2 Botany and Crop Improv[illegible] Ginger

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The genus *Zingiber* of the family Zingiberaceae is distributed in tropical and subtropical Asia and Far East Asia and consists of about 150 species. Zingiberaceae is of considerable importance as a "spice family." Besides ginger this family includes turmeric, cardamom, large cardamom, grain of paradise, and several others having economic and medicinal importance. Zingiberaceae was earlier divided into the subfamilies Costoideae and Zingiberoideae, which were later given independent family status as Costaceae and Zingiberaceae. Three tribes were recognized in the subfamily Zingiberoideae by workers such as Peterson (1889) and Schumann (1904); and the genus *Zingiber* was included in the tribe Zingibereae along with *Alpinia*, *Amomum,* and others. This tribe is characterized by the absence of lateral staminodes or staminodes that are united to the labellum, in comparison with tribe Hedychieae, in which the lateral staminodes are well developed. Later Holttum (1950) removed *Zingiber* from Zingibereae and renamed it as Alpinieae; his argument was that *Zingiber* is closer to the genera under the Hedychieae as their lateral staminodes appear as lobes at the base of the labellum, whereas in *Alpinia* these staminodes are well developed. Many later workers accepted the opinion of Holttum. Burtt and Smith, however, felt that the contention of Holttum is nomenclaturally incorrect and proposed that *Zingiber* should be in an independent tribe (Burtt and Smith, 1983).

The first documentation of ginger was by Van Rheede (1692) in his *Hortus Indicus Malabaricus* (Vol. 11), the first written account of the plants of India. Van Rheede described the cultivated ginger (*Z. officinale*) under the local name *inschi (inchi)*. The Indian species was first botanically described by Roxburg (1810), who reported 11 species, and placed them in two sections based on the nature of the spike: Section 1. spikes radical and Section 2. spikes terminal.

Baker (1882) has carried out an exhaustive survey of the Zingiberaceae of Indian Peninsula for *The Flora of British India* (J.D. Hooker). In this he recognized four sections:

1. Cryptanthemum Horan—Spikes are produced directly from the rhizome and are very short and dense; peduncle very short (11 species)
2. Lampuzium Horan—Spikes produced from the rhizome on more or less elongated peduncles with sheathing scariose bracts (10 species)
3. Pleurantheis Benth—Spike peduncle arising from the side of the leafy stem (1 species)
4. Dymczewiczia (Horan) Benth—Spikes terminal on the leafy stem (2 species)

This subgeneric classification was accepted by later workers including Schumann (1904) in his revision of Zingiberaceae.

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Zingiber Boehmer

Boehmer and Ludwig, Def.Gen.Pl.89,1760, nom.cons; Benth.&Hook.f.Gen.Pl. 3,646,1883; Baker in Hook.f.Fl.Br.India,7,243,1892; Schum.in Pflanzen.Zng.165,1904. Type species: *Z. officinale.*

Holttum (1950) provided the following description for the genus.

Rhizomes as or near surface of the ground, bearing leaf shoots close together. Leaf shoots short to moderately tall, often with many leaves. Leaves thin in texture, never very large (rarely to 50 cm long), sessile or with quite short petioles, the ligule short to long deeply bilobed or entire. Inflorescence on a separate shoot without normal leaves (rarely at the apex of the shoot); scape usually erect, short or long, clothed with two-ranked sheaths that are sometimes colored red; spike short or long, slender or thick, cylindrical, ovoid, or tapering to a narrow apex, elongating gradually. Bracts fairly large, usually brightly colored, red or yellow, usually thinly fleshy, closely imbricating or with apices free, margins plane or inflexed. One flower in the axil of each bract; flowers fragile or short lived. Bracteoles one to each flower, facing the bract, thin and narrower than bract, usually persisting and enclosing the fruit, split to the base, never tubular.

Calyx thin, tubular spathaceous usually shorter than the bracteole, but sometimes longer. Corolla tube slender, usually about as long as the bract; dorsal lobe usually broader than the others, erect, narrowed to the tip, and hardly hooded; edges inflexed, lateral lobes usually below the tip and on either side of it, sometimes joined partly together by their adjacent sides and to the tip; color usually white or cream. Labellum deeply three-lobed (the side lobes representing staminodes), or rarely the side lobes hardly free from the mid lobe, side lobes erect on either side of the stamen, mid lobe shorter than or not greatly longer than the lateral corolla lobes, its apex usually retuse or cleft; color cream to white or more or less deeply suffused with crimson or purple. Filament of stamen short and broad, anther rather long, narrow; connective prolonged into a slender curved beak-like appendage as long as the pollen sac, with inflexed edges, containing the upper part of the style. Stigma protruding just below the apex of the appendage, not thickened, with a circular apical aperture surrounded by stiff hairs. Stylodes usually slender and free, not surrounding the base of the style. Ovary glabrous or hairy, trilocular with several ovules in each loculus. Fruit with a fleshy wall when fresh, more or less leathery when dry, smooth, or hairy, enclosed by the persistent bract or bracteole, dehiscent loculicidally within the persistent bracts. Seed ellipsoid, black or dark brown, covered by a thin saccate white aril with irregularly lacerate edges.

The main distinguishing features of the genus are: (1) long, curved anther-appendage embracing the style, (2) the three-lobed lip (the side lobes are staminodes, which are relatively broad and fused more or less to the mid lobe or lip proper), and (3) the relatively large bracts, each with a single flower and a nontubular bracteole, more or less imbricating on a lengthening inflorescence (*Z. clarkei* from Sikkim is an exception that has two to four flowers to each bract). The bracts are often but not always colored; in some species, they change color as they grow older. The color of the lip is an important distinguishing character.

The genus contains 150 species: 34 species have been reported from China (Shu, 2003) and 24 species from India (Baker, 1882). The main centers of diversity are South China; Malaysia; Northeast India, Myanmar region, and the Java–Sumatra region of Indonesia; Shu (2003) has recently revised the Chinese species. The only species extensively used as flavoring for food is the true ginger, *Z. officinale.* Some species like *Z. zerumbet* and *Z. cassumunnar* are well known for their uses in native medicine. *Z. mioga* is used as a spice and its flower buds are in great demand in Japan as a vegetable.

Zingiber officinale Rosc.

Roscoe, New arrangements of the plants of the monandrian class usually called "Scitaminea," Trans. Linn. Soc. 8:348, 1807; Valeton, Bull. Buitenz, 2nd Ser., xxvii, 128, 1818; Fluckiger and Hanbury, Pharmacographia, 574, 1874; Engler, Pflanzenw.Ost.-Afrikes and Nachbargebiete, B. Natzpflanzen,.264,1895; Schumann, Zingiberaceae, in Das Pflanzenrich, 4,46,170,1904.

Inschi, Rheede, Hort. Malabaricus, 11,23–25, 1692.

Rhizome entirely pale yellow within or with a red external layer. Leafy stems to about 50 cm tall, 5 mm diameter, glabrous except for short hairs near base of each leaf blade; leaf blades commonly about 17 by 1.8 cm; rather dark green, narrowed evenly to slender tip; ligule broad, thin, glabrous, to 5 mm tall, slightly bilobed. Scape slender, to 12 cm tall, the upper sheaths with or without short leafy tips; inflorescence approximately 4.5 cm long and 15 mm diameter; bracts approximately 2.5 by 1.8 cm; green with pale submarginal band and narrow translucent margin; margins incurved, lower bracts with slender white tip. Bracteoles as long as bract; calyx with ovary 12 mm long; corolla tube 2.5 cm long, lobes yellowish, dorsal lobe 18 by 8 mm (flattened), curving over the anther and narrowed to the tip, laterals narrower. Lip (mid lobe) nearly circular, approximately 12 mm long, and wide, dull purple with cream blotches and base, sidelobes about 6 by 4 mm; free almost to the base, colored at mid lobe; anther cream, 9 mm long, appendage dark purple, curved, 7 mm long (Holttum, 1950). The species is sterile and does not set seeds (Figure 2.1, Figure 2.2, and Figure 2.3).

Taxonomical notes: Roscoe (1807) described *Z. officinale* from a plant in the Botanic Garden at Liverpool as "*Bracteis ovato-lanceolatis, laciniis corolla revolutis, nectario trilobato*" and referred to *Amomum zingiber* Willd. Sp.Pl 1:p6. Willdenow (1797) extended Linnaeus description "*Amomum scapo nude, spica ovata*" with "*squamis ovatis, foliis lanceolatisbad apicem margine ciliates.*" Linnaeus's (1753) *Amomum zingiber* is the basionym for the species. The genus *Amomum* of Linnaeus is a nomenclatural synonym of the conserved generic name, *Zingiber* Boehm (Burt and Smith, 1968). The specific epithet *zingiber* could not be used in the genus *Zingiber.* Thus, *Z. officinale* was adopted as the correct name for ginger. The specimens available in most herbaria are without flowers, and it is assumed that Linnaeus based his description on the account and figure given by Rheede in *Hortus Malabaricus.* The figure given by Rheede (Vol., 11, plate 12, 1692) is the designated lectotype of the species *Z. officinale* Rosc. (Jansen, 1981).

The species epithet *officinale* was derived from Latin, meaning "work shop," which in early Latin was used to mean pharmacy, thereby implying that it had a medicinal use.

Morphology and Anatomy

The ginger plant is a herbaceous perennial grown as an annual crop. The plant is erect, has many fibrous roots, aerial shoots (pseudostem) with leaves, and the underground stem (rhizome). The roots of ginger are of two types, fibrous and fleshy. After planting, many roots having indefinite growth grow out of the base of the sprouts. These are the fibrous roots, and the number of such roots keeps on increasing with the growth of

Figure 2.1 A ginger plant showing aerial shoots and inflorescence.

tillers. These fibrous roots are thin, have root hairs, and their function is mainly absorption of water and nutrients. As a ginger plant grows further, several fleshy roots of indefinite growth are produced from the lower nodes of the mother ginger and primary fingers. These roots are thicker, milky white in color, with few root hairs, and no lateral roots. Such roots carry out the functions of support as well as absorption (Figure 2.4).

During the initial growth, the apical bud of the rhizome piece planted grows out and becomes the main tiller or mother tiller. As this tiller grows, its base enlarges into a rhizome. This is the first formed rhizome knob and is often called the mother rhizome. From either side of the mother rhizome, branches arise and they grow out and become the primary tillers (Figure 2.5). The bases of these tillers become enlarged and develop into the primary fingers. The buds on these primaries develop in turn into secondary tillers and their bases into secondary fingers. The buds on the secondary fingers in turn can develop into tertiary tillers and tertiary fingers.

The aerial shoots have many narrow leaves borne on very short petioles and with sheaths that are long and narrow, and the overlapping sheaths produce the aerial shoot. A pair of ligules is formed at the junction of leaves and sheath. The leaves are arranged in a distichous manner.

Ginger is a subterranean stem (rhizome) modified for the vegetative propagation and storage of food materials. The stem has nodes with scale leaves and internodes. Except for the first few nodes, all the nodes have axillary buds. When the rhizome bit is used for planting ("seed rhizome" or setts), there may be one or more apical buds on it; however, normally only one bud becomes active. When large pieces are used, more than

Figure 2.2 Sketch of the ginger plant showing the origin of shoots, inflorescence, and flower. AS: Aerial shoot, R: Rhizome, Fl: Flower, P: Peduncle (scape), S: Spike.

one bud may develop simultaneously. If more than one branch from the parent rhizome is responsible for the ultimate growth and development of the adult rhizome, the branches of the mature rhizome lie in the same plane (Shah and Raju, 1975a).

The pattern of rhizome branching is illustrated in Figure 2.6. The main axis developing from the apical bud, which is the first developing branch, has 7 to 15 nodes, which later

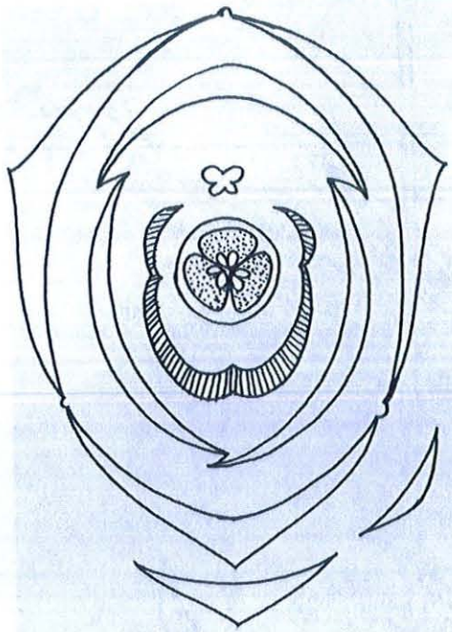

Figure 2.3 Floral diagram of ginger flower.

Figure 2.4 Ginger rhizome showing two types of roots—thick, white fleshy roots and the fibrous roots with root hairs.

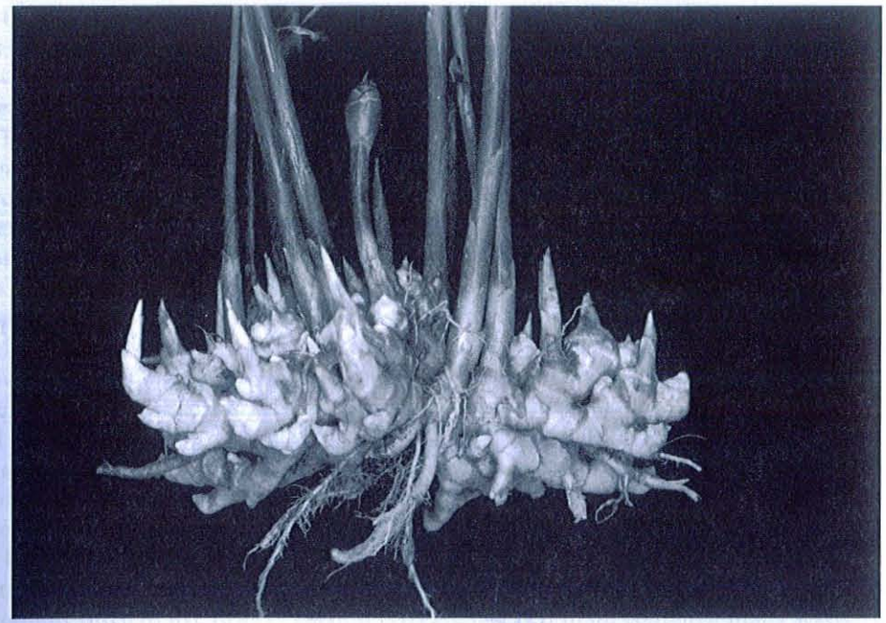

Figure 2.5 Ginger rhizome showing the conversion of branch apices into aerial shoots.

becomes an aerial shoot. Once this axis becomes aerial, the subsequent growth of the rhizome is due to the development of the axillary buds situated above the first two to three nodes of the underground main axis. These axillary branches are plagiotropic and then they quickly show orthotropic growth at their distal region and subsequently become aerial shoots (see Figure 2.5). The same pattern of growth is continued for successive branches to form a sympodial growth pattern. A few axillary buds at the distal end of the branch remain dormant. The number of primary branches may be two, three, or four. These primary branches arise on either side of the main axis. Subsequent development of the secondary, tertiary, and quaternary branches are on the abaxial side of the respective branches. Irrespective of the number of primary branches, the subsequent branches lie in the same plane, although alteration of this scheme is seen sometimes. A mature rhizome may consist of 6 to 26 axillary branches with foliage leaves or only with sheath leaves and they show negative geotropic response (Shah and Raju, 1975a).

The number of nodes in each rhizome branch varies. The main axis (mother rhizome) and the subsequent branches (primaries) have 6 to 15 nodes. The internodal length of the rhizome branches ranges 0.1 to 1.5 cm, and varies even in a single branch. The internodal length is more in secondary, tertiary, and quaternary branches, and in the aerial stem it ranges from 3 to 7 cm. In the underground stem the nodes have scale leaves that ensheath and protect the axillary buds. These scale leaves fall off or may be lost, so that in mature rhizomes only the scars remain. Young scale leaves have pointed tips that help in penetration of soil.

The distal few nodes of the rhizome have sheath leaves. At the early stage of development they lack any apparent slit due to the overlapping of their margins. Later a longitudinal slit is formed through which the shoot tip projects. After the development of 6 to 12 scale leaves and 3 to 5 sheath leaves, the foliage leaves are produced. A foliage

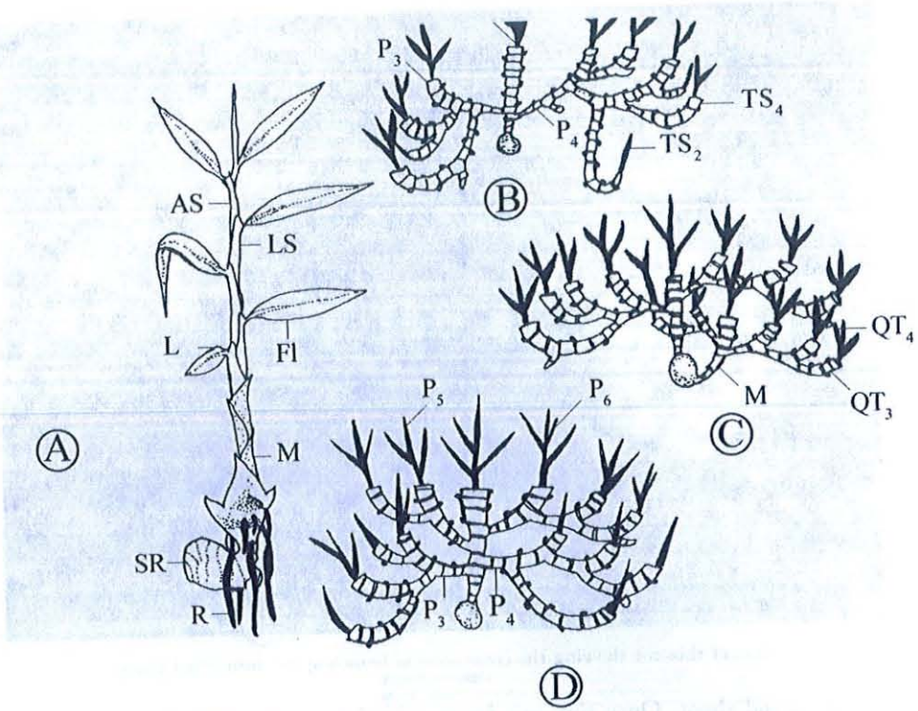

Figure 2.6 Growth pattern of the ginger rhizome.
A. Habit. B. Typical mode of growth pattern (nodes are represented by dark horizontal lines and dormant buds by a black spot). C. Two main axes developing from the seed rhizome, and their subsequent branches developing in the same plane. D. A main axis with four primary branches and their subsequent branches developing in the same plane. (Source: Shah and Raju, 1975a.)

leaf consists of a leaf sheath, a ligule, and an elliptical–lanceolate blade. The leaf sheath is about 15 to 18 cm and lamina about 12 to 15 cm long. Above its region of insertion, the sheath encircles the internode; and from the side opposite to its origin up to the ligule, the sheath is open longitudinally. A distinct mid rib is present only in the lamina. The phyllotaxy of the scale leaves on the rhizome and foliage leaves on the aerial stem is distichous, with an angle of divergence of about 180°. Within the bud, leaves have imbricate aestivation (Shah and Raju, 1975a).

Rhizome Anatomy

The early studies on the anatomy of ginger were carried out mainly by the pharmacognosists, and they concentrated on the officinal part, the rhizome, either dry or fresh (Futterer, 1896). A comprehensive survey on the anatomy of the plants belonging to Zingiberaceae was that of Solereder and Meyer (1930), in their classical work *Systematische Anatomie der Monocotyledonen* (Systematic Anatomy of the Monocotyledons). They provided anatomical notes on 18 genera and some 70 species (Tomlinson, 1956). Later Tomlinson (1956) supplemented the information and filled in the gaps. However, no information was available on the developmental anatomy. Some studies were carried out

by Pillai et al. (1961), Aiyer and Kolammal (1966), and Shah and Raju (1975b). More recently, Ravindran and colleagues investigated the developmental anatomy of rhizomes, oil cells, and associated aspects (Remashree et al., 1997; 1998, 1999; Ravindran, 1998). The following discussion is based on the studies of the above workers.

The transection of a fresh, unpeeled rhizome is almost circular or oval, about 2 cm in diameter, with the outline almost regular. The TS shows a light-brown-colored outer border and a central zone 1.2 cm in diameter marked off by a yellowish ring from an intermediate cortical zone. A distinct continuous layer of epidermis is generally present, consisting of a single row of rectangular cells; in some cases, it may be ruptured. Within this is the cork, varying in thickness from 480 to 640 µm and differentiated into an outer region 300 to 400 µm in thickness, composed of irregularly arranged, tangentially elongated, slightly brown-colored cells, and an inner zone of 6 to 12 regular rows of thin-walled rectangular to slightly tangential elongated cells arranged in radial rows. They measure 30 × 30 to 114 × 48 µm. (*Note*: Cork tissue develops after the harvest and during storing. So when a rhizome is cut soon after harvest, one may not encounter much cork tissue.) A cork cambium is not evident. Inner to the cork is the cortex that is about 4 mm in thickness, composed of thin-walled large hexagonal to polygonal parenchymal cells. The cortical cells are heavily loaded with starch grains. These grains are large, simple, and ovoid, in length varying from 15 to 65 µm. Scattered within the cortex are numerous oil cells that contain large globules of yellowish-green color. The outermost three to five rows of cortical cells are not rich in oil contents. Many scattered, collateral, closed vascular bundles are present, of which the greater number is seen in the inner cortical zone. The large bundles are partially or entirely enclosed in a sheath of septate fibers, whereas the smaller bundles are devoid of any fiber. Each vascular bundle consists of phloem, composed of small thin-walled polygonal cells with well-marked sieve tubes and xylem composed of one to nine vessels with annular, spiral or reticulate thickenings. These vessels have a diameter varying from 21 to 66 µm. In the enclosing sheath of fibers the number of cells varies very much. There are 4 to 48 fibers or occasionally more. These fibers are very long, but less than 1 mm, have a diameter from 10 to 40 µm, and are not straight, but undulate in character. The inner limit of the cortex is marked by a single-layered endodermis composed of thin-walled rectangular cells, much smaller than the cortical cells, with their radial walls slightly thickened and free from starch grains. The endodermis is lined by a pericycle composed of a single row of thin-walled slightly tangentially elongated cells devoid of any starch grains.

The stele that forms the bulk of the rhizome consists of parenchymal cells similar to those of the cortex, with starch grains and oil globules and a large number of irregularly scattered vascular bundles. Just within the pericycle a number of very small vascular bundles are arranged in a ring. These bundles have only one to three vessels and a small phloem. No fibers are present enclosing these small bundles. Generally, the vascular bundles present within the stele are slightly larger than those present in the cortex. The stele contains more oil cells and starch grains than the cortex (Aiyer and Kolammal, 1966).

Rhizome Enlargement

Rhizome enlargement in ginger is by the activity of three meristematic zones. Very early in the development of the rhizome, a zone of meristematic cells is formed at the base of a young scale leaf primordium of developing rhizome. These meristematic cells develop

into the primary thickening meristem (PTM) and procambial stands. The meristematic activity of the PTM is responsible for the initial increase in the width of the cortex. The second type is the actively dividing ground parenchyma. The third type is the secondary thickening meristem (STM), in which fusiform and ray initials are clearly visible. The STM develops just below the endodermoidal layer.

At a lower level in the rhizome from the shoot bud apex, the PTM can still be identified. The scattered vascular bundles are developing from the PTM or procambial cells. Such groups of cells can be identified by the plane of cell division. The differentiation of procambial cells into vascular tissue takes place at different stages of rhizome growth. Unlike in many monocots, in ginger rhizome there is a special meristematic layer along with the endodermoidal layer, and this layer consists of cambium-like cells. The cells are thin-walled and arranged in a biseriate manner. In certain loci, where the vascular bundles develop, these cells are elongated with tapered ends and appear similar to the fusiform initials with an average of 62.34 µm length and 8.12 µm width in mature stages. Between these fusiform initials, some cells show transverse divisions to form ray initials. The presence of the cambium-like layer is an important feature in rhizome development. From this layer inverted and irregularly distributed groups of xylem and phloem are formed along the intermediate layer. The cells outer and inner to the cambial layer become filled with starch grains.

Development of Oil Cells and Oil Ducts

Oil cells are present in the epidermis or just below the epidermis of the leaf, petiole, rhizome, and root. In the rhizome, oil cell initials are present in the meristematic region. They are spherical and densely stainable. The initiation of oil cells and formation of ducts occurs in the apical parts of shoots and roots and starts much before the initiation of vascular elements. Secretory ducts are formed both schizogenously and lysigenously (Remashree et al., 1998; Ravindran et al., 1998).

Schizogenous Type

The schizogenous type of secretory duct originates in the intercalary meristem of the developing regions. The ducts are initiated by the separation of a group of densely stained meristematic cells through dissolution of the middle lamella. Concurrent separation of the cells leads to the formation of an intercellular space bordered by parenchymal cells. These ducts anastomose and appear branched in longitudinal section. Further separation of the bordering cells along the radial wall leads to widening of the duct lumen.

Lysigenous Type

The lysigenous type of duct formation is more frequent in the meristematic region, but occurs in mature parts too. There are four stages involved in its development: initiation, differentiation, secretion, and quiescence. These steps are a gradual process that occurs acropetally (Figure 2.7).

Initiation and differentiation: In shoot apex, the meristematic cells are arranged in tiers. In between these cells, certain cells in the cortical zone are distinguishable from the rest by their large size, dense cytoplasm and prominent nucleus (see Figure 2.7A). Such cells act as the oil cell mother cell. Anticlinal and periclinal divisions of these cells result in

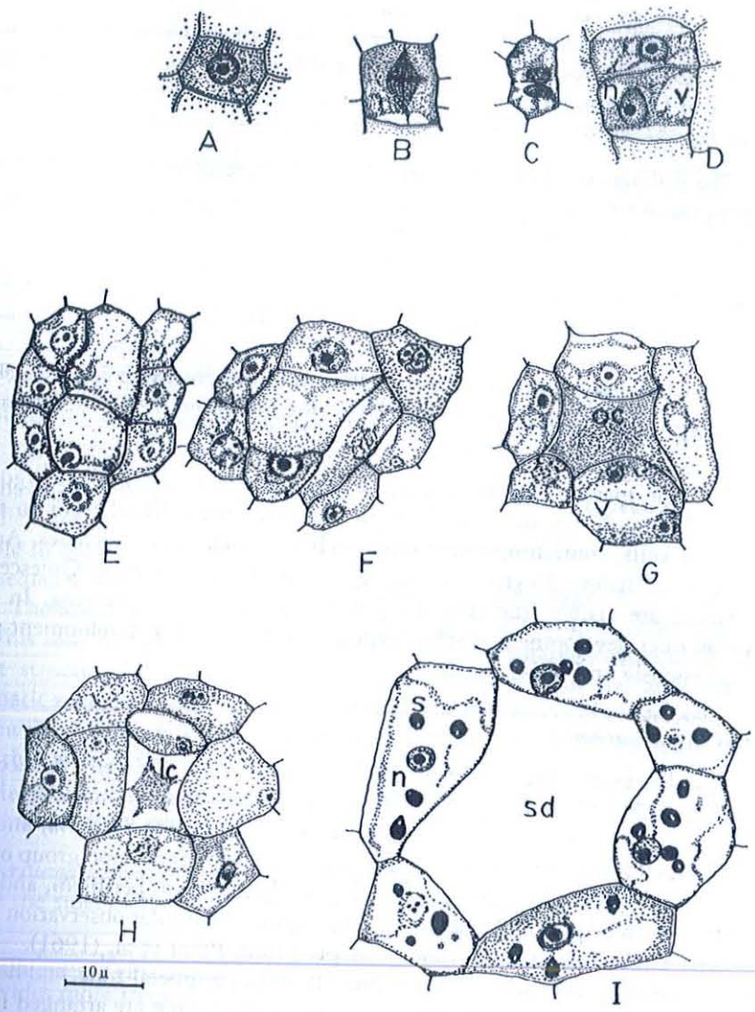

Figure 2.7 Ontogeny of oil cell in ginger: lysigenous development.
A. Oil cell mother cell. B–D. Division of mother cell. E. Nuclear disintegration of central cell. F. Nuclear disintegration (note the deformed cell). G. Cytoplasmic condensation. H. Darkening of cell contents and increase in vacuolation. I. Mature oil duct with scanty cytoplasm (lc, lysing cell; n, nucleus; oc, oil cell; sd, secretory duct; s, starch grain; v, vacuole).

a group of oil cell initials (see Figure 2.7B–E). Cyloplasmic vacuolation initiates in the oil cells at a distance of about 420 µm from the shoot apex. Subsequently the surrounding cells also enlarge in size, showing cytoplasmic and nuclear disconfigurations (see Figure 2.7E, F). Further development leads to the disintegration of nuclear content of the central cell, which stretches toward the intercellular space. Later the central cell disintegrates

and the contents spill into the cavity thus formed (see Figure 2.7I). This process that takes place in adjacent cells leads to the formation of a duct. The duct can be either articulated or nonarticulated, and becomes gradually filled up with the cell contents of the lysed cells. Once the lysogeny of the central cell is completed, the adjacent cells also lyse gradually in a basipetal manner, resulting in the widening of the duct lumen. These stages occur between 1500 and 3000 µm from the apex.

Secretion: The differentiated oil cells start a holocrine type of secretion and expel their contents into the duct. Then the next cell (in acropetal order) becomes differentiated into an oil cell and starts elimination of its contents followed by lysis. Simultaneously the primary tissues continue to become differentiated into new oil cells and reach the secretory stage. The secretion fills the duct in young stages, but the quantity becomes reduced gradually, and finally the ducts appear empty. This could happen because of the diffusion of oil basipetally and radially; such oil particles are deposited in the cells and can be seen as black masses inside cells as well as in the intercellular space. Such stages are noticed about 3,250 µm from the shoot tip (Ravindran et al., 1998; Remashree et al., 1999).

Quiescence: In the mature rhizome the ground parenchyma does not undergo further division and differentiation into the duct. In this stage the cells adjacent to the duct become storage cells, containing numerous starch grains and large vacuoles. An empty cell or cells with distorted cytoplasm appear along the duct lumen. Quiescence and secretory stages are visible from the third month onward after planting. In primary tissues the oil duct development is schizogenous, whereas further development proceeds both schizogenously and lysigenously.

Root Apical Organization

The root apical organization in ginger together with many other zingiberaceous taxa was first reported by Pillai et al. (1961). They found that the structural organization of ginger root apex differs from that of other taxa (such as *Curcuma, Elettaria,* and *Hedychium*). In ginger, all zones in the root apex are originated from a common group of initials. From the rim of this common group, calyptrogen, dermatogen, periblem, and plerome become differentiated. Raju and Shah (1977) also reported a similar observation in ginger and turmeric. The following discussion is adapted from Pillai et al. (1961).

The root cap is not differentiated into columella and a peripheral zone, and hence there are no separate initials for these regions. The cells in this region are arranged in vertical superimposed files. The cells arise by the activity of a meristem, which can be easily differentiated from the rest of the region. Pillai et al. (1961) named this meristematic region columellogen. In transections, the cells of the columella form a compact mass of polygonal cells in the center with the cells of the peripheral region arranged in radiating rows around it.

In the root body two histogens could be distinguished: (1) the plerome concerned with the formation of stele and (2) the protoderm–periblem complex concerned with the formation of the outer shell to the stele including periblem and dermatogen. The protoderm–periblem complex is located outside the plerome and is composed of a single tier of cells. The cells of this zone located on the flanks exhibit T-divisions, which help the tissue to widen out. Periblem consists of the initials of the cortex extending from the hypodemis to the endodermis. The hypodermis arises from the inner layer of the protoderm–periblem initials. The cells composing this tissue vacuolate earlier than the outer cells of the cortex.

Endodermis differentiates from the innermost periblem cells. Outside the plerome dome all cells of the periblem exhibit T-divisions initially but later in development show anticlinal divisions, and the endodermis is differentiated at that time.

Plerome has at its tip a group of more or less isodiametric cells. On the sides of the plerome dome is the uniseriate pericycle. Near the dome, cells take less stain because of their quiescent nature. The metaxylem vessel elements with wider lumens can be seen near the plerome dome. The isodiametric cells at the very center of the plerome divide like a rib meristem to give rise to the pith. In transections passing near the tip of the plerome dome, the initials can be distinguished as a compact mass of isodiametric cells surrounded by radiating rows of periblematic cells.

Cytophysiological Organization of Root Tip

The root tip can be distinguished into two zones on cytophysiological grounds:

1. The quiescent center: This zone is found at the tip of the root body, characterized by its cells having (a) cytoplasm highly stained with pyronin-methyl green and hematoxylin, (b) smaller nuclei and nucleoli, (c) cell divisions less frequent, and (d) vacuolation noticeable in most.

The median longisection of this group of cells is in the shape of a cup with the rim forward. The above characteristics show their state of rest and are called the quiescent center. This zone includes cells belonging to all the structural histogens of the root body (i.e., not structurally delimitable). It gradually merges with the zone outside, the meristematic zone. Raju and Shah (1977) studied the root apices of ginger, mango ginger, and turmeric with azure B staining to localize DNA and RNA contents in order to identify the quiescent center. A quiescent center was present in all the three cases as indicated by the light stainability of its cells. In longisection the quiescent center resembles an inverted cup.

2. The meristematic zone: This zone is shaped like an arch surrounding the quiescent center on the sides of the root body. The cells of this zone have the following features:

a. cytoplasm deeply stained with pyronin-methyl green and hematoxylin.
b. divides more frequently
c. have larger nuclei and nucleoli
d. vacuolation is absent or not prominent

The meristimatic zone includes the cells of all the structural histogens of the root body. The percentage of cell division is much lower in the quiescent center compared to the meristematic zone. This character combined with the response of these cells to stains such as pyronin-methyl green indicates that these cells are in a state of comparative repose and hence are not synthesizing nucleic acids (Pillai et al., 1961). The distance between the tip of the root body and the nearest mature phloem element, which carries the metabolic products required by the active cells, was reported to be 480 to 490 µm. This led to the suggestion that the cells at the tip of the root body go into quiescence because of the dearth of sufficient metabolites (Pillai et al., 1961).

Ontogeny of Buds, Roots, and Phloem

The ontogeny of ginger was studied by Shah and Raju (1975b), Remashree et al. (1998), and Ravindran et al. (1998). In a longisection, the shoot apex is dome shaped with a single tunica layer, below which the central mother cell zone is present. The flank meristem is situated on either side of the central mother zone. The leaf is initiated from the outer tunica layer and from the flank meristem. The shoot apical organization and acropetal differentiation of procambial strands are closely related to the phyllotaxy. At an even lower level basipetally in the rhizome axis, additional inner cortical cells are produced by a lateral PTM or procambium in which the resulting cells are radial rows.

The nature of the shoot apex: Shah and Raju (1975b) investigated the nature of the shoot apex in ginger. In the shoot apex in all stages, a single layer of tunica occurs, showing only anticlinal divisions. Cytohistological zonation based on staining affinity is not observed at any stage. The distal axial order (cr) includes the central group of corpus cells dividing periclinally and anticlinally and the overlying cells of the tunica (Figure 2.8). The peripheral zone (pr_1) is concerned with the initiation of the next leaf primordium and formation of the leaf sheath on the opposite side. It is delimited by the shell zone on the rhizome apices, which appears as an arc of narrow cells in median longitudinal section. The peripheral zone (pr_2) is associated with the initiation of the next leaf primordium. In the rhizome apices it is also associated with the initiation of the axillary buds. As the phyllotaxy is distichous, this zone is opposite to pr_1 in median longisections. Pith cells differentiate in the inner axial zone (rr).

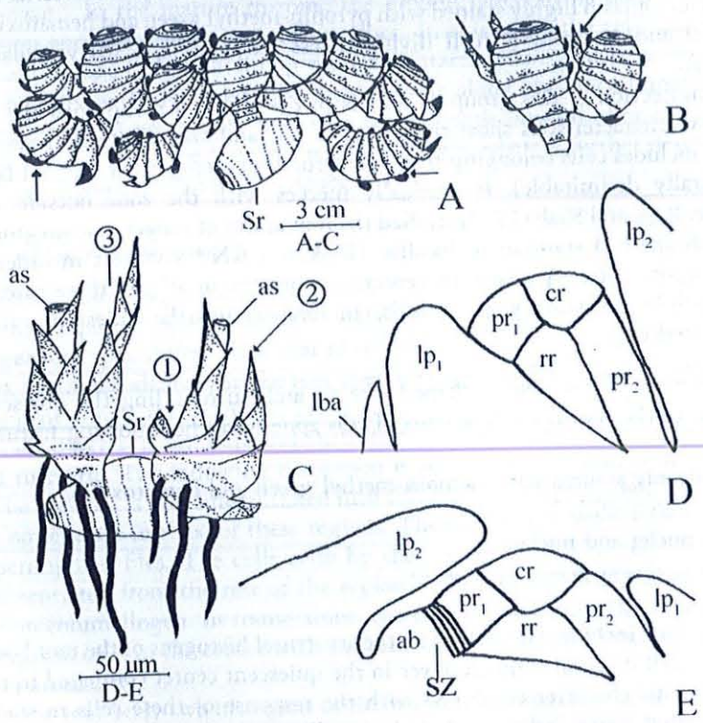

Figure 2.8 Ontogeny of shoot apex: (A) dormant rhizome with stage 1 root apices; (B) rhizome with stage 2 shoot apex; (C) rhizome with stages 5, 6, and 7 root apices; (D) aerial apex showing topographical zonation; (E) rhizome apex showing topographical zonation. ab, axillary bud; as, aerial shoot; cr, central zone; lba, leaf base; lp_1, lp_2, leaf primordium; pr_1, pr_2, peripheral zone; rr, inner aerial zone; sr, seed rhizome; sz, shell zone. (Source: Shah and Raju, 1975.)

Shah and Raju (1975b) recognized seven developmental stages of the apical bud. In stage one (dormant apex), the shoot apex lies in a shallow depression, the apex measures 116 to 214 µm by 45 to 70 µm. A few cells toward the flank showed increased concentrations of DNA as evidenced by dense staining. Some cells of pr_1 and pr_2 (see Figure 2.7) showed dense stainability for C-RNA (cytoplasmic RNA). The outer corpus cells show peripheral divisions. In stage two, the apex is dome shaped and its width and height are 94 to 165 µm and 35 to 75 µm, respectively. Zones pr_1 and pr_2 show denser histological staining than cr and rr zones. A biochemical zonation is present at pr_2 that shows deep staining for DNA. The apex at stage three measures 76 to 140 µm in width, and 53 to 86 µm in height and is dome shaped. The cells of the inner axial zone are vacuolated. The shoot apex dome at stage four is 140 to 160 µm high and 90 to 116 µm wide. Outer corpus cells are vertically elongated. At stage five, the apex is a low dome having 214 to 248 µm height and 53 to 75 µm width. Cells of the pr_2 zone show dense staining. The apex of stage six is prominently dome shaped having a width of 169 to 200 µm and height of 87 to 96 µm. During stage seven, the underground branch reaches the soil level. The shoot apex is 91 to 112 µm in width and 134 to 167 µm in height.

In ginger all the underground branches show a negative geotropic response. Two kinds of apices are found in ginger: (1) the apices are low dome and surrounded by either scale leaves or leaf bases, and (2) they are dome shaped and raised on an elongated axis. In the base of the rhizome apices, cells derived from the inner axial zone elongate tangentially and contribute to the widening of the axis. In certain cases these cells extend up to the base of the axillary buds. In a dormant apex they are thick walled and contain starch grains. These cells are distinct in the dormant or early active rhizome apex and constitute latitudinal growth meristem. During vascular differentiation a few cells of this meristem develop into procambium. During subsequent development of the rhizome apex the cells derived from the inner axial zone elongate and contribute to the pith.

Procambial differentiation: The peripheral or flank meristem divides periclinally and produces parenchymal cells. Some of the cells are distinguishable from the rest by deeper stainability, smaller size, less or no vacuolation, and darkly stained nuclei. These are the procambial initials and each such group contains 15 to 20 cells. Later these cells elongate, vacuolation increases, and they develop gradually into sieve tubes. Protophloem differentiation precedes that of protoxylem. The collateral differentiation of phloem and xylem with parenchymal bundle sheaths becomes distinct after an intermediate stage of random differentiation of the bundles. Ultimately the vascular bundles are found scattered in parenchymal ground tissue. In transection, an endodermoidal layer is also visible during the development (Remashree et al., 1998; Ravindran et al., 1998).

Axillary Bud

The development of leaves and scale leaves that encircle the shoot apex in ginger rhizomes is in a clockwise direction. The axillary bud meristem is first discernible in the axillary

position on adaxial sides of the third leaf primordium from the apical meristem as a distinct zone by the stainability of the constituent cells and multiplane division of the cells in the concerned peripheral meristem sectors. The axillary buds thus originate as a cellular patch in the adaxial side of a leaf or scale leaf of the node. In a fully developed axillary bud the cytohistological zones akin to the main shoot apex can be distinctly observed. The development of a new rhizome is by the enhancement of a dormant axillary bud, which acts just like the main shoot apex. The procambial cells and the ground meristem cells divide and parenchyma as well as vascular tissues add thickness to the newly enhanced axillary bud. Likewise, many buds become active during favorable conditions, each of which produces secondary or tertiary rhizomes. The axillary buds show vascularization by the activity of the procambial strands of the mother rhizome and procambial cells originated from the differentiation of parenchymal cells.

Development of the Root

The adventitious root primordia become differentiated endogenously from the endodermoidal layer of the rhizome. Roots always develop just below the nodal region. Transection of the rhizome reveals that the endodermoidal layer and the pericycle become meristematic and undergo periclinal and anticlinal divisions resulting in a group of root initials. This is in direct connection with the vascular ring situated beneath the endodermoidal layer. The root primordia are of the open type, having common initials for the cortical meristem, root cap, and protoderm. The actively dividing and deeply staining central cylinder shows vascular connections with the rhizome vasculature. As the enlarging root primordia emerge through the cortex, the cortical cells are crushed and torn apart. Normally, these roots originate from the lateral or opposite side of the axillary bud and scale leaf.

Phloem

As a rule there is no secondary growth in monocots. However, the rhizome structure of ginger gives evidence of both primary and secondary growth having a well-developed endodermoidal layer and cambium. The vascular bundles are collateral, closed, and scattered in the ground parenchyma. The phloem element consists of the sieve tube, companion cells, parenchyma and fiber.

Sieve tube: Phloem cells originate from a group of actively dividing procambial cells of PTM. These cells can be distinguished from the surrounding cells by their meristematic activity, stainability, and size of the nucleus. During development, a procambial cell elongates and becomes thick walled with cytoplasm and a prominent nucleus; this is the sieve tube mother cell. It undergoes a longitudinal unequal division, and the resulting smaller cell gives rise to the companion cell. This cell continues to divide, forming four to eight cells. The large cell is the sieve cell. It has cytoplasm and nucleus in early stages, which degenerate during its development into the sieve tube. During further development, the vacuolation increases and the cytoplasm shrinks and appears like a thread along the wall. At the same time, the nucleus disintegrates and the cell assumes the features of the enucleated sieve tube element. The transverse wall of the sieve tube changes to simple sieve plates with many pores and with very little callose deposition.

The first sieve tube element can be distinguished at a distance of 720 to 920 µm from the shoot apex.

In the ginger rhizome, four to eight companion cells per sieve tube element are arranged in vertical lines with transverse end walls. They may vary from 18 to 32 µm in length and 7 to 19 µm in width. The sieve tube elements are arranged end to end to form columns of sieve tubes. The length of a sieve tube element varies from 57.5 to 103.8 µm, the average being 76.8 µm. The width varies from 5.29 to 10.35 µm, the average being 8.76 µm (Remashree et al., 1998). At the early stage of development, the slime body is present in the sieve tube, which appears to be amorphous but homogeneous. Later the slime body disintegrates.

In ginger, development of sieve tube is pycnotic, similar to the second type of nuclear degeneration reported by Esau (1969) and Evert (1984). The sieve element passes through a "fragmented multinucleated stage," a unique feature in the ontogeny of the multinucleated sieve tubes as reported by Esau (1938).

Phloem parenchyma: The phloem parenchymal cells are comparatively larger than the companion cells and smaller than normal cortical parenchymal cells. The increase in size of the phloem element is proportional to the growth of the rhizome. Some older phloem parenchymal cells become lignified into thick phloem fibers.

Anatomical Features of Ginger in Comparison with Related Taxa

Many species-specific anatomical variations were noted in the genus *Zingiber*. These variations were presented in a comparative study of ginger and three other species (Ravindran et al., 1998). The salient features are given in Table 2.1, which presents the important anatomical similarities and differences among the four species: *Z. officinale, Z. roseum, Z. zerumbet,* and *Z. macrostachyum.* Ginger has distinct anatomical features compared to other species, such as the absence of periderm, short-lived functional cambium, the presence of xylem vessels with scalariform thickening, helical and scalariform type of xylem tracheids, scalariform perforation plate, outer bundles with a collenchymatous bundle sheath, and high frequency of oil cells. The oil cell frequency was found to be 17.8/mm^2 in ginger, whereas the corresponding frequency in the other species was 9.5, 5.3, and 2.8/mm^2 in *Z. zerumbet, Z. macrostachyum*, and *Z. roseum,* respectively. Species differences were also noticed in fiber length, fiber width, and fiber wall thickness. Histochemical studies indicated that *Z. zerumbet* has greater amount of fibers than the others.

In general, xylem elements in *Zingiber* consist mainly of tracheids and rarely of vessels. The secondary wall thickening in the tracheids of ginger is of two types, scalariform and helical. The rings, or helices, are arranged either in a loose or dense manner. The helical bands are found joined in certain areas giving ladder-like thickening. The width of helical tracheids is less than that of scalariform tracheids. Similar tracheids are present in *Z. macrostachyum*, whereas in *Z. zerumbet* and *Z. roseum,* only scalariform thickening occurs (Ravindran et al., 1998). Xylem vessels occur in ginger and not in other species. Snowden and Jackson (1990), while studying the microscopic characters of ginger powder, recorded that the vessels are fairly large, reticulately thickened, less commonly spirally, and annularly thickened.

Table 2.1 Comparative anatomy of four species of *Zingiber*

Tissue	*Z. officinale*	*Z. roseum*	*Z. zerumbet*	*Z. macrostachyum*
Epidermis	Single layered	Single layered	Single layered	Single layered
Periderm	Absent	Periderm with lenticel	Periderm present	Absent
Cortex (outer cylinder)	Not wide	Not wide	Not wide	Wide
Endodermis	Present	Present	Present	Present
Casparian strips	Present	Present	Present	Present
Cambium	Present	Not found	Not found	Not found
Central cylinder	Wider than the outer zone	Wider than the outer zone	Comparatively less wider than the outer zone	Not wider than the outer zone
Number of vascular bundles	Less in the outer cylinder than in the inner zone	Less in the outer zone than in the inner zone	Less in the outer zone than in the inner zone	More in the outer cylinder than the other 3 species but lesser than the inner zone
Nature of vascular bundles	Collateral closed	Collateral closed	Collateral closed	Collateral closed
Vascular bundles distribution	More toward inner cortex and scattered in the central zone	More toward inner cortex and scattered in the central zone	More bundles in the middle cortex and number of bundles is very less compared to other 3 species	Bundles are arranged in two rows in the middle cortex and only a few bundles in the inner cortex and the bundles are uniformly distributed in the central zone.
Pith	Present	Present	Present	Present
Xylem elements	Vessels, tracheids, and fibers	Tracheids, fibers	Tracheids, fibers	Tracheids, fibers
Vessels	Vessels few with scalariform/reticulate thickening	Not found	Not found	Not found
Xylem tracheids thickening	Helical and scalariform type	Scalariform	Scalariform	Helical and scalariform
Perforation plate	Scalariform type	None	None	None
Phloem	Sieve tube, companion cells, phloem parenchyma and phloem fiber	Sieve tube, companion cells, phloem parenchyma and phloem fiber	Sieve tube, companion cells, phloem fiber, and phloem parenchyma	Sieve tube, companion cells, phloem fiber, and parenchyma
Metaxylem width	Outer zone 57 μm Inner zone 84 μm	20 μm 53 μm	25 μm 53 μm	32 μm 76 μm
Bundle sheath	Outer vascular bundles possess collenchymatous bundle sheath	Absent	Absent	Collenchymatous sheath is present only in outer bundles
Oil cell frequency	Very high	Least	High	Less
Curcumin cell	None	Present	Present	None

Leaf Anatomical Features

Ginger leaves are isobilateral. The upper epidermal cells of leaf are polygonal and predominantly elongated at right angles to the long axis of the leaf. In the lower epidermis the cells are polygonal and irregular, except at the vein region, where they are vertically elongated and thick walled. The epidermal cells in the scale and sheath leaves (the first two to five leaves above the ground are without leaf blades) are elongated and parallel to the long axis of the leaf. Oil cells in the upper and lower epidermis are rectangular, thick walled, and suberized. Unicellular hairs are present in the lower epidermis of the foliage leaves. Occasionally, a hair is present at the polar side of the stomata.

Ginger leaves are amphistomatic. A distinct substomatal chamber is present. Stomata are either diperigenous or tetraperigenous. Occasionally, anisocytic stomata are also observed. The subsidiary cells are completely aligned longitudinally with the guard cell. The lateral subsidiary cells may divide to form anisocytic stomata. Occasionally, three to five lateral subsidiary cells are formed by further division (Raju and Shah, 1975).

The guard cells on the foliage leaves are 40.6 μm long, whereas those on the sheath and scale leaves are 28.9 μm long. The stomata on the scale leaves and rarely on the sheath leaves show pear-shaped guard cells with a large central pore. The nuclei of the guard cells are smaller than those in the subsidiary cells. Raju and Shah (1975) also reported the uncommon wall thickening at the polar ends of the guard cells. This wall thickening may be restricted to the outer wall at the polar regions or may also be extended to the common inner cell wall.

Tomlinson (1956) gave a brief note on the petiolar anatomy of ginger. The short petiole shows a swollen pulvinus-like appearance. A transection just above the pulvinus shows typical structure with two bundle arcs, air canals, and collenchyma. A transection through the pulvinus shows a different structure. Here air canals and assimilating tissue are absent, there is extensive hypertrophy of ground tissue parenchymal cells, and abundant deposition of tanniferous substances. The most striking feature according to Tomlinson (1956) is the collenchymatous thickening of the cells of the bundle sheath, Below the pulvinus the structure is again normal as that of the above pulvinus region.

Table 2.2 gives the comparative leaf anatomical features of four species of *Zingiber.* The stomata are tetracyclic in all the species. The first two subsidiary cells are parallel to the guard cells and the other two lie at right angles. In *Z. officinale*, *Z. roseum,* and *Z. macrostachyum* there is a special thickening in the upper and lower sides of the guard cell, but *Z. zerumbet* showed some extra thickening on the corners of subsidiary cells. The stomatal index was higher in *Z. zerumbet.* Guard cells were the largest in *Z. zerumbet*, followed by *Z. officinale* and *Z. macrostachyum.* In *Z. roseum* the guard cells were shorter and broader.

Stomatal ontogeny: Raju and Shah (1975) described the structure and ontogeny of stomata of ginger. Here the differentiation of a guard cell mother cell or a meristemoid occurs by an asymmetrical division of protodermal cells. The meristemoid is distinguished from the adjacent protodermal cells by its small size, dense stainability of cytoplasm, and less vacuolation. The anticlinal wall of the meristemoid appears lightly stained with periodic acid–Schiff (PAS) reaction than the lateral walls of the epidermal cell and the meristemoid. The epidermal cell on either side of the meristemoid divides to form a small subsidiary cell. This epidermal cell shows dense stainability for nuclear DNA. The young lateral subsidiary cells are smaller than other epidermal cells. Later the meristemoid

Table 2.2 Leaf anatomical characteristics in four species of ginger

Tissues	*Z. officinale*	*Z. macrostachyum*	*Z. zerumbet*	*Z. roseum*
Epidermis	Upper larger than the lower	Both epidermis equal	Both epidermis equal	Both epidermis equal
Hypodermis	2 layers on upper side, one layer on lower side	2-layered on both sides	2-layered on both sides	Upper cells are larger, lower cells smaller
Mesophyll palisade	Single layered on upper side	No palisade tissue	No palisade tissue	Single layered on upper side
Spongy tissue	3–4 layers, closely packed	4–5 layers, loosely packed	4–6 layers, loosely packed	4–5 layers, closely packed
Air cavities	Absent in lamina, present in the mid rib region	Present in the mesophyll tissue and more in the mid rib region	Few cavities in lamina, more in the mid rib region	Absent in lamina, present in the mid rib
Vascular bundle sheath	Present on both sides and extend to both epidermis	Present on both sides and extend to upper epidermis only	Present on both sides and extend to upper epidermis only	Present on both sides and extend to both epidermis
Stomatal Index Range, Mean, Std. deviation	5.8–8.9, 7.45, 1.4	7.8–10.3, 8.15, 1.08	8.9–13.2, 10.23, 1.4	8.01–12.03,9.11, 1.2

divides to form a pair of guard cells. The epidermal cells that are lying at the polar region of the guard cell may divide and occasionally completely abut the stomatal complex and appear as subsidiary cells (Raju and Shah, 1975).

Anatomical Features of Dry Ginger

In commercial ginger rhizome (peeled dried rhizome), the outer tissue consisting of cork, epidermis, and hypodermis is scraped off. So the transections of processed rhizome consist of cortex, endodermis, pericycle, and the central cylinder or the vascular zone. The epidermis (of dry unpeeled ginger) is frequently disorganized, consisting of longitudinally oblong rectangular cells; the hypodermis consists of a few layers of parenchymal cells. The cork consists of several layers of oblong–rectangular, thin-walled suberized cells. The cortex is made of (1) thin-walled parenchymal cells containing plenty of starch grains, (2) brown-colored oleoresin and oil cells scattered throughout the cortex, and (3) fibrovascular bundles. There is an unbroken endodermis made of tangentially elongated cells with thickened suberized radial walls. Below the endodermis there is a pericycle that consists of an unbroken ring of tangentially elongated cells.

The central cylinder consists of an outer and an inner zone. In the outer zone adjoining the pericycle there is a vascular bundle zone without fibers. Fibrovascular bundles and oleoresin cells occur in the central zone of the central cylinder. The ground tissue of the central cylinder consists of thin-walled parenchymal cells containing starch.

The fibrovascular bundles are large. In longisections the fibers are long with moderately thick walls and a wide lumen. The vessels are large and scalariform, except in the vascular bundle zone adjoining the pericycle, where large reticulate vessels, scalariform vessels, and some special vessels occur.

Starch grains are present in abundance. The granules are ovate and many are characterized by a protuberance at one end. They vary in size to about 45 μm in length and 24 μm in width. Under polarized light the granules exhibit a distinct cross through the hilum at the tapering end (Parry, 1962).

Microscopic Features of Ginger Powder

Ginger rhizome powder is pale yellow or cream in color with a pleasant, aromatic odor and a characteristic and pungent taste. The diagnostic characteristics of ginger powder given by Jackson and Snowden (1990) are:

1. The abundant starch granules are mostly simple, fairly large, flattened, oblong to subrectangular to oval in outline with a small pointed hilum situated at the narrower end; infrequent granules show very faint transverse striations. Compound granules with two components occur very rarely.
2. The fibers usually occur in groups and may be associated with the vessels; they are fairly large and one wall is frequently dentate; the walls are thin and marked with numerous pits, which vary from circular to slit shaped in outline; very thin transverse septa occur at intervals. The fibers give only a faint reaction for lignin.
3. The vessels are fairly large and usually occur in small groups associated with the fibers; they are reticulately thickened, frequently showing distinct, regularly arranged rectangular pits, and are often accompanied by narrow, thin-walled cells containing dark brown pigment; a few smaller, spirally or annularly thickened vessels also occur. All the vessels give only a faint reaction for lignin.
4. The oleoresin cells in uncleared preparations are seen as bright yellow ovoid to spherical cells occurring singly or in small groups in the parenchyma.
5. The abundant parenchyma is composed of thin-walled cells, rounded to oval in outline with small intercellular spaces; many of the walls are characteristically wrinkled; the cells are filled with starch granules or oleoresin. Occasionally, groups of parenchyma are associated with thin-walled tissue composed of several rows of collapsed cells.

Floral Anatomy

Rao et al. (1954), Rao and Pai (1959, 1960), and Rao and Gupta (1961) studied the floral anatomy of the members of Scitamineae, in which a few species of *Zingiber* were also included. The floral anatomy of *Z. ottensi, Z. macrostachyum, Z. cernuum,* and other *Zingiber* species was reported by these workers. Because of the basic similarities in floral characters, it is presumed that the floral anatomical features will also be identical. The following discussion is based on the reports of the above-mentioned workers. The floral anatomical features of *Z. cernuum* (which is different from *Z. officinale* only by the absence of staminodes) are given in Figure 2.9. The peduncle contains two rings of vascular bundles with a few strands in the central pith. The inner ring gives off three dorsal bundles of the carpels outward and the latter then divide into three large strands alternating in position with the dorsal bundles of the carpels. The central strands unite

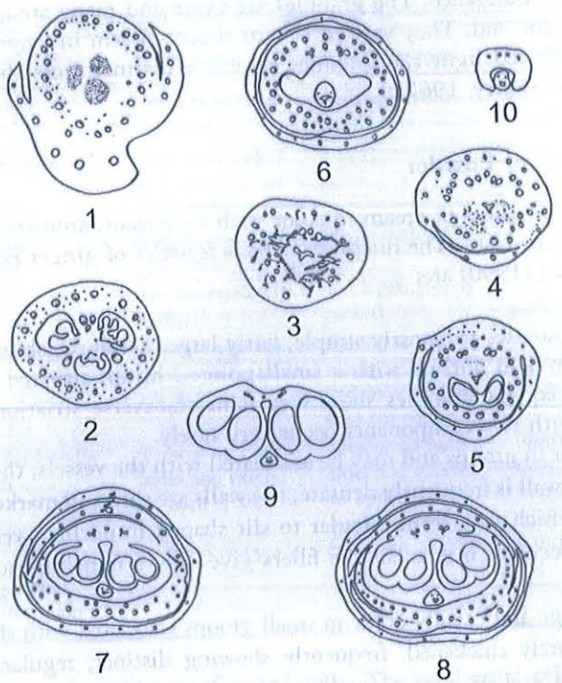

Figure 2.9 Floral anatomy of *Z. cernuum*. 1–10, different stages in the development of floral vasculature (for explanation, see text).

first into one bundle for a short length and fuse with the vascular tissue immediately to the outside. The three large bundles divide first into smaller inner placental bundles and a large outer parietal bundle. The placental bundle may branch off almost at its base. The parietal bundle travels into the septa and sends a few outward branches into the ovary wall. The placental bundles in the axile area bear the ovular traces. The posterior parietal bundle is larger and divides even at a lower level than the other two into two or three. A transverse section through the basal part of the ovary at this level shows: (1) a comparatively thick ovary wall in which there are numerous vascular bundles almost irregularly scattered, (2) in each of the three septa there is a prominent bundle that may divide into two, and (3) in the placental zone there are 6 to 10 strands that bear traces for the ovules. Most of the potential bundles are exhausted in supplying the ovules while one or two may fuse with the nearest parietal bundle. The loculi extend for a considerable distance above the ovuliferous zone, and in this terminal part of the ovary the number of bundles in the ovary wall is reduced by fusions among themselves, and all of them form almost a single ring near the level where the loculi end. Just on the top of the ovary, the three parietal strands, which have already divided into two or three bundles, extend laterally and form a broad network-like cylinder of vascular tissue. This network establishes vascular connections (anastamoses) with the peripheral bundles. The three loculi continue upwards into a Y-shaped stylar canal. After the anastamosis the vascular tissue directly forms (1) an outermost ring of about 15 small bundles for the calyx, (2) a next inner ring of about 25 larger strands for the corolla and androecial members, and (3) toward the center a number of small scattered strands arrange somewhat in the form of an arc. Two stylar traces are given off from the two margins of this arc-like group and they stand close to the two arms of the Y-shaped stylar canal. The numerous small bundles, arranged at first as an arc, break up into two groups, which supply the two epigynous glands present in anteriolateral positions. The tubular basal parts of the calyx containing the sepal traces referred to earlier are at first separated, and at the same level, the two epigynous glands also separate. A very short distance above, the style also separates.

The basal part of the floral tube contains a ring of vascular bundles, an additional bundle in the median posterior position, and a pair of closely placed bundles on either side. The median posterior strand and the double strands on either side constitute the supply to the functional stamen. One of the component bundles of each double strand divides into two in such a way as to result in a third bundle that lies toward the inner side with its xylem pointing to the outside. On the anterior side of the floral tube, the vascular bundles divide and form two rings, whereas on the posterior face, external to the stamen traces, there is only one ring of bundles. The latter are for the labellum, whose margins are fused for a short distance with those of the filament. The outer ring of bundles is for the corolla.

The flat filament receives: (1) a small median bundle; (2) a triple strand on either side of it, the constituent bundles of which more or less fuse together; and (3) two or four minute strands toward either margin. The lateral triple strands are opposite the line of attachment of the anther lobes to the filament. The minute marginal traces disappear quickly, leaving only a small median bundle and the two lateral large composite ones. These run in parallel manner upward, and the composite strands of each lateral group fuse together more or less completely, so that the anther connective contains a small median and two large lateral bundles. Above the level of the anther, the connective is continued upward as a narrow flat plate with margins incurved and enclosing the style. Each of the two composite lateral strands becomes smaller and divides into two. Thus, in the terminal part of the filament, five bundles are present, of which one is the median one. The median bundle fades out first, leaving a pair of bundles on either side. The bundles of each pair then fuse together giving only two bundles, which run right up to the tip and disappear.

The style receives only two traces and these run throughout its length without any branching. The styled canal is narrow, Y-shaped, the arms of the Y pointing to the posterior side. Toward the tip the arms of the stylar canal spread out so that the canal appears as a curved slit in transverse sections. It then widens out into a large canal, which opens freely to the outside. The two vascular bundles of the style become more prominent in this terminal part and then disappear (Rao and Pai, 1959).

Floral Biology

Ginger flowers are produced in peducled spikes arising directly from the rhizomes. The oval or conical spike consists of overlapping bracts, from the axils of which flowers arise, each bract producing a single flower. The flowers are fragile, short-lived, and surrounded by a scariose, glabrous bracteole. Each flower has a thin tubular corolla that widens up at the top into three lobes. The colorful part of the flower is the labellum, the petalloid

stamen. The labellum is tubular at the base, three lobed above, pale yellow outside, dark purple inside the top and margins, and mixed with yellow spots. The single fertile anther is ellipsoid, two celled, cream colored, and dehisces by longitudinal slits. The inferior ovary is globose, the style is long and filiform, and the stigma is hairy. Flowering is not common, and is probably influenced by climatic factors and photoperiod. On the west coast of India (Kerala), most cultivars flower if sufficiently large rhizome pieces are used for planting. When rhizomes are left unharvested in pots, profuse flowering occurs in the next growing season. Flowering is also reported from the east coast of India (Bhubaneswar in Orissa). However ginger does not usually flower or flowers very rarely in the growing areas of such locations as Himachal Pradesh, Utter Pradesh, West Bengal, and Northeast India. Holttum (1950) reported that ginger seldom, if at all, flowers in Malaysia. Flowering is reported from south China, but not from north China, and also from Nigeria. In general ginger does not flower under subtropical or subtemperate climatic conditions. Japanese workers reported that flowering leads to yield reduction. Ginger is shown to be a quantitative short-day plant (Adaniya et al., 1989).

Jayachandran et al. (1979) reported that the flower bud development took 20 to 25 days from the bud initiation to full bloom and 23 to 28 days to complete flower opening in an inflorescence. Flower opening takes place in an acropetal succession. Anthesis is between 1.30 and 3.30 P.M. under the west coast conditions of Kerala. Anther dehiscence almost coincides with the flower opening. The flower fades and falls on the next day morning. There is no fruit setting.

Das et al. (1999) reported floral biology in four cultivars of ginger (Bhaisey, Ernad Chernad, Gurubathan and Turia local). They found that anthesis under greenhouse and field conditions took place at around 1:00 to 2:00 P.M., under the coastal Orissa situations. Flowers were hermaphroditic with pin- and thrum-type incompatibility, and dehisced pollen grains did not reach the stigma. Selfing and cross-pollination did not produce any seed set.

Self-Incompatibility

Dhamayanthi et al. (2003) investigated the self-incompatibility system in ginger. They reported that heterostyly with a gametophytically controlled self-incompatibility system exists in ginger. Flowers are distylous, there are long ("pin") and short ("thrum") styles. The "pin" type has a slender style that protrudes out of the floral parts, which are short, covering not even half the length of the style. The stigma is receptive before the anthesis, whereas the anthers dehisce after 15 to 20 hours. The anthers are situated far below and hence the pollen grains cannot reach the stigma. In case of the "thrum" style, the stigma is very short and the staminodes are long and facing inward. However, the occurrence of thrum styles is very rare among cultivated ginger. According to the above-mentioned workers, this heterostyly situation may be a contributing factor to the sterility in ginger. However, this may not be very important as almost all cultivars are the pin type and pollination is entomophilous, mostly by honeybees. Dhamayanthi et al. (2003) have also reported inhibition of pollen tube growth in the style, and this was interpreted to be due to incompatibility. Adaniya (2001) reported the pollen germination in a tetraploid clone of ginger, 4 × Sanshu. Pollen germination was highest at around 20°C and pollen tube growth in the style was greatly enhanced at 17°C. At this temperature, the pollen tubes penetrated into the entire length of the style in

66.7% of the styles analyzed. Pollen stored for 3 hours at a relative humidity (RH) of 40 to 80% completely lost its viability, whereas pollen incubated at 100% RH retained relatively high germinability. When the RH was low, the pollen tube in the style stopped growing. Hence for pollen to germinate and grow in the stylar tissue, relatively low temperature (approximately 20°C) and 100% RH are essential.

Embryology

The embryology of ginger has not been investigated critically so far, and it is rather amazing that such an economically important species has been ignored by embryologists. One possible reason may be the absence of flowering and seed set in ginger in most growing regions. However, some information is available on a related species, *Z. macrostachyum*. The embryological features of the genera in Zingiberaceae are similar, and hence the information on *Z. macrostachyum* may as well be applicable to ginger.

The embryo sac development follows the *Polygonum* type (Panchaksharappa, 1966). The ovules are anatropous, bitegmic, and crassinucellate and are borne on an axil placentation. The inner integument forms the micropyle. In the ovular primordium the hypodermal archesporial cell cuts off a primary parietal cell and a primary sporogenous cell (Figure 2.10). The former undergoes anticlinal division. The sporogenous cell enlarges into a megspore mother cell, which undergoes meiosis forming megaspores. The chalazal spore enlarges and produces the embryo sac. Its nucleus undergoes three successive divisions resulting in a eight-nucleate embryo sac. Prior to fertilization in *Z. macrostachyum,* the synergids and antipodals degenerate. The fate of the nuclei in the embryo sac of ginger (which is a sterile species) is not known. However, some studies have indicated a postmeiotic degeneration of the embryo sac (Pillai, personal communication).

Cytology, Cytogenetics, and Palynology

Mitotic Studies

The chromosome number of ginger was reported as 2n = 22 by Moringa et al. (1929) and Sugiura (1936). Darlington and Janaki Ammal (1945) cited a report from Takahashi who claimed 2n = 24 for *Z. officinale*. A more detailed study was carried out by Raghavan and Venkatasubban (1943) on the cytology of three species, *Z. officinale*, *Z. cassumunnar,* and *Z. zerumbet,* and all three had the somatic chromosome number of 2n = 22. Based on the differences in ideogram morphology, the above-mentioned workers concluded that the chromosome morphology of *Z. officinale* was different from the other two species. Janaki Ammal (Darlington and Janaki Ammal, 1945) reported two "B" chromosomes in certain types of ginger in addition to the normal complement of 2n = 22. Chakravorti (1948) also found 2n = 22 in ginger. He concluded that in view of the normal pairing of 11 bivalents in species like *Z. cassumunnar* and *Z. zerumbet*, *Z. mioga* having a somatic chromosome of 2n = 55 is to be considered a pentaploid (Table 2.3).

Sharma and Bhattacharya (1959) reported the widespread occurrence of an inconsistency in chromosome numbers in several species of Zingiberaceae including *Z. officinale.* Sato (1960) carried out karyotype studies of 24 species belonging to 13 genera and concluded that the basic number of the genus *Zingiber* is x = 11 and that *Z. mioga*

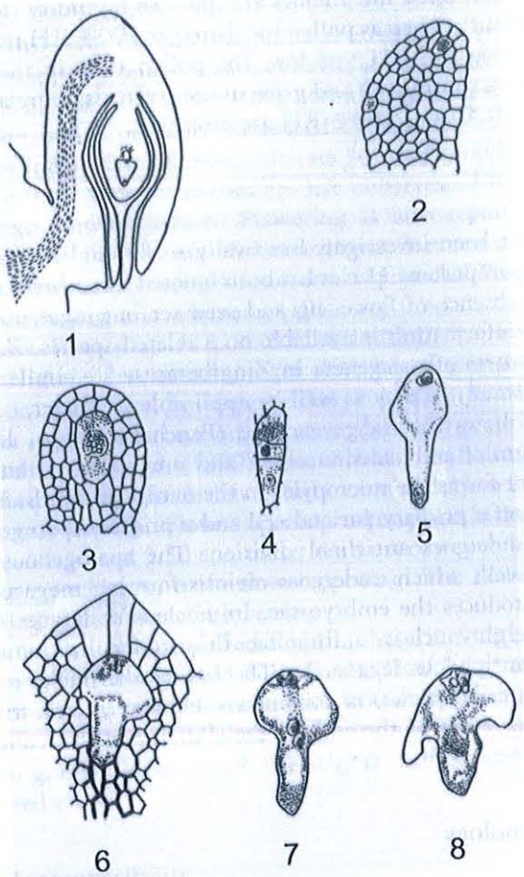

Figure 2.10 Embryology of ginger (*Z. macrostachyum*). 1–8, stages in the development of the embryo sac (for details see text).
1. L.S. of the anatropous ovule. 2. L.S. ovule showing archesporial cell. 3. L.S. ovule with meagspore mother cell. 4. T-shaped tetrad. 5, 6. 4- and 8-nucleate embryo sacs. 7, 8. Organized embryo sacs. Note the degenerated synergids and antipodals in 8.

having 2n = 55 is a pentaploid. Ramachandran (1969) studied the cytology of five species of *Zingiber* (*Z. macrostachyum, Z. roseum, Z. wightianum, Z. zerumbet,* and *Z. officinale*) and found a diploid number of 2n = 22 in all species. He found evidence of structural hybridity involving interchanges and inversions in ginger. Mahanty (1970) studied the cytology of Zingiberales. He reported 2n = 22 for *Z. spectabile* and *Z. cylindricum* and concluded that the genus *Zingiber* appears to be much more correctly placed in Hydychieae than in the Zingibereae.

Ratnambal (1979) investigated the karyotype of 32 cultivars of ginger (*Z. officinale*) and found that all of them possess a somatic chromosome number of 2n = 22 (Figure 2.11). The karyotype was categorized based on Stebbins's classification (Stebbins, 1958), which recognizes three degrees of differences between the longest and the shortest chromosome of the complement and four degrees of differences with respect to the

Table 2.3 Chromosome reports on *Zingiber*

Species	*n*	*2n*	*Reference*
Z. officinale		22	Suguira (1936)
		22	Moringa et al. (1929)
		22	Raghavan and Vankatasubban (1943)
		22	Chakravorthi (1948)
		22	Sharma and Bhattacharya (1959)
		22 + 2B	Darlington and Janaki Ammal (1945)
		24	Takahashi (1930)
	11	22	Ramachandran (1969)
	11	22	Ratnambal (1979)
Z. roseum	11	22	Ramachandran (1969)
Z. wightianum	11	22	Ramachandran (1969)
Z. spectabile		22	Mahanty (1970)
Z. cylindricum		22	Mahanty (1970)
Z. cassumunnar		22	Raghavan and Venkatasubban (1943)
		22	Ratnambal (1979)
Z. clarkei		22	Holttum (1950)
Z. ottensi		22	Holttum (1950)
Z. mioga		55	Moringa et al. (1929), Sato (1948)
Z. zerumbet	11	22	Ratnambal (1979)

proportion of the chromosome that are acro-, meta-, and telocentric. An asymmetrical karyotype of "1B" was found in all cultivars except in cvs. Bangkok and Jorhat, which have a karyotype asymmetry of 1A (Ratnambal, 1979). The karyotypes of various cultivars exhibited only minor differences (Table 2.4.). The total chromosome length varied from 22.4 μm in cv. Jorhat to 37.4 μm in cv. China. The length of the longest chromosome ranged between 2.8 μm (in cv. Jorhat) and 4.8 μm (in cv. China). The length of the shortest chromosome ranged between 1.2 μm (in cv. Rio de Janeiro) to 2.2 μm (in cv. China).

Ratnambal (1979) used the karyotype data in a generalized distance-D^2 statistics analysis. Based on the D^2 values, the cultivars were grouped into different clusters. Thirty-two cultivars fell into eight groups, A–H (Table 2.5). The relative distance between each group is a measure of the extent of divergence of the cultivars constituting the group. Cultivars Tafingiwa, Jamaica, Rio de Janeiro, Thinladium, Thingpuri, Maran, and Himachal Pradesh did not fall into any cluster, indicating their independence as well as divergence from the rest of the cultivars. *Z. zerumbet* and *Z. casummunar* did not fall into any group, but *Z. machrostachyum* fell into group B. It was also seen that geographical distances did not influence the clustering. This is expected in a strictly vegetatively propagated species, the planting materials that have been transported from

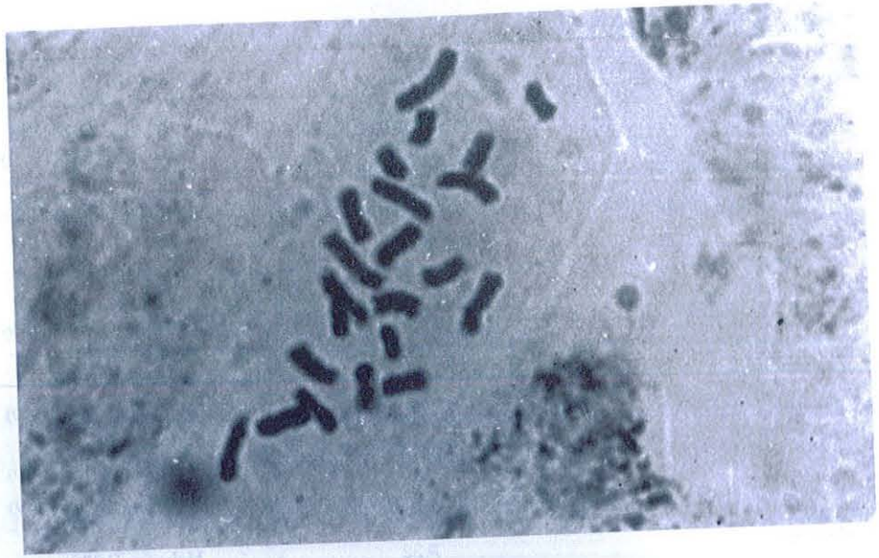

Figure 2.11 Mitotic metaphase showing 2n = 22 chromosomes.

Table 2.4 Karyotype variability in ginger cultivars

Sl. No.	*Karyotype character*	*Range*	*Cultivars with lowest and highest values*
1.	Total chromatin length (μm)	22.4–37.4	cv. Jorhat, cv. China
2.	Length of longest chromosome (μm)	2.8–4.8	cv. Jorhat, cv. China
3.	Length of shortest chromosome (μm)	1.2–2.2	cv. Rio de Janeiro, cvs. China and Poona
4.	No. of median chromosomes	1–9	cv. Jugijan, cvs. Mananthody and Arippa
5.	No. of submedian chromosomes	2–10	cv. Mananthody, cv. Jugijan
6.	No. of subterminal chromosomes	0–2	cvs. Kuruppumpadi, Poona, and Himachal Pradesh.
7.	No. of satellite chromosomes	1	In all cultivars
8.	Type of symmetry	1A	cvs. Jorhat and Bangkok, species Z. *macrostachyum*, Z. *zerumbet*, and Z. *casumunnar*
		1B	In all other cultivars

Source: Ratnambal (1979).

region to region and between countries. The karyotype of the cultivars remained relatively asymmetrical because of the lack of recombination and evolution by sexual processes.

Ratnamabal (1979) investigated the cytology of three species that are closely related to ginger. In Z. *zerumbet* the total chromatin length in the haploid compliment was 25.6 μm. The absolute length of individual chromosomes ranges from 2.9 to 1.6 μm. Six of 11 chromosomes have median centromeres and the remaining have submedian centromeres. Four chromosomes are long, four medium, and three short. The third chromosome with a median centromere has a satellite attached to its long arm. In Z.

Table 2.5 Grouping of ginger cultivars based on D^2 analysis of karyotype data

Group	*Cultivars in the group*
A	China, Assam, Burdwan
B	Wynad, Kunnamangalam, Sierra Leone, Kuruppumpadi, Jugidan, Jorhat
C	Narasapattam, Poona.
D	Arippa, Tura
E	Eranad, Manjeri, Nadia, Uttar Pradesh
F	Wynad local, Valluvanadu
G	Taiwan, Bajpai, Bangkok, Vengara
H	Eranad Chernad, Thodupuzha

Source: Ratnambal (1979).

macrostachyum the total chromatin length of the haploid complement is 29.6 μm. The absolute length of individual chromosomes varies from 3.5 to 1.9 μm. Chromosomes 1, 2, 4, 5, and 9 have submedian centromeres; 3, 6, 10, and 11 have median centromeres; and 7 has terminal centromeres. The second chromosome had a satellite on its longer arm. Z. *cassumunnar* had a total chromatin length of 24.7 μm; the individual chromosomes length varied from 2.9 to 1.6 μm. The karyotype is characterized by one subterminal, two submedian (one of which is satellited), and eight median chromosomes. There were three long, three medium, and five short chromosomes. In all three species the type of asymmetry is reported as being IA.

Das et al. (1998) carried out karyotype analysis and 4C DNA estimation in eight ginger cultivars. They recognized five types of karyotypes occurring in these cultivars.

Type A. Large- to medium-sized chromosome with primary and secondary constrictions nearly submedian in position, respectively
Type B. Large- to medium-sized chromosome with two constrictions, one in the submedian position and other in the subterminal position
Type C. Small-sized chromosome with nearly median to median primary constriction with satellite bodies on the long arm
Type D. Medium- to small-sized chromosome with nearly submedian primary constriction
Type E. Medium-sized chromosomes with nearly submedian primary constriction

All the types of karyotypes are found in the cvs. Bhitarkata local, Himachal Pradesh, and Tura. The A type was present in all the cultivars except in cvs. Raipur local and Wynad. The C type chromosome was common in all the cultivars except in cvs. Maran, Nadia, S-557, and Tura. D and E types were found in all the cultivars. The total chromosome length ranged from 64.80 μm in cv. S.557 to 98.12 μm in cv. Wynad. Total chromosome volume was from 84.35 μm^3 in S.557 to 1126.36 μm^3 in Wynad.

The 4C DNA varied significantly in different cultivars of ginger; from 16.234 picogram (pg) in cv. S.537 to 22.934 pg in cv.Wynad. The average chromosome length and volume ranged from 2.94 to 4.46 and 3.83 to 5.74 μm^3, respectively. The nuclear DNA content was directly proportional to the total chromosome volume, which in turn was

positively correlated with the chromosome length. The variability in DNA amount has been attributed to loss or addition of highly repetitive DNA sequence rather than the adenine-thymine (AT) or guanine-cytosine (GC) rich sequences in a genome, which reached a certain level and became stabilized during microevolution and gradual selection (Das et al., 1998).

Meiosis

Ratnambal (1979) and Ratnambal and Nair (1981) studied the process of meiosis in 25 cultivars of ginger. These cultivars exhibited much intercultivar variability in meiotic behavior. Cultivars like Karakkal formed only bivalents, whereas in cv. Taiwan two hexavalents, one quadrivalent, and three bivalents were present. Univalents were very common and much variability was noticed in respect of their number (Figure 2.12a, b). The presence of multivalent and chromatin bridges was found to be a common feature in most cultivars studied by Ratnambal (1979). The presence of multivalents in a diploid species indicates structural hybridity involving segmental interchanges, and four to six chromosomes are involved in the translocations as evidenced by quadrivalents and hexavalents. This structural hybridity might be contributing to the sterility in ginger.

Ratnambal (1979) also reported two to six univalents in various cultivars; the lowest was in the cv. Mananthody and the highest in cv. Karakkal. The number of univalents observed at metaphase 1 was more than that in diakinesis, and this has been attributed to the precocious separation of one or two bivalents. Most of these univalents end up in the formation of micronuclei and are lost subsequently. This leads to the production of gametes with deficiency and is likely to lead to sterility. A high percentage of abnormalities has been observed during the first and second divisions, as well as in the tetrad stage. The bridges noticed were presumed to be due to inversion heterozygosity or from chromosomal breakage and reunion in the early stage of meiosis. Unequal breakage of bridges at anaphase might be leading to the production of gametes with duplications and deficiencies (Ratnambal, 1979).

Structural chromosomal aberrations occurred at all stages of microsporogenesis in ginger. The predominant aberrations were laggards, bridges, and fragments at anaphase I; laggards, bridges, and fragments, irregular chromosome separation, and irregular cytokinesis at anaphase II; and micronuclei and supernumerary spores at the quartet stage (Table 2.6). Ratnambal (1979) had shown a positive linear regression between pollen sterility and chromosomal aberrations at anaphase II and aberrant quartets. Structural chromosomal aberrations have been attributed as the cause of sterility in ginger. But how such a diploid species as ginger came to acquire a complicated meiotic system that led to chromosomal sterility is not well understood. A hybrid origin followed by continuous vegetative propagation can be one reason for the abnormal chromosomal behavior (Ratnambal, 1979). Beltram and Kam (1984) studied meiotic features of 33 species in Zingiberaceae, including nine species of *Zingiber*. They observed various abnormalities such as aneuploidy, polyploidy, and B chromosomes. They also confirmed the diploid nature of the Malysian Zingiber (x = 11) and the pentaploid nature of the Japanese ginger, *Z. mioga*.

Das et al. (1998) studied meiosis and sterility in four cultivars (Bhaisey, Ernad Chernad, Gorubathany, and Thuria local) and reported a 30.35 to 40.5% meiotic index in them. Pollen mother cells showed incomplete homologous pairing at metaphase 1 and spindle

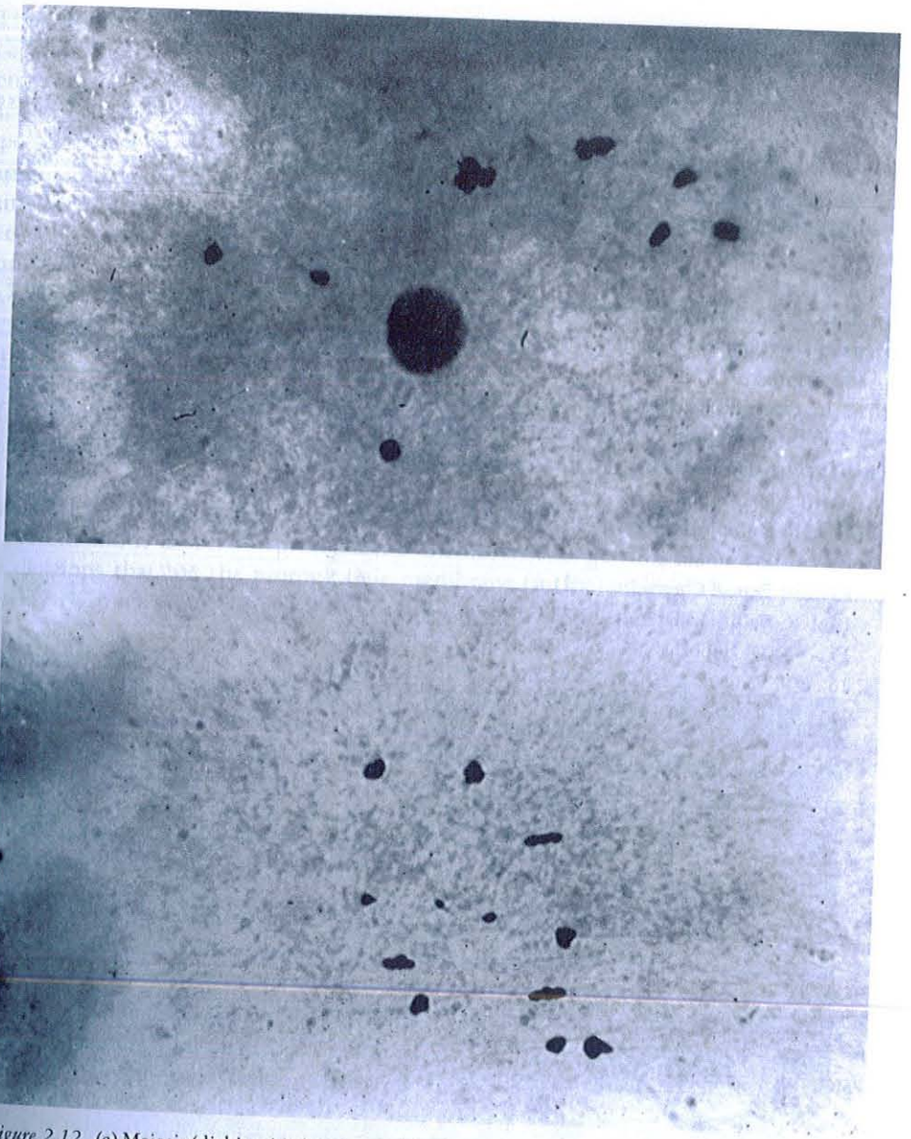

Figure 2.12 (a) Meiosis (diakinesis) showing multivalents. (b) Meiotic metaphase showing multivalents and univalents.

abnormalities (e.g., late separation, laggards, sticky bridges) at anaphase 1, leading to high pollen sterility. Das et al. (1999) felt that the sterility might be due to nonhomology of bivalents, with irregular separation of genomic complements leading to sterile gamete formation. The absence of germination pores on the pollen grains has also been indicated as an impediment to seed set.

Table 2.6 Chromosomal abnormalities and pollen sterility in ginger cultivars

Sl. No.	*Cultivars*	*Percentage of PMCs with anaphase I abnormalities*	*Percentage of PMCs with Metaphase II abnormalities*	*Abnormal tetrads*	*Percentage of pollen sterility*
1	China	31.0	45.8	52.9	81.0
2	Bangkok	33.3	51.7	42.9	82.0
3	Taiwan	8.1	40.0	51.9	82.8
4	Sierra Leone	47.2	55.1	52.2	85.0
5	Tafingiwa	11.0	34.4	48.8	82.9
6	Jamaica	11.6	30.2	54.2	54.4
7	Rio de Janeiro	17.6	71.2	70.6	90.2
8	Wynad local	5.5	39.4	37.9	76.7
9	Kunnamangalm	15.4	70.7	80.5	91.4
10	Mananthodi	21.1	60.2	42.2	82.5
11	Kuruppampadi	24.5	30.8	39.7	79.6
12	Eranad Manjeri	18.0	26.9	30.3	74.2
13	Eranad Chernad	21.4	41.5	56.7	84.4
14	Valluvanadu	20.0	39.4	33.8	85.6
15	Thodupuzha	9.8	69.2	61.2	86.4
16	Vengara	3.2	20.6	51.9	84.0
17	Karakkal	20.7	58.3	48.7	85.7
18	Uttar pradesh	32.9	67.0	58.8	86.1
19	Bajpai	34.2	61.4	5.5	85.5
20	Assam	38.4	61.2	51.6	78.5
21	Jorhat	18.7	81.1	79.4	88.7
22	Thingpuri	21.4	47.2	24.3	84.0
23	Jugidan	19.7	72.4	83.2	88.8
24	Burdwan	23.1	24.6	47.9	79.6
25	Maran	19.4	76.6	71.2	79.3
26	*Z. zerumbet*	28.4	19.3	15.2	9.0
27	*Z. casummunnar*	23.0	28.1	18.3	4.7

PMC, Pollen mother cells. Source: Ratnambal (1979).

Pollen Morphology

The earlier investigators (Stone et al., 1979; Zavada, 1983; Dahlgren et al., 1985) were of the opinion that the pollen grains of the family are exineless, possessing a structurally complex intine (Hesse and Waha, 1982). However later studies indicated that in the majority of the Zingiberaceae an exinous layer does exist, although it is poorly developed in many taxa (Kress and Stone, 1982; Skvaria and Rowely, 1988; Chen, 1989). Recent palynological studies have demonstrated differences in pollen structure between sections of *Zingiber*. The Sect. Zingiber has spherical pollen grains with cerebroid sculpturing, whereas Sect. Cryptanthium has ellipsoid pollen grains with spirostriate sculpturing (Liang, 1988; Chen, 1989).

The pollen of Zingiberaceae is usually classified as inaperturate, but *Zingiber* is an exception. Some workers described *Zingiber* pollen as monosulcate (Zavada, 1983; Dahlgren et al., 1985; Mangaly and Nair, 1990), whereas others reported the pollen as being inaperturate (Liang, 1988; Chen, 1989). Theilade et al. (1993) made a detailed study of pollen morphology and structure in 18 species of *Zingiber*. The pollen is spherical or ellipsoidal. The spherical pollen grains have a cerebroid or reticulate sculpturing. The grains are 55 to 85 µm in diameter. The elliptical pollen grains (in Sect. Cryptanthium) have a spirostriate sculpturing. The grains are 110 to 135 by 60 to 75 µm. The pollen grains have 2 to 3 µm thick coherent exine. The intine consists of two layers, a 5 µm thick outer layer and 2 to 3 µm thick inner layer adjacent to the protoplast. The outer layer is radially striated; the inner layer has a distinct, minute fine structure. No apertures are present. It has been indicated that the entire wall functions as a potential germination site (Hesse and Waha, 1982; Kress and Stone, 1982). Nayar (1995) studied germinating pollen grains of 22 taxa in Zingiberales including *Z. roseum* and *Z. zerumbet* and reported that the pollen grains possess an exine containing sporopollenin. Inside this layer there is a well-defined lamellatted cellulosic layer (described as the outer layer of intine by earlier workers), which is the medine. The intine is membraneous and consists of cellulose and protein and is in fact the protoplasmic membrane. At germination a solitary pollen tube develops that has the protoplasmic membrane (intine) as its wall and pierces the outer layers smoothly even in the absence of a germpore or aperture (Figure 2.13).

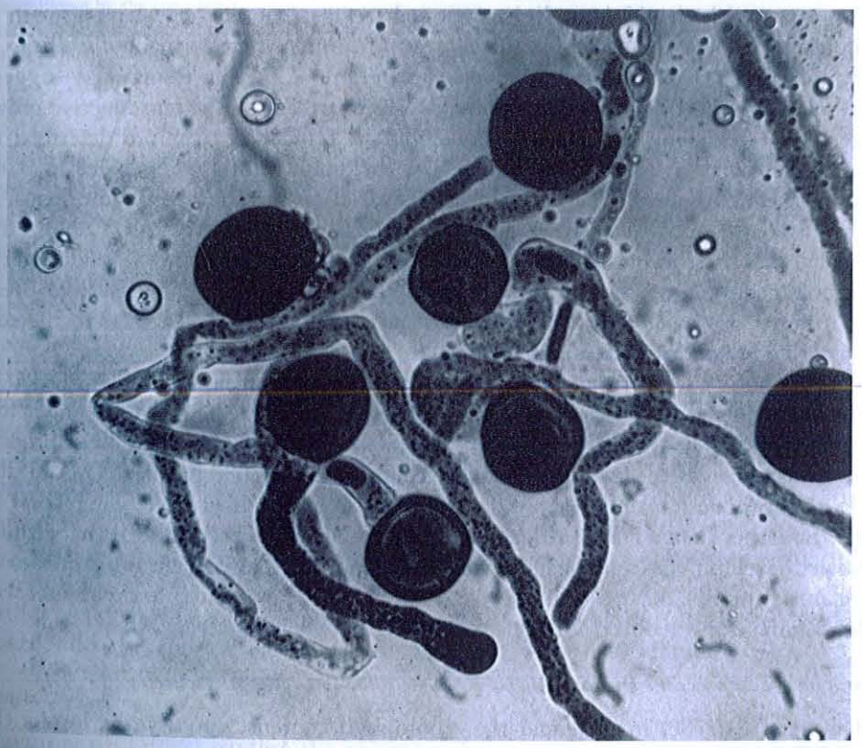

Figure 2.13 Germination of pollen grains.

The stainability percentage ranges from 14.7 (cv. Thingpuri) to 28.5 (in cv. Pottangi and China). Usha (1984) reported 12.5 and 16.4% stainability in cvs.Rio de Janeiro and Moran, respectively. Pollen germination ranged from 8 (cv. Sabarimala) to 24% (Moran) (Dhamayanthi et al., 2003). Pillai et al. (1978) reported 17% pollen germination in cv. Rio de Janeiro. The pollen tube growth under in vitro was maximum in cv. China (488 μm) and minimum in cv. Nadia (328 μm). The number of pollen tubes ranged from 6.5 (in cv. Nadia) to 16.7 (in cv. Varada) (Dhamayanthi et al., 2003).

Physiology of Ginger

Effect of Day Length on Flowering and Rhizome Swelling

Ginger is grown under varying climatic conditions and in many countries in both hemispheres. It is generally regarded as being insensitive to day length. Adaniya et al. (1989) carried out a study to determine the influence of day length on three Japanese cultivars (Kintoki, Sanshu, and Oshoga) by subjecting the plants to varying light periods in comparison with natural daylight. In the three cultivars, as the light periods decreased from 16 to 10 hours, there was inhibition of vegetative growth of shoots and the underground stem. The rhizome knobs became more rounded and smaller. As the day length increased to 16 hours, the plants grew more vigorously and the rhizome knobs were slender and larger and active as new sprouts continued to appear. When the light period was extended to 19 hours, there was reduction in all growth parameters, and it was on a par with the 13-hour light period. It seems that the vegetative growth was promoted by a longer light period up to a certain limit, whereas rhizome swelling was accelerated under a relatively short day length (Table 2.7). The results also suggested that a relatively short day length accelerated the progression of the reproductive growth, whereas relatively long day length decelerated it. Ginger is therefore described as a quantitative short-day plant for flowering and rhizome swelling (Adaniya et al., 1989). These workers have also observed intraspecific variations in photoperiodic response; cv. Sanshu responded most sensitively, and Kintoki was more sensitive than Oshoga. They concluded that such an intraspecific response to the photoperiod could be related to their traditional geographical distribution; Kintoki and Sanshu are early cultivars adapted to the northern part (Kanto district) and Oshoga is a late cultivar adapted to the south (Okinawa to Shikoku districts).

Sterling et al. (2002) studied the effect of photoperiod on flower bud initiation and development in *Zingiber mioga* (myoga, or Japanese ginger). Plants grown under long-day conditions (16 hours) and short-day conditions (8 hours) with a night break produced flower buds, whereas those under short-day conditions (8 hours) did not. This failure of flower bud production under short day was due to abortion of developing floral bud primordia rather than a failure to initiate inflorescences. It was concluded that although for flower development in myoga a quantitative long-day requirement must be satisfied, flower initiation was day neutral. Short-day conditions also resulted in premature senescence of foliage and reduced foliage dry weight.

Chlorophyll Content and Photosynthetic Rate in Relation to Leaf Maturity

Xizhen et al. (1998c) investigated the chlorophyll content, photosynthetic rate (Pn), MDA content, and the activities of the protective enzymes during leaf development. Both chlorophyll content and Pn increased with leaf expansion and reached a peak on

Table 2.7 Effect of photoperiod on the growth of underground parts

Cultivar	*Day length (h)*	*No. of rhizome knobs*	*Weight of rhizome (g)*	*Weight of a rhizome knob (g)*	*No. of primary roots*	*Percentage of swollen primary roots (%)*
Kintoki	10	27.0a[y]	75.2b	2.71b	39.8d	19.9a
	ND[x]	30.4a	118.2a	3.80a	127.0c	3.9b
	13	30.6a	102.0ab	3.15b	154.8bc	0.6c
	16	29.9a	128.5a	4.33a	204.4a	—
	19	28.5a	99.3ab	3.50a	184.9ab	—
Sanshu	10	26.7c	58.3c	2.18c	41.3d	2.3a
	ND	39.6b	151.4b	3.82b	77.1b	2.5a
	13	47.5a	152.1b	3.26b	55.0cd	0.5b
	16	45.2ab	212.3a	4.64a	146.7a	—
	19	27.8c	123.2b	4.48a	74.5bc	—
Oshoga	10	11.2b	68.9c	6.15b	26.9b	0.7a
	ND	13.8ab	190.4ab	13.80a	44.4a	0.5a
	13	15.9a	215.9a	13.58a	49.6a	—
	16	12.8ab	195.6ab	15.28a	44.6a	—
	19	10.8b	146.7b	13.58a	40.2a	—

Values followed by the same letters are not significantly different.
[x]Natural day length decreased from 13.46 h (June 29) to 10.41 h (Nov. 29)
[y]Mean separation with in cultivars by Duncan's multiple range test, 5% level.

the 15th day and then declined gradually (Table 2.8). In the first 40 days of leaf growth, the malondialdehyde (MDA) content of leaves remained constant and SOD (superoxide dismutase) activity showed a little decrease. After 40 days, the MDA content increased markedly and SOD activity dropped substantially. Peroxidase (POD) and catalase activities exhibited a steady increase during 60 days. Xizhen et al. (1998) concluded that senescence of ginger leaf sets in when leaf age reaches about 40 days.

Xizhen et al. (1998) also studied the photosynthetic characteristic of different leaf positions, and reported that the Pn of midposition leaves was the highest followed by the lower leaves and Pn was lowest in upper leaves. The light compensation point of different leaf positions was from 18.46 to 30.82 $\mu mol/m^2s^{-1}$; it was highest in midposition leaves and lowest in lower leaves. The light saturation point ranged from 624.8 to 827.6 $\mu mol/m^2s^{-1}$, the values were 624.8, 827.6 and 799. 5 $\mu mol/m^2s^{-1}$, respectively, in upper, middle, and lower leaves. CO_2 compensation points in upper, middle, and lower position leaves were 163.8, 29.6 and 71.4 μl/l, respectively. CO_2 saturation in upper, middle, and lower leaves were 1543.3, 1499.0 and 1582.0 μl/l. The diurnal variation of Pn in different leaf positions gave a double peak curve, the first peak was at about 9:00 A.M. and the second appeared from 1300 to 1400 hours.

Stomatal Behavior and Chlorophyll Fluorescence

Dongyun et al. (1998) studied the chlorophyll fluorescence and stomatal behavior of ginger leaves. Ginger leaves were enclosed individually in cuvettes and studied to find

Table 2.8 Changes of chlorophyll content and photosynthetic rate during development of ginger leaves

Leaf age (days)	*Chlorophyll content(mg · g^{-1})*	*Pn (μmol m^{-2} · s^{-1})*
1 day	1.80	6.11
5 days	1.98	7.58
10 days	2.02	9.16
15 days	2.58	10.30
20 days	2.56	0.20
25 days	2.43	9.86
30 days	2.47	8.54
35 days	2.51	8.69
40 days	2.56	8.48
45 days	2.30	7.62
50 days	2.01	7.11
55 days	1.89	6.65
60 days	1.77	6.21

Source: Xizhen et al. (1998b).

out the relationship between photosynthesis and changes in microclimate. Stomatal conductance (gsc) increased and was saturated at relatively low values of high intensity (400 μmol^{-1}). At different leaf temperatures, gsc peaked at 29°C, but transpiration (tr) increased with increasing irradiance and temperature. Increasing external CO_2 concentrations caused gsc to increase but were relatively insensitive to increasing soil moisture availability until a threshold was reached (0.5 to 2 g/g). At a soil moisture content of 2 to 3.5 g/g, gsc increased approximately linearly with increasing tr. Fluorescence (Fv/Fm, electron transfer in PS II) decreased with increasing photon flux density (PFD). In leaves exposed to high PFD and different temperatures, Fv/Fm was the lowest at 15°C, and the highest at more than 25°C. In leaves exposed to low PFD, Fv/Fm remained at a similar value over all temperatures tested.

Photosynthesis and Photorespiration

Zhenxian et al. (2000) measured, using a portable photosynthetic system and a plant efficiency analyzer, the photosystem inhibition of photosynthesis and the diurnal variation of photosynthetic efficiency under shade and field conditions. There were marked photoinhibition phenomena under high light stress at mid-day. The apparent quantum yield (AQY) and photochemical efficiency of PS II (Fv/Fm) decreased at midday, and there was a marked diurnal variation. The extent of photoinhibition due to higher light intensity was severe in the seedling stage. After shading, AQY and Fv/Fn increased and the degree of photoinhibition declined markedly. However, under heavier shade, the photosynthetic rate declined because the carboxylation efficiency declined after shading.

Shi-jie et al. (1999) investigated the seasonal and diurnal changes in photorespiration (Pr) and the xanthophyll cycle (L) in ginger leaves under field conditions in order to understand the role of L and Pr in protecting leaves against photoinhibitory damage. The seasonal and diurnal changes of Pr and L of ginger leaves were marked, and Pr showed diurnal changes in response to PFD, and its peak was around 10:00 A.M. to

12:00 noon. Pr declined with increasing shade intensity. The L cycle showed a diurnal variation in response to PFD and xanthophyll cycle pool. Both increased during the midday period, and peaked around 12:00 noon. The results, in general, indicated that Pr and the xanthophyll cycle had positive roles in dissipating excessive light energy and in protecting the photosynthetic apparatus of ginger leaves from midday high-light stress.

Xizhen et al. (2000) have also investigated the role of SOD in protecting ginger leaves from photoinhibition damage under high-light intensity. They observed that on a sunny day the photochemical efficiency of PS ll (Fv/Fm) and AQY of ginger leaves declined gradually in the morning, but rose progressively after 12:00 noon. The MDA content in ginger leaves increased but the Pn declined under midday high-light stress. SOD activity in ginger leaves increased gradually before 1400 hours, and then decreased. At 60% shading in the seedling stage, Fv/Fm and AQY of ginger leaves increased but the MDA content, SOD activity, and Pn decreased. Pn, AQY, and Fv/Fm of ginger leaves treated with diethyldithio carbamic acid (DDTC) decreased whether shaded or not, but the effect of DDTC on shaded plants was less than that on unshaded plants. These workers concluded that midday high-light intensity imposed a stress on ginger plants and caused photoinhibition and lipid peroxidation. SOD and shading played important roles in protecting the photosynthetic apparatus of ginger leaves against high light stress.

Xizhen et al. (1998a) have investigated the effect of temperature on photosynthesis of ginger leaf. They showed that the highest photosynthetic rate and apparent quantum efficiency was under 25°C. The light compensation point of photosynthesis was in the range of 25 to 69 μmol.m^{2}s^{-1}; it increased with increasing temperature. The light saturation point was also temperature dependent. The low-light saturation point was noted at temperatures below 25°C. The CO_2 compensation point and the saturation point were 25 to 72 and 1343 to 1566 μl/l, respectively, and both increased with the increase in leaf temperature.

Xianchang et al. (1996) studied the relationship between canopy, canopy photosynthesis, and yield formation in ginger. They found that canopy photosynthesis was closely related to yield. In a field experiment using a plant population of 5,000 to 10,000 per 666.7 m^2 area, they had a yield increase from 1,733 to 2,626 kg. The Pn increased from 8.16 (μmol CO_2 m^{-2} 1 (ground) s^{-1}) to 14.66; the leaf area index from 3.21 (m^2/m^2) to 7.02 m^2/m^2 (Table 2.9). The unit area of branches (tillers) and leaf area index were over 150/m^2 and 6 m^2/m^2, respectively, in the canopy of the higher yield class. The canopies over 7,000 plants per 666.67 m^2 satisfied these two criteria and among them there were no significant differences in height, tillers, leaf area index, canopy photosynthesis, and yield. Diurnal changes in the canopy Pn showed a typical single-peak curve, which was different from the double-peak curve obtained from the single-leaf Pn.

Effect of Growth Regulators

Studies have been carried out to find out the effect of various growth regulators on ginger growth, flowering and rhizome development. The main aims of such studies are to break the rhizome dormancy, to induce flowering and seed set, and to enlarge the rhizome followed by increased yield. Islam et al. (1978) studied the influence of 2-chloroethyl phosphonic acid (ethrel or ethephon) and elevated temperature treatments. Exposure of ginger rhizome pieces to 35°C for 24 hours or to 250 ppm ethrel for 15 min caused a

Table 2.9 Effect of plant density on growth, photosynthesis, and yield of ginger

Plant density (per 66.67 m^2)	*Plant ht. (cm)*	*Tillers (no/m^2)*	*Leaf area index (m^2/m^2)*	*Photosynthetic rate (μmol CO^2 m^2 (ground) · s^{-1})*	*Yield (kg/666.7 m^2)*
5,000	62a*	103a	3.21a	8.16a	1733.42a
6,000	64a	122b	4.25b	10.17b	1948.25b
7,000	67a	138c	5.31c	12.23c	2211.22c
8,000	73b	152d	6.15d	14.56d	2637.17d
9,000	74b	159d	6.63d	14.78d	2614.95d
10,000	74b	163d	7.02d	14.66d	2626.13d

*Same letters are not statistically significant

Source: Xianchang et al. (1996).

Table 2.10 Effect of temperature and ethrel on germination and early growth of ginger

Growth parameters	*Day 16 Pretreated*			*Day 23 Pretreated*		
	Control	*35°C*	*Ethrel*	*Control*	*35°C*	*Ethrel*
Shoots plus swollen buds (%)[a]	70.4	76.8	91.8***	86.2	81.4	92.6
Total length of shoots per rhizome piece (m)	2.63	3.49*	4.23***	3.72	5.36	6.83***
Length of longest shoot per rhizome piece (cm)	1.48	1.90*	2.36***	2.28	3.23	4.36*
Shoots having roots (%)	9.43	13.73	34.63***	25.83	41.83**	46.93**
Total number of roots per seed piece	2.45	2.78	9.81***	5.95	9.12	13.54**

Source: Islam et al. (1978), [a]Expressed as percentage of total number of shoots, swollen buds, and visible but apparently dormant buds; *, **, *** denotes significant differences from control treatment at P = .05, P = .01, and P = .001, respectively.

substantial increase in shoot growth during the first 23 days of growth (Table 2.10). Ethrel was more effective in increasing the number of roots per rhizome piece by a factor of 4.0 and the number of shoots having roots by a factor of 3.7 (both at day 16). Relatively low concentrations of ethrel (less than 250 ppm) were sufficient to produce maximum responses in terms of shoot length parameters, although significant increases in the number of shoots per seed piece, the number of rooted shoots, and the total number and length of roots per seed piece occurred even up to the highest concentrations of 1,000 ppm studied by Islam et al. (1978). Treatment of ethrel was found to be effective in reducing the variability in root growth, but shoot growth variability had increased particularly at concentrations below 500 ppm.

Furutani and Nagao (1986) investigated the effect of daminozide, gibberellic acid (GA_3), and ethephon on flowering, shoot growth, and yield of ginger. Field-grown ginger plants were treated with three weekly foliar sprays of GA_3 (0, 1.44 and 2.88 mM); ethephon (0, 3.46, and 6.92 mM), or daminozide (0.3, 13, and 6.26 mM). GA_3 inhibited

flowering and shoot emergence, whereas ethepon and daminozide had no effect on flowering but promoted shoot emergence. Rhizome yields were increased with daminozide and decreased with GA_3 and ethephon.

Ravindran et al. (1998) tested three growth regulators—triacontanol, paclobutrazole, and GA_3—on ginger to find out their effect on rhizome growth and developmental anatomy. Paclobutrazole- and triacontanol-treated rhizomes resulted in thicker walled cortical cells compared to GA_3 and control plants. The procambial activity was higher in plants treated with triacontanol and paclobutrazole. In the cambium layers, the fusiform cells were much larger in paclobutrazole-treated plants. Growth-regulator treatment did not affect the general anatomy, although dimensional variations existed. The numbers of vascular bundles were more in plants treated with paclobutrazole and triacontanol. Paclobutrazole-treated plants exhibited greater deposition of starch grains than other treatments. The fiber content in the rhizome was less in GA_3-treated rhizome. A higher oil cell index and higher frequency oil cells were observed in paclobutrazole-treated rhizome (Table 2.11). GA treatment also led to considerable increase in the number of fibrous roots.

Growth-Related Compositional Changes

Baranowski (1986) studied the cv. Hawaii for 34 weeks and recorded the growth-related changes of the rhizome. The solid content of the rhizome increased throughout the season, but there was a decline in the acetone extractable oleoresin content of dried ginger. However, the oleoresin content on a fresh weight basis was roughly constant (Table 2.12).

The (6)-gingerol content of ginger generally increased with the age of the rhizome on a fresh weight basis (Table 2.13) These results indicate the basis for the gradual increase in pungency with maturity. On a dry weight basis, gingerol generally exhibited a linear increase with maturity up to 24 weeks, followed by a steady decline through the rest of the period. The results, in general, indicate that it may be advantageous to harvest ginger early (i.e., by 24 weeks) for converting to various products.

Table 2.11 Effect of triacontanol, paclobutrazol, and GA_3 on rhizome characters of ginger

Treatment	*Mean internodal length aerial stem (cm)*	*Mean leaf length (cm)*	*Mean internodal length of rhizome (cm)*	*Mean rhizome girth (cm)*	*Mean oil cells per mm^2*	*Crude fiber content (%)*
Control	2.3	1.9	5.2	6.8	18.3	2.2
Tria-contanol	1.9	2.0	4.0	7.8	12.3	2.4
Paclobutrazole	0.8	1.8	0.7	4.6	22.2	2.6
GA_3	4.8	3.2	4.4	8.6	17.8	1.8

GA_3, gibberellic acid.

Source: Ravindran et al. (1998).

Table 2.12 Changes in yield and composition of ginger Hawaiian rhizomes during growth

			*Oleoresin (%)***	
Weeks after planting	*Wt.* (kg)*	*Solids (%)*	*Dry wt basis*	*Fresh wt basis*
12	0.1	6.4	18.7a	1.20a
16	0.5	5.1	19.7a	1.00c,d
18	0.4	4.9	18.4a	0.90d
20	0.8	5.3	16.8b	0.89d
22	0.9	5.7	16.7b	0.95c,d
24	1.5	6.1	15.4c	0.94c,d
26	3.0	7.0	14.7c,d	1.03b,c
28	3.4	8.8	13.6d	1.20a
30	3.7	9.2	12.1e	1.04a,b
32	3.1	10.4	10.0f	1.04b,c
34	5.0	13.8	7.1g	0.99c,d

*Average of four plants, cleaned rhizomes
**Means separated by Duncan's multiple range test (P = .05)
Figures followed by the same letters are not significantly different.

Source: Baranowski (1986).

Table 2.13 Changes in (6)-gingerol content during growth

Weeks after planting	*Wet weight basis (ppm)*[a]	*Dry weight basis (ppm * 10^{-3})*[a]
12	597	9.3
16	964	18.9
18	708	14.5
20	723	13.6
22	871	15.3
24	1001	16.4
26	1039	14.8
28	1184	13.5
30	1110	12.1
32	1238	11.9
34	1547	11.3

[a]Means separated by Duncan's multiple range test (P = 0.05)

Source: Baranowski (1986).

Genetic Resources

The history of domestication of ginger is not definitely known. However, this crop is known to have been under cultivation and use in India and China for the last 2,000 years or even more. China is probably the region where domestication had started, but little is known about the center of origin, although the largest variability exists in China. Southwestern India, known as the Malabar Coast in ancient times, traded ginger with the Western World from ancient times, indicating its cultivation. This long period of

domestication might have played a major role in the evolution of this crop that is sterile and propagated solely vegetatively. Ginger has rich cultivar diversity, and most major growing tracts have cultivars that are specific to the area; and these cultivars are mostly known by place names. Cultivar diversity is richest in China. In India the diversity is more in the state of Kerala and in the northeastern region of India. Being clonally propagated, the population structure of this species is determined mainly by the presence of isolation mechanisms and the divergence that might have resulted through the accumulation of random mutations. At present, more than 50 ginger cultivars possessing varying quality attributes and yield potential are being cultivated in India, although the spread of a few improved and high-yielding ones are causing the disappearance of the traditional land races. The cultivars popularly grown (cultivar diversity) in the various ginger-growing states in India are given in Table 2.14. Some of these cultivars were introduced into India, and the cultivar Rio de Janeiro, an introduction from Brazil, has become very popular in Kerala. Introductions such as China, Jamaica, Sierra Leone, and Taffin Giwa, are also grown occasionally.

Among the ginger-growing countries, China has the richest cultivar diversity. The important cultivars grown in China are given in Table 2.15. Less important ones are Zaoyang of Hubei province, Zunji big white ginger of Giuzhou, Chenggu yellow ginger of Shaxi, Yulin round fleshy ginger of Guangxi, Bamboo root ginger and Mian yang ginger of Sichuan, Xuanchang ginger of Ahuii, Yuxi yellow ginger of Yunnan, and Taiwan fleshy ginger. Many of these cultivars have unique morphological markers for identification.

In general, the cultivar variability is much less in other ginger-growing countries. Tindall (1968) reported that there were two main types of ginger grown in West Africa. These differ in color of the rhizome, one with a purplish red or blue tissue below the outer scaly skin, whereas the other has a yellowish white flesh. Graham (1936) reported that there were five kinds of ginger recognized in Jamaica known as St. Mary, Red eye, Blue Tumeric, Bull blue, and China blue. But Lawrence (1984) reported that only one cultivar is grown widely in Jamaica. According to Ridley (1915), three forms of ginger were known in Malaysia in earlier days: halyia betel (true ginger), halyia bara, or padi, a smaller leaved ginger with a yellowish rhizome used only in medicine; and halyia udang, red ginger having red color at the base of the aerial shoot. A red variety of ginger, *Z. officinale* var. *rubra* (also called pink ginger), has been described from Malaysia, in which the rhizome skin has a reddish color. A variety "withered skin" also has been reported. In Philippines two cultivars are known, the native and the Hawaiian (Rosales, 1938). In Nigeria the cv. Taffin Giwa (Bold, yellow ginger) is the common one, the other being Yasun Bari, the black ginger.

In Japan the ginger types are classified into three groups: (1) small-sized plants with many tillers and a small rhizome, (2) medium-sized plants with an intermediate number of tillers and a medium-sized rhizome, and (3) large-sized plants with fewer tillers and larger rhizomes. The common cultivars included in these groups are Kintoki, Sanshu, and Oshoga, respectively. A stabilized tetraploid line of Sanshu (4x Sanshu) is also being cultivated in Japan (Adaniya, 2001). In addition, *Z. mioga* (Japanese ginger) is also grown in Japan for spice and vegetable purposes. In Queensland, Australia, ginger was an important crop in earlier times. The ginger cultivars might have been introduced there, although the exact source is not known. The local cultivar, known as Buderim local, is the most commonly grown. Australia earlier introduced cultivars from Japan, Hawaii,

Table 2.14 Major ginger-growing states in India and their popular cultivars indicating the diversity in ginger

State	*Cultivar name*	*Specific trait/character*	*Reference*
Kerala	Rio de Janeiro (32.55 t/ha—fresh)	High yield	Thomas (1966);
	Burdwan, Jamaica	High yield	Muralidharan and Kamalam (1973)
	Nadia (28.55 t/ha—fresh) & 6.54 t/ha—dry), Maran, Bajpai, and Narasapattam	High yield	AICSCIP (1978); Khan (1959)
	Rio de Janeiro and Kuruppumpady	Ratoon crop	Sree Kumar et al. (1980)
	SG-666	Fresh rhizome	Rattan (1989)
	Rio de Janeiro (21.80 t/ha—fresh; 3.27t/ha—dry), Assam (17.23 t/ha—fresh), Maran (3.27 t/ha—dry), and Thingpuri (2.79 t/ha—dry)	High yield	Muralidharan (1973)
	Thingpuri, Rio de Janeiro, and China	High yield	Sreekumar et al. (1980)
	IISR-Varada (22.6 t/ha)		Muralidharan (1973)
	IISR-Mahima (23.2 t/ha) and IISR-Rejatha (22.4 t/ha)	Wider adaptability High yield	Sasikumar et al. (2003)
	V_2E_5-2 (33.83 t/ha), Rio de Janeiro (27.38 t/ha), Ernadan (25.11 t/ha), and Mananthavady (22.94 t/ha) (green ginger)	High yield	Pradeep Kumar et al. (2000)
Himachal Pradesh	Himachal Selection, Rio de Janeiro	High yield	Jogi et al. (1972)
	SG-646 and SG-666	High yield	Rattan (1989)
	Kerala local (3.76 t/ha) and B-1 (3.83 t/ha), Himachal selection (local) (10.9 t/ha) and Kerala local (9.6 t/ha)	Fresh ginger	Arya and Rana (1990)
	SG-534 (10.35 t/ha), V_1E_8-2 (8.92 t/ha), Acc. No. 64 (8.9 t/ha)	High-altitude areas	AICRPS (2000)
Assam	Nadia (6.7 t/ha) & Chekerella (5.7 t/ha)	High fresh rhizome yield	Aiyadurai (1966); Saikia and Shadeque (1992)
Nagaland	Thinladium, Nadia, and Khasi local (>30 t/ha)	High fresh rhizome yield	Singh et al. (1999)
Orissa	SG-666	High fresh rhizome yield	Rattan (1989)
	Rio de Janeiro and China (239 g/plant), Vingra selection, Ernad Manjeri, U.P., Thingpuri, Kuruppampadi, Wynad Kunnamangalam Thingpuri (2.20 t/ha)	High yield	Mohanty et al. (1981) Panigrahi and Patro (1985)
	V_1E_8-2 (25.13 t/ha)	High-altitude area	AICRPS (2000)
	V_3S_1-8 (22.12 t/ha)	High-altitude area	Naidu et al. (2000)
Andhra Pradesh	IISR-Varada		
Karnataka	Himachal Pradesh (19.97 t/ha), Jorhat (18.88 t/ha), Wynad local (18.68 t/ha)	High fresh rhizome yield	Gowda and Melanta (2000)
Meghalaya	Tura (26.69 t/ha), Poona (25.04 t/ha), and Basar local (24.88 t/ha)	Midhills area	Chandra and Govind (1999)
West Bengal	Gurubathan (27.9 t/ha) Acc. No. 64 (18.93 t/ha)	High yield	AICRPS (2001)
Madhya Pradesh	V_3S_1-8 (17.4 t/ha)	High yield	AICRPS (1999)

Table 2.15 Ginger varieties commonly grown in China

Sl. No.	*Category/Type*	*Varieties/Cultivars*
1.	Sparse seedling type	Gandzhou (sparse ringed, big fleshy ginger)
		Shandong Laiwu (big ginger)
2.	Dense seedling type	Guangzhow (dense-ringed fleshy ginger)
		Zhejiang (red-claw ginger)
3.	Edible medicinal type	Fujian red bud
		Hunan yellow heart
		Chicken claw ginger
		Xingguo ginger
4.	Edible processed type	Guangzhou (fleshy)
		Fuzhou ginger (purplish shoot)
		Tongling (white ginger)
		Fujian bamboo ginger
		Zunyi (big white ginger)
		Leifeng ginger
5.	Ornamental ginger examples	Laishe ginger
		Flower ginger
		Tea ginger
		Strong ginger
		Hengchum ginger
		Hekou ginger
6.	Other cultivar examples	Zaoyang (Hubei Province)
		Zunji big ginger (Giuzhou)
		Chenggu Yellow (Shaxi)
		Yulin round fleshy (Guangxi)
		Bamboo root ginger (Sichuan)
		Mianyang (Sichuan)
		Xuanchang (Ahuii)
		Yuxi yellow (Yunnan)
		Laiwu slice ginger (Shandong)
		Yellow claw (Zhejiang)
		Taiwan fleshy (Taiwan)

and India. Recently the Buderim Ginger Co. (2002) has released the first tetraploid commercial variety, called Buderim Gold, for cultivation in Queensland. *Z. mioga,* the myoga ginger, introduced from Japan, is also grown commercially for its unopened flower buds, which are a vegetable delicacy.

In many cases, the major production centers are far from the areas of origin of the crop concerned (Simmonds, 1979). This is true of ginger as well: the Indo/Malayan region is very rich in Zingiberaceous flora (Holttum, 1950). Considering the present distribution of genetic variability, it is only logical to assume that the Indo/Malayan region is probably the major center of genetic diversity for *Zingiber*. It may be inferred that geographical spread accompanied by genetic differentiation into locally adapted populations caused by mutations could be the main factor responsible for variations encountered in cultivated ginger (Ravindran et al., 1994). In India the early movement of settlers across the length and breadth of the Kerala state and adjoining regions, where the maximum ginger cultivation is found, and the story of shifting cultivation in northeastern India (the second major ginger-growing sector in India), are well-documented sociological events. The farmers invariably carried small samples of the common crops that they grew in their original place along with them and domesticated the same in their new habitat—in most cases, virgin forestlands. Conscious selection for different needs such as high fresh ginger yield, good dry recovery, and less fiber content over the years has augmented the spread of differentiation in this crop. This would have ultimately resulted in the land races of ginger of today (Ravindran et al.,1994).

Conservation of Ginger Germplasm

Major collections of ginger germplasm are maintained at the Indian Institute of Spices Research (IISR), Calicut, India, and the Research Institute for Spices and Medicinal Crops, Bogor, Indonesia. In India serious efforts are being made for conservation of ginger germplasm. At present, the ginger germplasm conservatory at IISR consists of 645 accessions that include exotic cultivars, indigenous collections, improved cultivars, mutants, tetraploids, and related species (IISR, 2002). In addition, 443 accessions are being maintained at different centers of the All India-Coordinated Research Project on Spices and the National Bureau of Plant Genetic Resources (NBPGR), Regional Station, Thrissur (AICRPS, 2001 Table 2.16). The major constraints involved in the conservation of the germplasm of ginger are the two soil-borne diseases: rhizome rot caused by *Pythium* spp. (such as *P. aphanidermatum, P. myriotylum,* and *P. vexans*) and the bacterial wilt caused by *Ralstonia solanacearum* (*Pseudomonas solanacearum*). Added to this, infection by leaf fleck virus is also posing serious problems for conservation. These diseases are extremely difficult to control or prevent under field conditions. Hence, in the National Conservatory for ginger at IISR, ginger germplasm is conserved in specially made cement tubs under 50% shade, as a nucleus gene bank to safeguard the material from deadly diseases and to maintain the purity of germplasm from adulteration,which is very common in field plantings. Each year, part of the germplasm collection is planted out in the field for evaluation and characterization (Ravindran et al., 1994). The collections are harvested every year and replanted in the next season in a fresh potting mixture. On harvesting the rhizomes, each accession is cleaned and dipped in fungicide and insecticide for protection and stored in individual brick-walled cubicles lined with sawdust or sand in a well-protected building.

In Vitro Conservation

In vitro conservation of ginger germplasm is a safe and complementary strategy to protect the genetic resources from epidemic diseases and other natural disasters. This is also an excellent method to supplement the conventional conservation strategies. Conservation

Table 2.16 Germplasm collections of ginger in India.

Sl.no	*Institute/University*	*No. of accessions*	*Reference*
1.	Indian Institute of Spices Research, Calicut	645	IISR (2002)
2.	Orissa University of Agriculture and Technology, Pottangi, Orissa	172	AICRPS (2003)
3.	Dr. Y.S Parmar University of Horticulture and Forestry, Solan, Himachal Pradesh	271	AICRPS (2003)
4.	Rajendra Agricultural University, Dholi, Bihar	103	-do-
5.	Uttara Bangala Krishi Viswa Vidyalaya, Pundibari, West Bengal	31	-do-
6.	Narendra Dev University of Agriculture and Technology, Kumarganj, Faizabad, Uttar Pradesh.	29	-do-
7.	Indira Gandhi Krishi Viswa Vidyalaya, Regional Station, Raigarh	35	-do-
8.	National Bureau of Plant Genetic Resources, Regional Station, Thrissur, Kerala	173	Ravindran et al. (2004)
9.	Department of Horticulture, Sikkim	58	Kumar (1999)
10.	Central Agricultural Research Institute, Port Blair, Andamans	33	Shiva et al. (2004)

of ginger germplasm under in vitro conditions by slow growth was standardized at IISR, Calicut (Geetha et al., 1995; Nirmal Babu et al., 1996; Geetha, 2002). By this method, ginger could be stored up to one year without subculture in half-strength Murashige and Skoog (MS) medium with 10 gl^{-1} each of sucrose, and mannitol in sealed culture tubes. The survival of such stored material is around 85%. At IISR, over 100 unique accessions of ginger are being conserved under in vitro gene bank as medium-term storage of germplasm (Ravindran et al., 1994; Geetha, 2002). The possibility of storage at relatively high ambient temperatures (24–29°C) by subjecting the ginger and related taxa to stress factors was explored by Dekkers et al. (1991). The increase in the subculture period was better with an overlay of liquid paraffin. After one year, 70 to 100% survival was seen.

Ravindran and coworkers (Anon. 2004) standardized the use of synthetic seeds in conservation. Synthetic seeds, developed with somatic embryos, encapsulated in 5% sodium alginate gel could be stored in MS medium supplemented with 1 mgl^{-1}. g/l can be substituted for gl^{-1} throughout the chapter (and also in other chapters) Benzyl adenine (BA) at 22 ± 2°C for 9 months with 75% survival. The encapsulated beads on transfer to MS medium supplemented with 1.0 mgl^{-1} Benzylaminopurine (BAP) and 0.5 mgl^{-1} Naphthalene acetic acid (NAA), germinated and developed into normal plantlets (Sajina et al., 1997). The conservation of germplasm through microrhizome production was also investigated and it was found that microrhizomes can be induced in vitro when cultured in MS medium supplemented with higher levels of sucrose (9 to 12%). Such microrhizomes can be easily stored for more than one year in culture. Six-months-old microrhizomes can be directly planted in the field without any acclimatization. The microrhizomes can thus be used as a disease-free seed material and for propagation, conservation, and exchange of germplasm (Geetha, 2002). This microrhizome technology is amenable for automation and scaling up.

Cryopreservation is a strategy for long-term conservation of germplasm (Ravindran et al., 1994). Efforts are going on at IISR and NBPGR for developing such strategies. Cryopreservation of ginger shoot buds through an encapsulation-dehydration method was attempted by Geetha (2002). The shoot buds were encapsulated in 3% sodium alginate beads and pretreated with 0.75 M sucrose solution for 4 days and dehydrated in an air current from laminar airflow and then immersed in liquid nitrogen. Beads conserved like this on thawing and recovery exhibited 40 to 50% viability. The cryopreserved shoot buds were regenerated into plantlets. The studies carried out at IISR showed that vitrification and encapsulation-vitrification methods are more suitable for the cryopreservation of ginger shoot buds (Nirmal Babu, unpublished data).

Characterization and Evaluation of Germplasm

A clear knowledge of the extent of genetic variability is essential for formulating a meaningful breeding strategy. Under a low-variability situation, selection programs will not yield worthwhile benefits. In any vegetatively propagated species the extent of genetic variability will be limited unless samples are drawn from distinctly different agroecological situations. Studies on genetic variability for yield and associated characters in ginger indicated the existence of only moderate variability in the germplasm. Little variability exists among the genotypes that are grown in the same area; however, good variability has been reported among cultivars that came from widely divergent areas.

Ravindran et al. (1994) characterized 100 accessions of ginger germplasm based on morphological, yield, and quality parameters. Moderate variability was observed for many yield and quality traits (Table 2.17). Tiller number per plant had the highest variability, followed by rhizome yield/plant. Among the quality traits, the shogaol content recorded the highest variability, followed by crude fiber and oleoresin. None of the accessions possessed resistance to the causal organism of leaf spot disease, *Phyllosticta zingiberi*. Quality parameters such as dry recovery and oleoresin and fiber contents

Table 2.17 Mean, range, and CV (%) for yield attributes and quality traits in ginger germplasm

Character	*Mean*	*Range*	*CV (%)*
Plant height (cm)	59.2	23.1–88.6	19.00
Leaf no./plant	37.1	17.0–52.0	18.22
Tiller no./plant	16.8	2.80–35.5	45.90
Leaf length (cm)	23.8	17.0–36.5	10.90
Leaf width (cm)	2.6	1.90–3.70	10.80
Days to maturity	226.0	214–236	13.5
Dry recovery (%)	21.7	14.0–28.5	14.3
Rhizome yield/plant (g)	363.1	55.0–770.0	39.3
Crude fiber (%)	4.31	2.1–7.0	23.3
Oleoresin (%)	6.1	3.2–9.5	21.7
Gingerol (%) in oleoresin	19.9	14.0–27.0	15.2
Shogaol (%) in oleoresin	4.1	2.7–7.5	24.3

Source: Ravindran et al. (1994).

are known to vary with the soil type, cultural conditions, and climate (Ravindran et al., 1994).

Mohanty and Sarma (1979) reported that expected genetic advance and heritability estimates were high for the number of secondary rhizome and total root weight. Genetic coefficient of variation was high for weight of root tubers. Rhizome yield was positively and significantly correlated with number of pseudostems (tillers), leaves, secondary rhizome fingers, tertiary rhizome fingers, total rhizome, plant height, leaf breadth, girth of secondary rhizome fingers, and number and weight of adventitious roots. Studies indicated that straight selection was useful to improve almost all characters except the number of tertiary fingers and straw yield. Rattan et al. (1988) reported that plant height was positively and significantly correlated with number of leaves, leaf length, rhizome length, rhizome breadth, and yield per plot. The number of leaves per plant was positively and significantly related to rhizome length, breadth, and yield. The rhizome length was also related to rhizome breadth and yield. Positive correlation of rhizome weight with plant height, number of tillers, and leaf number was reported by Sreekumar et al. (1980). Mohanty et al. (1981) observed a significant varietal differences for all the characters except for the number of tillers per plant and number of leaves per plant. Pandey and Dobhal (1993) observed a wide range of variability for most of the characters studied by them. Rhizome yield per plant was positively associated with plant height, number of fingers per plant, weight of fingers, and primary rhizome.

At IISR, Sasikumar et al. (1992b) studied 100 accessions of ginger germplasm for variability, correlation, and path analysis. They found that rhizome yield was positively correlated with plant height, tiller and leaf number, and leaf length and width (Table 2.18). Plant height also had a significant and positive association with leaf and tiller number as well as length and width of leaf. The association of leaf number with tiller number, leaf length, and leaf width was also positive and significant. Tiller number had a significant negative association with dry recovery. Leaf width had a positive significant association with dry recovery.

Table 2.18 Character associations in ginger

Character	*Leaf no.*	*Tiller no.*	*Leaf length*	*Leaf weight*	*Days to maturity*	*Dry recovery*	*Rhizome/ plant*
Plant ht.	0.69*	0.32**	0.59**	0.51**	0.12	0.18	0.47**
Leaf no.		0.26**	0.56**	0.36**	0.01	0.07	0.38**
Tiller no.			0.30*	0.13	0.03	0.29**	0.26**
Leaf length				0.42**	0.04	0.04	0.49**
Leaf width					0.01	0.42**	0.23**
Days to maturity						0.06	0.03
Dry recovery							0.10

** Significant at 1% level.

Source: Sasikumar et al. (1992b).

Yadav (1999) reported a high genotypic coefficient of variation for length and weight of secondary rhizomes, weight of primary rhizomes, number of secondary and primary rhizomes, and rhizome yield/plant. High heritability coupled with high genetic advance as a percentage of mean was observed for plant height, leaf length, suckers per plant, number of mother and secondary rhizomes, weight of primary rhizome, and rhizome yield per plant, indicating that desirable improvement in these traits can be brought about through straight selection. Plant height followed by number of tillers per plant and leaf length had a maximum direct effect on rhizome yield (Singh, 2001).

Nybe and Nair (1982) suggested that morphological characters are not reliable to classify the types, although some of the types can be distinguished to a certain extent from rhizome characters. All the morphological characters were found to vary among types except for breadth of leaf, leaf area index, and number of primary fingers. Manmohandas et al. (2000) found that all the cultivars differed significantly in tiller number and leaf number. Yield stability analysis revealed the superiority of cvs. Ernad and Kuruppumpadi as they expressed high mean yield, nonsignificant genotype-environment interaction and stability in yield.

Biochemical Variability

Oleoresin of ginger is the total extract of ginger containing all the flavoring principles as well as the pungent constituents. The oleoresin contains two important compounds—gingerol and shogoal—that contribute to the ginger pungency. On long-term storage, gingerol becomes converted to shogoal. The quality of ginger thus depends on the relative content of gingerol and shogoal. Zachariah et al. (1993) classified 86 ginger accessions into high-, medium-, and low-quality types based on the relative contents of the quality components (Table 2.19). There are many ginger cultivars with high oleoresin, a few them, such as Rio de Janeiro, Ernad Chernad, Wynad, Kunnamangalam, and Meppayyur, also had a high gingerol content. The intercharacter association showed a positive correlation with oleoresin, gingerol, and shogoal.

Shamina et al. (1997) investigated the variability in total free amino acids, proteins, total phenols, and isozymes, using 25 cultivars. Moderate variations were recorded for total free amino acids, proteins, and total phenols. Isozyme variability for polyphenol oxidase, peroxidase, and SOD was reported to be low, indicating only a low level of polymorphism.

The information available from various studies on germplasm evaluation is summarized in Tables 2.20 and 2.21.

Table 2.19 Range, mean, and coefficient of variance in ginger cultivars for the quality components

Quality constituents	*Range*	*Mean*	*CV%*
Oleoresin (%)	3.2–9.5	6.1	21.5
Gingerol (%) (in oleoresin)	14–25	19.9	15.0
Shogaol (%) (in oleoresin)	2.8–7.0	4.1	23.7

Source: Zachariah et al. (1993).

Table 2.20 Evaluation of ginger germplasm for rhizome yield and its attributes

Character/trait	*Variety/Cultivar/Accession*	*References*
1. High yield (fresh and dry)	U.P, Rio de Janeiro, Thingpuri, Karakkal, Suprabha, Anamika, Jugijan	Mohanty and Panda (1994)
	SG-646 (Kerala) (159 g/plant) and SG-666 (H.P) (151 g/plant)	Rattan (1989)
	Rio de Janeiro, Suprabha, Suruchi, Suravi, Jugijan, Thigpuri, Wynad local, Himachal, Karakkal, Varada, Maran Acc. Nos. 64, 117 and 35	Sasikumar et al. (1994)
	Rio de Janeiro (Av. 21 t/ha—fresh, Maran (Av. 20 t/ha, 4.40 t/ha—dry), Nadia (Av. 19 t/ha—fresh, 3.80 t/ha—dry), Narasapattam (Av. 3.80t/ha-dry)	Paulose (1973)
	Rio de Janeiro (32.55 t/ha), China (16.76 t/ha), Ernad Chernad (15.84 t/ha)	Thomas (1966)
	Wynad (9.0 kg/3 m^2, SG-700, SG-705, and BDJR-1226 (7.5–7.7 kg/3 m^2), V_2E_4-5, and PGS 43 (7.8 kg/3 m^2)	AICRPS (1999, 2000, 2001)
	SG-876, SG-882 (9.2 kg/3 m^2)	
2. Bold rhizome	China, Taffingiva, SG-35	
	Varada, Gurubathan, Bhaise, China, Acc. Nos. 117, 35, 15, 27, and 142	Sasikumar et al. (1994, 1999)
3. Slender rhizome	Suruchi, Kunduli local	Mohanty and Panda (1994)
4. Short duration	Sierra Leone	Mohanty and Panda (1994)
5. High dry recovery (%)	Tura local—2 (29.7%)	Mohanty (1984)
	Tura (28%)	Sreekumar et al. (1982)
	Thodupuzha (22.6%), Kuruppampadi (23.0%) and Nadia (22.6%)	Nybe et al. (1982)
	Tura and Maran	Nair (1969); Muralidharan (1972); CPCRI (1973)
	Tura (22.07%), Thinladium (21.03%), and Jorhat (20.60%)	Muralidharan (1973)
	Vengara (25%), Ernad (24.37%), Himachal Pradesh, and Sierra Leone (23.12% each)	Thomas (1966)
	Zahirabad, Jorhat local, Kuruppampadi, Ernad, Suruchi, Maran, Assam, China, Mowshom, Thingpui, Varada, Acc. Nos. 27, 117, 204, and 294	Sasikumar et al. (1994, 1999)
	SG-685	AICRPS (2000)
6. High oleoresin (%)	Assam (9.3%) and Manathody (9.2%)	Krishnamourthy et al. (1970); Natarajan et al. (1972)
	Kuruppampadi (7.1%)	Muralidharan (1972)
	Rio de Janeiro (10.5%), Maran (10.0%) and Wynad local (9.1%)	Nybe et al. (1980)

Table 2.20 (Continued)

Character/trait	*Variety/Cultivar/Accession*	*References*
	Rio de Janeiro (10.8%)	Sreekumar et al. (1980)
	Wynad, Kunnamangalam, Ambalavayalan, Ernad, Santhing Pui, Rio de Janeiro, Kuruppampadi, Himachal, Varada, and China	Sasikumar et al. (1994)
	Rio de Janeiro, Wynad, Kunnamangalam, Meppayur, Santhing Pui (Manipur-1), Ernad, Erattupetta, Tamarassery local, PGS-33, and PGS-11 (> 7.4%)	Zachariah et al. (1993)
	Acc. Nos. 14 (9.0%) and 118 (6.0%)	Sasikumar et al. (1999)
	Nadan Pulpally, Nadan, and Acc. No.57	Zachariah et al. (1999)
	Acc. Nos. 110, 582, 236, 388, 414, 6, and 3 (6.2–8.9%)	AICRPS (1999)
	V_1S_1-8, BDJR-1226, and Chanog-ll (8.3 to 8.7%)	Krishnamurthy et al. (1970); Lewis et al. (1972)
7. High Essential oil (%)	Mananthody (2.2%)	Nybe et al. (1982)
	Karakkal, (2.4%), Rio de Janeiro (2.3%), Vengara (2.3%), and Valluvanad (2.2%)	Sasikumar et al. (1999)
	Elakallan and Sabarimala	Zakariah et al. (1999)
	Acc. Nos. 118 (2.6%) and 14 (2.5%)	AICRPS (1999)
	Pulpally, Sabarimala, Nadan Pulpally, and Thodupuzha	AICRPS (2000)
	Acc. Nos. 418, 399, 389, 205, 110, 236, 104, and 296 (2.9–3.2%)	Nybe et al. (1982)
	BLP-6, SG-723, BDJR-1054, SG-55, and Maran (2.0 to 2.8%)	Sreekumar et al. (1980)
	Shilli, Bangi, Himgiri, Acc. No. 64, V_1E_4-4 PGS-23, and SG-706	Thomas (1966)
8. Low crude fiber (%)	China (3.4%), UP (3.7%), Himachal Pradesh (3. 8%), Nadia (3.9%)	Sasikumar et al. (1994)
	Tura (3.5%)	Sasikumar et al. (1999)
	China (3.43%), Ernad (4.43%)	Jogi et al. (1972)
	Zahirabad, Kuruppampadi, Mizo, PGS-16, China, UP, Nadia, Poona, and Jamaica	Zachariah et al. (1999)
	Acc. Nos. 287 (3.0%), 288, 22 and 18 (3.2%)	Muralidharan (1973)
	Varada, Acc. Nos. 15 and 27	Paulose (1973)
	Poona (4.62%), Nadia (4.84%), and Thinladium (5.01%)	
	Acc. Nos. 419, 386, 415, 200, 110, and 336 (2.2–3.3%)	
9. High yield of dry ginger (t/ha)	Rio de Janeiro, Maran (3.27 t/ha), and Thingpuri (2.79 t/ha)	
	Maran (Av. 4.40 t/ha), Nadia (Av. 3.80 t/ha), Narasapattam (Av. 3.80 t/ha)	

10. High gingerol and shogaol	Wynad, Kunnamangalam, Ambalavayalan, Ernad, Thing Puri, and Rio de Janeiro	Sasikumar et al. (1994)
	Mizo, Nadia, Maran, Ernad, Kada, and Narianpara (high gingerol—22% of oleoresin); Rio de Janeiro, Santhing Pin (Manipur-1), PGS-37, S-641, Maran, Erattupetta, Nadan Pulpally, Jorhat local, PGS-16, Mizo and Nadia (high shogaol)—5% of oleoresin)	Zachariah et al. (1993)
	Baharica and Amaravathy	Sasikumar et al. (1999)
11. High zingiberene and (6)-gingerol	Baharica and Amaravathy	Sasikumar et al. (1999)

Data collected from various sources.

Table 2.21 Screening of ginger germplasm against pest and disease incidences

Character/trait	*Variety/cultivar/accession*	*Reaction*	*References*
A. Reaction to pests			
1. Shoot borer	Rio de Janeiro	Tolerant	Nybe et al. (1980)
2. Rhizome scale	Wild-2	Least infestation	Mohanty (1984)
	Anamika	Least incidence	Sasikumar et al. (1994)
3. Storage pest	Varada, Acc. Nos. 215 and 212	Resistant	
4. Root-knot nematode	Valluvanad, Tura and H.P	Least infestation	Charles and Kuiyan (1981)
	Acc. Nos. 36, 59 and 221	Resistant	
B. Reaction to diseases			
1. Rhizome rot	Jorhat and Sierra Leone	Least incidence (11.25%)	AICSCIP (1975)
	Maran	Least infection	Nybe and Nair (1979)
	Narasapattam	Least susceptible (1–20%)	Mohanty (1984)
	Burdwan-1, Anamika, Poona and Himachal	Less susceptible	Sasikumar et al. (1994)
	BDJR-1226, Jamaica, BLP-6	Less susceptible	AICRPS (1999)
2. Bacterial wilt	V_2E_5-2, Rio de Janeiro	Least incidence	Pradeepkumar et al. (2000)
3. Leaf spot	Taffingiva, Maran Bajpai and Nadia	Most tolerant	Nybe and Nair (1979)
	Maran and Kunduli local	Less susceptible	Sasikumar et al. (1994)

Path Analysis

The partitioning of phenotypic correlation between yield and morphological characters into direct and indirect effects by the method of path coefficient analysis revealed that plant height exhibited a high direct effect as well as high indirect effect in the establishment of correlation between yield and other morphological characters (Ratnambal, 1979; Nair et al., 1982). Rattan et al. (1989) indicated that number of leaves per plant had maximum direct contribution to yield per plant, followed by rhizome breadth.

Das et al. (1999) reported very high positive direct effects of stomatal number, leaf area, leaf number, and plant height on rhizome yield; leaf temperature, relative humidity of leaves; stomatal resistance and rate of transpiration showed negligible effects. The direct effect of leaf number on rhizome yield was very high (0.631), and this trait is recommended for use as a selection criterion for improving rhizome yield. The study of Pandey and Dobhal (1993) revealed that the strongest forces influencing yield are weight of fingers, width of fingers, and leaf width. Singh et al. (1999) grouped 18 cultivars into three clusters under Nagaland conditions based on D^2 analysis. The major forces influencing divergence of cultivars were rhizome yield per plant and oleoresin and fiber contents.

Sasikumar et al. (1992b) carried out path analysis using 100 accessions of ginger. They reported that plant height followed by leaf length exhibited the highest direct effect on rhizome yield. Dry recovery had a negative direct effect on yield. All other direct effects were negligible. The highest indirect effect was for leaf number through plant height followed by leaf length, again through plant height. In turn, plant height exerted a moderately good indirect effect on rhizome yield. Moderate indirect effects were also noticed in the case of leaf width (through plant height), and leaf length and leaf number (through leaf length). However, these workers noticed a residual effect of 0.8217, thereby indicating that the variability accounted for in the study was only 18%. They concluded that plant height should be given prime importance in a selection program as this character had positive and significant correlation as well as a good direct effect with rhizome yield.

Multiple regression analysis by using morphological characters indicated that the final yield could be predicted fairly accurately by taking into consideration plant height, number of leaves, and breadth of last fully opened leaf at the 90th and 120th days after planting (Ratnambal et al., 1982). Rattan et al. (1989) found that to improve yield per plant, emphasis should be given to the number of leaves per plant and rhizome length by using partial regression analysis. Rai et al. (1999) reported that higher rhizome yields were strongly associated with chlorophyll-a, carbohydrate, and lower polyphenol levels in the leaf. Leaf protein contents showed significant correlation with carbohydrates and the chlorophyll a:b ratio. The chlorophyll a:b ratio also showed a highly positive correlation with the leaf carbohydrate content. However, polyphenols showed a significant positive correlation with chlorophyll-b and carotenoids with chlorophyll-a and chlorophyll-b.

Crop Improvement

Crop-improvement work in ginger is constrained due to the absence of seed set. As a result, clonal selection, mutation breeding, and induction of polyploidy were the crop-improvement methods employed. More recently, somaclonal variations arising through the callus regenerating system is also being made use of in crop-improvement work. Most of the work in this area was carried out in India. The major breeding objectives are: high yield, wide adaptability, resistance to diseases (such as rhizome rot, bacterial wilt, and *Fusarium* yellows), improvement in quality parameters (oil, oleoresin), and low fiber. Work in this area is carried out mainly at the IISR, Calicut, the AICRPS center at the High Altitude Research Station, Pottangi, under the Orissa University of Agriculture and Technology and at the AICRPS center at the Y.S. Parmar University of Horticulture and Forestry at Solan (Himachal Pradesh).

Crop-improvement work carried out so far has been confined mainly to germplasm collection, evaluation, and selection. A large number of collections have been assembled at the IISR, and these collections have been evaluated for yield and quality characters. In addition, a few introductions from other countries have also been made use of for breeding work. Some of the indigenous cultivars have been known to be high yielding and of good quality. In general, variability was found to be limited in cultivars grown in the same region, but wider variability is met within cultivars growing in geographically distant locations.

Khan (1959) reported the high yielding capacity of cv. Rio de Janeiro. In a trial with 18 cultivars, the yield of Rio was double of that of cv. China under Kerala conditions (Thomas, 1966). Kannan and Nair (1965), Thomas and Kannan (1969), and Muralidharan and Kamalam (1973) also found that cv. Rio de Janeiro was superior to other cultivars with respect to yield; however the percentage dry ginger was lower than that of cv. Moran. Randhawa and Nandpuri (1970) evaluated 15 cultivars for four years, and reported that none could out-yield the local cultivar (Himachal) under the colder climate of Himachal Pradesh. Jogi et al. (1972) also reported that the local cv. Himachal produced the highest yield, followed by cv. Rio de Janeiro.

The trials carried out at Kasaragod under the All India Coordinated Research Project indicated the high-yield potential of cvs Rio de Janeiro, Burdwan, and Jamaica (AICSCIP, 1978). In Assam cv. Nadia out-yielded other cultivars (Aiyadurai, 1966).

Nybe et al. (1982) evaluated 28 cultivars for fresh and dry rhizome yield and noted significant differences among them. Fresh rhizome yield was highest in the case of cv. Nadia, followed by cvs. Moran, Bajpai, and Narasapattam. Cv. Nadia also gave the highest yield of dry ginger. Sreekumar et al. (1982) found that cvs Rio de Janeiro and Kuruppumpadi were the best yielders.

Muralidharan (1973) studied the varietal performance of ginger in Wynad, Kerala, and concluded that the cv. Rio de Janeiro gave the highest fresh ginger yield, whereas the dry ginger yield was lowest in this cultivar. Dry ginger yield was highest in cv. Tura. Cvs. Moran, Nadia, and Thingpui are the other high yielders and were more or less on a par with cv. Rio de Janeiro. This worker recommended cv. Rio for fresh ginger production and cvs. Moran, Nadia, and Thingpui for dry ginger production.

Evaluation and Selection for Quality

Jogi et al. (1972) evaluated 14 cultivars and reported that the fiber content ranged from 4.62 (cv. Poona) to 6.98% (cv. Narasapattam). Cv. Karakkal was lowest in dry recovery followed by cvs. Wynad local and Rio de Janeiro. Cv. Rio had the highest oleoresin, whereas cv. Karakkal had the highest oil. Crude fiber was least in cvs. Nadia and China.

Nybe et al. (1982) evaluated 28 cultivars and reported that cvs. Rio de Janeiro and Moran had the highest oleoresin content, 10.53 and 10.05%, respectively. Essential oil was highest in Karakkal (2.4%) and crude fiber was highest in Kuruppumpadi (6.47%).

Sreekumar et al. (1982) found that the dry ginger recovery ranged from 17.7% in cv. China to 28.0% in cv. Tura. Cultivars having more than 22% dry recovery (cvs. Moran, Jugijan, Ernad Manjeri, Nadia, Poona, Himachal Pradesh, Tura, and Arippa) are suitable for dry ginger production.

Breeding Strategies

Conventional Method: the Clonal Selection Pathway

The clonal selection pathway has been the most successful breeding method in the absence of seed set. The steps involved are: collection of cultivars from diverse sources and their assemblage in one or more locations, evaluation of cultivars for superiority in yield, quality or stress resistance, selection of promising lines, replicated yield trials in multilocations, selection of the best performer, its multiplication and testing in large evaluation plots and finally release. For a cultivar to be released, it should give a yield increase of 20% or more over the ruling standard cultivar (Figure 2.14). This strategy has been used successfully for evolving the present day cultivars, which have been developed mainly for higher yield adaptability and quality (Table 2.22).

Table 2.22 Elite cultivars developed and released

Cultivar name	*Pedigree*	*Mean yield t/ha*	*Dry recovery (%)*	*Oil content (%)*	*Oleoresin (%)*	*Crude fiber (%)*	*Mean days to maturity*
Suprabha	Selection from Kunduli local	16.6	20.5	1.9	8.9	4.4	230
Suruchi	Induced mutant of Rudrapur local	11.6	23.5	2.0	10.0	3.8	220
Suravi	Selection from germplasm	17.5	23.0	2.1	10.2	4.0	225
IISR Varada	Do	22.6	19.5	1.7	6.7	3.3	200
IISR Mahima	Do	23.2	23.0	1.7	4.5	3.3	200
IISR Rajitha	Do	22.4	19.0	2.4	6.2	4.0	200
Himgiri	Clonal selection from Himachal Local	14.0	20.6	1.6	4.3	6.0	230
Buderim gold[a]	Induced tetraploid of cv. Queensland Local	NA	NA	NA	NA	NA	NA
4x Sanshu[b]	Induced tetraploid of cv. Sanshu	NA	NA	NA	NA	NA	NA

[a]Developed by the Buderim Ginger Co., in Queensland, Australia. Reported to be high yielder, having plumpy rhizomes.

[b]Developed in Japan, reported to be high yielding, and is cultivated commonly. More information on yield and quality are not available.

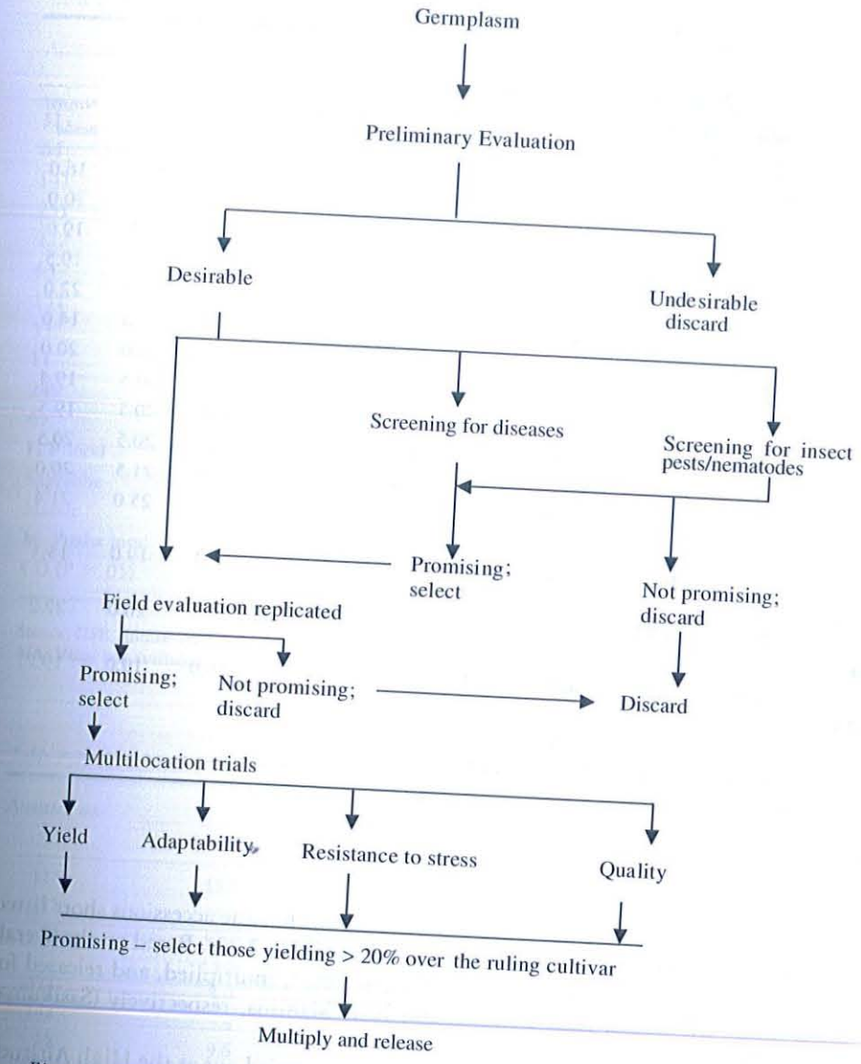

Figure 2.14 Breeding strategy—the clonal selection pathway.

The general breeding objectives in most breeding programs have been: high yield, high quality, resistance to fungal and bacterial pathogens, bold rhizomes, high dry recovery, and low fiber content. Resistance to *Pythium* (the causal organism for rhizome rot) and *Ralstonia solanacearum* (bacterial wilt pathogen) has so far not been encountered.

In one such selection program carried out at the IISR, Calicut, 15 cultivars short listed from germplasm evaluation were tested in replicated trials for four years in five locations (Table 2.23). This effort led to the selection of Varada, one of the most important ruling cultivars at present in south and central India (see Figure 2.14).

The data presented in Table 2.23 also demonstrate the influence of genotype–environment interaction. The quality characters of these accessions are given in Table 2.24.

Table 2.23 Yield and dry recovery of ginger at different locations

Accession Number	Mean fresh yield (kg/3 m² bed)					Dry recovery (%)			
	Peruvan-namuzhi	Muvatt-upuzha	Amaba-lavayal	Peechi	Niravi-lpuzha	Peruvan-namuzhi	Ambal-avayal	Peechi	Niravil-puzha
51	9.5	9.43	6.28	7.17	11.08	19.5	24.0	24.0	16.0
64	11.17	11.5	7.38	9.83	11.0	21.0	23.0	24.0	20.0
141	9.83	9.83	6.78	8.00	10.0	20.5	18.00	20.0	19.0
251	12.33	8.17	6.09	8.83	9.47	20.0	23.0	19.0	19.5
222	10.17	8.0	5.17	7.83	6.92	20.5	22.0	22.0	22.0
63	10.83	9.0	6.87	7.67	10.83	18.5	21.0	1.0	14.0
151	11.0	9.27	6.30	8.17	8.10	20.0	19.0	24.0	20.0
53	11.0	10.33	6.41	9.83	9.60	20.0	15.0	20.5	19.4
11	10.6	9.0	6.47	7.17	9.67	17.5	14.0	20.5	19.5
249	10.1	10.0	6.00	8.33	9.16	17.5	17.0	20.5	20.5
65	9.83	10.5	5.33	7.33	11.0	20.0	20.0	21.5	20.0
250 (Himachal)	10.17	10.5	6.10	8.16	10.23	21.0	22.5	25.0	21.4
293 (Suprabha)	11.17	9.67	7.25	7.83	11.28	18.5	15.0	19.0	15.1
295 (Maran)	10.17	8.83	7.23	9.0	7.36	21.5	19.0	20.0	22.2
252 (M puzha)	11.0	8.83	6.70	8.16	7.83	20.0	16.0	19.0	19.27
CD	0.62	0.51	0.54	0.745	0.90				
CV	47.48	17.19	11.27	12.1	12.6				

Source: IISR Annual report, 1994–1995.

In another trial for increasing the rhizome size, 15 bold rhizome accessions short listed from the germplasm were tested in multilocation plots (Table 2.25). Based on the overall superior performance, accessions 35 and 107 were selected, multiplied, and released for cultivation under the names IISR Rejatha, and IISR Mahima, respectively (Sasikumar et al. 2003) (Figure 2.15).

Clonal selection programs for crop improvement were carried out at the High Altitude Research Station in Potangi, Orissa, and at the Department of Vegetable Crops at the Y.S. Parmar University of Horticulture and Forestry in Solan (Himachal Pradesh). The former came out with the selections, Suprabha, and Suravi and the latter with the selection, Himgiri.

Mutation Breeding

Ginger is not amenable to any conventional recombination breeding programs due to its sterility. Induction of variability through mutations, chemical mutagens, ionizing radiations, and tissue culture (somaclonal variations) has been tried by a few workers (Gonzalez et al., 1969; Raju et al., 1980; Giridharan, 1984; Jayachandran, 1989; Mohanty and Panda, 1991; Nirmal Babu, 1997). The general scheme for a mutation

Table 2.24 Yield, dry recovery, and quality of promising ginger accessions at IISR

Accession no.	Quality		
	E. Oil (%)	Oleoresin (%)	Crude fiber (%)
51	2.1	6.8	5.7
64	1.9	6.0	5.4
141	1.9	6.5	4.0
251	2.4	9.0	6.6
222	2.0	7.0	3.9
63	2.3	7.0	4.9
151	2.0	7.0	6.0
53	2.5	9.9	5.1
11	2.0	7.0	4.0
249	2.4	9.0	3.5
65	2.7	8.0	5.3
H.P local	1.2	5.8	8.5
Suprabha	1.9	6.3	4.4
Maran	2.0	7.5	6.1
M. Puzha local	1.9	6.3	NA
CD ($P = 05$)			

Source: IISR Annual report (1993–1994).
NA: Value not available

Table 2.25 Yield and recovery of bold rhizome selections

Accession no.	1996		1997		1998
	Mean Yield (fresh)	Dry recovery (%)	Mean yield	Dry recovery (%)	Yield
117	13.5	22.0	9.9	25.5	11.0
35	14.7	17.5	11.9	21.2	14.7
49	12.3	22.0	10.3	21.3	9.3
27	13.0	22.0	11.3	26.3	11.8
3573	5.0	23.0	9.6	25.5	7.0
142	7.8	23.0	6.9	26.8	12.7
15	9.6	19.5	13.1	24.8	9.7
415	12.3	22.0	11.4	24.3	10.8
116	7.3	15.0	10.6	22.0	8.2
294	12.2	22.0	10.5	27.0	9.8
204	11.4	23.0	10.9	25.5	9.3
64	13.2	19.5	11.4	24.3	12.5
179	13.0	23.0	10.9	26.5	11.7
71	8.5	21.5	7.4	23.8	10.3
244	13.1	17.5	9.9	22.0	10.7
CD%	1.13	—	1.86	—	1.22

Source: IISR Annual Report (1997, 1998, 1999).

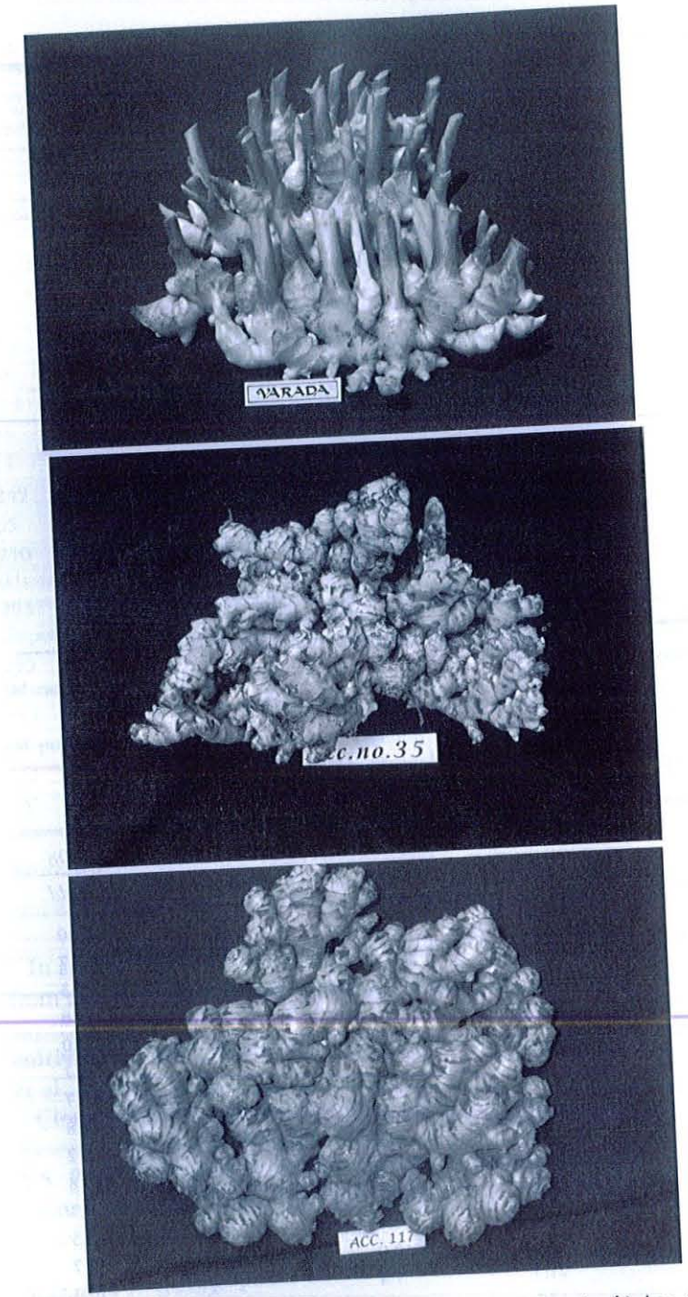

Figure 2.15 Improved selections of ginger (a) IISR Varada, (b) Acc. 117, (c) Acc. 35.

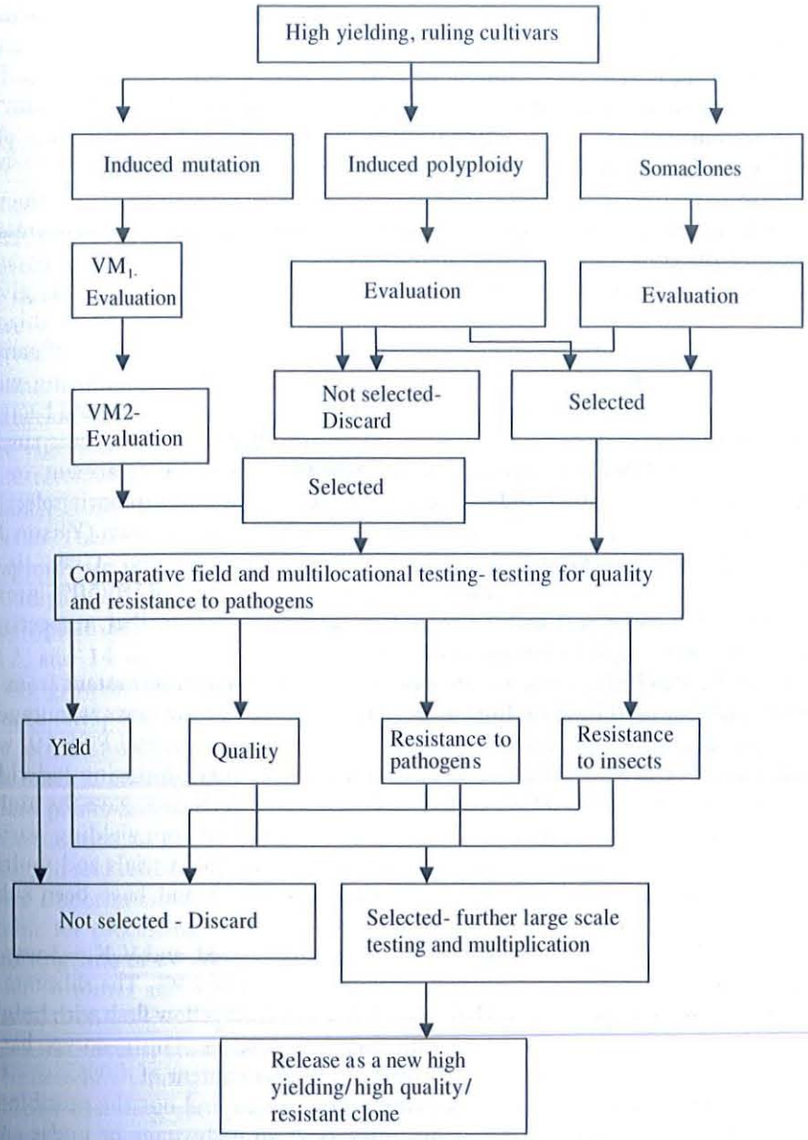

Figure 2.16 Breeding strategy—the unconventional pathway.

breeding program is given in Figure 2.16. Rhizome bits were treated with chemical mutagens or irradiated with gamma rays. Ginger buds are sensitive to irradiation and the LD_{50} was reported to be below 2 Krad. The LD_{50} (50% lethal dose) for germination was reported to be between 1.5 and 2.0 Krad (Giridharan, 1984). Jayachandran (1989) treated the cv. Rio de Janeiro with gamma rays at 0.5 to 1.5 Krads and Ethylmethane sulfonate (EMS) at 2.0 to 10.0 mM and studied VM_1-VM_3 generations with a view to isolate useful mutants. This study revealed that the percentage of sprouting, survival, and the height of plants decreased as the mutagen dose increased. The LD_{50} in the study

for sprouting and survival was between 0.5 and 1.0 Krad of gamma rays and below 8 mM of EMS.

Mutagen treatment affected tiller production; in 1.5 Krad gamma rays there was 45% reduction, whereas in 10 mM EMS there was 61% reduction in tiller production. The mutagen treatment did not affect pollen fertility or improve seed set. Rhizome yield was affected in a dose-dependent manner.

Jayachandran (1989) analyzed the VM2 generation and found a significant reduction in plant height as the dose increased. The mean tiller number indicated transgression to either side of the controls. Similarly, the mean rhizome yield in the VM2 generation indicated shifts in both the directions, with the lower doses of the mutagens giving positive shifts and the higher doses giving negative shifts. The variation in rhizome yield ranged from 1 to 1,320 g/plant. This same worker found that lower doses of gamma rays (0.5 and 0.75 Krad) and EMS (2 to 4 mM) are more effective in inducing wider variations. Screening against the soft rot pathogen, *Pythium aphanidermatum,* and bacterial wilt (caused by *Ralstonia solanacearum*) did not reveal any change in pathogenic susceptibility. Jayachandran (1989) observed that the effects of mutagen treatment in the subsequent generations vanished, indicating the operation of strong diplontic selection.

Nwachukwu et al. (1995) irradiated rhizomes of two Nigerian cultivars (Yatsun Biri and the yellow ginger Tafin Giwa) with 2.5 to 10 Gy gamma rays (Gy—Gray—is the unit of absorbed dose; 1 Gy = 100 rads). In these cultivars the GR50 (50% growth reduction) was found to be at 5 and 6 Gy in Tafin Giwa and Yatsun Biri, respectively, and LD_{50} was found to be 8.75 Gy for both cultivars.

Mohanty and Panda (1991) reported the isolation of a high-yielding mutant from the VM_3 generation. They used EMS, sodium azide, colchicine, and gamma rays as mutagenic agents and five cultivars (cv. UP, Rio de Janeiro, Thingpui, PGS-10, and PGS-19) were treated and studied in VM_1, VM_2, and VM_3 generations. Twenty promising individual clumps ("mutants") were selected for evaluation. One of them (V_1K_1-3) gave the highest yield of 22.08 t/ha, which was significantly higher than the top yielding variety, Suprabha. Six top yielders were further tested in comparative yield trials and multilocation trials—the results indicated the superiority of V_1K_1-3 and have been subsequently released for cultivation under the name Suravi.

The genotype differences were consistent over the locations tested, and V_1K_1-3 was out yielding the others in all locations. This line has a dry recovery of 23%. The rhizomes are plumpy with cylindrical fingers having dark glazed skin and dark yellow flesh with bulging oval tips and finger nodes that are covered with deep brown scales. This genotype has oil content of 2.1%, oleoresin content of 10.2%, and crude fiber content of 4.0%.

Tashiro et al. (1995) studied induced isozyme mutations to find out the possible use of isozyme analysis as markers for detecting mutants at an early stage or under an in vitro culture system. They used the cvs. Otafuku, Kintoki, and Shirome Wase and excised shoot tips were treated with 5 mM methyl nitrosourea (N-methyl-N-nitrosourea-MNU) for 5 to 20 minutes and cultured on MS medium supplemented with 0.05 mg NAA and 0.5 mg BA/l. Regenerated plants were analyzed for locating mutations in the following isozymes: glutamate dehydrogenase (GDH), glutamate-oxaloacetate transaminase (GOT), malate dehydrogenase (MDH), 6-phosphogluconate dehydrogenase (6-PGDH), phosphoglucomutase (PGM), and shikimate dehydrogenase (SKDH). Analysis of the untreated control gave uniform isozyme profiles for all the three cultivars. Five of 21 MNU-treated plants had isozyme profiles that differed from the basic pattern of GOT, 6-PGDH, PGM and SKDH. All these isozyme mutants expressed morphological variations such as multiple shoot formation, dwarfing, and abnormal leaves. The results indicated that treating shoot tips with MNU and then culturing them in appropriate media can recover mutants and that isozyme analysis is a good technique in detecting the mutation rate, and hence is useful in mutation breeding programs.

Polyploidy Breeding

Induced polyploidy has been tried in ginger for introducing variability, for improving pollen and ovule fertility, and for improving growth and yield. Ratnambal et al. (1979) reported induction of polyploidy in the cv. Rio de Janeiro through colchicine treatment. The tetraploids showed stunted growth and had reduced length and breadth of leaves. However, in this case a stable polyploid line could not be established and all the plants reverted to diploidy in the succeeding generations.

Ramachandran et al. (1982) and Ramachandran and Nair (1992) reported successful production of stable tetraploid lines in cvs. Maran and Mananthody. The polyploids were more vigorous than the diploids and flowered during the second year of induction. The stable tetraploid lines (2n = 44) had larger, plumpy rhizomes and high yield (198.7 g/plant). However, the essential oil content was lower (2.3%) than the original diploid cultivar. There was considerable increase in pollen fertility in the tetraploids. These tetraploids are maintained in the germplasm collection at IISR, Calicut.

Adaniya and Shirai (2001) induced tetraploids under in vitro conditions by culturing shoot tips in MS solid medium containing BA, NAA, and 0.2% w/v colchicine for 4, 8, 12, and 14 days and transferred the shoot tips to medium without colchicine for further growth. More tetraploids were recovered from buds cultured for eight days. Induced tetraploid line of the cultivars (4x Kintoki, 4x Sanshu, and 4x Philippine cebu1) were later transferred to the field where they flowered. These tetraploids produced pollen with much higher fertility and germinability than the diploid plants (0.0 to 1% in the diploid plants as against 27.4 to 74.2% in the tetraploids).

The commercial ginger company in Queensland, Australia, Buderim Ginger Co., has developed and released for cultivation a tetraploid line from the local cultivar. This line, named Buderim Gold, is much higher yielding and has plump rhizomes that are ideally suitable for processing (Buderim Ginger Co., 2003). Nirmal Babu (1996) developed a promising line of cv. Maran from somaclonal variants. This line is high yielding with bolder rhizomes and taller plants (Figure 2.17). In addition to somaclonal variation, other biotechnological approaches have been initiated for evolving disease-resistant genotypes (for details, see Chapter 4).

The breeding strategies currently in use will not be useful to solve many of the serious problems besetting the ginger crop. In spite of extensive search, no genes resistant to *Pythium* rot, *Fusarium* wilt, or bacterial wilt could be located in the germplasm. The absence of sexual reproduction and seed set imposes a severe constraint on our efforts to develop resistant cultivars. Recourse to biotechnological approaches may be useful. However, no effort is going on in this field in a concerted manner anywhere in the world. Resorting to r-DNA technology by using resistance genes to the target pathogen from other crop plants can be a viable alternative for evolving resistant ginger plants. Until such genetically modified ginger cultivars are available, one has to rely on disease avoidance through efficient phytosanitation, through crop rotation, and by the use of biocontrol organisms. However, the ginger breeders and biotechnologists around the world should put their brains together to evolve a future action plan to solve the difficult problems and constraints to which this crop is currently being subjected.

Figure 2.17 High-yielding somaclonal variant.

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