

TREE SEEDLING GROWTH IN
GAPS AND UNDERSTOREY

The importance of gap phase regeneration in maintaining species diversity in forest is well established. Regeneration in gaps involves colonization by new species and growth of hitherto suppressed seedlings and saplings. Most tropical trees depend on gaps for their successful regeneration (Hartshorn 1980, Whitmore 1984) and they show ecological differentiation in growth response to canopy openings (Ricklefs 1977, Connell 1978, Whitmore 1982, Pickett 1983, Brokaw 1985a). Most species are in some sense gap dependant since they positively respond to the locally enhanced light levels in the canopy openings. The canopy gaps created by treefalls, a major source of environmental heterogeneity in the close-canopied forest (Denslow 1980, Brokaw 1985a), are important for growth and reproduction of many forest trees (Richards and Williams 1975, Hartshorn 1980, Clark and Clark,

1987b). Gap microclimate is generally characterized by low humidity and high light intensity, temperature and soil moisture (Denslow et al 1990). The extent to which this increase in light and temperature and soil moisture regimes affects seedling growth depends on its physiological ability to utilize these resources. The effect of canopy gaps on the growth of tree seedlings in the tropical rain forests have been studied by Popma and Bongers (1988), Uhl et al (1988), Canham (1988) and Denslow et al (1990). Brokaw (1985b) and Denslow (1987) have emphasized the importance of relationship between gap size and growth abilities of tree species in determining the structure and composition of tropical forests, while Leigh et al (1982) and Brokaw and Scheiner (1989) have examined the effect of gap size on growth of tree species. However, only a few workers have compared the performance of tree juveniles in the gaps and understory (Clark and Clark 1987). Such studies on tree seedling performance in gaps and understory are completely lacking in India. Further, the effect of gap induced changes in forest microenvironment on the growth of tree seedlings is also not well understood.

The growth response of seedlings of dominant tree species in gaps of different sizes and in the forest understory studied in the Mawphlang forest has been presented in

this chapter. The influence of various microenvironmental factors on the growth performance of the seedlings has also been assessed.

METHODS

Growth performance of the tagged tree seedlings in the small, medium and large gaps and in the ten permanent quadrats in the understorey (cf. Chapter 6) were studied from August, 1988 to August, 1990. Various growth parameters such as shoot length, number of leaves, total leaf area and stem diameter of all seedlings were measured at monthly intervals. Leaf area was measured by a portable leaf area meter (LICOR, USA) and the stem diameter was measured just above the ground level with the help of a screw gauge. All the parameters were expressed on per seedling basis. By using these data, growth functions such as relative shoot growth rate (RSGR) and leaf area index (LAI) were computed according to the methods described by Combs et al (1985).

$$\text{RSGR} = \frac{\ln h_2 - \ln h_1}{t_2 - t_1}$$

where, t is the time in months, h_1 is the shoot length at time t_1 and h_2 is the shoot length at time t_2 .

$$\text{LAI} = \frac{\text{Total surface area of leaves}}{\text{Ground area covered by seedling canopy}}$$

Since growth in shoot length and leaf area was very slow, RSGR and LAI were calculated on seasonal basis. Thus the values of August, November, February and May were taken as representatives of growth during rainy, autumn, winter and spring seasons, respectively.

The effects of photon flux density, relative humidity, soil moisture, air temperature, soil temperature and litter depth on growth behaviour of seedlings were studied by computing partial correlation coefficients. In order to simplify the analyses, the four growth parameters described above were combined into a synthetic measure of growth using Principal Component Analysis (Poole 1974). The first Principal Component (PC I) explained about 75% variance among the four growth parameters of the seedlings in gaps and understory. Thereafter partial correlation coefficients (r) were computed between PC I of growth and microenvironmental variables. Multiple regression models were proposed for the different species to estimate the growth response of seedlings in a given set of micro-environmental factors (Zarr 1974).

RESULTS

Growth

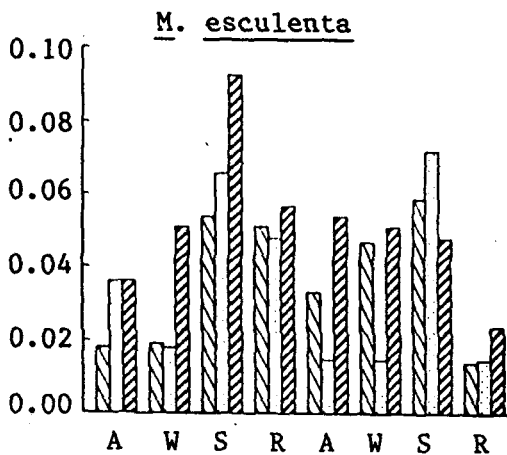
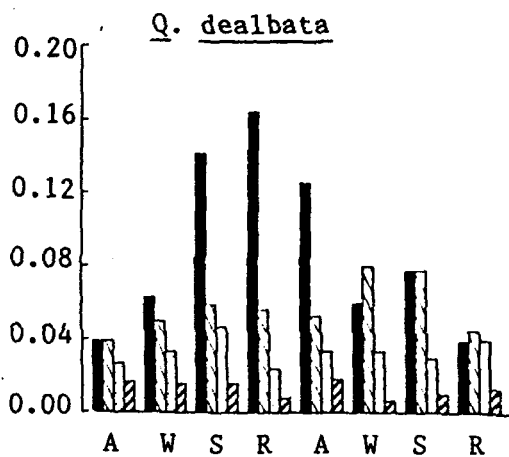
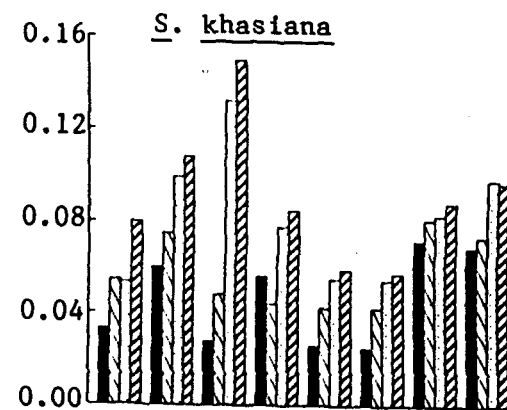
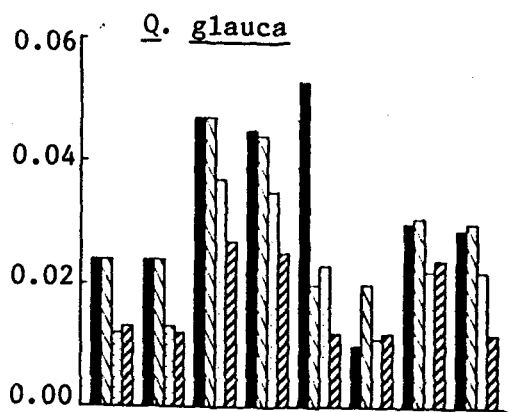
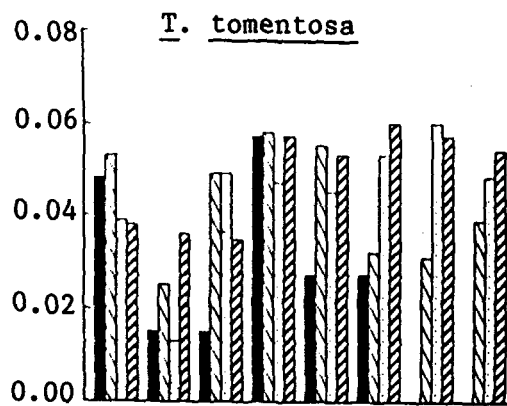
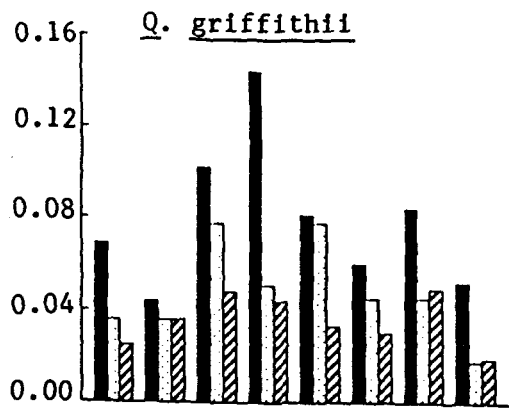
Relative shoot growth rate of three Quercus species was higher in the forest understorey than in the gaps but S. khasiana, M. esculenta and T. tomentosa seedlings showed better growth in the medium and large gaps (Fig.7.1). In general, all species showed maximum RSGR during rainy season. Basal area of all tree seedlings increased with time both in gaps and forest understorey (Fig.7.2). Difference in basal area along understorey-gap size gradient was prominent in case of M. esculenta, Q. griffithii, Q. glauca and T. tomentosa. In Q. glauca it was higher in the understorey and small gaps while in Q. griffithii the seedlings inhabiting understorey and medium gaps had higher basal area than those in large gaps. Basal area of M. esculenta seedlings was negatively related to gap size, but in T. tomentosa it was higher in the small gaps. In case of Q. dealbata and S. khasiana the trend was not clear (Fig.7.2).

Foliage dynamics

Figure 7.3 shows the foliage dynamics of tree seedlings in the Mawphlang forest. The behaviour of Q. glauca and Q. dealbata was similar, both having long leaf blade expansion period extending from May to February. In these

Fig.7.1. Relative shoot growth rate of tree seedlings in understorey (■) and small (▨), medium (▩), and large (▧) gaps during Autumn (A), Winter (W), Spring (S) and Rainy (R) seasons.

RELATIVE SHOOT GROWTH RATE (cm month⁻¹)

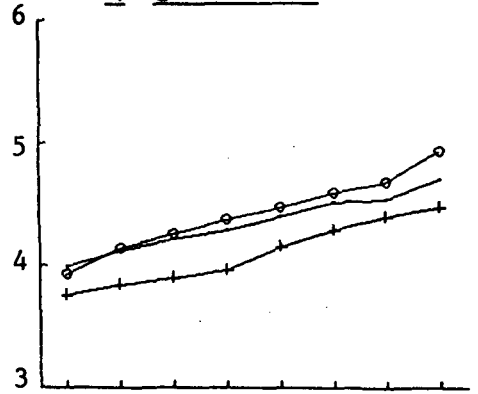


SEASONS

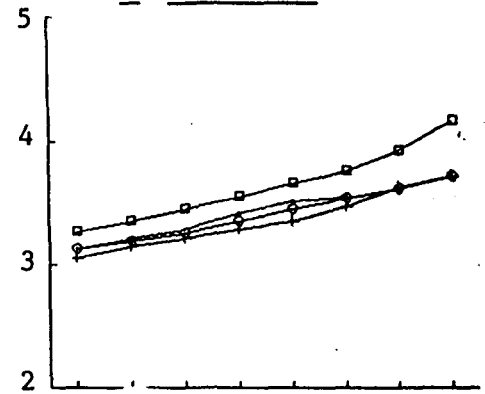
Fig.7.2. Seasonal increase in basal area of tree seedlings during two years of growth in understorey (-●-) and small (-□-), medium (-○-) and large (+) gaps. [Autumn (A); Winter (W); Spring (S); Rainy (R)].

BASAL AREA PER SEEDLING (mm²)

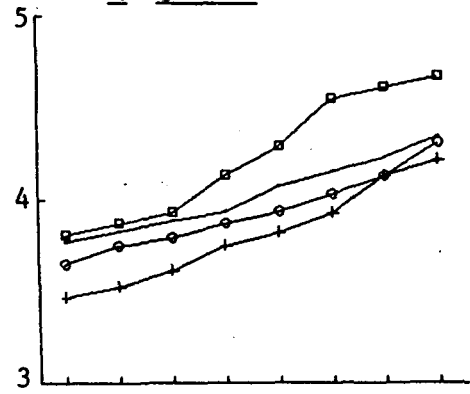
Q. griffithii



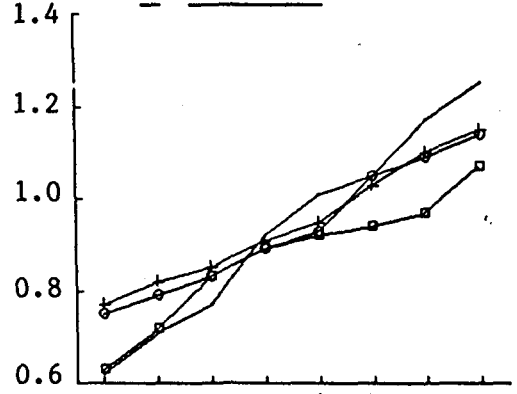
T. tomentosa



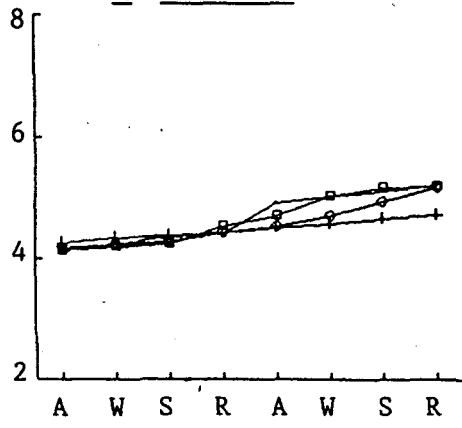
Q. glauca



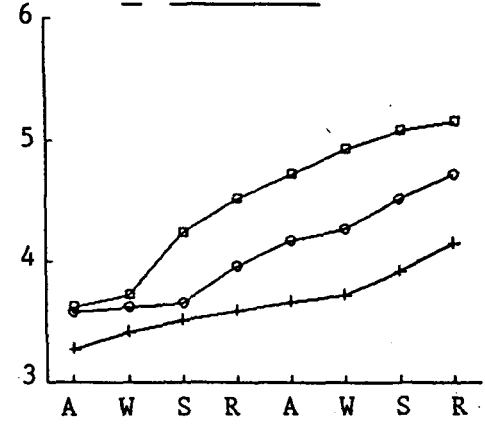
S. khasiana



Q. dealbata

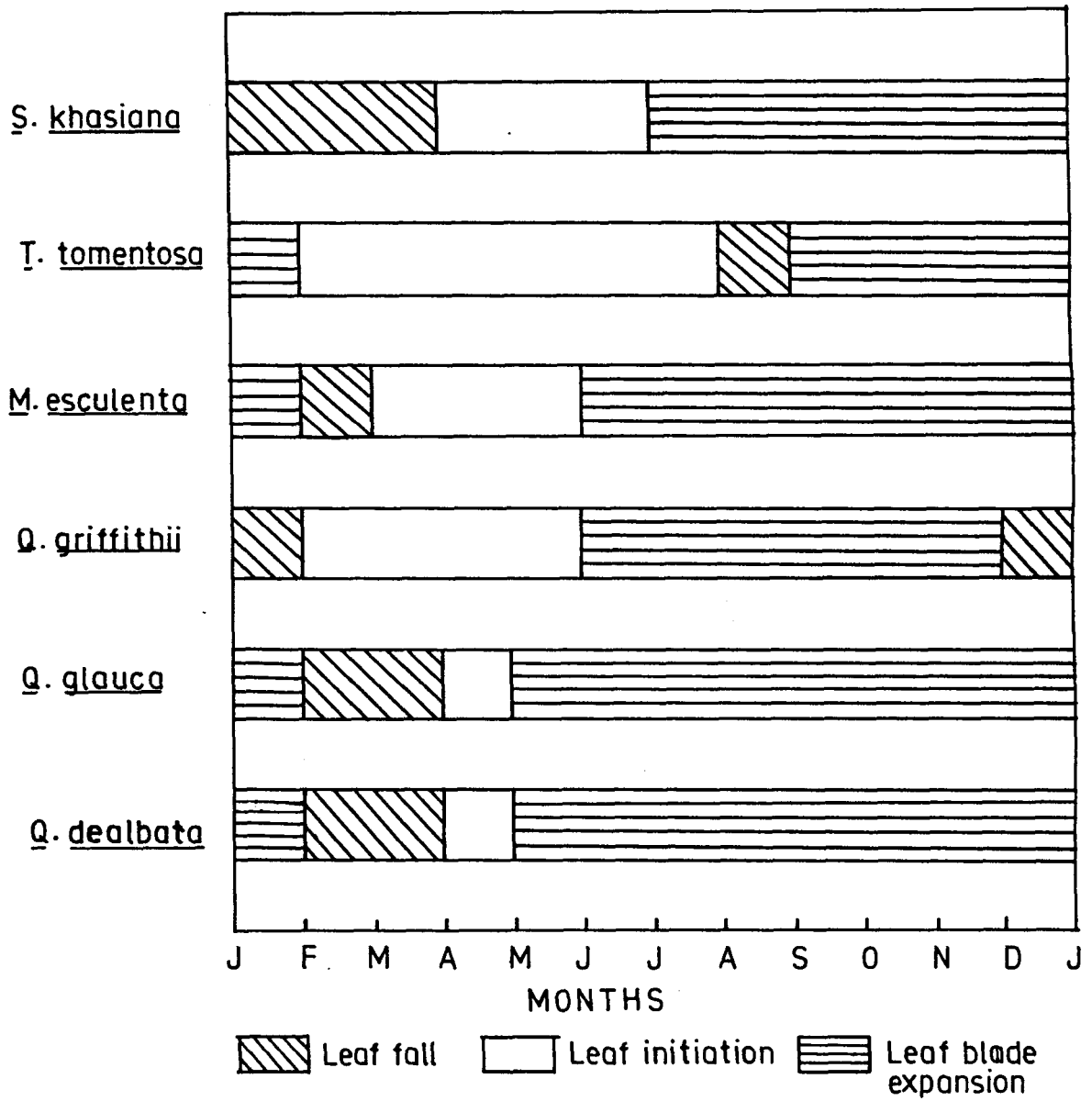


M. esculenta



SEASONS

Fig.7.3. Foliage dynamics of tree species in the Mawphlang forest.



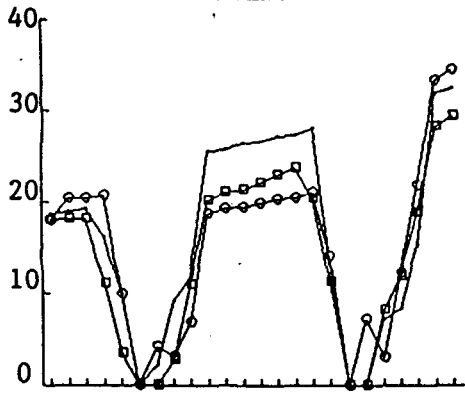
species leaf initiation occurs between April and May. Both the species show partial leaf shedding during spring (February to April). Q. griffithii is a deciduous species and leaf shedding is complete between December and February. New leaves appear during spring and early rainy season (March to July), and expansion of leaf blade takes place between June and December. Leaf blade expansion in M. esculenta extends from June to February. Leaf initiation in these two species takes place between May and June and February and August, respectively. Leaf fall in these species lasted for a brief period during winter. S. khasiana, a semi-deciduous species, partially sheds its leaves between January and April. Leaf initiation is observed between April and July and blade expansion occurs during July to January.

In general, leaf area per seedling increased with time. Q. griffithii and Q. dealbata showed maximum leaf area in the understorey, while other species showed higher values in large and medium sized gaps (Fig.7.4). Seasonality in foliage dynamics influenced the photosynthetic surface of seedlings as is clearly evident from the fall and rise of leaf area curves during different months of the year. The deciduous nature of Q. griffithii was responsible for the drop in leaf area to zero during winter. Among the other two Quercus spp, leaf shedding was prominent only in

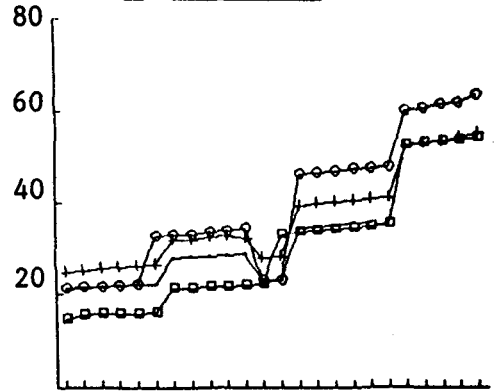
Fig.7.4. Changes in total leaf area of tree seedlings during two years of growth in understorey (—●—) and small (—□—), medium (—○—), and large (+) gaps.

LEAF AREA PER SEEDLING (cm²)

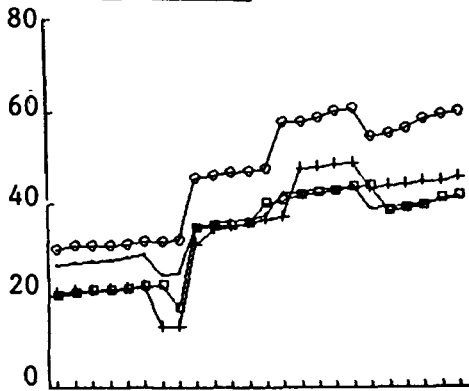
Q. griffithii



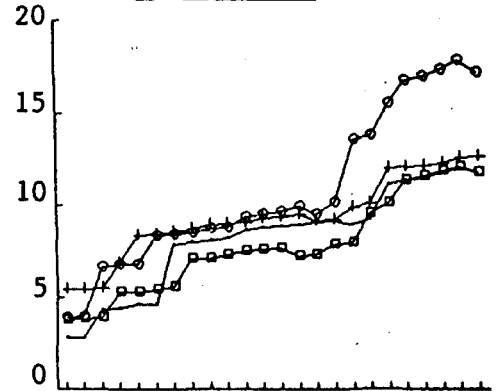
T. tomentosa



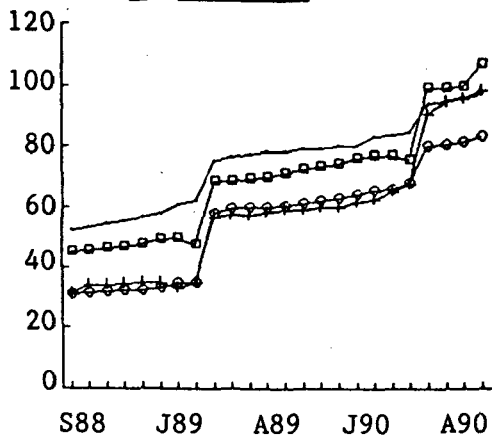
Q. glauca



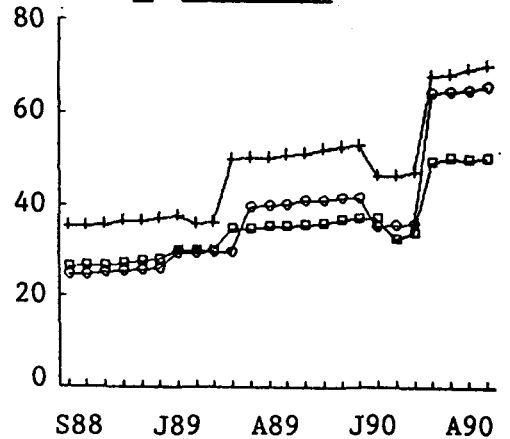
S. khasiana



Q. dealbata



M. esculenta



M O N T H S

case of Q. glauca. Seasonality in leaf area of M. esculenta and T. tomentosa was observed only during the second year of their growth. S. khasiana showed a gradual rise in leaf area during two years of study. In this semi-deciduous species, seasonality was not prominent due to overlapping of leaf fall and leaf initiation periods. In all species the period of sudden increase in leaf area corresponds to the period of leaf initiation (Fig.7.4).

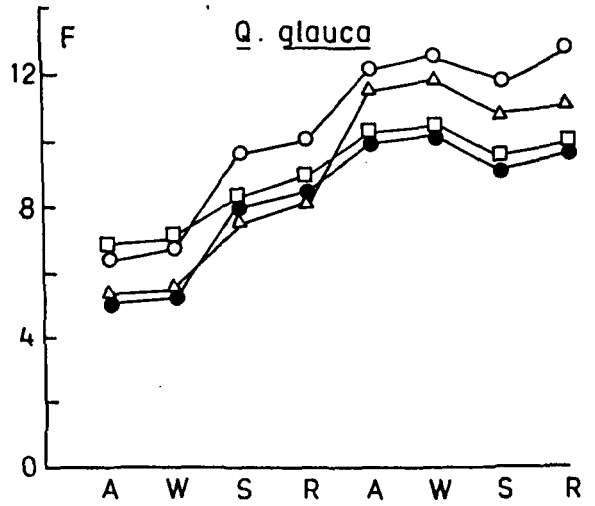
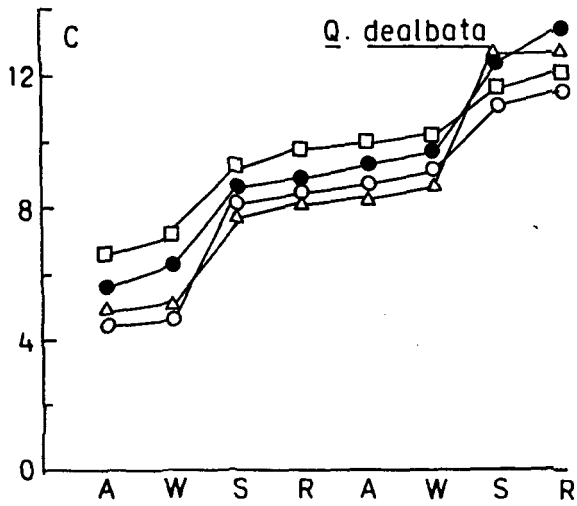
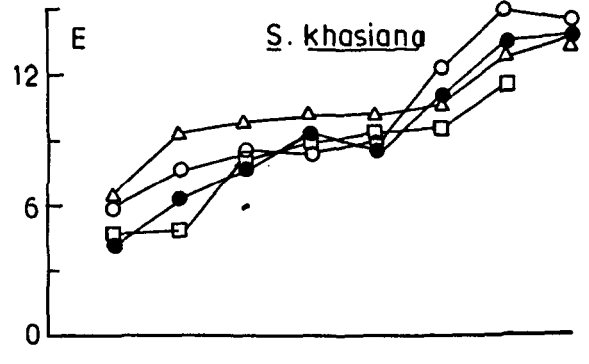
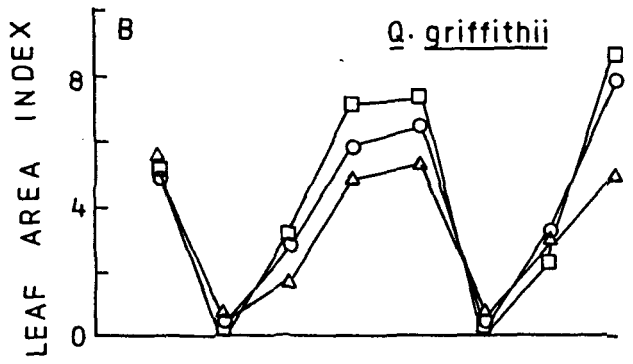
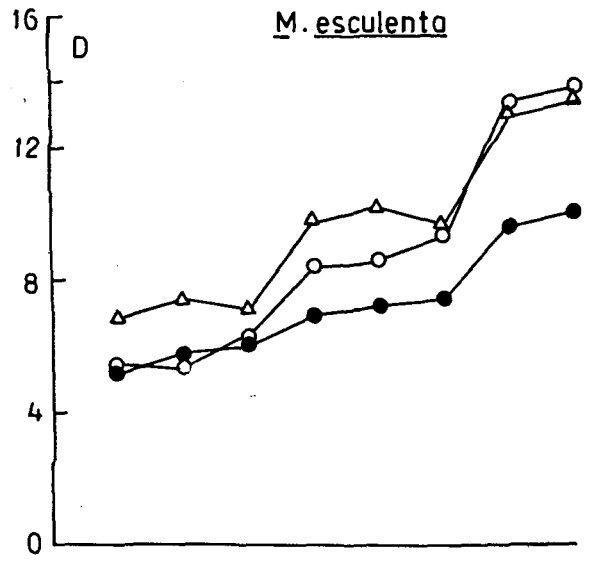
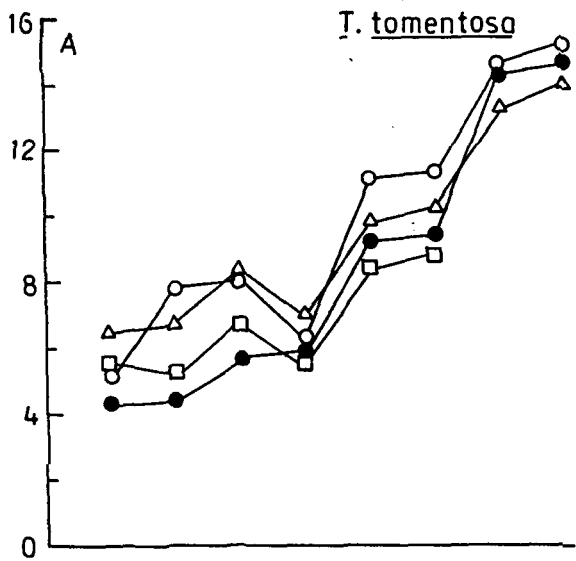
Leaf area index (LAI) of Q. dealbata and Q. griffithii was maximum in the understorey and minimum in the large gap. In case of Q. glauca and T. tomentosa it was higher in the medium sized gaps. S. khasiana and M. esculenta had highest LAI in the large gaps and lowest in the small gaps (Fig.7.5).

Relationship between seedling growth and microenvironment

The influence of various microenvironmental variables on seedling growth was evaluated by comparing significant ($P < 0.05$) values of partial correlation coefficients 'r' between PC I of growth and climatic and edaphic variables. These values are represented through a bar diagram in Fig.7.6.

Results indicate that growth of all species except M. esculenta in forest understorey was significantly affected

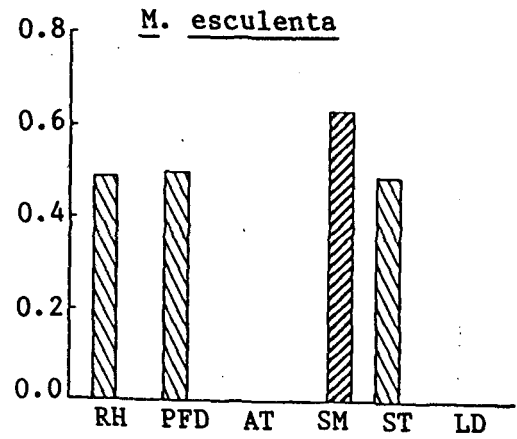
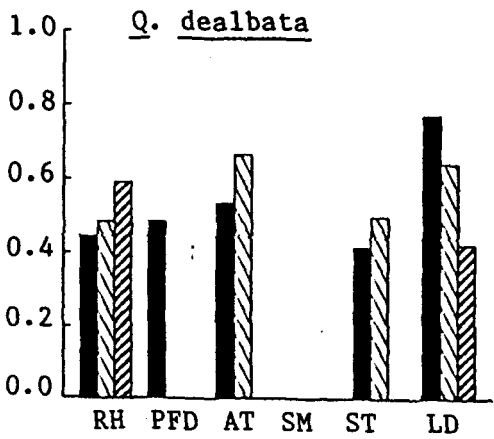
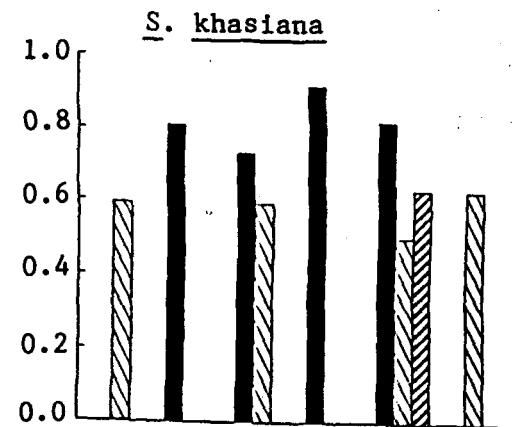
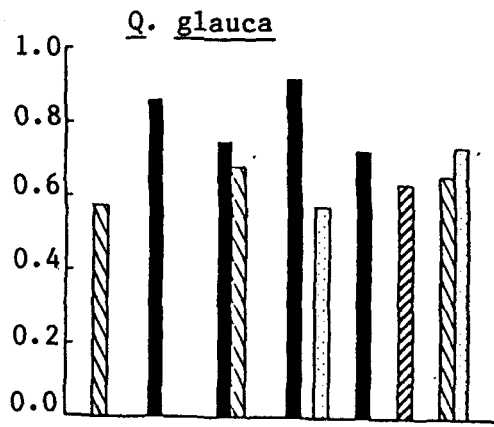
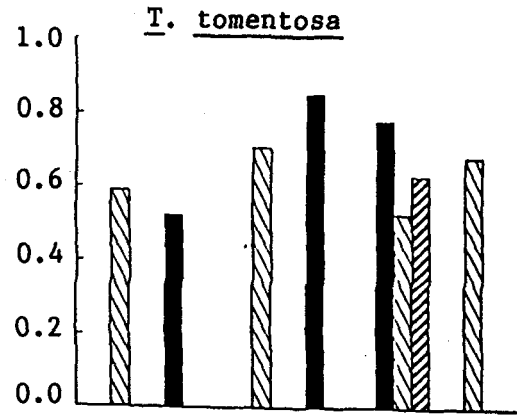
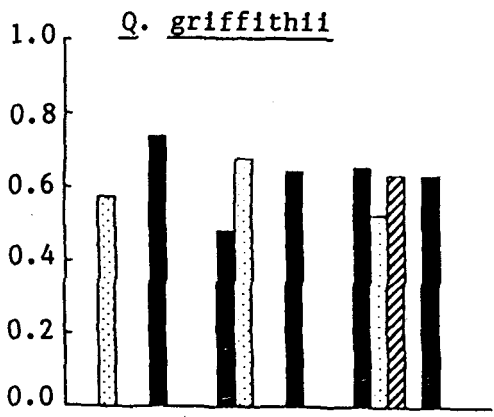
Fig.7.5. Leaf area index of tree seedlings in understorey (■) and small (▨), medium (▩) and large (▧) gaps during Autumn (A), Winter (W), Spring (S) and Rainy (R) seasons.



SEASONS

Fig.7.6. Partial correlation coefficients (r) between Principal Component-I of the growth parameters of tree seedlings and six microenvironmental variables in understorey (■) and small (▨), medium (▩) and large (▧) gaps. The values represented in the figure are significant at $P < 0.05$ (RH - relative humidity; PFD-photon flux density; AT-air temperature; SM-soil moisture; ST-soil temperature; LD-litter depth).

PARTIAL CORRELATION COEFFICIENT (r)



MICRO ENVIRONMENT

by photon flux density. For M. esculenta this factor was important in small gaps; in the large gaps soil moisture was found to be important. Relative humidity was important in small gaps for the seedlings of S. khasiana, M. esculenta, T. tomentosa, Q. dealbata and Q. glauca. It influenced the growth of Q. griffithii and Q. dealbata in medium and large gaps, respectively. In the understory, growth of S. khasiana, T. tomentosa and Q. glauca was strongly related to soil moisture. Seedlings of Q. griffithii were also affected by the soil moisture in the understory, although the relationship was less significant. Soil and air temperature and litter depth seemed to influence growth of most species in the understory and small gaps.

The multiple regression equations showing the relationship between PC I of growth and the microenvironmental factors have been given in Table 7.1.

DISCUSSION

Differential growth response of tree species in different micro-habitats in the forest has an important bearing on their spatial and temporal distribution patterns. Small scale disturbances like treefalls have been shown to

Table 7.1. Multiple regression equations showing relationship of PC I of growth with microenvironmental factors in the understory (US), small (SG), medium and large (LG) gaps.

Species	For- est stand	Cons- tant	Microenvironmental variables						R ²	n
			RH	PFD	AT	SM	ST	LD		
<u>Schima</u> <u>khasiana</u>	US	-18.213	NS	-0.163**	NS	-2.163**	2.165**	NS	0.843	21
	SG	-17.109	-0.112**	NS	-1.108**	NS	1.238*	5.418**	0.725	23
	MG	-10.990	NS	NS	NS	NS	NS	-0.307**	0.284	24
	LG	-18.434	NS	NS	NS	NS	1.858**	-0.140**	0.457	-
<u>M.</u> <u>esculenta</u>	US	-	-	-	-	-	-	-	-	24
	SG	- 1.691	-0.125**	NS	NS	NS	1.653*	NS	0.501	24
	MG	- 7.887	NS	NS	NS	NS	NS	NS	0.269	24
	LG	-18.92	NS	NS	NS	NS	1.879**	NS	0.485	24
<u>T.</u> <u>tomentosa</u>	US	-14.307	NS	-0.070*	NS	-3.601**	4.103**	NS	0.897	18
	SG	-17.395	-0.116**	NS	-1.168**	NS	1.178*	5.783**	0.746	24
	MG	-10.623	NS	NS	NS	NS	NS	NS	0.349	24
	LG	-12.522	NS	NS	NS	NS	1.306**	NS	0.442	24
<u>Q.</u> <u>dealbata</u>	US	-27.024	-0.21*	0.008*	0.458*	NS	NS	2.308**	0.775	24
	SG	-17.865	-0.082*	NS	-0.972**	NS	1.1015*	4.820**	0.706	24
	MG	- 7.711	NS	NS	NS	NS	NS	NS	0.274	24
	LG	- 9.213	0.111*	NS	NS	NS	NS	0.061*	0.481	24
<u>Q.</u> <u>griffithii</u>	US	-12.417	NS	-0.012**	0.425*	-0.643**	0.929**	2.067**	0.913	24
	SG	-	-	-	-	-	-	-	-	-
	MG	7.515	NS	NS	NS	-0.888**	NS	-2.16*	0.840	24
	LG	- 7.956	NS	NS	NS	NS	0.912**	NS	0.440	24
<u>Q.</u> <u>glauca</u>	US	9.465	NS	0.030**	1.504**	-3.153**	1.948**	NS	0.930	24
	SG	-15.538	-0.121**	NS	-1.169**	NS	NS	5.868**	0.703	24
	MG	0.995	NS	NS	NS	-0.047**	NS	-0.298**	0.690	24
	LG	-17.730	NS	NS	NS	NS	1.849**	-0.231**	0.450	24

* Significant at P<0.05

** Significant at P<0.01

NS Not significant

influence habitat heterogeneity (Orians 1982, Nunez Farifan and Dirzo 1988, McCarthy and Facelli 1990) which in turn affect the performance of individuals in the gaps (Dirzo 1988). The results of this study indicate that the species differed in their growth responses to gaps and understorey conditions. Seedlings of S. khasiana, M. esculenta and T. tomentosa showed better growth in medium and large gaps, while the three oak species showed little response to canopy openings and registered higher shoot growth rate in the understorey region. This is in accordance with the results of Brokaw (1985b) who found higher height growth rates in the gaps for pioneer species than the primary species, but does not support the findings of Augspurger (1984b) and Popma and Bongers (1988) who reported enhanced growth for all species in gaps. Spatial variation in light among gaps and understorey and its effect on tree growth has been extensively studied (Denslow 1980, Whitmore 1982, Brokaw 1985 and Canham and Marks 1985).

Simultaneous increase in LAI and shoot growth rates of different species in various micro-habitats does not agree with the findings of Canham (1988), who reported an increase in LAI in sugar maple saplings without any significant increase in shoot length. Based on the growth response of seedlings to the increased light intensity along the increasing gap size gradient, S. khasiana and

M. esculenta which showed maximum growth in the large gaps may be classified under the shade intolerant or gap phase species, while Q. dealbata, Q. griffithii and Q. glauca may be termed as shade tolerant or mature phase species. T. tomentosa seedlings whose performance was better in the small and medium gaps may be regarded as a species occupying an intermediate position between shade tolerant and shade intolerant species distributed along the understorey-gap size gradient in the forest.

The role of soil moisture in influencing growth of seedlings has also been studied by McLeod and Murphy (1977) and Mueller Dombois (1980). Leaf litter, apart from being the chief source of nutrients, also affects soil moisture and temperature of the forest floor (Hart et al 1962 Campbell 1982), thereby indirectly affects seedling growth by enhancing availability of soil moisture and nutrients. In this forest peak seedling growth during rainy season could be attributed to the increased availability of nutrients due to rapid decomposition of litter on the forest floor and also to the higher moisture content of the soil.

Thus the differential growth response of seedlings of different tree species to almost same set of microenvironmental conditions that varied along the gap size gradient

may be a species specific attribute which influence the physiological ability of plant for efficient utilization of environmental resources.

