THE HABITAT OF *ACACIA AURICULIFORMIS* AND PROBABLE FACTORS ASSOCIATED WITH ITS DISTRIBUTION

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BOLAND, D.J., PINYOPUSARERK, K., McDONALD, M.W., JOVANOVIC, T. & BOOTH, T.H. 1990. The habitat of *Acacia auriculiformis* and probable factors associated with its distribution. This paper describes the current distribution of *Acacia auriculiformis* in Australia (Northern Territory and Queensland), Papua New Guinea and Indonesia. Climatic data for six climatically defined groups within the species distribution are indicated. Details are given of past geological and climatic events that are likely to have been important in moulding the current distribution. The species is fairly primitive and may have evolved on rain forest fringes sympatrically with *Acacia aulacocarpa* and *Acacia crassicarpa*. In recent times it is likely to have expanded from monsoon vine forests and gallery rain forests when conditions were favourable. The species is opportunistic and very mobile. Rising sea levels and periods of aridity are probably the major factors determining its current disjunct distribution. Implications for seed collection programmes and for the interpretation of results from biosystematic studies are discussed.

Key words: *Acacia auriculiformis* - natural occurrence - population types - sea levels - biogeography

Introduction

Acacia auriculiformis Cunn. ex Benth. is a tropical species valuable for forestry, particularly in southeast Asia and the Indian subcontinent. Its important attributes are rapid early growth, good wood quality (for pulp, sawn timber, charcoal, fuelwood) and tolerance of a range of soil types and pH (mostly acid but it can also tolerate alkaline conditions). The species can also tolerate seasonal water logging and competition from *Imperata* grass. In particular its ability to fix atmospheric nitrogen and grow on nutrient-impoverished soils are important attributes for sites currently available for reforestation in the tropics. The species is widely grown in Vietnam, Thailand, Philippines, Indonesia and India and has been trialed in South and Central America and Africa. Large plantations currently exist in Karnataka (India) and new plantations are proposed for Zaire (Phambu Khasa personal communication 1989).

The species is adaptable to agroforestry situations. It was one of five priority species (*Eucalyptus camaldulensis, Acacia mangium, Leucaena leucocephala, Acacia auriculiformis* and *Bambusa* spp.) recommended by the International Union of

Forest Research Organisations (IUFRO) for intensive development in the humid tropical lowlands (IUFRO 1984). IUFRO further recommended that tree breeding and silvicultural research be commenced and this was taken up by USAID (through Winrock International) in the development of the Forestry/Fuelwood Research and Development Project (F/FRED) in Asia (Anonymous 1986). The F/FRED Project involves *A. auriculiformis* in growth and management trials and also cooperative ventures with Australia (ACIAR/CSIRO) in seed collections (B. Gunn *et al.* unpublished report) and work on field provenance trials, geographic variation of seedling morphology and a bibliography (Anonymous 1988). These activities led to the current study.

In developing this paper we have constructed a database of natural occurrences of the species in dBASE III Plus, using locations of herbarium specimens lodged in Australian and Indonesian herbaria, seed collection locations and other known natural stands (output of database available on request). One limitation of the study is that we are reconstructing environmental information essentially from the records of botanists and seed collectors and not from ecologists specifically studying the range of environmental conditions under which the species grows.

Care was taken to exclude sites where the species has been cultivated on the fringes of its distribution for example street trees on Ambon and Timor Islands, Indonesia. Generally, however, the species is not used in its natural range except as a minor species for fuelwood and rough construction (poles, posts *etc.*) In addition, most of its natural distribution occurs in sparsely settled areas and hence only limited agricultural clearing has taken place. In Papua New Guinea villagers may have cleared natural stands for village gardens. Human disturbance is thought to have had little impact in reducing or expanding its distribution within the range of its natural occurrence.

In domesticating *A. auriculiformis* it is important to document published information, define its natural distribution, study patterns of natural variation, examine its repoductive biology, conduct seed collections, develop appropriate breeding programs and associated provenance/progeny tests and explore a range of end uses to further its utility. This paper defines the natural distribution of *A. auriculiformis.* Attention is given to soil types, associated vegetation and current climates in order to provide details of the range of habitat conditions *A. auriculiformis* is associated with naturally. These details will assist in the domestication of the species and interpretation of results of genetic variation studies.

Present distribution of *A. auriculiformis*

The currently known distribution of *A. auriculiformis* is shown in Figure 1. In Australia the species occurs on Cape York Peninsula, Queensland, and the Top End of the Northern Territory. It does not occur in Western Australia (Kenneally & Beard 1987, B. Maslin personal communication 1989) although suitable habitats appear to exist in and near the numerous small patches of monsoon vine forests in the northern Kimberley area. In Papua New Guinea the species occurs in Western Province, Central District and neighbouring offshore islands. The distribution in Indonesia is less well known but it appears to be restricted to Irian Jaya including small offshore islands.

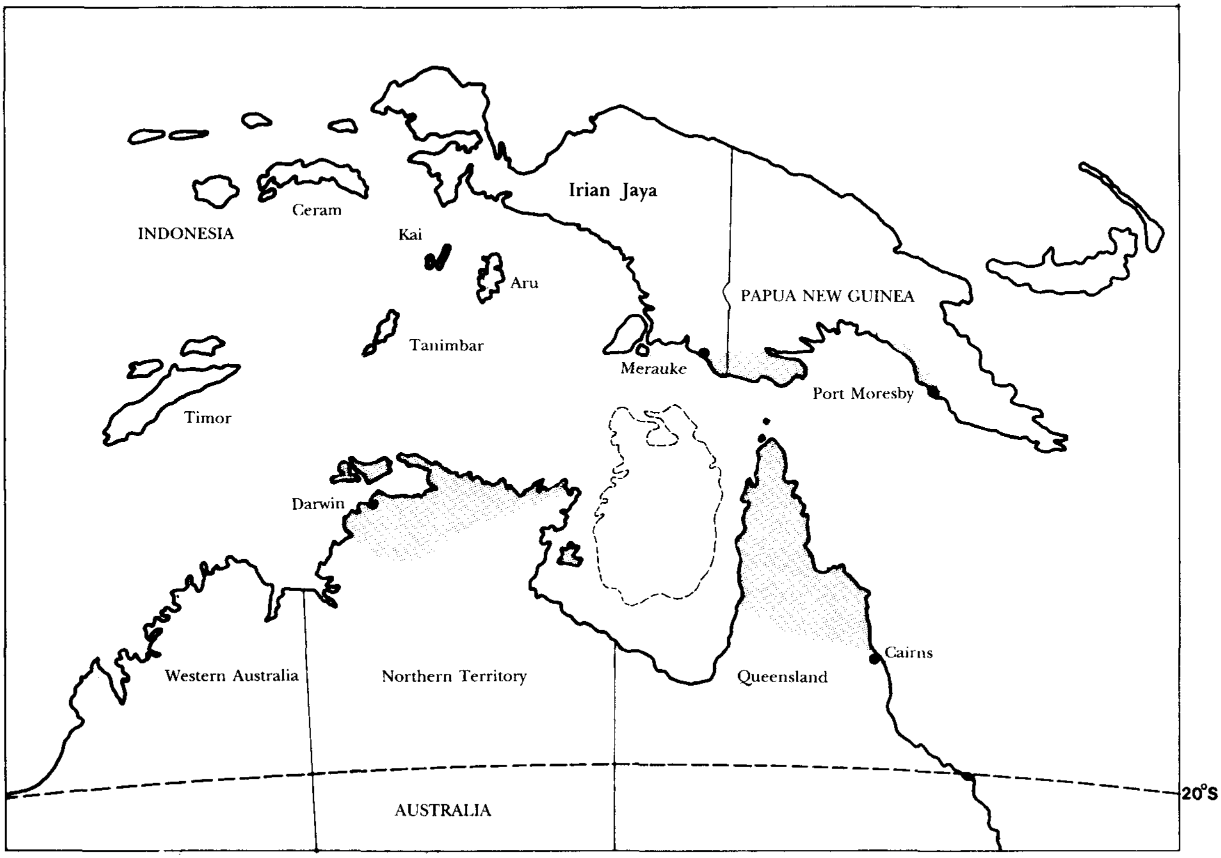

Figure 1. A map of the natural distribution of *A. auriculiformis* (Broken lines indicate the former position of Lake Carpenteria at its maximum extent)

A. auriculiformis is only found where its roots can exploit a supply of permanent or semi-permanent ground/surface water, that is, high watertable habitats (riverbanks, creekbanks, springs), run-on sites (floodplains, billabongs) and coastal landforms (estuaries, lagoons, foredunes). Details of specific locations within two Australian States, Papua New Guinea and Indonesia follow.

Natural occurrence in the Northern Territory, Australia

Distribution

The main area of occurrence extends from 11°S, 130°E (Melville Island) in the northwest, south to 14°S, 131°E (Douglas River) and east to 12°S, 135°E (western rim of the Arafura Swamp). This encompasses about 15 lowland river systems that have their origins on the Arnhem Land Plateau. In the Top End it also occurs on seven offshore islands, namely, Groote Eylandt (Levitt 1981), Elcho, Milingimbi, Croker, Melville, Bathurst and Peron Islands. It is uncommon in eastern Arnhem Land and known only from Oyster Beach on the mainland. In this region it is usually displaced by *A. leptocarpa* in riverine habitats. On the southwestern edge of the Gulf of Carpentaria a reported population near Borroloola (Maslin & Pedley 1982) has now been determined from herbarium material to be *A. leptocarpa* (L.A.J. Thomson personal communication 1989). The species occurs on Maria and Vanderlin Islands (Sir Edward Pellew group) in the Gulf of Carpentaria in areas adjacent to Borroloola.

The altitudinal range is from sea level (*e.g.* Cobourg Peninsula and Melville Island) to 150 *m* on the Reynolds River. The species extends inland for up to 120 *km.*

Population types

The populations of *A. auriculiformis* in the Northern Territory have been grouped into three broad types as discussed below:

Coastal and sub-coastal populations. These populations are found on a variety of landforms which include foredunes, tidal flats, saline lagoons, estuary banks and deltaic floodplains. They are exemplified by populations on the Cobourg Peninsula, the East Alligator River floodplain and Noogoo Swamp. *A. auriculiformis* is abundant on coastal landforms of the Cobourg Peninsula, particularly at Danger Point and Smith Point. At these sites it can occur as a shrub (2-3 *m* tall), colonising the foredune to the high-tide level associated with *Casuarina equisetifolia.* Small trees develop at the rear of these systems. Pure stands fringe saline lagoons or it may be associated with mangroves along the tidal estuaries. Soils of these populations may be derived from aeolian sands (pH 7.0-7.5), laterite (pH 6.0-6.5) or limestone (pH 8.0-9.0).

Extensive woodland stands of *A. auriculiformis* border the *Pseudoraphis* swamp grasslands along the deltaic floodplains of the East Alligator River. They occupy the broad transitional zone between the seasonally inundated flats and the elevated areas surrounding the floodplain. Soils are acidic alluvia composed of silty sandy clays.

At Noogoo Swamp *A. auriculiformis* dominates the tidal flat plant communities which fringe the highly saline zone. They are small trees up to 12 *m* tall which have prominent upright-branching crowns. The soils are black cracking clays (pH 5.0) subject to periodic inundation.

Riparian populations. *A. auriculiformis* is a component of the vegetation corridors fringing rivers and creeks of lowland drainage systems. These are the most wide-ranging populations. Occurrences include Douglas River (a tributary of the Daly River), Reynolds River, Finnis River, Elizabeth River, Darwin River, Adelaide River (south to the Mary River tributary), South Alligator River (south to Gerowie Creek tributary), Cooper Creek, East Alligator River (to tributaries south of Nabarlek), Goomadeer River, Mann River, Cadell River, Blyth River and Yarunga Creek (near Ramingining).

The vegetation structure of riparian populations ranges from closed forest to open forest. The form varies from tall trees (to 25 *m*) in monsoon vine forests to heavy crowned, short boled trees on open exposed sites.

When present in mixed riparian stands it may form a component of either of the two major riverine alliances of the Top End, that is the *Melaleuca* alliance (*M. leucodendra* - *M. argentea*, with *M. dealbata*, *M. cajuputi*, *Lophostemon lactifuus*, *Barringtonia acutangula* and *Pandanus spiralis* often associated) or the monsoon vine forest alliance (*e.g. Adenanthera pavonina*, *Breynia cernua*, *Carallia brachiata*, *Calophyllum* sp., *Canarium australianum*, *Carpentaria acuminata*, *Cupaniopsis anacardioides*, *Elaeocarpus arnhemicus*, *Euodia elleryana*, *Ficus* spp., *Hydriastele wendlandiana*, *Maranthes corymbosa*, *Myristica insipida*, *Nauclea orientalis*, *Syzygium* spp., *Terminalia* spp., *Timonius timon*, *Xanthostemon* spp. - B. Gunn *et al.* unpublished report). Its ability to extend from the monsoon vine forest to the *Melaleuca* alliance can be attributed to several factors such as its hardseededness and subsequent ability to regenerate after fires, an ability to grow in exposed open sites, tolerance of adverse soil conditions (especially periodic waterlogging), and its rapid early growth rate.

Soils are alluvia derived from sandstone and/or laterite. They drain poorly consisting mostly of clay. They vary from being acidic (pH 4.5) to slightly acidic (pH 6.5).

Riparian populations are perhaps the most dynamic as they colonise recent, alluvial landforms and may be subject to flood damage, seasonal fire and grazing by stock.

Isolated monsoon vine forest populations. *A. auriculiformis* is a component of the isolated patches of monsoon vine forests scattered widely throughout the Top End. These populations differ from those occurring in the wide-ranging riparian monsoon vine forests in that they are disjunct and possibly genetically isolated. They typically occur on landforms that are semi-permanently moist and protected from intense fire. They range in size from less than one hectare to large tracts of tens of hectares. Russell-Smith and Dunlop (1987) recorded the species in these isolated monsoon vine forests near lowland springs, rocky outcrops and sandstone springs.

Populations of *A. auriculiformis* occur in gullies that surround the Arafura Swamp. These are often represented by a small number of mature individuals (*e.g.* three trees present in a monsoon vine forest 18.6 *km* south of Ramininging, N.T.). In these closed forests individual trees may attain heights of 28 *m*. The gullies are spring-fed and soils acidic clay loams.

Natural occurrence in Northern Queensland, Australia

Distribution

The natural occurrence extends from 10°10' S, 142°15' E (Moa Island north of Cape York in Torres Strait) to 16°41' S, 145°18' E (Rifle Creek) near Mt. Molloy. It has been collected from the upper catchments of six west- (*i.e.* Wenlock, Archer, Holroyd, Mission, Jardine and Mitchell Rivers) and four east- (Stewart, Morehead, Normanby/Kennedy, and Endeavour Rivers) flowing drainage systems but potentially may be present on all river systems (*ca.* 50) north of the Mitchell River.

In contrast to occurrences in the Northern Territory and Papua New Guinea, populations of *A. auriculiformis* in north Queensland extend far inland up streams. It is common for populations to occur up to 150 *km* inland. At Rifle Creek *A. auriculiformis* is some 430 *km* inland (but only 30 *km* from the east coast) from the mouth of the Mitchell River.

There are several high continental or volcanic islands between Cape York and Papua New Guinea (Jennings 1972) and numerous coral cays and mud islands. The largest of the volcanic islands are Prince of Wales, Moa, Badu and Horn Island. The species occurs on hillsides on Moa island (B. Gray personal communication 1989) and possibly on neighbouring Badu island (J. Clarkson personal communication 1989). The species also occurs on Hammond Island (R.W. Gurraway 1905; one herbarium specimen) near the tip of Cape York. There are few islands in Queensland on the west side of Cape York and the species is absent from the Wellesley Islands in the Gulf of Carpentaria (J. Clarkson personal communication 1989).

The Laura Basin dry corridor of dry sclerophyllous forests (mainly eucalypts) is a barrier for many rain forest species between the Cape York forests of the Iron Range-Mcllwraith Ranges and the more southern rain forests around the Cairns-Atherton region (Laverack & Godwin 1987, Barlow & Hyland 1988). occurs either side of this barrier and is present along river systems flowing out from both areas. However it does not extend further south to the rivers or monsoon vine forests inland from Townsville (Kahn & Lawrie 1987).

The altitudinal range in Queensland is from 10 *m* (Silver Plains) to 380 *m* (Rifle Creek).

Population types

A. auriculiformis populations in Northern Queensland are predominantly riparian and wide ranging. In southern Cape York it occurs more frequently on the high river banks of braided streams or the fringes of gallery rain forests. In northern Cape York it occurs more commonly on the fringes of monsoon vine forests and evergreen forests (*e.g.* near Weipa and Bamaga) and in vine thickets on Moa Island. Population types are outlined briefly below.

Riparian populations. These populations are associated with or may intergrade into either the *Melaleuca* riparian forests (*e.g.* Morehead River, Archer River, Holroyd River) or the gallery rain forest alliance (*e.g.* Jardines Gardens, Normanby River, Croll Creek, Stewart River, Kings Plain and Archer River). Occurrences that have both alliances represented include the Coen River and Wenlock River populations.

Structural form may vary from open to closed forest. Tree heights of 20 to 30 *m* are common. In a population north of Bamaga trees up to 40 *m* tall have been recorded (C.A. Gardiner & J. Moriarty personal communication 1989).

Soils are alluvia derived from granite or meta-sedimentary substrate ranging in texture from loamy sands (pH 6.5) to clay (pH 4.5).

Coastal populations. These populations occur on various coastal landforms including the landward edge of the mangrove zone (*e.g.* Silver Plains where they occur as tall shrubs or small trees). At Somerset on the tip of Cape York a small population is present on the low rocky cliffs that line the foreshore (C.A. Gardiner personal communication 1989). There they occur as sparsely distributed shrubs. Soils are derived from aeolian sands or sandy alluvia.

Natural occurrence in Papua New Guinea

Distribution

The main occurrence of *A. auriculiformis* is in the Western Province of Papua New Guinea extending from 09°00' S, 143°15' E (Oriomo River) to 09°05' S, 141°00' E (the Irian Jaya border). Most populations occur within 20 *km* of the coast but extend to 70 *km* from the coast at Weam. Within this area it is most common on the coastal plains or along the lower reaches of river systems that drain the Oriomo Plateau.

In the Central District of Papua New Guinea the species occurs on the Brown River (*ca.* 25 *km* NW of Port Moresby) and herbarium material has been collected from several stands such as those at Kwikila (*ca.* 60 *km* SE of Port Moresby), Gally Reach (50 *km* NW of Port Moresby), Aroa River (ca. 60 *km* NW of Port Moresby) and Kairuku on Yule Island (*ca.* 100 *km* NW of Port Moresby). In the Gulf District herbarium material exists from stands at Mairu/Lese (*ca.* 160 *km* NW of Port Moresby) and Kerema (*ca.* 240 *km* NW of Port Moresby). Field inspections and seed collections from these stands are warranted.

The altitudinal range is generally within 5 to 20 *m* with an inland occurrence reaching an elevation of 35 *m* (at Morehead).

Population types

In Western Province the interaction of the high rain fall and a flat clayey terrain has produced a mosaic of swamp forests, savanna woodland swamps, and monsoon vine forests throughout the Oriomo Plateau. The plateau is incised by eight strongly-tidal river systems. Species that can tolerate long periods of seasonal inundation (up to five months), are a dominant feature of the vegetation. The occurrence of *A. auriculiformis* in Papua New Guinea falls into four broad population types as outlined below.

Floodplain and coastal populations. The extensive grassland (*Pseudoraphis*) floodplains of the Morehead and Bensbach Rivers are unique in Western Province (Skelton 1987). Here *A. auriculiformis* is sparsely distributed growing in extremely open and exposed situations along the riverbanks and swampy margins of the plains. It becomes more numerous where it intergrades into the *Melaleuca* swamp forests that surround the floodplains.

A. auriculiformis also occurs within 500 *m* of the coast amongst the littoral forests that colonise the beach ridge systems formed by longshore drift of silt deposits (Loffler 1974).

The floodplain and subcoastal form of *A. auriculiformis* is invariably short-boled with a broad spreading canopy. Plants are usually < 10 *m* in height.

Also scattered occasionally along the floodplains may be *Nauclea orientalis, Corypha elata, Cathormion umbellatum* or *Barringtonia tetraptera.* Genera of the littoral beach ridge forests include *Melaleuca, Aleurites, Alstonia, Dysoxylum, Intsia* and *Ficus* (Paijmans *et al.* 1971).

Soils are black cracking clays which are acidic (pH 4.5-5.5).

Riparian populations. Riparian populations favour the lower sections of rivers and are more extensive along the longer river systems such as the Morehead River and the Bensbach River. Other occurrences include the Wassi-Mai Kussa system, Pohaturi River, the Kura-Gugi system, Binaturi River, Oriomo River and the Bituri River (a tributary of the Fly River).

The structural form of the vegetation ranges from closed to open forests. It is not uncommon to observe trees of excellent form attaining 25 to 30 *m.*

These populations form a corridor that fringe riverbanks or the rear of mangrove zones. Associates, when present, include *A. aulacocarpa, B. tetraptera* and *N. orientalis.* It may also occur in monsoon vine forests if these occur in proximity to riparian populations.

Soils are alluvia ranging in texture from clay to clay loam to sandy clay loam. The pH is generally acidic (4.5-5.5). Neutral or slightly alkaline soils occur in periodically waterlogged sites.

Swamp forest and monsoon vine forest populations. Swamp forests containing *A. auriculiformis* are a special feature of the Papua New Guinean populations of the species. Often adjacent to riparian populations they extend inland over low lying terrain subject to seasonal inundation. Occurrences include stands at Morehead, Weam, Bensbach (Dog Track), Bandaber, Tonda and Mibini Swamp. *A. auriculiformis* may also occur in monsoon vine forests that have developed on favourable sites removed from drainage lines. Occurrences include Balamuk, Morehead, Ngou and Waidoro.

These populations occur as tall open-forests to tall closed-forests and are amongst the most impressive stands encountered throughout the species' natural occurrence. Trees may be up to 35 *m* tall with long boles and small crowns.

The swamp forest populations are co-dominant with tall (30 *m*) melaleucas such as *M. cajuputi* spp. '*platyphylla*' MS (Barlow) and *M. leucodendra. Lophostemon suaveolens, A. mangium, B. tetraptera* and *Dillenia alata* may also be present. Associates in the monsoon vine forest populations may have representatives from a number of rain forest genera such as *Flindersia, Syzygium* and *Terminalia.*

Soils are clay loams derived from alluvia with a pH range of 4.5 to 5.5.

Populations of disturbed sites. Essentially subpopulations of the riparian or monsoon vine forest populations, these colonise old garden sites that are abundant throughout the Western Province. The periodic rotation of village garden sites by native Papua New Guineans has ensured that species such as pioneering acacias and the aggressive *Imperata* grass regularly have a habitat to invade. *A. auriculiformis* occurs in these situations throughout its natural distribution in Western Province but is absent from disturbed sites along the upper sections of drainage systems.

They form mixed stands with other acacias (such as *A. mangium, A. crassicarpa, A. aulacocarpa* and *A. simsii*) and develop into woodland or open forests.

Soils range from clay to clay loam (pH 5.0-6.0).

Natural occurrence in Indonesia

Distribution

Little is known of the natural distribution in Indonesia. The species is known to occur naturally near Merauke (at Kolen Station and along the Merauke River), on Kai Islands (botanical collections of 1922 at Bogor Herbarium) and possibly near Sorong on the Vogelkop (unconfirmed sighting). Surprisingly there are no records for Aru island, a close neighbour of the Kai group.

Amenity plantings are common in Kupang, Kalabahi, Jayapura and Merauke.

Population types

Habitats near Merauke are apparently very similar to those on the Papua New Guinea side of the border. A herbarium specimen collected by P. van Royen (4450 Bogor) states on the label that the species is one of the main constituents of the *Acacia/Melaleuca* forests on the road between Mopah airstrip and Manggatrikke, Merauke district. He also records occurrences in light, open forest associated with *Alstonia schlolaris, Gigantochloa* sp. and grasses *Imperata cylindrica* and *Themeda* spp. on "grey, dusty, fine sands" (van Royen 1963).

Analysis of current climate

The climatic conditions occurring within the natural distribution of *A. auriculiformis* can be determined by interpolation techniques which allow mean climatic conditions to be reliably estimated for any given location in Australia and Papua New Guinea (but not Indonesia at this stage). Latitude, longitude and elevation data describing the location of 107 natural occurrences of *A. auriculiformis* were analysed using the BIOCLIM programme devised by Nix (1986). For each location the programme produces estimates of 12 climatic factors, including mean annual temperature, coldest month minimum temperature, hottest month maximum temperature and mean annual precipitation.

A climatic classification of the 107 specimen localities was derived using all 12 climatic estimates obtained from the above BIOCLIM analysis. Numerical classification was undertaken with the PATN package (Belbin 1987), following the method of Booth *et al.* (1989). Six climatic groups were identified; the distribution of specimen climatic types is presented in Figure 2.

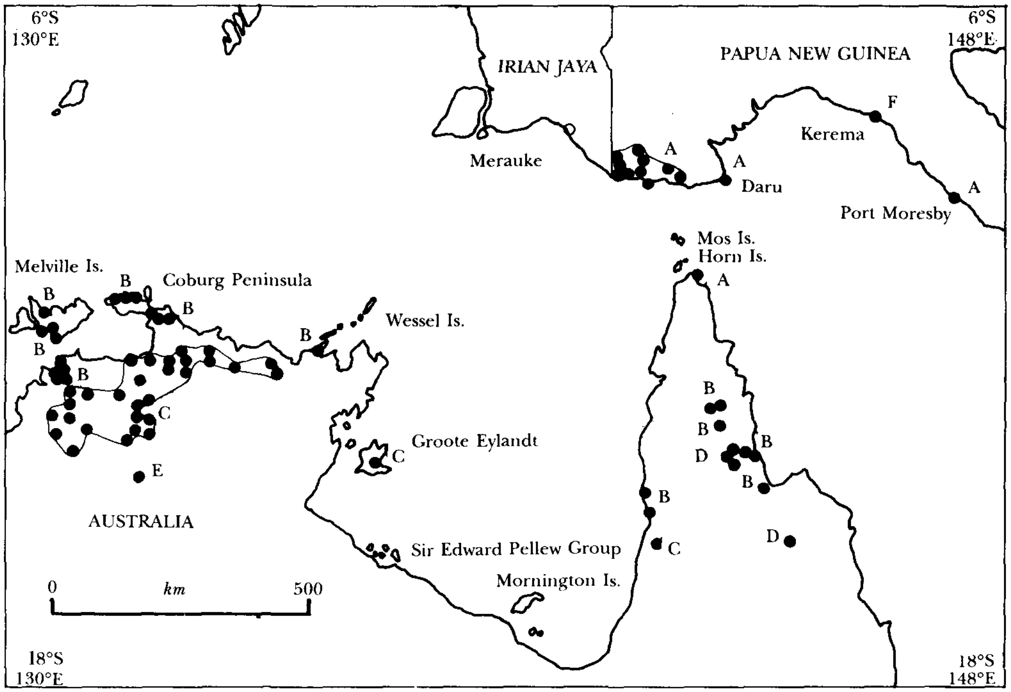

Figure 2. The six climatic groups of *A. auriculiformis* as defined by the classificatory programme PATN (Each of 107 localities for *A. auriculiformis* has been allocated to climatic groups labelled A, B, C, D, E and F; lines have been drawn to circumscribe sites with similar climatic conditions)

The analysis indicated that there are three main groups (A, B, C) and three small groups (D, E, F). Mean values for each of these groups for four important climatic factors are shown in Table 1. Notable features of this analysis are results for Groups A, C and D, and F. Group A receives high rain fall and high minimum temperatures, Groups C and D have low minimum temperatures, and Group F receives nearly twice the rain fall of any of the other groups.

Table 1. Mean climatic conditions for climatic grouping shown in Figure 2 as estimated from BIOCLIM

	Group					
	A	B	C	D	E	F
Number of climatic locations in group	23	37	40	5	1	1
Mean annual temperature (°C)	26.0	25.8	26.5	25.4	26.9	26.2
Coldest month min. temp. (°C)	20.4	17.7	12.5	16.3	12.6	21.1
Hottest month max. temp. (°C)	32.0	32.3	34.8	33.9	37.5	31.8
Mean annual precipitation (*mm*)	1370	1230	1150	940	960	3430

Past events affecting the natural distribution

A more complete understanding of the current distribution of *A. auriculiformis* involves and examination of past geological events, the origin of the species, the evolution of seasonally dry forests and associated palaeoclimates (including former sea levels), the evolution of landforms, soils and more recent events such as modern climates, fires and possible vectors aiding dispersal.

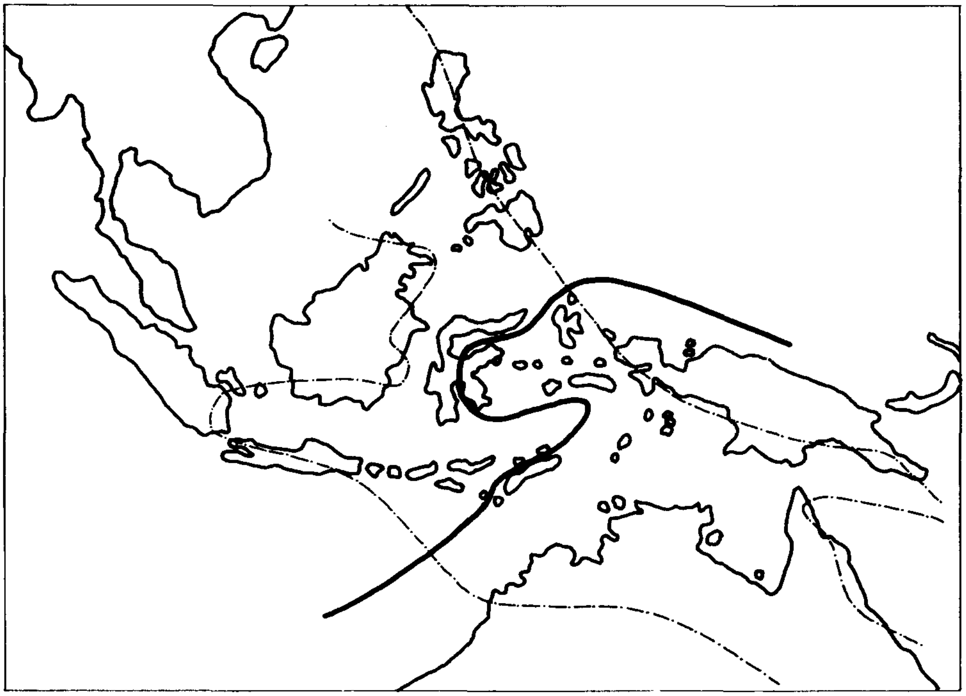

Figure 3. A map of Australia and southeast Asia marking the limits (bold line) of the Australian plate; the area between the two broken lines indicates the region that contains seasonally dry climates and monsoon forests, this suggests a potential corridor for the migration of species within this zone (Map modified from Barlow & Hyland 1988)

Plate tectonics and continental drift

Plate tectonics and continental drift theory suggest that the Australian plate separated from Antarctica during Cretaceous times about 55 million years ago (55 *Ma*) and then moved northwards (carrying a diverse Gondwanic flora) and finally collided with the Sunda plate during the Miocene about 20 *Ma.* From geological records the exact northern parts of the Australian plate are now reasonably well defined (Audley-Charles 1987). Figure 3 indicates islands north of Australia which are considered part of the original plate. The current distribution of *A. auriculiformis* occurs entirely within the old plate. The northern border of the plate includes the islands of Buru, Buton, Banggai-Sula, part of Sulawesi, Ceram, and the Lesser Sunda islands of the non-volcanic Outer Banda Arc (Kai, Aru, Tanimbar through to Timor and Roti). Some of these islands (*viz* Tanimbar, Timor, Ceram) lie on the northern side of the deep sea trench and such islands are either rafted fractured fragments of the leading edge of the old Australian plate or consist of sediments scraped off the subducting Australian plate (see Audley-Charles 1987). The close proximity of the younger volcanic islands of the inner Banda group to the outer Banda group is related to vulcanism associated with the contact zone of collision. The inner Banda islands include those east of Java in an arc through to Flores, Wetar and Banda. *A. wetarensis*, a close relative of *A. auriculiformis* (Pedley 1975), occurs on the Inner Banda Arc (Wetar only) and hence off the plate.

To the east of the present day Australian mainland the island of New Caledonia (which contains a close relative *A. spirorbis*) is geologically part of the old Australian plate. Further east, the islands of the New Hebrides came into existence (in the mid-Oligocene about 30 *Ma*) and are part of the plate edge phenomenon. They are believed to be volcanic in origin and have since been uplifted and weathered (B.M.R. Wilford personal communication 1989). *A. spirorbis* ssp. *solandri*, a relative of *A. auriculiformis*, occurs in the New Herbrides and thus just off the Australian plate.

Evolution of the Australian acacias and implications for the biogeography of A. auriculiformis and related species

Australian acacias - an overview

Acacia was widespread in Australia in the late Cretaceous (90-100 *Ma*) and at that time species with affinity to *A. auriculiformis*, *A. simplex* and *A. melanoxylon* moved away from the continent (Pedley 1986). By the end of the Oligocene (late Tertiary-22 *Ma*) *Acacia* would have been more or less confined to tropical areas in the north of the Australian plate (including parts of present day Papua New Guinea and Indonesia) with the least specialised group - the *Juliflorae* (to which *A. auriculiformis* belongs) predominating (Pedley 1986). The evolution of *Acacia* probably occurred on rain forest fringes or in seasonally drowned wetlands and was associated with the commencement of the breakdown of continuous rain forest cover on the Australian plate through the development of strongly seasonal climates (and hence the onset of dry seasons) and the general development of scleromorphy in the Australian flora. This change in climate also led to the extensive development of lateritic earths in northern Australia during the tertiary period (Specht 1988) due to the seasonal wetting and drying of soil profiles.

At this time it is also possible that other genera such as *Melaleuca* and *Eucalyptus*, which are current day ecological associates or neighbours of *A. auriculiformis*, evolved under similar environmental conditions (Barlow 1988). It is significant that species in the less-specialised group of *Melaleuca*, that is the *Melaleuca leucodendra* species complex (see Barlow 1988) also have similar distribution pattern to *A. auriculiformis* (and related *Acacia* species) but usually occur in sites which remain waterlogged for longer periods than those occupied by *A. auriculiformis.*

In overview, the early evolution of *Acacia* and progenitors of *A. auriculiformis*, the onset of climatic seasonality and finally the occurrence of continuous land on the northern end of the Australian plate were all factors conducive to the dispersal of progenitors of *A. auriculiformis* since at least Tertiary times.

Distribution of *A. auriculiformis* and related species - its relevance

Taxonomically *A. auriculiformis* belongs to section *Juliflorae*, a large group (219 species) of species having a mainly tropical distribution in the north and northwest (but also in the southwest) of Australia and often associated with rocky tableland areas (Hnatiuk & Maslin 1988, Maslin & Pedley 1988). The *Juliflorae* are the least specialised group (hence considered the more primitive) of Australian acacias. Within the *Juliflorae* the closest relatives of *A. auriculiformis* appear to be *A. crassicarpa*, *A. aulacocarpa*, *A. cincinnata*, *A. leptocarpa*, *A. polystachya*, *A. mangium*, *A. spirorbis* ssp. *solandri*, *A. spirorbis* ssp. *spirorbis* and *A. wetarensis* (L. Pedley personal communication 1990) and these ten acacias are considered to form the most primitive subgroup. *A. mangium* is perhaps the most ancestral of the true Australian acacias and slightly isolated taxonomically from the others (L. Pedley personal communication 1990). Within the subgroup the closest relatives to *A. auriculiformis* are *A. aulacocarpa*, *A. crassicarpa* and *A. wetarensis.* The last species is probably a more direct derivative of *A. auriculiformis* (Pedley 1975). Pedley (1987) also suggested close taxonomic links with other members such as *A. cincinnata* and *A. spirorbis.* No hybrids between *A. auriculiformis* and its three closest relatives have been recorded but the species does hybridise in the field with *A. mangium* and *A. leptocarpa.* Manipulated hybridisation studies may assist in resolving relationships in this group.

A generalised map of the distribution of these ten species (Figure 4) provides some important insights into their dispersal patterns. Basically all are tropical in distribution; two do not occur in Australia (*A. wetarensis* and *A. spirorbis* ssp. *spirorbis*), and six also have extra-Australian distributions. The distributions of several species are remarkably disjunct and are trans-Torresian.

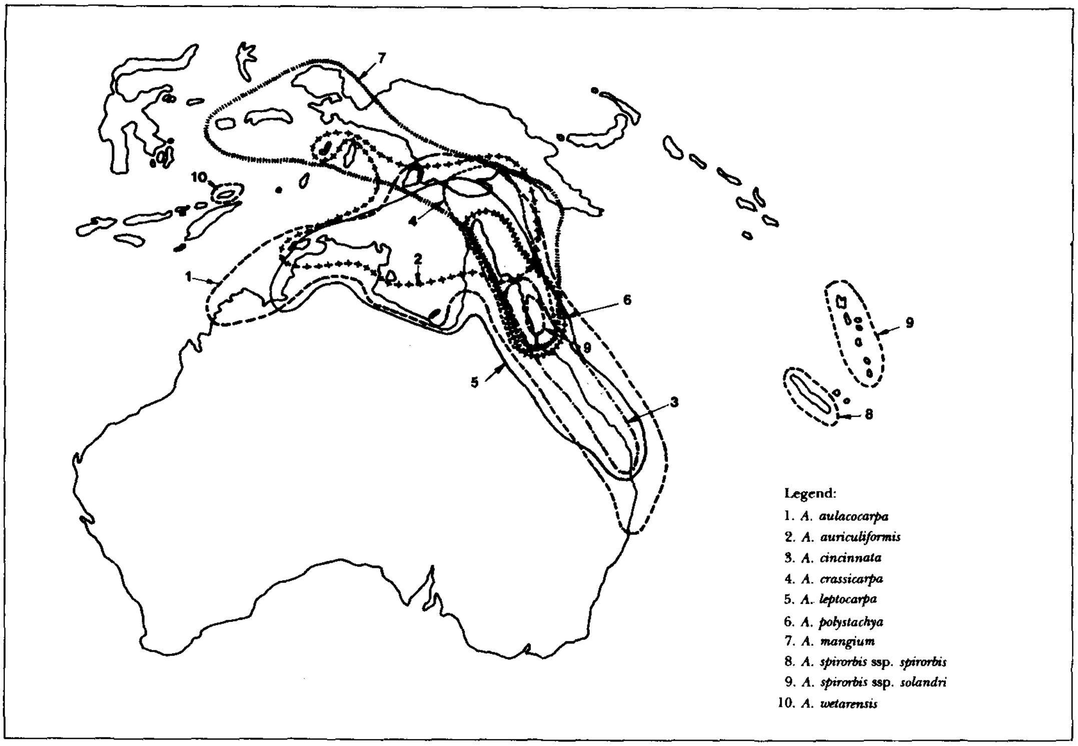

Figure 4. A generalised map of the distribution of *A. auriculiformis* and nine other closely related taxa

Such information provides circumstantial evidence that this group was relatively widely distributed prior to subsequent marine transgressions. The existence of related species namely *A. wetarensis* and *A. spirorbis* ssp. *spirorbis* (New Caledonia) far from the presumed Australian centre of origin tends to support this contention. Many members of *Juliflorae* are components of coastal strand vegetation and propagules could be blown, rafted or carried by birds across sea-ways and thus could have migrated. The alternate hypothesis to migration of fragmentation of populations after marine transgression seems more likely.

The distribution of the group is typical of one showing both sympatric and allopatric speciation. Two close allies of *A. auriculiformis* (*i.e. A. aulacocarpa* and *A. crassicarpa*) have a sympatric pattern while *A. wetarensis* and *A. spirorbis* are allopatric. It may also be useful to view *A. aulacocarpa*, *A. crassicarpa*, and *A. auriculiformis* as a catena of species capable of occupying successively more difficult sites with *A. auriculiformis* being the most successful away from rain forest fringes. *A. aulacocarpa* prefers more fertile soils than *A. crassicarpa* which in turn can grow on soils with impeded drainage. Most species in the group occur on rain forest fringes or near the margins of rivers, mangroves or swamps. Only *A. polystachya* could be considered a true rain forest species. Both *A. aulacocarpa* and *A. crassicarpa* can naturally regenerate vigorously on cleared rain forest sites (Pedley 1987), and the long lived *A. aulacocarpa* persists in many rain forest habitats.

One of the taxa closely related to *A. auriculiformis,* that is *A. wetarensis* occurs on new land associated with vulcanism on the edge of the continental plate. The progenitors of this taxa probably arrived across seawater barriers and speciation may have arisen by genetic drift, perhaps encouraged by new soil types derived from volcanic activity. Speciation processes at the plate edge have not yet been studied.

Evolution of seasonal dry forests and implications for the distribution of A. auriculiformis

It is axiomatic that the past distribution of a species must be related to conducive palaeo-climates. Evidence for a widespread favourable climatic conditions in the past is provided by the existence of well established "dry" monsoon vine forests extending in a mosaic pattern in a wide corridor from Australia northwards to western Papua New Guinea and western Indonesia (see Figure 3). Such forests are associated with a pronounced dry season. *A. auriculiformis* is often associated with these forests either as an edge species or growing in gaps within them. The monsoon vine forests are relictual, have low endemism and strong Sundaland links (suggesting a two-way migration) with the Australian component evolving directly from the more humid rain forests (Barlow & Hyland 1988). The maximum extent of continuous land in this region existed at various points in the late Pliocene (3 *Ma*) and Pleistocene (1-2 *Ma*), and the increase in climatic seasonality would likely have resulted in the expansion of monsoon vine forests at the expense of closed mesic forests. The potential for migration at this time was maximised because more land was available for colonisation.

The presence of *A. auriculiformis* in or near these forests may have been the original source of the riparian populations that dispersed along river systems and over deltaic plains when conditions for population expansion were favourable. That it evolved from rain forest progenitors is supported by the fact that its close relatives are essentially rain forest or rain forest fringe species.

Surprisingly, numbers of individuals in many of todays' isolated monsoon vine forests are typically small. The geographic fragmentation of these forests suggest that there is little genetic exchange of pollen and seed amongst them. However, Russell-Smith and Dunlop (1987) have challenged this assumption by pointing out that recruitment of new species from seed (brought in by birds and wind) and the numerous pollinators migrating between these stands is suggestive that there is considerable genetic exchange between many species. This situation may also apply to *A. auriculiformis.*

Russell-Smith and Dunlop (1987) drew attention to the mobile nature of monsoon forests with respect to the dominant and prevailing tropical eucalypt woodlands, and the ability of many monsoon forest species to colonise new depositional surfaces such as stream banks and expanding littoral zones associated with falling or rising sea levels. This is evident by the presence of monsoon forests on land surfaces of recent origin (Holocene shore lines) and the evident capacity of species to respond to environmental change. In the Northern Territory over 70% of the obligate monsoon vine forest flora is found on soils of recent origin. A species like *A. auriculiformis* possessing the ability to tolerate a wide range of environmental conditions has an advantage over many monsoon vine forest species in colonising new sites. This may help account for the more common riparian stands found over much of its range.

Dryland connections, marine transgressions and periods of aridity in the late Tertiary and Quaternary

In the Quaternary there were a series of major marine transgressions associated mainly with interglacial periods. Our interpretation of these events as they affect the distribution of *A. auriculiformis* is based on the assumption that relatively little broad-scale tectonic movement of the land surfaces occurred in the region under scrutiny in the Quaternary Epoch (Chappell personal communication 1989). An indication of size of these sea level changes is evident by the fact that 28,000 years ago sea level was about 44 *m* below current sea level (Chappell & Shackleton 1986). Sea level rises would have eliminated populations while falls would have been favourable for dispersal.

It is now known that the present water barriers of the Arafura Sea, Gulf of Carpentaria and Torres Strait would have been land during many of the Pleistocene sea level minima (Doutch 1972). A fall in sea level of only 15 *m* provides continuous land between New Guinea and Queensland across Torres Straits. Torres Straits is believed to have attained its present dimensions about 6500 years ago (Thom & Roy 1985) and strong sea currents across Torres Straits would have been an effective barrier for much rafted seed material.

The Quaternary Epoch has been marked also by cycles of aridity. The impact of these would have been the restriction of *A. auriculiformis* to moister refugia such as gorges in the sandstone Arnhem-land region (Northern Territory) and mountains in Cape York (Queensland) and towards the edges of mesic forests in PNG. No doubt expansions and contractions of populations during this period would have markedly affected genetic interchange. Periods of aridity may have been more severe in the southern part of the range of *A. auriculiformis* and the present large gap between populations in Queensland and the Northern Territory may have its origin in these periods.

Landforms and soils

The major landforms of the region under consideration relevant to the distribution of *A. auriculiformis* can be divided into erosional and depositional surfaces (Galloway & Loffler 1972).

In northern Australia the main erosional landscapes are Tertiary weathered land surfaces which vary from undissected to partially dissected, to the complete removal of Tertiary weathered land surfaces exposing a complex variety of underlying rocks. The species occurs in this area on erosional surfaces only occasionally and then is associated mainly with small isolated monsoon vine forests (Russell-Smith & Dunlop 1987).

Fine-textured Vertisols or Mitchell grass plains of the Barkley Tablelands are derived from Cretaceous sediments. The importance of these Vertisols as a barrier to speciation in Section *Juliflorae* was recognised by Hnatiuk and Maslin (1988). They conclude that the major centres of species concentration in northern Australia are the rocky tablelands east and west of these soils. These cracking clays are restrictive to most tree crops with species having deep tap roots being particularly susceptible. While the current disjunction of *A. auriculiformis* populations between Queensland and Northern Territory might be explained in terms of the current climate with its severe dry winters, a more generalised reason may be that *A. auriculiformis* is not suited to these soils.

Depositional landscapes in northern Australia are the landscapes on which *A. auriculiformis* thrives, particularly when the moisture relations are favourable. Late Tertiary depositional surfaces are particularly extensive on the western side of Cape York Peninsular, around the Gulf of Carpentaria and near Darwin. They produce predominantly red and yellow earths, deep weathering profiles and laterite. On river systems younger alluvial plains include extensive deltas such as the alluvial flats of the Mitchell, Normanby, Leichhardt and Gilbert Rivers, and smaller plains along lesser-rivers. Much of the country in the lower Gulf region is flooded during the wet season but is too dry between monsoons for *A. auriculiformis*. The coastal fringe is an almost continuous belt of recent marine and estuarine sediments 5 to 30 *km* wide, and is usually flooded for months at a time during the wet season. This youthful landscape has developed since sealevel attained more or less its present position (Galloway & Loffler 1972). This landscape is very similar to the southern coastal plains of Papua New Guinea.

In Papua New Guinea the main landforms relevant to the distribution of *A. auriculiformis* are depositional, and fall into three broad classes. The first of these are coastal plains which comprise deltaic fans and narrow bands of beach ridges, swales and mangrove flats. Soils are typically strongly alkaline marine clays. The second group are the recent alluvial plains and these form a band 5 to 35 *km* wide along present day river systems. These back-plains and swamps are often connected with blocked valley swamps and lakes formed by infilling of tributary valleys. Soils are mainly strongly gleyed alluvial clays. The third distinctive type comprise older alluvial plains which are generally above the floodlevel of present day streams and thus are not depositional sites. They are fossil soils but maybe partly flooded during the wet season. The largest portion of the Fly-Digoel lowlands is formed by such soils. The southern part of these lowlands is the Oriomo Plateau which extends from the mouths of the Digoel and Fly rivers and is between 20 to 50 *m* above sea level. It is considered to be a raised relictual alluvial plain rather than a plateau (Loffler 1974). Soils are strongly weathered loams.

One notable feature of the landforms in Australia and Papua New Guinea is that almost the whole distribution of *A. auriculiformis* is enclosed within a roughly circular catchment basin feeding into the Gulf of Carpentaria and Arafura Sea.

Of more localised importance during periods of Quaternary low sea levels (during the past 30,000 years) was the possible existence of a large closed basin, Lake Carpentaria (see Figure 1) between Papua New Guinea and Australia (Torgersen *et al.* 1983). This lake was extensive (at 53 *m* below current sea level it would have covered about 165,000 km^2, fed by a large water catchment from present day Papua New Guinea and northern Australia, with about 80% of the water coming from New Guinea. *A. auriculiformis* may have colonised many of these feeder streams. The lake would also have separated the eastern and western distributions of the species as sea level rose thus restricting more westerly populations perhaps towards refugia in the Arnhem Land region.

In conclusion, the bulk of the present distribution of *A. auriculiformis* is mostly on depositional land surfaces (alluvial soils). The species is thus a good coloniser. While the species may have evolved on Tertiary land surfaces its current preference for alluvial sites is marked, especially as it can cope with partially saline sites and seasonally waterlogged areas. Any past climatic events favouring these conditions is likely to have led to a rapid dispersal of the species. Also, during periods of aridity in the Quaternary period the species is likely to be restricted to moister upland refugia and to patches of monsoon vine forests and other sites where soil water conditions were relatively favourable.

Impact of fire

The monsoon vine forests and gallery rain forests are notable for the fragmentary nature of their occurrence in a broad belt across northern Australia. Individual forests are small in extent (often 5 *ha*), are seemingly relictual, and are mostly surrounded by open forests of eucalypts. Their patchiness has been variously ascribed to the climatic sifting of species, forest fires and various other environmental and biological causes. There is little doubt that fire is a potent present day determinant of this pattern and presumably has been an important factor since late Tertiary times, although fossil evidence is poor (Russell-Smith & Dunlop 1987).

With the onset of climatic seasonality and the breakdown of continuous closed forests, fire is likely to have been a constant feature of the environment of northern Australia. Natural fires caused by lightning strikes are most damaging in the late dry season when fuel loads are large and very dry. Aboriginal man has been in northern Australia for over 60,000 years. Firestick farming through the early wet and in the early dry season is also likely to have been an important determinant of the current distribution and circumscription of individual patches of monsoon forests. In other instances wet swamps, springs and rocky outcrops may have served to protect monsoon forest communities from fire (Russell-Smith & Dunlop 1987).

Fire is also important in the distribution of monsoon forests in Papua New Guinea. Fire is used by indigenous people to flush out game and in general cleaning operations associated with the establishment of gardens near settled areas. Wild fires caused by lightning also occur but their frequency is unknown. Several acacias, particularly *A. mangium, A. crassicarpa* and *A. aulacocarpa* regenerate profusely on abandoned gardens while *A. auriculiformis* does so occasionally.

The perimeters of monsoon forests are notable for the presence of many fire resistant species with good regenerative powers through coppicing. It is in this zone that *A. auriculiformis* has a competitive advantage. It also occurs in *Melaleuca* open-forests and rarely as an interspersive in eucalypt open-forests. In these situations fire tolerance and an ability to cope with strong irradiation, drought stress and grass competition are useful attributes. Such characteristics are more likely to be encountered in the Australian populations than in Papua New Guinea.

Long distance dispersal of propagules

Vectors for long distance dispersal include wind (cyclones), birds and water through rafting of propagules. The northern region of Australia is noted for intense storm activity and cyclonic winds each summer coinciding approximately with the time of seed ripening. The circular clockwise motion of cyclones could possibly carry material from Australia to New Guinea particularly when sea levels were lower. Cyclonic winds travelling from the northwest to southwest across the Gulf of Carpentaria could conceivably carry material to New Guinea and *vice versa.*

The seed of *A. auriculiformis* is usually enclosed within a tightly curled legume; when ripe the legume splits along the suture and releases a black coloured seed attached to the legume by a brightly coloured aril. This amounts to a generalised presentation mechanism and various birds such as parrots (red-wing, sulphur-crested or white cockatoos and Leuwin honeyeaters are known to eat acacia seed destructively (F. Crome & L.A.J. Thomson personal communication) in Northern Australia and New Guinea.

Ants and rats may facilitate short distance dispersal but the aril is a seemingly small reward for specialist seed transporting birds. However O'Dowd and Gill (1986) argue that the aril in some acacias (including *A. auriculiformis)* is a rich reward and seed dispersal by birds is common in acacias having large colourful arils and seedcoats. The seed, because of its hard seed coat, may also be passed through a bird in a viable state. Interestingly O'Dowd and Gill (1986) believe that bird transport of acacia seed in Australia is the more primitive,. and ant transport the more advanced, condition. To substantiate a theory of inter-island transport bird flight patterns, seed survival after ingestion, and likely bird vectors need to be clearly demonstrated. Because of the longevity of acacia seed, regeneration in new sites may not necessarily be the result of recent transportation.

General conclusions

The natural distribution of *A. auriculiformis* has been described in detail and many new locations for its occurrence documented. Analysis of the climate of its natural distribution has indicated six climatic groups; this analysis should be of assistance to foresters selecting seedlots for new pilot plantations or provenance trials. The information will also be of value in the interpretation of the results from provenance trials already established under the F/FRED programme.

A. auriculiformis is a species with fairly primitive characteristics, its progenitors probably evolving in northern parts of the Australian plate in late Cretaceous times. It is likely that the species evolved sympatrically with *A. crassicarpa* and *A. aulacocarpa* and thrived in marginally more difficult sites than its two allied species. It is likely also that the evolution and dispersal of *A. auriculiformis* has been aided by the climatic upheavals of the late Tertiary. The species distribution would have expanded and contracted during the climatically variable Quaternary with cycles of wetness and aridity and various marine transgressions on the northwestern part of the Australian plate.

The distribution of *A. auriculiformis* is restricted to the old Australian plate. While the species may have evolved on the margins of rain forest occupying relatively old erosional land surfaces, it currently occupies mainly young depositional landforms throughout its range. This distribution pattern reflects the great capacity of *A. auriculiformis* to colonise newly available sites. Disjunctions in the extant distribution of *A. auriculiformis* likely reflect both the influence of Late Tertiary and Pleistocene sea level changes, particularly in the region of the Gulf of Carpentaria and Torres Straits, as well as the species capacity for dispersal. The level of genetic difference between isolated populations occurring in Cape York, the Northern Territory, and Papua New Guinea is not known and awaits further study.

The occurrence of *A. auriculiformis* in many isolated monsoon vine forests has important implications for future seed collections and development of breeding strategies, particularly if many of these stands are genetically isolated. In addition competitive pressures in some of these stands appears to have selected straighter, taller and faster-growing genotypes. The analysis undertaken in this paper is important for the planning of future seed collections, and in the interpretation of results of biosystematic studies of other species having similar patterns of distribution to that of *A. auriculiformis.*

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