GENERAL DISCUSSION
Himalayan poplar (Populus ciliata) is one of the important fast growing species of the temperate Himalaya. Its distributional zone overlapping with apple region of the Western Himalaya warrants its future exploitation in packaging industry by evolving fast growing clones. The improvement programme of any species depends upon selection and breeding of appropriate clonal or seed material which is genetically superior, quantitatively adequate and geographically appropriate. What is geographically appropriate is determined by geneecological studies. Genetically superior material is that, which is superior to the wild form in certain desirable characteristics. It is obtained by selecting phenotypes exhibiting a high degree of desired characteristics, and then estimating the heritability of these characteristics by progeny tests. A quantitatively adequate supply of materials, in plants like Populus species, is obtained by the establishment of clonal orchards. These cannot be established until the information pertaining to variation within the species and climatic differences throughout its distributional zone are available (Hoche, 1970). The early assessment of geographic variation in forest trees can be undertaken by the study of biosystematics or experimental taxonomy, which was described as an attribute of geneecology by Hoche (1968) as it determines the habitat-correlated genetically-based variation within the
species (Puresson, 1923). Thus, the investigations of
infra-specific variation in relation to its environment is
truly a provenance study, which in turn forms a part of the
geneecological study in purpose, method and scope. To unravel
the broad pattern of geneecological variation in the species
these manifestations in the succeeding pages are being
discussed under three heads i.e., i) Systematics and
Evolution, ii) Adaptations and iii) Provenance Variation.

SYSTEMATICS AND EVOLUTION

The genus *Populus* after its emergence in the
Jurassic now comprises 30 living species. The ample fossil
records of the genus (page 11) indicate that the luxuriant
proliferation of the genus in the remote past was not only
checked by environmental calamities but many species became
extinct under this pressure while some survived by producing
neo-forms capable of invading the new ecological niches. The
richness of gene pool in determining genetic recombination to
produce new variants under natural selection is well
documented in literature (Stebbins, 1974). Dobzhansky (1951),
Simpson (1953) and Mayr (1963) on the basis of contemporary
species of animals have shown that major evolutionary
changes come about through the action of gene recombination
and natural selection. The author corroborates the
hypothesis of Stebbins (1974) to explain the gaps in the
living gene pool of the genus *Populus*, that in response to
any environmental change a population may respond to it.
either by evolving in a new direction, that is, by carrying out an adaptative shift or by becoming extinct.

Unlike other Salicaceous genera e.g., Betula and Salix which produced euploid series to survive and invade the new edaphic niches during glaciation, the genus Populus remained relatively stable with cytotypes restricted only to P. alba and P. nigra with 2n = 38 and 57, P. tomentosa with 2n = 38 and 76 and P. tremula with 2n = 38, 57 and 76. The occurrence of chromosomal races in the aforesaid species seems to be an attribute of domestication supported by suckering ability rather than an upsurge of ecological adaptation. No chromosomal variation was recorded in P. ciliata from as many as 150 taxa embracing 17 provenances. The genome of the genus with x = 19 like other primitive angiosperm representatives (Khosla and Sareen, 1981) attained an equilibrium with the existing environment by expending their capacities to bringforth a new-equilibrium for the stray seedlings with numerical irregularities to establish in nature. Therefore, paleo-amphiploid origin of the basic mode in the genus (7+12) also contributed a selective advantage to occupy new niches than the pre-historic mode which supposedly possessed x = 7 akin to primitive angiosperms.

Accordingly, it may be hypothesized that early amphiploidy in the genus, suckering ability, dioecy along with pioneering nature produced an adaptive strategy for the
survival of the genus, in general, and the origin of
P. ciliata and its migration in the Himalaya, in particular.
The species after its origin in Central Asia migrated
through Yunnan to Himalaya and was then cut off from the
parental gene pool by the emergence of the Tibetan Plateau.
Three species viz., P. ciliata, P. gamblei and P. clausa
emerged from this gene pool in Eastern Himalaya, and
P. ciliata due to its wide adaptability invaded the rest of
the Himalaya extending as far as Afghanistan.

The systematic position of P. ciliata, P. gamblei,
and P. clausa either in Leucodae or Tacamahaca has
remained controversial. The author proposes that on the
basis of the following characters i.e., leaves being ciliate,
bracts being ciliate, stamens being more than 40 and
capsules being 2-4 valued these three Himalayan species
warrant their placement in a separate section. This is
further supported by the fact that P. ciliata is cross-
incompatible with P. deltoidea and is difficult to root
from stem cuttings. A new section named 'Ciliata' is
suggested for the proper phylogenetic placement of these
three Himalayan species.

Adaptations

The progenies of a pioneer species, as is
Populus ciliata, occupy habitats considerably different from
their parents. They are known to grow and regenerate over a longer range of environments than species found near the climax stage (Stem and Roche, 1974). The Himalayan poplar embraces quite diverse ecological conditions throughout the Himalayan range, right from the extreme moist conditions of river flood basins to the company of coniferous genera, reputed for their water reducing morphological modifications. The adaptability of this species to grow on different soil substrata preferably freshly exposed soils, as also evident from present studies, explains its proliferation over wide heterogenous edaphic and climatic environments superimposed by discontinuous mountain ranges and river basins.

*Populus ciliata*, unlike other discontinuous species, does not reveal any morphological characteristics or any other productive feature sufficient enough to delimit discrete morphotypes. The isolated genotypes of discontinuous species reach an eco-genetic equilibrium with the environmental heterogeneity to produce distinct races or biotypes. The findings of Wright (1958, 1976, 1981) on geographic variation studies of several forest tree species depict that there is more variation in a species with disrupted distribution pattern in a mountainous range than in a species with a continuous distribution. The latter type on account of uniform climate may shape only clinal variation in response to local conditions of niche frequencies with heterogenous environments, selection coefficients of
single alleles, form of fitness set and mating type and migration rate (Stern and Roche, 1974). The clinal variation is also usual of several discontinuous species where each isolated physiographic feature, embodied with ecological gradient (ecocline), that with geographic factors (topocline), etc., shows a gradation in phenotypic (including physiological) characteristics. Critchfield (1957) reported clinal variation amongst isolated ecotypes of Pinus contorta.

The genetic isolation of P. ciliata is broken over the wide Himalayan region by obligate wind pollination and the dissemination of light and cottony seed over the physiographic barriers by air and the downstream transportation of both seed and juvenile seedlings by water currents. The suckering ability of the species enabled the escaped variants to multiply at new habitats which later mixed with local inhabitants to diffuse their genotypes by introgression. The wide adaptation of the species to varied climates may thus be due to intra-provenance hybrid vigour as enforced by above discussed biological adaptations of the species. However, the process of speciation seems to have come to a dead-end inspite of several factors that contributed to enrich its gene pool in the geological past. The pioneering nature of the species expanded the rich gene pool in order to meet the survival pressures for invading all available ecological niches in its temperate zone that the evolutionary guidelines in this case turned to eco-specific in nature. The aforesaid
factors thus checked the possibility of distinct morpho-
clinal differences except that the populations around the
river basins showed thin bark and better productivity of
wood while along with coniferous associates it possessed
thick and reticulated bark with poor growth rate.

The dioecy, which assured outcrossing to produce
new heterozygous combinations, needed to occupy different
ecological habitats, did not even affect the morphology or
the productivity of trees. The dioecious habit is thus
taken as a eco-physiological adaptation to increase the
genetic variegation of a pioneering species. The aberrant
bisexual catkin with self compatibility may be treated as a
relic to identify the pre-Populus stock of the genus to be
bisexual in nature. The dioecy thus served as an adaptation
for profusing the genetic variance to meet the environmental
changes in the geological clock. Viewing the occurrence of
dioecy and pioneering nature of several Salicaceous
representatives like Salix and Betula, the author opines that
dioecious species occupy more diverse habitats. However,
information on habitats of other dioecious species would be
meaningful to accept the above logistic postulation.

To meet the challenge of surviving in diverse
conditions the species has acquired many natural adaptations
with regard to growth, phenology and reproductive system
which enhance not only its genetic diversity but also augment
GROWTH

There exist remarkable differences in seasonal height growth patterns of different species of trees. Species differ markedly in total amount of seasonal height growth and in the length of their growing season. Although, height growth is determined by interaction of hereditary potentialities and environmental factors, the length of the growing season and the shape of the growth curve of a species are apparently controlled by hereditary factors and appear to be relatively independent of the normal fluctuations in environmental factors. The growth of the trees in natural stands have shown it to be uniform year after year though sometimes severe drought and unfavourable conditions have been found to check the growth temporarily. Kramer (1943) and Kozlowski and Ward (1957) were also of the view that severe droughts or excessively low temperatures may check height growth but the usual fluctuations in moisture and temperature apparently have little effect. The finding of root-shoot relationships have also revealed that the dormant phase of the species is in winter, though occasionally, during the growth period itself, there occur short breaks in the growth rate. Cannell and Millett (1976) have shown that differences in root-shoot ratios are purely seasonal and they cannot be expected to increase in subsequent years.
The intensive culturing of the species has been found to be feasible even without addition of any fertilizer. Being a pioneering species, the genotype of the species is so adapted that the new sites may or may not contain enough nutrients it is immaterial for its initial establishment. Conversely, the application of fertilizers have been shown by innumerable workers to be the mainstay in poplar cultivation.

**PHENOLOGY**

The flushing and anthesis, in general, was affected by temperature and photoperiod. The provenances at higher altitudes or cooler places were late in flushing as compared to lower altitudes. The temperature at a given site as determined by the shady and sunny region of the area also affected the phenological expression of these characters. Acock-Wood (1968) did not observe any correlation of latitude with leaf flushing in *P. deltoides* but reported a high degree of within-population variation in leaf flushing and flowering. The differences in time of flowering among trees are of considerable importance in breeding and management of seed orchards on account of physiological barriers which produce differential pollination checks for excessive inter-provenance crosses.

The concurrent occurrence of reproductive and vegetative pheno- phases in females i.e., simultaneous emergence of leafing and catkins reflects an adaptive strategy...
to render a more effective pollen carrying mechanism by way of increasing the total resistance area by the female trees to the passing current of air carrying pollen. The late budding in male trees allows the easy and free dispersal of pollen. Furthermore, the delayed budding in males helps to generate profuse flowering since males are required to produce large quantities of pollen for effective pollination.

**REPRODUCTIVE PHASE**

Seed dispersal was also found to be temperature dependent. Seeds could cover greater distances when dispersed during high temperatures. It has often been shown that genes in tree populations migrate via pollen or seed. Pollens usually travel greater distance than seed. Therefore, pollen dispersion distance is usually considered more critical than seed dispersion distance in most tree-genetics work (Knight, 1962). However, it is of importance to note that in very light seeded plants like poplars the seed dispersion distances are correspondingly greater, which may lead to higher rate of gene migration, through seed instead of pollen. This perhaps may be the reason for more or less continuous variation patterns as has been shown in the present studies and that of Pauley and Perry (1954) in *P. tricocarpa*. McKnight (1963) had also shown constant variation and migration along the rivers in *P. deltoides*. He expressed that waterways probably were the main migration routes for the species, as the seeds stay viable in water for much longer time than in air.
Sexual dimorphism was observed only in one tree occurring in the Narkanda provenance. It is presumed that the erratic environmental conditions which prevailed in the year prior to the observance of monoecious catkins might have caused differential activity of hormones. The temperature sum as postulated by Sarvas (1966) is assumed to be the main factor responsible for this aberration. The sex ratio has been confirmed to be 3 males:2 females as earlier reported by Khosla et al. (1979).

PROVENANCE VARIATION

There may be considerable differences between populations, between plants of the same population growing at different sites and even between plants of a single population growing together. The reason for these differences are partly genetic and partly environmental. Most wide-spread species, therefore, appear to be composed of geographical clines or moderately distinct geographic ecotypes (Wright et al. 1958). The true precision of such phenotypic variation from the wide geographic source of any species can be determined either through the quantitative aspect of natural variation or qualitative aspect of field trials. The objective of field trials is to assess the differences in performance between different genotypes in a given environment and, sometimes, to observe whether these differences are the same in two or more varying environments. The variation may occur on account of
several ecological variables like latitude, longitude, elevation above sea level, mean annual rainfall or precipitation, mean annual temperature, photoperiod, soil, slope, aspect, etc. The vegetation and the position of the species in succession also contribute to the clinal variation along with the general environment (climate, soil).

In trees to form a concise estimate of the variation a term often used is provenance. This is a term which does not exist in the taxonomic hierarchy and is purely a forestry term to denote the area on which any stand of trees is growing (Jones and Burley, 1973). It also denotes the trees having a given place of origin (Wright, 1976). The term, in general, overlaps with topocline, ecotype or biotype.

The provenance study is the most important applied aspect of geneecology, as it brings out the infra-specific variation in a plant species in relation to environment (Roche, 1968). It is well established that habitat-correlated heritable differences occur between the genotypes of different populations i.e., provenances. These differences are demonstrated in designed provenance trials conducted in the field, nursery or greenhouse (Mergen et al., 1974). No doubt that the natural variation study gives us the amount of variability, but it fails to identify the genetic control of a particular character, being totally phenotypic in observation. This aspect is analysed through provenance
trials which are seedling or clonal in origin. When the trials are carried out with the same provenance in two or more diverse environments, it is possible to detect the presence of interactions between the source-population genetic effects and the environmental effects at the planting sites. Such interactions are caused by the lack of additivity of the main effects and they are reflected in differential rankings or by differences in response of the provenances to different sites.

The present observations in the basic propositions of genecology i.e., variation in morphological and physiological characteristics, infra-specific variation in relation to habitat, and the extent of ecologically-correlated variation is attributable to the action of natural selection in moulding locally adapted populations from the available pool of genetical variation. This observation stems from the analysis of the quantitative variation in natural stands which exhibit tree-to-tree variation in various characters but ecological grouping disclosed that height-wise performance was better in ravines/river flood basins. Anatomical studies and wood chemical analysis were also not able to show any particular pattern of variation which could be linked to its habitat.

In the present studies the effect of sex of a tree was found to be non-significant in influencing variation range
of the species. It confirms the earlier studies in the species, where too no relationship of sex was found to growth characters (Khosla et al., 1979). Even in the wood chemical analysis, the influence of sex of the tree was also found to be insignificant in determining the chemical components, though a strong influence of fibre length on lignin and holocellulose content was found in females. In general, it emerges that the variation pattern in the species in the natural habitat is controlled more by environment than by any other factor.

The qualitative aspect of a provenance trial signifies the selection and propagation of superior inherent material for plantation programme. This was evident from the poor performance of Kalatop and Kandi provenances as compared to other provenances where Sahar provenance was superior. The seed germination and rooting capability studies also revealed variation in the provenance material. The selected provenance material was further tested under different climatic conditions, and the present studies reveal that the species is unsuitable for plantation in outer hills, while the suitability of provenances in mid and inner hills varied. Still the Sahar provenance performed well at two of the four sites tested.