Tuber Development of Three Orchid Species at Hokio, West of Levin

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INTRODUCTION

About forty years ago I undertook to make regular observations of tuber development of *Acianthus sinclairii*, *Corybas trilobus* and *Pterostylis alobula,* at that time growing in very large numbers in forest and scrub of the Horowhenua dune system at Hokio (NZMS 1 N152/728064). I had grown *Pterostylis banksii* in cultivation in the early 1930s and had observed root-like structures creeping over the soil surface. These subsequently produced new tubers at their ends. I was curious to find out how other terrestrial orchids spread vegetatively. Between June 1953 and June 1954 I made approximately monthly collections of the three species. All parts of each specimen were measured and sketched and notes taken for each collection.

The collecting site was on a stabilised dune ridge where the orchids grew mainly under kanuka scrub (*Kunzea ericoides*). Lower scrub, mainly *Cyathodes juniperina*, gave protection from side winds while the moss *Ptychomnion aciculare* and kanuka leaf litter formed a moisture-retaining ground cover. Later in the season some specimens were collected from nearby dune forest but the presence of many tree roots made it more difficult to separate the underground parts of the orchids.

SUMMARY OF OBSERVATIONS

1. The orchids *Acianthus sinclairii*, *Corybas trilobus* and *Pterostylis alobula* replace the current season's tuber with a new tuber. This generally starts to grow at the beginning of the season with its shoot, on top, developing at the same time. The habitat in summer is bone dry, but tubers continue to develop their shoots ready for next season's growth. The current tuber does not shrivel until the end of the season, by which time the replacement tuber is fully grown and, in favourable seasons, may be larger than the previous one.

   The new tuber forms just above the old one, either at the end of a short connective dropper or sessile at the base of the plant stem. None of the tubers grow directly out of the old one. Where the dropper is long, it places the new tuber lower than the old one. This tuber is found in the sand or soil well below the moss.

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2. Dispersal tubers: every plant, unless very undersized, grows one or more runners, each of which grows a small tuber at its tip. The runners travel more or less horizontally through the moss, often quite near the surface. At a very early stage, each runner has a pointed tip. Soon a swelling starts just behind this tip. This is the start of the new tuber which later develops mostly on its underside, weighting the tuber which is thus pulled downwards into the sand or soil below the moss. From an early stage of their growth, many of these tubers have a tiny shoot on top, developing for the following season's above-ground growth. Being dispersed on the ends of runners, these tubers serve to create a colony of plants at a reasonable distance from the parent and have to build up reserves of nourishment before becoming mature themselves.

   Runners which produce dispersal tubers:

   Acianthus sinclairii: one, occasionally two (replacement tuber grows on a dropper, or occasionally it is sessile.)

   Corybas trilobus: generally one but occasionally two (replacement tuber grows on a dropper.)

   Pterostylis alobula: 2-4, unless the plant is very small.

3. Influence of flowering: In flowering or fruiting specimens there is some delay in the formation of dispersal tubers as a rule, but their growth is made up later.

TUBER DEVELOPMENT OF THE THREE SPECIES

Acianthus sinclairii

THE ANNUAL CYCLE

In March it was possible to find a very few plants. The tuber was of reasonable size. The runner was absent or very small at this time. The replacement tuber was not yet developing.

By early June some mature plants were flowering. Their runners were fairly long. The droppers were short or almost non-existent but new replacement tubers were all present, the largest one on a flowering plant being 3 x 4 mm. A very small juvenile plant had a very small replacement tuber but this had a shoot developing. None of the replacement tubers on other plants had a shoot.

By the end of June all specimens had a shoot on the replacement tuber and a long runner showed a hook, the beginning of a dispersal tuber at its tip.

In the middle of July any flowers had shrivelled and seed capsules developing were very small. One mature and two non-flowering plants had shoots on the new tubers 1 mm or 1.5 mm long. Though it was usual for each plant to have one runner, a non-flowering plant of reasonable size had a very small extra runner at ground surface level.

By mid-August there were well-developed unripe seed capsules on some plants. Replacement tubers of whatever size had white shoots. On non-flowering specimens the replacement tuber had almost attained the size of the current season's tuber though there was no sign of any development of a dispersal tuber on the runner. On the other hand, on flowering specimens very small tubers were commencing on the runners.

Near the end of September, specimens collected from the dune forest showed that in most cases the replacement tuber was larger than its forerunner, which by this time was beginning to shrivel. Again, it was a non-flowering plant which had a small runner at ground level as well as another lower down, and a small flowering specimen also had two runners. By this time nearly all had well grown dispersal tubers. The shoots at the top of the new tubers, so conspicuous on the August specimens from the dune scrub, were not seen in the September collection except for a tiny knob on one tip. The forest conditions seem to have had a different influence on the timing of each growth. In general the plants were larger than those of the dune scrub.

By the end of December the leaves of mature plants were very withered. On non-flowering plants the leaves were still green and firm, and the runners still continuing to grow. New shoots on tubers showed various stages of development, the largest being on non-flowering plants. Old tubers of flowering plants were by this time very much shrivelled. A non-flowering specimen had a shoot 1.7 cm long on the new replacement tuber, while the old tuber of the same plant showed no sign of withering. It was seen at this stage that the shoot was ensheathed by a bract, either at its base or part of the way along the shoot.

DETAILED OBSERVATIONS (Table 1)

15 July 1953

The stem of *Acianthus sinclairii* bulges slightly just below ground level, and has a collection of tiny root-points. On one specimen examined, one of these hairlike points has produced a true root tip. Otherwise, each plant has only one rootlet (secondary root), growing out from the base of the swollen sub-ground level portion of the plant, in an almost horizontal position. The old tuber is at the base of the vertical root-line, with the replacement tuber growing on a lateral a short distance above. It was noticed that in most instances, especially in mature plants, the connectives were fairly long, thus placing the new tuber (and its subsequent plant) in a position somewhat removed from its predecessor. In six of the seven specimens examined, the direction taken by the rootlet was the same as that indicated by the tip of the leaf.

Well developed non-flowering specimens were more advanced with the production of the new tuber than specimens flowering or recently flowered. A specimen which was more advanced with its flowering showed tuber development equal to that of the larger non-flowering specimens.

Table 1. Seasonal development of *Acianthus sinclairii* at Hokio, Horowhenua.

Date	Specimen condition	Flowering state	Total length (cm)	Root length (cm)	Rootlet length (cm)	New tuber dimensions (mm)	New tuber connective length (mm)	Old tuber dimensions (mm)	Old tuber connective length (mm)
15 vii 53	mature	flowers shrivelled	6.7	2.0	3.0	2 x 2.5	4	5 x 5	9
	mature	small capsules	8.8	2.1	3.0	4 x 4	1.5	6 x 5	1.5
	mature	small capsules	5.6	1.7	4.5	2 x 2	1.5	4 x 3	6
	mature	flower eaten off	5.0	2.3	2.5	2 x 3	1.5	5 x 4	10
	juvenile	non-flowering	5.1	2.5	2.9	4 x 3.5	8	7 x 5	12
	juvenile	non-flowering	4.9	2.4	5.0	4 x 3.5	3	4.5 x 4	5
	juvenile	non-flowering	4.3	1.5	1.5	1.5 x 1.5	1	2.5 x 3	1
17viii53	mature	unripe capsule	8.4	2.4	8.6	2 x 2.5	—	4 x 4	—
	mature	ripe capsule	10.3	2.6	0.2	—	—	5 x 4	—
	mature	unripe capsule	10.3	2.9	1.0	2 x 2	—	6 x 4	—
	mature	unripe capsule	9.7	2.7	3.5	2 x 3	—	5 x 4	—
	mature	non-flowering	4.1	2.2	8.2	3 x 3	—	3 x 3.5	—
20ix53	mature	flower eaten off	8.5	3.3	5.2	8 x 7	—	7 x 7	—
	mature	flower eaten off	8.5	3.0	6.0	8 x 6.5	—	7 x 6.5	—
	mature	non-flowering	5.0	2.5	1.8(+)	6 x 5.5	—	4 x 4	—
	mature	spent capsules	9.2	2.8	10.5	3 x 3	—	5 x 5	—
	mature	spent capsules	8.8	2.6	1.7, 0.6	2 x 2.5	—	5 x 5	—
	mature	aborted capsules	7.9	3.0	0.3, 0.2	5 x 4	—	4 x 3.5	—
31xii53	mature	flowered	6.0	2.2	4.5, 7.5, 1.2	4 x 4, 6 x 5.5	—	5.5 x 3	—
	mature	flowered	5.1	2	1.5(+)	5.5 x 5	—	5 x 3	—
	juvenile	non-flowering	5.7	4.1	2.5, 0.4	5 x 4.5	—	3.5 x 3	—
11iii54	mature	—	3.1	1.8	1.0	—	—	5 x 4.5	—
	juvenile	—	3.5	1.6	—	—	—	3.5 x 4	—
02vi54	mature	flowering	7.1	1.7	0.6, 1.2	1 x 1	—	4.5 x 4	—
	mature	flowering	8.5	1.2	2.8, 1.0	3 x 4	—	5 x 5	—
	mature	flowering	9.1	2.7	1.5	1.5 x 1.5	—	5 x 5	—
	mature	in bud	5.7	2.5	—	1 x 1	—	4 x 4	—
	mature	flower stem broken	4.7	2.7	5.9	2 x 2	—	4.5 x 4.5	—
	juvenile	non-flowering	4	2.4	—	1 x 0.5	—	2.5 x 2	—
	mature	in bud	4	1.8	0.2	2 x 2.5	—	3.5 x 4	—
20vi54	mature	flowering	7.7	2.9	1.8	2 x 1	—	4.5 x 4	—
	mature	flowering	6.0	3.0	0.4	1.5 x 0.5	—	5 x 4	—
	mature	flowering	7.0	1.9	5.4(+), 0.3	3 x 1	—	4.5 x 5	—

The old tubers at this stage (15/7/53) are somewhat larger than those of the *Pterostylis* examined at the same date, and the development of the new tuber is more advanced. On the three specimens of *Acianthus* where tuber development is most advanced, a small vertical shoot, approximately 1 mm long is growing out of the top of the new tuber. The surface of the old tuber is granular.

17 August 1953
All new tubers (except those on very immature specimens, and those on root-tips) show white shoots on top. One rootlet on a large specimen showed an obvious knob on the tip. Others showed slight thickening under magnification, though not obvious to the naked eye. Some rootlets on small flowerless specimens showed very slight thickening. When removing dirt from around the tubers, I noticed a dead skin between the two tubers.

20 September 1953
As supplies of flowered specimens were running low in the original locality, specimens were collected from an adjacent ridge covered with mixed dune forest. The orchid roots were mixed in a tangle of roots and compost and sand, all rather dry. Above soil level, rather dry moss propped the *Acianthus* leaves so that they appeared sessile. As the horizontal rootlets were rather lengthy, they were entangled with each other, and with other roots in the soil, making it difficult to trace each rootlet for its complete length. In a sod about 12 x 15 cm were all the plants described, also a few *Corybas trilobus*. Unfortunately the tips of some of the rootlets (showing small tubers) were separated from their plants of origin. Specimens 1, 2, and 3 all have lost the tips of their rootlets, so the two unattached rootlets could belong to two of these.

Specimens 1 and 2 had such well-developed basal tubers that it was difficult to decide which was the new, and which the old. In nearly all of the plants examined in the previous months, and the more obvious ones of this group, the old tuber lies in the direction of the point of the leaf. I am inclined to the opinion that specimens 1 and 2 follow this position also. The tubers of specimens 1 and 2 which I have assumed to be the old tubers have a slightly more transparent appearance than their companion tubers. The old tuber of specimen 3 also shows this slight transparency, as it is commencing to shrivel. In the other specimens examined, most still show the older tuber as the larger one. Some have as yet no tuber on the horizontal rootlets.

The tiny shoots noticed on the upper side of the new basal tuber of the August collection, and on the best specimens of the July collection, were not seen on the September specimens, except, perhaps, for the tiny knob on the top of No. 2's new tuber. Perhaps the drier and more fibrous soil in which September's specimens were growing could have an influence in discouraging sprouting.

The "skin", as noted next to the tubers of August specimens, was again noticed. It looks as if the new tuber changes its skin in the course of growth, as

flakes of adhering skin were noticed. The dry sand was clinging very tightly to the tubers, even after being soaked, complete removal of the sand was found to be impossible, thus making clear observations difficult.

31 December 1953

Flowering specimens, being better developed plants in the first place, have larger replacement tubers. Old tubers are now very much shrivelled, and the size of any side tubers has apparently attained the maximum. Side rootlets show lack of vitality and comparative flaccidity. Leaves fading badly. New shoots (on tubers) are in varying stages of development.

The leaf of the non-flowering specimen is still green and firm. Side roots are apparently still developing. The shoot on the new tuber has grown to a considerable length (1.7 cm). The old tuber is showing little discoloration and no withering.

Specimen 1, with a reasonably well developed shoot on its replacement tuber, shows that the tuber is in the sheath of a bract nearly as long as itself. Specimen 3, with a long shoot, shows a bract commencing (and finishing) halfway along its length. Its shoot is much stouter than any other part of the root system.

Corybas trilobus

The flowering times of this orchid range over a six-month period depending on latitude and altitude. In Horowhenua the range is four months, from June on the coastal dunes to September-October only a few kilometres inland and in the lower foothills, so it is unlikely that the timing of growth will be exactly the same everywhere. This account follows the behaviour of Hokio dune scrub specimens.

The distinction between the replacement tuber and the dispersal tuber is not so clear in this species, probably because the replacement tuber is normally borne on a short dropper which could be mistaken for a runner, although the dropper sometimes issues direct from the old tuber and generally turns downwards, at least at some stage of its development. The runner is more or less horizontal and the tuber on this grows more quickly than the one on the dropper though they finish more or less equal in size. The tubers of this orchid are always small even when fully grown.

THE ANNUAL CYCLE

In mid-May everything was underground but the tubers all had small shoots of varying lengths.

At the beginning of June, perhaps sometimes even earlier, there were some flowers still tipped forward with only the greenish galea showing at the top. Later the flower tipped back and the dark red labellum was stretched across the humped-up seed capsule. The leaves were small, as yet poorly developed and

hidden amongst the moss. There were no new tubers commencing. The leaves were just unfurling, having been rolled over from sides to middle, but there was plenty of underground development. Some leaves were barely emerging from their scale-bract above the tuber. Towards the end of June a flowering plant and all the juveniles were showing a slight thickening at the ends of their runners where dispersal tubers were beginning to form.

Runners developed in July, the upper usually quite long but the lower which appeared to be a dropper for a replacement tuber was quite short. The knobs at the tips of runners were recorded in June, 1954, but the previous season there was no sign of them at the equivalent time, so some seasons are more advanced than others.

Mid-August showed that mature plants which had flowered but had not developed seeds had a new dispersal tuber at the end of a runner and another tuber at the end of the dropper. Some new tubers had a tiny shoot. Mature plants which had set no seed had no sign of new tubers, though juveniles had two as stated above.

By late September all specimens, whether mature with ripe seeds or juveniles, had two new tubers, all about the same size. Exceptions to this were extremely small juveniles with no sign of new tubers.

At the beginning of November one mature plant had a new tuber on the runner and a swollen tip on the dropper, while a flowerless plant had a new tuber on a runner and a small replacement tuber just above the current season's tuber. It appears that replacement tubers of this species develop late in the season.

By the end of December the leaves of two medium specimens were thinning and fading. Runners were commencing to wither. Two new tubers each had small shoots on top. Most of January to April and probably much of May are underground periods. In March, however, though all are underground, all tubers have shoots of varying lengths.

FLOWERING TIMES

Hatch (1947, page 575) gives details of the flowering times of *Corybas trilobus* as follows:

At sea level, Auckland, early June;
At 400 ft on the Volcanic Plateau, early December;
At sea level in Stewart Island, from August to September.

In the Levin district I have recorded habitats and flowering times as follows (altitudes are approximate only):

a. Hokio Dune Scrub (10 m a.s.l.) June, July, August. On sand.
b. Ngawakahianee forest, Poroutawhao, (6 m) September. On older dune surrounded by extensive area of swamp land.
c. Papaitonga bush, "has flowered" - 26/10/47. Under trees on sandstone promontory, north side of Papaitonga Lake (36 m).

d. Totara forest NW of Ohau railway station, October. On river gravel (15 m).
e. By Ohau River bridge on Muhunoa East Road, "1 flower, 2 seeding", 13/10/62. In bush on river gravel (58 m).
f. North of the east end of Kimberley Road, October. In bush on river gravel (60 m).
g. North end of Forest Reserve, Tararua foothills, in bush (90 m) large leaves. No flowers seen.
h. Bush beside Tunnel Creek, near western end of Ohau Gorge (90 m). Large leaves but no flowers seen.

(It flowers in October in beech forest, Silverstream, Hutt Valley – A. P. Druce, *pers. comm.*.)

The variation of flowering times owing to differences of altitude and latitude could hardly be the reason for so much difference in the flowering times from such places as Hokio Dune Scrub, and lowland places a few miles inland, and the beech forest at Silverstream. There is not much difference in altitude or latitude between any of these habitats, so another reason is to be sought. A quicker seasonal warming up of the coastal soil offers a solution of the problem. Hatch's record of *C. trilobus* flowering in Auckland at sea level in early June seems to be added evidence that flowering time is related to the warming up of the soil to optimum temperature. This would occur earlier in the dune forest and scrub, Hokio, and in Auckland forests and scrub, than it would in other lowland and foothill habitats of Horowhenua, and in Silverstream.

TUBERS

E. D. Hatch (1947, p. 576) says "Each flowerless plant produces several terminal tubers on long root fibres". In my experience, the flowering plants produce just as many as the non-flowering plants. It is seldom that fewer than two new tubers are produced by any plant, of whatever size, except extremely undersized plants which produce one only. Very occasionally three new tubers are produced. I have no evidence that the circumstances of flowering or producing seed have any effect on the size or number of tubers; but flowering specimens are about one month later in forming their tubers.

The old tuber is replaced by a new one which erupts from the main root above the old tuber. The stalk may be very short. Often the stalk takes a downward plunge, thus finishing with the new tuber somewhat lower in the ground than the old tuber. The other new tuber is borne on a much longer stalk erupting from higher up the root and travelling for some distance in a roughly horizontal direction. Being near the surface it occasionally shows that it is affected by light, having a greenish tinge. Though the thickening near the tip of the rootlet is evenly distributed at first, further development of the new tuber is on the underside, and its weight seems to cause the rootlet to take a downward direction near the tip.

In several years after the collections were made, long dry seasons killed out most of the growth (*Cyathodes juniperina*, etc.). The wind was able to enter the damp hollow to dry it up. Most of the moss died and the orchid growth the following season was of poor quality, the majority of plants reverting to pre-flowering size, and there being fewer in number.

E.D. Hatch (1959) states "*Corybas trilobus* begins to flower at this time also, although the flowering plants are very tiny, and few in proportion to the size and numbers of the barren plants which appear later, and so is easily overlooked". I would be inclined to explain that this way - while all of the plants are very small, and many still hidden in moss, the more vigorous ones flower, even though leaf-development has not proceeded very far. These plants are seen because their flowers make them more conspicuous. While flowering, these plants do not increase the size of their leaves. After flowering, their leaves increase in size, and the flowerless plants, having nothing to take the strength from the leaves, come into view with larger leaves. In the mixed collections I have not noticed any indication that there is permanent retardation of leaf-size in flowering specimens as they make up the size later. In the sand country, where the season comes on with a rush before the leaves have had time to attain much size, the general average of leaf-size at maturity tends to be much smaller and less lobed than where the plant is in moister conditions and takes longer to come to flowering. Barren plants, wherever growing, greatly outnumber the flowering ones.

DETAILED OBSERVATIONS (Table 2)

June: Early flowering season:

a. Flowering specimens, many in early stages. Galea showing. (Later the flower tips back.) Leaves small and relatively undeveloped. (Hidden in moss, *Ptychomnion aciculare*.) No sign of new tubers. Two "roots".
b. Juvenile: Leaf only just unfurling. Each lobe rolled inwards from side to centre, very small as yet. Root development relatively good. Leaf green.
c. Another juvenile: Leaf green, but barely emergent from scale-bract.
d. Smaller flowering specimens show shorter second root. The lower root emerges on the same side as the scar on the tuber, then works around $^{3}/_{4}$ of the circumference of the root-stem, (by mid-August), then swings away at right angles from the main root.

20 June 1953

a. Flowering specimen: Tiny mucro at tip of each rootlet, but the thickening of an incipient knob on upper rootlet.
b. Juvenile (but well-developed): Tips of rootlets beginning to develop knobs.
c. Juvenile (small): Tip of upper rootlet shows slight thickening.

Table 2. Seasonal development of *Corybas trilobus* at Hokio, Horowhenua.

Date	Specimen condition	Flowering state	Total length	Root length	Rootlet length		Tuber dimensions (mm)	Connective length (mm)	New tubers
					Upper	Lower			
15 vii 53	mature	flower nipped off; remains of peduncle	6.2	3.1	9.4	2.1	6 x 5	3	—
	mature	flower fading	5.4	4.0	6.3	2.0	6 x 5	2	—
	mature	flower in prime	3.2	1.7	4.4	2.7	5 x 4.5	2	—
	mature	flower in prime	5.2	3.4	2.6	0.8	5 x 4	1.5	—
	immature	non-flowering	7.4	2.8	6.5	0.5	3 x 3	2.5	—
	immature	non-flowering	5.4	2.1	3.5	0.5	2 x 1.5	2	—
	mature	flower nipped off; remains of peduncle	4.4	2.4	5.3	0.8	4.5 x 4; 3 x 2	4	—
	immature	—	1.7	1.0	1.9	1.2	3 x 3	1	—
	immature	—	1.5	0.6	1.9	—	2 x 2.5	—	—
17viii53	mature	ripe capsule	11.0	2.3	7.7	2.4	6 x 4.5	4	0
	mature	unripe capsule	7.6	3.4	6.3	—	5.5 x 4.5	9	0
	mature	flower destroyed	3.0	2.3	4.8	2.2	4 x 4	—	2
	mature	no sign of flower	3.0	1.3	1.2	—	4 x 3	—	2
	mature	no sign of flower	4.1	2.3	8.0	1.2	4 x 3.5	1	2
	small	—	3.2	2.7	3.5	2.0	3 x 3	3	2
	small	—	3.4	2.2	2.9	—	3 x 3	1	2
20ix53	mature	ripe seeds	11.9	2.7	5.5	1.5	5 x 4	—	2
	mature	almost ripe seeds	9.5	3.7	1.8(+)	1.4	5 x 4	—	2
	well-grown	non-flowering	6.3	2.8	3.2	0.5	3 x 3	—	2
	small	non-flowering	8.0	6.7	1.5	0	3 x 2.5	—	1
	small	non-flowering	4.1	1.4	3.0	1.5	2 x 2	—	2
	small	non-flowering	3.7	3.0	1.3	<0.1	2 x 2	—	1
	very small	—	0.9	0.6	1.7	1.4	3.25 x ?	—	0
	medium	non-flowering	7.3	1.0	4.3	1.7	3 x 3	—	2
01xi53	mature	ripened capsule	10.0	1.4	3.4	3.0	4 x 3.5	—	1
	—	non-flowering	3.9	3.1	3.1	—	3 x 3	—	2
	—	non-flowering	6.0	4.3	3.4	—	3.5 x 3	—	1
	—	non-flowering	3.5	1.4	2.2	—	3 x 2.5	—	2
	—	non-flowering	3.4	1.3	3.0	1.1	3 x 2.5	—	2
31xii53	medium	—	8.0	3.7	4.3	4.5	3 x 2.5	6	2
	medium	flower nipped off; remains of peduncle	6.6	2.5	1.5(+)	0.7	4 x 3	2.5	1
	medium	—	8.5	4.3	2.2	0.7	3.5 x 3	3.5	1
02vi54	mature	early flowering	5.6	2.6	4.5	0.8	4 x 4	—	—
	juvenile	new leaf	2.0	1.0	2.7	1.2	3 x 3	—	—
	juvenile	new leaf	2.3	2.0	1.0	0.3	2.5 x 2	—	—
20vi54	mature	flowering	4.7	1.4	2.4	0.4	5 x 4	—	—
	mature	flowering	3.8	2.9	8.4	3.0	7 x 5	—	—
	mature	flowering	5.7	2.8	5.0	0.6	5 x 4	—	—
	mature	flowering	7.3	4.4	—	0.4	5 x 4	—	—
	juvenile	—	4.5	1.8	2.0	1.5	3 x 3	—	—
	juvenile	—	2.5	1.6	3.6	0.6	4 x 3	—	—

15 July 1953

Long-petioled specimens were growing in a very damp situation, in amongst *Ptychomnion aciculare*. They were spindly and flaccid, with comparatively small tubers.

All flowering specimens were growing in harder (drier?) conditions. The top of the root system is slightly swollen just below ground level with a generous sprinkling of "root-points" (scales? hairs?), these continuing more sparsely along the lower parts of the root-system.

Lengthy rootlet is almost horizontal. The majority lie in the direction of the leaf-tip. A smaller rootlet springs from a short distance above the tuber and points in any direction.

Tuber usually heart-shaped, bearing a small round brownish scar (with dark dot in centre) on the top, roughly opposite to the direction of the large rootlet. No sign of new tuber.

All tubers had granular surface. In very small specimens, the surface of the tubers (under magnification) was dotted with purple. There was a good development of rootlets in spite of the small size of the plants.

17 August 1953

By now there is considerable root-change. On non-flowering specimens, and those on which the flower had been destroyed or had not set seed, all showed early development of two new tubers. (On long rootlets; the tuber grows on the underside of the tip.) In some cases a small pyramidal shoot was showing on the top of the tuber, next to the end of the rootlet.

By studying the lines of the tissue forming the rootlets, it was noticed that the lower rootlets commenced forming on the side where the round scar was noticed on the old tubers. After growing up the line of the main root, the rootlets swung around to separate from the main root at right angles, three quarters of the way round from the side on which they commenced development.

Specimens which had set seed had good long rootlets, but a careful examination under a lens failed to show any sign of new tuber development. In specimen 4 the new tuber was very advanced, and was lower than the old tuber. The new tuber was showing a noticeable shoot at its apex. Specimen 3 appeared to be an unusual development, showing rootlets issuing direct from the old tuber. This was seldom seen in other specimens examined.

A careful check of leaf-angle was kept. The level of the leaf being taken as parallel with the ground level. Roots were growing at all angles, presumably taking the line of least resistance through compost of soil surface. Part of one specimen travelled quite a distance in a horizontal position through a rotting twig, before being able to break through to the surface. Others in more crumbly soil took a more direct upward thrust. Scar present in all instances, but less noticeable than the previous month.

20 September 1953

As the supply of flowered specimens in the kanuka scrub had run out, specimens were obtained from mixed forest nearby. In general they did not look very different from the previous month's specimens. It was seen, however, that fruited specimens were developing two young tubers, thus showing that by setting seed they only retarded tuber development, but did not prevent it altogether. None of the old tubers were showing any signs of shrinking, nor any other part of the plants, though where seeds were present, they were ripe, or almost so. In well-developed specimens (other than fruiting ones) there was generally one of the new tubers almost as large as the old one. Very small specimens showed good root development with no sign of new tubers forming yet; whereas slightly larger plants showed poor development of rootlets, but one, or even two new tubers developing well.

Very small tubers are white with purple dots, and show the characteristic scar on the upper surface. Apparently the leaves of this species are above ground for a long period. Rootlets at or near ground surface show a greenish tinge. The first direction followed by the upper rootlet is slightly upwards, then more or less horizontal, with a kink downwards near the tip. The lower rootlet rises at its origin, thereafter taking a slightly downward course, so the new tuber produced on the lower rootlet tends in time to become lower than the old tuber.

The soil in the mixed dune forest was drier and more fibrous than that of the kanuka scrub, so rootlets were not so lengthy. Also, some difficulty was experienced in separating the root and tuber systems from the surrounding chaffy and fibrous matter, so there was a tendency to lose some of the tubers when cleaning the roots.

In one instance the lower rootlet was growing directly out of the top of the old tuber. In several instances it was growing at the extreme lower end of the main root, i.e., immediately above the old tuber. Another was very similar but the tip of the upper rootlet showed just a slight knob, which was greenish, probably being in the surface of the soil or moss.

1 November 1953

From specimens examined at this time the conclusion could be drawn that the time would not be long before the tubers became separated from their rootlets as the latter had become very filamentous, making it difficult to remove the debris from around the tubers without knocking them off. Apparently the first new tuber to be produced is the one on the long rootlet, as this is in all cases the larger of the two new ones. (Of course, very small specimens produce only one tuber, to replace the old one.) In many cases the larger of the two new tubers exceeds the old tuber in size. The old tuber is not showing signs of shrivelling, however. Whether on account of drier weather conditions, or for normal seasonal reasons, one cannot say, but the earth debris is much more tightly stuck to the tubers and roots, and is very difficult at this stage to remove.

13 December 1953
Leaves mostly show some sign of withering. Many leaves have already done so. Many of the leaves are more irregular in shape than those of the early season, which in the shaded dune areas are noticeably roundish. (Leaf-growth continues after the early flowering season.)

Tubers are all fairly small. The lower (old) tubers show little sign of shrivelling. The larger of the new tubers – the uppermost one where such is present - sometimes shows good development of the new season's shoot. There are indications that this is only so where the ground is fairly damp. *Corybas trilobus* in a dry lump of sand (gathered some months previously) show the tubers (greenish) of a comparable size with any of the dune ones, but all evidence of leaves and roots have vanished, and there are no apparent shoots.

(For comparison, *Corybas macranthus* collected 13/12/53 from damp peaty soil in shade showed very well-developed shoots and no sign of withering.)

2 June 1954 (one year after the beginning)
Masses of flowers in evidence, all in early stages, galea the obvious thing showing, mostly not yet tipped back. Leaves small and relatively undeveloped, hidden in moss (*Ptychomnion aciculare*). No sign of new tubers. Smaller flowering specimens showed shorter second rootlet. Lower rootlet always starts on same side as scar and works around about 1/4 of root-stem before emerging as an independent rootlet. Elsewhere (August previously) I had noted that the shoot works around 3/4 of the distance, therefore it grows from 1/4 to 3/4 by August.

Pterostylis alobula

THE ANNUAL CYCLE

At the beginning of March or slightly sooner the leaves started to unfurl. By mid-March there were two leaves. There was one tuber, sometimes with a withered piece of connective. Some of the more advanced specimens were already developing two or three short roots, the longest 6 mm and the lowest growing downwards, which may be a dropper for a replacement tuber.

By early June some plants were already flowering and others had well developed flower buds. Three, sometimes four, roots were present, the longest 9 mm. The flowering specimens had attained a height of 15-16 cm from base of tuber to top of flower. The replacement tuber growing just above the current season's tuber was approximately 1 mm long in flowering specimens, but in some juvenile specimens it was 3 x 1.5 mm. In some cases a minute shoot showed at the tip of these larger replacement tubers. In some cases the withered connective was still present, hanging to the main tuber which later showed a scar when the connective had disappeared.

By mid-July, some flowers were finished and others still in their prime. Mature specimens had four roots, juveniles three or two. Replacement tubers, present on all plants, were flask-shaped (and growing closely above the main tuber). On

juvenile plants, or where the plant had flowered earlier, new tubers were well grown, but they were much smaller on plants still flowering.

Mid-August showed flowered specimens with seed capsules either well developed or infertile. There were also a few plants flowering. As many as seven roots were present. An infertile specimen had a new tuber larger than the current season's one, the new tuber bearing on its top a shoot about 2 mm long. On the specimen still flowering, one of its four roots was starting to shrivel. On juvenile specimens all short roots were shrivelling, but in addition to these there were several long runners of recent growth.

Well into September many plants which flowered had failed to set seed, or the seed stalk (or flower stalk) had been eaten off. In these cases the roots, all of the short order, were limp. The current season's tuber was becoming depleted and was shrivelling. Most of the replacement tubers were larger than the ones they were to replace. Stalks and some leaves were changing colour, preparing to die down. Most juvenile specimens had two dispersal tubers beginning to form on long runners and new replacement tubers were large. Old tubers were shrivelling. Where the top runner was near the surface of the ground or moss it had green colouration.

By the beginning of November all short roots were shrivelling. The long runners developed later than the short roots all had dispersal tubers of good size, whether the plant had borne a flower or whether it was a juvenile. In plants where the seed capsule had ripened, any new dispersal tubers were still only small knobs, though some replacement tubers were full size.

By the end of December there were only a few juvenile plants above ground, their leaves fading. Others had died down altogether. A small juvenile specimen examined had no sign of new dispersal tubers on two runners. It is possible that this retarded specimen had developed well on in the growing season from a very small tuber (2 x 2 mm); very small plants with only one or two leaves having no runners.

January is the dormant month, but judging by the shoots which showed on the replacement tubers almost from their beginnings, it is doubtful if there is a complete cessation of growth. Above ground shoots are seen again early in March, occasionally earlier, thus completing their cycle.

The three or four short roots produced during the flowering time only are not concerned with growing tubers. They probably have a dual purpose of providing some nutrition and for stabilising the tall, narrow plant during the flowering period, and their life is very short. The long runners all produce dispersal tubers and, growing where they are affected by light, they usually contain chlorophyll.

FLOWERING TIME

At Hokio, in the dune forest and scrub, this orchid flowers during June, July, or August, but probably not all of that time during any one season. In 1960,

Mr I. D. Parsons collected flowers from this dune area in late September. I have found it in flower in June, at Ohau on the outskirts of totara forest growing on a low shingle terrace near the Ohau River. It seems that the time of flowering is related to the seasons rather than to the situation, thus differing from *Corybas trilobus*, the flowering times of which vary so considerably within the Horowhenua district, according to the distance inland, or perhaps substratum (sandy soil warming up earlier). This factor appears to have no noticeable effect on the flowering time of *Pterostylis alobula*.

DETAILED OBSERVATIONS (Table 3)

15 July 1953

Just below ground level, a slightly bulging portion of the stem is fairly generously studded with root-points. These continue more sparsely down the main elongated line of the root system. Branching off the main root line are rootlets, four in mature specimens, fewer in immature specimens (spathulate-leaved). The old tuber grows at the extreme tip of the root-line. Closely situated above this is the new tuber, growing out of the root, not directly connected with the old tuber. Near the new tuber is a rootlet, sometimes erupting from the root line above the new tuber, and sometimes lower, and generally from the opposite side of the root.

The new tuber (replacing the old tuber) commences forming as the flower comes to maturity. At first it is pear-shaped. As the flower fades, the tuber develops rather rapidly. Juvenile (i.e., non-flowering) plants develop their new tubers earlier, their energy being put straight into the formation of these at the same time as the flowering period of mature plants.

The total length of the root system does not seem to have any connection with the age of the plant, but rather with the depth at which the soil occurs. A layer of leaf-mould and moss constitutes the top layer, where the rootlets spread out to feed. But the tubers are formed in the soil proper, in this instance, almost pure sand. There is no uniformity about the position or size of the rootlets except that a rootlet is always to be found close to the new tuber. When no other rootlets are present, this would be the only feeding tip. It would appear that the plant remains without flowers until it has accumulated sufficient nutriment to form a reasonable-sized tuber and four feeding rootlets in addition to its seasonal leaf production. The size of the main tubers shows remarkably little variation. The surface of the old tubers is granular.

17 August 1953

Old secondary roots (short) are now withering. New rootlets, for the most part long, are travelling fairly near the surface, so in some cases they are showing a green tinge. These long rootlets are only noticed on well grown but flowerless specimens. In some cases, small flowerless specimens have one long rootlet as a connective for the new tuber; otherwise the new tubers are mostly sessile

Table 3. Seasonal development of *Pterostylis alobula* at Hokio, Horowhenua.

Date	Specimen condition	Flowering state	Total length (cm)	Root length (cm)	Length of secondary roots					Tuber dimensions (mm)	
					1 (top)	2	3	4	5	Upper (new)	Lower (old)
15 vii 53	mature	flower shrivelled	15.5	2.8	12	7	11	7		4 x 3	5 x 4
	mature	flower shrivelling	12.6	2.8	7	11	7	6		3 x 1	4 x 3
	mature	flowers in prime	12.8	3.7	10	5	6	5		1.5 x 1	5 x 3
	juvenile	non-flowering	5.5	2.0	9	9	9	—		3.5 x 3	5 x 4
	juvenile	non-flowering	4.7	2.8	2	6	2	—		3 x 2	4 x 3.5
	juvenile	non-flowering	4.0	2.8	5	4	—	—		4 x 3.5	4 x 3.5
17viii53	mature	seed capsule	17.4	4.1	18	10	12	10	—	2 x 1	7 x 5
	submature	flowering	12.2	3.6	7	17	9	4	—	—	5 x 4
	mature	infertile capsule	12.3	2.4	10	3	3	—	—	5 x 5	4 x 4
	juvenile	—	6.8	3.8	79	7	55	4	6	3 x 4	5 x 4
	juvenile	—	2.7	1.5	65	12	11	—	—	2 x 2	3 x 2
	juvenile	—	5.5	5.0	47	7	7	—	—	3 x 2	4 x 3
	small	—	4.9	3.5	—	—	—	—	—	4 x 3.5	4 x 4
20ix53	mature	unripened capsule	11.5	3.0	4	15	6	6	—	6 x 6	5 x 4
		defoliated	14.0	2.8	15	14	14	—	—	4 x 4	5 x 2.5
	mature	unripened capsule	11.2	2.7	1	10	12	9	—	6 x 5	6 x 4
	juvenile	largely defoliated	4.5	1.5	140	12	9	—	—	3 x 2.5	6 x 4
	juvenile	—	5.2	1.8	48	4	9	—	—	5 x 5	5 x 3
	very small	—	2.1	0.9	40	59	3	4	—	3.5 x 3	3 x 2
	small	—	5.0	3.0	3	2	—	—	—	4 x 3	3 x 2.5
	juvenile	—	4.0	1.0	51	20	8	—	—	3 x 2.5	—
01xi53	mature	infertile capsule	9.2	2.1	72	7	38	16	14	4.5 x 4	6 x 4
		ripe capsule	10.5	3.7	—	5	6	5	—	5 x 4	5 x 4
	juvenile	—	1.8	0.8	80	93	3	14	—	3 x 2; 4.5 x 4; 4.5 x 4	2 x 2
	juvenile	—	3.2	2.2	15(+)	140(+)	30	11	8	7 x 6.5; 2.5 x 2.5	5 x 4
31xii53	juvenile	—	2.1	2.4	47	53	—	—	—	3 x 2	2 x 2
11iii54	juvenile	—	3.8	2.4	3	3	4	—	—	—	4.5 x 4
	juvenile	—	2.0	0.7	—	—	—	—	—	—	4 x 3.5
	juvenile	—	3.0	2.0	6	4	—	—	—	—	4 x 3
	mature	—	2.9	2.3	5	4.5	—	—	—	—	5 x 4.5
	mature	—	5.0	3.6	—	—	—	—	—	—	6 x 5.5
2vi54	mature	flowering	15.1	2.5	6	6	6	9	—	1 x 1	5.5 x 5
	mature	in bud	16.1	3.7	8	5	6	—	—	1 x 1	6 x 4.5
	juvenile	—	5.0	3.0	6	4	—	—	—	3 x 1.5	4 x 3
	juvenile	—	3.8	2.4	7	4.5	—	—	—	3 x 1	4.5 x 3
	indeterminate	—	4.0	0.9	43	70	10	12	—	—	4 x 3

and now showing a white shoot 2 mm long, coming out of the top. Very young flowerless specimens (one or two leaves) do not produce these secondary rootlets, but in some instances the tubers are quite large and well developed, and compare favourably with those of the larger specimens. One with a fertilised and well grown seed capsule has very little development of the new tuber. Following observations of the previous month's specimens, this bears out the theory that plants producing seed are retarded in the development of the new tuber. The new rootlets showed no thickening at their tips.

1 November 1953

The specimens of 20/9/53 showed no long rootlet development on mature plants, the tuber production being in such cases just one near the base to replace the old tuber. This month's specimens show a slightly different picture. The two mature specimens were both "young-mature", i.e., they had petiolate leaves towards the base of the stem, with narrower, amplexicaule leaves towards the top. Specimen 1 which had flowered but had set no seed, had very good long-root development; one tip was broken off, but the other showed a well developed tuber at its tip. The new tuber at the base, replacing the old tuber, had been broken off. Or it may have been that the remaining one was the new one and the old one had been broken off. The incomplete root tip remained.

Specimen 2 was more in line with the mature specimens of 20/9/53. There were no long rootlets, and indeed very poor root development of any sort; though the plant had flowered and developed a good-sized seed capsule. The new tuber at the base was about the same size as the one which it was replacing. Higher up the root-line, however, one of the small rootlets appeared to be swelling at the tip, as if to produce a belated tuber; while a new young root-tip near the top of the root-line looked as if it might have developed a tuber also.

A specimen collected when flowering (no date stated), was kept under a damp cloth till 20/8/54. The flowers died off but the leaves remained. This year's tuber shrivelled, but new tubers were formed on the end of shoots; the largest one being 3 x 2.5 mm.

(The specimen was an intermediate plant, flowering, but with basal rounded petiolate leaves. It showed shoot development (i.e., side roots) comparable with that of well developed juvenile plants – longer shoots than those on mature flowering specimens.

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