Woody Legumes (excluding Acacias)

S Harris, University of Oxford, Oxford, UK

Introduction

The Fabaceae (or Leguminosae) is the second largest family of flowering plants. Furthermore, no family, except perhaps the Poaceae, has a wider geographical distribution in a broader range of habitats. Legumes are distributed throughout every continent, except Antarctica, and in almost every habitat from the freshwater lakes of Amazonia, through the tropical and subtropical forests of the New and Old Worlds to the deserts of Central Asia and the arctic-alpine vegetation of the temperate region. The reason for the ecological success of the family has been suggested as the ability to form root nodules with nitrogen-fixing bacteria, although not all Fabaceae fix nitrogen. Together with their ecological diversity, the Fabaceae have habits that range from annual herbs through lianas to shrubs and very tall trees (at approximately 88 m, the tallest tropical angiosperm is the Southeast Asian tree *Koompassia excelsa*). In tropical and subtropical regions, legumes are primarily woody, whilst in temperate regions they are herbaceous. It is the herbaceous legumes that have the most obvious economic value to humans (particularly the genera *Phaseolus* and *Glycine*). However, the economic value of woody legumes is also immense, particularly in the tropics, and ranges from timber, fuelwood, and forage production to sources of resins, toxins, and dyes. The present article, which focuses on the woody legumes (excluding the genus *Acacia*), will provide an overview of Fabaceae systematics together with information on their ecological and reproductive diversity. Finally, the utility of woody legumes is reviewed.

Systematics

The Fabaceae comprises approximately 640 genera and 18 000 species, which have traditionally been divided into three morphologically distinct subfamilies (Mimosoideae, Caesalpinioideae, Papilionoideae) (**Table 1**), although some classification systems have also recognized these subfamilies as families. Molecular and morphological data strongly support the monophyly of the Fabaceae, although the monophyly of only two (Mimosoideae, Papilionoideae) of the three subfamilies is supported. Subfamily Caesalpinioideae is paraphyletic, with some genera more closely related to the Mimosoideae and some to the Papilionoideae than they are to each other. The three subfamilies have disproportionate distributions of species with the tree habit; more than 80% of subfamilies Caesalpinioideae and Mimosoideae are trees, whilst less than 40% of the Papilionoideae are trees. Furthermore, the Caesalpinioideae and Mimosoideae are primarily tropical whilst the Papilionoideae are primarily temperate.

Each subfamily is divided into tribes (**Table 2**); the Papilionoideae contains the largest number of tribes, of which fewer than half contain tree species. Molecular data indicate that temperate herbaceous lineages are more recently derived from woody tropical lineages, although it is unclear how many origins of the herbaceous habit have occurred. Furthermore, within the Papilionoideae, *Swartzia* and the tribe Sophoreae appear to be basal groups.

The Fabaceae contains some of the largest and most diverse genera in the plant kingdom, e.g., *Acacia*, *Astragalus*, and *Mimosa*. Furthermore, these genera may contain high numbers of endemic species, for example, *Mimosa* in central Brazil.

Table 1 Characteristics of the three subfamilies in the Leguminosae

	Mimosoideae	*Caesalpinioideae*	*Papilionoideae*
Genera/species (approximate)	64/2950	153/2175	425/12 150
Habit	Trees or shrubs, some herbs	Trees or shrubs, some herbs	Herbs or shrubs, some trees
Leaves	Usually bipinnate	Usually pinnate or bipinnate	Pinnate to trifoliate, occasionally unifoliate
Corolla	Actinomorphic. Petals just touching. Not showy	Usually zygomorphic. Petals overlapping, upper petal usually innermost. Usually showy	Mostly zygomorphic. Petals overlapping, upper petal outermost. Showy
Stamens	Ten to many. Showy	One to 10. Usually not showy	Ten. Not showy
Pollen	Monads, tetrads, polyads	Monads	Monads
Pleurogram	Present	Usually lacking	Lacking
Root nodule occurrence	60–70%	25–30%	>95%

Table 2 Distribution of woody taxa among the Fabaceae tribes; only those tribes containing trees are shown

Tribe	*Habit*	*Distribution*	*Example genera*
Caesalpinioideae (four tribes total)			
Caesalpinieae	Trees or shrubs, rarely herbs	Primarily tropical	*Erythrophleum* *Caesalpinia* *Parkinsonia*
Cassieae	Trees or shrubs, rarely herbs	Tropical and subtropical	*Ceratonia* *Dialium* *Senna*
Cercideae	Trees or shrubs	Mainly tropical, one genus north temperate	*Cercis* *Bauhinia*
Detarieae	Trees; some suffrutices	Tropical	*Cynometra* *Afzelia* *Brachystegia*
Mimosoideae (five tribes total)			
Parkieae	Trees	Tropical	*Parkia* *Pentaclethra*
Mimoseae	Trees or shrubs, rarely herbs	Tropical and subtropical, rarely temperate, most numerous in tropical South America and Africa	*Mimosa* *Prosopis* *Entada*
Acacieae	Trees or shrubs, rarely herbs	Mainly tropical and subtropical	*Acacia* *Faidherbia*
Ingeae	Trees or shrubs	Mainly tropical	*Inga* *Calliandra* *Albizia*
Papilionoideae (31 tribes total)			
Swartzieae	Trees, rarely shrubs	Tropics	*Swartzia* *Mildbraediodendron*
Sophoreae	Trees or shrubs, rarely herbs	Tropics	*Sophora* *Myroxylon* *Ateleia*
Dipteryxeae	Trees	Neotropics, mainly Amazonia	*Dipteryx* *Pterodon*
Dalbergieae	Trees or shrubs	Tropics, mainly tropical America	*Dalbergia* *Macherium* *Pterocarpus*
Millettieae	Trees or shrubs	Mainly tropical	*Derris* *Lonchocarpus* *Millettia*
Robinieae	Trees, shrubs or herbs	Temperate and tropical New World, *Sesbania* pantropical	*Sesbania* *Gliricidia* *Robinia*
Psoraleeae	Small trees or shrubs, rarely herbs	Widespread, rarely tropical	*Psoralea*
Amorpheae	Small trees, shrubs or herbs	New World	*Amorpha* *Dalea*
Carmichaelieae	Small trees or shrubs	New Zealand	*Carmichaelia*
Brongniartieae	Trees or shrubs	New World	*Brongniartia*
Podalyrieae	Small trees or shrubs	South Africa	*Podalyria*
Genisteae	Small trees, shrubs, or herbs	Worldwide	*Genista* *Ulex*

Ecology

The morphological diversity of legumes reflects ecological diversity, where species occupy habitats as diverse as the deserts of Central Asia, estuarine tropical forest to temperate and alpine forests. However, it is in the tropical habitats that the greatest diversity of tree legumes is found. Legumes are important ecosystem components wherever they are found, although some habitats are dominated by tree legumes, for example, the miombo woodlands of southern Africa. In other cases, legumes may be infrequent; for example, despite the value of the timber, large-scale commercial exploitation of *Ormosia* species in Southeast Asia is limited because the low density of individuals makes selective harvesting uneconomic.

In addition to their dominant role in some natural habitats, woody legumes may also be important components of pioneer and secondary forest vegetation, for example, *Mimosa* species in the neotropics. Furthermore, changes in human activities (e.g., pasture management) may cause considerable changes in legume domination. Another major effect of humans on the distribution of woody legumes has been the intercontinental movements of species, for example, neotropical species being moved to Africa and Asia. The consequences of such movements have been unpredictable; some species can be highly productive in part of the introduced range whilst destructive in other parts of the range, for example the high value of *Leucaena leucocephala* as a fodder in Australia but its major role as a weed in Hawaii.

Legumes generally form symbiotic relationships with the bacterial genus *Rhizobium*, producing root nodules and fixing atmospheric nitrogen, although this is not always the case, particularly in the Caesalpinioideae (**Table 1**). In addition to root nodules, legumes may also have mycorrhizae.

Reproductive Biology

In legumes, the pollination unit is either the inflorescence or the flower, and pollen is usually released as monads (single cells), although in the Mimosoideae pollen is also often released as tetrads or polyads (groups of pollen grains). Mechanisms to promote outcrossing in legumes include: (1) protogyny, where the stigma is receptive to pollen before pollen in the same flower is released; (2) andromonoecy, where male and hermaphrodite flowers occur on the same plant; and (3) self-incompatibility, where successful fertilization is determined by the genotype of the pollen. Rarely are legumes dioecious (e.g., *Ateleia*). The structure of the legume inflorescence suggests that the majority of species are pollinated by insects, including Coleoptera, Diptera, Hymenoptera, and Lepidoptera, although others are pollinated by mammals (e.g., *Parkia*) and nectarivorous birds (e.g., *Erythrina*). However, some legumes (e.g., *Ateleia herbert-smithii*) are wind-pollinated. In addition to sexual reproduction, vegetative reproduction may also be important in both natural (e.g, *Albizia*) and artificial (e.g., *Gliricidia sepium*) ecosystems.

Seed dispersal in legumes is usually by gravity or mechanical means. Many genera have elastically dehiscent fruits, whilst others may be dispersed by water (e.g., *Entada*) and wind (e.g., *Centrolobium*, *Pterocarpus*). However, mammals (e.g., for *Inga*, *Tamarindus*) and birds (e.g., for *Pithecellobium*) may play an important role in seed dispersal. Humans are an important means of long-distance dispersal of legume seed, whether it is seed for establishing plantations (e.g., *Calliandra*), cultivation of ornamentals (e.g., *Delonix regia*), movement of multipurpose species (e.g., *Gliricidia sepium*), or transport by their livestock (e.g., *Mucuna*).

Many legume seeds have hard seed coats (particularly Caesalpinioideae and Mimosoideae) and need to be scarified before they will germinate. Scarification may occur naturally by passage through animal guts, although for plantation establishment it is necessary to use other treatments (e.g., damaging the seed testa or treatment with boiling water). Many legume seeds may be lost through predation of the developing ovules by beetle larvae (Bruchidae) at the early stages of fruit development.

Utilization

Timber

The morphological and ecological diversity of legumes are reflected in their wood properties, ranging from hard, durable woods (e.g., *Xylia*) to soft, perishable woods (e.g., *Erythrina*). Potentially, therefore, legume woods are suitable for all purposes, from building (e.g., *Koompassia*) to boat construction (e.g., *Copaifera*, *Pterocarpus*) and carving (e.g., *Dalbergia*). For example, legumes provide some of the most highly prized woods for the manufacture of fine furniture, marquetry, and veneers, including the rosewoods (*Dalbergia*) of South America and Southeast Asia, Jichimu (*Ormosia*) of China, and *Afzelia* of Africa and Southeast Asia. Trade in some species has threatened natural populations (e.g., *Pericopsis mooniana* in Southeast Asia and *Dalbergia latifolia* in India), whilst the properties of some genera have influenced how they are extracted from forests. For example, the wood of *Cynometra* species is so dense that trunks sink in water and hence they must be moved over land rather than floated down rivers.

Tannins and Resins

The pods of *Caesalpinia* species (e.g., *C. brevifolia*, *C. coriaria*, *C. spinosa*) and the bark of *Robinia pseudoacacia* are important sources of vegetable tannin (used in leather and adhesive manufacture). Species of *Hymenaea* and *Copaifera* are important sources of resin for the manufacture of high-quality varnishes, particularly as copals.

Human Food and Ornamentation

Tree legumes are minor sources of human foods, particularly in their native areas; for example, the immature pods of *Leucaena* species are used as a vegetable in Mexico and *Prosopis juliflora* pods are used for the manufacture of flour, syrup, and coffee substitutes (**Figure 1**). Some species (e.g., the pulp of *Tamarindus indica* fruits) have both local and international markets. The fruits of *Ceratonia siliqua* are an important source of edible gum (locust gum) and are used as a cocoa substitute. Tree legumes can also be important sources of nectar for honey production (e.g., *Robinia*, *Calliandra*) or habitats for bees (e.g., *Koompassia*). Brightly colored legume seeds (e.g., *Erythrina*, *Ormosia*, *Adenanthera*) are often used in ethnic jewelry whilst *Dipteryx* seeds are a source of perfume.

Fodder

Legume trees are important food components of animal diets in natural populations, whilst there are significant economic uses of the foliage and green pods as livestock fodder of many genera (e.g., *Calliandra*, *Gliricidia*, *Leucaena*, *Prosopis*, *Ulex*). In the case of *Leucaena*, a nonprotein amino acid called mimosine is found which at high concentrations may result in reduction in weight gain, hair loss, and abortion in nonruminant animals. Furthermore, fodder species may also have additional uses, e.g., fuelwood and charcoal. Legumes may also be important shade trees in some agroforestry systems, e.g., *Inga* species as shade trees for coffee production in South America.

Ornamentals, Dyes, Poisons, and Medicines

Legume species are planted throughout the tropics as street trees, e.g., *Delonix regia* and *Albizia lebbeck*, whilst others (e.g., *Laburnum*, *Robinia*, *Wisteria*) are important temperate ornamentals. Indigo (*Indigofera tinctoria*; Asia) and logwood (*Hymantoxylum campechianum*; Mexico) provide two of the most important plant-derived dyes, whilst historically other important dyes have been isolated from the genera *Caesalpinia* and *Genista*. *Derris elliptica* and *Lonchocarpus* species are used as fish poisons in South America but have recently attracted attention as environmentally friendly insecticides. Numerous traditional products are derived from legume trees. For example, *Erythrophleum suaveolens* bark is used as an ordeal poison throughout Africa. The seeds of *Sophora secundiflora* (mescal bean) are used by native North Americans to induce hallucinations, although the psychoactive alkaloid (cytisine) is very toxic. Many legume genera (e.g., *Cassia*) yield both locally and internationally important medicines.

Weediness

Many woody legumes have become serious weeds, particularly in the tropics. Genera introduced for forestry purposes may have unforeseen weedy

Figure 1 Examples of inflorescences from the three legume subfamilies. (A) *Leucaena greggii*, a mimosoid legume; (B) *Bauhinia* sp., a caesalpinoid legume; (C) *Pterodon pubescens*, a papilionoid legume.

consequences, e.g., *Leucaena leucocephala*, *Parkinsonia aculeata*, *Prosopis juliflora* and *Robinia pseudoacacia*, whilst changes in management practice may make previously valuable species potential weedy species, e.g., *Ulex europaeus* in Scotland. The weediness of woody legumes means that their use in agroforestry and amenity situations must be considered very carefully.

See also: **Biodiversity**: Biodiversity in Forests. **Ecology**: Reproductive Ecology of Forest Trees. **Genetics and Genetic Resources**: Molecular Biology of Forest Trees; Population, Conservation and Ecological Genetics. **Landscape and Planning**: Landscape Ecology, Use and Application in Forestry. **Medicinal, Food and Aromatic Plants**: Edible Products from the Forest; Forest Biodiversity Prospecting; Medicinal and Aromatic Plants: Ethnobotany and Conservation Status. **Tree Breeding, Practices**: Tropical Hardwoods Breeding and Genetic Resources. **Tropical Forests**: Monsoon Forests (Southern and Southeast Asia); Tropical Dry Forests; Tropical Moist Forests.

Further Reading

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