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Seed germination patterns in a Himalayan moist temperate forest

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Abstract: A study was conducted in a Himlayan moist temperate forest in Mandal to identify the patterns of seed germination and major germination syndromes operating in the forest and to understand the role of primary selective factors in controlling germination in the plant community and how groups of species respond to such factors. The germination pattern was bimodal with the peak time of emergence in June followed by February-March. Along the altitudinal gradient (1650 to 2600 masl), the maximum number of seedlings emerging per transect was at the middle elevations of which more than 80% was understorey species while in the higher elevations canopy tree species seemed to dominate in the regeneration transect. The mean length of dormancy (MLD) of species recorded in field nursery trials in Mandal ranged from 10 days to 285 days. Seasonal analysis of the germination pattern revealed that maximum number of species dispersed their seeds during dry season (Oct-Jan) as compared to rainy or pre-rainy season. Three germination groups: delayed-rainy (DR), intermediate-dry (ID) and rapid-rainy (RR) were identified as the major germination syndromes in the study area. Among the four ecological groupings of species, the season of seed dispersal and dispersal type explained most of the variance, in MLD among species. The synchronization in the pattern of emergence within species and between species in Mandal forest was best illustrated by the pattern of seedling emergence in the four oak species (*Quercus semecarpifolia*, *Q. floribunda*, *Q. leucotrichophora* and *Q. glauca*) and four under storey species (*Euonymus tingens*, *Symplocos paniculata, Lindera pulcherrima* and *Sarcococca hookerana*).

Resumen: Se realizó un estudio en el bosque húmedo templado himalayo en Mandal con el fin de identificar los patrones de germinación de semillas y los principales síndromes de germinación que operan en estos bosques, y para entender el papel de los factores selectivos primarios en el control de la germinación en la comunidad vegetal y cómo los grupos de especies responden a tales factores. El patrón de germinación fue bimodal con un pico de emergencia en junio, seguido por otro en febrero-marzo. A lo largo del gradiente altitudinal (1650 a 2600 m snm), el número máximo de plántulas que emergieron por transecto se presentó a elevaciones medias, de las cuales más del 80% eran especies del sotobosque, mientras que a elevaciones mayores las especies arbóreas del dosel parecieron dominar en el transecto de regeneración. La duración media de la latencia (DML) de las especies registradas en los ensayos de vivero en el campo en Mandal varió de 10 a 285 días. El análisis estacional del patrón de germinación mostró que el mayor número de especies dispersaron sus semillas durante la estación seca (octubre-enero) en comparación con las épocas de lluvias o de pre-lluvias. Se identificaron tres grupos germinativos como los principales síndromes de germinación en el área de estudio: retrasada en lluvias (DR), intermedia en secas (ID) y rápida en lluvias (RR). Entre las cuatro agrupaciones ecológicas de las especies, la estación de dispersión de semillas y el tipo de dispersión explicaron la mayoría de la varianza en DML entre las especies. La sincronización en el patrón de emergencia dentro y entre especies en el bosque de Mandal estuvo bien ilustrada por el patrón de emergencia de plántulas en las cuatro especies de encinos (*Quercus semecarpifolia*,

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Q. floribunda, *Q. leucotrichophora* y *Q. glauca*) y cuatro especies del sotobosque (*Euonymus tingens*, *Symplocos paniculata, Lindera pulcherrima* y *Sarcococca hookerana*).

Resumo: Foi efectuado um estudo numa floresta temperada dos Himalaias em Mandal para identificar os padrões de germinação das sementes, os maiores síndromas ocorrendo na floresta e compreender o papel dos factores selectivos primários controlando a germinação na comunidade vegetal bem como os grupos de espécies que respondem a tais factores. O padrão de germinação era bimodal com um pico de tempo de emergência em Junho seguido pelo de Fevereiro-Março. Ao longo do gradiente de altitude (1650 a 2600 m), o número máximo de plântulas emergentes por transecto ocorreu nas elevações médias das quais mais de 80% eram de espécies do sub-coberto enquanto que nas maiores elevações pareciam dominar as espécies arbóreas do docel no transecto de regeneração. O tempo médio de dormência (MLD) das espécies registadas nos ensaios de campo em viveiro, em Mandal, oscilaram entre os 10 dias e os 285 dias. A análise estacional dos padrões de germinação revelou que o maior número de espécies dispersou as suas sementes durante a estação seca (Outubro-Janeiro) quando comparada com a estação das chuvas ou de pré-chuvas. Três grupos de germinação foram identificados como os maiores síndromas na área de estudo: chuva retardada (DR), seca intermédia (ID), chuva rápida (RR). Entre os quatro agrupamentos ecológicos das espécies, a estação de dispersão das sementes e o tipo de dispersão explicaram a maior parte da variância entre espécies em relação ao MLD. A sincronização no padrão de emergência dentro das espécies e entre espécies na floresta de Mandal encontrava-se melhor ilustrada pelo padrão de emergência nas quatro espécies de carvalhos (*Quercus semecarpifolia*, *Q. floribunda*, *Q. leucotrichophora* e *Q. glauca*) e quatro espécies do sub-coberto (*Euonymus tingens*, *Symplocos paniculata*, *Lindera pulcherrima* e *Sarcococca hookerana*).

Key words: Dispersal, elevation gradient, germination syndromes, mean length of dormancy, synchronization, seed dormancy.

Introduction

The natural timing of seed germination in a community is determined by a host of biotic selective factors acting simultaneously often in opposing directions. A community level study of germination can provide an insight into the role of primary selective factors in controlling the timing of germination in the community and in understanding how groups of species respond to such factors in identical ways. Some of the selective factors identified in controlling the timing of germination in previous studies (Frankie *et al.* 1974; Garwood 1983; Mayer & Polkajoff-Mayber 1982) include soil moisture, length of growing season, timing of seed dispersal and seed dormancy. Factors responsible for interspecific and intraspecific variation in length of dormancy as well as the adaptive significance of the length of dormancy period has been speculative. An attempt to address this problem has been made in the current study by contrasting the length of dormancy of seeds of the same or different species that are dispersed at different times or had different dispersal mechanisms or life form. In addition to this, the major seed germination syndromes present in a high altitude Himalayan moist temperate forest community were identified and an attempt was made to interpret its ecological significance.

Materials and methods

Study area

The present study was conducted during 1990-1994 in a small forest patch known as Mandal forest which is a part of the Trishula reserve forest of Kedarnath forest division bordering the Kedarnath Wild Life Sanctuary (KWLS) in the Garhwal region of Western Himalaya (Fig. 1). The natural

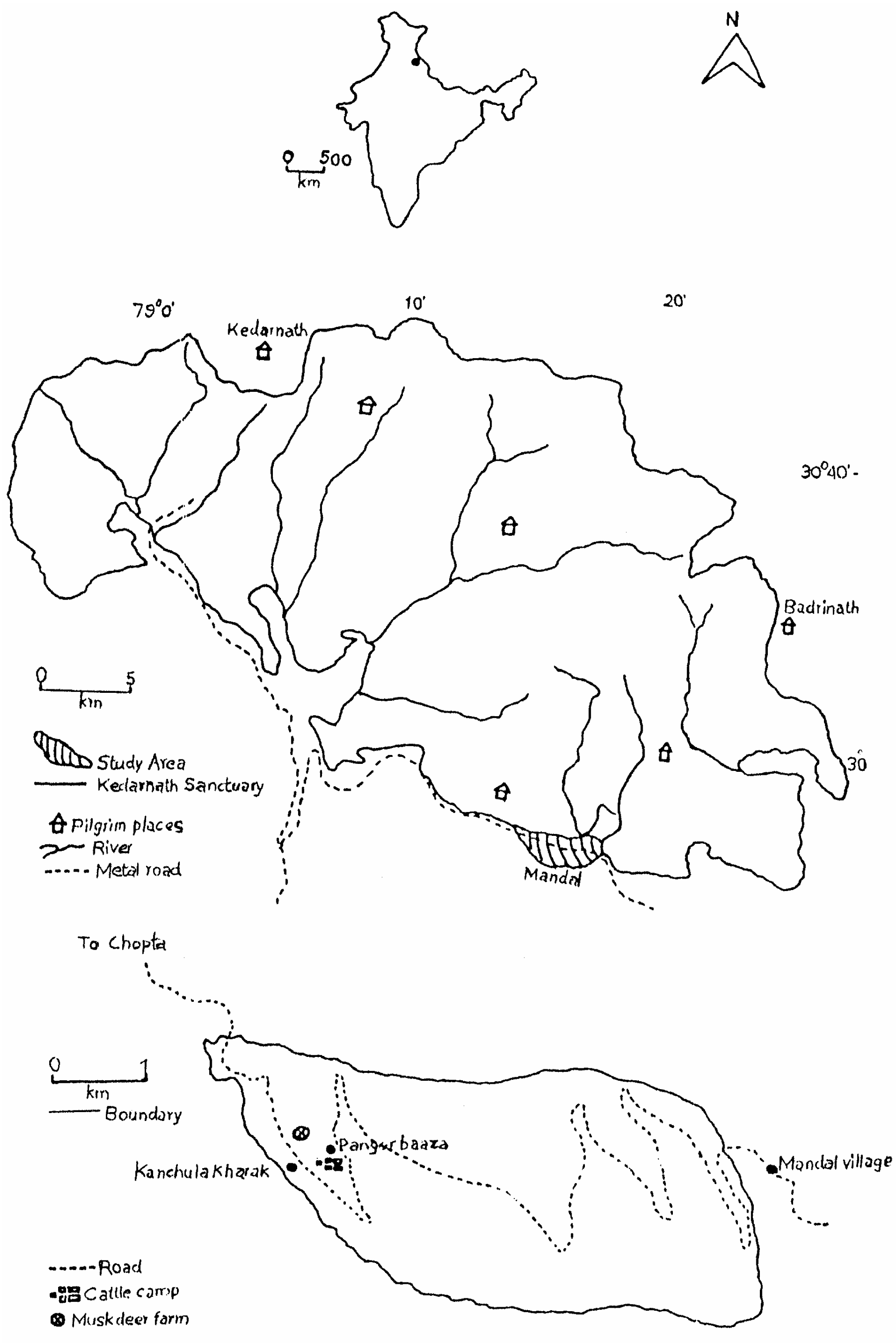

Fig. 1. Location map of the study area.

altitudinal zonation of the vegetation is well reflected from 1600 m asl in Mandal village at the base to 2700 m asl above Kanchula Kharak. The vegetation consists mainly of *Quercus leucotrichophora* (Banj) oak forests at lower elevations of 1600 m – 2000 m and *Quercus semecarpifolia* and *Q. floribunda* forests mixed with *Abies pindrow* at higher elevations. Other prominent species in the 1600-3000 m range include *Acer* spp, *Aesculus indica*, *Alnus nepalensis*, *Betula alnoides*, *Carpinus viminea*, *Juglans regia*, *Ilex dipyrena*, *Hovenia dulcis*, *Persea* spp, *Rhododendron* spp, *Lyonia ovalifolia* and *Buxus wallichiana*. In Kanchula kharak, located at the higher reaches in the study area, nearly 87% of the mean annual rainfall (2600 mm) was observed in the monsoon between June and September and 10% fell as snow in winter between December and March during the study period (1990-1994). Frost is common during winters while the higher elevation experience heavy spells of snowfall which may persist up to April-May in some shady locations. Average air temperature varied from 5.7°C to 23°C in Mandal Gharzari (1700 m) and 0.5°C to 14°C in Khanchula Kharak (2600 m).

Experimental design and sampling

Starting from the edge of the forest at 1625 m asl six (1 x 100 m) non adjacent transects (at least 150 m apart in the elevation gradient) were laid out perpendicular to slope alongside a six km loop of infrequently used trail that pass through Mandal forest. Approximately at two month intervals (starting from June 1990 till June 1992) all emerging dicot seedlings with expanded cotyledons or first leaves ≥ 0.25 cm^2 were removed from the transects. The seedlings were identified at species level. Periodical census of seedling emergence above the leaf litter were used to estimate the timing of germination in the community. The community was sub divided into ecological groups of species by life form, dispersal type, season of seed dispersal and germination groups. Life form groups include canopy trees (Ct) and understorey trees (Ut) while dispersal types included wind dispersed and animal dispersed species. Three distinct seasons of seed dispersal recognized in the study were: dry (D), pre-rainy (P) and rainy (R).

The median time of emergence of each species each year (by pooling individuals of each species from all transects), total number of seedlings of all species per transect in each collection period and the mean (± SE) number of species per transect in each collection period were also calculated. The number of seedlings emerging in each collection period was transformed into rate of seedling emergence (number/transect/two months) and the mean (± SE) rate of emergence computed. The time of seed dispersal and the time of seedling emergence was compared by condensing the two year seedling emergence data into a single distribution. The season of seed dispersal was determined by personal observation. To gather information on germination capacity and mean length of dormancy under natural conditions, freshly fallen seeds of about 38 species were collected from the forest during the study period. The seeds were sown on soil surface in raised forest nursery beds in Mandal Gharzari and Kanchula kharak. Germination counts were taken at weekly intervals. Time taken for germination since sowing was noted in the case of dormant seeds and the mean length of dormancy worked out. Germination data from all nursery beds of a species sown on the same date were pooled when the number of seeds available for that particular species was limited. Sample sizes (N) per species per sowing date ranged from 20 to 100. For each planting of a single species, the mean length of dormancy (MLD) was calculated from the length of dormancy of all seeds that germinated in the replicates. The data collected on the mean length of dormancy (MLD) for each of the recorded species was compared by grouping the species based on germination type, season of seed dispersal, dispersal type and life form. The values were then log transformed and mean (x) and variance (s^2) worked out for each of the subgroups within the main groupings. Hartlett's test of homogeneity was performed to test the homogeneity of variances between different subgroups within each main group and level of significance noted.

Results

Patterns of germination

A bimodal germination pattern was noticed during each year of the observation period (Fig. 2). For seedlings of some species like *Acer sterculiaceum, A. caesium, Quercus leucotrichophora, Q. glauca* with seed fall at end of autumn (September-October), the emergence of seedlings started in February and peaked by April. These species seemed to require an over wintering or pre chilling prior to natural regeneration. In some species like *Acer caesium, Acer caudatum and Acer sterculiaceum* due to accumulated snow fall during the early months of the year at higher elevations, the germination started only by April. In both the years June 1990 to April 1991 and June 1991 to April 1992, the peak time of emergence was June during the onset of first rains of the season (Fig. 2). The number of emerging seedlings was significantly skewed to the right. The average number of species emerging per collection period also showed a similar pattern. The maximum number of spe-

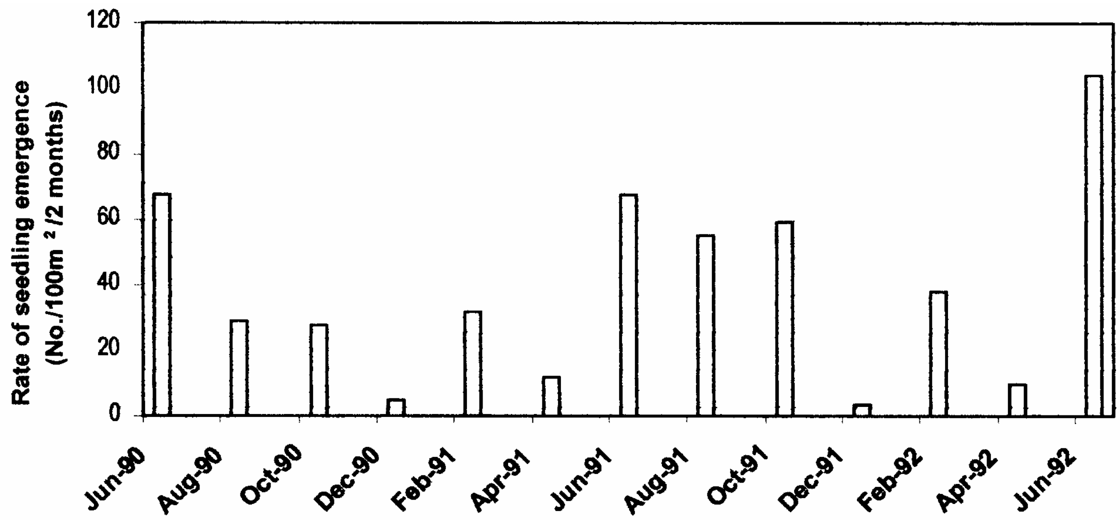

Fig. 2. Mean rate of seedling emergence (N = 6 transects) during the study period (1990-1992) in Mandal forest.

cies germinated in April and June. For more than 50% of the species, the median time of emergence was before April while nearly 35% of species had emerged by June and 15% by October during 1991. The corresponding figures in 1991-92 was 52, 32 and 16%. The rate of emergence of canopy tree species and understorey species also showed distinct patterns with under storey species dominating in April and June. Along the elevation gradient, the maximum number of seedlings emerging per transect was around middle elevation of which more than 70% were understorey species (Fig. 3). However, in the higher reaches, most of the emerging seedlings were of canopy tree species. This trend in regeneration was noticed in both the years along the elevational gradient. The peak in seedling emergence noticed during 1991-92 in middle elevations may be attributed to increased seed production in under storey species like *Symplocos paniculata* and *Sarcococca hookerana* (Fig. 3).

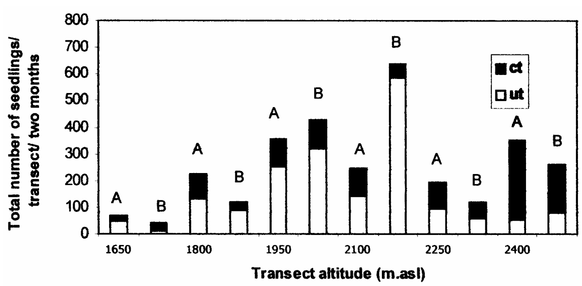

Fig. 3. Regeneration pattern along the gradient in Mandal forest during June 1990-1991 (A) and June 1991-1992 (B). Shaded bars represent canopy tree (ct) and unshaded bars under storey species (ut).

The pattern of emergence of four oak species and four under storey species (*Euonymus tingens, Symplocos paniculata, Lindera pulcherrima* and *Sarcococca hookerana*) illustrate a synchrony between and within species. Distribution of the four oak species followed a distinct pattern along the elevation gradient. *Quercus semecarpifolia* (Kharsu oak) and *Quercus floribunda* (Moru oak) were found in higher elevations (2200 m and above) while *Quercus leucotrichophorai* (Banj oak) and *Q. glauca* (Harinj oak) were distributed in the lower elevations (1650 m to 2000 m). For *Quercus semecarpifolia* and *Q. floribunda* in the higher elevations, the seed germination started immediately after seed fall in July-August. For lower elevations oaks (*Quercus glauca* and *Q. leucotrichophora*) a brief chilling period was necessary and seed germination took atleast two to three months after seed fall (October). *Moru* and *Kharsu* oak seemed to lack clear-cut dormancy and took advantage of the close synchronization between seed fall and the commencement of the rainy season in June-July.

Among the under storey species, the germination patterns in *Euonymus tingens, Symplocos paniculata, Lindera pulcherrima* and *Sarcococca hookerana* were notable and constituted the maximum number out of the total seedlings germinating in transects around middle elevations (Fig. 3). In *Sarcococca hookerana* the seeds germinated almost throughout the year with peaks before the rains. In *Lindera pulcherrima* the seeds were dispersed in the beginning of the rainy season and germination was noticed soon after whereas in *Symplocos paniculata* the peaks in seed germination was noticed during the beginning of rainy season even though the seeds were dispersed in the dry season (October to January).

Variation in length of dormancy

The germination data for 38 species revealed that the mean length of dormancy (MLD) ranged from 10 days in *Quercus semecarpifolia* to 285 days in *Persea duthiei.* The germination capacity of the tested species was high –11%; intermediate – 32%; low – 33%; very low – 24%. The mean length of dormancy differed significantly for seeds dispersed during the three different seasons (rainy, dry and pre-rainy). Within the rainy season seed dispersed species, two groups can be distinguished; one group consisting of species which have an average dormancy of two weeks or less designated as 'rapid rainy' and another category of species whose seeds remained dormant for a period more than 20 weeks (delayed rainy). Of the species which dispersed seeds during the dry season (October to January) the dormancy ranged from 5 to 24 weeks (Fig. 4a). Hence this group could be described as intermediate – dry as far as germination was concerned. Of the 13 identified species which dispersed seeds in rainy season, eight species had short dormant period (rapid rainy) while five others had long dormant period (delayed rainy) (Fig. 4b). For species which disperse seeds in the season following the winter (March to May) and described as pre-rainy, the dormancy varied from 7 to 10 weeks (Fig. 4c). For seeds of the delayed rainy group and intermediate dry group the length of dormancy was approximately equal to the time between dispersal and the beginning of the next rainy season.

Germination syndromes

For nearly 78% of the seedlings that germinated between January to April, the seeds were dispersed during the rainy season and dry season. The dry season accounted for nearly 50% of the species in which seed dispersal was recorded between January to April while the rainy season accounted for nearly

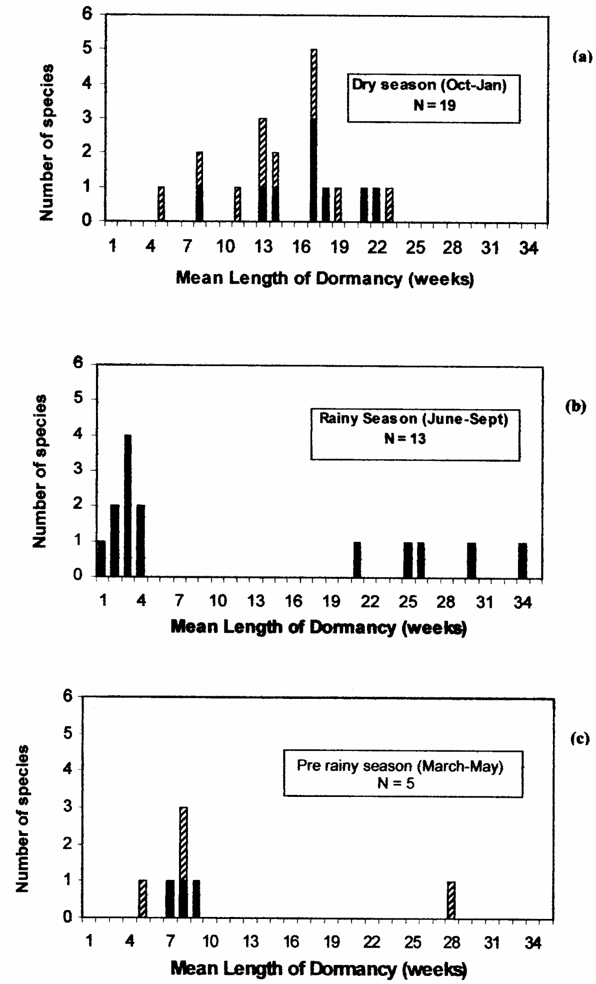

Fig. 4. Mean length of innate dormancy of species whose seeds are dispersed in dry season, rainy season and pre-rainy season. Hatched bars represent wind dispersed species.

36%. Species like *Daphne papyracea, Quercus floribunda, Q. semicarpifolia, Sarcococca hookerana* and *Lindera pulcherrima* the seeds were dispersed during the rainy season and germination would begin within the same season. For the regeneration pattern of four oak species, times of seedling emergence and season of seed dispersal, were not independent. The seedling emergence time of seeds dispersed in the early and late rainy season were not significantly different but the seedling emergence time of seeds dispersed in dry season differed from those dispersed during early rainy or late rainy season. The maximum number of species seem to be dispersed in the dry season (Oct-Dec) as compared to rainy/pre-rainy season (Fig. 4).

Three germination groups distinguished based on the period of dormancy for the species recorded in Mandal include Rapid rainy (RR), Delayed rainy (DR) and Intermediate dry (ID). The rapid rainy group dispersed seeds in the rainy season, had short dormant period (20-25 days) and would germinate in the same rainy season in which they were dispersed. The typical species include *Euonymus tingens, Daphne papyraceae, Meliosma delleniifolia, Lindera pulcherrima* and *Phoebe lanceolata*. The delayed rainy group disperse seeds towards the end of the rainy season and had a fairly long dormant period (Mean MLD = 235 days). For most of the species a minimum pre chilling requirement was needed for the seeds to germinate. Typical examples are *Persea duthiei* and *Persea odoratissima*. Germination in this group would begin following the first rains of the spring season. In some of the species the seeds would germinate only in the following rainy season in June; e.g.: *Ilex dipyrena*. The intermediate dry group dispersed seeds in the dry season (Oct-Dec) and had an intermediate length of dormancy (Mean MLD = 101 days). The seeds would germinate in the spring season following the first rains after winter in February or in the beginning of the rainy season in June. By grouping species in this manner, the variance within germination group was lower than that of the groupings based on season of dispersal (Table 1). Hence this grouping explained best the difference in MLD noticed in Mandal forest.

Discussion

A bimodal germination pattern appears to be prominent for the identified forest community. The seedlings of many prominent tree species like maples and lower altitude oaks (*Quercus leucotrichophora* and *Q. glauca*) in which seeds were shed in dry season (intermediate-dry category), start to emerge in February and peak by April. This resulted in a trend which showed more skewness towards the right. In temperate forests most of the tree species require varying periods of pre chilling before germination. This is achieved naturally when the seeds are shed in October-November and in following winter, the pre chilling requirements are met. This phenomenon has been reported in other temperate species like *Elaegnus umbellate* (Fowler & Fowler 1987) and in *Aesculus indica* (Maithani *et al.* 1990). This pattern of emergence is in contrast to patterns recorded in a tropical evergreen forest in Barro Colarado island (Garwood 1983) where the emergence of maximum number of species was in June, with the onset of rains whereas in Mandal forest there was a peak in February-March just after snowmelt followed by another peak in germination with the onset of the

Table 1. Mean (x) and variances (s^2) of the natural logarithm of mean length of dormancy (MLD) in days for different groupings of 37 species. Result of Hartlett's test of homogeneity of variances within each group is given beside the variance of each group. N = number of species.

Comparison	$\log_e$ MLD			
	N	x	s^2	Mean MLD
1. All species	37	4.625	0.776	102.3
2. Germination groups				
Intermediate dry (ID)	24	4.619	0.238^{NS}	101.37
Rapid rainy (RR)	8	3.032	0.124	20.75
Delayed rainy (DR)	5	5.46	0.052	235.2
3. Season of Seed Dispersal				
Rainy (R)	14	4.729	1.585*	113.23
Dry (D)	18	4.774	0.249	107.15
Pre rainy (P)	6	4.034	0.12	56.5
4. Dispersal type				
Animal	21	4.665	1.155*	106.24
Wind	16	4.569	0.265	96.5
5. Life forms				
Understorey species	17	4.084	0.769^{NS}	59.41
Canopy trees	20	4.757	0.767	116.45

*0.05 ≥ P > 0.01; NS, not significant

rainy season in June. The prominent species germinating at that time included Moru and Kharsu oak, designated in the category of rapid-rainy.

The pattern of emergence of the four oak species best illustrates the synchrony within the species with regard to intra specific variation in length of dormancy as an adaptive mechanism for seed survival and establishment. Moru and Kharsu oak seemed to lack clear-cut dormancy and took advantage of the close synchronization between seed fall and the commencement of the rainy season in June-July. Moreover, they are largely insensitive to moisture variations for germination and possessed the added advantage of viviparous germination which helped seedling establishment even in forest floor with high litter content (Singh & Singh 1992). Seed germination in Banj and Harinj is delayed until the availability of sufficient soil moisture for seedling establishment is ensured with the commencement of monsoon. The advantage of this seasonal periodicity is that it ensures that seedlings do not have to encounter a long period of winter and summer drought immediately after emergence and by the next season's drought they are fairly established in their micro habitat. Alternately this also means that seedlings of Kharsu and Moru oak are more susceptible to mortality. Rao & Singh (1986) have recorded higher mortality rate (35%) in an year for oak seedlings initiated during rainy season as compared to 20.6% mortality rate for oak (Banj and Harinj) seedlings in which initiation occurred prior to rainy season.

Regeneration of the high altitude oaks was high in rainy season in Mandal. Kharsu oak accounted for nearly 36%, 21% and 22% of total regeneration in transects in June 1990, June 1991 and June 1992 respectively while Moru oak accounted for nearly 52% and 27% in the month of October in successive years. For both the oaks the peak regeneration was during rainy season while for Banj and Harinj oaks the regeneration started by late December and staggered regeneration continued until April-June in successive years of the study. Winter chilling is required to promote seed germination in Banj and Harinj which disperse their seeds during the dry period in October. The longer residence period of oaks acorns on the forest floor was found to increase the susceptibility of acorns to weevil infestation especially *Sitophilus glandium* Marshall. This weevil accounted for nearly 83.7% infestation level in oak acorns during the winter for Banj oak forests in Nainital in Kumaon Himalayas (Singh & Singh 1992). Such high levels of infestation could even adversely affect the natural regeneration in Banj oak in the absence of natural enemies of the weevil.

The regeneration of under storey species also showed distinct patterns of germination behaviour. The overall pattern of regeneration was similar to that of canopy tree species. However, when individual transects were considered at each point along the elevation gradient, under storey species seemed to dominate in transects at the middle elevations during successive years. Regeneration of understorey species accounted for more than 60% of the total regeneration during 1990-91 and 1991-92 period. This could be correlated to the species richness, diversity index values and dominance of under storey species in the vegetational composition at the middle elevations (Viswanath 1999). Although early emergence maximizes the length of the first growing season and allows time for development of a potentially large root system which might ensure survival through the first dry season (Frankie *et al.* 1974), these may not be the primary selective factors for an early emergence species survival strategy. If that were so then the adaptive mechanism of later emerging species to compensate for shorter growing season available to them would have been a larger seed size or large seed reserve for rapid growth. In Mandal, some species like banj oak, harinj oak and *Aesculus indica* which are dispersed in the late rainy season or dry season have relatively large seeds. These seeds remain in the soil delaying germination to emerge in early rainy or pre rainy season. Differences in times of emergence of different life forms may also be attributed to their different life history patterns. Most of the understorey species like *Lindera pulcherimma, Neolitsea pallens, Symplocos crategoides* emerged during the rainy season. However, early emerging seedlings in shaded under storey did not seem to gain a competitive edge over those emerging late in the rainy season. Garwood (1983) suggested that the emergence of understorey species throughout the rainy season is because of lack of any advantage to early emergence. The prolific regeneration of understorey species in the middle elevations (2000 m) could be correlated to favourable microsite conditions and species richness.

Both seed dispersal and timing of seed dispersal are important adaptive behaviours controlling timing of seed germination in the broad leaved temperate forests of Mandal. Species with delayed germination behaviour are clearly dormant and those with immediate rapid germination behaviour are not. Species with intermediate dormancy bridge the gap. If intermediate germination behaviour can be termed as dormancy then clearly 78% of the species studied in Mandal are dormant. The season in which the seeds are dispersed accounted for some of the variation in duration of seed dormancy as measured by the mean length of dormancy (MLD).

The three germination groups: delayed – rainy (DR), intermediate-dry (ID) and rapid-rainy (RR) appear to be the major germination syndromes in the present community even though they may not correspond to the types recognised by Angevine & Chabot (1979). In the delayed-rainy syndrome, dormancy prevent germination during the rainy season in which the seeds are dispersed and during the following dry season until the pre-rainy season four to seven months later. Seeds dispersed earlier were dormant longer because of the beginning of the next rainy season was further away. The flowering in most of the DR species was after the rainy season and seeds are dispersed in the late-rainy season. Dormancy allows germination early in the next rainy season but may be costly because energy and/or nutrients must be expended for thick protective seed coats or chemical defenses to deter predators during this long period (Garwood 1983). In the intermediate-dry syndrome (ID), dormancy prevents germination during the dry season in which seeds are dispersed. Dormancy period is shorter than in DR syndrome. Most of the species in ID syndrome flower and fruit in the dry season and seeds are dispersed primarily in March-April. Timing the dispersal close to the beginning of the rainy season is thus an important component of this syndrome because it reduces the time. Seeds are exposed to post dispersal predators and decreases the frequency of encountering false starts of the rainy season or unpredictable rains of the dry seasons (Foster 1982). Dormancy prevents germination during environmentally unpredictable periods and reproduction is shifted to a less favourable but more costly time period to ensure germination in early rainy season. In the rapid-rainy (RR) syndrome, seeds are dispersed during the rainy season and germinate in that season itself though not early in the season. Earlier dispersed seeds do not seem to germinate faster or may be even slower than those dispersed late in the rainy season. Flowering of species in this RR syndrome is usually just before or at the beginning of the rainy season and fruits are dispersed before the late rainy season. This strongly lends credence to the suggestion that selection for flowering early in the rainy season has been stronger than selection for early germination. According to Garwood (1983) either germination occurs at a less optimal time or RR species do not benefit from early germination. Hence delay in germination of RR species may not prove costly in terms of early seedling establishment.

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