colonizes cells of the cortex to form distinct structures called arbuscules, which are sites of nutrient transfer.

The AM fungus receives carbon from the plant, and the plant, in turn, may receive a range of benefits, including improved plant growth and fitness (through increased mineral nutrition, principally phosphate), improved water relations and protection from pathogens. The growth of hyphae from the mycorrhizal root increases the volume of soil from which nutrients and water can be absorbed, thus extending the root system. The complex inter- and extra-cellular relationship between plant roots and AM fungi requires a continuous exchange of signals to ensure the proper development of the symbiosis. Plant **hormones** and certain flavonoids in root exudates, such as biochanin, may play a role in the regulation of the symbiosis, and many similarities between the signalling in the rhizobial and the AM symbiosis have been found. Several aspects of sexual reproduction can be influenced by AM, including the timing of reproductive events and number of flowers, fruits and seeds. Seed quality can also be strongly influenced by mycorrhizal infection, resulting in variation in seedling vigour and resultant competitive ability.

1. Inoculation and potential uses

The beneficial effects of AM on plant growth and health have prompted an increased interest in the use of mycorrhizas, exploiting this association as one of the most useful biological means of assuring high quality plant production with minimal input of chemicals.

Mycorrhizal inoculation is most beneficial where indigenous mycorrhizal fungi are absent or scarce, such as disinfected soils – normally used in commercial horticulture and forestry nurseries – inert substrates, micropropagation techniques, artificial landscapes, amenity and urban settings. However, the successful use of AM fungi can only be achieved under certain conditions: benefits will only be obtained by a careful selection of compatible host/AM/substratum combinations.

A variety of mycorrhizal inoculants are commercially available – some being blends of AM and ectomycorrhizas. AM fungi are obligate biotrophs unable to grow in pot cultures; hence inoculum has to be produced on living roots, and includes spores, mycelia and mycorrhizal root fragments. These are normally incorporated into a carrier, such as sand, soil, **peat**, clay, **vermiculite** and other substrates. The development of seed**coating** or liquid delivery systems has been limited mainly by the propagule size and most commercial inoculants are granular formulations.

The most common application method places the inoculum below the seed or seedling before planting, which ensures close proximity with the developing root for effective colonization. The development of an efficient AM at the nursery and seedling stage is essential to produce high quality seedlings and the general rule is that the earlier the inoculant is applied, the greater the benefit. AM inoculation of turf grasses at seeding is becoming a common practice on golf courses and football pitches, where inoculants are applied at 20 g/m^2 with calibrated granule applicators. Many commercial horticulture and ornamental crops, such as tomatoes, aubergines, peppers, leeks, asparagus and Gerbera, are also being routinely inoculated at seeding time, for example in Japan and Thailand (see: **Rhizosphere microorganisms**). Also, all **orchids** have a requirement for mycorrhiza at germination (Basidiomycetes mainly of genus *Rhizoctonia*); though *in vitro* germination of some species is possible without a fungal symbiont, cultivation requires infection for continued development of the protocorm. (IA)

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Archaeobotany

Archaeobotany (or palaeoethnobotany) is the study of plant remains from archaeological sites, with the aim of understanding past human diet, food gathering and cultivation, and environmental change. The term encompasses both macroremains (seeds and wood/charcoal) and microremains (pollen and phytoliths). Most archaeobotanists work on seed remains, including in modern forensic science, here broadly defined to include all kinds of propagules.

1. History

Interest in archaeobotany started in the late 19th century, with the discovery of desiccated plant remains in ancient Egyptian tombs, and Oswald Heer's classic 1865 report on Neolithic plant-remains from Swiss lake villages. Until the 1960s, archaeobotany was usually a part-time occupation of botanists and agronomists. Recovery of plant remains by excavators of archaeological sites was piecemeal and depended on the discovery of obvious deposits, such as burnt storerooms containing jars or silos of seeds. With exceptions, such as the work of the pioneering Danish archaeobotanist Hans Helbaek (1907–1981), reports were of variable quality. In the 1960s archaeologists developed a stronger interest in economic and environmental aspects of ancient societies, and the development of flotation techniques allowed far more reliable recovery of plant remains. Archaeobotany is now a discipline in its own

Table A.7. Seed remains found in jars at the Late Bronze Age shipwreck (1300 BC) at Ulu Burun, off the southwest coast of Turkey.

Fig	*Ficus carica*
Grape	*Vitis vinifera*
Pomegranate	*Punica granatum*
Olive	*Olea europaea*
Almond	*Amygdalus communis*
Pine	*Pinus pinea*
Coriander	*Coriandrum sativum*
Black cumin	*Nigella sativa*
Sumac	*Rhus coriaria*

Note the concentration of fruits and spices, rather than the cereals and pulses typical of daily subsistence.

right, and an integral part of many archaeological projects. The work of archaeobotanists is now mainly carried out within academic or commercial archaeological organizations, although the cross-disciplinary work continues to require strong botanical skills.

2. Preservation and recovery

Most seeds either germinate and establish seedlings, or are consumed by animals or microorganisms. Uncharred seeds and other plant parts only survive from antiquity under unusual conditions. One such case is in hyper-arid areas, such as the deserts of North Africa or the American southwest. At dry sites such as Qasr Ibrim, in southern Egypt, vast quantities of plant remains survive, ranging from food debris to baskets and paper documents. Permanently waterlogged sites, such as the Viking levels at the city of York in northern England, Windover in the wetlands of Florida, or the cargoes of shipwrecks, also preserve a wide range of plant materials (Table A.7), although with some loss of soft tissues such as **endosperm**. Comparable preservation occurs in mineral-rich deposits such as latrines, where carbonates and phosphates replace plant tissues leading to the survival of mineralized plant remains.

Except in these unusual cases, by far the most widespread form of preservation is by charring in fires. Plant materials that fall into ash, or which are in heaps or jars, will char and turn black at temperatures between about 150 and 400°C. Charring preserves the shape of seeds remarkably well, and also fine features such as seed anatomy and **seedcoat** cell patterns. Wood and tubers also char well, but light seeds and plant parts, such as leaves, tend to burn to ash. In addition to favouring more solid plant parts, charring will also disproportionately favour plants used for fuel. For example, cereal chaff and straw is often used to fuel fast fires or as kindling, so is likely to be charred. Spices and medicinal plants will be carefully hoarded and are less likely to be burnt. Charred seeds can also derive from a less direct route – burning of animal dung, which contains undigested seeds from the animals' forage and fodder. In general, charred plant remains are dominated by food and fuelplants, and other uses of plants will be more difficult to trace in the archaeological record. Unlike seeds in **soil seed banks** or pollen in lake beds, archaeological seeds cannot be considered a fully representative sample of plants used at or growing near a settlement.

Fragments of DNA have been successfully extracted from **ancient seeds**, but appear to be less degraded in desiccated material than in charred. It is often claimed that ancient seeds, particularly grain from Egyptian tombs ('mummy wheat') can be germinated. However, with the exception of the sacred lotus, *Nelumbo nucifera* (*ca.* 1200 years old), there are no documented cases of germination of truly **ancient seeds**. The degree of fragmentation of DNA and other chemicals within the seed rules this out. (**See: Longevity; Seed banks**)

3. Identification

Most seed material can be identified using gross morphology, by comparison to a seed reference collection of modern, identified material. Seed identification manuals have a limited role, as they often depend on characters that are lost in waterlogged or charred material, such as colour or appendages. Scanning electron microscopy is much used for observation of seedcoat patterns. Published identifications vary in quality, depending on the researcher's experience and access to reference collections. In particular, species-level identifications are problematic unless published in sufficient detail as to explain how the other candidate species were excluded. (**See: Seedcoats – structure; Structure of seeds – identification characters of seeds**)

4. Forensic science

Although less commonly used than entomology and palynology, seed identification is an important tool in specific instances. Seeds are used as trace and contact evidence, when their presence may indicate that two or more objects or people have been in contact, and in search and location enquiries for missing people. It is rare that seeds can be demonstrated to come from a single location, but it is often the case that they derive from plants with very specific habitat preferences, which can be highly informative in a local context. For example, presence of seeds on a body, from plants absent from the scene of crime, may help point to prior hiding places. Seed identification is also important in the investigation of human and animal stomach contents, both in cases of accidental or deliberate poisoning, and in characterizing meal contents and time of death. The comminuted nature of stomach contents means that plant anatomical skills are usually necessary for identification of seedcoat fragments. In 2003 a plant anatomist at Kew Gardens was able to identify fragments of the seedcoat of the toxic calabar bean (*Physostigma venenosum*) in the intestines of an unidentified body, recovered from the River Thames, London. Calabar bean's use as an ordeal plant in West Africa suggested a motive for the murder. (**See: Pharmaceuticals and pharmacologically active compounds; Poisonous seeds**)

The Tyrolean Iceman, dating to the Neolithic period (*ca.* 5300 years old), is a well-known example of the application of forensic skills to an archaeological case. Minute quantities of the Iceman's colon contents were examined through transmitting and scanning electron microscopes. The main component was bran of **einkorn** wheat (*Triticum monococcum*), with small quantities of muscle fibres (perhaps from ibex meat), pollen, and the eggs of an intestinal parasite, whipworm (*Trichuris trichiura*). The small size of the bran particles suggests they had been finely ground, probably for preparation of bread rather than gruel.

5. Key issues in archaeobotany

(a) *Hunter-gatherers.* Plant remains are poorly preserved at archaeological sites more than 20,000 years old. From the Late Upper Palaeolithic (Old World) or Palaeoindian (New World) (*ca.* 20,000–10,000 years ago) onwards, archaeobotany has proved informative about the role of plants in the pre-agrarian, foraging societies that subsisted on wild animals and plants. Grinding stones and mortars are abundant in some areas, and it is likely that seeds would have been processed for human consumption using these tools and fire, for example in roasting nuts or extracting oil.

Archaeobotany has demonstrated that seeds were a major resource in ancient foraging societies: the energy costs of processing seeds to food are offset by the seeds' abundance, storability and nutritional quality (e.g. **storage protein, oils**). The evidence also shows that a very diverse range of species was consumed: for example, seeds of over 150 species of edible plant were recovered from the Epipalaeolithic site of Abu Hureyra in Syria; tubers, edible greens and other plant parts would also have been eaten. This conforms with ethnographic evidence that hunter-gatherer diets are generally high in protein and fibre and low in saturated fat, with high levels of micronutrients. Ethnographic evidence suggests that perhaps 65% of energy would have been derived from plant foods. (**See: Ethnobotany**)

(b) *Domestication*. Archaeologists have devoted much attention to crop domestication and the origins of agriculture, because of farming's central role in the evolution of complex, literate civilizations. Domesticated plants can be distinguished by a range of adaptations to cultivation, most notably the loss of the capacity to disperse seed without human intervention. The wild ancestors of seed crops also typically have smaller seeds. Many claims for early finds of domesticated plants have proved over-optimistic. The relatively new technique of accelerator radiocarbon dating has allowed individual seeds to be dated, demonstrating that many archaeological plant remains are more recent than previously thought. Dates obtained before the mid-1980s must be treated with caution. (**See: Domestication**) In particular, re-dating of plant remains suggests that agriculture in the Americas is significantly younger than once thought. Claims for domestication as early as 10,000 years ago for potato and 7000 years for maize and bean are not supported by direct dating of early plant remains.

Agriculture evolved independently in at least six areas. In the Fertile Crescent of the Near East, **wheat, barley, lentils** and **peas** were domesticated about 10,000 years ago, eventually spreading as crops through much of the temperate Old World. The beginning of farming in the Fertile Crescent may have been triggered by climate change at the end of the last Ice Age, leading to increased populations that could not be supported by foraging for wild foods. In the rest of the world, domestication occurred later, without obvious climatic triggers, and is still poorly documented by archaeological remains. In Southeast Asia, **rice** was probably first domesticated in the Yangtze valley *ca*. 8000 years ago. The third independent centre of domestication in the Old World is thought to be sub-Saharan African, where **sorghum** and **pearl millet** were domesticated by 4000 years ago.

In the New World, agriculture also appears to have started in three centres. Archaeobotanical evidence from Mexico shows that the classic Mesoamerican group of crops, **maize, squash** and **common beans** were domesticated at different times, with maize appearing by 6000 years ago and beans 4000 years ago. In the Andean highlands of Peru, incomplete evidence shows that common bean (domesticated independently from that in Mesoamerica), **lima bean**, potato and **quinoa** were domesticated by 5000 years ago. In eastern North America, research in the last two decades has shown that a range of small-seeded crops, such as goosefoot (*Chenopodium berlandieri*) and marsh elder (*Iva annua*), were domesticated by 4000 years ago, prior to the arrival in the region of Mesoamerican crops such as maize. (**See: Cereals; Legumes; Pseudocereals**)

(c) *Agriculture*. Archaeobotany has proved to be a powerful tool for identifying the range of crops grown in past societies and, more interestingly, in identifying crop husbandry regimes. When combined with studies of field and settlement distribution, archaeobotany can be used to identify economic changes in farming that link to wider socio-political changes. Identification of cultivation regimes, e.g. fallowing, manuring, and irrigation, depends on accurate identification of ancient weed seeds, and their ecological interpretation. Ethnographic work in current-day traditional farming settlements has given insights into the taphonomy of archaeological plant remains, i.e. the processes that lead to the incorporation of plant remains into the archaeological record. The resulting studies of crop-processing and fuel use have proved essential in interpreting ancient plant remains, and are also of interest to a wider user group of ethnobotanists and agronomists.

(d) *Foods*. There has been increasing interest in studying the consumption of plant foods, in addition to the aspects of production discussed above. Food is a difficult subject for archaeology because, by their very nature, plant-based foodstuffs are consumed and do not enter the archaeological record. Rare exceptions include desiccated coprolites (preserved faeces) from dry areas such as the American southwest, and the stomach contents of the Iron Age bog bodies of northern Europe. Prehistoric coprolites from the Lower Pecos region of Texas and New Mexico contain a wide range of seed types, dominated by prickly pear (*Opuntia ficus-indica*) and wild grass seeds. Ritual food deposits, such as beer residues and bread loaves, made from **emmer** (*Triticum dicoccum*) and **barley** (*Hordeum vulgare*) have been found in ancient Egyptian tombs. Studies of consumption therefore depend on integrating evidence from archaeobotany with that for food-processing tools, cooking installations such as hearths and ovens, with evidence from ethnography. (MN)

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Archegonia

Female sexual organs producing and containing the female **gametes**; fully developed in bryophytes and pteridophytes (mosses and ferns) in the broadest sense, only rudimentary in gymnosperms. True archegonia are absent from angiosperms (with the three-celled egg apparatus as the homologue – egg cell flanked by two synergids). (**See: Reproductive structures, 1. Female**)

Aril

Pulpy structure that grows from some part of the **ovule** or **funiculus** after fertilization and covers part of, or the whole seed. Some authors on occasion distinguish so-called localized arils or 'arillodes' that develop from some part of the ovule (e.g. **exostome, raphe, chalaza**) from 'true', funicular arils.

The Encyclopedia of Seeds

Science, Technology and Uses

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