INTERNATIONAL PROVENANCE RESEARCH ON CENTRAL AMERICAN PINES

By R. H. KEMP

Commonwealth Forestry Institute, University of Oxford, United Kingdom

SUMMARY

An international provenance research programme on Central American Pines was started in 1969 and international provenance trials are now in progress. Study of the natural forests of both species has confirmed their potential value for plantation in many tropical countries, especially on seasonally dry and infertile sites. Variation observed both within and between the natural populations offers possibilities for improved adaptation to site and production requirements. Some natural populations are in danger of depletion or extinction and further international action is needed to conserve and develop their genetic resources.

THE CENTRAL AMERICAN Pine Provenance Research Project was initiated in October, 1969, at the Commonwealth Forestry Institute, Oxford, under a grant from the U.K. Ministry of Overseas Development (now the Overseas Development Administration of the Foreign and Commonwealth Office). Further support has been given by the United Nations Organisation through the F.A.O. Panel of Experts on Forest Gene Resources. Field work on the two principal species, *Pinus caribaea* Morelet and *P. oocarpa* Schiede, has been previously noticed in the Review (Vol. 50 (1), p. 26 and Vol. 51 (1), p. 24 and many tropical countries both within and without the Commonwealth are co-operating in the international provenance trials. The fact that this research was initiated and is largely financed by a country which itself does not grow the species concerned, but is undertaking it as part of a programme of technical assistance to developing countries, is important in its effect on the strategy of exploration, seed collection and field trials.

Principles of international provenance research

Provenance research on a species of wide natural distribution may logically be conducted in three stages, starting with range-wide sampling and followed successively by trials from a restricted area or areas of the range and finally by crop-performance studies of a small number of provenances (Burley, 1969). Ideally these successive trials are done on all relevant site-types in the country concerned. Bearing in mind the powerful influence of environment on many important characters of the tree and also the need to provide a broad genetical base for future selection and breeding, especially when it may be difficult or impossible to return later to the wild populations for fresh introductions, the sampling procedure attempts to transfer as much as is practicable of the useful variation to the new environment. This means collecting from relatively large numbers of trees broadly representative of the populations at each site (provenances).

Stratification by such environmental factors as latitude, altitude, climatic regime, geographical isolation and so on is clearly desirable to assist efficient sampling. Within each stand sampled it is reasonable to ensure that the best phenotypes, to the extent that they can be readily recognised by visual assessment, are included in the collection. Bearing in mind that time and money are limited it is also reasonable to exclude the obviously undesirable phenotypes whose defects are likely to be at least partly genetic in origin. However the exclusion of "minus" stands at the range-wide sampling phases should be done only after taking into account site conditions and history since populations growing under severely adverse conditions, and particularly those at the extremes of the natural range, may contain genetic material of great value for use elsewhere.

In an international provenance research programme, which aims to serve a whole climatic region, such as the tropics, many countries concerned will be at an early stage in the trials sequence. The range of possible site types to be tested will be much greater than in any single country and the risk of exposure to exceptionally severe conditions at some stage in the life of a crop is likely to be increased also. A part of the research effort must therefore be put into exploration and conservation which may give no immediate gain, as a form of insurance against future needs. It must look beyond the first generations of selection to such possibilities as the incorporation of what may appear at first sight less promising strains in the production of synthetic varieties. The main factor limiting tree growth on most tropical sites is dry-season water availability, while the soils of deforested areas have also frequently suffered impoverishment by leaching, burning and surface erosion. The search for species and strains capable of high productivity under such conditions is therefore particularly important.

With these general considerations in mind the tactics of exploration and collection are determined largely by conditions in the collection zone, such as the geographical and ecological range covered by the species, the extent and pattern of variation both between and within stands at different points in the range, the present state, past history and future security of the stands and so on. Many of these conditions may be very imperfectly known. Of the two principal species in the present project *P. caribaea* is widely known by reputation but is generally represented in introductions by only one or two provenances. A comprehensive monograph on this species is now in the press and will be issued shortly (Lamb, 1973) and a corresponding volume on *P. oocarpa* will appear later. The following brief account is therefore concerned only with the main points of distribution, ecology, variability and present state of the natural forests of these two species. The botanical varieties *P. caribaea* var *bahamensis* and *P. caribaea* var *caribaea* are not found in Central America and are not considered here, although they are represented in the full international provenance trials of the species.

Pinus caribaea var hondurensis Barr. et Golf.

The coastal stands

These form by far the major part of the natural forests of this variety, extending in a generally narrow band along the Atlantic coast from about 12° 13′ N in Nicaragua almost to the northern border of British Honduras, at 18° N. There are major discontinuities in this distribution, particularly along the northern coast of Honduras Republic where the high mountain ranges approach quite closely to the sea without the broad coastal plain on which the species is typically found. At the southern extremity of its range the pine is in small stands, separated by broad areas of swampy ground carrying only grass and sedge, and isolated from the more extensive stands further north by dense broadleaf forest.

Climatic conditions throughout the coastal range are generally rather similar with mean annual rainfall increasing progressively southwards from about 1,500 mm (59 inches) in northern British Honduras to more than 3,800 mm (150 inches) near the most southerly stands. Nowhere along this coastal strip is there appreciably less than 76 mm (3 inches) of rain in the driest month, although on the more freely-drained sites the grasses dry out sufficiently in the three-month dry season to burn fiercely, especially in years of exceptionally low rainfall. The soils of the coastal plain are also generally similar throughout its length, being composed of recent alluvium, with the pines confined to the better-drained sites.

The pine stands on the Atlantic coastal plain of eastern Honduras and north-eastern Nicaragua are practically inaccessible overland from the main centres of human population and industry which lie far to the west. Wherever access to large areas of pine forest has been possible from the sea, unhampered by extensive swamps and lagoons, the stands were very heavily logged, especially during the

period from 1945 to 1960. Where exploitation was most intensive only badly formed or unsound trees were left and since dry-season fires were frequent during and after exploitation regeneration is generally sparse or absent. Only where a well planned and properly equipped project for reforestation through fire protection exists, as in north-eastern Nicaragua, is there hope of restoring and maintaining satisfactory pine populations as gene pools.

Great variation in individual tree form, and particularly in branching habit, is found throughout the entire coastal range and indeed in all natural stands of *P. caribaea* var *hondurensis*. Although such features as total height and straightness of stem, length of clear bole and branch persistence are clearly influenced by site factors, including the effect of other vegetation and fire, nevertheless where well stocked young stands exist, frequently near old camps or sawmill sites, individual variation in angle, length and thickness of branches is always evident. In view of the probable effects of site and past accidental influences, and the great individual variation which leads to the occurrence of both highly desirable and highly undesirable phenotypes in all areas visited, none of the coastal provenances can be judged clearly superior in form to any of the others on the basis of observations in the natural stands alone. Predictably the best looking stands are in areas which have mainly escaped exploitation, such as some of the more southerly coastal occurrences in Nicaragua, and on more sheltered, well drained sites.

Sampling of the coastal forests for provenance research has therefore been done by collecting at intervals of about 60 km, or half-degrees of latitude, along a north-south gradient which in fact parallels the climatic gradient of rainfall increase. The pines have apparently migrated progressively southwards through Central America, from a centre of diversity in present-day Mexico and the Caribbean. The most southerly, isolated stands of *P. caribaea* which occur at sea level, only 1 km or less from the coast, between areas of swamp and of broadleaf forest on slightly higher ground, are the most equatorial natural occurrences of pine in the Americas and have therefore been given special attention. Their existence may be attributed to periodic fires in the strips of grassland between the perenially wet swamp and the evergreen rainforest but there are signs that pine regeneration is now being severely affected by the frequent severe fires resulting from human activity in the area. Seed production in these stands in 1970 and 1971 was extremely low and this may be due in part to unfavourable conditions for pollen dispersal resulting from high rainfall. If so years of high seed production are likely to be very infrequent in this part of the range. The sparse crop is further reduced by parrots, which invade the small stands from the surrounding broadleaf forests shortly before the cones ripen. The Nicaraguan government development agency, which together with F.A.O. has established an effective system of reforestation of the pine forests in the north-eastern areas, has plans to extend its work progressively southwards (F.A.O., 1969). The future of these potentionally valuable gene pools is therefore more secure than most other areas of pine forest in Central America. However there is still cause for concern over the future of the most southerly stands which are too small and isolated to be included within the proposed area of management and reforestation, but which may be sources of valuable genetic variation.

The inland stands

The Mountain Pine Ridge forests of British Honduras are undoubtedly the best known inland occurrence of *P. caribaea* var *hondurensis* and have been fully described, notably by Lamb (1950 ; 1973), Loock (1950), Hunt (1962) and Lückhoff (1964). They are also the major source of seed for plantation of this variety and are well represented in plantations throughout the tropics, while the original sites have been under effective fire-protection and regeneration for over twenty years.

The Poptun stands of northern Guatemala, now separated from those on the Mountain Pine Ridge by about 40 miles of broadleaf forests, are at present the

second most important seed source for other tropical countries and thus the continued existence of this provenance is also in some way assured. Nevertheless there is strong evidence of a rapid reduction in the total area of these natural stands in recent years and regeneration of the remaining areas is far from satisfactory (Haufe, 1969). Destruction of the natural regeneration is largely due to regular and frequent burning associated with cattle raising, but commercial seed collection is also contributing to the damage. In recent years there have been up to 500 or more collectors competing for the cone crop during the two-month season and the methods used not only remove the current year's cones but in many cases the following year's also, and may severely damage the trees. So far the stands have escaped intensive felling since there has been no all-season road link with the main centres of human population and industry in the south. Commercial logging in the pine forests may begin very soon and it will then be essential to ensure adequate regeneration, and deliberate conservation of the most valuable genetic resources. The Poptun stands which are found at an elevation of about 500 m (1,600 feet), in a mean annual rainfall of about 1,690 mm (65 inches), are possibly the best natural forests of *P. caribaea* var *hondurensis*. Although the same variation in stem and branch characters can be found there as in all natural occurrences of this variety there is an unusually high proportion of good and excellent stems, with desirable branching habit. This may in part be due to the lack of past selective logging that has affected most stands and to favourable site factors, but the strong possibility that the Poptun populations have inherently better form justifies the introduction of special conservation measures.

Over most of its range in Central America *P. caribaea* has not been found at elevations above 800 m (2,600 feet) and in the mountainous areas of southern Guatemala and most of the Republic of Honduras it is therefore restricted to the valleys and foothills of the main mountain ranges. Wherever it occurs it is certainly the most accessible and sometime the only pine species present and has therefore suffered most severely from exploitation, accompanied and followed by fires severely destructive to regeneration. Increasing spread of cattle grazing, and associated grass burning late in the dry season to stimulate fresh growth, have introduced a fire regime which being annual and virtually complete destroys seedlings before they develop resistance. The introduction from Africa of the pasture grass *Hyparrhenia rufa* (Nees) Stapf., now widespread in many parts of Central America, has almost certainly increased the severity of grass fires. The future existence of many of these inland stands is very doubtful. From continuous areas of open pine forest most have been reduced to scattered groups of trees which are satisfactory neither as a breeding population nor as a unit of management. The further slow reduction of these scattered groups to isolated trees and their final disappearance seem under present circumstances inevitable.

In the mountainous interior of Honduras the distribution of *P. caribaea* is much wider than is commonly realised but, now at least, discontinuous. Lückhoff (1964) lists most of the known occurrences although additional areas have been found in the course of the present project, in the south-west of the country and in valleys along the north coast. It is significant that even in 1957 he found most of the forests of this species heavily cut over already and a few stands that had not then been heavily exploited and which he reported to be "generally well stocked with 50 or more stems per acre" have since been reduced to scattered groups of poorly formed or unsound trees by intensive logging, followed by fire. It seems very probable that *P. caribaea* was more continuously distributed until the recent past along many of the valleys of interior Honduras, which could have served as a link between the forests of this species in northern Nicaragua and those along the north coast of Honduras and on the Atlantic coastal plain far to the east. The largest area still remaining is in the Department of Olancho, to the east of Catacamas. These stands, although virtually unexploited, are much less impressive than the

Poptun stands with a much higher incidence of poor stem form and branching habit and greater apparent tendency to severely spiral grain.

The inland stands in Honduras Republic which may be of greatest value as seed sources for arid areas are found in severely dry conditions, in the broad upper valley of the Rio Choluteca. In this area of low, rocky hills, around 700 m (2,300 feet) above sea level, the soil is thin, poor in nutrients and freely drained, while the mean annual rainfall is only 650 to 900 mm (25 to 30 inches) with a prolonged dry season. It was on the better soils in this general area, possibly with a somewhat higher rainfall, that Lückhoff (1964) reported finding the largest specimen of *P. caribaea* he encountered in all of Central America with a diameter of over 122 cms (4 feet) and a height of approximately 37 m (120 feet). In the dry zone the few remaining older trees are now restricted mainly to hilltops, among boulders and rock outcrops, and are generally of very poor form but some small open stands of straight young trees are found (provenance collection No. K56). The contrast between the ecological conditions of these stands and those on the Atlantic coastal plain is very great.

Pinus oocarpa Schiede

Until very recently little was known of this species from its natural range outside Mexico, where several botanical varieties have been recognised and described (Martinez, 1948). Its range within Central America is extremely wide, extending from Baja Verapaz and Huehuetenango, close to the Guatemalan border with Mexico at 16° N as far south as 12° 45′ N in Nicaragua. Within the Republic of Honduras alone it is, or was, distributed almost continuously over an area more than 160 kms (100 miles) from north to south and more than 300 kms (180 miles) from east to west, extending further north and west into Guatemala and El Salvador, and southwards into Nicaragua. The herbarium specimens, amounting in total to several hundred, collected throughout the area in the course of the present research project, and brought to Oxford, are the first comprehensive collections of the species in its range outside Mexico. Observations made during the course of collecting indicate that it is highly variable botanically and detailed examination of material collected is being continued at Oxford by Dr. B. T. Styles. Oleoresin analysis of samples from different parts of the natural range is also in progress, at the Tropical Products Institute, London.

To any visitor to Central America who is familiar with dry savanna woodland sites elsewhere in the tropics, as found for example over large areas of Africa, the potential of *P. oocarpa* as a plantation species is immediately apparent. In comparison with *P. caribaea* it appears to be adapted to a longer and more severe dry season. *P. oocarpa* is normally found at higher elevations, generally between 700 m (2,300 feet) and 2,000m (6,500 feet) above sea level. The present study has been directed principally at the low level occurrences and it has been found as low as 250 m (800 feet) above sea level in one area of Guatemala. At altitudes below 800 m (2,600 feet) it is commonly in mixture with *P. caribaea*. Over large parts of its range, mean annual rainfall is generally between 700 mm (27 inches) and 1,500 mm (59 inches) with a severe and prolonged dry season. Although exact climatic data are frequently lacking it is clear that in many areas where *P. oocarpa* is the main pine species there is a continuous period of six months with mean monthly rainfall less than 50 mm (2 inches) and mean monthly maximum temperatures between 26°C and 32°C.

It is found on a very wide range of parent materials including granites, gneisses, micaceous schists, shales, mudstones, volcanic tuff and ignimbrites. Since it grows mainly on steep slopes the soil is usually very thin above the parent rock, and drainage is free to excessive. The herb layer is dominated by grasses adapted to annual fires, or in more favoured situations by bracken and shrubs, such as *Byrsonima crassifolia, Quercus* spp and some *Melastomaceae*.

Since *P. caribaea* is already well known and much sought after as a plantation species the comparison of the growing conditions of the two pine species in a region in which both are found naturally is of great interest. The different altitudinal range is evident and also the very different rainfall regime between the inland mountains where *P. oocarpa* is found and the wet coastal plain which is the main climatic zone for *P. caribaea*. The rain-bearing winds come mainly from the north-east and since the mountain ranges are aligned approximately at right angles to these winds they cast a rain shadow on the southern side. Interesting examples of this are the Sierra de las Minas in Guatemala and the Sierra de Dipilto in Nicaragua. The former range reaches almost to the Atlantic coast, below the southern border of British Honduras, and rises progressively higher to the west. At the extreme eastern end no pine is found but *P. caribaea* appears about 50 kms (30 miles) inland and continues along the foothills for a distance of about 50 kms. With increasing distance westward and increasing height of the mountain range, the rain shadow effect becomes progressively greater and *P. caribaea* is progressively replaced by *P. oocarpa*. Over a distance of about 35 kms the two species can be found growing together at elevations from 250 m (800 feet) to 750 m (2,500 feet) above sea level. Other factors, of course, change in the same direction, as there is a slow increase in level of the valley floor, where the natural vegetation has been largely modified by human activity, and the slopes of the hills at the foot of the range tend to become steeper.

A parallel situation exists in the Sierra de Dipilto, along the northern border of Nicaragua. Here the mountain range is bordered on the east by the broad coastal plain with high rainfall and again casts an increasingly deep rain shadow with increasing distance westward. On the foothills and valley floor at the eastern end *P. caribaea* is the only pine species but it is progressively replaced to the west by *P. oocarpa* at elevations of 600 m (2,000 feet) and above, or by thorn scrub and grasslands at lower elevations. Again the decreasing rainfall gradient runs parallel to an increase in elevation and in steepness of slope of the mountains.

The driest site on which *P. caribaea* has been found is in the upper Choluteca valley near to Los Limones (provenance seed collection No. K56), in the southern part of Honduras Republic. In the vicinity of these stands only a few trees of *P. oocarpa* are to be found, but in the foothills at the edge of the valley, at only slightly greater elevations, it is once more dominant and above 800 m replaces *P. caribaea* completely.

From observations in the Mountain Pine Ridge in British Honduras, where *P. oocarpa* does occur together with the much more widespread *P. caribaea*, Lamb (1966) concluded that *P. oocarpa* was found on the more favourable sites, particularly on the steep-sided valleys in the slate and shale which also carry a more dense shrubby vegetation. Such sites burn occasionally in extremely dry years leaving an almost clean floor. Whereas the cones of *P. caribaea* mature and drop their seed within a period of about three months in any one area (during the rainy season, although the actual calendar months of seed fall vary in different parts of its range) the cones of *P. oocarpa* reach maturity over a longer period of six months or more and those cones which mature after the onset of the rainy season may retain their seed until the start of the following dry season. The majority reach maturity at the height of the dry season and thus the species is in a favourable position to occupy sites burnt by fires at any time throughout this period.

There is ample evidence throughout the range of *P. oocarpa* of its ability to colonise dry, exposed sites left bare by fire and/or erosion. It is very intolerant of shade and the dense regeneration that in many areas followed where mortality from the severe *Dendroctonus* attack of 1964 was most heavy is evidence of this. *P. caribaea* appears to be less susceptible in this respect and where adequate seedling regeneration of both pine species occurs on the same site therefore, it is

likely that either in direct competition between the two, or separately through competition with other vegetation, *P. caribaea* may become dominant if other conditions are favourable to it.

The rôle of fire in determining the relative distribution of pines and broadleaf species has been well reviewed by Johannessen (1959), Denevan (1960), Taylor (1963) and others, who concluded that the upland pine communities in which both *P. caribaea* and *P. oocarpa* are found are fire-induced disclimaxes, due largely to the relative shade intolerance of seedlings of both pine species as compared with the neighbouring broadleaf species. However it seems possible that fire may affect regeneration of one pine species more severely than the other according to the timing, intensity, speed of movement, flame height and so on. In addition to the differences in time and duration of seed fall, there appear to be differences between the species in the fire-tolerance of seedlings and young saplings.

Where the two species are found together in unburnt areas *P. oocarpa* may most readily be distinguished by the bark of large seedlings and young saplings which in addition to its deep orange colour in the early stages is almost invariably smoother and thinner than in *P. caribaea* of equivalent size. At the same time the needles of the latter species form more dense, deeper green clusters around the growing points of stem and branches whereas in most *P. oocarpa* the needles, being finer, more flexible and less densely clustered, affort less protection. It is probable therefore that a fire which damages the bark, or which reaches up to all the tips of stem and branches, will kill relatively more *P. oocarpa* than *P. caribaea*.

Of possibly greater significance is the remarkable capacity of young saplings of *P. oocarpa* to produce fresh shoots from the root collar region after the stem has been killed by fire. Although there have been very few published reports of this ability it was observed in the course of the present research project in stands throughout the entire range of the species in Central America, excepting British Honduras; failure to observe it there may have been due partly to the very brief period spent there and also to the effective fire prevention practised on the Mountain Pine Ridge. In many other areas where large numbers of saplings had been recently killed by fire the majority of them were producing shoots in dense tufts and some shoots were observed growing strongly to a height of more than two metres, parallel and close to the dead stem. It is common also to find young seedlings with multiple shoots clustered around a taller main shoot and with no evidence of having suffered fire damage. This habit could be of value in increasing chances of survival in light grass fires. Chable (1967) reported cases in Honduras in which young saplings were burned back for several years in succession, during which time a dense root system was developed, until finally the saplings got past the stage at which they could be killed by fire. This behaviour may partly explain the high incidence of basal sweep or of multiple stems arising at or slightly above ground level, as found in some areas of the natural stands. Exactly similar behaviour is seen of course in many indigenous trees of the African savanna woodlands, and several eucalypts in Australia, where severe grass fires occur in the dry seasons. *P. caribaea* has never been observed to produce such basal shoots and while it is capable of surviving fires which kill practically all the needles and severely scorch the bark, if the apical meristems are killed there is no recovery.

On steep slopes, where upward-moving fires reach greater flame height and intensity, and on sites where more favourable moisture or nutrient status support a denser vegetation which may burn fiercely in very dry years, it might be supposed that *P. oocarpa* would have a better chance of becoming established than *P. caribaea*. It seems probable therefore that the relationship between a parent material or soil type and the species of pine found growing on it may not be simple and direct but may act through their influence on such factors as associated vegetation or angle of slope which in turn modify the effect of fire on pine regeneration.

Despite the great variability of *P. oocarpa,* in almost all natural stands trees with

Regrowth of *P. oocarpa* after death of the main stem from fire. Honduras Republic.

good or excellent stem form are to be found. Branching habit and branch-shedding are generally good although the development of long clear boles may be due partly to the influence of fire. The most serious defect in stem form is a tendency to sinuousity sometimes visible not only in the main shoot but in the branches also. Production of multiple stems, perhaps as a result of "coppicing" after fire, has already been mentioned. Forking of the main stem is also common in some

stands, particularly where selective felling may have caused damage to the leading shoots.

Timber testing of *P. oocarpa* from the natural forests has been restricted so far to only two or three sites and to very few trees. Tests at Yale (Hess, Wangaard and Dickinson, 1950) suggest that its strength properties are inferior to *P. caribaea* from the natural forest but equal to and in some characters better than *P. palustris* Mill. Of greater significance is the increased demand for the timber for export to the U.S.A. and Europe and the fact that in practice no distinction is made between the timber of this species and that of *P. caribaea*. The suitability for pulp and papermaking is equal to that of the southern pines of the U.S.A. and in some respects better than that of *P. caribaea* (Schafer and Chidester, 1961).

Priorities for international research

Several countries are embarked on extensive plantation schemes with *P. caribaea* var *hondurensis*, using the Mountain Pine Ridge and Poptun seed sources, which have been virtually the only supplies available. In a few countries important genetic gains have already been achieved in such features as stem straightness, by selecting from within the introduced populations. Although it seems probable that these two sources of seed are among the most suitable for many tropical sites there can be no certainty of this without conducting range-wide provenance trials under a variety of conditions. *P. caribaea* was originally chosen as a plantation species because it was one of the few fast-growing tropical conifers, with wood qualities comparable to some of the valuable temperate conifers and with the capacity to grow at low elevations. *P. oocarpa* has been more recently and less widely introduced as an exotic but is now in great demand for similar reasons. However other qualities possessed by both species which are at least as important in the long-term are their great variability both within and between populations, and the ability of some populations to grow under severely adverse conditions, on dry and infertile sites.

There can be little doubt that their inherent variability has been largely responsible for the southwards advance of these two species on to a variety of sites beyond the southern limits of any other pine on the American continent. Although this variation is most apparent in the gross morphology of the tree, it is ultimately physiological controls which determine the patterns of growth and which strongly influence the ability to survive and grow under adverse conditions. Great inherent variability in physiological traits such as the production of growth regulators is almost certainly to be found among the wild populations of both species, and must be responsible for the frequently unpredictable behaviour of provenances or progenies when introduced to a new and different environment. The comparatively uniform growth patterns shown by the two botanical varieties of *P. caribaea* which are confined to relatively uniform island environments in Cuba and the Bahamas, even when transferred to new and different environments, is an indication of less inherent variability than that shown by the mainland variety. While such uniformity may be an advantage in a short term introduction and selection programme it imposes limitations on a long term breeding programme, unless used in combination with other material by inter-varietal or inter-specific hybridization.

While natural selection has produced some varieties, strains and families that are immediately useful, it is probable that further large improvements are possible by selection and breeding within a highly variable species. These gains can most easily be achieved by establishing large populations under a given set of environmental conditions and then selecting and propagating the most productive individuals. There is nevertheless a danger that some potentially valuable traits might be lost in this process unless the original wild populations can somehow be perpetuated as well. Moreover it is practically impossible to establish populations large enough to support a long term breeding programme on all the possible sites

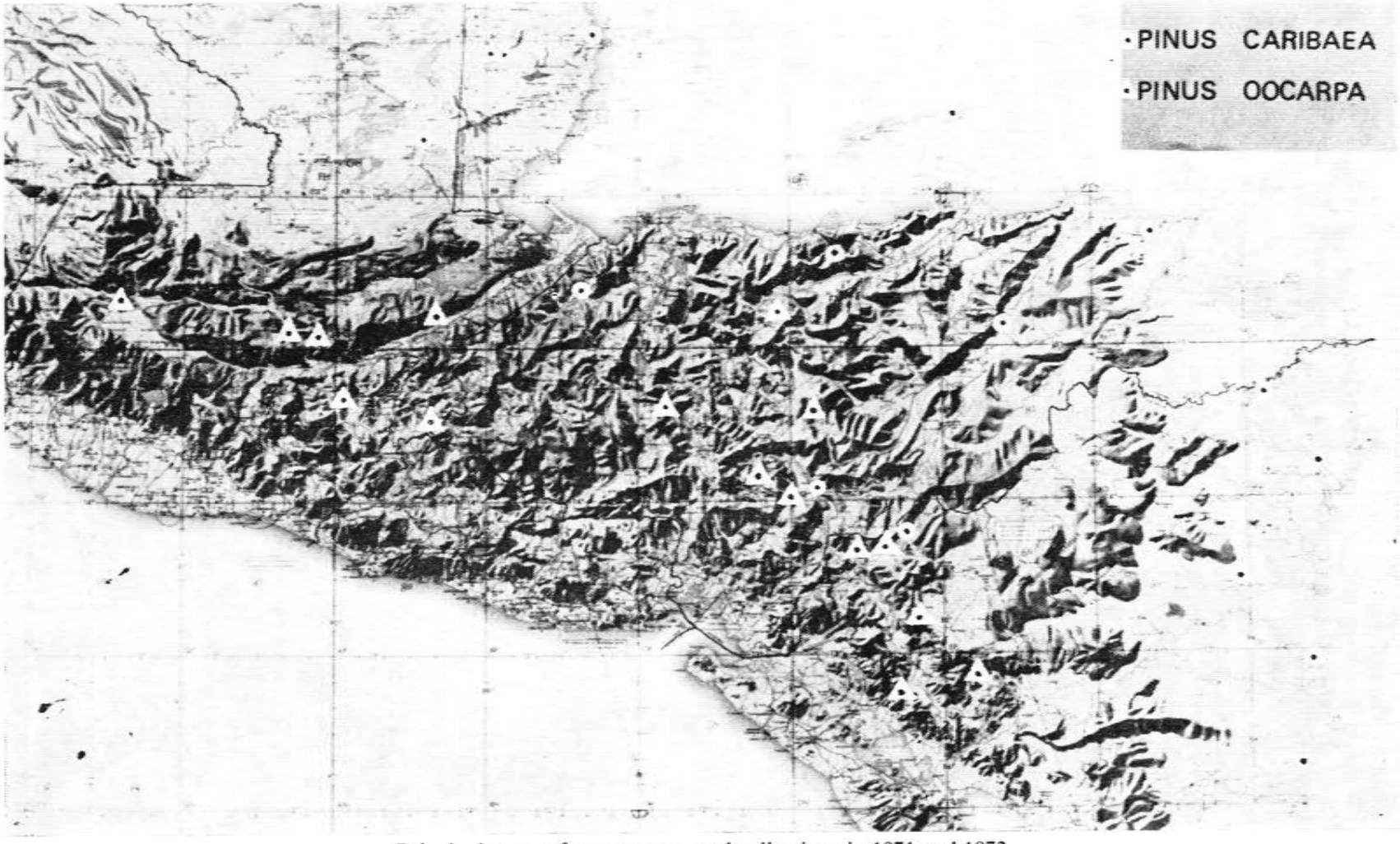
in all interested countries. An alternative, or at least complementary approach is therefore to study those characters which are of greatest value in fitting the plant to the desired environment and end use, and their heritability and interaction with each other or with the environment. Both these approaches require a research programme extending over a very long period of years before appreciable gains are made. To what extent can such a programme be justified if, as is sometimes suggested, the industrial rôle of wood may in future be filled by synthetic substitutes?

Although the questioning of the future industrial rôle of wood and wood products has been valuable in stimulating discussion it is far from being a sound basis for deciding research policy. Recent concern over environmental pollution and exhaustion of non-renewable resources is likely to lead to the restriction of industrial growth within limits that are not set by technological or economic considerations alone. The rational use of renewable resources which contribute in both life and death to natural ecosystems is continuing to gain support. In economic terms the prospects for forestry in the tropics are good. Potential rates of growth are high and with an investment in research, and the development of the means to efficient management, such as have gone into temperate forestry, very high production rates at low cost are clearly attainable. Large areas of land are available and many which are at present unproductive as a result of past misuse may gain additional benefits from the restoration of a forest cover as well as wood production.

The potential value of some populations of *P. caribaea* and *P. oocarpa* in the reforestation of degraded and seasonally arid tropical sites is apparent from the natural stands and a programme of selection and breeding, based on the most suitable provenances and informed by study of the more important characters, could extend the capacity of both species to utilise sites at present considered unplantable. Such an achievement would continue to bring lasting benefit as the pressures on land increase and would have its greatest impact where the shortage of wood is already most severe. In the short term the conversion of areas of closed forest of low productivity to high yielding plantations will give much quicker and more certain returns on investment. However in the long view the low productivity of many mixed tropical hardwood forests, being limited largely by marketing and harvesting problems, may be more apparent than real.

It is often difficult for a forestry department in a developing country to obtain funds to finance development projects which involve a long initial research investment before tangible benefits are achieved. Political pressures frequently enforce a short term view to achieve rapid results. An international research programme can assist with provision of material for such national programmes and proposals for international action, particularly on *P. caribaea*, have already been made (Nikles, 1971). At the same time there is an overriding international responsibility to ensure that global resources of valuable genetic variation are not lost unnecessarily but are conserved and developed (Kemp et al, 1972).

So far in the provenance research programme for *P. caribaea* and *P. oocarpa* priority has been given to the early assembly of representative range-wide seed collections for international provenance trials. At the same time an attempt is being made to collect large quantities of seed of those provenances which appear in their natural habitat to be in the greatest danger or of the greatest potential value as seed sources. Seed for over 150 provenance trials, each containing up to 16 provenances, and for some selection/conservation stands of individual provenances, has already been distributed. It has not been possible to provide enough seed for trials on all possible site types in all interested countries but by analysis of genotype-environment interaction effects under different conditions it may be possible to assess the suitability of a provenance for sites where no trial has yet been made. At the same time the trials will provide comparable material for study



Principal areas of provenance seed collections in 1971 and 1972.

of a variety of morphological, anatomical and chemical characters. The same provenances are also being studied under greenhouse conditions.

This work is clearly only the first stage in a long research and development programme. When the Oxford programme of research on fast growing tropical timber species was first started in 1963, with particular emphasis on *P. caribaea*, three phases of operation were proposed. The first was to be the comprehensive study of the species performance in plantation throughout the tropics and sub-tropics and the second was a systematic investigation of seed sources in the countries of origin. Pending the results of provenance trials a third phase was proposed, to establish a tree breeding centre in the area of origin. More recently proposals have been put forward for a global project with U.N.D.P. participation and involving research centres in several countries as well as the country of origin. (Kemp et al, 1972.) Both *P. caribaea* and *P. oocarpa* are clearly of great potential value to many tropical countries and a co-ordinated international programme is needed urgently to conserve and develop the genetic resource of these two species.

(Editor's Note. The author supplied a lengthy list of locations of provenance seed collections in 1971 and 1972—space does not permit of its inclusion—interested readers could contact him direct.)

REFERENCES

BURLEY, J., 1969. Methodology for provenance trials in the tropics. Unasylva 23 (3) No. 94.

CHABLE, A. C., 1967. Reforestation in the Republic of Honduras, Central America. Ceiba. Vol. 13 No. 2.

DENEVAN, W. M., 1961. The upland pine forests of Nicaragua. Univ. of Calif. Publ. in Geography Vol. 12 No. 4.

F.A.O., 1969. Survey of agricultural and forest resources in Nicaragua. Final Report. FAO/SF: 49/NIC-2, Rome.

HAUFE, H. H. R., 1969. Inventario forestal complementario de los bosques de pino (*Pinus caribaea* Morelet) de Poptun, Peten. Empresa de Fomento y Desarrollo Economico del Peten, Guatemala.

HESS, R. W., WANGAARD, F. F. and DICKINSON, F. E., 1950. Properties and uses of tropical woods. Trop. Woods No. 97.

HUNT, D. R., 1962. Some notes on pines of British Honduras. Emp. For. Rev. 41 (2): 134-145.

JOHANNESSEN, C. L., 1959. Geography of the savannas of interior Honduras. Dept. of Geogr. Univ. of Calif., Berkeley.

KEMP, R. H., BURLEY, J., KEIDING, H., and NIKLES, D. G., 1972. International co-operation in the exploration, conservation and development of tropical and sub-tropical forest gene resources. Proc. VII World For. Cong. Argentina, 1972, F.A.O., Rome.

LAMB, A. F. A., 1950. Pine forests of British Honduras. Emp. For. Rev. 29, No. 3, 1950.

LAMB, A. F. A., 1966. Report on further data from the forests where *Pinus caribaea* and *P. oocarpa* are indigenous. Comm. For. Inst., Oxford (mimeog.).

LAMB, A. F. A., 1973. *Pinus caribaea.* Fast growing timber trees of the lowland tropics (Series) No. 6, Comm. For. Inst. Oxford.

LOOCK, E. E. M., 1950. The pines of Mexico and British Honduras. Union of S. Africa. Dept. For. Bull. No. 35

LUCKHOFF, H A., 1964. The natural distribution, growth and botanical variation of *Pinus caribaea* and its cultivation in South Africa. Annals Univ. Stellenbosch Vol. 39, Series A No. 1.

MARTINEZ, M., 1948. *Los pinos Mexicanos.* 2nd ed. Ediciones Botas, Mexico.

NIKLES, D. G., 1971. A proposal for international co-operation in the breeding of certain conifers, with special reference to *Pinus caribaea* Morelet. Proc. of Symp. on Selection and Breeding to improve some tropical conifers, Vol. 2, Gainesville, 1971.

SCHAFER, E. R. and CHIDESTER, G. H., 1961. Pulping and papermaking experiments on certain pines of Mexico and Central America. Report No. 2217. For. Prod. Lab., Madison, Wisconsin, U.S.A.

TAYLOR, B. W., 1963. An outline of the vegetation of Nicaragua. Journ. of Ecol. 51 (1).