1

What are Cucurbits?

DISTRIBUTION AND ECOLOGY

The Cucurbitaceae is a family of frost-sensitive and predominantly tendril-bearing vining plants that are found in subtropical and tropical regions around the globe. There are only a few species that are native to temperate climates; they are either prolific seed-producing annuals, perennials that live for one season until killed by frost, or xerophytic perennials whose succulent underground parts survive the winter. Ecologically, the family is dichotomous; many genera flourish in the humid tropics, particularly in southeastern Asia and the neotropics, whereas other genera are native to the arid regions of Africa, Madagascar and North America. Members of the latter group, the xerophytes, usually have large perennial roots and succulent stems that are clambering and creeping and at least partially subterranean; in some cases, tendrils or leaves are lacking or greatly modified.

Although most crops in the Cucurbitaceae have been selected from the mesophytic annuals, concern over famine and fuel sources in arid countries has led to interest in turning some of the xerophytes into agricultural crops.

NOMENCLATURE

'Cucurbits' is a term coined by Liberty Hyde Bailey for cultivated species of the family Cucurbitaceae. Beginning in the early 20th century, the term has been used not only for cultivated forms, but also for any species of the Cucurbitaceae, and it will be so used in this book.

Other vernaculars applied to the family and various of its members are 'gourd', 'melon', 'cucumber', 'squash' and 'pumpkin'. Of these, squash and pumpkin are the most straightforward, almost always referring to species of *Cucurbita*. An exception is the fluted pumpkin, which is *Telfairia occidentalis*. The unqualified terms melon and cucumber usually define *Cucumis melo* and

Cucumis sativus, respectively. However, confusion develops when modifiers are added to these terms. Whereas muskmelon or sprite melon refers to a specific type of *C. melo*, watermelon is *Citrullus lanatus*, wintermelon is *Benincasa hispida* and bitter melon is *Momordica charantia*. Gourd generally is used to describe a cucurbit fruit with a hard, durable rind; usually it refers to bottle gourd (*Lagenaria siceraria*), or a wild species of *Cucurbita*, or an ornamental form of *Cucurbita pepo*. However, various other cucurbits also are called gourds, such as luffa sponge gourd (*Luffa aegyptiaca*), ridge gourd (*Luffa acutangula*) and some that do not have hard rinds, such as bitter gourd or bitter melon (*M. charantia*) and ivy gourd (*Coccinia grandis*). Sometimes the term refers to tough-rinded species of other plant families, such as the tree gourd (*Crescentia cujete* L., Bignoniaceae).

Complicating matters further, more than one common name is often applied to a single species. For example, names for *B. hispida* include ash gourd, white pumpkin, wax gourd and winter melon. Sometimes different names refer to distinct crops within a species, such as pumpkin, zucchini and acorn squash in *Cucurbita pepo*. In other cases, the different common names for the same species are used interchangeably. Frequently used common names for cucurbit crops are given in the Appendix.

Popular terms for the cucurbits may be confused in other languages as well. Cucumber and melon are sometimes considered the same in India. Older terminology in Chinese included 'guo-kua', which is translated into English as 'melon', but it includes watermelon (*C. lanatus*) as well as melon (*C. melo*). Also, 'tsaikua', which usually translates as 'gourd', refers to *B. hispida*, *C. sativus*, *M. charantia* and species of *Cucurbita* and *Luffa*. This is no longer a problem in China, since the names in Mandarin are now precise.

TAXONOMY

The family Cucurbitaceae, which is not closely related to any other plant family, consists of two well-defined subfamilies, eight tribes (representing varying degrees of circumscriptive cohesiveness) and about 118 genera and 825 species (Jeffrey, 1990). The four major cucurbit crops (watermelon, cucumber, melon, squash) and five other important crops (luffa, bottle gourd, chayote, wax gourd, bitter gourd) in the family belong to the Cucurbitoideae subfamily. Four of these – watermelon, luffa, bottle gourd and wax gourd – belong to the tribe Benincaseae. The classification of these and other cultivated species is given in Table 1.1. Many more wild taxa have actual or potential economic value, making Cucurbitaceae one of the most important plant families for human exploitation.

Taxonomic studies of cucurbits at all hierarchical levels have been done. They include comparative analyses of morphology (including specialized studies on trichomes, stomata, palynology and seed coat anatomy), cytology,

Table 1.1. Taxonomy of cultivated cucurbit species.

Latin name	Common name[a]	Frequency and place of cultivation[b]	Usage
Tribe Actinostemmateae			
Actinostemma tenerum Griff.	He-zi-cao, Goki zuru	Localized (S)	Medicinal
Bolbostemma (syn. *Actinostemma*) *paniculatum* (Maxim.) Franq.	Pseudo-fritillary	Localized (S)	Medicinal
Tribe Benincaseae			
Acanthosicyos horridus Welw. ex Hook. f.	Butterpips, Naras	Localized (A)	Food, medicinal, ornamental
Benincasa fistulosa (Stocks) Schaef. & Renner (formerly *Praecitrullus fistulosus*)	Round melon	Localized (W)	Food
Benincasa hispida (Thunb.) Cogn.	Wax gourd, winter melon	Frequent (W)	Food, medicinal
Citrullus colocynthis (L.) Schrad.	Colocynth	Sporadic (W)	Medicinal
Citrullus lanatus (Thunb.) Matsum. & Nakai.	Watermelon	Common (W)	Food, medicinal
Coccinia abyssinica (Lam.) Cogn.	–	Localized (A)	Food
Coccinia grandis (L.) Voigt	Ivy gourd	Sporadic (W)	Food, medicinal
Cucumis anguria L.	West Indian or burr gherkin	Localized (W)	Food
Cucumis dipsaceus Ehrenb. ex Spach	Teasel gourd	Sporadic (W)	Ornamental
Cucumis melo L.	Melon	Common (W)	Food
Cucumis metuliferus E. Mey. ex Naud.	African horned melon	Sporadic (W)	Food
Cucumis sativus L.	Cucumber	Common (W)	Food
Diplocyclos palmatus (L.) C. Jeffrey	Lollipop climber	Localized (O)	Ornamental
Lagenaria siceraria (Molina) Standl.	Bottle gourd	Common (W)	Utilitarian, ornamental, food
Melothria sphaerocarpa (Cogn.) Schaef. & Renner (formerly *Cucumeropsis mannii*)	White-seeded melon, Egusi-itto	Localized (A)	Food

Continued

Table 1.1. Continued.

Latin name	Common name[a]	Frequency and place of cultivation[b]	Usage
Tribe Bryonieae			
Bryonia alba L.	White bryony	Sporadic (W)	Medicinal, ornamental
Bryonia cretica L.	Bryony	Localized (O)	Medicinal
Bryonia dioica Jacq.	Red bryony	Sporadic (W)	Medicinal, ornamental
Ecballium elaterium (L.) A. Rich.	Squirting cucumber	Sporadic (O)	Ornamental
Tribe Cucurbiteae			
Cayaponia kathematophora R. E. Schult.	–	Rare (N)	Ornamental
Cayaponia ophthalmica R. E. Schult.	–	Rare (N)	Medicinal
Cucurbita argyrosperma C. Huber	Squash, pumpkin	Localized (W)	Food
Cucurbita ficifolia Bouché	Malabar gourd	Localized (W)	Food
Cucurbita ecuadorensis H. C. Cutler & Whitaker	Squash, pumpkin	Localized (N)	Food
Cucurbita maxima Duchesne	Great pumpkin	Common (W)	Food
Cucurbita moschata Duchesne	Squash, pumpkin	Common (W)	Food
Cucurbita pepo L.	Squash, pumpkin	Common (W)	Food
Sicana odorifera (Vell.) Naudin	Casabanana	Sporadic (N)	Food, ornamental
Tribe Gomphogyneae			
Gynostemma pentaphyllum (Thunb.) Mak.	Jiao-gu-lan, Doloe	Localized (S)	Medicinal
Hemsleya amabilis Diels	Luo-guo-di	Localized (S)	Medicinal
Tribe Joliffieae			
Telfairia occidentalis Hook. f.	Fluted pumpkin	Localized (A)	Food
Telfairia pedata (Sims) Hook.	Oyster nut	Localized (A)	Food

Tribe Momordiceae			
Momordica angustisepala Harms	Sponge plant	Rare (A)	Utilitarian
Momordica balsamina L.	Balsam apple	Frequent (W)	Medicinal, ornamental
Momordica charantia L.	Bitter gourd	Common (W)	Food, medicinal
Momordica cochinchinensis (Lour.) Spreng.	Cochinchin gourd	Sporadic (W)	Medicinal, ornamental
Momordica cymbalaria Hook. f.	–	Rare (O)	Food
Momordica dioica Roxb. ex Willd.	Kaksa	Localized (S)	Food
Tribe Sicyoeae			
Cyclanthera brachybotrys (Poepp. & Endl.) Cogn. (*Cyclanthera,* incl. *Rytidostylis* & *Pseudocyclanthera,* incl. *C. explodens* synonym of *C. brachystachya*)	Springgurka	Localized (W)	Food
Cyclanthera pedata (L.) Schrad.	Achocha, Stuffing cucumber	Sporadic (W)	Food, medicinal
Echinocystis lobata (Michx.) Torr. & Gray	Wild cucumber	Sporadic (W)	Ornamental
Hodgsonia macrocarpa (Bl.) Cogn.	Lard plant	Infrequent (S)	Food, medicinal, ornamental
Luffa acutangula (L.) Roxb.	Angled loofah	Frequent (W)	Food, medicinal
Luffa aegyptiaca Mill. (formerly *L. cylindrica*).	Smooth loofah	Common (W)	Utilitarian, food, medicinal
Sechium edule (Jacq.) Swartz	Chayote	Common (W)	Food, medicinal
Sechium tacaco (Pittier) C. Jeffrey	Tacaco	Localized (N)	Food
Trichosanthes costata Blume (formerly *Gymnopetalum cochinchinense*)	–	Rare (S)	Food
Trichosanthes cucumerina L.	Snake gourd	Frequent (W)	Food, medicinal
Trichosanthes dioica Roxb.	Pointed gourd	Localized (S)	Food, medicinal

Continued

Table 1.1. Continued.

Latin name	Common name[a]	Frequency and place of cultivation[b]	Usage
Trichosanthes kirilowii Maxim.	Chinese snake gourd	Localized (S)	Medicinal
Trichosanthes lepiniana (Naud.) Cogn.	Indreni	Localized (S)	Medicinal
Trichosanthes pilosa Lour. (formerly T. ovigera)	Japanese snake gourd	Frequent (S)	Food
Trichosanthes villosa Blume	Mi-mao-gua-lou	Localized (S)	Food
Tribe Siraitieae			
Siraitia grosvenorii (Swingle) A. M. Lu & Zhi Y. Zhang	Buddhafruit, Monk fruit, Luo-han-guo	Localized (S)	Food, Medicinal
Tribe Thladiantheae			
Thladiantha dubia Bunge	Red hail stone, Chi bao	Sporadic (W)	Medicinal, ornamental
Tribe Triceratieae			
Fevillea cordifolia L.	Antidote vine	Rare(N)	Medicinal

[a]For most species, the common name given is English or an English translation. Common names in other languages are listed in Kays and Silva Dias (1995) or US NPGS GRIN Taxonomy (2017).
[b]Locations: A=Africa, N=neotropics, O=Old World, S=Asia, W=widespread.

DNA, isozymes, flavonoids, cucurbitacins, amino acids and fatty acids in seeds, biogeography and coevolving insects. A monograph has been written on *Cucumis* (Kirkbride, 1993), and the taxonomic relationships within the Cucurbitaceae are being improved using molecular markers (Schaefer *et al.*, 2009; Chomicki and Renner, 2014). These new studies have been useful to the areas of crop improvement and germplasm conservation.

MORPHOLOGY AND ANATOMY

Seedlings

Most cucurbit seedlings are epigean, germinating with the tips of the cotyledons initially inverted but later erect. As it emerges, the hypocotyl straightens and the cotyledons ascend as the seed coat is dislodged by the peg, an outgrowth on one side of the hypocotyl. The function of the peg is to open the seed coat and permit the cotyledons to emerge. The photosynthetic cotyledons of most cucurbit seedlings are more or less oblong in shape. Between them lies the inconspicuous developing epicotyl.

Roots

Cucurbits generally have a strong taproot, which may penetrate the soil to a depth of more than 2 m, as in the case of squash. Even in cucumber, the tap root can extend 1 m into the soil. Cucurbits also have many secondary roots occurring near the soil surface. In fact, most roots are in the upper 60 cm of the soil. Lateral roots extend out as far as, or farther than, the above-ground stems. The cortex of the primary root is apparently involved in the development of secondary roots in cucurbits. Adventitious roots may arise from stem nodes in squash, luffa, bitter gourd and other cucurbits, sometimes without the stem having contact with the soil or other substrate.

Some xerophytic species have massive storage roots that enable the plant to survive severe drought. Those of *Acanthosicyos* can reach up to 15 m in length. The central taproot on one buffalo gourd plant weighed 72 kg (Dittmer and Talley, 1964). The above-ground parts of this species may die from lack of water or in response to freezing temperatures, but the plant regenerates from surviving stem tissue at the root–shoot transition area when favourable conditions resume.

Older vessels in the secondary xylem are often plugged with tyloses (extensions of the parenchyma cells), especially in watermelon, which can contribute to drought resistance. The sieve tubes in the secondary phloem are among the largest found in angiosperm plants.

Stems

The herbaceous or sometimes slightly woody stems are typically prostrate, trailing, or climbing, angled in cross-section, centrally hollow, sap-filled and branched. Primary and secondary branches can reach 15 m in length. Bush forms of cucurbits have much shorter internodes as well as total stem lengths than vining cultivars.

Many of the xerophytic cucurbits are true caudiciforms; that is, the lower part of the perennial stem, which is usually subterranean or at ground level, is thickened, succulent and drought resistant. In *Marah*, the large underground tubers originate from the hypocotyl and stem base (Stocking, 1955). The succulent stems of *Ibervillea sonora* (S. Wats.) Greene can continue to sprout new growth annually during periods of drought lasting 8 years or more (Macdougal and Spalding, 1910).

The vascular bundles of cucurbit stems are bicollateral (phloem to the inside and outside of the xylem), discrete, usually ten, and arranged in two rings around the pith cavity. The relatively large sieve tubes are also scattered in the cortex in some cucurbits (e.g. squash), serving to join all phloem elements together. The anomalous stem anatomy of cucurbits and other vines may serve to increase stem flexibility, to facilitate nutrient transport, to promote healing of injuries, or to provide protection against stem destruction via redundancy (Fisher and Ewers, 1991).

Many cucurbits have soft to rough hairs (trichomes) on their stems and foliage, whereas chayote, smooth luffa, stuffing cucumber and some other cucurbits are glabrous or nearly so. Trichome morphology is quite variable: hairs are glandular or eglandular, unicellular to multicellular, and simple or branched.

Leaves

Cucurbit leaves are usually simple (i.e. not divided into leaflets), palmately veined and shallowly to deeply three- to seven-lobed. There is usually one leaf per stem node. Along the stem, leaves are helically arranged with a phyllotaxy of 2/5; in other words, there are two twists of the stem, which segment contains five leaves, before one leaf is directly above another. This means that the angle of divergence between neighbouring leaves is 144° (2/5 of 360°).

Leaf stomata are mostly anomocytic, lacking subsidiary cells. The petiole in cross-section often has a crescent or ring of unequal vascular bundles, the larger ones bicollateral. Stipules at the base of the petiole are typically absent, but have been transformed into photosynthetic thorns in *Acanthosicyos*. Extrafloral nectaries, which frequently attract ants, occur on some cucurbit leaves (e.g. ivy gourd).

Succulent leaves are rare, even among the xerophytic cucurbits. Those of *Xerosicyos* have large water-storage cells in the inner mesophyll and perform crassulacean acid metabolism (CAM). However, the deciduous leaves of *Seyrigia* only perform C_3 photosynthesis even though the succulent stem performs CAM. The large ephemeral leaves of most cucurbits adapted to an arid environment avoid heat damage by maintaining high levels of transpirational cooling (Rundel and Franklin, 1991).

Tendrils

Most cucurbits have solitary tendrils at their leaf axils. Tendrils are unbranched in species such as cucumber and branched in luffa and other taxa. They are often coiled, helping plants to cling to trellises and other supports. Terminal adhesive pads develop on the tendrils of several species, allowing attachment to tree trunks and other large textured objects. Some cucurbits lack tendrils, e.g. squirting cucumber and bush cultivars of summer squash, while other cucurbits may have more than one tendril per node.

Tendrils in most of the cucurbit crops are interpreted as modified shoots. However, in luffa and other species, they are considered a stipule–stem complex. There are still other interpretations concerning the anatomical origins of cucurbit tendrils and research is ongoing. In cucumber, a single nucleotide polymorphism (SNP) resulted in the transition from tendrils to tendril-less, removing the plant's ability to climb (Wang *et al*., 2015).

Flowers

Many cucurbits have large showy flowers that attract pollinating insects, but *Echinocystis*, *Sechium* and some other genera have small, rather inconspicuous flowers. The typically unisexual flowers occur in leaf axils, either alone or in inflorescences. They are often white or yellow, but may be red (e.g. *Gurania*) or other colours. The hypanthium is cup- or bell-shaped. The sepals or sepal lobes, typically numbering five, and the corolla, which is usually five-lobed and more or less fused, extend beyond the hypanthium. Flowers have radially symmetrical, bell-shaped corollas that may differ between male (staminate) and female (pistillate) flowers.

Staminate and pistillate flowers on monoecious cucumber and squash plants are originally bisexual, with both stamen and pistil primordia initiated. During ontogeny, depending on the hormonal status of the tissue near the floral bud, development of the anthers may be arrested and a pistillate flower develops, or development of the pistil is retarded and a staminate flower is produced. Undeveloped stamens (staminodia) can be seen in mature pistillate flowers, and there is a rudimentary pistil (pistillodium) in staminate flowers (Fig. 1.1).

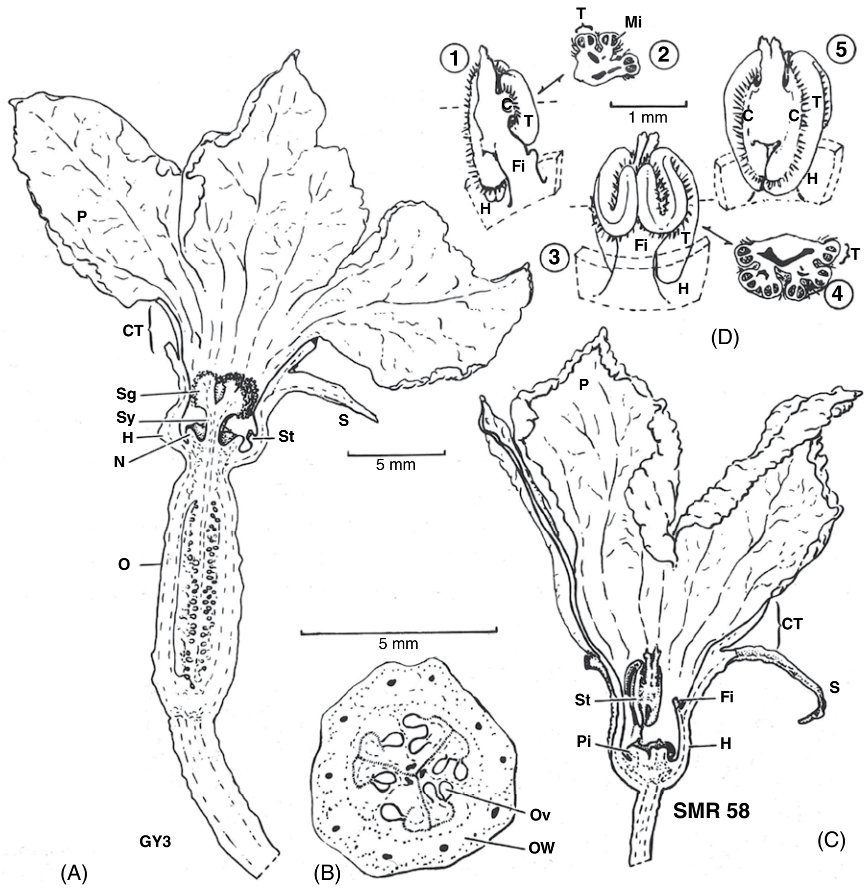

Fig. 1.1. Comparison of female and male cucumber flowers. (A) Female flower at anthesis, longitudinal section. (B) Tricarpellate ovary, transection at anthesis. (C) Male flower at anthesis, longitudinal section. (D) Simple stamen (1, 2) and two compound stamens (3–5). C, anther connective; CT, corolla tube; Fi, filament; H, hypanthium; Mi, microsporangium; N, nectary; O, ovary; Ov, ovule; OW, ovary wall; P, petal; Pi, pistillodium; S, sepal; Sg, stigma; St, stamen or stanimodium; Sy, style; T, theca. (Goffinet, 1990. Reprinted courtesy of Cornell University Press.)

Stamens are attached to the hypanthium and alternate with corolla lobes. The basic number of stamens in the Cucurbitaceae is five. Some cucurbits (e.g. *Fevillea*) have five free stamens, whereas all five stamens are fused together in *Cyclanthera*. During evolution, fusion of two pairs of stamens has resulted in some genera (e.g. *Cucumis*) having one small unilocular and two large bilocular stamens. The three stamens are usually attached to each other to some degree by their anthers, as in squash; filaments are short and often united also.

In the Cucurbitaceae, the subfamily Zanonioideae has relatively homogeneous pollen morphology. In the subfamily Cucurbitoideae, pollen is quite variable, but consistent within genera. For example: in squash, pollen grains are very large, spherical and spiny, but in cucumber the pollen grains are more globular and smooth.

Pistillate flowers have an inferior ovary below the hypanthium. The pistil, which often has a fused style but separate stigma lobes, generally has three or five carpels. The fleshy placentae bear numerous ovules in most species, but only one in chayote.

Floral nectaries attract pollinating insects. These structures are borne inside and at the base of the hypanthium in both staminate and pistillate flowers. The nectary forms a continuous ring surrounding the base of the style(s) in the female flower, whereas the nectary and its associated pistil rudiment form a button-shaped mound at the centre of the male flower.

Fruit

Fruit of the Cucurbitaceae are extremely diverse in many characteristics, including size, shape, colour and ornamentation. Those of bryony are small (ca 5 mm), spherical, and green, red or black in rind colour. Angled luffas are club-shaped, about 60 cm long, and prominently ribbed. Some of the many shapes of bottle gourds are described in Chapter 4. The striped, mottled, bicoloured or solid-coloured fruit of squash are smooth, wrinkled, warted, furrowed or ridged. *Sicyos* has stiff, dry spines, whereas those on the teasel gourd are soft and fleshy.

Cucurbita maxima is well named, for it is this species that is the giant of the plant kingdom. Every year, there is a contest to grow the world's largest pumpkin. In this contest any squash fruit with an orange skin is considered a pumpkin, and the winners are invariably *C. maxima*. Weights crossed the 500 kg threshold in 1999 and the 1000 kg threshold in 2014. The winning fruit in 2016 weighed an astounding 1193 kg. Giant watermelon contests are also run, with the winning fruit in 2015 weighing 137 kg.

Cucurbit fruit are generally indehiscent 'pepos', usually with one or three ovary sections or locules (Fig. 1.2). A pepo is a fleshy fruit with a leathery, non-septate rind derived from an inferior ovary. However, fruit of some cucurbit genera, e.g. *Momordica* and *Cyclanthera*, split at maturity. Fruit of squirting cucumber forcefully eject their seeds through a blossom-end pore. Fruit may be dry when mature, as in luffa, where seeds fall out through a hole at the bottom of the pendulous fruit. Mature fruit of many cucurbits have a hard, lignified rind, but various squash cultivars have been bred to have a tender rind.

Cucurbit fruit flesh is generally white to pale yellow and moist, but cultivated cucurbits such as melon, squash and watermelon have been bred to have a range of flesh colours. Melon and squash have also been bred to include green

Fig. 1.2. Frontal and cross section of female flower from *Cucurbita pepo* (spaghetti squash).

or orange flesh, and watermelon flesh can be white, salmon yellow, canary yellow, orange, coral red or scarlet red. In melon, watermelon and squash, the flesh is derived from the fruit wall. In other species, including cucumber, the edible flesh may be mostly placental in origin.

Many cultivated cucurbits produce a fleshy fruit at maturity. Others, such as gourd and luffa, dry at maturation. When a luffa fruit matures and dries, what is left is a papery outer skin and a fibrous mass surrounding the seeds. This tangled mass of modified vascular bundles, consisting mostly of fibre cells, makes up a luffa sponge.

Seeds

There may be only one seed in the fruit, as in chayote, or more typically, tens to hundreds of seeds. Cucurbit seeds, which are rarely winged, are usually flat. The seed coat encloses a collapsed perisperm, an oily embryo and little or no endosperm. The tiny endosperm is consumed during seed development. Two cotyledons make up much of the contents of the seed. Seeds of some cucurbits are enveloped in a false aril of placental origin; in bitter gourd this sarcotesta is red and fleshy, attracting birds as seed dispersal agents.

Seed size, shape and colour vary greatly among the cultivated cucurbits (Fig. 1.3). The largest unwinged seed is that of *Hodgsonia*, measuring about 7 cm long. The nearly spherical seed of *Bryonia* is sometimes less than 3 mm in diameter. Cultivars within a crop, including watermelon and squash, may differ considerably in their seed sizes and other seed characteristics. Depending on the cultivar, watermelon seeds are white, tan, brown, black, red, or green. They can also have patterns on them, referred to as dotted, rimmed (dark seed margin), tipped (dark seed tip) or clump (dark seed centre).

The complex seed coat anatomy of cucurbits has been well studied (Singh and Dathan, 1990). The testa develops from the outer integument of the

Fig. 1.3. Seeds of the Cucurbitaceae. The largest seed (*Fevillea cordifolia*) shown here measures ca 53 mm across. Also shown are seeds of *Cucurbita*, *Siraitia*, *Marah*, *Momordica*, *Sicana*, *Trichosanthes*, *Luffa*, *Lagenaria*, *Echinocystis* and *Melothria* (the smallest seeds).

anatropous, bitegmic, crassinucellate ovule. The inner integument degenerates in fertilized ovules. The mature seed coat in the subfamily Cucurbitoideae consists of an epidermis, hypodermis, main sclerenchymatous zone, aerenchymatous zone and inner parenchymatous or chlorenchymatous zone. In the Zanonioideae, the sclerenchymatous layer is poorly or not differentiated from the hypodermis, and the well-developed aerenchyma has distinctive lignified thickenings. Within each subfamily, there is further anatomical diversity among genera.

GROWTH AND DEVELOPMENT

Seed germination

Seed maturation usually continues until the fruit starts to yellow with senescence. Some seed producers store mature cucurbit fruit after harvest to permit the seeds to develop further. However, if seeds are left too long in some fruit, they may germinate *in situ*. In a few cucurbits, such as chayote, germination is naturally viviparous.

Seed dormancy, which is common in various wild species, is not usually a serious problem in the major crops. Dormancy can occur in freshly harvested seeds of some cultivars, but this dormancy can be broken by a month or more of after-ripening, i.e. storing seeds in the fruit after harvest. Light and low temperature (< 15°C) are strong inhibitors of germination for many species. Under amenable conditions (e.g. low light levels, temperatures of 25–30°C and adequate but not soaking moisture), germination takes 2 days to 2 weeks if the seeds are not dormant. See Chapter 6 for experimental studies investigating seed germination physiology.

Plant growth and movement

Most cucurbits grow rapidly in warm weather, with stem extension growth outpacing leaf development in the tuberous perennials. In a single growing season, a wild buffalo gourd plant produced 360 shoots covering an area 12 m in diameter with a total vine length of over 2000 m (Dittmer and Talley, 1964). Among the annuals, bottle gourd stems can elongate up to 60 cm in 24 h, and wild cucumber (*Echinocystis lobata*), which is adapted to the short growing seasons of southern Canada, is considered one of the fastest growing vines. Holroyd (1914) reported that a single annual squash (*C. pepo*) plant produced 450 leaves on a vine measuring 43 m. Cucurbit root growth is also rapid, occurring at a rate of 6 cm per day for squash when conditions are favourable. Elite cultivars of pickling cucumber will go from seed planting to first harvest in 39 days if grown at the optimum growth temperature (32°C).

In large-fruited vining squash plants, total leaf area increases exponentially throughout the season until fruit set creates a large reproductive sink and vegetative growth is suppressed. During the period between flower primordia initiation and the start of fruit development in West Indian gherkin, differentiation of new vegetative organs decreases, the growth rate of existing vegetative organs increases, and water and nutrient intake drops; soon after fruit development begins, vegetative differentiation and water and nutrient intake resurge (Hall, 1949).

Biomass productivity differs among species and cultivars and is influenced by cultural practices (e.g. planting density, irrigation, fertilizer application) as well as local environmental conditions. Environmental factors most affecting growth rates are photoperiod and ambient temperature, either of which can affect the intake and effective utilization of water and nutrients. Many investigations of the relationship between growth and environmental factors have been carried out on species of *Cucumis*, particularly cucumber. The results of these studies, which were discussed in detail in Whitaker and Davis (1962) and Wien (1997), are summarized below.

1. The growth rate curve for a single leaf under continuous light is generally an S curve, but is affected by light intensity.
2. The rate of stem elongation is greater during 8 h days than during 16 h days, and plants grown under short-day conditions produce more nodes and leaves, but smaller total leaf and root areas.
3. Overall stem length may be greater under a long-day versus a short-day regime when nitrogen levels are high.
4. Under low-nitrogen conditions, plants grown during long days contain more carbohydrates at anthesis than plants grown during short days, but this carbohydrate relationship is reversed at fruit maturity.
5. Stem extension and leaf area growth rates are linearly dependent on mean ambient temperature during periods of optimum temperatures for growth

(20–30°C, depending on other environmental conditions). However, in the range of 15–27°C, Grimstad and Frimanslund (1993) found that plant dry weight of cucumber had a sigmoidal response curve with inflections at about 17°C and 24°C.

6. When temperature rises above the optimum, leaf growth rate in young plants declines as material is redistributed to the stems, and cell division in developing leaves is reduced.

7. At below-optimum temperatures, relative leaf growth rate is independent of temperature and is controlled instead by light intensity.

8. Stem extension rates are lower than normal when night temperatures exceed day temperatures.

9. Low temperatures slow the development of apical buds.

In *C. pepo*, bushy plants with short internodes possess an allele that reduces biosynthesis of endogenous gibberellin. When these plants are treated with a high concentration (2.9–4.3 mmol l^{-1}) of gibberellic acid, internode lengths become as long as those of naturally viny squash plants.

Breeders have also selected for bush cultivars in *C. maxima*. Research on bushy versus viny plants of this species indicates that bush cultivars have a more uniform growth pattern, respond better to high-density planting, and produce a greater percentage of fruit versus vegetative biomass during short growing seasons (Loy and Broderick, 1990). This last effect is partly due to the fact that fruiting begins sooner in bush cultivars, which in turn suppresses vegetative growth. However, photosynthetic rates in bush plants increase during fruit set in response to increasing sink demand, which may be possible because of a proportionally thicker palisade layer in bush plant leaves (Loy and Broderick, 1990).

In climbing cucurbits, the stems often revolve, twist and extend upwards. Darwin (1906) made several interesting observations on the revolving nature of cucurbit stems and tendrils. He noted that the average rotation rate was 100 min per revolution in wild cucumber. Light affects this movement, with stem tips, including the two uppermost internodes subtending the apical meristem, following the sun throughout the day.

Generally, the slightly curved tendril becomes sensitive to mechanical stimulus on its concave side when it is one-third grown. At that stage, it reacts quickly (in under 2 min), with coiling caused by the elongation of parenchymatous cells on the convex side of the tendril. The revolving movement of a tendril does not stop after it has coiled, but its ability to coil is limited after it stops revolving.

Sex expression

No cucurbit species is known to have only or primarily functionally hermaphrodite flowers. Instead, most cucurbits are monoecious; that is, they have separate male and female flowers on the same plant. Among its genera, the Cucurbitaceae also has a high rate of dioecy, where staminate and pistillate flowers occur on separate plants. Some genera have only dioecious species. Half of the 135 cucurbit species surveyed in India by Roy and Saran (1990) were dioecious, a much higher proportion than is typical for angiosperm families. Cultivated cucurbits that are dioecious include oyster nut, fluted pumpkin, ivy gourd, pointed gourd and monk fruit (luo-han-guo, *Siraitia grosvenorii*).

Primitive cucurbits are typically monoecious, as are the majority of domesticated cucurbits. Most squash and watermelon cultivars are monoecious, although genes for different forms of sex expression are known for these crops. For example, some watermelon cultivars may have three types of flowers on the same plant: staminate, pistillate and perfect (hermaphrodite). The wild-type watermelon is andromonoecious (staminate followed by perfect flowers). Many cucumber cultivars are monoecious, but others are gynoecious or predominantly gynoecious, and round-fruited cucumber such as 'Lemon' and 'Crystal Apple' are andromonoecious. All seven sex types have been identified in cucumber: androecious, gynoecious, hermaphroditic, monoecious, andromonoecious, gynomonoecious, and trimonoecious (staminate, perfect and pistillate flowers). Angled luffa is monoecious with some exceptions, such as the cultivar 'Satputia', which has only hermaphrodite flowers. Most round-fruited melon cultivars are andromonoecious, with the fruit formed from perfect flowers. The bisexual flowers of these plants are often borne on the first or second node of the lateral branches. There are exceptions, however. Monoecious cultivars such as 'Athena' have been selected to have short, almost round fruit developing from pistillate flowers. 'Banana' and other melon cultivars of the Flexuosus Group are monoecious. The group includes snake melon (Armenian cucumber) and pickling melon, with long fruit having crisp white bland flesh, similar to cucumber.

Monoecy is the ancestral condition in cucurbits. Dioecy and other forms of sex expression have arisen in various evolutionary lines in the family. Single genes can determine the occurrence of unisexual plants in normally monoecious species, as in the case of dioecy (all male or all female flowers on a plant) in *C. pepo*. In melon, cucumber and many other cucurbits, two or more genes are involved in sex expression, sometimes (as in *Luffa*) with each gene having three or more alleles. The development of heteromorphic sex chromosomes (e.g. ivy gourd) to determine dioecy is considered to represent the ultimate degree of evolution from monoecy in the Cucurbitaceae.

Monoecious cultivars may differ in degree of female sex expression, some having a higher proportion of female to male flowers. Generally, they produce many more staminate than pistillate flowers and go through a progression of floral development. Nitsch *et al.* (1952) determined that young squash plants are initially vegetative, then bear only underdeveloped male flowers. Later, they produce only normal male flowers, then bear normal female as well as male flowers. The proportion of female to male flowers increases as the plant grows older, and the plant eventually produces only female flowers. If squash plants are not pollinated, ultimately they may produce enlarged female flowers and parthenocarpic fruit.

Although staminate flowers usually appear a few days to a few weeks before pistillate flowers on squash vines, a few cultivars and some wild populations of *C. pepo* may produce female flowers first (Fig. 1.4), especially when spring temperatures are low. These wild populations also tend to have a higher ratio of female to male flowers than most cultivars (Decker, 1986).

In their search for early staminate flower production in cucumber, Walters and Wehner (1994) examined 866 cultivars, breeding lines and plant introduction accessions. Earliness was normally distributed for the cultigens and ranged from 26 to over 45 days from planting to first staminate flower.

Sex expression in the Cucurbitaceae is controlled by environmental as well as genetic factors. Unfavourable growing conditions (e.g. lack of water) can reduce flower production. In general, female sex expression is promoted by low temperature, low nitrogen supply, short photoperiod and high moisture availability, i.e. conditions that encourage the build-up of carbohydrates. These environmental factors influence the levels of endogenous hormones (especially ethylene, auxin and gibberellic acid), which in turn influence sex expression. Most studies examining this role of hormones have been conducted on

Fig. 1.4. Accession means of the number of days from seed germination to the first male and female flowers on plants of 30 cultivars and eight wild populations of *Cucurbita pepo*. (Data from Decker, 1986.)

cucumber, followed by squash, melon and watermelon. See Chapter 7 for details on the use of exogenous hormones to control sex expression.

Temperature affects anthesis and, in squash, the length of time that a flower is open. Squash pollen is released at temperatures as low as 10°C, whereas cucumber, watermelon and melon flowers require higher temperatures for anther dehiscence. Warmer temperatures cause anthesis in squash to occur earlier in the morning. However, high temperatures (ca 30°C) accelerate squash flower closing, causing the corollas to close by mid- to late morning.

Fruit development

Pollen tube growth and ovule fertilization stimulate ovary enlargement. Subsequent fruit set depends on the quality of pollination (i.e. having enough ovules fertilized) and is affected by the presence of already developing fruit, leaf area, daylength and other environmental factors. Fruit on a plant may inhibit the production of additional pistillate flowers and the development of subsequent fruit. In cucurbit crops such as melon, watermelon and squash, fruit-thinning will allow fruit that remain on the vine to grow larger.

If fruit are not developing on a plant by the end of the growing season, then the last group of ovaries may develop parthenocarpically. Parthenocarpy in cucumber and squash is promoted by low temperature, short daylength, old plant age and genetics. Some cucumber cultivars have genes for parthenocarpy and will set fruit without pollination. Parthenocarpic cultivars are common in the greenhouse trellis type, the Middle Eastern greenhouse (Beit Alpha) type and, more recently, field slicers and field pickles. Parthenocarpic pickling type has become popular in northern Europe and most of the USA, due to seedless fruit and higher yield. Field production of parthenocarpic cultivars depends on isolation from conventional cultivars having staminate flowers, as well as the exclusion of beehives from the area.

Anderson (1894) determined that a developing squash fruit gained weight at an average rate of 1 g per minute. The greatest weight increase was at night. The growth rate for cucurbit fruit is influenced by exogenous conditions (e.g. higher temperatures and greater light exposure increase the growth rate) as well as by endogenous plant conditions, such as the presence of other developing fruit, which retards growth.

Several studies on the inheritance and development of fruit shape in squash (*C. pepo*) were conducted by Sinnott (1932). He reported that fruit shape is evident in the shape of the immature ovary, with ultimate shape affected by both genetic and environmental factors. Also, fruit that are set first may be shaped differently than those set later, the difference being evident in the shape of the ovaries.

Immature ovaries are usually green, although those of squash cultivars with gene *B* may be yellow. Fruit of various cucurbits, including luffa and bottle gourd, remain green until fruit senescence, at which time they turn tan or brown. Other cucurbits develop rind coloration changes during maturation. In these, chlorophyll depletion reveals the presence of additional pigments after pollination. For example, the green fruit of many squash cultivars become yellow or orange as they age. Colour changes usually begin at the blossom end of the fruit. In most wild and cultivated *Cucurbita*, rind patterns, such as stripes or mottling, are lightly visible on the ovary, becoming more distinct soon after pollination. However, the white fruit of 'Mandan' (*C. pepo*) reach almost full size before the dark green markings appear. Fruit markings persist at maturity for some squash cultivars, but fade away in senescent fruit of others.

In young melon fruit of the Cantalupensis Group of cultivars, rapidly dividing cork cells develop below the epicarp. Near maturity, this growth breaks through to form a network of grey corky tissue covering the rind, as is evident in the netting of muskmelon cultivars.

A unique case of adaptation to a particular ecological niche is exemplified by *Cucumis humifructus* Stent. This African species has a geocarpic fruit, similar to that of peanut. After flowering and setting fruit above ground, similar to other *Cucumis* species, the developing fruit is thrust downward and completes its development several inches below the soil surface. In its native land, the African anteater or aardvark (*Orycteropus afer*) consumes the subterranean fruit. It is a symbiotic relationship, with the aardvark using the fruit as a source of food and water in the arid area where the plant often grows, and providing a means of seed dispersal for the plant. *C. humifructus* is called aardvark cucumber because of this relationship, but it is more closely related to melon than to cucumber.