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THE ESTABLISHMENT, SPREAD AND HOST RANGE OF *PAROPSIS CHARYBDIS* STÅL (Chrysomelidae) IN NEW ZEALAND

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Abstract: *P. charybdis* Stål became established in the South Island in 1916. It spread rapidly, causing considerable damage, but declined in the late thirties. In 1956 it again increased, invaded the North Island, spread throughout the country by 1965, then declined again. It has been recorded from 59 species of *Eucalyptus*, and the adults apparently disperse prior to hibernation.

There is good correlation between increased abundance of *P. charybdis* and weather which is believed to stress plants making them more nutritious for the insects. The abundance of food may have been largely responsible for the fluctuations in its numbers.

HISTORY OF INVASION AND SPREAD (fig. 1). The Australian chrysomelid, *Paropsis charybdis* Stål was first recorded in New Zealand in 1916 in the Port Hills of the South Island (Thomson, 1922). It spread rapidly over the eastern South Island, by 1930 being recorded in Dunedin and the Kaikoura Range (Clark, 1930). Specimens were collected in Nelson in 1921, but it was not abundant there until 1932. In 1938 it was recorded in Southland.

There was one unconfirmed record in 1925 of a specimen at Bulls in the North Island (Miller, 1925) but no subsequent collections were made from the North Island.

After 1938 there were few reports until 1951 when some specimens were collected in Canterbury. From 1952 increasing numbers were reported from various localities in the South Island and in 1954 it was recorded for the second time at Queenstown.

In 1956[2] specimens were collected in the Palmerston North-Bulls area and from Titahi Bay. It was also found by others at this time (Gurr, 1957). The species was firmly established in the North Island and spreading fast.

By the autumn of 1957 it had spread up the west coast and throughout the Manawatu, reached the central King Country, and Hawkes Bay. A year later it had advanced to Turangi and reached just north of Napier and New Plymouth. By the end of the 1958-59 summer Rotorua and an isolated belt of country between Te Kauwhata and Puketutu Island were infested. Next season it spread rapidly, extending over the Bay of Plenty and the Waikato, north to Warkworth, up the Coromandel Peninsula, south from Te Kauwhata to Te Kuiti, and up the east coast.

The rate of spread was slower than expected in 1960-61, but *P. charybdis* was dis-

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2. From this time until it had colonized the whole of the country, intensive sampling was maintained by the Forest Biology Survey of the N. Z. Forest Services; over 1500 samples were collected.

covered for the first time in Westland.

By the autumn of 1962 all the East Cape and the Coromandel Peninsula had been colonized, the northern limit was a line from Waipu to Dargaville, and in Westland it

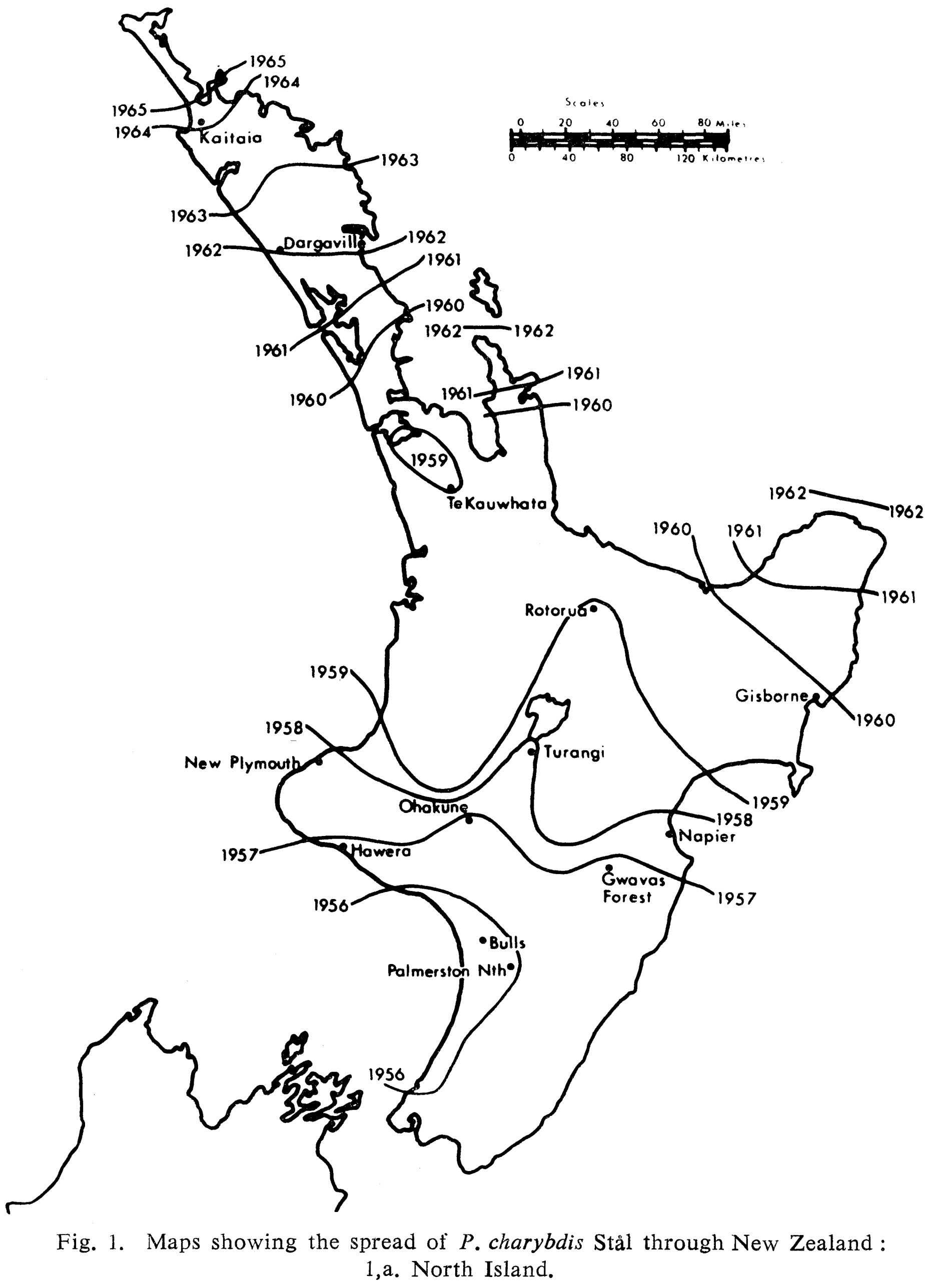
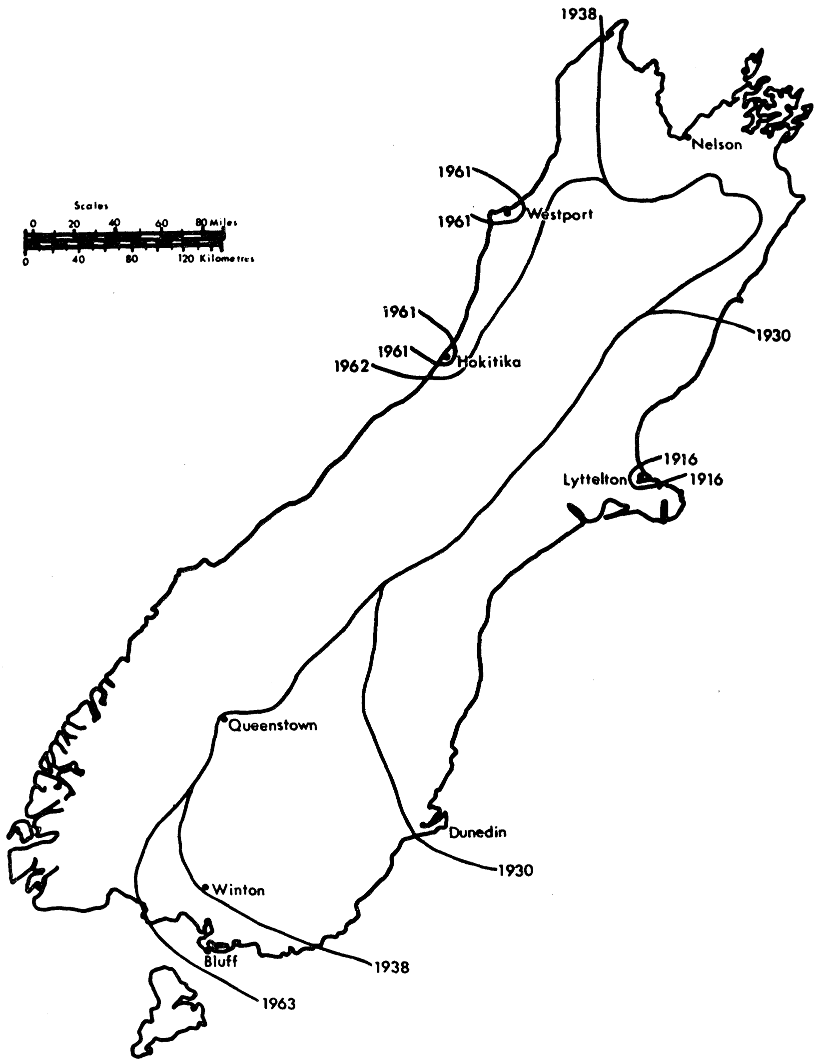


Fig. 1. Maps showing the spread of *P. charybdis* Stål through New Zealand : 1,a. North Island.



1,b. South Island.

had extended its range. In the 1962-63 season it was found at the Bluff, and north to Kaikohe. By the following year it was established everywhere eucalypts were growing, with the exception of Stewart Island and the northern tip of the North Island. From about 1965 its numbers declined throughout New Zealand.

DISPERSAL. Clark (1930) reported that the beetles clung tenaciously to the hood of a motor car for many miles. They remained on the smooth surface of a modern car travelling at 80-97 kph for more than 48 kilometers. Dispersal on trains, motor vehicles and light aircraft is therefore quite possible, especially from areas of great abundance. Perhaps the introduction to the west coast of the South Island in 1961 could be attributed to this cause, but the rapid rate of spread from initial points of colonization in both islands would suggest a more efficient mode of dispersal, as would the successful invasion of the North Island in 1955–56.

Although the flight behaviour of *P. charybdis* has not been studied, general observations have shown that the adults fly strongly and persistently in warm, sunny weather, particularly in the late summer when there are large numbers of adults feeding prior to hibernation. That such behaviour is conducive to widespread and effective dispersal (Lewis & Taylor, 1965) is supported by the following records. The D. S. I. R. collection in Nelson includes beetles taken on Mt Arthur (1372 m) in 1921 and on Mt Peel (1739 m) in 1943. Gibbs & Ramsay (1960) recorded "numerous beetles" on three separate occasions and sites between 1220 and 1520 m in the Tararua Ranges. In 1959 large numbers of adults were found at the summit of Mt Egmont (1910 m). In 1959 and again in 1960 very large numbers of beetles (a solid band several kilometers long) many still alive, were washed up on the east coast beaches of the Bay of Plenty at Matakana Island and Mt Manganui. Also in 1959 (or possibly earlier) the Puketutu Island–Te Kauwhata area was infested some 161–322 kilometers ahead of the general boundary of spread. Clark (1930) noted that the rapid spread and scattered nature of the infested areas in the South Island suggested dispersal with the prevailing winds, and the pattern of spread in the North Island also reflected an advance with the prevailing SW winds.

The successful colonization along the SW coast of the North Island probably became possible because many beetles were blown out to sea from Nelson after they became abundant there in the early 1950's. This invasion and the subsequent spread eastward through the Manawatu Gorge and on into Hawkes Bay is remarkably similar to that of *Eriococcus coriaceus* Mask 30 years earlier (Clark, 1938).

HOST RANGE AND FEEDING PREFERENCES. Clark (1930) recorded that *Eucalyptus globulus*, *E. radiata* and *E. viminalis* were the favoured hosts of the species, and that *E. regnans*, *E. gunnii*, *E. obliqua*, *E. macarthurii* and *E. eugenioides* were also attacked. The few records between 1930 and 1958 either did not name the host, or stated only "*Eucalyptus* sp."

Since the 1958–59 season all collections of *P. charybdis* sent to the Forest Research Institute by Forest Biology Observers either included a specimen of the host plant for check identification, or came from trees already authoritatively identified. As a result this insect was recorded feeding on 59 species of *Eucalyptus* (Table 1). Of these, only six (*E. deanei*, *E. globulus*, *E. leucoxylon*, *E. macarthurii*, *E. resinifera* and *E. viminalis*) were extensively and repeatedly defoliated. A further eleven species (*E. amplifolia*, *E. botryoides*, *E. fastigata*, *E. gunnii*, *E. maidenii*, *E. obliqua*, *E. ovata*, *E. pauciflora*, *E. punctata*, *E. radiata* and *E. saligna*) were sometimes heavily attacked, but not so badly as the first group. The remaining 42 species were only ever slightly damaged, and then very infrequently. But it would seem that the picture of host susceptibility is more complex than this. Local and intermittent exceptions to the above groupings often occurred. Although these three categories of susceptibility held true in general, the degree of attack on an individual tree of any one species varied with its age, vigour and site. Of interest in this connection are some data collected by P.B. Carne in 1967 (pers. comm.). At 154 sites in Nelson and Marlborough, chosen to represent extremes of favourability and unfavourability for growth of eucalypts, he classified the *E. macarthurii*

Table 1. Species of *Eucalyptus* upon which *Paropsis charybdis* Stål has been recorded feeding in the field in New Zealand.

aggregata D. & M.	*ficifolia* F. Muell.	*oreades* R.T. Bak.
amplifolia Naudin	*fraxinoides* D. & M.	*ovata* Labill.
amygdalina Labill.	*globoidea* Blakely	*paniculata* Sm.
bauerana Schau.	*globulus* Labill.	*pauciflora* Sieb. ex Spreng.
blakelyi Maiden	*grandis* Hill ex Maiden	*pellita* F. Muell.
blaxlandii Maiden & Cambage	*gumifera* (Gaertn.) Hochr.	*pilularis* Sm.
bosistoana F. Muell.	*gunnii* Hook. F.	*piperita* Sm.
botryoides Sm.	*haemostoma* Sm.	*propinqua* D. & M.
bridgesiana R.T. Bak.	*leucoxylon* F. Muell.	*punctata* D.C.
camaldulensis Dehn.	*linearis* Dehn.	*radiata* Sieb. ex D.C.
capitellata Sm.	*longifolia* Link & Otto	*regnans* F. Muell.
cinerea F. Muell ex Benth.	*macarthurii* D. & M.	*resinifera* Sm.
cladocalyx F. Muell.	*maculata* Hook.	*robusta* Sm.
cornuta Labill.	*maidenii* F. Muell.	*saligna* Sm.
dalrympleana Maiden	*mannifera* Mudie ssp. *maculosa* (R.T. Bak.) L. Johnson	*sideroxylon* A. Cunn. ex Woolls
deanei Maiden	*microcorys* F. Muell.	*sieberi* L. Johnson
delegatensis R.T. Bak.	*muellerana* Howitt	*tasmanica* Blakely
diversicolor F. Muell.	*nitens* Maiden	*tereticornis* Sm.
eugenioides Sieb. ex Spreng.	*obliqua* L'Herit.	*urnigera* Hook. F.
fastigata D. & M.		*viminalis* Labill.

and *E. viminalis* trees on them according to their vigour and the amount of dieback of their crowns. A 4 × 2 contingency test of these data (Table 2) suggests that the success of *P. charybdis* on these two species is positively correlated with the degree of environmental stress already experienced by the trees.

In addition it should be noted that in spite of extreme and widespread defoliation,

Table 2. A 4×2 Contingency Test of observations of the condition of *Eucalyptus macarthurii* and *E. viminalis* trees growing on good and poor sites after being attacked by *P. charybdis* Stål for several years.

Assessment of Site	Condition of Tree: Severe dieback & weak crown		Mod. dieback & weak crown		Slight dieback & weak crown		No dieback & strong crown		Total Trees
	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected	
Poor to very poor (exposed hillsides, shallow or eroded soils, rocky hilltops)	23	13.4	27	17.9	16	20.2	3	17.5	69
Good to excellent (gullies & flats with rich soil, well watered)	7	16.6	13	22.1	29	24.8	36	21.5	85
Total trees	30	30	40	40	45	45	39	39	154

$\chi^2_3 = 44.2 \quad P < 0.001$

a general recovery and regrowth of even the most susceptible species followed after the invasion of both the South and North Island.

DISCUSSION. *P. charybdis* is now present virtually wherever eucalypts occur in New Zealand. This was achieved in two brief, approximately ten year "bursts"— one in the South Island following its introduction in 1916 and the other in the North Island after it had gained a foothold there in 1956. In both instances the numbers declined to low levels after the original spectacular colonizing outbreak. The beetles became much less abundant on the more susceptible species of *Eucalyptus* and virtually disappeared from many of the less susceptible species. Seasonal and local fluctuations continued at these lower levels but there was a general recovery and regrowth of most of the trees that had been attacked. Agitation for control measures during outbreaks subsided when the outbreaks subsided.

The repetition on the North Island of a similar sequence of events to what had occurred 40 years earlier in the South Island, together with an accompanying resurgence of the South Island population, suggests a common cause. A conventional explanation might involve predation, but there is no record of parasitism and only very few records of predation or disease (Styles, 1970). And twice there has been a marked decline in abundance in the absence of any parasitism or observed increase in predation. Another explanation might be that *P. charybdis* ate out its food supply as *Cactoblastis* did in Queensland (Dodd, 1936), but there is no evidence for this. Indeed most trees seem now to carry as much succulent foliage as they did before they were attacked.

The best explanation for these two outbreaks may be found in the theory of the stress index put forward by White (1969). According to this theory trees may be stressed when a series of unusually wet winters is accompanied by a series of unusually dry summers. Trees that are stressed by such changes in soil moisture tend to respond by increasing the nitrogen content of their leaves, particularly the soluble nitrogen of the phloem sap. This makes them much more suitable food for phytophagous insects.

The stress indices for a number of localities in New Zealand have been calculated according to the formula of White (1969) and are presented in fig. 2. The correlation of positive or increasing values of the stress index with the spread and multiplication of *P. charybdis* is good. For example for Christchurch where *P. charybdis* was first reported in 1916, the stress index increased sharply between 1915 and 1918, becoming positive in 1917–18 and remaining so for most of the time until 1924–25, when it again increased steeply before falling in 1929–30. It was during this period that *P. charybdis* spread so rapidly in the South Island (fig. 2a).

The stress index for Nelson increased steeply from 1952 to 1958, and that for Palmerston North from 1955 to 1958. *P. charybdis* had been increasing in the Nelson district since 1951, and became established near Palmerston North in 1955–56 (fig. 2b). In 1925 when it was reported near Palmerston North, but did not become established there, Nelson's stress index was positive, but Palmerston North's was strongly negative. At that time *P. charybdis* was still quite abundant in Nelson, so that many may have been blown out to sea with the prevailing SW winds. But any reaching the North Island would have had little chance of surviving on the unstressed trees.

The stress indices for Palmerston North, Hamilton and Auckland were all essentially similar between 1955 and 1965, remaining positive apart from a short negative period

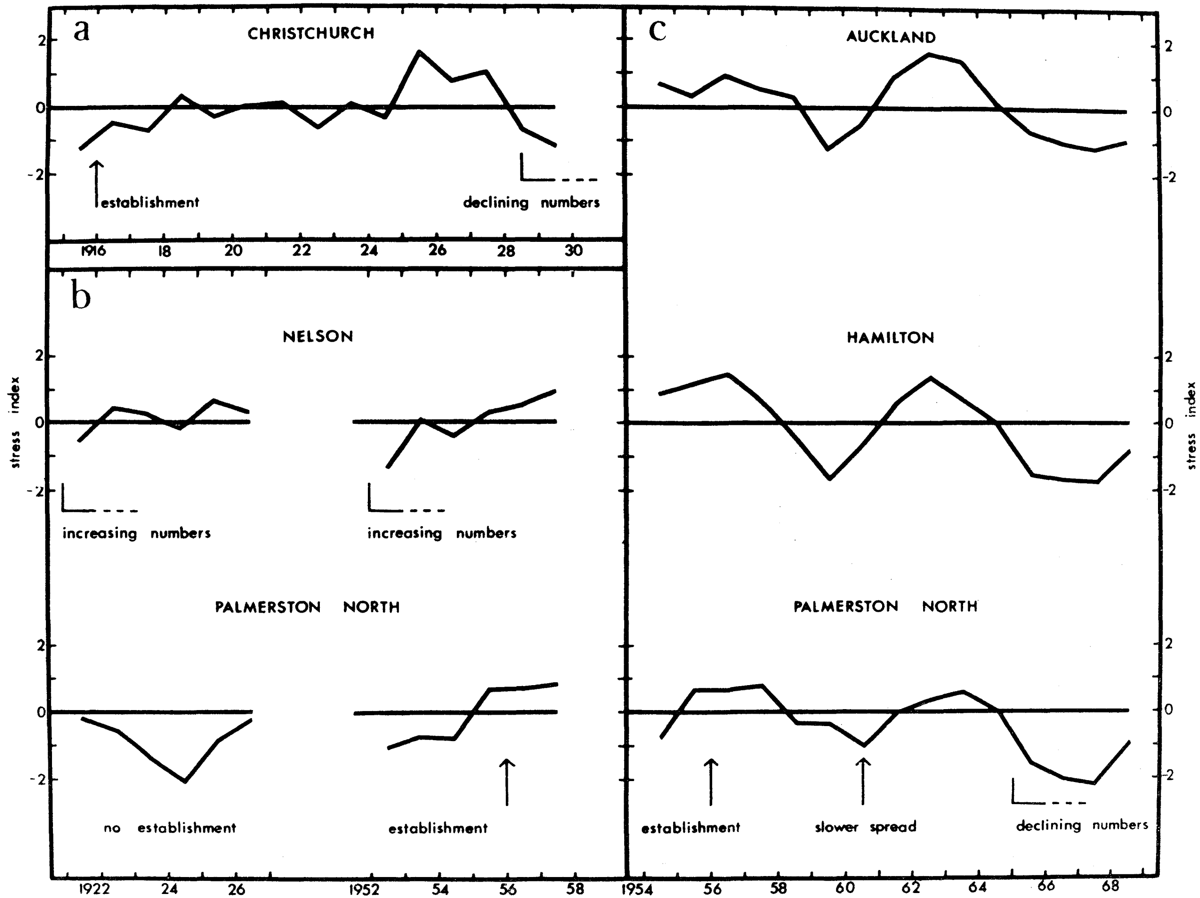


Fig. 2. Stress indices for selected locations in New Zealand calculated from rainfall data supplied by the New Zealand Meteorological Service. For discussion see text.

from 1959 to 1961. (fig. 2c) During these years the beetle spread rapidly in the North Island and was in great abundance except for the 1960-61 season when it was generally not so abundant, and its rate of spread was much less than had been expected.

Since 1964-65 the stress index in the North Island has been negative, and it is noteworthy that from 1965 onwards *P. charybdis* has been much less abundant. The fact that other sorts of phytophagous insects were more abundant on eucalypts when *P. charybdis* was in great abundance, and Carne's observations on the correlation of attack with site, would support this idea that stressed trees are a better source of food for *P. charybdis.*

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