

An Appraisal of Factors Controlling the Latitudinal Distribution of Mangrove (*Avicennia marina* var. *resinifera*) in New Zealand

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ABSTRACT

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The latitudinal distribution of mangroves (*Avicennia marina* var. *resinifera*) in New Zealand has traditionally been considered to be controlled by climatic stress, particularly air temperature. This paper reviews the influence of climate factors, particularly frost, and the dispersal of mangrove propagules on the present-day mangrove distribution.

There is no strong evidence to show that the southern limit of mangroves in New Zealand is a function of climatic conditions, or that the present mangrove distribution is in equilibrium with climatic conditions. It is probable that coastal processes affecting propagule dispersal are more important controls on the mangrove distribution within New Zealand than climatic factors. In particular, tidal asymmetry inhibits mixing of east and west coast mangrove populations around northern-most New Zealand, and low coastal current velocities and large distances between suitable habitats makes natural establishment south of present limits unlikely.

ADDITIONAL INDEX WORDS: *climate, dispersal, littoral drift, manawa, tidal currents, wind drift.*

INTRODUCTION

There is only one mangrove species, *Avicennia marina* var. *resinifera*, in New Zealand. *Avicennia marina* var. *resinifera*, or manawa, is often referred to as the southernmost growing mangrove (MORTON, 1976; GREGORIE, 1980), but this distinction goes to the Australian mangrove which occurs within Corner Inlet (38°54.8'S), Victoria (TOMLINSON, 1986; MILDENHALL and BROWN, 1987). The Australian mangrove, which has been previously identified as *Avicennia marina* var. *australis*, is now recognised as conspecific with the New Zealand mangrove (TOMLINSON, 1986).

However, it is clear that the New Zealand mangrove is close to the southern limit of the natural range of mangroves. It is commonly accepted that this limit is a function of climatic factors (CRISP *et al.*, 1990), particularly temperature, whether this is manifest as water temperature (TOMLINSON, 1986), air temperature (NATURE CONSERVATION COUNCIL, 1984), or the frequency of frosts (Chapman and RONALDSON, 1958; KÜCHLER, 1972).

Comparison between records of mangrove occurrences in New Zealand during the 1800's and

present distributions indicate that mangroves have become more abundant within their accepted range (NATURE CONSERVATION COUNCIL, 1984), although the range has not extended southwards. The increase within the northern regions of the natural range is commonly attributed to increased sedimentation following land clearance (NATURE CONSERVATION COUNCIL, 1984). Studies undertaken by the Department of Earth Sciences at the University of Waikato indicated that mangroves are also becoming more abundant towards their southernmost limit (*viz.* SHEFFIELD, 1991).

It was suggested that the increased abundance of mangroves may be partially in response to global warming, since paleontological evidence reveals a more southerly limit during the climatic optimum (MILDENHALL and BROWN, 1987). This led us to query whether the present distribution was in equilibrium with climate and could therefore be used to assess global warming, or if some other factor or factors controlled the latitudinal distribution. Accordingly, the aims of this paper are to review the influence of climate factors, particularly frost, and the dispersal mechanisms of mangrove propagules on the present day mangrove distribution.

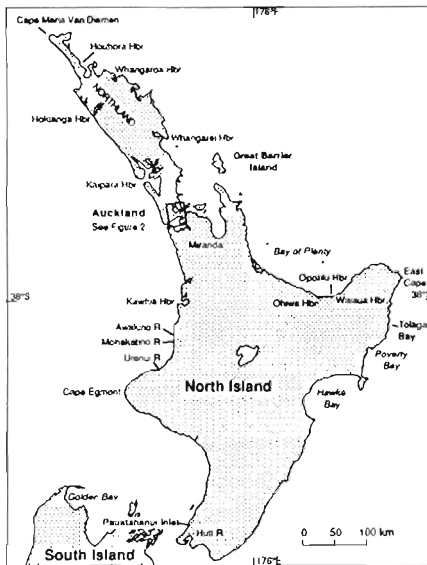


Figure 1 Map of the locations referred to in the text. See Figure 2 for an enlargement of the Auckland region.

NEW ZEALAND DISTRIBUTION

Mangrove in New Zealand have a natural distribution north of latitude 38°S (Figure 1), corresponding to Kawhia Harbour in the west and Ohiwa Harbour in the east (CRISP *et al.*, 1990; P. J. de Lange *personal observation*). Of these, Ohiwa Harbour contains the most southerly specimen at Kutarerer (38°03'S). South of these natural populations, mangroves have been successfully established along the west coast at the Awakino, Mohakino and Urenui Rivers, effectively extending their southward range to 39°S. The Awakino and Mohakino plantings were made for stream bank protection by the Department of Lands and Survey (P. DINGWALL, 1984; CRISP *et al.*, 1990). The origin of the Urenui plantings is unknown. Plantings were also made at Tolaga Bay (38°23'S) in 1980, which subsequently flowered and produced viable propagules (DANIEL 1986; CRISP *et al.*, 1990).

Two 0.5 m high plants have also been reported from Parapara Inlet, Golden Bay (40°43'S), in the South Island of New Zealand (WALSBY, 1992). These were planted and have since been removed by the Department of Conservation. Finally, a planted mangrove flourished for many years on the Hutt River (41°13'S) before being smothered by landfill (I. FLUX, *personal communication*,

1990). It is not known whether the mangrove produced any propagules.

HOOKE (1864) reported an occurrence of *Avicennia marina* from the Chatham Islands (44°S), which are exposed to the East Auckland geostrophic current flowing away from New Zealand (HEATH, 1985). CHEESEMAN (1906) and METCALFE (1972) consider this report to be a mis-identification of *Olearia traversii*, and there have been no other reported occurrences of mangrove at this locality. Therefore, we consider that the natural occurrence of mangrove in New Zealand is restricted to the North Island as discussed above.

CLIMATIC CONSTRAINTS ON MANGROVE DISTRIBUTION

HUTCHINGS and SAENGER (1987) noted *Avicennia marina* in Australia are found north of sites where mean daily temperatures are between 4 °C and 7 °C in July (mid-winter), and where minimum air temperatures are greater than 0 °C. While it was accepted that *Avicennia* was susceptible to frost, it was observed that the degree of susceptibility varies with species and geographic location. McMILLAN (1975) showed that *Avicennia* plants from different sites had different responses when subjected to the same frost intensity. In particular, southern populations were hardier than northern populations, and some were tolerant of recurrent low winter temperatures.

DUKE (1990) examined the leaf fall and reproductive phenology of *Avicennia marina* from 23 sites in Australia, 1 in Papua New Guinea and 1 in New Zealand (Auckland). He concluded that reproduction was initiated when day length exceeded 12 hr, and that growth rates were a linear function of mean daily air temperature, with a 2 to 3 fold increase in growth rate for each 10 °C rise. He stated that the southern limit probably coincides with zero reproductive success resulting from short summer growth periods. The critical factor in reproductive success was taken to be the mean daily summer temperature with zero success occurring at temperatures < 18 °C.

Frost

CHAPMAN and RONALDSON (1958) suggested that the southern limit of mangroves in New Zealand is determined by frosts, based on the observation that 50% of the mangroves in Henderson Creek, Auckland (Figure 2), were seen to be dying following a frost which occurred during the period June 28 to July 4, 1951. This was taken to imply

that mangroves could not occur south of a line where coastal frosts exceed -2.2°C and occur at least once every 5–10 years thereby preventing the plants from flowering (CHAPMAN and RONALDSON, 1958). This assertion has not been questioned by most subsequent studies (viz. KÜCHLER, 1972; DANIEL, 1984). An examination of the freezing resistance of mangroves by SAKAI and WARDLE (1978) reported that the leaf tissues could not withstand 4 hr of freezing to -3.0°C , so an ultimate intolerance to winter chilling at -3.0°C is generally accepted (WARDLE, 1985; DUKE, 1990).

Frost is reported to affect terminal buds which influence the growth of the crowns of mangroves, so that only low horizontal branches can continue growth (CHAPMAN, 1976). It is suggested that the combination of these effects leads to a progressive decline in the maximum height of mangroves towards the south, and a concomitant decline in the size of mangroves away from tidal creeks (CHAPMAN, 1976). KÜCHLER (1972) suggested the decline in mangrove height away from tidal creeks is due to the warmth of water within the tidal creeks ameliorating the effects of frost. This effect involves the formation of warm water advection fogs, which form a protective blanket to restrict the emission of thermal radiation, thereby reducing the chilling effect of radiation frosts (OKE, 1987).

PROBLEMS WITH NEW ZEALAND CLIMATIC CONSTRAINTS

Sensitivity to Frost

Some difficulties are evident with the above data concerning frost influence on mangrove distribution. There is considerable uncertainty as to the actual frost temperature associated with the mangrove mortality in Henderson Creek (CHAPMAN and RONALDSON, 1958). At Oratia (~5 km inland from Henderson Creek), the daily minimum screened air temperatures for the period of frosts (June 29 to July 2, 1951) were -2.2°C (28.0°F), -3.8°C (25.2°F), -2.8°C (27.0°F), and -1.4°C (29.4°F) (CHAPMAN and RONALDSON, 1958). CHAPMAN and RONALDSON (1958) appeared to base their -2.2°C frost limit on the initial frost recorded at Oratia. If this inland temperature is an acceptable measure of the air temperature over Henderson Creek, it is unclear why the maximum frost recorded, -3.8°C , was ignored. A screened thermometer located on the salt marsh at North-

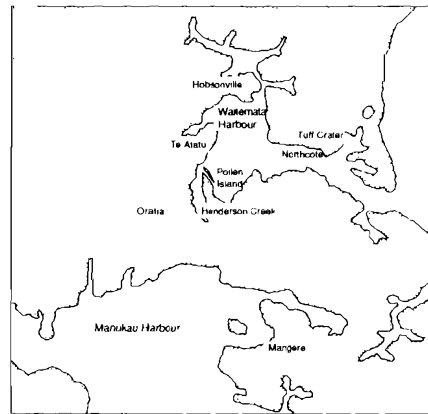


Figure 2. Map of the Auckland region showing locations referred to in the text.

cote recorded a maximum frost of -0.2°C (31.6°F) during the same period (CHAPMAN and RONALDSON, 1958), which suggests that the Oratia readings may not be pertinent to Henderson Creek due to the ameliorating effect of the surrounding water (OKE, 1987). CHAPMAN and RONALDSON (1958) also noted that mangroves assumed to be killed by frost had recovered by 1953, which indicates that the observed frost may not correspond to the critical threshold frost value. Other sources note that once *Avicennia* becomes established, it is quite capable of surviving in sites where frosts exceed -2°C (WALTHER cited in CHAPMAN, 1977).

SAKAI and WARDLE (1978) conducted freezing tests on *Avicennia* using 5 shoot samples obtained from one tree at Auckland. They determined that leaf tissues of *Avicennia marina* var. *resinifera* could not withstand 4 hr of freezing to -3.0°C . *Avicennia marina* in Australia show a differing response to low temperatures depending on location, with southern populations more resistant than northern ones (McMILLAN, 1975). A latitude dependent response to freezing is not unusual and is observed in a number of other New Zealand species (SAKAI and WARDLE, 1978; WARDLE, 1985). If *Avicennia marina* in New Zealand also display this behaviour, observations of Auckland mangroves in response to frost events or during freezing tests should not be used to define the behaviour of Ohiwa or Kawhia populations. Further, since west and east coast mangroves appear to be different genetic populations (DAWSON, 1989;

Table 1. Summary of mangrove substrate data sets used to assess whether non-climatic variables may influence mangrove growth form in New Zealand. Analyses refers to the number of textural determinations averaged for each site.

Location	Latitude, Longitude	Analyses	Mean Weight Percentage			
			Coarse Sand 2,000–200 μm	Fine Sand 200–20 μm	Silt 20–2 μm	Clay < 2 μm
Hobsonville	36°48'S, 174°39'E	1	1.1	17.5	36.0	45.4
Houhora Harbour	34°48'S, 173°06'E	3	28.4	68.7	1.1	1.8
Kaipara Harbour	36°12'S, 174°06'E	3	3.1	44.1	41.3	11.4
Mangere	36°58'S, 174°48'E	2	0.1	16.7	39.7	37.5
Miranda	37°11'S, 175°19'E	3	8.9	32.1	50.8	8.2
Ohiwa Harbour	37°59'S, 177°09'E	3	15.1	31.7	46.6	7.2
Pollen Island	36°52'S, 174°40'E	8	2.0	32.2	31.1	34.7
Tuff Crater	36°48'S, 174°45'E	4	8.7	44.1	39.7	7.5
Whangarei Harbour	35°48'S, 174°24'E	3	4.2	11.3	41.2	27.3
Whangaroa Harbour	35°04'S, 173°44'E	3	3.6	27.4	48.4	20.6

CRISP *et al.*, 1990), the response of Kawhia mangrove may also differ from those at Ohiwa.

We accept that frost is an important climatic control on mangrove distribution. However, the data published in the literature do not provide a reliable measure of the ultimate limits for *Avicennia marina* var. *resinifera* in New Zealand.

Size Variation with Latitude

A decrease in maximum mangrove height with increasing latitude is often cited as evidence for the influence of frost on the survivability of mangrove (*viz.* DANIEL, 1984; CRISP *et al.*, 1990; WALSBY, 1992). Therefore, to assess the importance of frost or minimum air temperature further, we examine the reported relationship between mangrove size and latitude. With respect to the apparent reduction of mangrove size with increasing latitude in New Zealand, NICKERSON (1980) noted that comparison of the southernmost mangroves at Ohiwa with northern specimens did not support this suggestion. Comparison of the maximum size of mangroves at a variety of localities along the east and west coasts indicates that although some mangroves in the north are larger than the maximum sizes in the south, in general, there is no systematic trend in size with increasing latitude (DINGWALL, 1984; authors *personal observation*).

We collated a limited data set to test this assertion. As far as possible, we selected data for mangroves of similar age, under similar conditions, other than varying latitude and sediment texture. Three growth forms were identified, based on the original descriptions:

(1) Stunted forms— those with a well developed

trunk, restricted height, and a large areal extent;

- (2) Tall forms— those significantly higher than the average mangroves in any given region, and forming an incomplete canopy cover;
- (3) Normal forms— those not specifically identified by the data source as either stunted or tall.

Table 1 lists the sites included and their average textural parameters. A regression analysis between latitude and the textural parameters gave a very poor correlation ($r = 0.10$, which is not significant at the 95% confidence level), so the data were considered suitable to compare the relative influences of latitude and sediment texture. A Student's *t*-test between the latitudes of stunted and tall forms indicated no difference for all significance levels < 38%, suggesting that there is no systematic relationship between latitude and growth form.

Mangroves are terrestrial trees which are capable of coping with some salinity, but are not fully marine (TOMLINSON, 1986; HUTCHINGS and SAENGER, 1987). Therefore, they live in a stressful environment, and numerous factors may interact to result in reduced growth to produce a stunted form or enhanced growth to produce larger than normal (tall) forms. These include salinity, nutrient availability, and sediment texture (HUTCHINGS and SAENGER, 1987). Limited data are available for these parameters for New Zealand mangrove. To examine whether non-climatic variables may directly influence size variations in New Zealand mangrove, we considered especially the influence of sediment texture.

Figure 3 shows the frequency of occurrence of

stunted, tall, and normal forms in relation to the percentage mud (sediment finer than 20 μm) in the substrate. Although this figure indicates a slight overlap between stunted and normal forms, the raw data indicate that mangroves growing on substrates with <50% mud display a stunted growth form, but there is no clear distinction between normal and tall forms at higher mud concentrations. Student's t-tests on a variety of sediment textural classes, such as percentage mud (< 20 μm) and percentage fine sand (200–20 μm), indicate that there is a difference at the 99% confidence level between stunted and normal + tall forms for any textural parameter. These data suggest that there may be a difference between the growth forms of mangroves in the sandy Ohiwa Harbour (RICHMOND *et al.*, 1984) and the muddy Whangaroa Harbour (BURNS, 1982) due to substrate textural differences. These two sites are quoted as proof of climatic controls on growth form by DANIEL (1986) and CRISP *et al.* (1990) and are both included in the data set analysed (Table 1). We suggest that the data are equivocal and the presence of stunted forms in Ohiwa Harbour cannot be taken as proof that they have reached a southern climatic limit. Further, the fact that mangroves planted at localities south of the 'natural limit' successfully reproduced and produced viable propagules suggests that mangrove in New Zealand have not reached a climatic southern limit.

THE ROLE OF PROPAGULE DISPERSAL

Avicennia exhibit cryptovivipary (HUTCHINGS and SAENGER, 1987) where the embryo, while developing within the fruit, does not enlarge sufficiently to rupture the pericarp. This protects the embryo from damage. Once the pericarp is ruptured, seedling establishment must take place or the propagule dies. Thus, the timing of propagule dispersal is important if the plant is to achieve maximum dispersal, since damage to the pericarp by wind or water can lead to premature death of the embryo.

Avicennia in Australia avoid damaging the pericarp by dropping propagules during low tide (CLARKE and HANNON, 1971). This means that *Avicennia* propagules are usually dispersed locally. The propagule of the Australian *Avicennia marina* generally has a 4 day period of maximum buoyancy before the pericarp starts to shed (STEINKE, 1975). Shedding is encouraged by high temperatures and decreasing salinities, the con-

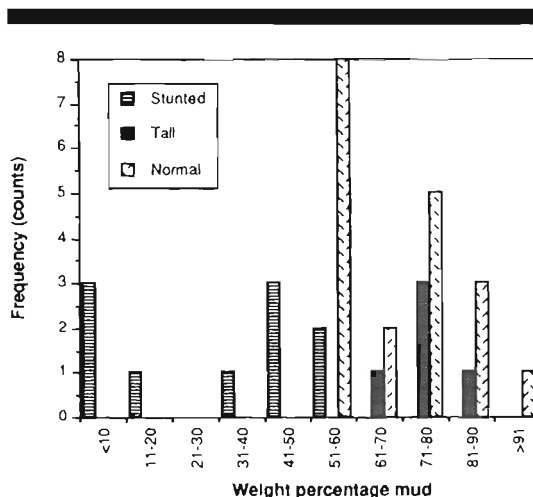


Figure 3. Frequency of occurrence of stunted, tall and normal mangrove growth forms (as defined in the text) versus the percentage mud (sediment finer than 20 μm) in the substrate. Data from the sets defined in Table 1.

ditions normally associated with estuarine environments. Root development only appears to occur once the propagule is stationary (TOMLINSON, 1986). If *Avicennia* propagules reach open ocean, they are unlikely to take root (CLARKE and HANNON, 1971).

Therefore, evidence from Australia indicates that *Avicennia marina* propagules are not suited to long distance dispersal by ocean currents and have a limited viability controlled by temperature and salinity. In New Zealand, mangrove propagules are found along much of the coastline (CRISP *et al.*, 1990), which has been interpreted as indicating that they are suitable for long distance dispersal, although little is known of the viability of these disseminules. BURNS (1982) undertook a series of experiments to investigate the processes involved in the dispersal of *Avicennia marina* var. *resinifera*; specifically the rates at which the pericarp is lost and the propagules sink. He found that the shedding of the pericarp was salinity dependant with shedding being encouraged by decreasing salinity, and that most propagules had shed their pericarp and sunk within 5 d regardless of salinity.

BURNS (1982) also observed that the propagules began refloating after a few days. The duration of the period during which the propagule remained submerged depended on salinity, with the duration increasing with increasing salinity. He

attributed this to slower metabolic processes within the propagule occurring at high salinities. BURNS (1982) assumed the propagules which re-floated were still viable.

Based on the Australian observations, it is probable that the propagule is only viable for a limited time following pericarp shedding, and that the majority of propagules which refloat are no longer viable. Further, since root development only occurs while the propagule is stationary (BURNS, 1982), rooting is most likely to occur when the propagules do not float.

BURNS (1982) demonstrated experimentally that establishment is also a function of the number of obstacles available to trap propagules. He noted that the maximum density of obstacles capable of trapping mangrove propagules in estuaries occurred around established mangrove populations due to the presence of pneumatophores.

CRISP *et al.* (1990) stated that *Avicennia* is well suited to long distance dispersal and establishment, but they did not quantify these claims. It is clear that propagules can be transported great distances, but they have probably shed their pericarp during the initial stages and are unlikely to be viable on arrival.

The evidence discussed above indicates that mangroves are adapted for restricted dispersal to ensure that propagules become established in the immediate vicinity of the parent. It is unlikely that propagules can successfully establish more than 4–5 d travel from source.

NEARSHORE CURRENTS AND MANGROVE DISPERSAL

Long distance dispersal requires that the propagule be swept out of the estuary, transported along the coast or across the ocean, and then deposited in a suitable habitat (normally estuarine). As indicated above, this needs to occur within 4–5 d, if the propagule is to remain viable. On the west coast of the North Island, almost all of the major estuaries are located north of 38°S (Figure 1). South of this point, there are a limited number of river-mouth estuaries with the only major estuary being the Pauatahanui Inlet. On the east coast, there are a few suitable river-mouth estuaries and lagoons mainly in Poverty Bay and Hawke Bay, and no significant estuaries south of Hawke Bay. Further, on both coasts the shoreline is predominantly rocky for at least 200 km along the coast 'south' of the present limits of mangrove and muddy shores are rare.

Therefore, suitable habitats for mangrove beyond the current distribution are small in extent, sparse, and widely separated. Major geostrophic currents flow along the Coast in the vicinity of the shelf break: the West Auckland current travels north along the west coast; and the East Auckland travels south along the east coast as far as East Cape, where it splits into two branches, one of which (East Cape Current) flows south along the coast before turning east to the south of Hawke Bay (HEATH, 1985). The velocities associated with these currents are low ($\sim 0.1 \text{ m sec}^{-1}$), so they can only transport propagules 30–40 km within 4–5 d. This is further limited by the time taken for the propagule to move offshore into the geostrophic current, and then back onshore to become established. We consider it more likely that successful propagules would be transported to suitable sites for establishment by nearshore currents such as wind-induced drift, tidal currents, and littoral drift.

Wind-Induced Drift

Observations of wind-induced drift are limited for New Zealand (WILLIAMS, 1985), but an appreciation of the influence of wind-induced drift may be obtained by assuming that the wind-induced drift velocity is a constant proportion of the wind velocity. Wind-induced drift velocities are normally between 3% and 7% of the wind velocity, with values of $\sim 3.5\%$ being considered appropriate for total surface drift over long fetches (WU, 1975). Since the mangrove propagules are buoyant and travel in the surface layer, we will assume a higher drift of 5% of the wind velocity.

The dominant wind direction for New Zealand is from the southwest (HARRIS, 1990) so that within the regions of relevance to mangrove dispersal winds are mainly offshore for the east coast and onshore for the west coast. Winds generally change direction progressively over a 5–7 d cycle associated with the passage of low pressure systems across New Zealand and usually do not persist in any one direction for more than a few days (HARRIS, 1990). During extremes of the Southern Oscillation, it is possible for some wind patterns to be sustained for longer periods, particularly southwesterly winds during El Niño extremes and northeasterly winds during La Niña extremes.

The west coast generally experiences stronger winds than the east coast. Data for the Maui A oil production platform southwest of Cape Egmont (REID, 1991) and the Taharoa ironsand de-

velopment south of Kawhia Harbour (FRANKLIN, 1973) suggest average wind drift velocities of 0.2–0.3 m sec⁻¹ in the northwards alongshore direction.

These are comparable to the measured surface current velocities of 0.15–0.30 m sec⁻¹ reported by STANTON and GREIG (1991) for sites off the west coast of the South Island. The net drift observed over 180 days was close to zero, but there were intervals when the flow was predominantly in one direction for up to 5 d, the maximum period available for the establishment of mangrove. Therefore, a southwards directed wind-induced drift current could transport a propagule up to 130 km. This is insufficient to take a Kawhia harbour sourced propagule to the nearest suitable habitat at the Pauatahanui Inlet (Figures 1 and 4).

On the east coast, BRADSHAW *et al.* (1991) recorded bottom currents in the northern Bay of Plenty of up to 0.40 m sec⁻¹ which they interpreted as wind-induced. However, measurements of near surface velocities made offshore from Tauranga by one of us (W. de L.) showed non-tidal residual currents of < 0.20 m sec⁻¹. These are consistent with wind measurements at Tauranga assuming a 3.5% wind factor, and also the calculated wind-induced currents of HARRIS (1985). Even taking the higher velocity value, the maximum travel distance over 5 d is < 175 km which is insufficient for Waiaua propagules to reach the next suitable habitat around East Cape (Figure 4). During the more sustained periods of northeasterly winds associated with La Niña events, the wind drift direction is opposite to that needed to travel around East Cape.

Tidal Currents

Tidal currents are clearly important for dispersing propagules within estuaries, but the current velocities outside estuaries die off rapidly with distance from the entrance (WILLIAMS, 1985). Coastal tidal currents around New Zealand are generally too weak to transport sediment (HEATH, 1985), although negligible velocities are required to move floating mangrove propagules. Further, due to the oscillatory nature of tidal currents, the important component to consider is the tidal residual. Shelf tidal residual currents around New Zealand are low, << 0.05 m sec⁻¹ based on our measurements off Tauranga, so they are unlikely to transport propagules further than 20 km for most of the New Zealand coast. The major exception relevant to mangrove dispersal is the tidal resid-

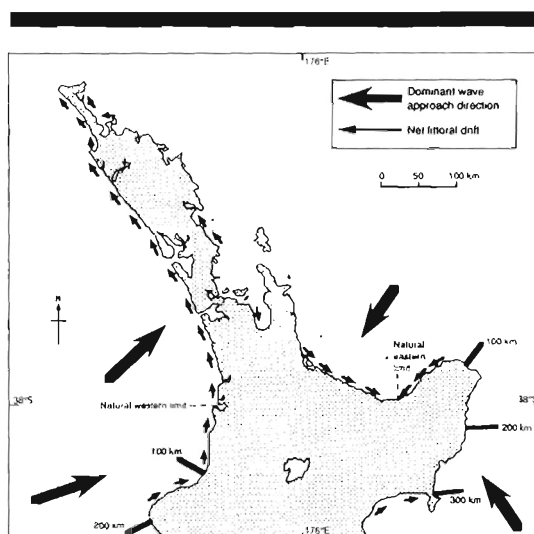


Figure 4 Dominant offshore wave approach directions and directions of littoral drift for the northern half of the North Island of New Zealand. Also marked are the distances along the coast from the last occurrence of mangrove

ual currents produced by a marked tidal asymmetry around the Northland Peninsula (HEATH, 1981, 1985). This asymmetry dominates the time-averaged mean flow, and hence determines the direction of transport (HEATH, 1981). The net direction of sediment transport is westwards around the north coast with a null point at Pandora Bank southwest of Cape Maria van Diemen. This is taken to be primarily due to the influence of tidal currents (HEATH, 1981).

Littoral Drift

The direction of littoral drift is determined by the wave climate and the orientation of the coast. Figure 4 summarises the wave approach directions (PICKRILL and MITCHELL, 1979) and dominant littoral drift directions for the northern half of the North Island. Although littoral drift currents are not persistent and may reverse direction for considerable durations, it is clear that any southwards dispersal of mangroves along the west coast by littoral drift is less likely than northwards dispersal.

Littoral drift in the Bay of Plenty is weaker than on the west coast due to the lower wave climate (PICKRILL and MITCHELL, 1979; HARRIS, 1985). The direction of drift is clearly towards the southeast as far as Ohiwa Harbour (RICHMOND *et*

al., 1984) and towards the southwest from East Cape towards Waiau Harbour (WILLIAMS, 1985). However, littoral drift is restricted to the surf zone, and it is probable that any propagules within this region will be cast onto the beach if they are still bouyant. Further, they may be damaged by turbulence and interaction with other materials in the surf. Therefore, littoral drift currents are unlikely as a suitable mechanism for transporting viable propagules. More likely propagules are jetted out of estuaries by tidal currents and then transported by wind-induced currents beyond the surf zone.

Implications

Tidal currents are only significant at the northern limit of mangrove in New Zealand and, therefore, exert no influence on the southern limit. However, since tidal currents only tend to transport mangrove propagules a very limited distance westwards around northernmost New Zealand, they may be responsible for maintaining the separate west and east coast genetic populations reported by DAWSON (1989).

Of the remaining processes considered, wind-induced drift currents are probably the most important transport processes with littoral drift having a secondary effect close to the shore. From the limited data available, it is probable that the maximum transport in any one direction during the 4-5 d establishment period of mangrove propagules is ~175 km. Since the coasts beyond the present limits are predominantly rocky within this distance, it is unlikely that mangroves will naturally increase their distribution in New Zealand.

The distribution of the conspecific mangrove in Australia may also be controlled by similar factors. Southwards extension of the mangrove distribution in Australia requires dispersal of propagules across Bass Strait to Tasmania. This is unlikely to occur as tidal current flows in Bass Strait are predominantly east-west with very little north-south movement (BLACK, 1992). Surface wind induced currents can be estimated as ~5% of the wind velocity as discussed above. Southward movement is associated with north-easterly wind conditions involving maximum mean winds of 15 m sec⁻¹ for durations of 1-3 d. These winds produce velocities <0.75 m sec⁻¹ (BLACK *et al.*, 1990) which are insufficient to transport propagules the >200 km necessary to reach the Tasmanian coast during the available time.

SUMMARY

There is no strong evidence to show that the southern limit of mangroves in New Zealand is solely a function of climatic conditions, particularly the frequency of winter frosts. Indeed, there is no strong evidence to show that the present mangrove distribution is in equilibrium with climatic conditions, and it is evident that mangroves can grow further south given that the other environmental conditions are suitable.

The New Zealand mangrove probably behaves in the same way as its Australian counterpart: *i.e.*, it is not suited to long distance dispersal and establishment with most plants establishing in suitable sites within 4-5 d travel distance from the parent plant. This makes dispersal by the major geostrophic currents unlikely. Dispersal is more likely determined by nearshore wind-induced currents with successful establishment favoured by dispersal within estuaries rather than between estuaries.

In the North Island of New Zealand, moderate to large estuaries are mainly located north of 38°S, which is coincident with the distribution of mangrove. South of this latitude, the coasts are primarily rocky and muddy shores are rare. Given the availability of suitable habitats for mangrove and the general pattern of nearshore currents, several conclusions may be drawn about the dispersal of mangrove propagules and hence the distribution of mangrove in New Zealand:

- (1) Tidal asymmetry around northernmost New Zealand tends to isolate western populations from eastern populations;
- (2) The main process controlling dispersal of viable propagules between estuaries appears to be wind-induced drift currents; and
- (3) The limits of the distribution are likely controlled by the lack of suitable habitats within 4-5 d travel time *via* coastal currents.

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