Ecological Importance of Ectomycorrhizae in World Forest Ecosystems.

Pragya Agarwal* and Pankaj Sah**

*Department of Botany, Kumaun University, Nainital-263002, Uttarakhand State, India.

**Department of Applied Sciences, Higher College of Technology (HCT), Muscat, Sultanate of Oman.

pragya_ntl@yahoo.com
pankaj@hct.edu.om, drpankajsah1@gmail.com
drpankaj_sah2002@yahoo.com

Abstract: During the last two decades, mycorrhizal research has received much attention and studies on plant-fungus mycorrhizal association have indicated that applied work on this research may compliment the so called *"green revolution"* to increase plant yield through the use of modern technology. Long-term productivity is measured in terms of sustainable ecosystem processes that maintain fertility and the over all *"ecosystem health"* as well as recovery after adverse disturbances. Over the last several decades in Indian Central Himalaya due to a variety of uncontrolled uses, *Quercus* species are heavily lopped, and grazed resulting in a poor stocking density, poor regeneration and eventually elimination. The forest cover is shrinking significantly. A number of environmental condition (moisture, mineral, nutrients, pollutants) and biological factors (interaction with the soil organisms) affect the root development and ectomycorrhizal formation. In this paper we have explained the ecological benefits of mycorrhiza to the Himalayan Forest Ecosystems and their role in rejuvenating the Himalayan forests. Now-a-days most research on inoculation with ectomycorrhizal fungi has been based on two working premises. First, any ectomycorrhizal association in tree seedlings is far better than no such association at all. Secondly, some species of ectomycorrhizal fungi have proven to be more beneficial to trees under certain environmental conditions than others. [Nature and Science. 2009;7(2):107-116]. (ISSN: 1545-0740).

Keywords: Ectomycorrhizae, Himalaya, Forest Ecosystems.

Introduction: Botanically, the mycorrhiza is a mutualistic association (non-pathogenic association) between soil borne fungi and the root of the higher plants. The term mycorrhiza *(Gr. Mykes=Fungus or Mushroom; Rhiza=Root)* i.e. *"Fungal Root"* was coined by the German Pathologist (Frank 1885) to describe the union of two different beings to form a single morphological organ in which the plant nourishes the fungus and fungus does the same for the plant. Mycorrhiza confers many attributes to plants such as growth stimulation due to increased nutrient uptake, tolerance of plants to adverse conditions and bio-control of root disease (Molina *et al.,* 1992).

The mycorrhizal symbiosis between plant roots and fungus is essential for the survival of both the partners (Harley and Smith, 1983) and it has been suggested that this symbiosis was a prerequisite for the successful colonization of the terrestrial environment by plants some 400 million years ago (Pyronzinski and Mallock, 1975). The term mycorrhiza describes a range of symbiotic structures formed between the fine root and different fungi.

Being highly specialized in their nutritional requirement, the mycorrhizal fungi obtain simple sugars, amino acids and plant growth substances from the host for growth & development. Mycorrhizae also benefit the host directly by influencing important ecosystem properties such as soil structure (Finley and Söderström, 1992). The biological requirement of many forest tree species in respect of the ectomycorrhizal association was initially observed when attempts to establish plantation of exotic pines routinely failed, and this could only be overcome by the introduction of symbiotic fungal associates (Gibson, 1963; Madhu, 1967). Thus mycorrhizae should be regarded as an integral part of the natural and normally functioning root system of plants, taking part in symbiosis and function as dynamic biological linkages.

Types of Mycorrhizae:

In early days, mycorrhizae were classified into two main groups, based upon the structure of the root fungus association, namely endomycorrhizae and ectomycorrhizae (Payronel *et al.*, 1969), which were subsequently renamed as endotrophic for endomycorrhizae and ectotrophic for ectomycorrhizae. The latest classification of mycorrhizae has seven groups, namely *Vesicular-Arbuscular Mycorrhizae* (VAM), *Ectomycorrhizae*, *Ectendomycorrhizae*, *Arbutoid mycorrhizae*, *Monotropoid mycorrhizae*, *Ericoid mycorrhizae* and *Orchid mycorrhizae* (Harley and Smith, 1983).

Morphologically several distinct types of mycorrhizae have been described to be associated with a particular vegetation type (Fig. 1).

(1) Vesiular Arbuscular Mycorrhizae (VAM): In the first group Vesicular Arbuscular Mycorrhizae (VAM) belonging to the fungal order Endogonales of the Zygomycetes with aseptate hyphae (lower fungi) has been included. In the other six groups the endophytes are fungi with septate hyphae (higher fungi) belonging to Ascomycetes or Basidiomycetes. In all these mutualistic types, the mycorrhizal association contributes significantly to the host health, in exchange for photosynthates (Barker *et al.*, 1998).

The most common VAM (vesicular arbuscular mycorrhiza) found in the most herbaceous and graminaceous species. These fungi belong to the family *Endogonaceae*. Vesicular arbuscular mycorrhizal association generally lacks specificity. Individual species of VAM fungi can associate with diverse plants groups from herbs to long-lived woody perennials. Similarly, VAM plants often associate with many VAM fungi. (Molina 1979) found *Festuca* spp. associated with 11 species of Endogonaceae in habitats scattered over the Western United States. Repeated failures to isolate and grow aexenic cultures of VAM fungi indicate the obligate nature of VAM fungi. VAM plants, on the other hand, range widely from facultative to obligate dependency on mycorrhizal association. Many facultative plants are VAM in some ecological settings but may lack mycorrhizae in others (Trappe, 1987).

(2) Ericoid mycorrhizae: Ericoid mycorrhiza develops on the members of Angiospermic order Ericales (*Ericoideae*, *Vacciniodeae* and *Rhododendroidae* of most *Ericaceae* as well as *Epacridaceae* and *Empetraceae*). A septate fungus forms intracellular coils, restricted to the epidermal cells. Each epidermal cell is colonized individually with little change in root morphology. These fungi seem to have broad host range among ericaceae plant family and are restricted to these.

(3) Monotropoid mycorrhizae: Monotropoid mycorrhizae are associated with achlorophyllous members of the *Ericaceae family* (the *Monotropoideae*). The fungi involved in this relationship often have narrow host range. Monotropoid hosts thus appear to share wide receptivity similar to arbutoid hosts, most certainly an ecological advantage given the proven dependency of achlorophyllous plants on carbon of mycorrhizally linked EM plants (Bjorkman, 1960; Furman & Trappe, 1971).

(4) Arbutoid mycorrhizae: Arbutoid mycorrhizae belong to two genera of plant family Ericaceae and these genera are *Arbutus* and *Arctostaphylos.* These mycorrhizae resemble ectendomycorrhizae in that their hyphae colonize both intercellularly and intracellularly. The fungi that form arbutoid mycorrhizae on *Arbustus* and *Arctostaphylos* also form EM on other hosts (Molina and Trappe, 1982a; Zak, 1976a, b). Ericoid mycorrhizae and EM may also occur on Arbutoid hosts (Largent *et al.*, 1980; Mejstrik & Hadac, 1975; Trappe, 1964; Zak, 1973, 1974).

(5) Orchid mycorrhizae: Orchid seeds germinate only when infected with endomycorrhizal fungi that subsequently colonize the entire plant (Harley, 1969). Specificity patterns in Orchid mycorrhizae are complicated in that two types of colonization may occur: primary, involving the germinating seed and seedling and secondary, involving new roots (Harley & Simth, 1983).

(6) Ectendomycorrhiza: An intermediate type of mycorrhizal association is also found on coniferous and deciduous trees in nurseries and burned forest sites. The ectendomycorrhiza type forms a typical EM structure, except the mantle is slight or missing and hyphae in the *"Hartig net"* may penetrate root cortical cells. The ectendomycorrhiza is replaced by EM as the seedling matures. The fungi involved in the association were initially designated *"E-strain"* but were later shown to be ascomycetes and placed in the genus *Wilcoxina*. (Sylvia *et al.* 2005).

(7) Ectomycorrhizae: The most important type of mycorrhizal association found in temperate regions is known as Ectomycorrhizae (sheathing mycorrhiza). The ectomycorrhizae characteristic of all colonize temperate to boreal forest trees, are also present in the tropical forest trees. In Central Himalaya, ectomycorrhizal tree species are dominant in most of the forests along an elevation gradient from foothills to the timberline. Most of the ectomycorrhizal fungi belong to Basidiomycetes; some also belong to Ascomycetes. These fungi occur naturally on the plants belonging to some families of angiosperms viz. Dipterocarpaceae (e.g. *Shorea robusta*) and Fagaceae (e.g. *Quercus leucotrichophora* and other spp.). Most of the conifers are also associated with these fungi including all species of the family Pinaceae (e.g. *Pinus roxburghii*). Strict host specificity is rare and one plant may form mycorrhizal associations with different fungi simultaneously. Such sheathing mycorrhizae forming fungi are bio-tropic in their host relationship and ecologically obligate parasites in their mode of carbon (energy) nutrition.

In this mycorrhizal symbiosis the fungus grows into the root of the host plant and the hyphae penetrate between outer cortical cells, forming a typical structure called the "Hartig net". On the root surface the fungus forms a mantle or sheath, a structure, typical of ectomycorrhizae. This structure is typically connected to the hyphae or hyphal aggregates, which penetrate the surrounding soil and often form extensive mycelium. In this way, the mycorrhizal roots acquire access to a much greater soil volume in contrast to uninfected ones and therefore the effective surface area for nutrient absorption is greatly increased. The infected feeder roots undergo morphogenesis. These may be forked, unforked, bifurcated, nodular, multiforked or coralloid. The ectomycorrhizal roots can be distinguished from non-mycorrhizal roots.

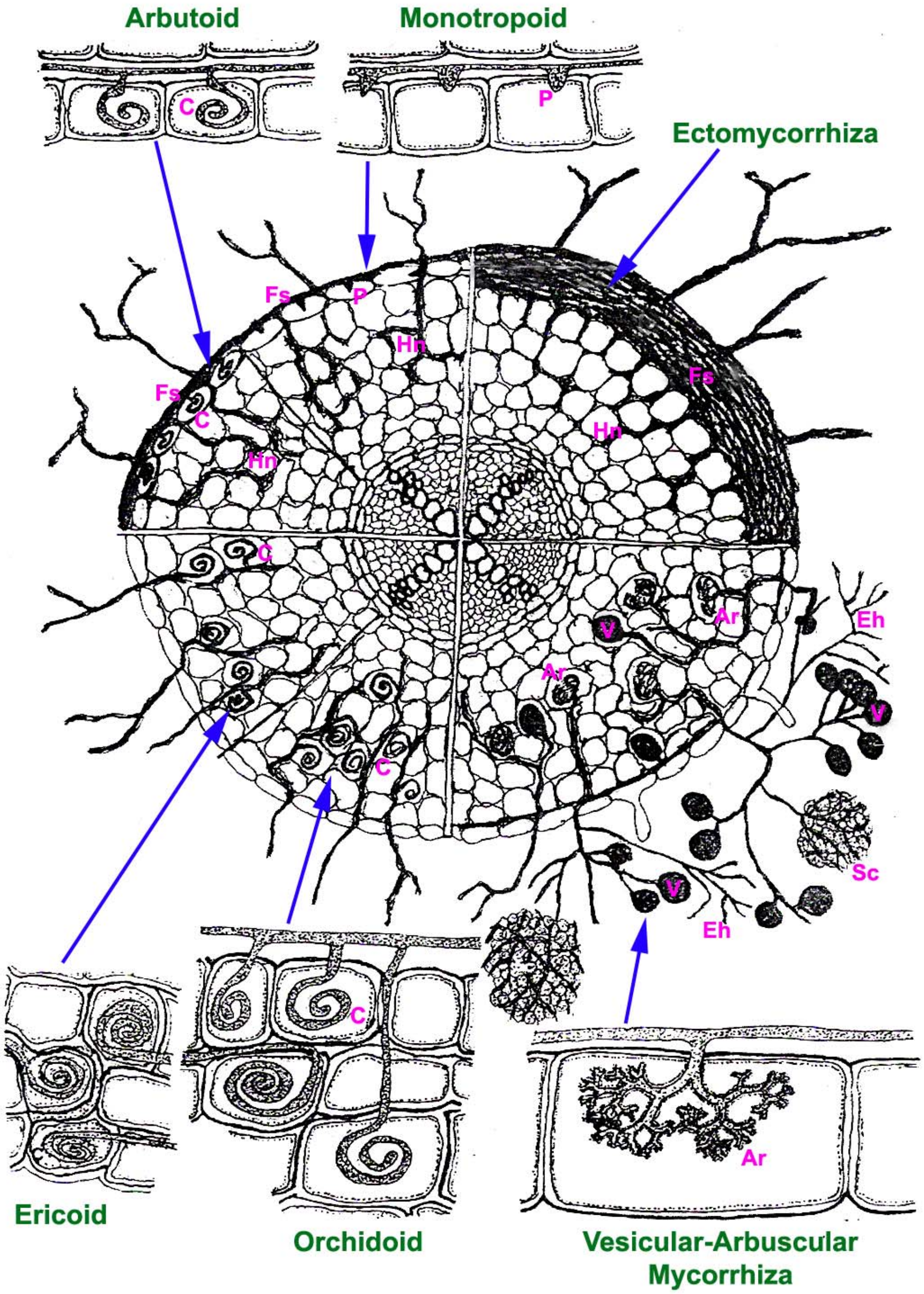

Fig. 1 Diagrams showing different types of mycorrhizae (derived from Mycorrhial Biology by K.G. Mukherji, B.P. Chamola and Jagjit Singh). **Ar** = Arbuscules, **C** = Coiled hyphae, **Eh** = Extrametrical hyphae, **Hn** = Hartig net, **Fs** = Fungal sheath, **P** = Protrusion, **Sc** = Sclerotia, **V** = Vesicles.

Importance of Ectomycorrhizae: Ectomycorrhizal symbiosis is important on a global scale because the dominant trees in most of the world's temperate and boreal forests and in large areas of tropical and subtropical forests are ectomycorrhizal (Allen, 1991; Read, 1991). It is more prevalent in temperate and sub-temperate region than in tropical and sub-tropical region where soil acts as a more important storage compartment for the minerals nutrient and the climatic conditions lead to restricted vegetative activity (Meyer, 1973). Pinaceae and Fagaceae, which dominate temperate forest together with members of Myrtaceae and Dipterocarpaceae from sub-tropical region, are the predominant ectomycorrhizal families (Smith and Read, 1997). It is considered that nearly 95% of wild flora is characteristically mycorrhizal (Barker *et al.,* 1998), although mycorrhizal status has been examined for only about 3% of the total (Smith and Read, 1997). Though the majority of plants show VAM symbiosis, the plants of temperate region are predominantly ectomycorrhizal. Thus ectomycorrhiza is always an integral component of forest ecosystem showing mutual dependency between fungus and the higher symbiont for natural function and survival.

There are over 5,000 fungi belonging to Basidiomycetes, and Ascomycetes involved in forming ectomycorrhizae on about 2,000 plants. However, about 2000 fungi could form ectomycorrhizae with Douglas-fir alone (Trappe, 1977). Already 400 taxa of ectomycorrhizal fungi, mostly belonging to *Russulaceae*, *Boletaceae*, *Canterallaceae*, *Amanitaceae* and *Cortinariaceae* have been described from African forest and woodland, and similar number is likely to be reported in future (Castellanio *et al.,* 2000).

Among the fungi belonging to Basidiomycetes, species of Hymenomycetes such as *Boletus*, *Cortinarius*, *Suillus*, *Russula*, *Gomphedries*, *Hebelema*, *Tricholoma*, *Laccaria*, and *Lactarius* and species of Gasteromycetes, e.g. *Rhizopogon*, *Scleroderma*, *Alpara*, and *Pisolithus* form ectomycorrhizae. Certain orders of the Ascomycetes such as, Tuberales and Pezizales have species that also form ectomycorrhizae (Marx, 1991). The importance of mycorrhiza for Pines and Oaks was clearly experienced when these species were planted in the tropics or in grasslands, where the particular types of fungi that they required were not present (Mikola, 1973). Without their fungal species, seedlings did not survive, or even if they grew, they could not perform well (Shemakhanova, 1967). It is reported that trees planted on highly disturbed areas receive high mortality unless given the proper mycorrhizal fungus (Marx, 1991; Singh. 2001). Review of mycorrhizal specificity commonly emphasizes a "lack of specificity" in mycorrhizal associations, i.e., there is no known example of gene-for-gene level of host fungus specificity (Molina *et al.,* 1992).

Numerous studies on the beneficial effects of ectomycorrhizal fungi on seedling growth and development in artificially regenerated forest sites and drastically disturbed land have been conducted (Marx *et al.,* 1991).

The Himalayan region can be divided into three zones on the basis of altitudinal variation, *viz*. Sub-Tropical, Temperate and Alpine representing a variety of forest types (Champion & Seth, 1968; Tewari, 1982; Adhikari *et al.,* 1989; Singh *et al.,* 1994) from the dry tropical deciduous in the foothills to the alpine scrub forest (Adhikari *et al.,* 1989; Garkoti, 1992) near the timberline. Himalayan belt can be divided into three regions Western, Eastern and Central. The Himalayan region of Uttaranchal comprises of about 50,000 km^2 and is often referred to as the Indian Central Himalaya.

The fungal diversity of local region is poorly known in India as well as in the Himalayan region. A few preliminary studies done in these forest sites basically deal with the symbiosis rather than the function of ectomycorrhizae in the forest ecosystem (Dubey *et al.,* 1998; Ginwal 1994) used soil inoculum for introduction of mycorrhizal fungi in *Quercus leucotrichophora* seedlings in nurseries. Recent researches conducted in glass-house experiments from Indian Central Himalaya also showed significant increase in root: shoot ratio and plant biomass in mycorrhizal seedlings as compared to uninfected once (Pande, 2003; Agarwal, 2007).

The importance of mycorrhizae for the Dipterocarp forest ecosystem and its management has only recently been realized. (Smits 1983) suggested that ectomycorrhizae might play an important role for successful regeneration after logging in lowland dipterocarp forests; much more attention was paid to the ecological aspects of dipterocarp ectomycorrhizae. Only a few studies concerning ecological aspects of mycorrhizae in dipterocarp forest ecosystems have been undertaken so far (Becker, 1983; Smits, 1983, 1994; Yasman, 1993). Dipterocarp are among the few species in the tropical forests of which the seedlings can survive and grow under very low light intensities on the forest floor, and may be benefited from interaction of their root system with a mature tree through ectomycorrhizal connection as described for other plants.

Based on the degree of dependency of plant species on mycorrhizae, plants can be grouped into three categories namely Non-Mycorrhizal, Facultative Mycorrhizal and Obligate Mycorrhizal (Bagyaraj, 1989). A number of studies confirm that dipterocarp species are obligatory ectomycorrhizal (Noor and Smits, 1988; Oman, 1994; Smits, 1994). The poor development of ectomycorrhizae on roots of dipterocarps explains the poor regeneration of dipterocarp trees on former skid roads and open areas (Smits, 1983; Julich, 1989; Smits, 1994). For instance, suggested that low availability of phosphorus in the soil and lack of season in a tropical soil might cause tropical species to depend upon mycorrhizal activities for survival and growth (Janos 1985).

Different types of mycorrhizal symbiosis may have different threshold of carbohydrate level. Ectomycorrhizal fungi may require more photosynthetic products (Carbohydrates) from their host than VA-mycorrhizal fungi from similarly dependent hosts for one of the following reasons- first because of a greater biomass of fruiting bodies, hyphae and rhizomorphs in ectomycorrhizae than in VA-mycorrhizae, hence a higher carbon cost if equal hyphae respiration rates of ectomycorrhizal and VA-mycorrhizal fungi are assumed; second, ectomycorrhizal fungi are a stronger sink for photosynthetic products than VA-mycorrhizal fungi, because ectomycorrhizal fungi produce plant hormones that influence translocation of carbon compounds, and convert the host sugars into storage sugars. Therefore in the forest ecosystem when the ectomycorrhizal species predominate as in dipterocarp forest, the role of ectomycorrhizae in the carbon allocation of the ecosystem is expected to be of primary importance (Yasman, 1995).

Much of the information on ectomycorrhizal fungi associated with temperate forest is based on research undertaken on the Northwest Pacific forest of America. Some of the important studies pertaining to the species richness of ectomycorrhizal fungi of forest North America include: spruce and hard wood forest of West Virginia (Bills *et al.,* 1986) and lobally pine (Cibula and Overvo, 1988) and Alder forest in Alaska (Brunner *et al.*, 1992). These forests are characterized by summer dry conditions, most of the area dominated by conifers; in contrast, the climate of Himalayan area has a characteristic monsoon that provides a different situation, such as broadleaf species rather than conifers dominating much of the area. As a result, difference in vegetation and climate would influence the ectomycorrhizal diversity in this region. In India, emphasis is being laid on boosting the afforestation programme in hills, particularly species of *Quercus* (Ginwal, 1994).

Authors for correspondence:
Pragya Agarwal
Department of Botany, Kumaun University, Nainital-263002, Uttarakhand State, India.

Pankaj Sah
Department of Applied Sciences, Higher College of Technology (HCT), Muscat, Sultanate of Oman.

pragya_ntl@yahoo.com
pankaj@hct.edu.om, drpankajsah1@gmail.com
drpankaj_sah2002@yahoo.com

References:

Adhikari, B.S., Ram, J., Sharma, S. and Bhatt, Y.D. 1989. Quantitative vegetational analysis of forest between 2000-3300m altitudes in Nanda Devi Biosphere Reserve. In: Singh, S.P. (ed) *Pattern of soil and vegetation and factors determining their forms and hydrological cycle in Nanda Devi Biosphere Reserve*. First Annual Report, Govt. of India, New Delhi, pp, 7-29.

Agarwal, P. 2007. Ectomycorrhizal Fungi in Three Major Forest Types in Central Himalaya and their Effect on Seedling Growth. Ph.D. Thesis, Kumaun University, Nainital, India.

Allen, M.F. 1991. *The ecology of mycorrhiza* . Cambridge University Press, Cambridge, UK, 184p .

Bagyaraj, D.J. 1989. Mycorrhizas. In "Tropical Rain Forest Ecosystem: Biographical and ecological studies" edited by Leith, H. and Werger, M.J.A. Elsevier, Amsterdam-Oxford-New York- Tokyo. Pp,

Barker, S.J., Tagu, D. and Delp, G. 1998. Regulation of root and fungal morphogenesis in mycorrhizal symbiosis. *Plant Physiology*, 116: 1201-1207.

Becker, P, 1983. Mycorrhizas of *Shorea* (Dipterocarpaceae) seedlings in a lowland Malaysian rain forest. *The Malayan Forester*, 42(2): 146-170.

Bills, G.F., Holtzmann, G.I. and Miller, O.j.Jr. 1986. Comparison of ectomycorrhizal Basidiomycetes communities in red spruce versus northern hardwood forest of West Virginia. *Canadian Journal of Botany*, 64: 760-768.

Bjorkman, E. 1960. *Monotropa hypopitys* L.-an epiparasitic on tree roots. *Physiologia Plantarum*, 13: 308-327.

Brunner, I.; Bunnere, F. and Laursen, G.A. 1992. Characterization and comparison of macrofungal communities in an *Alnus tumuifolia* and an *Alnus crispa* forest in Alaska. *Can. J. Bot*. 1992 70: 1247-1258.

Castellano, M.A., Verbeken, A., Walleyn, R. and Thoen, D. 2000. Some new and interesting sequestrate Basidiomycota from African Woodland Karstenia, 40: 11-21.

Champion, H.G. and Seth, S.K. 1968. *A revised survey of the forest types of India*. Govt. of India Publication, New Delhi, 404p.

Cibula, W. and Ovrevo, C. 1988. Mycosociological studies of mycorrhizal fungi in two loblolly pine plots in Missisipi and some relationship with remote sensing data. In remote Sensing for Resource Inventory Planning and Management (eds, J.D. greer) *American Society for Photogrammetric Remote Sensing*. Falls Church, Va. Pp. 268-307.

Dubey, R.C., Ginwal, H.S. and Singh, R.P. 1998. Comparative study of ectomycorrhizae of different forest of *Quercus* spp. In Kumaun Himalaya: Vertical distribution along soil depth. In: Rai, P. and Dkhar, M.S. (eds.) *New Trends in Microbial Ecology*. International Society for conservation of natural Resources, Varanasi, Dept. of Botany, BHU, India, pp 306-314.

Finlay, R. and Soderstrom, B. 1992. Mycorrhiza and carbon flow to the soil. In Allen, M.F. (eds.) Mycorrhizal functioning: An integrative plant fungus process, Chapman and Hall, The Netherlands, pp, 134-160.

Frank, A.B. 1885.microbiology. Bishan Singh Mahendra Pal, Dehradun, India. Pp. 83-114.

Furman, T.E. and Trappe, J.M. 1971. Phylogeny and ecology of mycotrophic achlorophyllous angiosperms. *Quarterly Review of Biology*, 46: 219-225.

Garkoti, S.C. 1992. *High altitudinal forest of Central Himalaya: Productivity and nutrient cycling*. Ph. D. Thesis, Kumaun University, Nainital, India, 211p.

Gibson, J.A.S. 1963. “Eine Mitteilung uber die Kiefernmykorrhiza in den waldern Kenias”. In: Rawald W. and Lyr. H. (Eds) “Mykorrhiza, fisher, Jena, pp. 49-51.

Ginwal, H.S. 1994. Studies on ectomycorrhizae in different central Himalayan oak forests and their role in nursery practices. Ph.D. Thesis, Kumaun University, Nainital, U.P.

Harley, J.L. 1969. “The biology of ectomycorrhizae” 2nd edition Leonard Hill. London. P. 334.

Harley, J.L. and Smith, S.E. 1983. Mycorrhizal symbiosis, Academic Press, London. 334 pp.

Janos, D. 1985. Mycorrhizal fungi: Agent for symptoms of tropical community composition, in R. Molina (eds.) *Proc. 6th North American Conference on Mycorrhizae*. P, 98-103.

Julich, W. 1989. Dipterocarpaceae and Mycorrhizae. German Forestry Group. GFG-report no. 9. Mulaearman University Samarinda Indonesia. 103 pp.

Largent, D. L., Sugihara, N. and Wisher, C. 1980. Occurrence of ectomycorrhizae on ericaceous and pyroloceous plants in northern California. *Canadian Journal of Botany*, 58: 2274-2279.

Madhu, M. 1967. The biology of ectotrophic mycorrhizal with reference to the growth of pines in Nigeria. Obeche. J. Tree club. Uni. Ibadan. 1: 9-16.

Marx, D.H. 1991. The practical significance of ectomycorrhiza. Use in forest establishment. In: Ecophysiology ectomycorrhizae of forest trees. The Marcus Wallenberg Foundation Symposia Proceedings 7, pp, 54-90.

Marx, D.H., Ruehle, J.L. and Cordell, C.E. 1991. Methods for studying nursery and field response of trees to specific ectomycorrhiza. Method Microbial, 24:383-411.

Mejstrik, V. and Hadac, E. 1975. Mycorrhizae of *Arctostaphylos* uva-ursi. *Pedobiologia*, 15: 336-342.

Meyer, F.N. 1973. Distribution of ectomycorrhizae in native and man-made forests. In: Marks, G.C. and Kozlowski, T.T. (eds) *Ectomycorrhizae: their ecology and physiology*. Academic Press, New York, pp, 79-105.

Mikola, P. 1973. Application of mycorrhizal symbiosis in forestry practice: In: Marks, G.C. and Kozlowski, T.T. (eds) Ectomycorrhizae: their ecology and physiology. Academic Press, New York, pp, 383-411.

Molina, R. 1979. Pure culture synthesis and host specificity of red alder mycorrhizae. *Can. J. Bot*. 57: 1223-1228.

Molina, R. and Trappe, J.M. 1982a. Patterns of ectomycorrhizal host specificity and potential among Pacific Northwest conifers and fungi. *For. Sci*. 28: 423-458.

Molina, R., Massicotte, H. and Trappe, J.M. 1992. Specific phenomena in mycorrhizal symbiosis; Community ecological consequences and practical implications. In: Mycorrhizal functioning an integrative plant fungi process. Ed. My Allen. Pp. 357-423. Chapman and Hall, New York.

Noor, M. And Smits, W.T.M. 1988. Pengaruh intensities cahaya dan suhu tanah ternadop ektomikoriza dan pertumbuhan anakan *Shorea cf. polyandra*. In Soemarna, K . et. al., (eds) Prosiding symposium hasil-hasil penetration Dipterocarpaceae, pp, 11-28.

Oman, R.M. 1994. Pengaruh jenis cendawan mikoriza dan media tumbuh terhadap perkembangam stek Shorea leprosula Miq. M.Sc. Thesis, Institut Pertanian Bogor 'Unpublished'. 115 pp.

Pande, V. 2003. Diversity and biotechnical applications of ectomycorrhizae associated with oaks of Central Himalaya. Ph.D. Thesis, Kumaun University, Nainital, India.

Payronel, B., Fassi, B., Fontana, A. and Trappe, J.M. 1969. Terminology of Mycorrhizae. *Mycologia*. 61: 410-411.

Pyronzinski, K.A. and Mallock, D.W. 1975. The origin of lands plants: a matter of mycotrophy. *Biosystems* 6: 153-164.

Read, D.J. 1991. Mycorrhiza in ecosystem. *Experientia*, 47: 376-391.

Shemakhanova, N.M. 1967. Mycotrophy of wood plants. USDA and NSF, Washington, DC, Israel Program for Scientific Translation, 329p.

Singh, S. 2001. Role of mycorrhiza in tree planting in the field. II: field inoculation, fungal succession, and effect of climatic and edaphic factors. *Mycorrhiza News*, 12: 2-12.

Singh, S.P., Adhikari, B.S. and Zobel, D.B. 1994. Biomass, productivity, leaf longevity and forest structure along an altitudinal gradient in the Central Himalaya. *Ecological Monograph*, 64(4): 401-421.

Smith, S.E. and Read, D.J. 1997. *Mycorrhizal Symbiosis (2nd edition)*, Academic Press, London.

Smits, W.T.M. 1983. Dipterocarpaceae and Mycorrhizae. An ecological adaptation and a factor in forest regeneration. *Flora Malesiana Bulletin*, 36: 3926-3937.

Smits, W.T.M. 1994. Dipterocarpaceae: Mycorrhizae and regeneration. Tropenuos Series, 9-243 pp.

Sylvia, M. David ; Fuhrman, J.Jeffrey ; Harlet G. Peter and Zuberer A. David. 2005. Principles and Applications of Soil Microbiology (2nd Edition). Prentice Hall.

Tewari, J.C. 1982. *Vegetational analysis along altitudinal gradients around Nainital.* Ph. D. Thesis, Kumaun University, Nainital, India, 570p.

Trappe, J.M. 1964. Mycorrhizal hosts and distribution of *Cenococcum graniforme*. Lloydia, 27: 100-106.

Trappe, J.M. 1977. Selection of fungi for ectomycorrhizal inoculation in nurseries. *Ann. Rev. Phytopath*. 15: 203-222.

Trappe, J.M. 1987. Phylogenetic and ecological aspects of mycotrophy in the angiosperms from an evolutionary standpoint. In Ecophysiology of VA mycorrhizal plants (ed. Safir, G.R.). CRC Press, Boca Raton, Fla., 2-25.

Yasman, I. 1993. Ectomycorrhizal sporocarps appearance in Dipterocarp forest East Kalimantan. Indonesia In Proc. Inter. Workshop Bio-Refor held in Jogyakarta, pp, 179-181.

Yasman, I. 1995. Dipterocarpaceae: Tree-Mycorrhizae seedling connections. Ph. D. Thesis., Wageninger Agricultural University. The Netherlands.

Zak, B. 1973. Classification of ectomycorrhizae. In "ectomycorrhizae" (Eds. G.C. Marks and T.T. Kozlowski) pp, 43-78. Academic Press. New York and London.

Zak, B. 1974. Ectendomycorrhiza of Pacific Madron (*Arbustus menziessi*). *Transaction of the British mycological Society*, 62:201-203.

Zak, B. 1976a. Pure culture synthesis of bearberry mycorrhizae. *Canadian Journal of Botany*, 54:1297-1305.

Zak, B. 1976b. Pure culture synthesis of Pacific Madron of ectendomycorrhizae. *Mycologia*, 68:362-369.

1/10/2009