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THE ECOLOGY OF *DACTYLANTHUS TAYLORII* AND THREATS TO ITS SURVIVAL

Summary: *Dactylanthus taylorii*, a root parasite in the family Balanophoraceae, is New Zealand's only fully parasitic flowering plant. It grows attached to the roots of a wide range of hardwood trees and shrubs, often in fire-induced secondary forest on the margin of podocarp-hardwood forest. It is inconstantly dioecious with a skewed sex ratio of approximately 5:1 male to female inflorescences. The inflorescences, especially the males, contain a large quantity of nectar, up to 1.6 ml, and can produce 0.5 ml per day for 10 days. The morphology of the inflorescences, the quantity and chemistry of the nectar, time-lapse video monitoring and other evidence suggest that the *Dactylanthus* flowers are adapted for pollination by short-tailed bats. Ship rats are also effective pollinators but occasionally destroy the inflorescences. Kiore completely destroyed all the inflorescences observed on Little Barrier Island in 1992 and 1993, although some seed was found there in 1991.

Dactylanthus plants have been successfully cultivated by sowing seeds close to the roots of broadleaf plants. Germination was very slow with the highest rates occurring nearly five years after the seed was sown. Further research is needed to clarify the role of fungal hyphae found inside the cells of a young plant and that of the sheath processes which may assist vegetative reproduction.

Video monitoring provided evidence that the introduced possum, by browsing the inflorescences, threatens the survival of *Dactylanthus* at most North Island sites. Where possums were present, and the plants unprotected, almost all the inflorescences were browsed. Adult plants at the main study site had a half-life of only 8.5 years. Conservation management to ensure the survival of *Dactylanthus* will require protection of the plants from possums, rats and humans and adequate areas of secondary forest containing abundant host plants.

Keywords: *Dactylanthus taylorii*; ecology; threatened plants; conservation; pollination; short-tailed bats; possums.

Introduction

Dactylanthus taylorii, also known as the wood rose, the flower of Hades, pua o te reinga (Taylor, 1870), or wae-wae-atua (Hill, 1909), is the only fully parasitic flowering plant in New Zealand's indigenous flora. It is the sole member of the genus and the most southerly occurring member of an otherwise tropical and subtropical family of root parasites, the Balanophoraceae.

Dactylanthus plants consist mainly of a round warty tuber (Fig. 1) up to 50 cm in diameter, attached as a parasite to the root of a host tree or shrub. In response to the infection by *Dactylanthus*, the host root enlarges and forms a placenta-like attachment area shaped like a fluted wooden flower. The *Dactylanthus* plant has no green leaves or roots of its own and obtains its nutrients from the host through this enlarged root area. The leaves, which lack stomata (Moore, 1940; Kuijt and Dong, 1989), are reduced to non-photosynthetic floral bracts and the minute flowers are clustered into inflorescences (Fig. 2) that emerge from the tuber. Moore (1940) and

other authors (Cheeseman, 1920; Thomson, 1927; Macphail and Mildenhall, 1980) made no mention of nectar and thought the flowers were pollinated by insects attracted by the heavy perfume. Govindappa and Shivamurthy (1975), who describe the insect pollination of *Balanophora abbreviata* Blume, state

> "The only recorded observation on pollination in the family (Balanophoraceae) is that of Moore (1940) [on *Dactylanthus*] who did not examine the mechanism involved".

Dactylanthus was listed, without comment, among the pollens identified in lesser short-tailed bat (*Mystacina tuberculata*) guano collected in May 1975 from Omahuta Forest, Northland (Daniel, 1976; Holloway, 1976). Had the bats visited *Dactylanthus* flowers for nectar or had they eaten insects which had visited the flowers?

The distinctive pollen grains of *Dactylanthus* have been found in middle to late Pliocene sediments in coal measure sequences from both the North and South Islands, as far south as Southland (Macphail and Mildenhall, 1980). They have also been found in deposits dated between 1800 and 50 000 years ago in
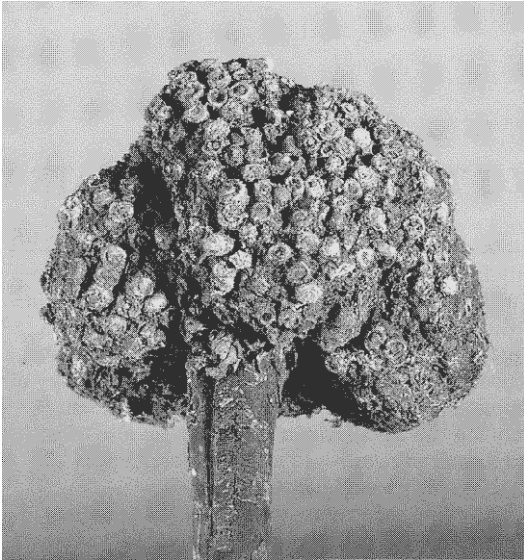
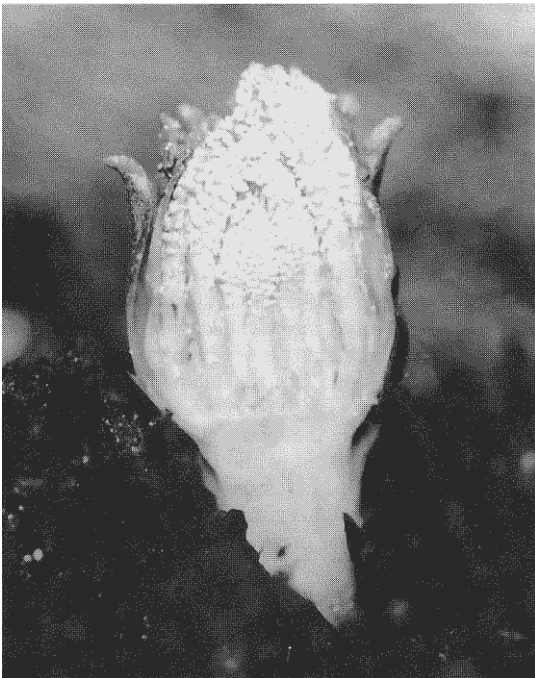Figure 1: Dactylanthus *on a host root, showing the tuber's warty surface formed by old peduncle bases.*

Figure 2: *A longitudinally sectioned* Dactylanthus *inflorescence showing the minute whitish male flowers clustered on the spadices and surrounded by the scale leaves (floral bracts).*

the Tongariro region, lowland Taranaki, and near Porirua (McGlone and Topping, 1977, 1983; Mildenhall, 1993; McGlone and Neall, 1994). Fresh looking *Dactylanthus* pollen was found in lake muds and peats from a site in the South Island, 35 km south of Cape Farewell, suggesting that either *Dactylanthus* still occurs in north-west Nelson or it has done so until recently (Macphail and Mildenhall, 1980).

The first reported European sighting of *Dactylanthus* was in March 1845 when the Reverend Richard Taylor saw it about 12 km south of Raetihi (Springer 1994). Herbarium specimens and published records over the last 150 years show a distribution for the species from Hokianga in Northland to the Orongorongo Valley near Wellington (Lane-Taylor, 1970; Ecroyd, 1995). However, it has not been reported for at least 25 years from many sites where it used to grow, particularly the northern, eastern and southernmost sites, for example, near Warkworth, Huia, Cape Colville, Thames, Nuhaka, Wairoa, Puketitiri, Kaitoke (Cheeseman, 1906) and the Orongorongo Valley.

Dactylanthus taylorii is currently rated as 'Endangered' in the recent listing of the threatened plants of New Zealand (Cameron *et al*., 1995). The main threats to *Dactylanthus* were considered by Wilson and Given (1989) to be habitat destruction and collectors of the 'wood rose', the modified host root.

In March 1989, during the expected period of peak flowering of *Dactylanthus* (Moore, 1940), *Dactylanthus* plants on the Mamaku Plateau, near Rotorua, were found surrounded by the broken off remains of inflorescences. No intact inflorescence was seen on any plant. The spadices had been completely and very neatly removed from every inflorescence leaving only the peduncle and bracts. A clump of plants was covered with netting to see whether it would protect the flowers. Two weeks later this clump was covered in inflorescences, and from this trial a six year study of the species developed.

The purpose of this study was to improve the understanding of the ecology and reproductive biology of this species, especially results of interference with flowering and seed production, to provide a basis for management to ensure its long-term survival.

Methods

Individual *Dactylanthus* plants are difficult to distinguish as they usually grow in tight clusters and are at least partially buried. The term 'clump' refers to a close group of one or more tubers which appear to have formed more than one haustorium and may comprise one or several individual plants**.**

Where authorities are not given, nomenclature follows Brownsey and Smith-Dodsworth (1989) for ferns, Connor and Edgar (1987) and references therein for other native vascular plants and King (1990) for mammals.

Distribution

To locate further *Dactylanthus* plants at the Mamaku site (site 6, Table 1) intensive searches were made and clumps marked and numbered when they were found. Searches of other localities in the known range with similar habitat and host species present, and information or assistance from people who had previously found *Dactylanthus*, helped to locate plants in 14 of the Ecological Districts mapped by McEwen (1987).

Hosts and habitat

To characterise the habitat of *Dactylanthus*, sites were selected covering its currently known geographical range (Table 1 and map in Ecroyd, 1993). Site factors including altitude, aspect, slope and physiography were recorded. At 24 of these sites a list was compiled of tree and shrub species occurring within 10 m of a selected *Dactylanthus* clump (Table 2). The canopy cover and ground cover of higher plants, bryophytes, litter, soil and rock was estimated for each plot except at site 1 (Table 3).

The host species were identified only when this was possible without excavating the root systems which would have risked damage to the host plant and the *Dactylanthus*. Hosts were sometimes determined by relating the death of a *Dactylanthus* plant to the death of a nearby tree.

Phenology and reproductive biology

Visits to site 6 were made from 1989 to 1995 and flowering records kept for 65 clumps with visits every four to five days from early February until mid May during the 1991 season. Visits in other years were more irregular but usually about every 14 days during the flowering season. Records of flowering were also kept for other sites visited during the flowering season.

Pollination
To indicate whether the flowers were adapted to attracting diurnal or nocturnal visitors, nectar was collected from 30 inflorescences at dawn and dusk each day for five days and the nectar flow measured. A paired *t*-test was used to test for differences between the diurnal and nocturnal nectar production. Ten of these inflorescences were males just starting

to open, ten were males in full flower and ten were females. The nectar was sampled from a clump of *Dactylanthus* which was covered in fine mesh cloth to prevent any nectar being taken by insects or other small animals. Samples of nectar were chemically analysed (see Ecroyd *et al.*, 1995).

Inflorescences were viewed under ultraviolet light to see whether there was any indication of adaptation for pollinators using this part of the spectrum.

To identify the pollinators of *Dactylanthus taylorii* flowers, observations were made on more than 100 occasions during the day and on more than 55 occasions at night, from 1989 to 1995, while the plants were flowering.

Data on insects visiting the *Dactylanthus* flowers were obtained using three 6 cm diameter pitfall traps placed close to inflorescences, two modified 'mini Malaise' type traps (Townes, 1972), 20 cm high, placed over the inflorescences and a small 50 cm high, square 360° Malaise trap suspended above the inflorescences from early April until mid May 1991.

To detect larger animals such as ship rats (*Rattus rattus*) and mice (*Mus musculus*) in the vicinity of the flowers, a footprint recording system (King and Edgar, 1977) was used near eight clumps at site 6 in 1991. Three *Dactylanthus* inflorescences were placed in enclosures with green tree geckos (*Naultinus elegans* Gray) to test whether geckos were attracted to the flowers.

A time-lapse video security system fitted with infra-red lighting (Ecroyd, 1993; Innes, Crook and Jansen, 1994), was used to monitor *Dactylanthus* inflorescences at 14 sites for 55 nights between March 1992 and April 1995.

Browsing of inflorescences
By 1991 about half of the 66 clumps of *Dactylanthus* at site 6 were protected with wire mesh exclosures. Five exclosures were constructed of 12 mm mesh to exclude rats, mice and possums (*Trichosurus vulpecula*), a further 11 were of 50 mm mesh to exclude possums and larger animals and other exclosures were of intermediate mesh sizes. From 1991 to 1994, the Department of Conservation reduced possum numbers at this site by trapping and poisoning with cyanide or pindone, but in 1995 brodifacoum (Talon[TM]) and sodium monofluoroacetate (1080) were used in bait stations. The effectiveness of these methods in regard to the prevention of browsing of inflorescences was monitored. By 1995 selected clumps were protected by exclosures at 31 of the *Dactylanthus* sites and some of these clumps were used for video observations and flowering records.

Cayenne pepper, naphthalene and an acrylic paint and egg mixture (Crozier and Ledgard, 1988) were applied as potential possum repellents, on or very close to unprotected *Dactylanthus* inflorescences which were monitored for browsing.

Fruit development, dispersal and seed germination

Fruits were collected from plants in August, October and November 1990 for germination trials and examined for soundness. They were cut and described as being sound if the endosperm was whitish and occupied most of the testa.

Soil samples of *c*. 10 g were collected downhill from a seed-producing female plant at site 12 at 20, 40, 60 and 80 cm intervals, to provide information on fruit dispersal and to determine whether there was a seed bank in the soil. The soil was sieved to extract the fruits.

To provide information on germination, fruits collected from sites 6 and 12 were sown in December 1990 on damp filter paper, sphagnum moss, sterile perlite, foam plastic and in standard seed sowing mix in seed trays. Fruits were also prepared for a germination trial on sterile nutrient media. Some were soaked in 50% bleach for 20 minutes, rinsed in water overnight, surface sterilised in hydrogen peroxide for six minutes and then double rinsed in sterile distilled water, while others were soaked in 30% bleach for 30 minutes and then double rinsed in sterile distilled water. After this surface sterilisation, they were placed on four different sterile nutrient mixes solidified with 9 g l^{-1} agar (half strength MS nutrient medium without hormones (Murashige and Skoog, 1962); R&W nutrient medium (Risser and White, 1964); and LP nutrient medium (Quoirin and Lepoivre, 1977) with and without 5 mg l^{-1} activated charcoal) and kept in the dark in a growth room.

Several hundred *Dactylanthus* fruits were sown in the vicinity of suitable host tree roots in natural forest conditions at five sites in 1989. In 1995 samples of soil from four of these sites were searched for fruits using a stereomicroscope and then the soil was sieved to recover further fruits. Fruits were also sown close to the roots of five kohuhu (*Pittosporum tenuifolium*), and five broadleaf (*Griselinia littoralis*) plants established in a partitioned glass-sided planter box in 1990. The root systems were monitored without disturbance by removing the cover from the glassed side. In November 1992 some of the plants were removed and carefully examined for *Dactylanthus* seedlings. The remaining plants were removed in May 1995. Samples of a possible *Dactylanthus* seedling were fixed in glutaraldehyde, dehydrated in acetone and critical point dried in carbon dioxide before being examined using a scanning electron microscope.

Population trends, growth rates and life span

Live and dead *Dactylanthus* clumps found on single visits to 27 sites were counted to provide an estimate of the proportion of live to dead plants.

At site 23 the larger and more exposed *Dactylanthus* plants were measured in 1994 to obtain an estimate of their growth rate. It was assumed that colonisation by native trees and shrubs occurred soon after the planting of pines at this site in 1974 (J. Barkla, *pers. comm*.; DoC, Wanganui, N.Z.), and the *Dactylanthus* plants would be less than 20 years old when visited.

To estimate the age of *Dactylanthus* plants, cross sections of three host roots, each bearing a large wood rose, were sanded and the growth rings counted using a binocular microscope.

Eight recently dead *Dactylanthus* plants from site 6 were collected and isolations made for fungal pathogens.

Results

Distribution

Sites where the occurrence of *Dactylanthus* has recently been confirmed are all between latitude 37°40' and 39°50'S (Table 1), except for Little Barrier Island at latitude 36°10'S where 11 clumps were found in 1992 (for map see Ecroyd, 1993). *Dactylanthus* pollen found in the guano of lesser short-tailed bats collected in Northland (35°10'S) in May 1975 (Daniel, 1976) indicates its probable existence even further north, however, recent searches of likely sites failed to find any. The majority of sites found are in the central North Island.

Despite considerable response from the general public with information concerning *Dactylanthus* sites, there have been no confirmed recent sightings of this species from areas where it was previously recorded near Auckland, Thames, on the Coromandel Peninsula, Hawke's Bay (except site 36), Kaitoke (despite a search in suitable habitat), or in the South Island. Unconfirmed recent reports suggest a wider occurrence in the vicinity of site 37, which is currently the most southerly confirmed site.

Hosts and habitat

Dactylanthus has previously been reported to grow on the roots of about 30 species of native hardwood trees and shrubs (Ecroyd, 1995). Broadleaf, fivefinger (*Pseudopanax arboreus*), kohuhu, lancewood (*Pseudopanax crassifolius*), lemonwood

Table 1: *Location and characteristics of study sites.*

Site No.	Ecological District	Latitude (S)	Longitude (E)	Alt. (m)	Aspect (°)	Slope (°)	Physiography
1	Little Barrier	36° 10'	175° 10'	380	180	30	face
2	Pukeamaru	37° 40'	178° 20'	160	200	30	face
3	Kawhia	38° 00'	175° 10'	900	330	20	ridge
4	Rotorua	38° 00'	176° 30'	300	190	2	terrace
5	Rotorua	38° 10'	176° 40'	400	170	15	face
6	Tokoroa	38° 10'	176° 00'	560	140	2	terrace
7	Atiamuri	38° 20'	176° 10'	740	310	15	ridge
8	Atiamuri	38° 30'	176° 10'	500	20	2	terrace
9	Pureora	38° 30'	175° 30'	540	150	5	face
10	Pureora	38° 30'	175° 30'	560	320	5	terrace
11	Pureora	38° 30'	175° 30'	560	270	5	terrace
12	Pureora	38° 30'	175° 30'	560	255	2	terrace
13	Taupo	38° 30'	175° 40'	500	100	5	terrace
14	Taupo	38° 40'	175° 50'	360	90	55	face
15	Taupo	38° 40'	176° 10'	700	290	20	face
16	Taupo	38° 50'	176° 10'	700	270	5	gully-head
17	Taupo	38° 50'	176° 10'	720	310	5	terrace
18	Taupo	38° 50'	175° 40'	650	315	30	face
19	Taupo	39° 00'	175° 40'	600	160	7	gully-head
20	Taupo	39° 00'	175° 50'	600	80	5	terrace
21	Taumarunui	38° 50'	175° 30'	800	5	2	terrace
22	North Taranaki	38° 50'	174° 50'	460	340	25	gully-head
23	North Taranaki	38° 50'	174° 50'	520	270	20	face
24	Tongariro	39° 00'	175° 40'	660	140	25	face
25	Tongariro	39° 00'	175° 50'	680	40	10	face
26	Tongariro	39° 00'	175° 30'	790	90	10	face
27	Tongariro	39° 00'	175° 30'	640	80	5	face
28	Tongariro	39° 10'	175° 20'	750	230	7	face
29	Tongariro	39° 10'	175° 20'	740	180	5	terrace
30	Tongariro	39° 10'	175° 20'	760	225	12	face
31	Tongariro	39° 20'	175° 20'	780	180	15	face
32	Tongariro	39° 20'	175° 20'	820	360	10	face
33	Tongariro	39° 20'	175° 20'	810	190	2	terrace
34	Tongariro	39° 20'	175° 30'	840	240	5	face
35	Egmont	39° 10'	174° 00'	1060	350	20	face
36	Kaimanawa	39° 20'	176° 20'	530	160	15	face
37	Rangitikei	39° 50'	175° 50'	400	25	10	ridge

(*Pittosporum eugenioides*), mahoe (*Melicytus ramiflorus*), mamangi (*Coprosma arborea*), and putaputaweta (*Carpodetus serratus*) were confirmed as common hosts. These are among the more common tree species found at sites where *Dactylanthus* is known to occur (Table 2). Most of the observed hosts were over 5 m tall except at site 35 which is near the upper altitudinal limit of trees and shrubs and has a canopy less than 5 m in height. Many of these host species are seral and occur abundantly on forest margins. Thus, one of the most common sites for *Dactylanthus* found today is in old fire-induced secondary forest on the margins of tall podocarp-hardwood forest.

Pseudopanax species were recorded at most sites. The genera *Podocarpus*, *Prumnopitys*, *Dacrydium*, and *Phyllocladus* were often recorded at *Dactylanthus* sites (Table 2) and there are anecdotal but unconfirmed reports of some of these conifers being *Dactylanthus* hosts (e.g., R. Whittle, *pers. comm.*; Puketitiri, N.Z.). *Nothofagus* is another reported host genus (Hooker, 1859) for which there has been no recent confirmation.

Dactylanthus is sometimes found growing close to the base of a particular tree but is actually attached to the roots of another species growing several metres away. It is often very difficult to identify the host with certainty without excavating the root system.

Dactylanthus grows in a wide variety of climates, from the relatively mild frost-free slopes of Little Barrier Island to near National Park in the

Table 2: *Tree species over 5 m tall growing at 24* Dactylanthus *sites.*

Species	1	2	6	8	9	11	12	13	14	17	18	19	21	22	23	24	26	28	29	31	34	35	36	37	Total
Agathis australis	*																								1
Alectryon excelsus																							*		1
Aristotelia serrata									*																1
Beilschmiedia tawa	*	*						*															*		4
Brachyglottis repanda															*										1
Carpodetus serratus								*			*	*				*		*							5
Coprosma arborea	*																								1
Coprosma grandifolia									*																1
Cordyline australis					*				*																2
Dacrydium cupressinum						*		*											*		*				4
Dysoxylum spectabile	*																								1
Elaeocarpus hookerianus																			*						1
Fuchsia excorticata				*																					1
Griselinia littoralis			*		*										*	*									4
Hebe "arborea"		*																							1
Knightia excelsa		*																							1
Kunzea ericoides	*	*							*																3
Leptospermum scoparium									*																1
Libocedrus bidwillii																		*							1
Melicytus ramiflorus		*		*								*										*	*		5
Myrsine australis	*				*			*															*		4
Neomyrtus pedunculata																		*							1
Nestegis cunninghamii																		*		*					2
Nestegis lanceolata					*						*										*		*		4
Phyllocladus alpinus					*		*						*			*									4
Pinus radiata															*										1
Pittosporum eugenioides									*														*		2
Pittosporum tenuifolium				*			*	*	*																4
Podocarpus hallii					*		*				*	*				*	*	*	*						8
Podocarpus totara					*																		*		2
Prumnopitys ferrugineus					*											*							*		3
Prumnopitys taxifolia					*											*				*					3
Pseudopanax arboreus		*				*	*	*	*	*															6
Pseudopanax colensoi																			*						1
Pseudopanax crassifolius			*		*	*	*					*			*	*	*	*							9
Pseudopanax simplex																		*							1
Schefflera digitata														*	*										2
Sophora microphylla																							*		1
Sophora tetraptera								*																	1
Toronia toru					*																				1
Weinmannia racemosa							*		*	*		*	*			*				*	*				8

central North Island where frosts and snow are common. There is also a wide altitudinal range from near sea level at East Cape to 1060 metres a.s.l., near the limit of shrubby vegetation, in Egmont National Park. Sites range from north-facing to south-facing and from vertical rocky faces to flat terraces (Table 1).

Dactylanthus sites typically have good drainage, but are not drought prone, and generally have a moderately dense forest canopy and relatively open ground cover (Table 3). It is often found growing around the heads of small streams and it has been found at some sites where there is a dense covering of *Astelia fragrans* or kiokio (*Blechnum* sp. 1). However, it is very difficult to locate in areas of dense ground cover and may be more common than is thought in such situations. Site 23 is unusual as the *Dactylanthus* plants grow on the roots of the native understorey trees in a radiata pine (*Pinus radiata* D.Don) plantation. *Dactylanthus* is likely to have colonised this site from seeds remaining in the soil after the native forest was cleared or from seeds dispersed from the adjacent native forest.

Table 3: *The main ground cover categories and % canopy cover at 23* Dactylanthus *sites.*

Site No.	Canopy %	Ground cover %				
		Higher plants	Bryophytes	Litter	Soil	Rock
2	70	30	0	60	5	5
6	60	40	10	50	0	0
8	80	5	0	90	5	0
9	80	5	2	93	0	0
11	85	10	1	84	5	0
12	80	30	5	65	0	0
13	70	20	15	65	0	0
14	90	50	15	25	10	0
17	85	5	0	80	15	0
18	80	20	10	70	0	0
19	80	10	10	80	0	0
21	75	5	0	95	0	0
22	80	60	0	40	0	0
23	90	10	5	85	0	0
24	80	10	0	60	30	0
26	75	70	10	20	0	0
28	70	50	10	40	0	0
29	85	10	5	85	0	0
31	75	30	15	50	5	0
34	70	55	10	35	0	0
35	85	5	15	80	0	0
36	50	5	20	25	0	50
37	70	10	5	70	15	0
Mean	77	24	7	63	4	2

Phenology

Flower buds are usually evident from December until May and flowering occurs from late summer to late autumn. At site 6 flowering was recorded from late February to mid May with the peak in mid March to mid April, varying slightly from year to year (Fig. 3). Some unseasonal flowering can occur and a total of seven male inflorescences were recorded in late May, June, and August 1991 at this site, but buds which failed to produce inflorescences by mid May were usually found to be rotten. The flowering observed at 20 other central North Island sites was predominantly in the months of March and April. A few inflorescences were open in late February at site 36 and at site 22 some inflorescences were already finished by late February indicating that flowering probably started in early February. At the most southern location, site 37, one inflorescence was reported in mid December 1992 and by late February 1993 there were 13 male inflorescences under one exclosure (J. Barkla, *pers. comm.*). On Little Barrier Island flowering did not start until late March in 1992.

There is considerable variation from year to year in the number of inflorescences and in the proportion of male and female inflorescences produced by a clump of plants (Table 4). This variation however, is not always typical of the whole population. The trends in annual variation for the male inflorescences under 14 exclosures were similar to those for the single clump but the number of male inflorescences were consistently greater than the number of female inflorescences. Most, but not all, mature plants produced some flowers every year.

Reproductive Biology

Dactylanthus plants produce flowers aggregated in relatively robust cup-shaped inflorescences 2-4 cm in diameter surrounded by an involucre of scale leaves (Fig. 2). The scale leaves are normally dull purplish to yellow-brown or grey-brown but sometimes greenish and occasionally bright yellow or red (Ecroyd, 1993). The average female inflorescence (Fig. 4) was found to consist of 20 spadices with 183 flowers on each spadix. Male inflorescences have fewer flowers per spadix. At all the sites visited, except for site 4, there have been many more male inflorescences than female. Only one plant, a female, has been found at site 4. At site 6 between 1989 and 1995 the average ratio of male inflorescences to female was approximately 5:1.

Most of the *Dactylanthus* inflorescences contained flowers of only one sex but there have been exceptions. Two inflorescences with female
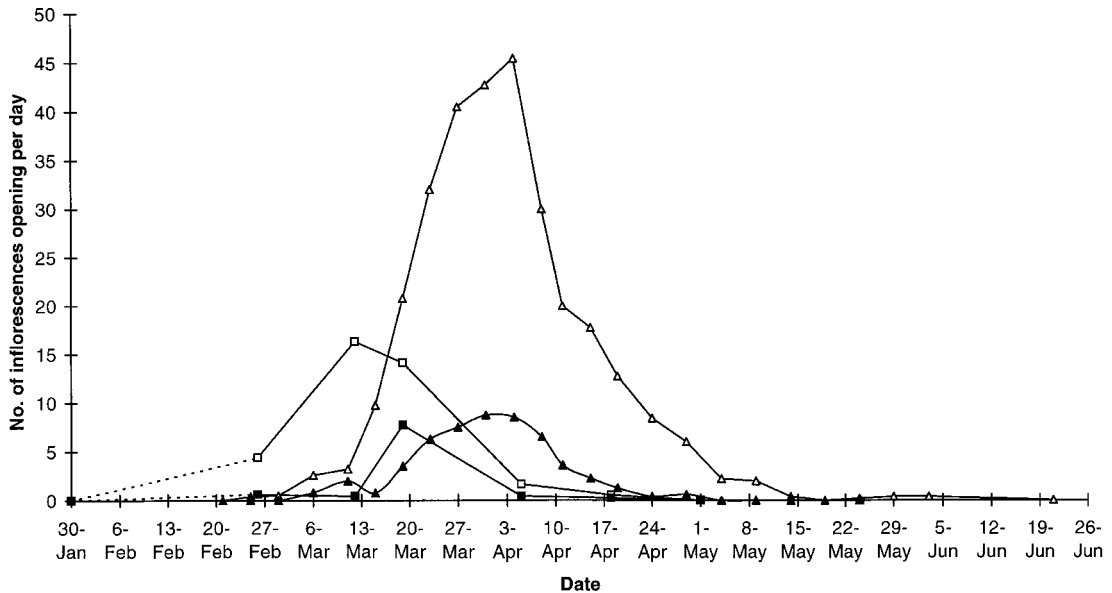
Figure 3: *Flowering of* Dactylanthus *under 26 exclosures at site 6 in 1990 (males - open square, females - solid square) and 1991 (males - open triangle, females - solid triangle).*

Table 4: *Production of inflorescences by protected plants at site 6, 1989-1995.*

Year	Under 1 exclosure			Under 13 other exclosures		
	Male infl.	Female infl.	% Male	Male infl.	Female infl.	% Male
1989	3	20	13	-	-	-
1990	10	32	24	284	47	86
1991	68	43	61	526	104	83
1992	39	10	80	410	32	93
1993	87	12	88	404	67	86
1994	35	5	88	209	14	94
1995	44	9	83	225	71	76
Mean	41	19	62	343	56	86

flowers on the lower third of the spadices and male on the upper two thirds have been found out of more than 6800 inflorescences seen at site 6. A careful inspection through a stereo-microscope of spadices from these mixed sex inflorescences confirmed that the flowers of both sexes were fully formed (Fig. 5). No seed was produced by the female flowers in these inflorescences as the remaining spadices rotted soon after flowering.

Two exclosures contained clumps in which inflorescences of only one sex were produced for several years after which inflorescences of the opposite sex were found in the same places. These could have been single plants changing sex or two plants growing in close proximity with one of them

flowering for several years and then ceasing as the other plant started to flower.

Pollination and browsing
Each male inflorescence remains open and produces nectar for about 13 days before starting to decay. They produce an abundance of cohesive pollen. The female inflorescence also produces nectar for about 13 days but the quantity is less than that produced by the male inflorescences (Fig. 6). If pollinated, the inflorescence then gradually matures with the spadices elongating and the fruits ripening over the next six months. Some of the female infructescences were still firmly connected by live tissue to the plant in November, about eight months after pollination.

Figure 4: *A fully open* Dactylanthus *inflorescence with the dark female flowers surrounded by floral bracts.*
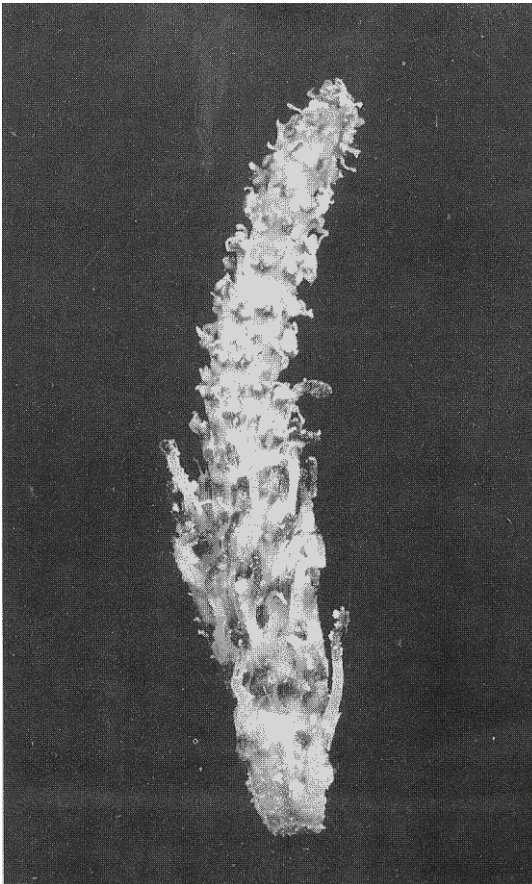

Figure 5: *A spadix with male flowers above and female flowers below.*

Up to 1.6 ml of nectar was found in one male inflorescence and the average nectar production for the male inflorescences was 0.5 ml per day for ten days (Ecroyd, 1996). Statistical analysis to compare the nectar flow during the day with the flow during the night, using a paired *t*-test, showed they are not statistically different (t = -0.5, 3 d.f.) (Fig. 6). The nectar has been described as having a cloyingly sweet fragrance, but with a slightly fatty backnote. A detailed composition of the steam-volatile fraction of *Dactylanthus* nectar from the inflorescences of male plants is given in Ecroyd *et al.* (1995). Squalene is a major constituent although the inflorescences from male plants sampled contained approximately twice the amount of squalene as that detected in the inflorescences of female plants. The nectar also contained sugars, principally sucrose, with some fructose and a trace of glucose.

The small 360° Malaise trap was the most successful system used for catching insects near the flowers and a summary of the insect species caught in 1990 and 1991 is presented in Table 5. The introduced common wasp (*Vespula vulgaris*) was the most abundant insect visitor and large numbers could be found at the flowers during the day and at night from late March to the end of April. Many of the inflorescences which were frequently visited by these wasps were damaged and had bracts partially eaten. A few individuals of the German wasp (*V. germanicus*) were found in the flowers in 1990 but were absent in 1991. The fly *Allophylopsis scutellata*, and the beetles *Saphobius* sp. and *Peristoreus trilobus* were also common visitors. The flies *Silvicola dubia* and *Drosophila immigrans* Sturtevant were reared from senescent inflorescences. In general, the Coleoptera and Diptera (beetles and flies) were associated with the older, senescent inflorescences, while the Hymenoptera (ants and wasps) were found in flowers in good condition and holding quantities of nectar. All insects collected directly from the flowers had very small quantities of pollen adhering to their bodies, with the largest amount being carried by the common wasps. Except for the insects associated with the senescent flowers, there was no strong association of any native insect with the flowering of *Dactylanthus*, even at sites where wasps were not seen.

Of the 52 tracking papers placed near inflorescences, 14 recorded mice, eight recorded ship rats, 13 recorded wetas (Stenopelmatidae), and 37 recorded other unidentified insects, but it was not known whether any of these recorded animals visited the *Dactylanthus* flowers or were just close to them. There was no sign of geckos visiting the inflorescences.
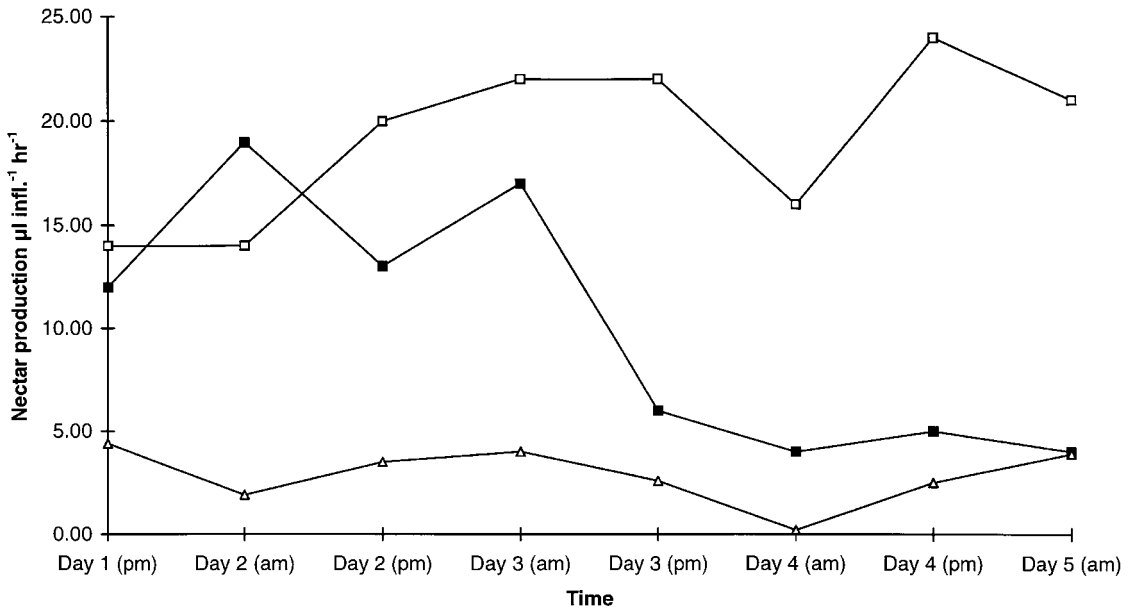
Figure 6: *Nectar flow from young male (open square), mature male (solid square) and female (triangle)* Dactylanthus *inflorescences measured morning and evening over five days.*

Table 5: *Insects frequently occurring in traps near* Dactylanthus *inflorescences at site 6 in 1990 and 1991.*

| | | Insects caught in small 360° Malaise trap in 1991 | | | | | | | Other Traps | |
	March 26	2	4	5	April 8	15	19	24	May 19		Total
Coleoptera											
Hydrophilidae (two undet. spp.)				1						9	10
Pactola fusicornis Broun	1				2						3
Peristoreus trolobus (Pascoe)		5	1	10	6	3	3	1	9	2	40
Saphobius sp.										14	14
Staphylinidae (three undet. spp.)							1			6	7
Diptera											
Allophyllopsis scutellata Hutton		2		3	4	3	3		1	8	24
Calliphoridae spp.		2			3	2				1	8
Silvicola dubia (Marquart)	1	1		1		4	4	4	2	7	24
Hymenoptera											
Formicidae (undetermined)	5	2	5		1					3	16
Vespula germanicus (F.)										3	3
Vespula vulgaris (L.)	1	13	8	1	9	18	22	3		64	139

Dactylanthus inflorescences did not strongly reflect ultraviolet light but they were infra-red reflective on VHS video film taken using infra-red lighting and an IR sensitive camera, with the reflection coming mostly from the pollen.

The first video tapes of flowering plants at site 12 in early March 1992, showed possums and ship rats visiting the *Dactylanthus* plants, the possums browsing any accessible inflorescences but the rats appearing to consume only nectar, leaving the flowers relatively intact (Table 6). Tapes recorded on Little Barrier Island later that month showed kiore (*Rattus exulans*) browsing and completely destroying inflorescences before they had fully opened. Reports were later received that all the inflorescences monitored on Little Barrier Island in

Table 6: *Animal visits to* Dactylanthus *flowers recorded by video monitoring at 14 sites between March 1992 and March 1995. The mean number of visits per night was calculated using only sites within the known range of these animals: kiore only at site 1, possums, ship rats and mice only at North Island sites, and bats at sites 1, 10, 11, 12, and 22 (King, 1990; Molloy, 1995).*

Site No.	No. of nights monitored	No. of visits to flowering plants by:					
		Possum	Ship rat	Kiore	Bat	Mouse	Birds
1	8			12			
6	1	1					
10	4	1	25		2		
11	11	4	25		130		
12	5	4	5		15		
13	3	1					
18	4	7	3				
19	2	5					
22	1						
25	6	12	5				
26	2	2					
30	4	1				1	
31	2	2	27				1
33	2						
Mean no. of visits night^{-1}		0.85	1.91	1.50	5.07	0.02	0.02

1992 and 1993 were destroyed before fully opening (S. Scarborough and C. Smuts-Kennedy, *pers. comm.*; DoC, Little Barrier Island, N.Z.). No other animals were observed visiting the *Dactylanthus* inflorescences on Little Barrier Island. However, in June 1991 one female plant at this site had been observed with good seed set on 16 infructescences and another plant had a single infructescence with fruits on three remaining spadices (Table 7).

In April 1992 further video recording was carried out at site 11 to check the behaviour of ship rats at the small clump of flowering plants chosen for observation. Fine 12 mm mesh which had been covering it and preventing access by rats to the flowers was replaced with 50 mm mesh wire netting. Over one night ship rats were recorded visiting the flowers 12 times but when a ship rat was not in the immediate vicinity a short-tailed bat appeared, entered the exclosure protecting the *Dactylanthus* from possums and fed from the inflorescences. There were 47 visits to inflorescences at this site by short-tailed bats in this one night. The next morning the inflorescences had no nectar remaining, virtually all the pollen was gone from the flowers with much of it scattered on the ground and the floral bracts were slightly damaged (Fig. 7). Pollen was also scattered over the only female inflorescence. The plants were covered again with the fine mesh and a few months later the female inflorescence was observed with abundant seed set.

In 20 nights of monitoring flowering *Dactylanthus* plants at site 10, 11 and 12, short-

Figure 7: *Three male inflorescences before (upper) and after (lower) 12 visits by ship rats and 47 visits by short-tailed bats during a single night.*

Table 7: *The number of live and dead* Dactylanthus *clumps, unbrowsed inflorescences (not protected from possums) and presence of possum sign recorded during single visits to 27 sites.*

Site No.	No. of live clumps	No. of dead clumps	No. of unbrowsed inflorescences	Presence (+) or absence (-) of possum sign
1	2	30	17	-
2	65	39	0	+
3	4	2	0	+
4	1	1	0	+
5	0	12	0	+
7	0	5	0	+
8	82	25	3	+
9	18	6	0	+
12	75	26	6	+
13	55	29	0	+
14	111	13	0	+
15	60	10	0	+
16	5	3	0	+
17	54	16	0	+
20	23	30	0	+
21	10	3	0	-
24	54	21	0	+
26	10	4	0	+
27	15	65	0	+
29	5	3	0	+
30	2	2	0	+
31	7	9	0	+
32	1	0	0	+
33	3	1	0	+
34	3	2	0	-
35	50	10	0	+
36	4	10	0	+
Total	719	377	26	

tailed bats were recorded on nine nights (Table 6). There were an average of 16 visits to the inflorescences on each of these nine nights. Other evidence that the short-tailed bat is an important pollinator of *Dactylanthus* is provided by photographs which show pollen covering the bat's face (Ecroyd, 1993), the presence of pollen on the stigmas after bats have visited and subsequent seed set on inflorescences.

Ship rats were also frequent visitors to *Dactylanthus* inflorescences, with 90 visits recorded over 21 nights, but their impact on the flowers is less clear. Abundant seed set has been observed on female plants they have visited. However, video monitoring has shown that they sometimes destroy the inflorescences. They left chewed-off spadices from female inflorescences scattered over the ground at site 10 and similar damage was noted under one 50 mm mesh exclosure at site 35.

A mouse was filmed visiting the inflorescences on one occasion and appeared to take only nectar,

leaving the inflorescence undamaged. A mouse also visited site 11 one night but a possum had browsed all the inflorescences and the mouse was attracted to other food sources nearby. The only bird recorded near the inflorescences was a North Island robin (*Petroica australis longipes* (Lesson)) which very briefly pecked at the inflorescences, probably searching for insects. Although lizards were present at some of the monitored sites none were recorded on video.

Fruits have been found on plants protected from possums by wire mesh exclosures at most sites visited. The infructescences should remain relatively conspicuous for at least a year, but 40 North Island *Dactylanthus* sites have been visited over the last five years and only about 20 infructescences have been found on unprotected plants at sites with no possum control. Evidence of possums, including faecal pellets, scratching, and bite marks, was found around unprotected plants at most sites except site 1 (Little Barrier Island) and sites where possum

numbers had recently been reduced, for example sites 21 and 34 (Table 7). The numerous broken inflorescences were browsed in a consistent manner, with all the spadices removed. Video film of possums browsing *Dactylanthus* inflorescences and subsequent inspection of the damaged inflorescences have shown that possums consistently browse them in this manner (Fig. 8). On average, there was nearly one possum visit per night for the 47 nights of video monitoring at North Island sites (Table 6). *Dactylanthus* inflorescences, which are attractive to possums while in bud and then for the *c*. 13 days of flowering, are very unlikely to escape browsing if possums are in the area. Plants under exclosures constructed of 50 mm mesh netting which allowed rats and mice access to the flowers, but which excluded possums, showed none of the typical possum browsing damage.

It is estimated from the flowering of plants at site 6 and from observations at several other North Island sites, that less than 1% of inflorescences on unprotected plants at North Island sites escape possum damage (Ecroyd, 1996). Monitoring with video has also shown that possums will sometimes dig for the newly emerging flower shoots and in the process may damage the host root and the *Dactylanthus* tuber.

Since 1989, plants have been illegally dug up and removed, presumably for the wood roses, at four of the 31 sites where plants were protected with exclosures. An alternative to using exclosures for protection is to reduce the numbers of possums. At site 9 possums were reduced to very low numbers in

Figure 8: Dactylanthus *inflorescences with their spadices removed by possum browsing.*

June 1992 by aerial and ground application of the poison 1080. Assessment of bait acceptance within the 111 700 ha poisoned area indicated a reduction of possums by approximately 87% (G.D. Butcher, *pers. comm.*; Waikato Regional Council, Hamilton, N.Z.). The reduction was effective for the 1993 flowering season, as a full crop of fruit was observed on 26 clumps, and no possum faecal pellets were found. However, in the following flowering season all the inflorescences were destroyed and fresh possum faecal pellets were noted. Monitoring 14 clumps at site 6 over four flowering seasons, when cyanide, pindone and traps were used for possum control, showed that over 90% of the *Dactylanthus* inflorescences were still browsed with 16 unbrowsed inflorescences found in 1991, 14 in 1992, nine in 1993 and only four in 1994. In 1995, when 1080 and Talon[TM] (brodifacoum) were used in bait stations from 27 February until 10 April, 202 unbrowsed inflorescences were found. None of the possum repellents proved effective at protecting the inflorescences from browsing.

Fresh rooting by pigs (*Sus scrofa*) was noted at sites 6, 12 and 16 but there was no sign of associated damage to the *Dactylanthus* plants, although exclosures were sometimes moved or damaged.

Fruit development and dispersal

The small nut-like *Dactylanthus* fruits take at least six months to mature. When first fully formed they have a thin fleshy ectocarp layer over a woody, much-hardened endocarp, enclosing a single seed. Within a few months the ectocarp dries out. The fruit with the remains of the style attached is on average 2.3 mm long and 1.1 mm wide and without the ectocarp 1.5 mm long and 1.0 mm wide.

Fruits collected in August from site 6 were immature and consequently they dried out and shrivelled a few days after collection. Of 1622 fruits collected in November 1991 and sown in soil, 80% were sound when recovered in May 1995. However, out of 100 fruits which had been attached to an infructescence and had remained *in situ* for four years from flowering only two were sound. Most of the sound seeds had probably fallen off and were gradually becoming buried in the forest litter. Seven fruits were recovered 20 cm from a parent plant, none at 40 cm, nine at 60 cm and one at 80 cm. The fruits disperse small distances downhill, probably assisted by heavy rain, and eventually become buried in the soil. *Dactylanthus* plants have been found on the edge of small watercourses and close to lake margins where water could have dispersed the fruits. Nearly all sound *Dactylanthus* seeds, however, sank when placed in water (S. Holzapfel, *pers. comm.*; Waikato University, Hamilton, N.Z.).
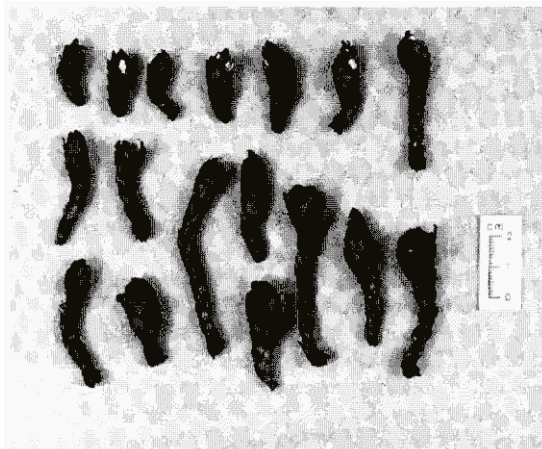
Seed germination

After two years there was no germination of any seeds sown on any of the media and many of the seeds had decayed because of attack by fungi or bacteria. However, out of 600 fruit stored under moist conditions for four years in a refrigerator 2.3% were splitting and some of the split fruits were still attached to spadices.

No *Dactylanthus* seedlings could be found attached to the roots of the kohuhu plants which were removed from the planter box in November 1992. However, two small *Dactylanthus* plants were found attached to the roots of two broadleaf plants removed at the same time. There were other root deformities which may have been young *Dactylanthus* plants but it was impossible to be certain without destroying the plants. The two broadleaf plants were replanted into a garden area and in September 1993 one was dug up and a *Dactylanthus* plant measuring 5 x 8 x 8 mm was removed. This *Dactylanthus* tuber was sectioned and its identification confirmed by SEM examination of the cell structure (Fig. 9). Some of the SEM sections showed fungal hyphae inside a few of the *Dactylanthus* cells. At least four other *Dactylanthus* seedlings had established on these host plants by May 1995.

Of 100 fruits recovered from the planter box four years after being sown, 62 were sound and of these six had split and one was starting to germinate.

No seedlings have been found at any of the five forest sites where seeds were sown. Of 164 fruits recovered from one of these sites in August 1995, 19% were germinating, 6% had split but were not visibly germinating, 15% were sound but had not split and 60% were hollow. Most of the germinating
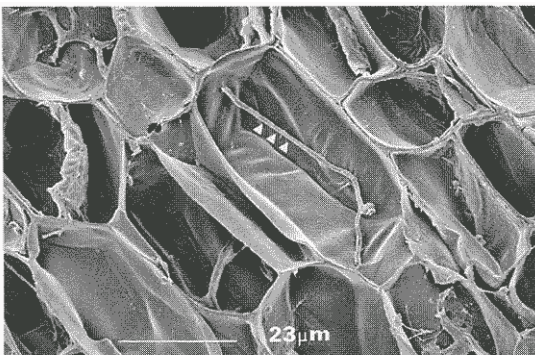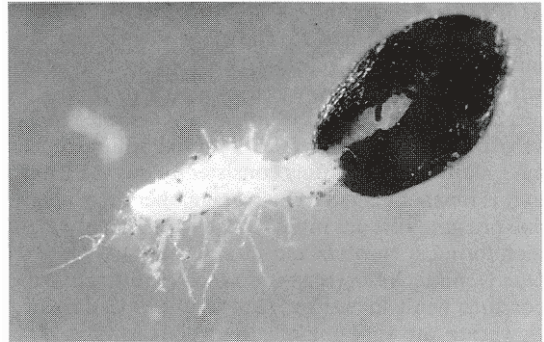
Figure 10: *A germinating* Dactylanthus *seed with long hairs growing from the 'radicle'.*

seeds were several centimetres away from host roots and some had exhausted their endosperm (S. Holzapfel, *pers. comm.*) without attaching to a host. Hairs or anchorage tubules (Shivamurthy, Arekal and Swamy, 1981), sometimes branched, and up to 2.2 mm long, were noticed growing from the emerging 'radicle' and ramifying through the soil (Fig. 10). One radicle 1.9 mm long, was growing towards a young root tip and its hairs appeared to touch the root just behind the growing tip.

Population trends, growth rates and life span

From information collected at 27 sites there was, on average, approximately one dead clump of *Dactylanthus* for every two live clumps (Table 7). While this high proportion could be the result of dead plants remaining intact and recognisable for many years, it is considered more likely to be an indication of a species in decline. At site 6, where observations of 67 *Dactylanthus* clumps have been made since 1989, 21 clumps have died during this period giving a half-life of only 8.5 years. Most of these clumps died as a result of their host's death, a few died of unknown causes and one clump was dug up and removed by a wood rose collector. There was a high proportion of dead *Dactylanthus* plants at several sites, such as site 27, where the host species were at the end of their life span and were being replaced by other non-host species.

The diameters of the *Dactylanthus* tubers measured at site 23 were up to 24 cm in 1994 and assuming that they became established soon after the site was cleared for planting in 1974 the average diameter growth rate of the larger plants would be approximately 1.2 cm per year.

Up to 30 growth rings have been counted on *Dactylanthus* host roots and assuming these rings are

Figure 9: *SEM photo of the cell structure of a* Dactylanthus *seedling cultivated from seed. Note the fungal hypha (indicated by arrows) inside the central cell.*

annual and that the *Dactylanthus* seedling established on the root when it was very young (Moore, 1940), then *Dactylanthus* plants can live for at least 30 years. The maximum life span of *Dactylanthus* is dependent on the life span of the host species which in many cases would greatly exceed 30 years, however, the host may be old when the *Dactylanthus* attaches and the host may live longer than the individual host root the *Dactylanthus* is on. *Dactylanthus* tubers have been found measuring up to 50 cm diameter but it is difficult to be certain that they are only one plant.

Pests and Diseases

Hyphae of the root-rot fungus *Armillaria novae-zelandiae* (Stevenson) Herink were extensive in four out of eight collections from recently dead *Dactylanthus* plants or their host roots and may have contributed to their death by killing either the *Dactylanthus* tuber or the host root. The fungus was extensive in one *Dactylanthus* specimen which had been alive less than two months previously, suggesting that it contributed to its demise. Another fungus, a species of *Cephalosporiopsis*, not regarded as pathogenic, and abundant bacteria, were isolated from a rotting area of an otherwise healthy plant.

Discussion

Neither the ecological range of the host trees nor the dispersal methods of *Dactylanthus* explain adequately its discontinuous distribution (Moore, 1940). The current distribution can, however, be explained as scattered populations of a previously much more common and widespread species.

It is suggested that *Dactylanthus* flowers are adapted for pollination by short-tailed bats. A larger species of short-tailed bat (*Mystacina robusta*) now thought to be extinct (Daniel, 1990) could have also been a pollinator. The short-tailed bats and *Dactylanthus* have declined in numbers and distribution since the arrival of man, rats and possums in New Zealand. Early irruptions of the kiore could have browsed the *Dactylanthus* flowers as they did on Little Barrier Island, and through competition, and possibly predation, they would have caused a decline in the abundance of its pollinator, the short-tailed bat, which was much more common and widespread 1000 or more years ago (Daniel, 1990; Worthy and Holdaway, 1994). For two cryptic species there is a remarkable similarity between the distribution of the short-tailed bat and *Dactylanthus*. Records from the last 150 years indicate that both species were on Little Barrier Island, near Omahuta Forest, Coromandel

Peninsula, East Cape, scattered through the central North Island, in the Tararua Ranges near Wellington and in north-west Nelson (Molloy, 1995; Ecroyd, 1995, 1996). However, less than a hundred years ago short-tailed bats were also in the southern part of the South Island and on Stewart Island and are still on nearby Codfish Island (Daniel and Williams, 1984) while there are only pollen records of *Dactylanthus* from these parts of New Zealand (Mildenhall and Crosbie, 1979).

The abundance and distribution of *Dactylanthus* must also have diminished as a consequence of forest clearance by firstly Maori and then European settlers (Atkinson and Cameron, 1993) and the impact of further introduced land mammals, particularly the possum and ship rat. Wood rose collection past and present, is another factor contributing to the decline of populations in some areas.

The common hosts listed by Cheeseman (1914) and Moore (1940) and the hosts identified during this study (Ecroyd, 1995) have all been shrub hardwoods characteristic of secondary conifer-broadleaved forest and its forerunners. Root parasites generally show little specialisation with regard to hosts (Kuijt, 1969), but it would be of interest if a survey of the host species represented in the wood rose collections confirmed that conifers were hosts of *Dactylanthus*.

Dactylanthus has a long flowering period (Moore, 1940) with the peak of flowering usually in March or April (Cheeseman, 1920). Flowering was recorded for up to 11 weeks, starting from late February, at one site. Moore reported a similar flowering season with flowers collected on 14 January 1934 on Mt Pirongia and at the end of May of the same year at Huia. As could be expected for an autumn flowering species, *Dactylanthus* seems to flower slightly later at warmer lowland sites such as Little Barrier Island, than at colder higher altitude sites.

There is some controversy in the literature as to whether *Dactylanthus* plants are dioecious or monoecious. Hooker (1859) mentions female plants implying that the species is dioecious but Cheeseman (1920) states that

"as the result of the examination of very numerous specimens Mr. Townson has definitely proved that the mature plant is monoecious".

Hill (1926) and Moore (1940) who also examined numerous specimens found no evidence to support Cheeseman's statement and concluded that the species is dioecious. Our data suggests that *Dactylanthus* is usually but not strictly dioecious and spadices with both sexes present as illustrated by

Cheeseman (1914) can very occasionally occur (Fig. 5). Modern DNA techniques may be useful to distinguish individual plants, enabling plants to be sexed and the ratio of 'male' to 'female' plants to be calculated.

With robust, dull-coloured inflorescences producing copious quantities of sweet, strongly scented nectar over many weeks, *Dactylanthus* flowers are well adapted to attract the short-tailed bat. This bat, with its agility on the ground, and ability to fly rapidly between sites many kilometres apart (Daniel, 1976), in return would provide a very effective means of cross pollination, assisting gene flow between widely dispersed clumps of *Dactylanthus*.

The quantity of nectar produced by the *Dactylanthus* inflorescences is in the range reported for other bat-pollinated flowers (Scogin, 1980; Opler, 1983) and is close to the amount of honey water (*c*. 1 ml) short-tailed bats are reported to consume per feeding bout (B. Lloyd, *pers. comm*.; DoC, Wellington, N.Z.). It is greater than the amount generally reported for insects or birds (Opler, 1983; Craig and Stewart, 1988). Bats were the native animal most frequently recorded visiting the flowers (Tables 5 and 6) and there was no evidence of pollination by lizards or birds.

There are similarities between the scent composition of *Dactylanthus* nectar (Ecroyd *et al*., 1995) and that of other bat-pollinated flowers (Kaiser and Tollsten, 1995; Knudsen and Tollsten, 1995). Squalene, one of the main volatile chemicals found in the nectar and also found in the scent mark of cotton-top tamarins (*Saguinus oedipus oedipus* L.) (Belcher *et al*., 1988), could be one of the principal chemicals attracting the short-tailed bats. The lipid components in the nectar, a chemical group some bats can readily smell (Schmidt, 1987), could provide the pollinators (and the browsing animals) with essential fatty acids (Baker and Baker, 1982) in addition to the sucrose, fructose and glucose present.

Dactylanthus does not, however, fit all the characteristics typical of the bat-pollinated syndrome, or chiropterophily (Heithaus, 1982; Wyatt, 1983). The flowers remain open for 10-14 days with nectar continually present, not just at night, and all other bat-pollinated species reported in the literature flower well above ground (Baker, 1961), whereas *Dactylanthus* flowers at ground level. However, the short-tailed bat is unusual in the amount of time it spends feeding on the ground (Daniel, 1979) and flowers of a given 'syndrome' often lack one or more of the expected features (Opler, 1983).

Eighty million years of isolation have allowed the evolution of a distinctive biota in New Zealand (Daugherty, Gibbs and Hitchmough, 1993; Towns and Ballantine, 1993). For example, in the absence of terrestrial mammalian predators such as rats and possums, the short-tailed bat has become well adapted to feeding on the ground and has evolved a mutually beneficial relationship with *Dactylanthus*, a plant which flowers at ground level. This specialised pollination system is even more unusual considering New Zealand's depauperate pollinator fauna and the constraints this has imposed on the evolution of the flora (Webb and Kelly, 1993).

Unfortunately, today there are probably only a few sites where the short-tailed bats and *Dactylanthus* still coexist. At the sites where bats are now absent the flowers which survive browsing will have to depend on insects, rats, mice or other animals for pollination. Insects are likely to pollinate only a very small percentage of the flowers. Rats may be effective pollinators when they do not destroy the female inflorescences. Mice could pollinate the flowers but they are not likely to be common in native forest, preferring disturbed habitats such as road edges (Murphy and Pickard, 1990). To maintain populations of *Dactylanthus* in areas where there are no longer short-tailed bats, ship rats or mice, artificial pollination may be necessary.

This study shows that possums are the most serious threat to the long term survival of *Dactylanthus* in the North Island. With their acute sense of smell they can easily find the strongly scented inflorescences regardless of how well hidden they are on the forest floor. Some current *Dactylanthus* sites are, however, near areas where possums were liberated many years ago. For example, possums were liberated near sites 3, 16, 22, 23, 28, 33, and 35 between 1902 and 1929 (Pracy, 1974) suggesting that there is no strong relationship between the areas where *Dactylanthus* has become extinct and the early liberation points of possums. Other factors such as the population density of possums or the long life span of *Dactylanthus* plants and long seed dormancy period, may be important to its survival. Only a very low percentage germination of *Dactylanthus* seeds has been observed over five years, and with its hard, woody endocarp the fruit is well adapted to survive in the soil for many years. In the absence of browsing animals there is the potential for a large seed bank to accumulate in the soil.

Although exclosures have proved to be an effective way of protecting the plants from possums they make it easier for people to locate them unless they are very well camouflaged. Trapping, cyanide and pindone, used over small areas for limited time periods, are largely ineffective probably due to the

rapid reinvasion of the area by possums (Clout and Efford, 1984), increasing numbers of trap-shy or cyanide-shy animals, or ineffective poison. Some possums will survive even after eating 1 kg of double strength pindone bait (Eason *et al.,* 1993). The success of 1080 at site 9 was probably because of the large size of the area treated and the use of 1080 in bait stations close to the *Dactylanthus* site. Other factors in the success of 1080 and brodifacoum as evident at site 6 could have been the effectiveness of the poison, the placement of bait stations close to the *Dactylanthus* plants and the timing of the operation.

Kiore destroyed the *Dactylanthus* inflorescences on Little Barrier Island in 1992 and 1993 but there were *Dactylanthus* infructescences present with excellent seed set at the same site in 1991. The difference between the years may have been due to fluctuations in the kiore population (Atkinson and Moller, 1990). Ship rats have shown variation in behaviour from being pollinators to destroying the inflorescences and this could also be due to population levels or food shortages.

After pollination the fruit takes many months to mature fully and will remain attached to the infructescence for at least a year. The whole infructescence may be dispersed a short distance before the fruit becomes detached (Moore, 1940). Most *Dactylanthus* fruits would disperse no more than a metre or two aided only by gravity and water except on steep slopes. Occasional longer distance dispersal however, must have occurred. For instance *Dactylanthus* has widely recolonised the Taupo district after the region was devastated by volcanic eruptions 1800 years ago (Pullar and Birrell, 1973). Perhaps the fruit was at least occasionally dispersed by species of ground-feeding birds or lizards, now extinct or uncommon on the mainland. North Island brown kiwis (*Apteryx australis mantelli* Bartlett), for example, have been found to have a wide range of seeds in their gizzards (Reid, Ordish and Harrison, 1982).

Hill (1909) carried out unsuccessful experiments with the seed and seeds have been supplied to several highly skilled nurserymen with no reports of successful germination. Although *Dactylanthus* plants were successfully cultivated from seed for the first time during this study the precise mechanism by which germination and seedling establishment occurs remains a mystery. Kuijt (1969) suggests initiation of germination may be a response to a biochemical exudate produced by the host root and Arekal and Shivamurthy (1976) observed that *Balanophora* seed germinated when lodged near newly formed host rootlets. However, many of the germinating *Dactylanthus* seeds were not adjacent to host roots and clean seeds split after being stored for four years in a refrigerator. It is suggested that the *Dactylanthus* seeds split, start to germinate and produce long tubular hairs which can sense a host root. The radicle then grows towards the host root. Alternatively, the hairs on the 'radicle' of the germinating seed may be tubules which secrete a sticky substance and anchor the fruit to a host rootlet in the same way as that reported for two species of *Balanophora* (Arekal and Shivamurthy, 1976; Shivamurthy *et al.*, 1981).

The presence of fungal hyphae inside the cells of *Dactylanthus* seedlings and in the 'radicle' of the germinating seed (Moore, 1940) raises the possibility of fungal involvement in the germination and early attachment stage. The possibility of mycelia assisting with the germination of the related parasitic plant *Balanophora japonica* Makino was reported by Watanabe (1942).

Moore (1940) comments on the close resemblance between the 'radicle' and the processes from the basal sheaths of the peduncles. This resemblance has recently been investigated and Moore's findings are supported (S. Holzapfel, *pers. comm.*). These processes may be a means by which the *Dactylanthus* tuber can attach to new roots and eventually form new plants. If vegetative reproduction can readily occur this would explain the dense clusters of plants often found and further explain the persistence of *Dactylanthus* at sites which have been accessible to possums browsing for 90 years or more.

Dactylanthus plants are relatively long lived for their size and under good conditions can grow relatively vigorously with diameter increases of about 1.2 cm per year. The health of *Dactylanthus* is however, dependent on the health of the host tree and its root system and if the host tree or host root dies so will the *Dactylanthus* plant. There is a continuing downward population trend evidenced by the number of dead plants found exceeding that of live plants at many sites and the very low half-life at site 6. If *Dactylanthus* is to survive at some of these sites management of the forest structure to ensure an adequate population of host plants will be necessary.

Conclusions

Dactylanthus taylorii is one of the few New Zealand plant species adapted to pollination by the endangered short-tailed bat. Previously much more widespread in New Zealand, *Dactylanthus* is continuing to decline in population sizes and distribution. Contributing factors to this decline, which probably started about 1000 years ago with the introduction of the kiore and

humans, are habitat destruction and collection of wood roses as curios and ornaments. Today, however, browsing of the inflorescences by possums and to a lesser extent rats, is the most serious threat to its long term survival. Once established and in the absence of destructive agents, *Dactylanthus* is well adapted to long-term survival with its relatively long potential lifespan and ability to form large seed banks in the soil. Its health and survival are, however, completely dependent on the host plant. Effective pollination could be a problem at sites where short-tailed bats are now extinct and ship rats absent. In the absence of an effective pollinator and without protection from possums, *Dactylanthus* is unlikely to survive long term.

Acknowledgements

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