INTRODUCTION
Aerial roots, common in tropical plants, exhibit a wide spectrum of form, function and morphogenetic response (Fahn, 1974; Gill & Tomlinson, 1975; Kramer & Kozlowski, 1979). However, this interesting organ of the angiosperms has not attracted much attention. They have been defined from time to time by various authors (Hill et al. 1950; Dycus & Knudson, 1957) and yet no satisfactory definition is available. Recently, Gill & Tomlinson (1975) have recognised 3 types of aerial roots: i) roots arising from an aerial stem, but still embedded within, or enclosed by other plant tissues or organs, ii) roots which arise from an aerial (or even a subterranean) organ, become exposed, but remain appressed to some adjacent surface of the substratum, and iii) roots exposed to air for at least 50% of each day and free of any support or substrate; they may originate either above or below ground.

Aerial roots can be categorised into the following recognised types based on specific functions:
root thorns. The aerial roots which do not adhere to any one of the above types are reviewed and examined as miscellaneous type.

I.A. - Review of literature

I.A.1 - Studies on naturally growing aerial roots

I.A.1.a. Types of aerial roots:

(1) **Pneumatophores or breathing roots**: Generally, the pneumatophores are specialized, negatively geotropic aerial roots with plenty of lenticels found in the mangrove plants like *Avicennia*, *Sonneratia*, *Ceriops*, and *Laguncularia* which inhabit muddy swamps poor in oxygen (Venkateswarlu, 1974). They do not develop on plants growing on well drained soil (Jenik, 1967); though attributed to have aerating function, this may not be true for all species (Jenik, 1967; Gill & Tomlinson, 1975).

The pneumatophores of the mangroves exhibit variation in size, shape and structure (Scholander et al., 1955; Jenik, 1970; Venkateswarlu, 1974; Gill & Tomlinson, 1975; Sen, 1980; Snedaker et al., 1981), and develop either through localized secondary thickening or by an apical meristem on the upper surface of horizontal roots (Fayle, 1980). Although pneumatophores are characteristic of some mangroves, rarely, non-mangrove plants like *Elaeis* (Yampolsky, 1924), *Areca* (Bhavappa & Murthy, 1961; Davis, 1961;
Ghosh & Ghose, 1971; Davis et al., 1978; Phoenix (Davis, 1968), Eugeissona, Taxodium and Jussieua (Venkateswarlu, 1974) produce pneumatophores. The respiratory function of the pneumatophores has been experimentally demonstrated (Chapmann, 1944).

(ii) Stilt roots: Stilt roots are well-developed in species of Pandanaceae and Rhizophoraceae and to some extent in Poaceae (Venkateswarlu, 1974).

Stilt roots are aerial adventitious roots which may arise from and around the base of the trunk or lateral branch or even from anchored aerial roots (Gill & Tomlinson, 1977) and grow obliquely downwards into the ground and assist in the mechanical tensile support (Mc Lean & Ivimey-Cook, 1951; Venkateswarlu, 1974; Gill & Tomlinson, 1975). Often, owing to the decay of the lower part of the stem the stilt roots offer good support to the plant, covering large areas (Venkateswarlu, 1974). Gill & Tomlinson (1969, 1971, 1975, 1977) provide extensive information on the developmental, structural and functional aspects in the stilt roots of Rhizophora mangle.

The extent and size of the aerial roots, in species of Pandanus which arise from the base of the trunk
vary considerably from those arising from the branches (Gill & Tomlinson, 1975). These aerial roots lack secondary thickening and possess a many-layered root cap of several centimetres long, with the individual layers eventually becoming papery (Gill & Tomlinson, 1975). Nevertheless, Dutta (1968) considers the 'cap' as a multiple one although Periasamy & Gopal (1978) deem it to be pseudomultiple. In nature, these root caps may function as an important microhabitat for epiphytes and insects (Van Steenis, 1948).

(iii) Prop roots: Prop roots are aerial and particularly characteristic of various species of Ficus. Prop roots in the species of *Ficus benghalensis* and *F. benjamina* attain a considerable size. The morphology and anatomy (Kumar, 1944; Mohan Ram & Rustagi, 1964; Kapil & Rustagi, 1966; Zimmermann et al., 1968; Periasamy & Gopal, 1978), grafting (La Rue, 1952; Rao, 1966), and experimental studies (Mohan Ram & Rustagi, 1964; Periasamy & Gopal, 1978; Gopal, 1981) on the aerial roots of different species of *Ficus* appear significant.

In a broad sense, the stilt roots of *Pandanus* spp. and that of Poaceae members have been considered as prop roots (Fuller & Tippo, 1954; Haupt, 1956).
(iv) **Buttress roots:** Many tropical trees show remarkably well-grown buttress roots around the base of the trunk just above the ground. They are formed by the main roots, in which secondary thickening is asymmetrical chiefly on the upper side (Venkateswarlu, 1974). Though the buttress formation appears to be genetically determined, its actual expression seems to be regulated by the environment. It is not clear whether the excessive thickening on the upper surface of lateral roots starts when the root is completely buried in soil or only after the bark is exposed (Fayle, 1980). Buttresses tend to develop on the windward side, presumably lending support rather than providing compression as implied by the word 'buttress' (Grace, 1977).

(v) **Climbing roots:** Many tropical climbers, especially of the family Araceae, make use of clasping roots, which are ageotropic but respond negatively to light and are markedly sensitive to touch (McLean and Ivimey-Cook, 1951; Venkateswarlu, 1974). In addition to the underground root system, the aerial adventitious roots develop at the nodes and internodes. Nourishing roots (Venkateswarlu, 1974) or absorbing roots develop in addition to the short clasping roots in some cases and they directly grow downwards and eventually enter the soil. Aerial roots of both types are evidently modifications of one common
root-form. They differ from one another by the absorbing root possessing larger-lumened vessels and the clasping roots with more sclerenchymatous cells (McLean & Ivlimey-Cook, 1951; Venkateswarlu, 1974). The climbing roots of Heptapleurum venulosum (Thirumalachar et al., 1942), Scindapsus officinalis and Piper betle (Periasamy & Gopal, 1978), and Monstera deliciosa (Hinchee, 1981) have been investigated and reported.

(vi) **Tendrillar roots:** Venkateswarlu (1974) has cited the incidence of tendrillar roots in Vanilla aromatica, an orchid, which hang freely in air and on coming in contact with some object twine around. Ponnaiya (1982) has reported that the aerial root of V. planifolia adheres to the wall by means of two fleshy outgrowths developed on either side.

(vii) **Cortical roots:** Cortical roots occur in some monocotyledons (McLean & Ivlimey-Cook, 1951; Venkateswarlu, 1974; Gill & Tomlinson, 1975; Lamont, 1981). They originate in the pericycle of the stem and penetrate through the cortex forming a pseudocortex.

(viii) **Photosynthetic roots:** Photosynthetic roots occur in Orchidaceae (and also in Podostemaceae). In epiphytic orchids like Taeniophyllum and Angraecum fasciola, incidence of photosynthetic roots are known (Venkateswarlu, 1974).
Energy from aerial root photosynthesis is claimed to support the entire plant (Withner, 1959).

(ix) Nest roots of epiphytes: The nest roots are negatively geotropic, grow out of the substratum, and form nest-like masses. Humus gets accumulated in between the roots and the minerals essential for nutrition are absorbed by some of the branches. *Anthurium ellipticum*, *Oncidium altissimum*, and *Grammatophyllum speciosum* (Orchidaceae) are some examples for nest roots (Venkateswarlu, 1974).

(x) Epiphytic velamen roots: Velamen roots are a special kind of absorbing roots known in members of Orchidaceae, Amaryllidaceae and Araceae (Haberlandt, 1914; Solereider & Meyer, 1930; Engard, 1944; Shushan, 1959; Deshpande, 1960, 1961; Esau, 1965; Capesius & Barthlott, 1975; Barthlott and Capesius, 1975; Benzing et al., 1982). Velamen tissue originates from protoderm (Mulay et al., 1958) and the number of layers varies from 1-10 in different species (Mulay & Deshpande, 1959). The single layered velamen develops only by anticlinal divisions in the protoderm whereas the multilayered one develops by both anticlinal and periclinal divisions (Mulay & Deshpande, 1959).
(xi) **Aerial root thorns**: Generally, occurrence of aerial root thorns is rare in plants. Aerial root thorns are of determinate growth and have well-developed root caps, but the root apex ultimately gets aborted and become sclerified (Parija & Misra, 1933; Mc Lean & Iv IMey-Cook, 1951; Gill & Tomlinson, 1975). Parija & Misra (1933) in Bridelia, Mc Arthur & Steeves (1969) in Cryosophila cuagara, Jenik & Harris (1969) in a number of woody dicotyledonous members of Euphorbiaceae, Irvingiaceae, Burseraceae, Guttiferae, Loganiaceae, and Sterculiaceae, Gill & Tomlinson (1975) in Pandanus spp., Socratea sp., and Iriartea sp., have observed and described the aerial root thorns. Such roots have been used as natural graters in Panama (Mc Lean & Iv IMey-Cook, 1951) by aboriginal people (Gill & Tomlinson, 1975). Aerial root thorns have been implicated to be protective in function in palms (Uhl & Moore, 1973).

I.A.1.b. - **Abnormal position of aerial roots on plants**:

Occasionally, aerial roots develop on various types of unusual organs of plants. Ayyangar & Nambiar (1937) have observed aerial roots on the earheads of a *Sorghum* variety. There is an instance on record in which aerial roots arose from a wound in the leaf sheath of sugarcane (In : Ayyangar & Nambiar, 1937).
Krishnaswamy & Ayyangar (1941) have recorded the development of aerial roots on almost every node of *Eleusine* plants raised from X-rayed seeds. Jones & Pope (1942) have observed aerial roots in the panicles of X-rayed rice varieties called ——→Calora and Nira. Later, Butany & Nair (1959) recorded the occurrence of such roots in a hybrid variety (Ac 1780 x Ac 1765) of rice. Davis (1958) has reported the development of a cluster of 24 aerial roots from the callus region on the internode of a sugarcane variety, Co 302. Mohan Ram & Nayyar (1974) have recorded the unusual occurrence of aerial roots, in cluster, along with the foliage and the scale leaves, in the axils of petals of a few flowers of *Nymphaea mexicana*. Periasamy & Gopal (1978) and Snedaker et al. (1981) have observed the anomalous development of positively geotropic aerial roots from the trunk of *Avicennia officinalis* and *A. germinans*, respectively.

**I.A.l.c. Fasciation in aerial roots:**

Information regarding fasciation in aerial roots is scanty (Worsdell, 1905; Kumar, 1944; White, 1948; Gill & Tomlinson, 1977; Unni & Philip, 1978 and Gopal & Lakshmanan, 1981).
Gopal & Lakshmanan (1981) reported the occurrence of fasciation in the aerial roots of *Cissus quadrangularis*, *Dracaena* sp., *Ficus benjamina*, *F. benghalensis*, and *Vernonia* sp. They have also classified the root fasciation into stable and unstable types. While the fasciated condition is retained permanently throughout the ontogeny in the stable type, it reverts to the original cylindrical condition in the unstable type.

Subsequently, Gopal & Lakshmanan (1982) have demonstrated the existence of eccentric stele in the fasciated aerial roots of *Impatiens balsamina*. The varied number of vascular bundles in transverse sections at different levels of the same fasciated roots has been attributed to frequent forking and fusion of vascular strands. The unequal distribution and activity of the periblem cells are supposed to be responsible for the eccentric position of the stele.

I.A.1.d. Aerial root grafting:

Root grafts have been reviewed by Graham & Dornmann (1966) and natural grafting has been reported to be frequent in the aerial roots (La Rue, 1952; Rao, 1966). However, artificial grafting on aerial roots is wanting.
I.A.l.e. Ecology of aerial roots:

Regarding the phytogeographical distribution of aerial roots, Sen (1980) suggests that though they are predominantly distributed in tropics, they also occur in extra-tropical regions. Place of emergence, longitudinal growth, biotic and a variety of environmental factors are known to affect the general distribution and entire system of aerial roots.

I-A.l.f. Apical organisation in aerial roots:

Although, quite a number of reviews (Guttenberg, 1960, 1961; Clowes, 1961, 1967; Esau, 1965; Pillai, 1972) are available on the apical organisation of radicular and underground roots, there is a dearth of information on the apical organisation in aerial roots. Nonetheless, few reports are available on apical organisation in aerial roots. While Turner (1934) has described three distinct sets of initials in the aerial root apex of *Vitis rotundifolia*, Shah et al. (1977) have reported a common group of initials in *Cissus quadrangularis* in the same family Vitaceae. Popham & Henry (1955) have observed separate sets of initials for stele and cortex and a common source of initials for epidermis and root cap in the aerial root apices of *Kalanchoe fedtschenkoi*. 
Recently, Periasamy and Gopal (1979) have brought out five different types of apical organisation in the aerial roots of eleven species of both monocotyledons and dicotyledons. The two types of aerial roots, positively geotropic and negatively geotropic, of *Avicennia officinalis*, exhibit the same type of apical organisation namely transverse meristem. In this species, there is no clear demarcation between root body and root cap. However, a columella is distinguishable at the distal end enclosed by a continuous cork. *Piper betle*, *Tinospora cordifolia* and *Pandanus odoratissimus* exhibit a transverse meristem at the aerial root apices. *Duranta plumieri* shows triangular common source of initials. A third type of organisation is that, where a single layer of initials is present e.g. *Combretum ovalifolium* and *Vernonia noveboracensis*. An inverted cup-shaped promeristem occurs in the aerial root apices of *Ficus benghalensis* and *Scindapsus officinalis*. A three-layered organisation is the fifth type represented in *Saccharum officinarum* and *Sorghum vulgare*, with three separate sets of initials - one for stele, another for root cap and the third a common source for cortex and epidermis.

**I.A.1.g. Tissue differentiation and organisation in aerial roots:**

Tissue differentiation and organisation have been studied, either singly or together, in the aerial

I.A.I.h. Root hairs:

It is well documented that root hair is an epidermal cell of the root that undergoes tubular elongation, (Haberlandt, 1914; Fitting et al., 1930; Eames & MacDaniels, 1947; Foster, 1949; Esau, 1965, 1977; Cutter, 1969; Fahn, 1974; Russell, 1977) at right angles to the surface of the root (Cormack, 1962). Root hairs are confined to a definite region on the root where elongation has ceased. However, root hairs are not present in all plants (Venkateswarlu, 1974). Several significant reviews (Snow, 1905; Cormack, 1949, 1962) on root hairs in general are available.
Various external and internal factors influence the development of root hairs. The role of the external factors, moisture (Schwarz, 1883; Snow, 1905; Farr, 1925a, b, 1928a,b,c,d,e; Farr, 1927; Cormack, 1935, 1944, 1949), temperature (Snow, 1905), light (Wilson, 1936, Cormack, 1937; King, 1943; Dale, 1951), Calcium (Cormack, 1949), pH (Farr, 1928a,b,c; Cormack, 1935) and growth regulators—IAA (Cormack, 1949), 2,4-D (Mohan Ram & Rustagi, 1964; Rao, 1972), GA₃ (Rao, 1972) and ethylene (Cormack, 1937) on the induction of root hairs has been studied.

Cormack (1947) stresses on the degree and extent of vacuolation in the epidermal cells that decide the ability to develop root hairs. There is a general notion (Kapil & Rustagi, 1966; Hinchee, 1981) that root hairs are absent on the aerial roots. On the contrary, Vijayaraghavan and Rao (1938) in Sorghum sp., Thirumalarchar et al. (1942) in Heptapleurum venulosum, Banerji (1943) in Plumeria acutifolia, Rao (1966) in Ficus globosa and Lamont (1981) in Kingia australis have observed root hairs on the aerial roots.

Popham & Henry (1955) and Gopal (1981) have reported multicellular root hairs on the aerial roots of several species of Kalanchoe. By changing the environment the aerial root epidermis of Kalanchoe has been made
to develop different types of root hairs or none (Gopal, 1981). Flask-shaped, club-shaped, spiral, circinate and variously branched abnormal hairs are also observed by Gopal (1981).

I.A.1.1. **Comparison between the aerial and underground roots:**

The anatomy of the aerial roots has been compared with that of the subterranean roots of the following plants: *Ficus benghalensis* (Kapil & Rustagi, 1966), *Cucurbita maxima* (Mandakini & Subrahmanyam, 1975), *Rhizophora mangle* (Gill & Tomlinson, 1975, 1977) and *Selaginella kraussiana* (Grenville & Peterson, 1981).

I.A.2. **Experimental studies on aerial roots:**

Very little information appears to be available on experimental studies on aerial roots.

I.A.2.a. **Induction of aerial roots:**

Aerial roots have been induced around the trunk of *Cocos nucifera* by heaping soil-manure (Menon et al., 1955). Gill & Tomlinson (1975) have induced aerial roots in *Ficus platyphylla* by ringing a branch. They have also been induced by applying chemicals -
Potassium naphthaleneacetate in *Kalanchoe daigremontiana* (Zimmerman & Hitchcock, 1937), NAA in *Nicotiana tabacum* (Bangarayya & Pal, 1965) and NAA and TIBA in orchids (Goh, 1983).

I.A.2.b. **Induction of buds on roots:**

As early as 1928, Sabnis succeeded in inducing root buds on root cuttings in soil medium. It is clear from the review (Peterson, 1975) that shoot buds have been induced in underground roots of the aerial roots. Recently, Rao & Mohan Ram (1981) have induced shoot buds from the roots of *Limnophila indica* under *in vitro* conditions. But no report is available on the induction of buds in aerial roots of any category.

I.A.2.c. **Induction of root fasciation:**

Though several reports on the experimental induction of fasciation in underground and radicular roots are available (Allsopp, 1952; Mohan Ram & Satsangi, 1963; Dunlop & Schmidt, 1964, 1965; Rao, 1972; Balasundaram, 1980; Gopal & Lakshmanan, 1981), there are only very few instances on induced fasciation in aerial roots (Shah et al., 1977; Gopal & Lakshmanan, 1981).
Eventhough, the word fasciation has not been used by the authors, root fasciation has been observed in their experimental studies by Dunlop & Schmidt (1964, 1965) and Shah et al., (1977).

I.A.2.d. Surgical experiments on roots:

Surgical manipulation has been performed (Lopriore, 1892; Clowes, 1954; Kadej, 1956; Pillai & Sachdeva, 1960; Pillai & Pillai, 1962; Periasamy & Gopal, 1978; Sivaramakrishna & Vijayaraghavan, 1979) on the root apices (including aerial roots) of various plant species to probe into the structure, activity and regenerating potentiality of the apical meristem.

I.A.2.e. Induction of laterals on aerial roots:

The aerial roots, in general, do not produce branches unless the tip is injured or pierced into the soil (Srivatsava, 1951; Gill & Tomlinson, 1975; Hinchee, 1981). However, laterals on the aerial roots of various plant species have been induced by severing the growing tip of roots (Moore, 1933), main stem (Goh & Sung, 1978) or by applying growth substances (Zimmerman & Hitchcock, 1935, 1937; Pfeiffer, 1937).
I.A.2.f. The effect of various chemicals on the aerial roots:

Only very few attempts have been made to study the histomorphological effects of various chemicals on the aerial roots of different plants. Contributions of Zimmerman & Hitchcock (1935, 1937), Pfeiffer (1937), Mohan Ram & Rustagi (1964), Shah et al. (1977) are significant in this respect.

I.A.2.g. The effect of different environments on the structure of the aerial roots:

Gill & Tomlinson (1977) have studied the effect of water, sand or mud on the structural features of the aerial roots of Rhizophora mangle.

I.B. Scope of the present investigation

Metcalf (1972) feels that after completing a detailed survey of a restricted number of species, there is always a danger that we may jump to the conclusion that our findings will apply equally to other groups of organisms that we have not actually examined, only to find that this is not necessarily so when taxonomically wider investigations are subsequently undertaken. So, in order to arrive at some useful and valid conclusions,
aerial roots of about 73 plant species from a broad spectrum of families of angiosperms have been investigated.

In spite of a large number of tropical plants exhibiting a remarkable pattern of aerial roots, only some of them have been investigated from the viewpoint of their morphology, anatomy, physiology and ecology. While the aerial roots of certain plant species have been repeatedly studied, the aerial roots of the others, particularly of annuals and the perennials which develop aerial roots seasonally, have been escaping attention.

Observational studies record the results of Nature's own experiments. Natural experiments are often more difficult to interpret than those designed by man, because the number of interdependent influences that are simultaneously operating on the organisms under observation (Metcalf, 1972). So, some experiments on aerial roots were designed in order to get a better insight into the structure and behaviour of the aerial roots.

The present work carried out over the last seven years on various aspects of aerial roots of about 73 plant species reports the following.

2. Anatomy of aerial roots - a) apical organisation, b) primary tissue differentiation and organisation, c) secondary growth d) structure of abnormal forms of aerial roots and e) development of laterals.

3. Experimental investigations - a) to induce aerial roots, root hairs, grafting, shoot buds and laterals on aerial roots. b) to have a comprehensive idea about the influence of the environmental factors on aerial roots. c) to study the effect of chemicals and magnetic field and also to assess the morphogenetic potentiality of the aerial roots by surgical manipulations.