.A.* **110**: 7978-7985.

Flavell, R.B. 2016. Greener revolutions for all. *Nature Biotechnology* **34**: 1106-1110.

Foley J.A. et al. 2011. Solutions for a cultivated planet. *Nature* **478**: 337-342.

Foyer, C.H. et al. 2016. Neglecting legumes has compromised human health and sustainable food production. *Nature Plants* **2**: 16112.

Gepts, P. 2004. Who owns biodiversity, and how should the owners be compensated? *Plant Physiology* **134**: 1295-1307.

Godfray, H.C. et al. 2010. Food security: the challenge of feeding 9 billion people. *Science* **327**: 812-818.

Hibberd, J.M., Sheehy, J.E. & Langdale, J.A. 2008. Using C4 photosynthesis to increase the yield of rice – rationale and feasibility. *Current Opinion in Plant Biology* **11**: 228-231.

Lemmon, Z.H. et al. 2018. Rapid improvement of domestication traits in an orphan crop by genome editing. *Nature Plants* **4**: doi: 10.1038/s41477-018-0259-x

Losey, J.E., Rayor, L.S. & Carter, M.E. 1999. Transgenic pollen harms monarch larvae. *Nature* **399**: 214.

Mitchell, P.L. & Sheehy, J.E. 2006. Supercharging rice photosynthesis to increase yield. *New Phytologist* **171**: 688-693.

Nature Outlook. 2017. Food Security. *Nature* **544**: S1-S21.

Pollan, M. 2002. The Potato. Chapter4, In: *The Botany of Desire – A Plant's-Eye View of the World*. Random House, New York.

Pallottini, L., Garcia, E., Kami, J., Barcaccia, G. & Gepts, P. 2004. The genetic anatomy of a patented yellow bean. *Crop Science* **44**: 968-977.

Quist, D. & Chapela, I.H. 2001. Transgenic DNA introgressed into traditional maize landraces in Oaxaca, Mexico. *Nature* **414**: 541-543.

Ruddiman, W.F. et al. 2015. Late Holocene climate: natural or anthropogenic. *Review of Geophysics* **54**.

Sage, R.F. (2004). The evolution of $C_4$ photosynthesis. *New Phytologist* 161: 341–370.

Surridge, C. 2002. The rice squad. *Nature* **416**: 576-578.

Tilman, D., Balzer, C., Hill, J. & Befort, B.L. 2011. Global food demand and the sustainable intensification of agriculture. *Proceedings National Academy of Sciences, U.S.A.* **108**: 20260-20264.

ETC Group. The New Biomasters. Synthetic Biology and the Next Assault on Biodiversity and Livelihoods. http://www.etcgroup.org/en/node/5232

'Terminator' technology - United States Patent 5,723,765: Oliver, et al. March 3, 1998: http://www.uspto.gov

The C4 Rice Project
http://irri.org/our-partners/networks/c4-rice

Robobees. Could this pollinating drone replace bees and butterflies?
http://www.sciencemag.org/news/2017/02/could-pollinating-drone-replace-butterflies-and-bees

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