Essential oil

Mixture of volatile constituents of plants generally obtained by steam distillation. Components are highly aromatic, consisting largely of benzene and terpene derivatives. They are present in seeds of many species. Contrast with **fixed oils**. (See: **Spices**)

Establishment

The stage at which seedling **emergence** from the soil or growing medium is complete (allowing for any subsequent post-emergence losses), usually assessed at the point of development of an agreed number of true leaves.

Ethene

An alkene gas with hormone activity that is produced by plant cells. Although often still described within the plant science community as **ethylene**, ethene is now the systematic name preferred by the International Union of Pure and Applied Chemistry (IUPAC).

Ethnobotany

1. Introduction

Ethnobotany is the study of traditional uses of plants by humans. It is a broad field, encompassing both the use of wild plants and of indigenous varieties of cultivated plants. As a field of study, ethnobotany may be said to have begun when the expanding European empires first colonized Africa, Asia and the Americas. Early colonial histories and travel books dating from the 16th to the 18th centuries are still a rich source of information on uses of plants, in cultures now disappeared or greatly altered. The aim of most ethnobotanical work in the last 200 years has been to draw on traditional knowledge for wider economic development, particularly through the development of new crops and medicines.

The Convention on Biological Diversity (The Rio Earth Summit of 1992) was a milestone in its recognition of national and local rights to plants, animals and indigenous knowledge. In the last decade ethnobotanists have learned to work in close partnerships with local communities, aiming to further sustainable harvesting of wild plants with benefits for local economies and for plant conservation. The methodologies of ethnobotany have also changed, with a strong emphasis on use of quantitative techniques drawn from **ecology**. While ethnobotany still straddles multiple disciplines, including botany, anthropology, nutrition and medicine, it is now emerging as a discipline in its own right. This article focuses on ethnobotanical aspects of wild foods as this represents the main use of seeds (here broadly defined to include fruits and **nuts**). Traditional management of seed crops is covered in the appropriate entries.

2. Nutritional value of seeds

The quality and quantity of plant foods varies considerably, but must be assessed in the context of overall consumption. For example, 'edible greens' (the leaves of wild plants) are low in energy, but are an important resource for vitamins, minerals and dietary diversity in the spring, when other foods are scarce. Energy values are also affected by the energy required for processing, such as shelling, dehusking or detoxifying nuts. Studies on hunter-gatherers rank seeds, nuts and roots and tubers roughly equal in terms of net energy yield, well below meat, but above foliage. In practice, choice of foodstuffs in foraging societies must balance the energy return of the food against the ease and predictability with which it can be obtained: unlike animals, plants are not mobile and, after harvest, can be easily stored.

There are also differences between wild and domesticated plants. The latter have often been selected for higher concentrations of carbohydrates, and reduced elements such as toxins that affect palatability. In contrast, wild foods are richer in fibre, vitamins, minerals and a range of phytochemicals, many with nutritional and medicinal significance (see: **Pharmaceuticals, medicines and biologically active compounds – an overview**).

The likely health benefits of wild foods, including wild animals which typically have fewer, healthier fats, have led some scholars to propose reversion to a 'Palaeolithic diet', replicating the characteristics of prehistoric hunter-gatherer diets. Ironically, such a diet would be expensive and difficult for most people to achieve today, given the high productivity of the carbohydrate-rich crops that are so central to our diet, and its likely impact on health is controversial.

3. Diet in foraging societies

Living hunter-gatherers have been much studied as case studies of pre-agricultural foraging societies. The most extensive studies are of the Kung San bushmen of the Kalahari desert, who collect fruits, roots and other parts from some 200 plant species (see: **Legumes, 1. Origins and domestication**). Overall, about 70% of Kung San dietary energy derives from plants (about half of this from the mongongo nut, *Schinziophyton rautanenii*) and the remainder from animals. It is likely that plants dominated hunter-gatherer diets, except in high latitudes where peoples such as the Inuit until recently subsisted almost entirely on hunting meat.

One major obstacle to the use of ethnographic data is that hunter-gatherers are now mainly restricted to areas too arid or too cold for farming. In areas like this, in which plant resources are scarce, they tend to follow plant resources as they ripen: people move, rather than resources. Such societies are highly mobile, and are often characterized by relatively little investment in management of wild resources. Observations of the ample leisure time available to Kung San bushmen led anthropologists to coin the phrase 'The Original Affluent Society' in the 1960s. However, older ethnographic records show that hunter-gatherer groups in more favourable environments (now occupied by farmers) were sedentary and territorial, with permanent villages forming the base from which resources were collected, and at which they were stored. Well-known examples are the salmon societies of British Columbia and the acorn-based economies of Californian native Americans in the 19th century. Like mobile hunter-gatherers, they consumed a wide range of species, though with some, such as wild grass seeds or nuts, often dominant. Archaeological evidence shows that sedentary hunter-gatherer societies were widespread prior to the beginning of farming.

4. Evolution of human diet

The changing dietary importance of seeds as food is thought to have played an important role in human evolution, although the exact nature and timing of dietary shifts and their importance for human behaviour are much debated and remain controversial. Three types of evidence are used: non-human primate diet, recent hunter-gatherer societies, and hominid fossils.

Current-day apes and monkeys obtain up to 95% of their dietary energy from plant foods, with the remainder derived from invertebrates, rather than meat. Lower quality, easy-to-acquire plant foods such as leaves are a major food resource; higher quality plant foods derive from ripe fruits, rather than the more difficult to acquire seeds, nuts and tubers. Overall, compared to apes and monkeys, the hunter-gatherer diet (and human diet in general) is characterized by higher quality, harder-to-acquire resources, including meat, roots, hard seeds and nuts, with a much smaller role for forage, ripe fruit and insects. Fossil evidence from teeth suggests that this dietary shift began with the first hominids, *Australopithecus* of 4–2 million years ago. The 'Expensive-tissue hypothesis' suggests that the shift to higher quality foods during human evolution is linked to increasing relative brain size. Since both the brain and the gut have high metabolic requirements, the relatively large brains of human primates could only evolve if the gut shrank – only possible through the consumption of higher quality foods. In addition to more sophisticated foraging techniques, hominids also used food processing tools and cooking to enhance nutrient availability, although there is no evidence for human control of fire prior to 400,000 years ago, and grinding stones first appeared in the time of anatomically modern *Homo sapiens*, from 20,000 to 5000 years ago in different parts of the world.

5. Wild seeds in human diet

The role of wild seeds in agricultural societies follows three patterns: integral staple, famine (or emergency) food, or luxury food. Prior to the widespread adoption of modern agricultural techniques in the 1940s, many rural communities depended on wild harvests as a major supplement to farm produce, for example grains of lyme grass in Iceland, or acorns in eastern Turkey. Wild grasses still maintain this role in large parts of Africa. Famine foods are those that are less preferred, perhaps because of taste and/or toxicity, but which become important at times of food shortage (**see**, for example: **Chickling pea**). Their role in famine relief has only recently been recognized by emergency nutritionists, which has led to a substantial increase in research into their nutritional quality and availability. Luxury foods are wild plants gathered because they are valued primarily for their taste properties or cultural associations; examples include sloe fruits (*Prunus spinosa*) for flavouring alcoholic drinks in Europe, and Australian plant foods, once staples for hunter-gathering aborigines, now high-value foods for urban consumers, e.g. the **macadamia** nut.

6. Grasses

The **caryopses** (grains) of grasses are easily collected, by beating stands of plants, and form a stable, storable food resource, mainly composed of **starch**, with **storage protein** contents of 5–10%. Although harvesting of wild grass seeds was often abandoned after the introduction of domesticated cereals, they are or were recently important staple foods in some farming communities, mainly in arid zones. On the fringes of the Sahara, *Panicum turgidum* (*merkba*, *afezu*), *Stipagrostis pungens* and *Cenchrus biflorus* (*kram-kram*) are used by the Tuareg and other peoples. In sub-Saharan Africa wild grains are harvested from seasonally flooded lakes and swamps, including species of *Panicum*, *Eragrostis*, *Paspalum* and *Echinochloa*, as well as **wild rice** species indigenous to Africa (e.g. *Oryza barthii* and *O. longistaminata*).

In 19th-century North America, wild grains were harvested from *Panicum sonorum* and *P. hirticaule* in the Sonoran desert, and *Panicum*, *Eragrostis* and *Oryzopsis* from the arid Great Basin of California. Here the Owens Valley Paiute sometimes irrigated wild stands of grasses. Today, only the wild rice indigenous to North America (*Zizania palustris*) is widely harvested, in the Great Lakes region (**see: Rice**). Both the wild form and the non-**shattering** form developed in the 1960s command high prices as a luxury food. In 19th-century Australia wild grasses such as *Panicum* and *Eragrostis* were harvested on a large scale in the arid interior. Wild grasses were important in some parts of Europe until the mid-20th century. Manna grass (*Glyceria fluitans*), named on account of its sweet taste, was extensively harvested from marshes in central and northern Europe. Crabgrass (*Digitaria sanguinalis*) was both collected and cultivated in eastern Europe, while lyme grass (*Leymus arenarius*) was an important food staple in Iceland.

Grass caryopses are usually well protected by **hulls** (the **lemma**, **palea** and **glumes**), which in part account for their keeping qualities. The husks were often made brittle by parching (contact with dry heat on a metal plate or in an oven), and then threshed with a flail or in a mortar and pestle. Wild grains were often consumed as a gruel or porridge, some ground into flour for bread.

7. Nuts

Botanists use the term nut to refer to one-seeded dry fruits, with a woody pericarp, such as the acorn, **hazelnut** (filbert) and beechnut. In everyday use, nut refers to any edible kernel within a hard shell, such as **walnut**, **Brazil nut**, **almonds** and **pine nuts**. Most nuts in trade are now derived from domesticated trees grown in plantations, but the relative late domestication of many nut trees, and easy availability of wild nut trees in their native habitat, means that wild nuts have not been entirely replaced by cultivated sources (**see: Nut**).

Both the acorn and **chestnut** are rich in starch, and have been staple foodstuffs. Wild chestnuts (*Castanea sativa*) were widely consumed in southern Europe, often mixed with wheat flour for bread. Acorns have a long history as a food staple, with archaeological finds dating to 21,000 years ago at Ohalo II in Israel, and were staple foods in North America, particularly in California, the Mediterranean and Near East, and Japan and Korea. Some species have sweet acorns, but most acorns contain bitter tannin and must be roasted or leached before use.

The other nuts have high **oil** contents (50–70% by weight). These nuts are more often highly appreciated supplementary foods than staples on the scale of acorns, although the hazelnut (*Corylus avellana*) is found in huge quantities in Mesolithic, pre-agrarian settlements in northern Europe. The **pecan** nut (*Carya illinoinensis*) was an important wild resource for native Americans in the southern USA. Many pine species bear edible nuts: the best known is the Mediterranean stone pine, *Pinus pinea*. Other nuts that were locally used, and are now traded, include *Pinus edulis*, in the southwest USA, and *P. koraiensis* in China. The similar nuts of another conifer, the monkey puzzle tree, *Araucaria araucana*, are collected in Chile. The best known nut of Australia is the macadamia nut (*Macadamia ternifolia* and *M. tetraphylla*), now cultivated, but with a long history of aboriginal use. Tropical nuts include the Brazil nut, *Bertholletia excelsa*, still mainly harvested from wild trees in Amazonia.

8. Fruit

As with nuts, domesticated fruits, whether juicy, starchy or oily, have largely displaced wild fruits as important elements of diet. The continuing role of wild fruits owes much to the ease with which they can be used as flavouring for food or beverages, or be dried or fermented as a means of storage. Nutritional properties such as high vitamin C are now less important. Not all fruits are sweet, and many wild fruits in the Rosaceae family contain cyanogens, which can be removed by cooking.

Collection of wild berries is still popular in Scandinavia and eastern Europe, where lingonberry (*Vaccinium vitis-idaea*), bilberry (*V. myrtillus*), cranberry (*V. oxycoccus*) and bearberry (*Arctostaphylos uva-ursi*), all in the Ericaceae family, are popular. Jam-making is a common use in Europe for sour fruits such as these, or brambles (*Rubus* sp.), or cornelian cherry (*Cornus mas*) in the Balkans. *Vaccinium* species were also used by native Americans, as cakes of fruit, or pounded with meat, but commercial cranberry (*V. macrocarpon*) and blueberry (*V. corymbosum*) are both domesticated today.

A very wide variety of fruits is used in other regions. Some well known examples include the noni fruit (*Morinda citrifolia*) of Polynesia, now marketed as a health food in North America, the latex-rich cow tree of Amazonia (*Brosimum utile*), and the baobab tree of western Africa (*Adansonia digitata*).

(MN)

(See: **Archaeobotany; Poisonous seeds; Psychoactive seeds**)

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Ethylene

Ethylene is a hormone made by all seed plants and also by some bacteria and fungi. It was discovered by Dimitri Neljubow in 1886 after he discovered that the gas used for lighting affected the growth of plants. It is the simplest of the alkenes with the chemical formula C_2H_4. Although **ethene** is now the systematic name preferred by chemists, plant scientists continue at present to refer to it as ethylene.

Ethylene is made in most tissues of plants. It may be induced developmentally, for instance in germinating seeds, seedlings (particularly in the plumular hook), in senescent leaves and ripening fruit. It is also induced by environmental stresses and other factors such as diurnal cycles, drought, flooding, high and low temperature, physical stresses (touch and pressure), wounding and attack by pests and pathogens. Finally, ethylene may be induced by auxin, which may be further enhanced by cytokinin and or ABA. Ethylene may also regulate its own synthesis either positively or negatively, depending upon the tissue. (See: **Germination – influences of gases**)

Ethylene is biosynthesized from 1-aminocyclopropane-1-carboxylic acid (ACC), which is in turn synthesized from S-adenosyl-L-methionine (SAM). In addition to being a methyl donor in numerous other enzyme reactions, SAM is the common precursor of both ethylene and **polyamines**. The first committed step in ethylene biosynthesis, therefore, is the conversion of SAM to ACC and 5′-methylthioadenosine. The valuable methylthio- group of methylthioadenosine is recycled back to methionine and SAM by the Yang cycle, named after Shang Fa Yang, who did much of the early work on it (Fig. E.9).

The formation of ACC is carried out by the enzyme ACC synthase (ACS), which requires pyridoxal phosphate as a cofactor (and hence is sensitive to inhibitors of pyridoxal phosphate such as aminoethoxyvinyl glycine and aminooxyacetic acid) and probably functions as a dimer. It is encoded by a small family of genes each member of which is regulated by different signals. It has been generally accepted that the production of ACC is the rate-limiting step in ethylene production. However, this may not be universally true because several treatments that promote ethylene production also induce ACC oxidase genes.

ACC oxidase (ACO), which was formerly known as ethylene-forming enzyme (EFE), carries out the final step in ethylene biosynthesis: the conversion of ACC to ethylene. It is a dioxygenase, requiring Fe^{2+} ions, ascorbate and molecular oxygen. There is also a requirement for carbon dioxide and the enzyme is inhibited by Co^{2+}. The reaction produces cyanide, which is detoxified to β-cyanoalanine. The *Aco* gene family is small and there is again some evidence that the genes are differentially induced by different stimuli.

When subjected to high concentrations of externally applied ethylene, plant cells will convert it to ethylene glycol via the intermediate of ethylene oxide. However, it is not clear that this happens at normal physiological concentrations of the gas. The important control is to remove the immediate precursor of ethylene by converting it to its malonyl conjugate (MACC). This seems to be irreversible *in planta*. Germinating peanut seeds that contain considerable amounts of MACC seem to make ethylene from newly synthesized ACC. However, inhibition of the enzyme that makes MACC, ACC N-malonyl transferase, does increase ethylene synthesis so malonylation is a method of regulating ethylene production. Exogenously applied ethylene-generating compounds, e.g. ethephon, can have practical applications in seed enhancement treatments (See: **Priming – technology, 2. Techniques and terminologies**).

(GL, JR)

(See: **Signal transduction – hormones**)

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