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GROWTH AND ESTABLISHMENT OF SEEDLINGS OF INDIGENOUS SPECIES INSIDE PLANTATIONS AND THE ADJACENT NATURAL FOREST

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GROWTH AND ESTABLISHMENT OF SEEDLINGS OF INDIGENOUS SPECIES INSIDE PLANTATIONS AND THE ADJACENT NATURAL FOREST

A thesis submitted to the School of Graduate Studies Addis Ababa University in partial fulfillment of the requirements for the Degree of Master of Science in Botanical Science

By

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Abstract

Eucalyptus and *Pinus* plantations and adjacent natural forest in Shashemene-Munessa State Forest were studied to investigate growth and establishment of seedlings of three indigenous species: *Podocarpus falcatus*, *Bersama abyssinica* and *Croton macrostachyus*. Density, distance from individual plantation trees, seedling architecture, transpiration and photosynthetic performance of understory indigenous plants were measured in order to investigate the nursing effect of plantation trees for the development of indigenous flora under their canopies. Examination of growth and establishment of study plants exhibited variations not only between plantations and adjacent natural forest but also between plantations themselves. Based on the results from measurements of density, distance from plantation trees and architecture of regenerated study species, plantations supported higher natural regeneration development (stem/ ha) of indigenous species than adjacent natural forest (1950 vs 1260). *P. falcatus* was found to be the most successfully regenerated species in both plantations and adjacent natural forest. More regeneration (stem/ha) and closer establishment to individual trees of plantation species of understory plants were found in *Eucalyptus* plantation indicating its better nursing effect than *Pinus* plantation. All study species had large number of individuals along the edge of *Eucalyptus* plantation. The seedling population of *P. falcatus* in *Eucalyptus* plantation had a density distribution inversely related with distance from seed source: with large number of individuals near the seed source and few individuals at further distance away from the seed source. Seedlings of *P. falcatus* and *B. abyssinica* exhibited differences in architecture in the two stands. Seedlings of both species in *Eucalyptus* plantation had more biomass distribution to branches and/or leaves to increase lateral growth than those in *Pinus* plantation. These differences in seedling architecture (stem growth and lateral growth) would probably reveal more need of silvicultural treatments for growth and establishment of indigenous plants in *Pinus* than *Eucalyptus* stand. Analysis of fluorescence parameters in the leaves of study species showed no significant difference in the level of F_v/F_m, $\Delta F/F_m'$, ETR and NPQ among species developed inside plantations and adjacent natural forest. In *Eucalyptus* plantation seedlings of *P. falcatus* and *E. saligna* had similar photosynthetic performance. From measurements of transpiration considerable variation was found between indigenous species and plantation species. Seedlings of *E. saligna* lose much more water through their leaves than those of *P. falcatus* and *B. abyssinica* with increasing vapor pressure deficit (VPD). Most importantly, large difference in water relation of *E. saligna* and *P. falcatus* was recorded which indicates its better water use. Comparison of photosynthetic performance and water relations of seedlings of *P. falcatus* with *E. saligna* indicated the potential of *P. falcatus* to grow inside *Eucalyptus* plantation. The study supported the suggestion that plantations had nursing effects for growth and establishment of indigenous flora under their canopies. Furthermore, the importance of seed availability and overstory species composition on the natural regeneration development of study species was also evident in the study.

1 Introduction

1.1 Background and justification

Forests have always played crucial roles in the economic and social development of mankind. Not only do they provide an indispensable source of food, fuel and materials for shelter, but they also play a vital role in protecting and maintaining the stability of our natural environment.

Humans are changing the landscape and altering the ecological balance that prevailed prior to the onset of large-scale, intensive human activity. Peoples living near or in tropical forest ecosystems have traditionally extracted forest products for their livelihood. Such practice does not create too much disturbance when the population is sparse, and the product is only for their own needs. When population pressure becomes greater, and the motive of extraction is profit, then the disturbance becomes serious threats to the environment (Riswan and Hartanti, 1995). Overharvesting of forests, together with land clearing for agriculture and overgrazing, reduces their numerous functions and the services they provide. These are being threatened not only by deforestation but also by reduction of biodiversity which affects the substituting tree cover formation (FAO, 2000).

Forest clearing, forest degradation through human disturbance and deterioration of land productivity due to inappropriate agricultural practices are the major problems in the tropics. They are caused by high population growth, rural poverty, market and policy failure and underdevelopment (Riswan and Hartanti, 1995; FAO, 2001). High rates of these problems generally result in rapid decline of natural forests throughout the tropical countries of the world (Parrotta *et al.*, 1997; Feyera *et al.*, 2002). As a result the destruction and degradation of tropical forests has been recognized as one of the greatest environmental threats and tragedies of all time

(Riswan and Hartanti, 1995). Because tropical forests are characterized by their high diversity of both plant and animal species, large number of endemic plants and animals, closed nutrient cycle, storage of high nutrient capital in the plant biomass and since they are largely responsible for water cycle and climatic condition, their destruction will result in biodiversity loss, loss of soil fertility and change in water cycle and climatic balances.

Tropical forest loss and degradation of lands, which formerly supported forest, are proceeding at alarming rates. According to FAO (2001) the world's natural forests continued to be converted to other land uses at very high rate during the 1990s. The estimated net annual change in forest area worldwide during the past decade (1990-2000) was -9.4 million hectares, representing the difference between the estimated annual rate of deforestation of 14.6 million hectares (14.2 million hectares in tropical areas and 0.4 million hectares in non-tropical areas) and the estimated annual rate of forest area increase of 5.2 million hectares. Thus major tasks of management include conservation of the remaining natural forests, expansion of forest plantation and thereby restoration of abandoned degraded areas.

The loss of natural forests at alarming rates confirms the need to slow down or preferably halt the decline before a more desperate situation is realized. There is high and increasing demand for wood for industrial and fuel needs especially in developing countries of the tropics with their increasing population. There is increasing evidence that forest plantations can play a key role in harmonizing long-term forest ecosystem rehabilitation or restoration with near-term socio economic development objectives (Parrotta, 1995; Parrotta *et al.*, 1997; Feyera, 1998; Yitebitu, 1998; Feyera *et al.*, 2002). In tropical regions where extensive degradation of forests, range lands and agricultural lands often has severe socio-economic implications, plantation programmes designed and managed to satisfy local needs for a diverse forest product mix are likely to have an increasing important role in the future (Brown and Lugo, 1994).

The role of forest plantations in sustainable forest management has been the subject of considerable attention. One reason for this is the current and future increase in demand for wood that may be largely met by plantations (FAO, 2001). They are considered to be an efficient means to produce forest products on relatively limited land base, and they are therefore seen by many others as helping to reduce deforestation and degradation of natural forests. Thus establishment of sufficient area of forest plantations may reduce logging pressure on natural forests by providing alternative source of wood supply. In the north-western United States, for example, over 25,000 ha of high yielding forest plantations were established between 1992 and 1997 in response to both increased demand for popular wood and decreased supply from natural forests (FAO, 1999).

To narrow or preferably fill the gap between supply and demand for wood, reducing the pressure from natural forests, forest tree plantations were initiated in the early 20th century in many tropical countries (Feyera *et al.*, 2002). Forest plantations cover an area of over 270,000 ha in Ethiopia (Pandey, 1995), 1.4 million ha in South Africa (Geldenhuys, 1997) and 4 million ha (*Eucalyptus* spp.) in Brazil (Da Silva *et al.*, 1995). Worldwide, the average rate of successful plantation establishment over the decade (1990-2000) was 3.1 million ha per year, of which 1.9 million ha were in tropical areas and 1.2 million ha in non-tropical areas (FAO, 2001).

In tropics there are silvicultural, economic and environmental benefits which make plantation forestry attractive. Any tree species (indigenous or exotic) that is adapted to degraded site can be planted to accelerate forest rehabilitation. Although indigenous tree species have been tried for afforestation of degraded lands, the majority of successful plantations in tropics consist of exotic species. Mainly exotic species of *Eucalyptus, Cupressus, Acacia, Pinus and Casuarina* have been and still are used for afforestation. Establishing plantation of indigenous species has often been either difficult or unsuccessful due to lack of adequate knowledge on their biology, ecology and silviculture (Parrotta, 1995; Geldenhuys, 1997; Powers *et al.*, 1997; Feyera *et al.*, 2002). On the contrary, plantation establishment using exotic species is more successful and has increased due to readily available information on their propagation techniques, silvicultural behavior and management activities; high productivity and rapid growth in relatively short period of time.

Not only plantations could be used as means for maintenance of the remnant natural forests by reducing the pressure imposed on, but also by fostering the regeneration of indigenous species under their canopies which would be developed into secondary indigenous forest with time. Several studies have shown that plantations can have a fostering effect on the regeneration of natural forest biodiversity and can be used as management tools for restoration of degraded lands (Parrotta, 1995; Michelsen *et al.*, 1996; Loumeto and Huttel, 1997; Parrotta *et al.*, 1997; Yitebitu, 1998; Feyera *et al.*, 2002). These studies suggest that, under certain circumstances, the facilitating role of plantations is due to changes in understory microclimate conditions, increased vegetation structure complexity, and development of humus and litter layers that occur during the early years of plantation growth. These changes lead to increased seed inputs from the neighboring indigenous forests by seed dispersing wildlife attracted to the plantation, suppression of grasses or other light demanding species that normally prevent tree seedling germination or seedling survival, and improved light, temperature and moisture conditions for seedling growth.

It has been noted that in the absence of silvicultural management aimed at eliminating woody understory regeneration, the monospecific plantation system is replaced by a mixed forest composed of planted species and increasing number of indigenous tree species drawn from surrounding forest areas (e.g. Parrotta *et al.*, 1997; Feyera, 1998; Yitebitu, 1998;). Alternatively, since the planted species are usually short-lived and light demanding (Lugo *et al.*, 1993) and if the planted species are gradually removed without removing woody understory regeneration, a floristically diverse secondary forest could develop with time.

Although exotic tree plantations in the tropics have clearly played a very important role in world wood supply thereby reducing the pressure on remnant natural forests, there is concern that exotic tree plantations especially *Eucalyptus*, are detrimental to the environment. Fast growing exotic species may exert higher competitive strength for water, nutrients and light than indigenous plants; hamper germination, establishment and growth of others particularly indigenous plants. However, such influences of exotic tree plantation depend on management activity, history of land use, age of plantation, distance from seed source and dispersal of those seeds, composition of seed banks and microclimatic conditions which need to be investigated (Parratta, 1995; Parratta *et al.*, 1997; Yitebitu, 1998; Feyera *et al.*, 2002). Several studies in different parts of the world have been initiated to study the effect of afforestation with exotic tree species (Parrotta *et al.*, 1997). Plantations may harbor a significant proportion of the indigenous plant diversity with time and can facilitate forest succession in their understory. It has been shown that tree plantations can have a nurse effect and foster the regeneration of indigenous plants under their canopies.

Such observations have been made in the Shashemene-Munessa Forest Area by Feyera (1998), Yitebitu (1998) and Feyera *et al.* (2002). They investigated natural regeneration of indigenous woody species inside *E. saligna, E. globulus, P. patula* and *C. lusitanica* plantations in association with the adjacent natural forest. Feyera (1998) found a total of 55 naturally regenerated woody species beneath the different plantation stands. Yitebitu (1998) also observed plantations supporting a total of 15 indigenous tree species under their canopies. They suggested the importance of species selection, seed availability and human intervention for successful development of indigenous species inside plantations and stressed the need for further investigation and follow-up. Our study becomes a good addition to them by evaluating how the regenerated species such as *P. falcatus* make such association with plantation tree species and whether plantations could limit further growth of indigenous species established beneath.

In the present study we investigated the establishment and growth performance of three indigenous species: *Podocarpus falcatus, Bersama abyssinica* and *Croton macrostachyus* under different site conditions, i.e. under the canopies of *Eucalyptus* and *Pinus* plantations and adjacent natural forest of Shashemene-Munessa State Forest. The aim of the study was to evaluate the nursing effect of plantations for the establishment of indigenous seedlings.

1.2 Objective of the study

General objective:

To evaluate establishment and growth performance of indigenous tree seedlings inside plantation and adjacent natural forest and generate information that may be important for the maintenance of our remnant natural forests.

Specific objectives:

- To compare density and seedling architecture of indigenous species in plantation understories and adjacent natural forest.
- To compare distance of indigenous species from individual trees of plantation species among them and across plantation stands.
- To examine the influence of distance from the seed source on the regeneration of indigenous species inside plantations.
- To compare some water relation parameters and photosynthetic performance of seedlings of indigenous species inside plantations and adjacent natural forest.

2. Materials and methods

2.1 Description of study area

The study was conducted in the Shashemene-Munessa State Forest, Eastern Escarpment of the Great Rift Valley, Ethiopia. This forest is one of the 58 Priority Forest Areas of Ethiopia. It is located about 240 km south of Addis Ababa at 7° 13'N and 8° 37'E and covers an altitudinal range between 2100 and 2700 m a.s.l. The bed rock is volcanic and the soils are reddish, freely draining and medium to heavy texture. The main rainy season extends from mid June to mid October with maximum rainfall occurring between July and August. There is also a short rainy season called "Belg Rain" between March and May. The mean annual temperature ranges 15-20^{0}C. The 10 year that is from 1993 to 2002 temperature and rainfall data of the study site (Degaga) is given in Fig. 1.

Shashemene-Munessa State Forest covers a total area of 98,169 ha out of which 17,223 ha is remnant natural forest and 6791 ha is exotic tree plantations. For this study *Eucalyptus* plantations at Degaga (near the village Degaga) and *Pinus* and *Eucalyptus* plantations at Kuke were chosen. The two sites are 4 km apart.

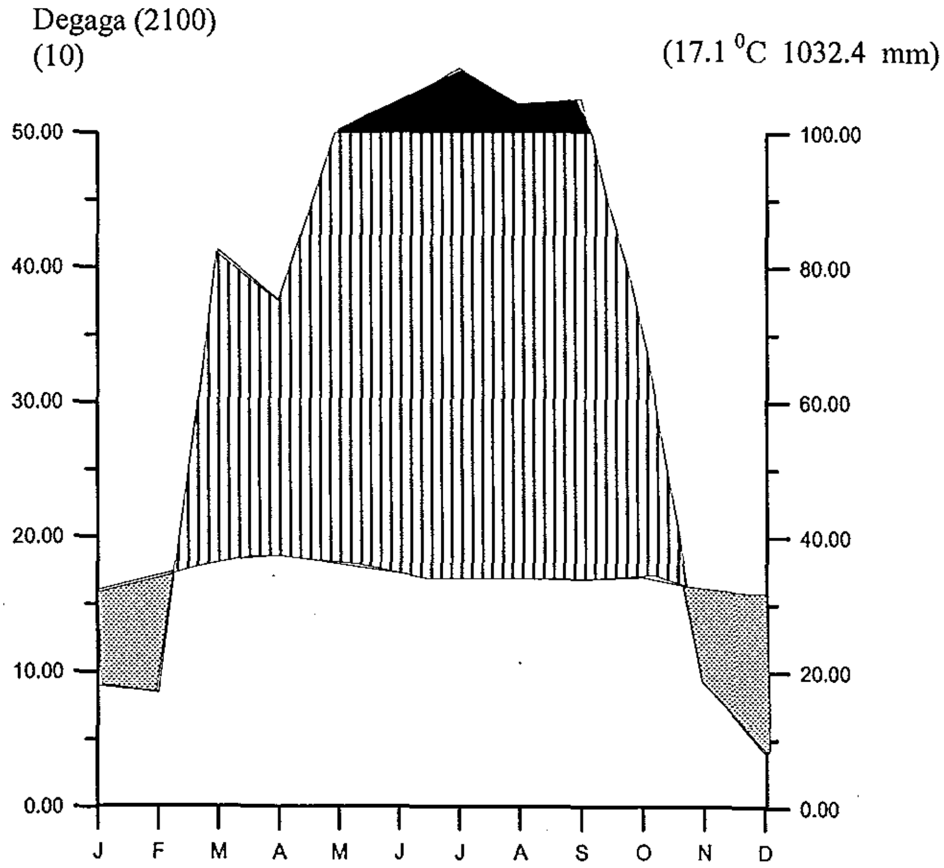

Fig.1. Mean annual temperature (^{0}C) and rainfall (mm).

2.2 Natural distribution and description of study species

2.2.1 Overstory species

Different stands composed of three plantation species, *Eucalyptus globulus* Labill., *E. saligna* Smith., *Pinus patula* Schlechtendal and Chamisso and adjacent natural forest were selected for the study. The species were chosen because of their variation in canopy structure, floor characteristics and management histories which are expected to influence growth and establishment of understory indigenous species. .

Eucalyptus globulus

E. globulus is indigenous to Australia, and has been planted in many countries around the world. It is a tree, usually up to 45 m, sometimes reaching 70 m, with a straight main stem and heavy rounded and open crown. The bark is smooth, white to cream, yellow, bluish-green or grey. The young leaves are opposite, sessile, cordate, ovate, grey-green, with strong difference in colour between the two sides, 7-16 cm long. Adult leaves are alternate, petiolate, lanceolate, sometimes falcate, acuminate, green, uniform in colour, very long and thin to 30 cm (Edwards *et al.*, 1995). The species is suitable for high altitude areas as it tolerates frost (Azene Bekele, 1993), and is characterized by its rapid growth and high rate of germination and survival. It performs well in Ethiopian highlands in altitudes between 1700-2800 m a.s.l. (Edwards *et al.*, 1995).

Eucalyptus saligna

E. saligna is a tall tree indigenous to Australia usually growing up to 55 m and is widely planted in the tropics for fuel (Azene Bekele, 1993; Edwards *et al.*, 1995). It has a straight main stem and medium irregular to rounded crown. The bark is smooth, white or blue-grey. The young leaves are alternate, petiolate, ovate to broadly lanceolate, green but with strong difference in colour between the two sides, 3-6 cm long. Adult leaves are alternate, petiolate, long acuminate, lanceolate, green but with strong difference in colour between the two sides, 9-17 cm long. In Ethiopia it grows well in areas with altitude between 1700-2300 m a. s. l. (Edwards *et al.*, 1995). It is the dominant *Eucalyptus* species grown in the highlands in the Arsi region.

Pinus patula

P. patula is indigenous to Mexico and is probably the most widely planted pine in tropical Africa. It is a tree with a straight trunk and growing up to 35 m in height. The bark is grey to dark-brown and fairly smooth. The leaves are long slender needles, soft but hard tipped, 15-23 cm long (Azene Bekele, 1993).

2.2.2. Understory indigenous species

Three indigenous species namely, *Podocarpus falcatus* (Thunb) Mirb., *Croton macrostachyus* Del. and *Bersama abyssinica* Fresen. were studied under different site conditions, i.e. under the canopies of plantation forests and adjacent natural forest.

Podocarpus falcatus

P. falcatus (*Podocarpaceae*) is one of the two most important coniferous species indigenous to the country. It is an evergreen and dioecious tree that grows up to 45 m in height and 3 m in diameter. The bark is grey to dark-brown, cracking and scaling into irregular rectangles. The leaves are linear to linear-oblong, shiny dark green, 2.5 cm in length. The young leaves are larger and brighter. Its trunk is straight and cylindrical (Azene Bekele, 1993; Demel Teketay, 1994&

1997). The seed is greenish-blue and oval. It turns yellow then purple as it ripens. Monkey and birds eat the seeds dispersing the tree (Demel Teketay, 1994). The natural distribution with respect to altitude ranges between 1500-2800 m a. s. l. *P. falcatus* is found to be the dominant tree in dry afromontane forests, often persisting in relic forest patches, frequent as relic tree left in derived grassland and farmland. The species is now rare due to over- exploitation (Azene Bekele, 1993; Friis, 1992; Demel Teketay, 1997).

Bersama abyssinica

B. abyssinica (*Melianthaceae*) is an evergreen shrub or small tree up to 18 m in height. Bark is brown and smooth becoming grey and rough. Leaves are odd pinnately compound with 5-21 leaflets, up to 1 m long. Leaflets are lanceolate to oblong or ovate-oblong, glabrous to hairy, 3.5-22 cm long (Hedberg and Edwards, 1989; Azene Bekele, 1993; Friis, 1992; Demel Teketay, 1997). Its natural distribution with respect to altitude is between 1700-2715 m a.s.l. and essentially found in *Juniperous-Podocarpus* or *Podocarpus* forest or degraded remnant of it; as well as in grasslands, open woodlands and cultivation. This species easily regenerates under mature trees and it may invade cultivated land if it is left fallow even for few years. (Hedberg and Edwards, 1989; Azene Bekele, 1993; Demel Teketay, 1997)

Croton macrostachyus

C. macrostachyus (*Euphorbiaceae*) is a deciduous tree with slender trunk, rounded crown and spreading branches, reaching up to 30 m in height. Bark is pale-grey, fairly smooth when young and longitudinally fissured when old. Leaves are simple, petiolate, ovate, base rounded to cordate (Azene Bekele, 1993; Edwards *et al.*, 1995; Demel Teketay, 1997). Its natural distribution with respect to altitude ranges between 500-2500 m a.s.l. and frequently occurs in secondary forest and forest edges, along rivers, cultivated fields, disturbed areas and along edges of roads (Friis, 1992; Edwards *et al.*, 1995; Demel Teketay, 1997).

2.3 Site Selection and Sampling methods

Following a reconnaissance survey of the study area on the first week of November 2002, three stands in *Eucalyptus* plantations and one stand in *Pinus* plantation were selected for investigation. These stands were selected because they supported natural regeneration development of indigenous species, had different management histories and floor characteristics. For comparison and evaluation of the catalytic effect of plantations for the establishment of indigenous flora, stands in adjacent natural forest and grassland (unplanted) area were also identified and included in the study.

Forty plots of size 20 m x 20 m were systematically laid down across the vertical line transacts in *Eucalyptus globulus* and *Pinus patula* plantations and adjacent natural forest and used to measure density, size and distance of indigenous species from the individual trees of plantation species. In *E. saligna* plantation, due to the narrow strip nature of the plantation, eight plots of size 10 x 20 m were sampled. The influence of distance from seed source on the regeneration of *Podocarpus falcatus* was also examined in 12 plots (1200 m^2) sampled at various distance from the nearby seed source in *E. saligna* and *E. globulus* plantations. Stand characteristics of sampled stands are summarized (Tab. 1&2).

Table 1 Sampled stand characteristics (LAI, DBH, age, etc) at Shashemene-Munessa State Forest

Plantation stands (location)	Altitude	Age (years)	LAI	Plots sampled	Density (stem/ha)	DBH (cm)	Silvicultural treatments
E. saligna (Degaga)	2100	30	-	11	* 1400	-	3rd coppice
E. globulus (Degaga)	2100	25	-	19	** 8472	-	2nd coppice
E. saligna (Kuke)	2300	17	2.5	3	1212	31	1st rotation thinned
P. patula (Kuke)	2300	31	2.4	17	823	33.5	1st rotation 3 x thinning
Natural forest	2300	-	1.8	10	-	-	-
Open area (Degaga)	2100	-		5	-	-	-

* Based on number of stumps
** Number of stems resprouted from stumps

Table 2 Size and density of plantation species at Degaga (coppice stand)

Species	Site	Variables	
		DBH (cm)	density (stem/ ha)
E. globulus	Edge of plantation	≤3.2	2500
		3.2-6.4	5300
		> 6.4	200
	Center of plantation	≤3.2	3900
		3.2-6.4	5000
		> 6.4	7

2.4 Seedling architecture and leaf area determination

Architecture and leaf structural characteristics of seedlings were measured in both plantation and natural forest. The mean height and size (diameter at 30 cm height) of representative seedlings of each species were measured by measuring tape (Tab. 7). An average of 20 representative seedlings per species per site was used for measurement. The mean distance between two successive branches (branch internode length) and mean number of lateral branches per main branch (for *P. falcatus* seedlings), internode length (for *B. abyssinica* seedlings), leaf area and leaf dry weight were measured. Healthy, matured and fully expanded leaves were used to determine leaf area. From each sampled leaf 0.25 cm^2 and 4 cm^2 discs were cut from leaves of *P. falcatus* and *B. abyssinica*, respectively. After drying the discs and the remaining leaves at 80^0C for 24 hours, the total leaf area was calculated from the known area of the discs, the dry weight of the discs and the total dry weight of the leaves.

2.5 Transpiration measurement

The transpiration rate of study species was determined using steady state porometer (Licor-Nebraka USA) on both sides of the leaves. Only leaves that were healthy and fully developed were used for measurement. As much as possible measurements were taken on leaves in their natural position.

2.6 Chlorophyll fluorescence measurement

Chlorophyll fluorescence was determined with a portable pulse-amplitude modulated photosynthesis yield analyzer (Mini-PAM, Heinz Walz Gmbh, Effeltrich, Germany) equipped with a standard 2030-B leaf clip holder. The maximal efficiency of photochemistry of PS II $(F_m-F_o)/F_m=F_v/F_m$) was measured following Lüttge *et al.* (2001) in the early morning and during the day after darkening the leaves for 30 min, where F_o is the minimal fluorescence level of dark adapted leaves with all PS II reaction centers open, F_m is the maximal fluorescence level with all PS II reaction centers closed determined by a saturating light pulse at 3000 µmol m^{-2} s^{-1} on dark adapted leaves and F_v is the maximal variable fluorescence level. Effective quantum yield of PS II was calculated as $(Fm - F)/F_{m'} = \Delta F/F_{m'}$ (Genty *et al.*, 1989), where F is the steady-state value of fluorescence of light adapted leaf and $F_{m'}$ is the maximal fluorescence level in the light adapted state determined by saturating light pulse at 3000 µmol m^{-2} s^{-1} superimposed on the prevailing environmental light flux. Non-photochemical quenching (NPQ) was calculated by Stern-Volmer equation as $NPQ = (F_m/F_{m'}) - 1$ (Bilger *et al.*, 1995). Apparent rate of photosynthetic electron transport (ETR) was determined as $\Delta F/F_{m'}$ x PAR x 0.5 x 0.84, where the factor 0.5 accounts for the excitation of PSII and the factor 0.84 assumes a reflection of 16% PAR (photosynthetically active radiation) at the leaf surface (Schreiber *et al.*, 1994).

2.7 Data analysis

The data obtained were analyzed by ANOVA using SPSS Version 10.00 Software and Microsoft Excel. The differences between treatment means were tested at 5 % level of significance.

3 Results

3.1 Regeneration of indigenous plants inside natural forest and plantation understories

Regeneration density of indigenous species is shown in Fig. 1. High regeneration density of understory indigenous species was found in plantation forests. Plantations supported more than 1.5 times the density of study species found beneath the adjacent natural forest. In all sites, *P. falcatus* had the highest regeneration.

There was more regeneration of indigenous plants in *Eucalyptus* plantation than in *Pinus* plantation. Density (s/ha) of *P. falcatus*, *B. abyssinica* and *C. macrostachyus* in *Eucalyptus globulus* plantation was greater by more than 30, 81 and 34 per cent of their densities in *Pinus* plantation, respectively. The density of *P. falcatus* was the highest in both sites followed by *C. macrostachyus* (Tab. 3). The density of indigenous plants also showed considerable variation in the center and at the peripheral zone of *Eucalyptus* plantation. All the study species had higher densities in the edge than in the center of plantation (Tab. 4). Even the two edges of *Eucalyptus* plantation at equal distance from the seed source supported different densities of *P. falcatus*. The edge adjacent to the open area (unplanted area covered by grass) exhibited more regeneration of *P. falcatus* than the edge adjacent to a plantation (Tab. 5).

Table 3 Density (stem/ ha) and distance (cm) from plantation trees of understory indigenous plants in *Eucalyptus* and *Pinus* plantations and adjacent natural forest

	E. globulus plantation		*P. patula* plantation		Natural forest	
	Density	Distance	Density	Distance	Density	Distance
P. falcatus	1545	50.5	1188	75	605	-
B. abyssinica	343	54	90	110	540	-
C. macrostachyus	420	62.5	313	139	115	-

Table 4 Density (stem/ ha) of regenerated indigenous species in the edge and center of E. globulus plantation at Degaga.

Species	Regeneration density	
	Edge	Center
P. falcatus	2883	206
B. abyssinica	417	267
C. macrostachyus	539	300

Furthermore; the regeneration of *P. falcatus* was highly influenced by distance from seed source. Its density greatly declined with increasing distance from the parent plant (Fig. 2).

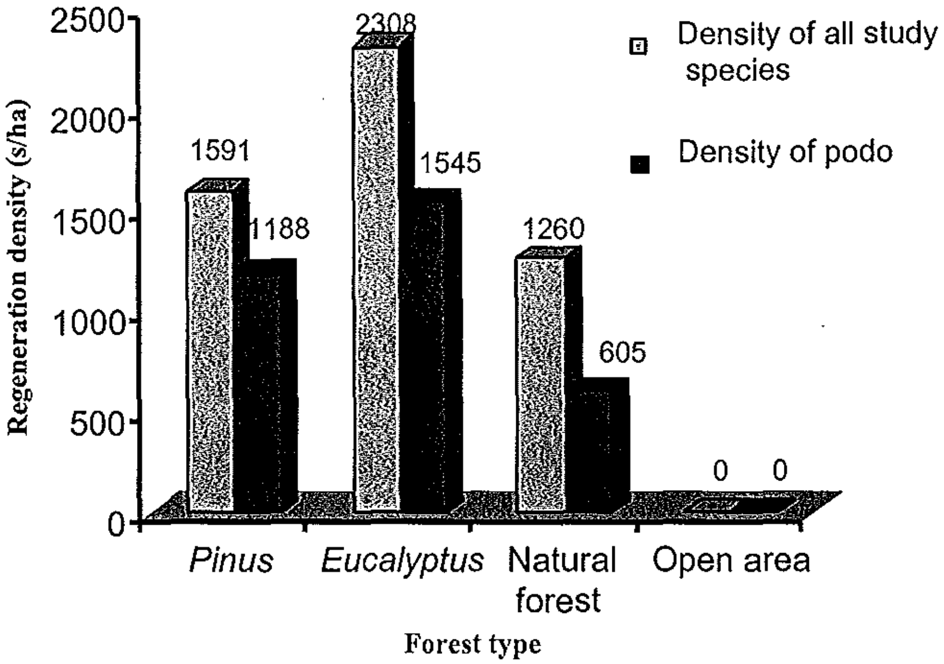

Fig.2 Regeneration (stem/ ha) of *P. falcatus.*, *B. abyssinica* and *C. macrostachyus* under different forest types

Table 5 Density (stem/ha) of *P. falcatus* at the two edges of *E. globulus* plantation at Degaga

Site	Density	
	E. globulus (Coppice)	*P. falcatus*
E[a]	8050	11950
E[b]	9250	2600

E[a] Edge of the plantation adjacent to open area (unplanted area covered by grass).

E[b] Edge of plantation adjacent to a plantation

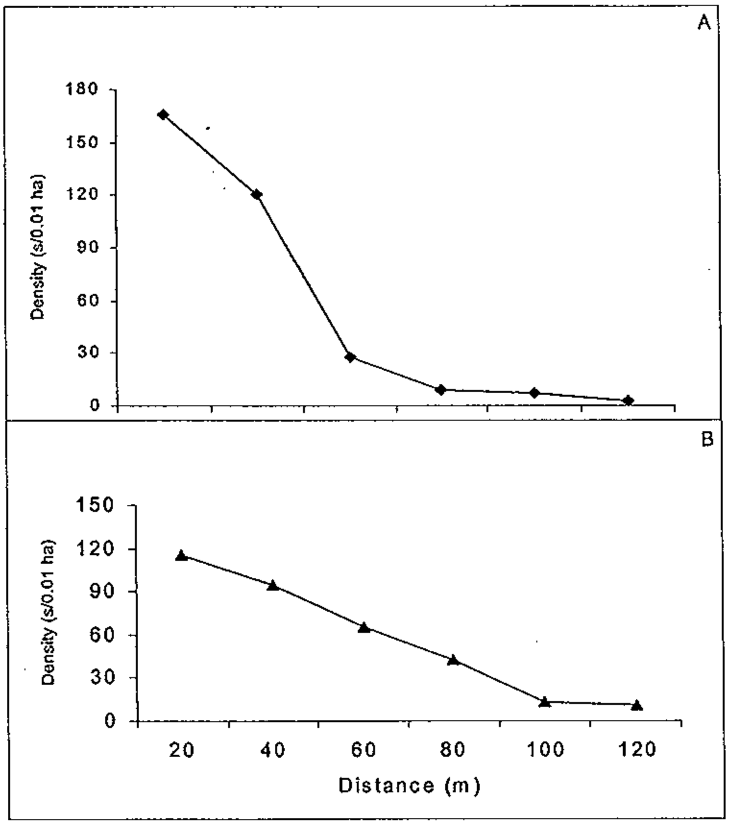

Fig. 3 Regeneration (stem/0.01 ha) of *P. falcatus* and distance (m) from seed source in *E. globulus* (A) and *E. saligna* (B) plantations at Degaga

Considering distance from individual trees of plantation species, understory indigenous species exhibited differences among themselves and between sites (Tab. 3). All the understory indigenous species considered tended to establish closer to individual plantation trees of *Eucalyptus* plantation than *Pinus* plantation. The distance of *B. abyssinica* and *C. macrostachyus* from individual trees of plantation species in *Pinus* plantation was more than twice that of the *Eucalyptus* plantation. In terms of closeness of indigenous species to the individual trees of plantation species at the two sites: *P. falcatus* ranked first, *B. abyssinica* second and *C. macrostachyus* last.

3.2 Population structure of understory indigenous plants in plantations and adjacent natural forest

In the three sites the density of each study species more or less declined with increasing size (height), that is, with more number of individuals at lower size classes. The difference in the regeneration density of indigenous species established in plantations and natural forest was minimum at the smallest size class (≤ 1.5 m height) and maximum at the sapling stage (1.5-3 m height). Fewer but bigger individuals of *P. falcatus* and *C. macrostachyus* were found in *Pinus* plantation.

Table 6 Comparative demography of understory indigenous plants considering differences in density (stem/ ha) and height classes (m) in *E. globulus* plantation (E), *P. patula* plantation (P) and the adjacent natural forest (N).

Height classes	Regeneration density								
	P.falcatus			*B. abyssinica*			*C. macrastachyus*		
	E	P	N	E	P	N	E	P	N
≤1.5	573	263	360	253	65	345	135	110	25
1.5-3	680	400	85	90	25	130	228	105	15
3-5	245	473	45	0	0	60	58	90	15
5-7	48	53	35	0	0	5	0	8	10
≥ 7	0	0	80	0	0	0	0	0	50

3.3 Leaf structural characteristics and seedling architecture of understory indigenous species

Leaf structural characteristics and architecture were measured only for seedlings of *P. falcatus* and *B. abyssinica*. These species generally had smaller values of leaf characteristics and internode length in natural forest than in plantations. Seedlings of both species had relatively larger leaf area and heavier leaf dry weight in *Eucalyptus* plantation.

Table 7 Leaf structural characteristics and architecture of: *P. falcatus* (P) and *B. abyssinica* (B) seedlings (n=20)

Characterstics	Sites					
	Pinus plantation		*Eucalyptus* plantation		Natural Forest	
	P	B	P	B	P	B
Mean height (cm)	143	95	139	97	122	90
Mean diameter (cm) at 30 cm	1.6	1.5	1.6	1.6	1.7	1.5
Branch internode length (cm)	12	-	8.7	-	8.1	-
Number of lateral branches	7.5	-	9.4	-	6.2	-
Internode length (cm)	-	3.7	-	2.5	-	2.1
Leaf dry weight (g)	0.049	0.298	0.053	0.304	0.055	0.293
Leaf area (cm^2)	3.69	50.74	4.06	51.2	3.92	38.02

Seedlings of *P. falcatus* had longer branch internode length and fewer number of lateral (secondary) branches per main branch in *Pinus* plantation than in *Eucalyptus* plantation. Similarly seedlings of *B. abyssinica* also had longer leaf internode length in *Pinus* plantation

(Tab. 7). In general, there was a tendency towards more biomass distribution in leaves and/or branches of indigenous plants growing inside *Eucalyptus* plantation which in turn enhance lateral growth and stem growth of understory indigenous plants in *Eucalyptus* and *Pinus* plantation, respectively.

3.4 Transpiration and vapor pressure deficit

Transpiration measurements were made for seedlings of *P. falcatus* and *B. abyssinica* in *E. saligna* plantation at Kuke. For comparison leaves of seedlings of *E. saligna* were also included in the measurement. All the species transpired on both sides of their leaves, but the amount of water lost on the two sides differed among species (Tab. 8). *P. falcatus* transpired almost equally on both sides of its leaves, whereas *B. abyssinica* transpired more on the lower surfaces of its leaves. Proportionally very significant amount of water is lost on the lower leaf surfaces of *E. saligna*.

Table 8 Comparison of transpiration (mmol m^{-2} s^{-1}) on the upper and lower leaf surfaces of study species in *E. saligna* plantation at Kuke

Species	Transpiration	
	Lower surface	Upper surface
P. falcatus	0.414	0.567
B. abyssinica	1.25	0.189
E. saligna	2.21	0.043

The effect of increase of vapor pressure deficit (VPD) on the transpiration rate of study species is illustrated in Fig. 3. Comparison of the diurnal transpirational behavior of the three plant species revealed differences in transpiration rate to increased VPD. Rate of transpiration in the three species increased with increasing VPD. Transpirational rates were highest in the plantation species (*E. saligna*) and the relationship between transpiration and VPD was also steeper in plantation species than in understory indigenous species.

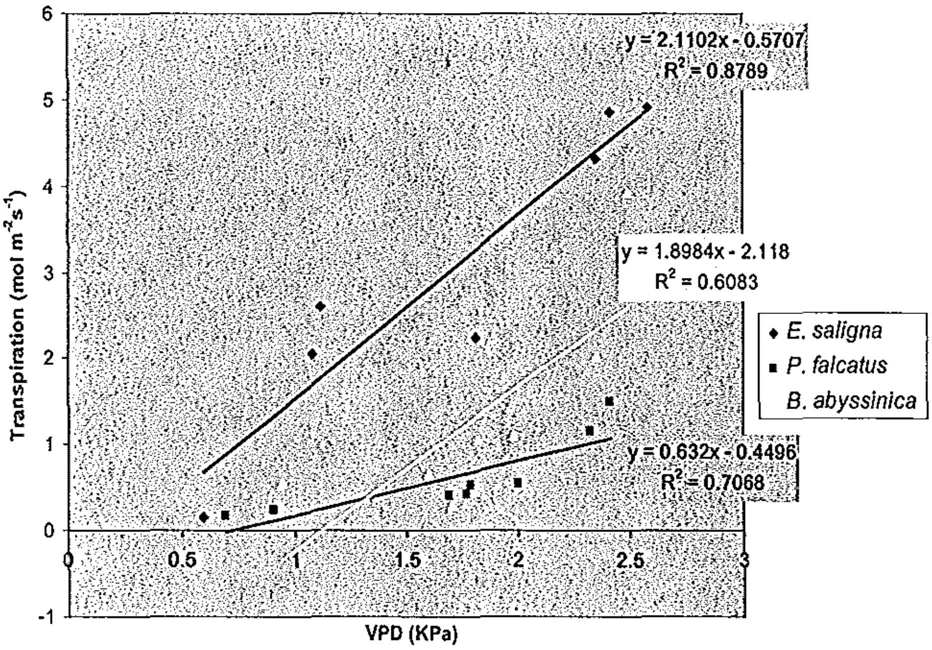

Fig. 4 Relationship between VPD and Transpiration of study species.

3.5 Chlorophyll fluorescence parameters in leaves of seedlings growing inside plantations and adjacent natural forest

No significant difference in photochemistry of PS II was found among leaves of indigenous plants established in plantations and the adjacent natural forest. The maximal photochemical efficiency of PS II in the dark-adapted state, F_v/F_m, which is used as a measure of potential maximum quantum yield of PS II (Demmig and BjÖrkman, 1987; Krause and Weis, 1991), is shown in Fig. 4. The value of F_v/F_m remained almost constant throughout the day and no significant difference was found in leaves of study species in both plantation and natural forest. Furthermore, the ratio F_v/F_m was not significantly different from 0.8, which could indicate optimal quantum efficiency of unstressed leaves (Demmig and BjÖrkman, 1987). The value of $\Delta F/F_{m'}$, however, declined around midday (Fig. 5). Here the species also showed no significant difference across the ±ites. ETR and NPQ in light adapted leaves of study species are given in Tab. 10. Both *P.falcatus* and *B. abyssinica* had little larger ETR and NPQ in plantation forests whereas *C. macrostachyus* had somewhat larger values of these parameters in the natural forest. Similar results were obtained among leaves of seedlings of understory indigenous species and plantation species (Tab. 11).

Table 9 Mean values (± SD) of ETR (μmol $m^{-2}s^{-1}$) and NPQ in leaves of study species at the study sites during the course of a day. For each plant and each parameter values followed by the same letter are not significantly different.

Species	Site	ETR	NPQ
P. falcatus	Natural forest	8.06a (4.8)	1.03a (0.29)
	Pinus plantation	9.49a (6.1)	1.57a (0.82)
	Eucalyptus plantation	8.26a (5.3)	1.33a (0.48)
	Clearfelled	29.5b (6.6)	4.07b (2.44)
B. abyssinica	Natural forest	2.98a (2.0)	1.1a (0.14)
	Pinus plantation	3.87a (3.8)	1.21a (0.28)
	Eucalyptus plantation	2.11a (2.8)	1.25a (0.31)
C. macrostachyus	Natural forest	13.89a (10.9)	1.58a (0.57)
	Pinus plantation	10.06a (6.5)	1.56a (0.54)

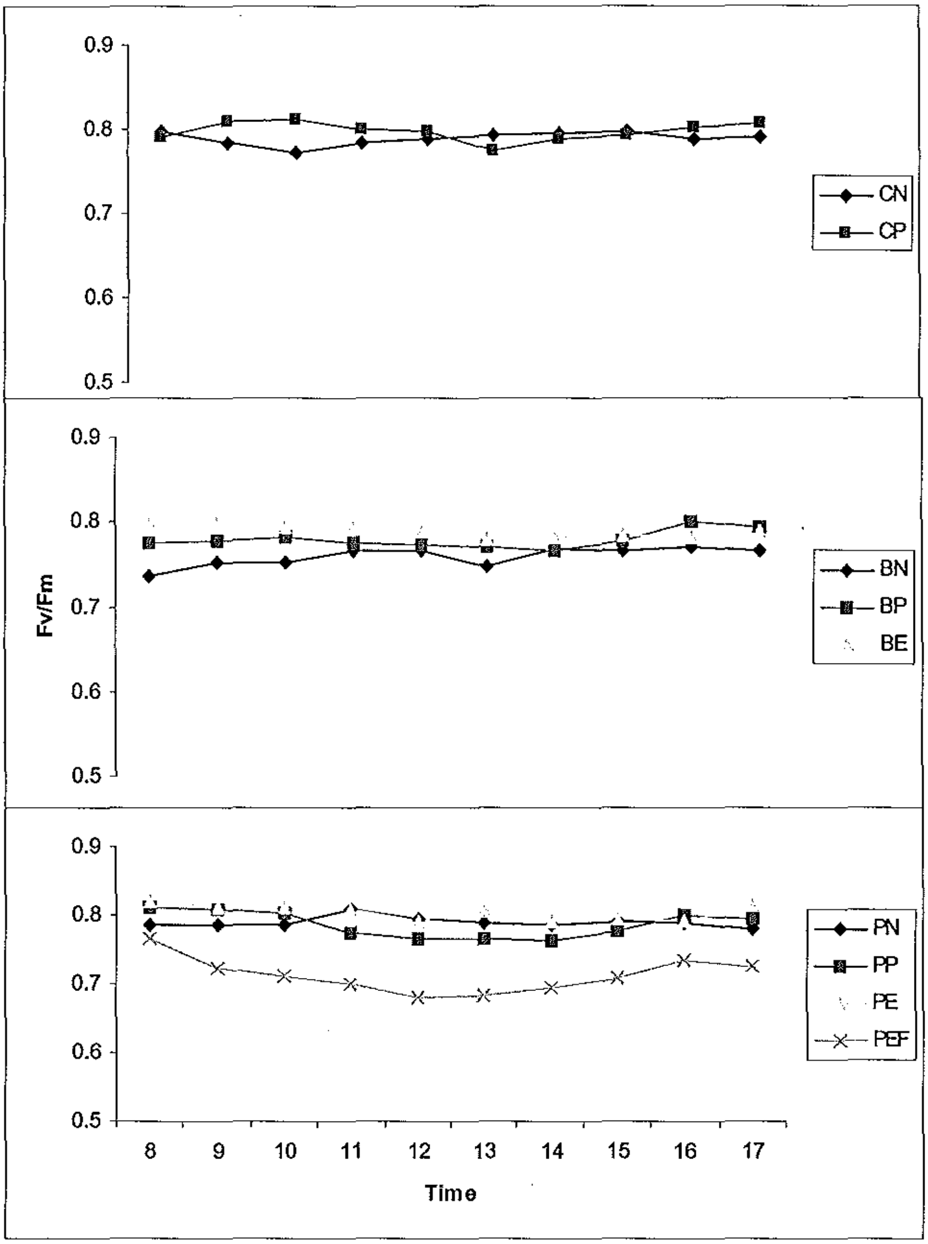

Fig. 5 Daily courses of F_v/F_m in leaves of *P. falcatus* (P), *B. abyssinica* (B) and *C. macrostachyus* (C) in natural forest (N), *Pinus* plantation (P), *Eucalyptus* plantation (E) and in the clearfelled plantation site (EF)

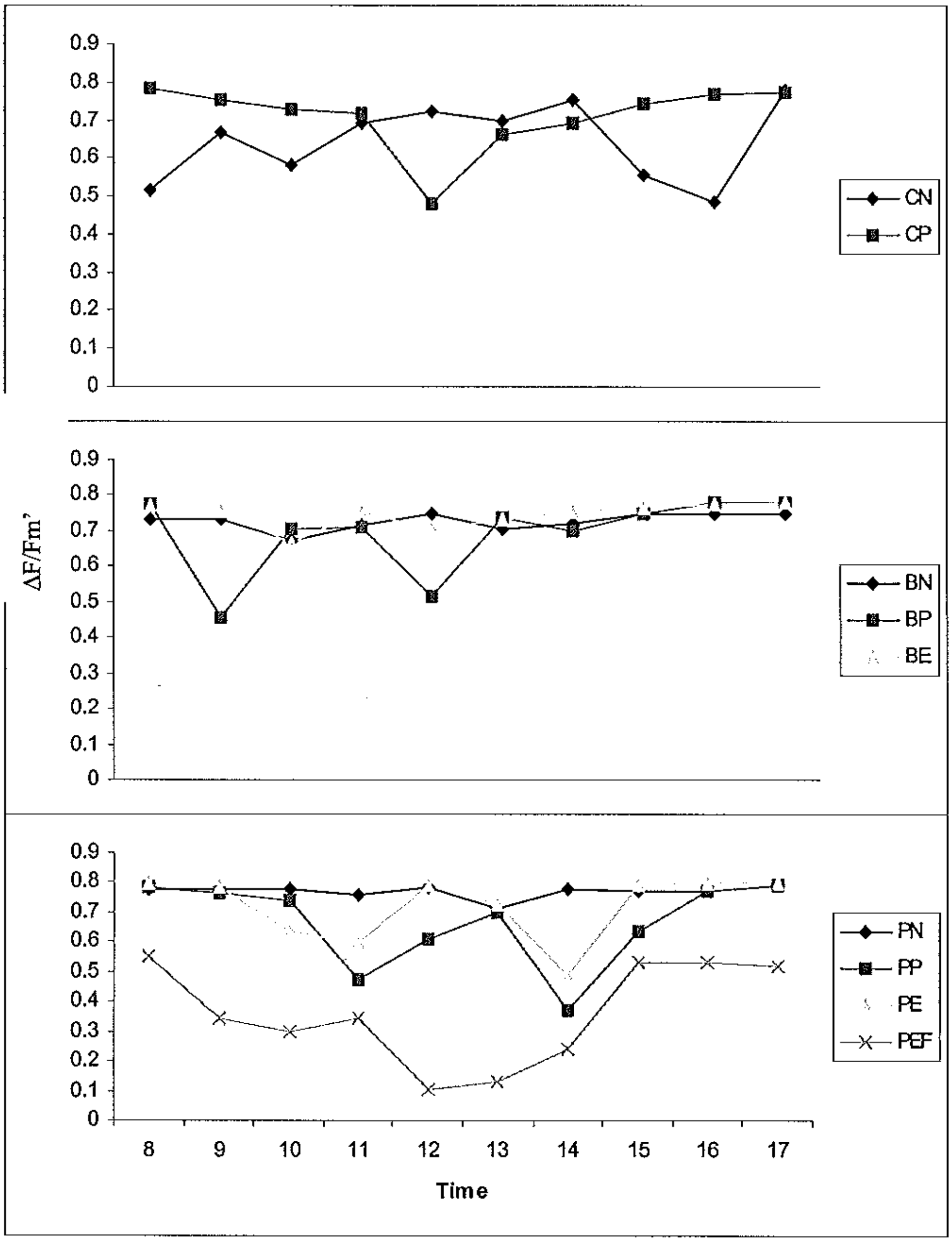

Fig. 6 Daily courses of $\Delta F/F_m'$ in leaves of *P. falcatus* (P), *B. abyssinica* (B) and *C. macrostachyus* (C) in natural forest (N), *Pinus* plantation (P), *Eucalyptus* plantation (E) and in the clearfelled plantation site (EF)

For more investigation of the potential of plantation forests for the establishment of indigenous plants under their canopies, chlorophyll fluorescence parameters in leaves of *P. falcatus* seedlings developed inside forests were compared with those left on the clearfelled plantation site which were exposed to direct sunlight (Tab. 9&10). All fluorescence parameters obtained from leaves developed inside forests were significantly different from those exposed to intense light in the open area. Leaves in the clearfelled had higher ETR and NPQ but Lower $\Delta F/F_m$' and F_v/F_m.

Table 10 Comparison of the mean values (± SD) of initial fluorescence (Fo), maximal fluorescence (Fm) and photochemical efficiency of PS II (Fv/Fm) in leaves (30 min dark adapted) of *P. falcatus* seedlings in forest understories and in the clearfelled during the course of a day. For each parameter values followed by the same letter are not significantly different.

Fluorescence parameter	Natural forest	*Pinus* plantation	*Eucalyptus* plantation	Clearfelled
F_o	850a (31.2)	837a (94.0)	745b (70.4)	740b (16.2)
F_m	4052a (382.0)	3775b (437.4)	3824ab (287.9)	2632c (366.8)
F_v/F_m	0.79a (0.06)	0.79a (0.05)	0.8a (0.11)	0.71b (0.07)

Table 11 Comparison of photosynthetic performance of understory indigenous species and overstory species in *E. saligna* plantation at Kuke. For each species and each parameter values (mean ± SD) followed by the same letter are not significantly different.

Species	F_v/F_m	$\Delta F/F_m'$	ETR	NPQ
P. falcatus	0.8a (0.11)	0.72a (0.01)	9.49a (5.3)	1.33ab (0.48)
B. abyssinica	0.79b (0.04)	0.74a (0.01)	2.11b (2.8)	1.25a (0.31)
E. saligna	0.83c (0.09)	0.74a (0.01)	10.41a (5.7)	1.58b (0.25)

Photosynthesis light response curves for species grown inside plantations and adjacent natural forest were generated using photosynthesis yield analyzer, Mini-PAM and are shown from Fig. 6 to 11. Yield ($\Delta F/F_m'$) significantly declined with increasing light level while apparent electron transport rate (ETR) and non-photochemical quenching (NPQ) increased with increasing light intensity with ETR being leveled off at high light (750-1040 µmol $m^{-2}s^{-1}$).

Species exhibited no marked differences among them and across sites in the level of light intensity at which ETR was maximal. They had maximum ETR at 750 µmol $m^{-2}s^{-1}$except seedlings of *B. abyssinica* in *Pinus* plantation and *C.macrostachyus* in *Pinus* plantation and natural forest, which had maximum ETR at 1040 µmol $m^{-2}s^{-1}$. However, there were little differences in the minimum values of $\Delta F/F_m'$ and maximum values of ETR. In seedlings of *P. falcatus* and *B. abyssinica* these parameters are high in *Pinus* plantation and low in natural forest. While *C. macrostachyus* had low values of the above parameters in *Eucalypts* plantation and high values in natural forest. *P. falcatus* and *B. abyssinica* had steeper light response curves in natural forest in the early phases of the response curves. Whereas, *C. macrostachyus* had its steeper response curves in the early phase in *Eucalyptus* plantation.

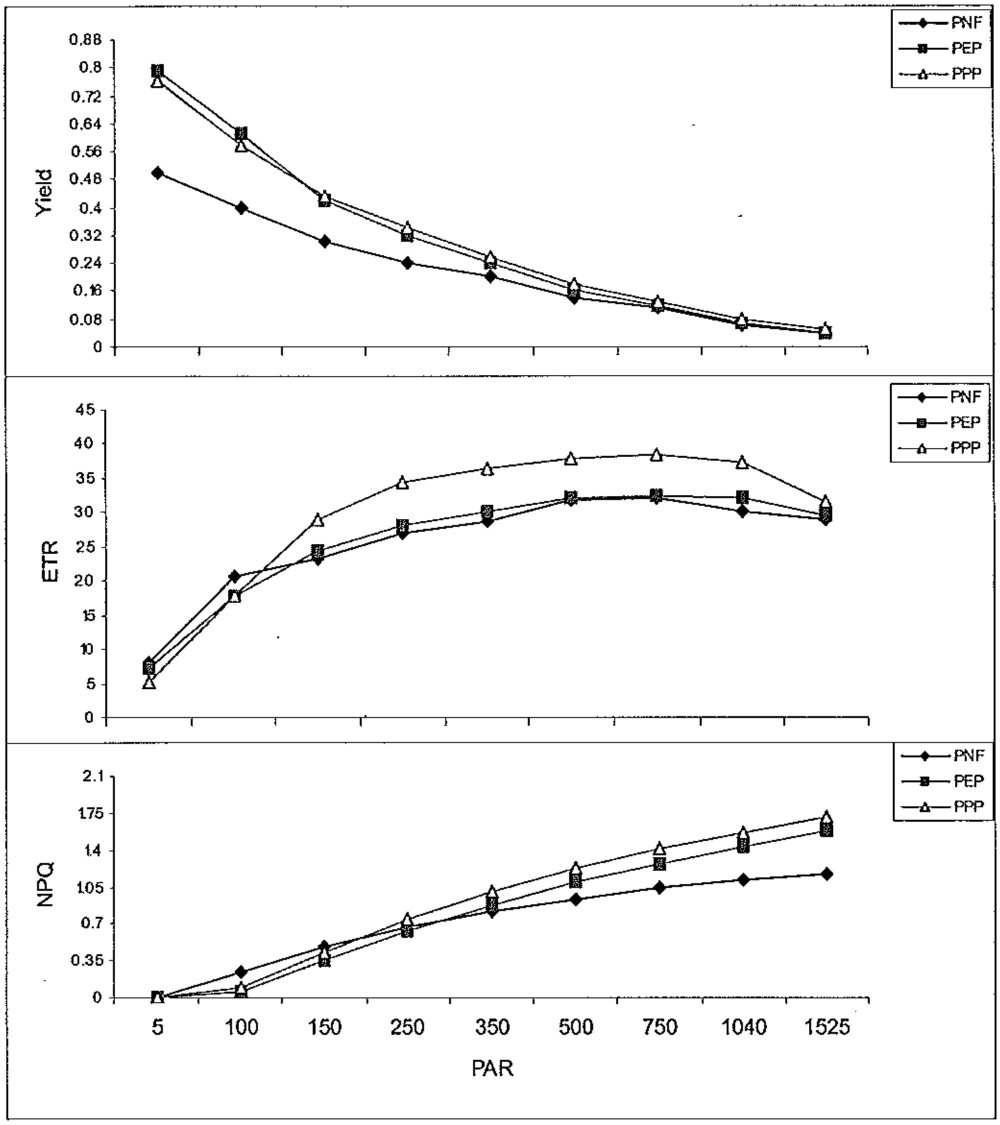

Fig. 7 Yield, ETR and NPQ as a function of incident light intensity in leaves of seedlings of *P. falcatus* grown in natural forest (NP), *Eucalyptus* plantation (EP) and *Pinus* plantation (PP).

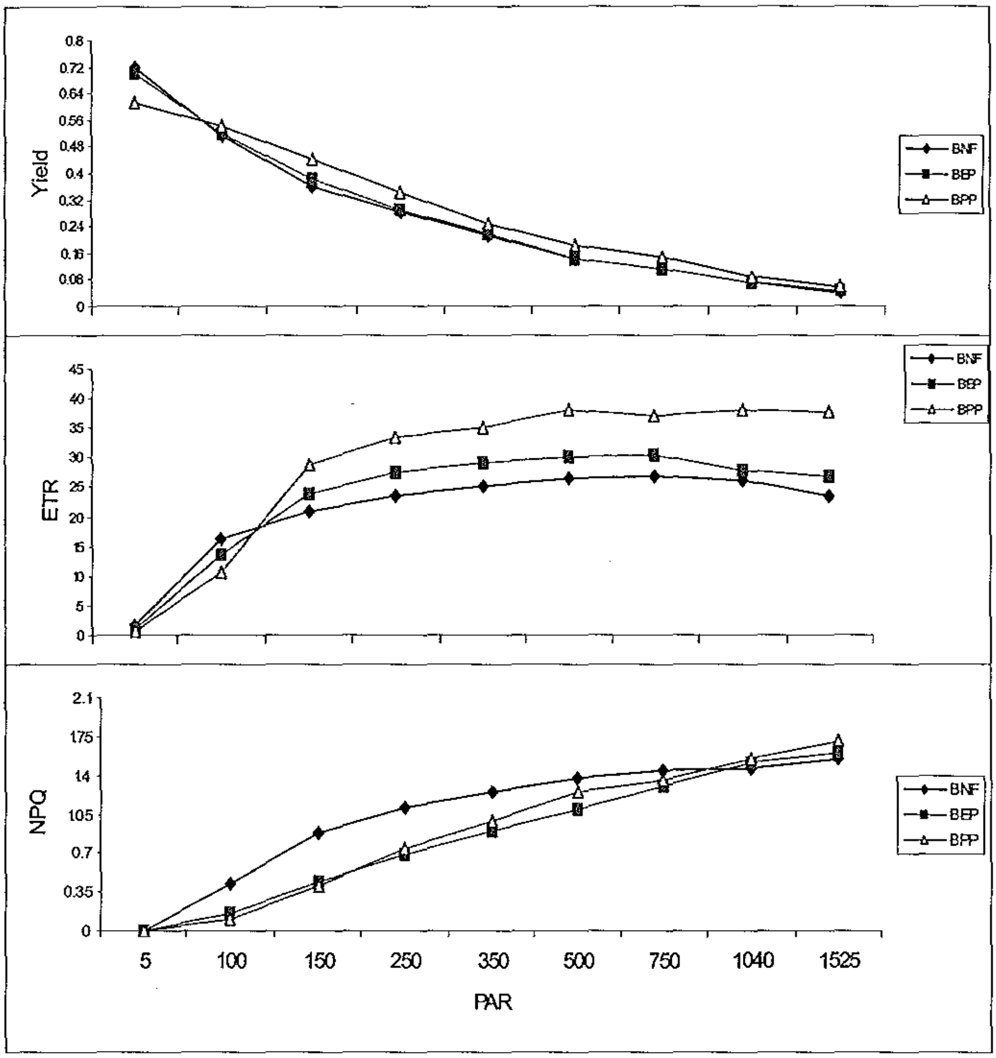

Fig. 8 Yield, ETR and NPQ as a function of incident light intensity in leaves of seedlings of *B. abyssinica* grown in natural forest (NP), *Eucalyptus* plantation (EP) and *Pinus* plantation (PP).

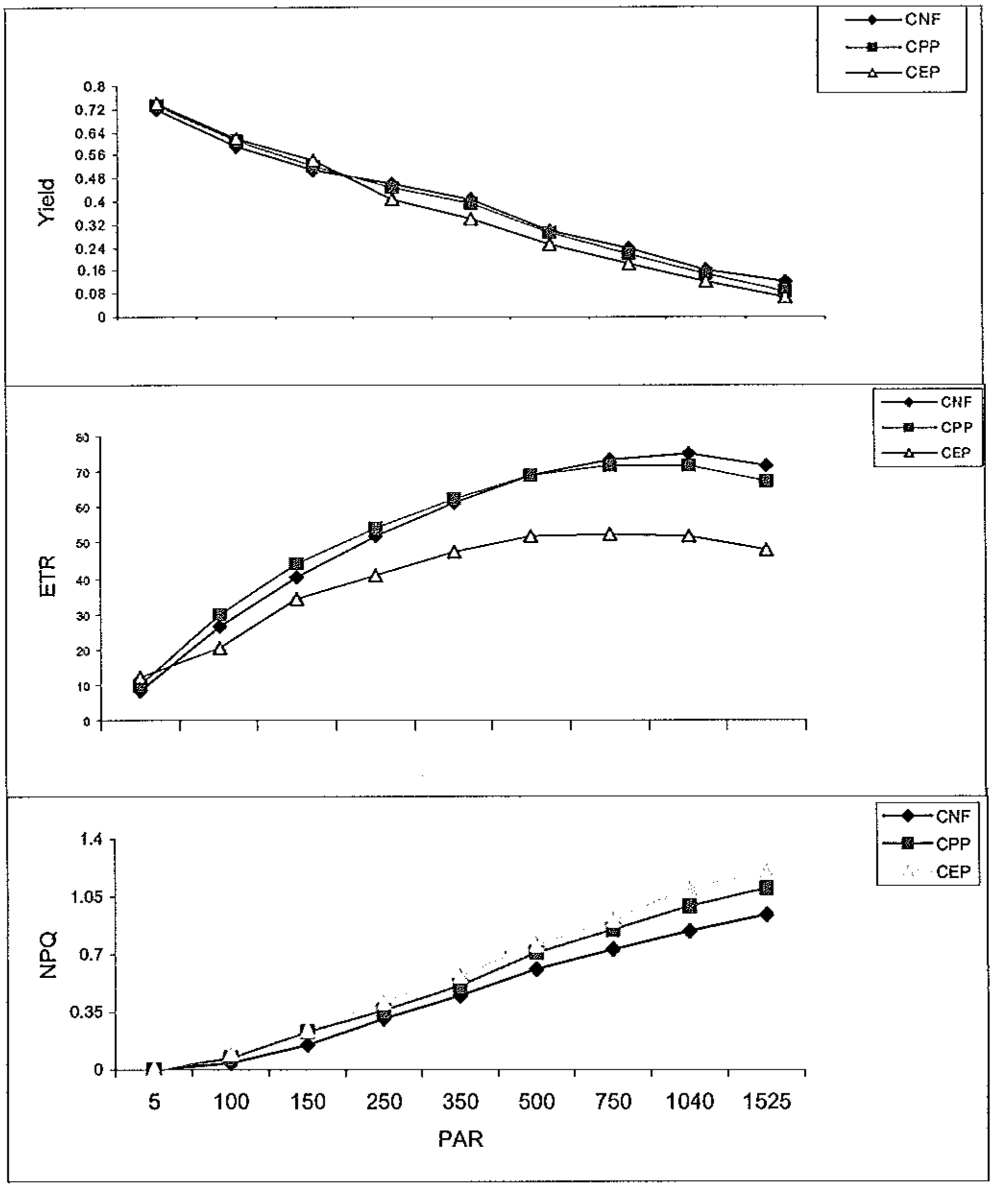

Fig. 9 Yield, ETR and NPQ as a function of incident light intensity in leaves of seedlings of *C. macrostachyus* grown in natural forest (NP), *Eucalyptus* plantation (EP) and *Pinus* plantation (PP).

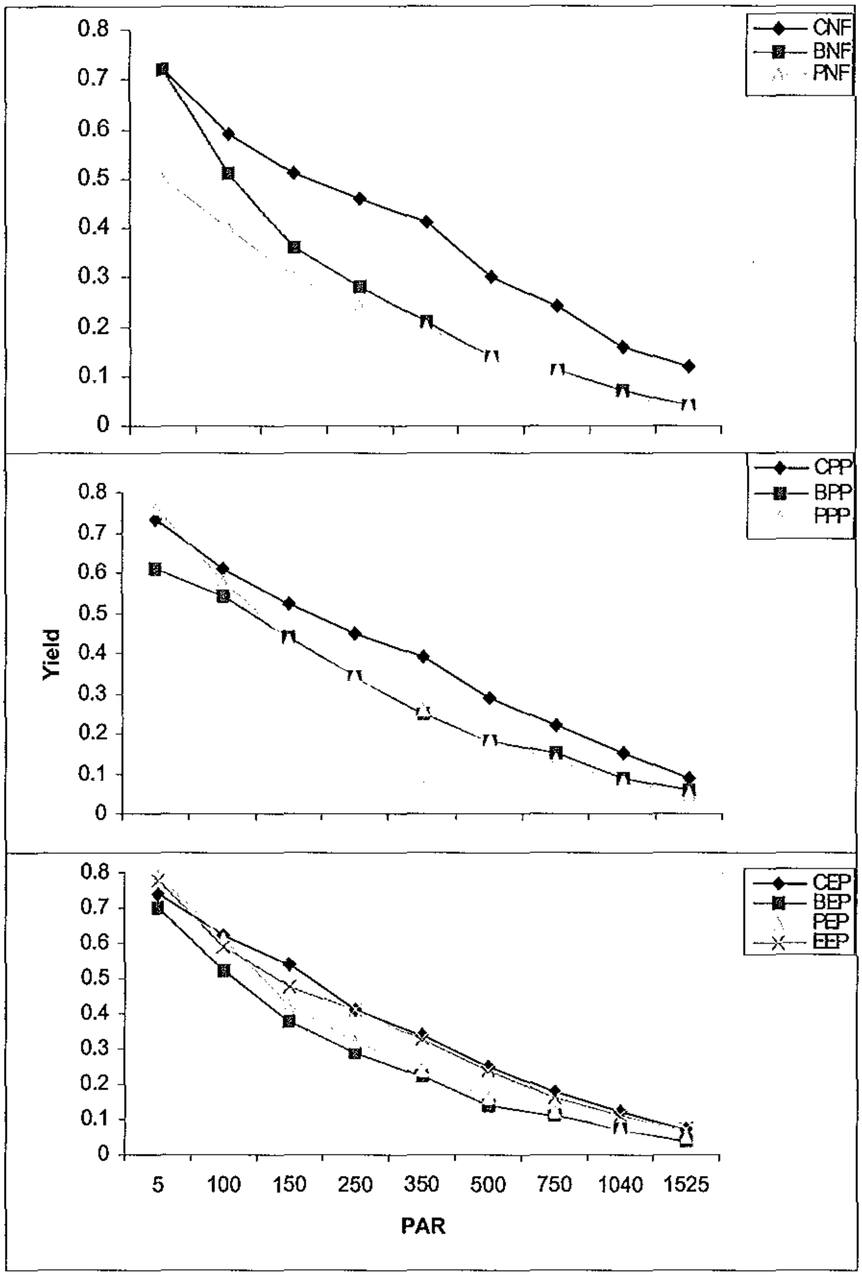

Fig. 10 Yield as a function of incident light intensity in leaves of seedlings of *C. macrostachyus* (C), *B. abyssnica* (B), *P. falcatus* (P) and *E. saligna* (E) grown in natural forest (NP), *Eucalyptus* plantation (EP) and *Pinus* plantation (PP).

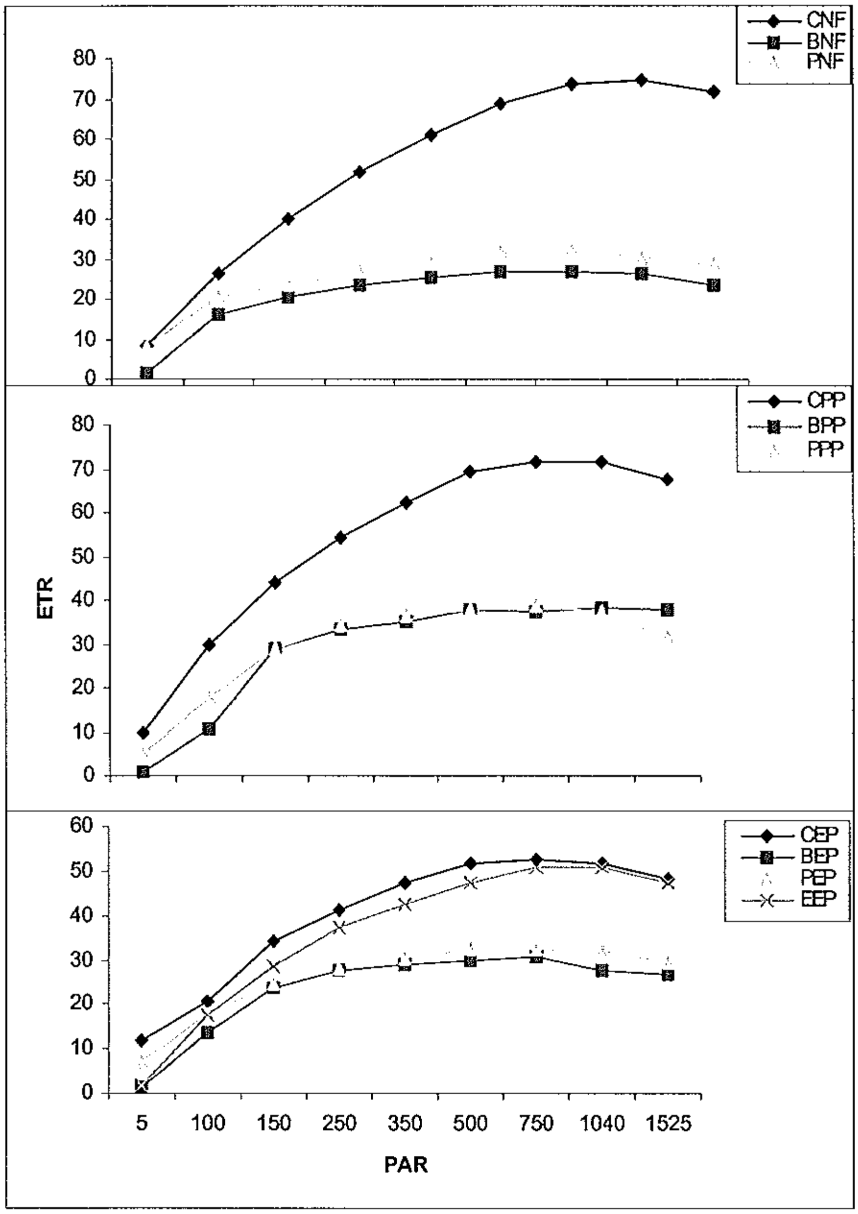

Fig. 11 ETR as a function of incident light intensity in leaves of seedlings of *C. macrostachyus* (C), *B. abyssnica* (B), *P. falcatus* (P) and *E. saligna* (E) grown in natural forest (NP), *Eucalyptus* plantation (EP) and *Pinus* plantation (PP).

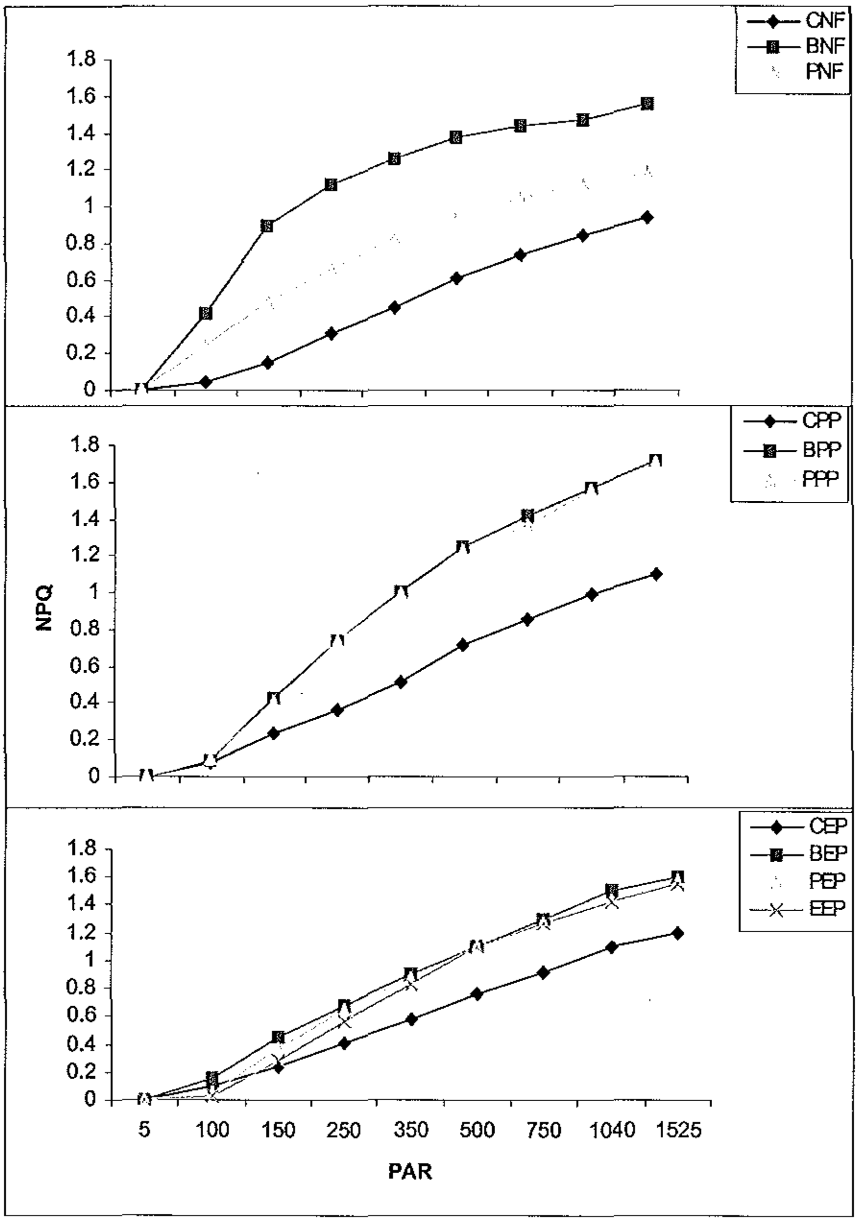

Fig. 12 NPQ as a function of incident light intensity in leaves of seedlings of *C. macrostachyus* (C), *B. abyssnica* (B), *P. falcatus* (P) and *E. saligna* (E) grown in natural forest (NP), *Eucalyptus* plantation (EP) and *Pinus* plantation (PP).

4 Discussion

4.1 Regeneration of indigenous plants inside plantation and adjacent natural forest

In this study we observed that there was a much denser regeneration of indigenous plants in plantation forests than in adjacent natural forest. Moreover, clear difference in the regeneration of indigenous plants was also observed between plantation forests and unplanted (open) area. There was high regeneration of indigenous plants inside plantation forests as compared to unplanted area where little or no regeneration occurred. This high regeneration density of indigenous seedlings inside plantation forests may be due to factors associated with creation of favorable microsite conditions and seed availability (Lugo, 1992; Parrotta, 1992; Parrotta, 1995; Loumeto and Huttel, 1997; Parrotta *et al.*, 1997; Power *et al.*, 1997; Wunderle; 1997).

The observed difference in the regeneration density of indigenous seedlings across sites can indicated their successful development inside plantations. Based on the results obtained it is possible to suggest that exotic tree plantations facilitate the regeneration of indigenous species at least far better than unplanted (open) areas. Since planted species usually fail to regenerate under their own canopy (Lugo *et al.*, 1993) and / or human intervention (management activities) are possible, plantations that supported high seedling density of indigenous species more possibly could allow them to reach the canopy than the natural forest. Overall, plantation forests may potentially improve physical and biological site conditions fostering subsequent successional development towards a secondary indigenous forest.

Low density of study species in the adjacent natural forest may also be attributed to high disturbance scale. As compared to the natural forest, plantations are better protected from disturbance by humans and livestock (personal observation). This disturbance probably hinders regeneration development of woody species. The absence or little regeneration of indigenous plants in unplanted area may be associated with high disturbance, absence of roosting sites and high light intensity that favors the dominance of grasses (Parrotta, 1992, 1993).

The difference in density of study species in plantations and natural forest becomes more and more pronounced as one moves upwards from seedling class into sapling and tree size stem classes. The relatively higher decline in density of indigenous species at higher size classes (sapling and tree size classes) in natural forest could aggravate the changes on future forest structure and composition in two ways. First, it inhibits the development of saplings into the higher stages of the plant. Second, it brings changes in the microclimatic conditions of the forest floor which this in turn affects growth and establishment of understory woody species favoring mainly the development of high light demanding herbs and shrubs.

4.2 Plantation species and regeneration of indigenous plants

Exotic tree plantation species seem to have considerable differences in their effects on the establishment of indigenous plants. There was higher regeneration density and shorter distance from individual trees of plantation species of study species in *Eucalyptus* plantation than in *Pinus* plantation. Among the study species, *P. falcatus* had the highest number of individuals and the smallest distance from individual plantation tree species in both stands which may indicate its potential to establish near the tree boles. The presence of large number of individuals and closer establishment of understory indigenous plants indicate their better successful regeneration in *Eucalyptus* plantation. Denser regeneration and closer establishment to individual plantation trees of study plants particularly *P. falcatus* in *Eucalyptus* plantation reveal that *Eucalyptus* provides better favorable conditions for understory colonization which in turn indicate more nursing effect and less competitive aggressiveness of *Eucalyptus* than *Pinus* in fostering undergrowth of these species (Turvey *et al.*, 1983; Bi and Turvey, 1994).

The difference in regeneration development of study species inside plantation forests may be affected by several factors. Plantation species and silvicultural treatments seem to have exerted a significant influence. The choice of plantation species is likely to influence understory colonization as tree species will differ in their facilitating effect (Michelsen *et* al., 1996; Parrotta, 1995; Keenan *et al.*, 1997; Loumeto and Huttel, 1997; Parrotta *et al.*, 1997; Yitebitu, 1998). According to Yitebitu (1998), for example, *Eucalyptus* plantation had light crowns and thin litter layer which allow penetrations of more light to the forest floor and reduce influence litter as a barrier for seedling emergence. *Pinus* plantation had dense crowns and thick litter layer which may have influence on the growth and establishment of seedlings of indigenous plants. The variation in litter thickness can thus partly explain the presence of fewer but bigger individuals of indigenous plants inside *Pinus* plantation. In addition, since the two plantation stands had different histories of management past silvicultural activities might contribute to the difference in regeneration of indigenous plants. Coppicing of *Eucalyptus* plantation at about 5 to 7 year interval can enhance better growth of understory woody species. On the contrary, only periodic thinnings which create small openings have been made in *Pinus* plantation.

Although the two plantations had variations in the above respects, population structure of indigenous plants growing inside them indicated more or less an increment in density towards lower size classes in both stands. This would probably show a healthy regeneration and if some management activities are involved the understory woody species will replace the overstory species.

Seed availability played an important role in the development of indigenous vegetation inside plantation forests. Its influence was examined inside *E. saligna* and *E. globulus* plantations at Degaga. The density of understory indigenous species was higher in the edge than in the center of *Eucalyptus* plantation. More regeneration of indigenous plants in the edge of the plantation may be attributed to the difference in seed availability. They had very slight differences in size and distance from the tree trunk of plantation species at the center and edge of the plantation. Surprisingly the two edges of *E. globulus* plantation at equal distance from the seed source supported significantly different density of *P. falcatus*. These above situations may indicate the importance of seed availability for the difference in the regeneration density of indigenous species at the central and peripheral zone of plantation stands. The high decline in the density of *P. falcatus* at further distance from the seed sources, which were located at about 10 m from the plantation stands, may indicate the difference in seedrain and the possibility to maximize or accelerate natural regeneration of indigenous species by leaving patches of natural forest or individual parent trees near or inside the plantation stands.

The clustered distribution of indigenous species especially *P. falcatus* near the edge of plantation could be due to preference for trees as roosting by vectors near the edge. Large numbers of bigger trees were found along the edge of the plantation. This agrees with the observation of Parrotta

(1995) where marked differences in seedling density of colonizing species were found in the center and at the periphery of plantation. Parrotta *et al.* (1997) and Loumeto and Huttel (1997) also found reduction in density and diversity of colonizing species with increasing distance into the plantation from seed sources. These authors suggested that the fostering effect of plantations generally decreases with increasing distance from seed sources. This supports our observation where the density of *P. falcatus* seedlings significantly declined with increasing distance from the seed source. The variation in density of indigenous species at the central and peripheral zone of plantation and with distance from the seed source seems to indicate that seed dispersing agents may be operating in a different way across these parts of the plantation area.

The results support the hypothesis that proximity to potential seed sources significantly affects understory colonization of plantations by indigenous species and suggest seed dispersal is increasingly a limiting factor at greater distances from seed sources. Thus, while the plantation program has been successful in creating favorable environment for regeneration of indigenous plant species, further management intervention such as enrichment planting, leaving patches of indigenous parent plants and better understanding of behavioral ecology of seed dispersal agents may be required to accelerate regeneration.

4.3 Plantation species and seedling architecture of understory indigenous plants

Seedlings of *P. falcatus* and *B.* abyssinica exhibited variability in their growth in both stands. They had more height growth in *Pinus* plantations and lateral growth in *Eucalyptus* plantation. The trade-off between height growth and lateral growth can be used to account for intraspecific differences between seedlings established inside *Eucalyptus* and *Pinus* plantations. The difference may indicate trade-off between biomass distribution to increase lateral growth and height growth. Allocation of more biomass to leaves and/ or branches to increase lateral growth helps to survive in the forest understory by intercepting much of the available light while more biomass allocation to stem growth increases height growth which allows to reach high light levels in the canopy (Kohyama, 1987; Kohyama and Hotta, 1990; King, 1991; Whitmore, 1996).

Species with height growth are favored following gap creation because taller seedlings are most likely to become established in gaps (Brown and Whitmore, 1992). On the other hand, according to Kohyama (1987) species with lateral growth are favored by at sites if time between germination and gap creation is long relative to the survivorship of those seedlings with height growth in shade. Height growth allows plants to grow into better illuminated regions. More height growth of species in *Pinus* plantation indicates the need for exposure to a relatively high irradiance. Therefore, more silvicultural treatments such as periodic thinnings are required to favor establishment of understory indigenous plants in *Pinus* plantation than in *Eucalyptus* plantation.

Because of past management activities such as coppicing and thin crown trees, understory indigenous species in *Eucalyptus* plantation obviously experienced exposure to increased level of light intensity. However, indigenous seedlings in *Eucalyptus* plantation produced relatively larger leaf area than those in *Pinus* plantation. The larger leaf area allows to trap more light available in the forest understory which increase their competitive ability for light with *Eucalyptus* trees.

4.4 Water relation of plantation species and regenerating understory indigenous plants

The three species compared showed distinct differences in their transpiration rates under increasing vapor pressure deficit. It is interesting to note that the extent of rise in water loss by transpiration with increasing VPD was considerably higher in *E. saligna* than in *P. falcatus* or *B. abyssinica*. This difference in transpiration indicates better water use or low water requirement by indigenous species. Thus, although eucalypts have high water consumption which is consistent with their high rate of growth, low transpiration rate of indigenous species may reveal their ability to compete well with eucalypts with respect to water-use. This in turn indicates the possibility of indigenous species to grow inside eucalypt plantations. In addition, increased water loss via transpiration with VPD showed that leaves were supplied with a sufficient amount of water (Fitter and Hay, 1989).

The difference in transpiration rate between the two sides of the leaves could be due to the difference in stomatal density or microenvironment in the vicinity of the leaf surfaces or responsiveness to the prevailing environmental conditions. There was insignificant difference in temperature and relative humidity on the two sides of the leaves of study species. Also there was proportional increase of transpiration with VPD. Thus, difference in stomatal density (i.e. more number of stomata on the lower sides of the leaves) may be responsible for the difference in transpiration rate of the two sides (Jones, 1992).

4.5 Comparison of characristics of PS II photochemistry among plants developed inside plantations and adjacent natural forest.

Fluorescence parameters help to assess photosynthetic responses of plants to light such as photochemical efficiency of PS II, the degree to which Q_A, the primary stable electron acceptor for PS II, is reduced and the degree to which excessive energy is dissipated as heat (Maxwell and Johnson, 2000). Measurements of fluorescence parameters in the leaves of understory indigenous plants in plantations and the adjacent natural forest indicated that the photochemical systems of these plants responded similarly during the course of the day. Species in both plantations and natural forest exhibited no significant variations in the characteristics of PS II photochemistry investigated, that is, F_v/F_m, $\Delta F/F_m$, ETR and NPQ. Since light is a major limitation to photosynthesis most commonly to tree seedlings growing in forest understories, photosynthetic response of plants to various irradiances can be influenced by the irradiance where they were grown (BjÖrkman, 1987; Riddoch *et al.*, 1991). The marginal differences in photosynthesis yield of indigenous species in the study sites may therefore show that plantations did not limit the light environment for the growth of indigenous seedlings.

The value of F_v/F_m, which is used as a measure of potential quantum yield of PS II (Demmig and BjÖrkman, 1987; Krause and Weis, 1991), remained almost constant throughout the course of the day. Values of F_v/F_m below 0.8 generally indicate photoinhibition (BjÖrkman, 1987). The values of F_v/F_m in leaves of study plants in plantations and adjacent natural forest were not significantly different from the above value indicating optimal quantum efficiency of unstressed leaves and hence the leaves were not under stress conditions prior to the measurement (BjÖrkman, 1987). Because high irradiance may potentially impair photosynthetic capacity and induce photoinhibition if plants are exposed to a high light intensity higher than that experienced during earlier growth (BjÖrkman, 1987), the absence of photoinhibition and insignificant difference in the value of F_v/F_m in leaves of understory indigenous seedlings indicated that plantations provide moderate microsite conditions.

However, chlorophyll fluorescence emitted by dark-adapted leaves (30 min) of *P. falcatus* in the clearfelled plantation site revealed the occurrence of photoinhibition. F_v/F_m of 0.71 was obtained which was significantly smaller than the value in leaves of seedlings inside forest understories. This reduction of F_v/F_m (photoinhibition) shows the influence of complete clearance of overstory species on the growth of colonizing understory vegetation and the protective effect of plantation forests from high light stress. On the other hand *P. falcatus* leaves in the clearfelled had lower F_m and F_0 and higher ETR and NPQ which might indicate the absence of photodamage to PS II (Demmig and BjÖrkman, 1987; Demmig-Adams and Adams, 1992; Anderson *et al.*, 1997; Lovelock *et al.*, 1998). High levels of ETR and NPQ can therefore be seen as a regulatory response to light stress reducing the probability of photodamage to PS II. The potential of *P. falcatus* to grow in forest understories and in the open by protecting its photosynthetic apparatus thus showed its wide ecological tolerance. This agrees with the investigation of Gemedo (1999) where *P. falcatus* has been observed to grow both in forest understories and in clearings.

To assess the potential photosynthetic performance of study species at different sites, light response curves were obtained and no significant differences were observed in the level of yield, apparent electron transport rate and non-photochemical quenching indicating that species were experiencing similar light environment. The similarity in light saturation behavior of indigenous species inside plantations and the adjacent natural forest suggests the potential of plantations for the development of indigenous vegetation under their canopies.

Seedlings of *P. falcatus* and *B. abyssinica* had a sequence of shade-adapted to light-adapted behavior in Natural forest > *Eucalyptus* plantation > *Pinus* plantation. *C. macrostachyus* had a sequence of the above behavior in *Eucalyptus* plantation > *Pinus* plantation > Natural forest. It needs to be noted however that the natural forest where measurements from *C. macrostachyus* were taken was more open compared to that of *P. falcatus* and *B. abyssinica*. Almost in all sites, values of $\Delta F/F_m'$ and ETR were low in *B. abyssinica* and high in *C. macrostachyus*. The light response curve suggested a sequence of shade-adapted to light- adapted behavior of *B. abyssinica* ≈*P. falcatus* > *E. saligna* ≈*C. macrostachyus*. Overall, differences in photosynthetic responses of individuals of each species across sites were minimal as compared to differences among individuals of different species at the same site.

Altogether the results from the investigation of fluorescence parameters in leaves of indigenous seedlings grown in plantations and adjacent natural forest indicated the role of exotic plantation tree species as nurse trees for growth of indigenous seedlings under their canopies.

5. Conclusion

The results of the present study indicate that plantations have a marked fostering effect on the development indigenous vegetation and hence can greatly accelerate forest succession at least far better than open (unplanted) areas. There was high regeneration of study species in *Pinus* and *Eucalyptus* plantations, whereas relatively low regeneration occurred in the adjacent natural forest. Few or little regeneration of study plants was found in open areas. Of all the study species *P. falcatus* was found to be the most successfully regenerating indigenous species in both plantations and natural forest. With the high density of regeneration of study species under the canopy of exotic tree plantation, it is possible to conclude that plantation stands can promote a high density (stem/ ha) of species for natural regeneration.

Plantations could more possibly allow or facilitate successional development of understory vegetation into secondary indigenous forest if some management practices are also implemented. This can be partly justified by the development of *P. falcatus* trees of size > 10 cm (DBH) in *E. saligna* plantation which had density of about 1400 s/ha. Since loss of tropical forests is continuing at alarming rates (FAO, 2001), the role of plantation forests for the maintenance of remnant natural forests by seeding up growth of indigenous species under their canopies through their effect on microsite conditions is significant

The two plantation stands also had different potential for regeneration of indigenous plants under their canopies. The successful regeneration of study plants inside plantation forests was influenced by planted species, seed availability and past management histories. These results suggest that with careful selection of overstory species and management activities and further study of the behavioral ecology of seed-dispersal agents, forest plantations could be a promising tool for maintaining species diversity on degraded or deforested areas by reducing pressure on the remnant natural forests and fostering forest succession.

So far management activities for high overstory wood yields have continued to be important while considerable effort is exerted to control or eliminate understory vegetation. Management practices that facilitate natural successional processes and the development of species rich understories need to be primary goal so that plantations could contribute more and play a great role for maintenance of patches of natural forests by reducing pressure and fostering growth of indigenous flora under their canopies.

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