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国立民族学博物館学術情報リポジトリ National Museum of Ethnology

PART2 : COLOCASIA ESCULENTA IN NEW ZEALAND : NGA TARO O AOTEAROA

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Here I report results of the New Zealand study introduced in Part 1. Previous accounts of taro in New Zealand consisted of scattered ethnographic records of use and cultivation by the Māori, mainly in the nineteenth century. In previous reports of chromosome numbers in taro, the possibility was raised that New Zealand taro arrived from Melanesia in pre-European times. This suggestion had radical implications for theories of human voyaging and cultural diffusion in the Pacific before written history, since it was (and remains) generally accepted that Māori ancestral and cultural origins lie somewhere in eastern Polynesia.

The research described here was an attempt to determine the historical status of taro present in New Zealand in the early 1980s. Chapters Four to Eight have been adapted from Matthews (1984).

Chapter Four

New Zealand Historical Context and Present Aims

Colocasia esculenta (L.) Schott (taro) is a crop plant not previously described for New Zealand. An initial study of the variation and distribution of taro has been made which provides a basis for future investigation of the plant both within and outside New Zealand. The present research has been directed towards an understanding of the history of taro in New Zealand.

C. esculenta (L.) Schott (taro) is an ancient crop now grown throughout the tropics and sub-tropics in subsistence economies (Plucknett et al. 1970; Herklotts 1972; Leon 1977). Early ethnographic records and Māori traditions (Best 1976) clearly establish that taro was introduced to *Aotearoa* in pre-European times.

Despite the nineteenth century disintegration of traditional Māori agriculture, taro has retained some economic importance. Diamond (1982) recorded the use of taro by Northland's bushmen and poor rural transients in the first half of this century, and Ishida (1966) described taro as a component of contemporary subsistence gardening in rural Māori communities of the North Island. Cultivations were also briefly noted in these communities by Yen and Wheeler (1968) and Matthews (1982b).

Some cultivation is found in the Chinese community (Yen and Wheeler 1968) but was not investigated in the present study. Casual observation indicates that taro is quite widespread in the urban Auckland district, where it is cultivated as a leaf crop in the gardens of Pacific Islander households (J. Watson, pers. comm. 1982).

A large demand for imported taro corms exists amongst the various Pacific and Asian ethnic groups in New Zealand. Imports from the Pacific Islands amount to approximately 49×10^3 kg per week (J. Watson, pers. comm. 1982).

Chromosome numbers have been used to identify likely routes of introduction of taro into the Pacific (Yen and Wheeler 1968). An origin for New Zealand's taro in Melanesia was indicated by the discovery in both New Caledonia and New Zealand of plants with chromosome numbers of $2n = 42$. Taro with this chromosome number also have been recorded in the Solomon Islands of Melanesia (Jackson et al. 1977), and in Timor, the Philippines, the Rykuyus, Japan, China, and India (Yen and Wheeler 1968). The $2n = 42$ number has not yet been reported elsewhere in the South Pacific east of New Caledonia. On the other hand, taro with a chromosome number of $2n = 28$ have been found throughout the South Pacific and in Asia (Yen and Wheeler 1968). Yen and Wheeler (1968) drew no definite conclusion from their discussion of whether the possible introduction from Melanesia occurred before, or after, the arrival of Europeans in New Zealand. The present research was undertaken in an attempt to resolve this discussion.

In recent years there has been considerable international interest in the conservation

of crop genetic resources (Frankel and Hawkes 1975; Simmonds 1979; New Zealand Nature Conservation Council 1980; Plucknett et al. 1983). Apart from the common potato (*Solanum tuberosum*), little is known about the many important root and tuber crops, including taro. Traditional methods of taxonomy do not appear to work well with root and tuber crop species (Leon 1977). Nevertheless, ethnobotanical studies by botanists and anthropologists have provided important insights into the interactions of cultivators and crop-plant gene pools (for example, Panoff 1972; Yen 1974; Jackson et al. 1980; Sillitoe 1983). Yen (1974) and Jackson et al. (1980) combined observations of cultural practices with botanical observations of morphological and cytological variation, and of distribution, in studies of sweet potato and potato respectively. A similar ethnobotanical approach was taken in the present study of New Zealand taro.

For the present report, observations of natural growth and dispersal of taro were made and, where possible, associated cultural practices were recorded to provide insight into possible historical explanations. These observations were made during wide-ranging field surveys. Botanical descriptions of New Zealand taro are presented in the chapters that follow, based on material observed in the field and in a living plant collection. Informal nomenclature is adopted and the New Zealand taro are described as 'variants'. Observations of root-tip chromosome numbers and karyotypes were made on fully provenanced accessions held in a living plant collection.

Three common variants of taro were found to be widely distributed in the North Island: var. RR (red petiole and rounded blade); var. GR (green petiole and rounded blade); and var. GP (green petiole and pointed blade). The distributions of these variants differ in both geographic range and in relationship to human settlement. Each has a chromosome number of $2n = 42$. Two variants with the chromosome number $2n = 28$ were found but are rare and have little or no economic importance in the areas surveyed.

These observations lend circumstantial support to the suggestion of a pre-European introduction of taro with $2n = 42$ from the western Pacific, but alternative explanations are readily apparent. The observations of natural and artificial dispersal have important implications for future studies of the evolution of taro and its relationship with people.

Chapter Five

Taxonomy and General Observations

5.1 Introduction

In the course of field surveys in the North Island of New Zealand, three variants of taro with major distributions were recognised. Observations of growth habit and flowering, and a key for their identification, are presented here. Their cytology is reported in Chapter Six, and their distributions are described in Chapter Seven.

Six other variants of limited known distribution are noted but not discussed. Use of the botanical name *Colocasia esculenta* (L.) Schott follows Hill (1939) and Purseglove (1972), and refers to a polymorphic species of the tribe Colocasioideae and family Araceae. The term ‘variant’ represents informal nomenclature adopted for the present study of variation in New Zealand taro. Where other authors referenced have used the term ‘variety’ in either a formal or informal sense, that use is retained here.

Taro is the Māori common name for *Colocasia* in New Zealand, and is cognate and synonymous with Polynesian terms such as *kalo* and *talo*. Taro also is presently a common name used generally in the Pacific and in literature, and is applied both collectively and singly to the edible aroids *Alocasia*, *Colocasia*, *Cyrtosperma*, and *Xanthosoma*.

The taxonomy of *Colocasia* is highly confused, a situation which is considered characteristic of ancient, vegetatively propagated food crops such as *Colocasia* (Purseglove 1972; Leon 1977; Plucknett 1983).

Although nine names of botanical varieties are listed by Plucknett (1983) in the most recent review of the taxonomic literature, their use appears to have been limited by the lack of any readily available descriptions for them. Debate has centered on the species or varietal status of the names ‘*esculenta*’ and ‘*antiquorum*’.

Haudricourt (1941), Massal and Barrau (1956), Barrau (1957), and Cooper (1969) propose two major subspecies or varieties of *Colocasia* distinguished on the basis of floral morphology. Cooper (1969) records the flowering of *C. esculenta* (L.) Schott in New Zealand and describes two varieties as follows:

‘var. *esculenta* (formerly *typica*), in which the sterile appendage of the spadix is shorter in length than the male inflorescence. This variety also has been defined as that in which the sterile appendage is short and is freed when the spathe tube opens. var. *antiquorum* (Schott, Hubbard and Rehder), in which the sterile appendage is equal to or greater than the length of the male flowers. This variety also has been defined as that in which the appendage is longer, and remains caught in the terminal part of the spathe when

the tube opens.'

Further observations of flowering in New Zealand are presented here. Plucknett (1983) states that there are two general types of crop plants in the cultivated *Colocasia*, and that in general they can be delineated as follows:

(1) Plants that produce a large edible main corm with few cormels (sometimes called sucker corms); e.g. four or eight or so. Generally this group has twenty-eight chromosomes and can be grown under a wide range of water conditions, from flooded (as in Hawai'i and other parts of the Pacific Islands) to rain-fed upland conditions. This plant is *C. esculenta* var. *esculenta*.

(2) Plants that produce a small or medium-sized main corm that often may be inedible because of acidity and a large number (fifteen or twenty or so, to as many as forty or more) of small edible cormels. Some cormels may possess some degree of dormancy. Generally this group has forty-two chromosomes and is grown as an irrigated crop like many other vegetables or as a rain-fed upland crop. This group of plants probably developed in Japan or China. This plant is *C. esculenta* var. *antiquorum* (sometimes called *C. esculenta* var. *globulifera*).

In addition to varieties which produce cormels (synonyms: sucker corms, side-corms), Whitney et al. (1939) describe two varieties forming rhizomes or stolons. Stolon formation also is discussed by Wilson (1982). Both growth habits have been observed among the New Zealand variants described here.

Leaf shape in *Colocasia* ranges from ovate to sagittate, and is entire with an acuminate apex and rounded basal lobes (Strauss 1983). A major diagnostic feature of *Colocasia* is the presence of peltate leaves in contrast to the leaves of other aroids having marginal petiole insertion (illustrated by Massal and Barrau 1956; Strauss 1983). An exception is the '*piko*' group of Hawai'ian cultivars, with marginal petiole insertion (Whitney et al. 1939).

The three major variants recognised in the present study were distinguished in the field by leaf shape and colour. A key based on these characters is presented (section 5.3.1), together with a quantitative analysis of leaf shape using data from the field. Only one collection has been made in New Zealand of what may be a '*piko*' variant of taro.

Whitney et al. (1939) present a botanical classification of 200 taro varieties collected largely from the Hawai'ian Islands and from as far afield as China and Japan. Among these they recognise 84 distinct varieties after observation of the collections, for from one to three generations, under cultivation at the Pensacola Branch Station, Hawai'i. Accessions thought to be similar were grown side by side for close comparisons.

The authors classify 74 of the varieties in a key based on vegetative characters. Floral characters could not be observed in all varieties, and observations of some varieties were insufficient for classification.

Observations were made on plants grown under 'normal' conditions, and close to the

period of maximum top growth between four to eight months after planting. After this stage, leaves decrease markedly in size until the time of full corm maturity. Whitney et al. (1939) also note that stage of growth affects qualitative characters: the colour and markings of petioles and corm flesh, the development of side-corms and rhizomes, and the branching of corms. Extremes of fertility, moisture, and sunlight also affect both quantitative and qualitative characters.

The above outline of the study by Whitney et al. (1939) is presented for two reasons: (1) it sets a precedent for reducing the number of named varieties when varieties already named according to a traditional folk taxonomy are classified by the Linnaean approach. (In the present study only three variants were recognised, although Best, 1976, presents a list of 45 Māori names of taro varieties; see Appendix 9 for further information); and (2) it identifies environmental and developmental factors affecting phenotype and relevant to the following account of variation in New Zealand taro.

5.2 Materials and Methods

5.2.1 Field measurements and analysis

Field notes and photographs were made to record habitats, growth habits, and flowering. The measurement of inflorescence parts followed Cooper (1969) except where upper and lower parts of the spathe were measured separately. Inflorescences chosen for measurement were generally at uniform developmental stage, with the upper spathe yellow.

Leaf measurement and sampling

Leaves measured within a patch of taro were individually identified by shoot number and leaf position (innermost first). Sites, site sample sizes, and annotated site descriptions are presented in Appendix 5. The characters measured are illustrated in Figure 5.1 and an example data sheet is shown in Appendix 6.

In general the selection and measurement of leaves was made by the author, with another person recording. The measurements were made in centimetres to one decimal place, in general, and to the nearest centimetre with difficult measurements of larger dimensions.

Twelve leaves were generally measured per site per variant. This number was chosen after a pilot total-population survey of 62 leaves at site NZMS 259/1 (Little Barrier Island) in August, 1981 (data not presented), and was subjectively considered sufficient to describe a patch without taking too much time. Occasionally, greater multiples of twelve were recorded when time and the number of plants permitted. For the analysis of leaf shape, the measurements from sites were pooled for each variant to give large samples incorporating the variation of each variant over a wide geographical range.

Selection of leaves for measurement within a site was not random. Taro generally form clumps within which individual plants (shoots) vary widely in age and size. The clumps within sites also vary widely in age and size, and the dispersion of clumps, in non-cultivated and wild sites, appears highly dependent on characteristics of local water

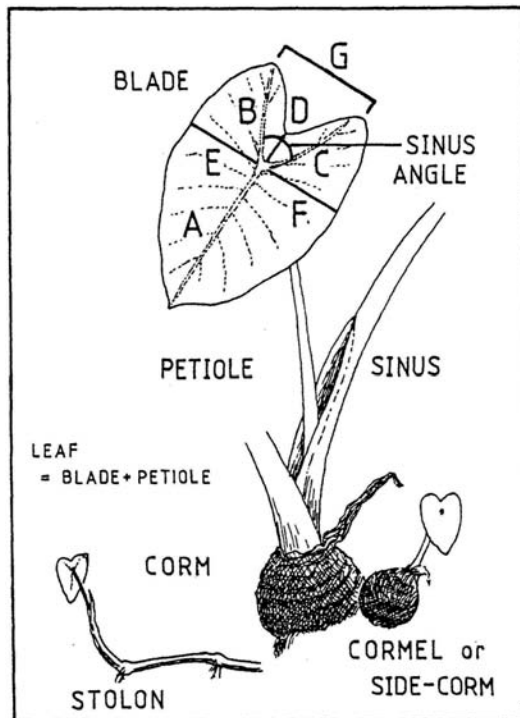


Figure 5.1 Morphology of *C. esculenta*. Illustration of terms and the blade dimensions (A to G) measured to describe shape. (A) to (F) are distances measured from the petiole junction (centre of blade) to edge of blade, and (G) is the distance between the tips of the rear lobes.

flow. In this situation, there is no readily apparent random sampling strategy which can be applied with any consistency from site to site.

In order to minimise the chance of creating apparent differences between variants through sample selection, sampling was aimed at maximising intrasite representation of variation. Leaves were selected which were felt to span the full size range of mature leaves present. Size was subjectively judged largely by the dimensions of petiole height, blade width, or blade length — to what degree shape affected judgement cannot be assessed.

Since leaves at the extremes of size range are less common, most leaves were selected from between extremes, and for this range more or less random walks were taken through patches. No consistency could be achieved with respect to within-plant sampling as the number of measurable intact leaves per plant is determined by its age, the degree to which older leaves have suffered weather damage, and other effects of micro-environment. Some sites contained too few intact, mature leaves to allow much choice about which leaves to select.

Intact, mature leaves were chosen to the exclusion of:

- (1) young leaves not yet fully unrolled and expanded;
- (2) the first, tiny leaves of shooting side-corms, since these have marginal petiole insertion rather than peltate structure — similar to the first leaves of taro seedlings illustrated by Kikuta et al. (1938), and
- (3) ripped, rotted, wilted or obviously malformed leaves.

Analysis of leaf shape

The analysis of leaf data was performed with the University of Auckland central IBM computer using the SAS statistical package (SAS Institute 1982 a, b) and the procedures PROC MEANS (for univariate descriptive statistics) and CANDISC (canonical discriminant analysis).

The statistical theory of discriminant analysis assumes that the discriminating variables have a multivariate normal distribution and that they have equal variance-covariance matrices within each group (in this study, within each taro variant). In practice, the technique is very robust and these assumptions need not be strongly adhered to (Klecka 1975).

Descriptive statistics obtained by the PROC MEANS command indicate that the untransformed leaf measurements are approximately normally distributed with generally slight right-skewness for each of the blade characters measured. Bivariate plots of different combinations of blade characters show scatter increasing with size of character (heteroscedasticity). Log transformation of the data linearised the bivariate plots, and was performed prior to the canonical discriminant analysis to help normalise the multivariate frequency distributions, and homogenise the variance-covariance matrices within each group. Nevertheless, it is suggested that the assumptions required for the discriminant analysis are only approximately satisfied. Because taro leaves are highly symmetrical (Appendix 6), redundant information was present in the original set of characters measured (Figure 5.1). Characters C and F were arbitrarily excluded from the discriminant analysis, and their equivalents, characters B and E, retained with the other blade characters A, D, and G.

5.2.2 Living plant collection

Collection

Accessions to the living plant collection were collected from a wide range of sites during field surveys and also were received from a number of correspondents and other fieldworkers. The accessions were numbered with the prefix AKL (= Auckland) in order of their arrival at the Department of Botany (Appendix 3).

Collection of taro for propagation does not require special care as both corms and side-corms have numerous adaxial meristems in addition to the central meristem. For transport, whole corms, the cut tops of corms (petiole plus top few centimetres of corm), side-corms, and stolon nodal sections were either placed with damp soil in unsealed bags or wrapped without soil in damp newspaper. Under cool or shaded conditions, material was stored for up to two weeks without rotting or dehydration of meristems.

Maintenance

The collection was held in four areas, as space permitted: glasshouse, poly-house, shade-house, and on an outside scoria bed. The plants were generally potted in black PVC bags of sizes PV 3 (100 × 100 × 200mm) and PV 6 ½ (130 × 130 × 280mm). Potting mixes used were fertilised 1 : 1 peat and pumice; and fertilised John Innes soil, peat, and pumice mix (supplied by the Mount Albert Research Centre, Auckland). Plants were multiplied by separation of side-shoots.

Glasshouse plants placed in watering trays were highly prone to spider mite and white fly infestation. Use of insecticide sprays was avoided because leaves were used for a biochemical investigation. Removal of the outermost leaves (usually the most seriously infested) at one- to three-week intervals delayed insect population explosions quite successfully. Periodically all leaves were removed to clear heavy infestations. Plants grown outside and with overhead watering in the poly-house and shade-house remained free of insects.

Observations

Plants were visually checked for constancy in phenotype after removal from the field. Occurrences of flowering were recorded and the inflorescences measured as described above for the field observations. To compare growth habits in variants RR, GR, and GP (described below), cut tops of each were placed in large PV 40 bags (230 × 230 × 460mm) half-filled with brown garden loam, and placed outside on the scoria bed. These were harvested after approximately one year (23.9.82 to 14.10.83) and photographed.

5.3 Observations

5.3.1 A key for distinguishing three New Zealand variants of *Colocasia esculenta* (L.) Schott

An initial key was developed after the first field survey in the central Bay of Islands (Matthews 1982), and with material received from a number of collectors prior to later field surveys. The key below recognises variability observed during the course of these later surveys. Anatomical terms are illustrated in Figure 5.1, and the three variants are shown in colour in Figure 5.2.

- a. Blade peltate, broadly ovate and entire, with obtuse rear lobes. Margins not undulate.
- b. Petioles predominantly greenish bronze to dark carmine, colour development greatest over basal half of petiole (degree of colouration variable within and between plants (younger petioles generally greenish bronze, immature petioles completely green)). Margin of petiole sinus greenish bronze or carmine (variant RR).
- bb. Petioles bright green or yellowish green. Some slight carmine colouring may develop at tip of petiole and along a small distance beneath the blade on the major veins. Carmine colour also appears in a narrow band of variable width along the margin of the petiole sinus (variant GR).
- aa. Blade peltate, ovate and entire, with attenuated rear lobes. Margin coarsely undulate.

Petioles predominantly pale green. Light, greenish bronze colour may develop over more than half the length of the petiole, from base. Some slight carmine colouring may develop at the tip of petiole and along a small distance beneath the blade on the major veins (variant GP).

In practice, variants may be recognised in the field simply as with red petioles and rounded blades (variant RR), green petioles and rounded blades (variant GR) or green petioles and pointed blades (variant GP).

Variants RR and GR are grouped together in the key above because other morphological similarities distinguish them from variant GP (described below).

5.3.2 General observations in the field and the living plant collection:

Areas and dates of fieldwork are set out below:

Northland:

Bay of Islands, May 1982

Cavalli Islands, December 1982

Hokianga to Kaitia, February 1983

Hauraki Gulf:

Little Barrier Island, August 1981

Waiheke Island, February 1983

Kawau Island, January 1983

Northern Great Barrier Island, January 1983

Coromandel Peninsula, August 1983

East Cape:

Opotiki to Gisborne, January 1983

Habitat range

The limits of habitat range have not been established, since not all areas known to have taro have been explored.

Taro were encountered in a diverse range of habitats, some of which are noted in Appendix 5, or may be seen in Figures 7.1. and 7.2. The most common attribute of sites with wild taro appears to be a plentiful water supply either seasonally, as in small creek or swamp sites, or year-round, as in bigger creek or swamp sites below larger water catchments. The presence of taro in sites lacking natural water flow can generally be attributed to planting by people.

Growth habits (variants RR, GR, and GP)

In the temperate climate of New Zealand the growth of taro is highly seasonal, with a major flush of leaf production over the summer months. Plants in areas prone to frosts, for example parts of Coromandel, were reported by local informants to survive frosts but

with growth set back. Plants with recently rotted and torn leaves were observed in open ground near Waikawau River, Coromandel, during August 1983, and appeared to be damaged by both frost and wind. At other Coromandel sites at this time, plants growing in narrow streams at the entrances of exposed coastal gullies appeared limited in size to the height of the banks which sheltered them.

Conditions that favour large size and a high rate of growth of leaves appear to include shelter, heat, and wet boggy ground (see Figure 7.2).

A clumping growth habit was observed with each of the variants RR, GR, and GP. Clumps in a patch may contain corms and side-shoots varying widely in age. The leaves produced over the summer by young side-shoots attain a smaller maximum size than do leaves from corms a number of years old. Etiolated petioles were frequently observed on shaded plants.

Petioles observed in the field ranged from only a few centimetres to almost two metres in length. Variants could not be distinguished in the field on the basis of size range, although visual comparisons of potted plants indicate that variant GP may be characterised by longer petioles on average than the variants RR and GR.

Variants RR and GR are similar in both their corm morphology and vegetative propagation. They produce undulating central corms with numerous side-corms where the parent is buried or lies against a damp surface. Side-corm production was observed in potted plants (Figure 5.2), and in the field (Figure 5.3).

Corms which have rotted at the base, and dislodged or abscised side-corms, are readily carried downstream by water flow, so that clumps of taro originating from an upstream site may eventually be dispersed within a watershed over considerable distances (to more than one kilometre).

Variant RR has been seen to produce short stolons, but only under highly artificial conditions: in the glasshouse, with roots highly pot-bound, and watered irregularly.

Stolon production is characteristic of variant GP in the field and under all conditions of potting (Figures 5.2 and 5.3). In the field stolons were not always seen, but in all sites prolific side-shoot formation was observed. These appear to grow without an intermediate cormel stage and develop into large corms similar to the parent corm. These side-shoots do not detach as readily as side-corms and it is sometimes difficult to collect propagating material. This close growing habit may be reflected in the extremely dense clumping seen in some sites, covering large areas (possibly more than 1000m² at site N14/30, Reena, North Hokianga).

Formation of stolons appears on casual observation to occur only in dry or damp conditions, rather than in bog or submerged in water. The older corms of variant GP often appear massive compared to those of the other variants (Figure 5.3), but also show undulations. The undulating shape of corms is believed to reflect seasonal growth over a number of years.

Other Variants

Six accessions from Rarotonga, Cook Islands (five of these from a collection at the Totokoitu Research Station, Appendix 3), were maintained in the living plant collection.

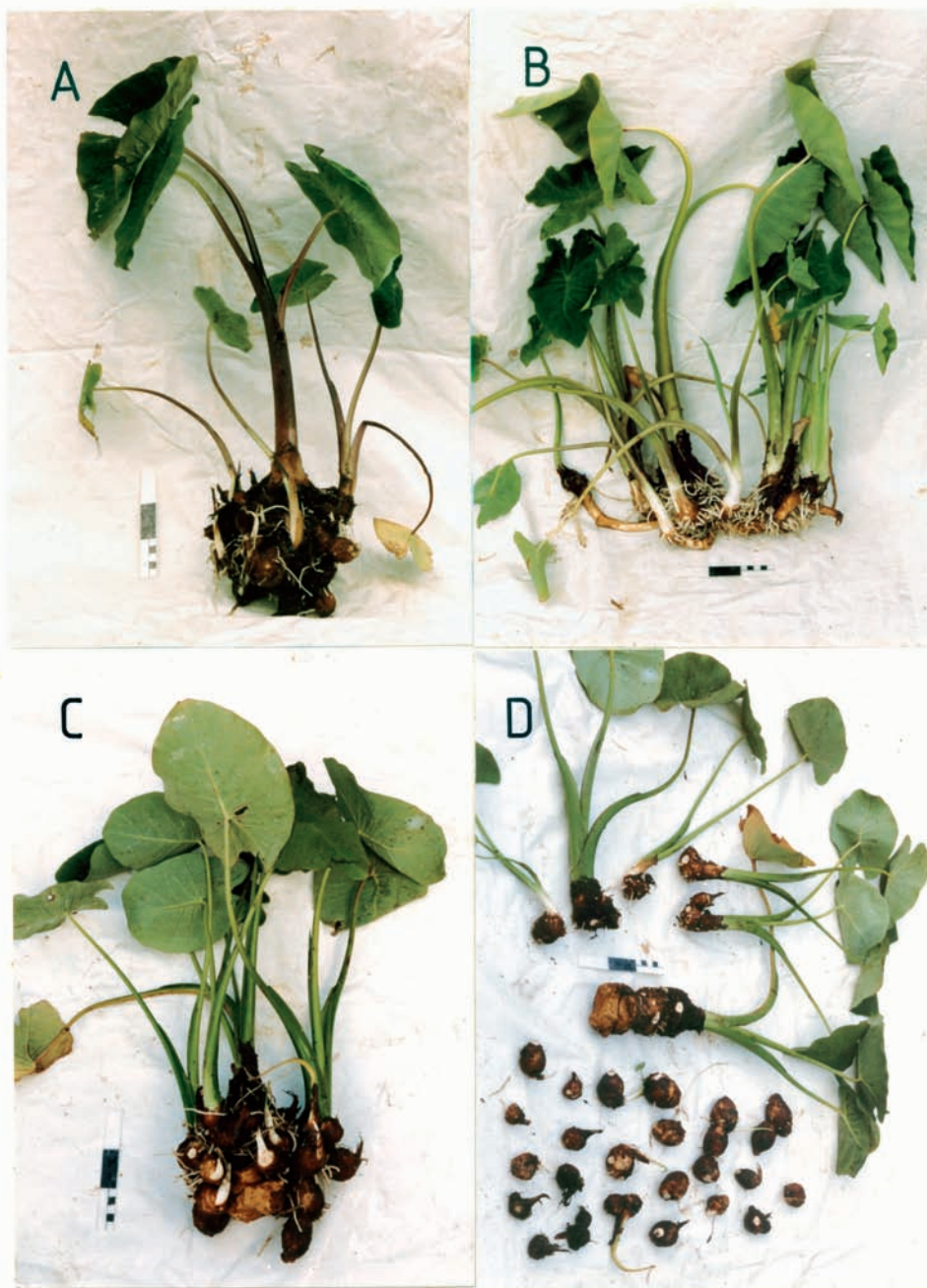


Figure 5.2 Growth habits of New Zealand variants of *C. esculenta*. Plants from potted corms after one year outside (late winter, 1982, to late winter, 1983) at Auckland. Scale bar = 15 cm. (A) Variant RR, AKL 2, tight clump formed with secondary and tertiary side-corms. (B) Variant GP, AKL 29, spreading clump formed with stolons. (C) Variant GR, AKL 37, tight clump formed with secondary and tertiary side-corms. (D) Same as C, dissected.

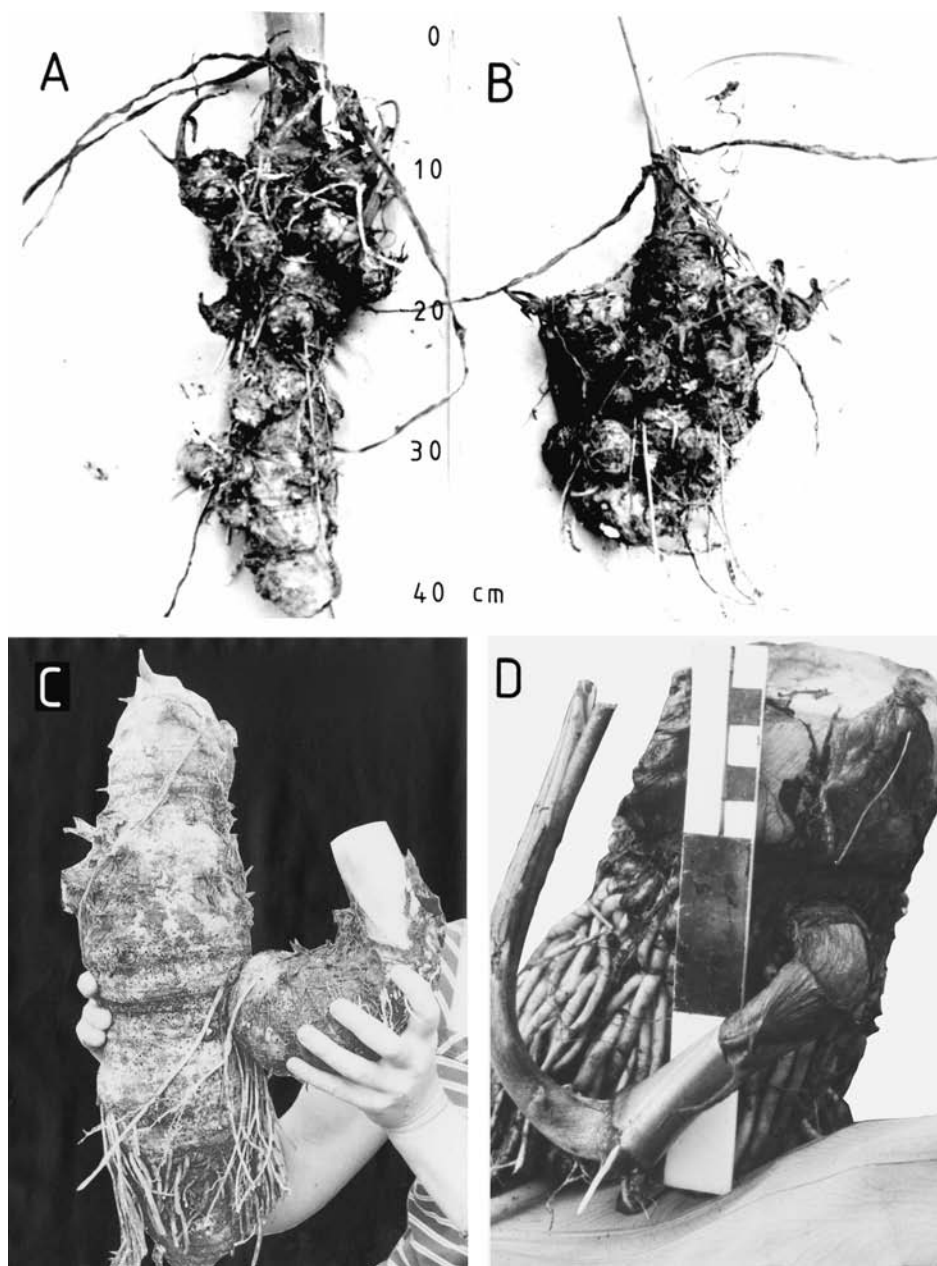


Figure 5.3 Growth habits of New Zealand variants of *C. esculenta*, in the field A and B: from same site (N39/6), Coromandel Peninsula, August 1983; non-cultivated, growing at surface of wet, forest topsoil beside small stream. (A) Variant RR, corm with side-corms; (B) Variant GR, corm with side-corms. C and D: Variant GP, non-cultivated, from boggy ground beside. (C) Corm growing above ground, with secondary corm developed from side-shoot, North Hokianga (site N14/30), February 1983; (D) cut top of corm with petiole base, roots, and stolon. A young root has emerged from the second node of the stolon. The shoot above the second node has had leaves removed. Bay of Islands (site N15/4), May 1982. Scale bar = 15 cm

None of these appeared the same as the New Zealand variants, so descriptions will not be presented.

New Zealand variants collected, other than those already described, are AKL 34, AKL 79, AKL 80, AKL 81, AKL 82, and AKL 87. All of these are known only from single garden sites. Cytological observations have been made on only AKL 34 and AKL 79 (Chapter Six).¹⁾

AKL 34 appears, on limited observation of potted material, to attain a smaller stature than the variants RR, GR, and GP, with shorter petioles and smaller blades. This may be due to its habit of proliferating rapidly, with many tiny side-corms quickly forming shoots around the small, spherical central corm. The size that would be reached after prolonged growth is not known. The blades and petioles are pale green to yellowish green with no traces of red pigmentation. A traced outline of one blade is shown in Figure 5.4.

AKL 79 is like AKL 34 in growth habit but has purple/carmine colouration up part of the petiole, from the base, and in the veins of the blade. The blade has a rather dark appearance. A traced outline of one blade is shown in Figure 5.2.

AKL 80 and 81 are said to differ in petiole length, blade texture, and venation, and whether or not they flower (G. Fuller, pers. comm. 1982, 1983). However, both flowered while maintained in the Auckland collection, and both have very similar general morphology.

AKL 82 is the only variant with marginal petiole insertion and recorded here as '*Colocasia* (?)'. Only one shoot has been observed: the petiole is completely dark purple/carmine, with this colour predominant in the veins of the blade. Staff at Pukekura Park, New Plymouth (G. Fuller, pers. comm. 1983) are familiar with *Xanthosoma* (marginal petiole insertion also) and are certain that AKL 82 is not of this genus. This accession may belong to the '*piko*' group of cultivars noted in the introduction above. A traced outline of one blade is shown in Figure 5.4.

Mutations

At termination, the living plant collection contained fifty-six accessions of variant RR; nine accessions of variant GR; ten accessions of variant GP; and twelve single accessions of other variants or varieties from New Zealand and Rarotonga. No obvious vegetative mutations were observed.

Diseases and pests

All taro seen during the field surveys appeared remarkably free of diseases and pests. Occasionally, leaf damage like that described as 'hopper burn' (Mitchell and Madison 1983) was seen in association with breeding populations of the passionvine hopper, *Scolypopa*.

Four occurrences of possible virus infection were noted in New Zealand taro:

(1) minor vein banding symptoms (feathering) in a succession of leaf blades of AKL 1 (from Little Barrier Island), variant RR, in January 1982, a number of months after collection and growing outside at Mount Albert, Auckland;

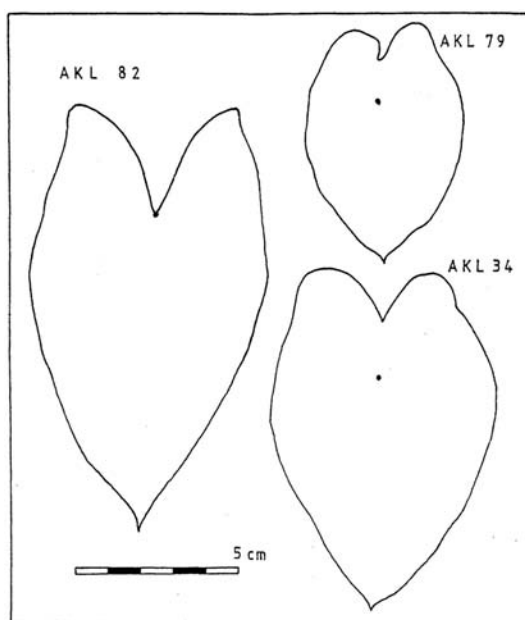


Figure 5.4 Leaf-blade outlines, each from a single leaf. AKL 34 and AKL 79: *C. esculenta*, peltate. AKL 82: *Colocasia?*, marginal petiole insertion. Petiole insertion points shown for each.

(2) recurrent interveinal chlorosis and deformed blade development in a potted plant of AKL 2 (from Little Huia, Auckland), variant RR, in August 1982, several months after collection and growing in a glasshouse in some proximity to virus-infected accessions of taro from Rarotonga (most of the Rarotongan varieties show obvious symptoms of virus infection, Figure 5.7),

(3) yellowed veins over one entire blade (Figure 5.7) in a patch of variant GP, growing wild at Omaio, East Cape (site N70/4), in January 1983; and

(4) chlorosis and deformity (Figure 5.7) in two leaf blades in a patch of variant GP growing wild at Herekino, Northland, (site N9+13/5), in February 1983.

Highly tentative diagnoses of these symptoms are, for each occurrence numbered: (1) dasheen mosaic virus (see Figure 13 in Jackson 1980); (2) dasheen mosaic virus (see Figure 3 in Zettler et al., 1978); (3) small bacilliform virus (see Figure 9 in Jackson 1980); and (4) unknown, symptom unlike previously described symptoms. Re-collection from the original sites, and further diagnostic investigation are needed to confirm these observations as first records of virus infection in New Zealand taro.

In a number of sites the torn ends of petioles indicated browsing by some herbivore. Pigs, goats, horses, sheep, cattle and pukeko were variously mentioned by informants in the field as animals which attack taro. Generally the large stock only eat the tops and

only in times of hunger, while pigs and goats may eat both tops and corms. Pukeko, reported only once, apparently slash the plants while searching amongst them for insects.

5.3.3 Flowering

The inflorescences of *Colocasia* are comprised of a spathe surrounding a spadix that contains zones of female, male, and sterile flowers (Strauss 1983). The structure of an inflorescence and the parts measured are shown in Figure 5.5.

General

Records of taro flowering in New Zealand, both recent and old, are listed in Table 5.1. During summer field work in North Auckland, in February 1983, prolific flowering by variant GP was observed in five sites.

Floral measurements are recorded in Table 5.2. No fruit formation was observed, and older spadices were seen withered and rotted to various degrees at the same time as younger spathes, on the same plant, were seen emerging (Figure 5.6) or shedding pollen.

As it was nearing the end of summer it was thought likely that increasing coolness would prevent any fruit development later.

Table 5.1 Records of *C. esculenta* flowering in New Zealand. For some, site number is given as the origin for collected material, or to specify the location of flowering. Collected material is identified by the plant accession number. Reference numbers for measured flowers are given for cross reference to the measurements in Appendix 8. G = garden; c = cultivated; nc = non-cultivated; d = derelict. For definitions of terms see Chapter Seven.

Variant	Origin	Plant acc. no.	Botany Department site no.	Site description	Flowering location	Region	Date or approx. period	Flowers measured (ref. no.)	Informant
RR	N23/1			G,c	Tekawa Stn	Dargaville	Feb 1983		A. Stilwell pers. comm. 1983
RR	N41/2	AKL 2		Glasshouse potted	Botany Dept	Auckland	Mar 1982	Yes (1)	P. Matthews
RR	?		N41/2	G, nc, nd	Little Huia	Auckland	Oct - Nov		J. Walsh pers. comm. 1982
RR	NZMS259/1	1		Glasshouse potted	Botany Dept	Auckland	Mar 1982	Yes (2)	P. Matthews
RR	NZMS259/1	1		G,c	Mt. Albert	Auckland	July 1982	Yes (3)	P. Matthews
RR	NZMS259/1	1		G,c	Mt. Albert	Auckland	Dec 1982		P. Matthews
RR	NZMS259/1	1		G,c	Mt. Albert	Auckland	Mar 1983	Yes (4)	P. Matthews
RR	N33/1			G,c	Ponsonby	Auckland	May 1982	Yes (5)	I. Lawlor pers. comm. 1982
GR	?		N18+22/2	G, nc, nd	Waimamaku Beach Road	Hokianga	Feb 1983		P. Matthews
GP	?		N14/3	G, nc, d	Mitimiti Rd	Hokianga	Feb 1983	Yes (6)	P. Matthews
GP	?		N14/30	Wild	Reena	Hokianga	Feb 1983	Yes (7)	P. Matthews
GP	?		N9+13/1	Wild	Herekino	Herekino	Feb 1983	Yes (8)	P. Matthews
GP	?		N9+13/10	Wild	Tauroa Pt.	Kaitaia	Feb 1983		P. Matthews
GP	?		N9+13/5	Wild	Ngaire St.	Kaitaia	Feb 1983	Yes (9)	P. Matthews
?	?			?	Waimate	Bay of Islands	Feb 1895		T.F. Cheeseman 1)
?	?			Wild	Lava Point	Raoul Island	June 1956	Yes	R.C. Cooper (1969)
?	Samoa			Garden	Henderson	Auckland	April 1967		T. Harris 1)
?	?			Garden	Henderson	Auckland	March 1964		T. Harris 1)
esculenta	Edmund St			Garden	?	Auckland	Feb 1968		A.T. Pycroft 1)
esculenta	Bay of Islands			Garden	Edmund St	Auckland	April 1962	Yes	A.T. Pycroft 1)
esculenta	?			?	Ngaire Bay	Whangaroa	Dec 1963	Yes	A. Leahy 1)
esculenta	?			?	Kerikeri Beach	Bay of Islands	Dec 1963	Yes	A. Leahy 1)

?	?			?	Mataka Beach	Bay of Islands	Jan 1961		A. Leahy 2)
antiquorum	?			?	?	Kaitiaia	April 1921	Yes	R.H. Matthews 1)
antiquorum	?			?	Whareora	Whangarei	Sept 1968	Yes	J.C. Nicholson 1)
?	?			?	Te Araroa	East Cape	'recently'		R. McConnell pers. comm. 1982
?	?			?	?	Northland	Jan		K. Reynolds pers. comm. 1982
?	?			?	?	Northland	May		K. Reynolds pers. comm. 1982
?	?			?	?	Northland	June		K. Reynolds pers. comm. 1982
antiquorum	?			?	Remuera	Auckland	May 1970		Herbarium specimen AK 123004
RR	Opotiki			?	Remuera	Auckland	Feb 1974		Herbarium specimen AK 151544
tarohoia	Hokianga			?	Remuera	Auckland	Apr 1980		Herbarium specimen AK 151597
AKL 80	N109/2	AKL 80		Glasshouse, potted	Botany Dept	Auckland	Sept 1983	Yes (10)	P. Matthews
AKL 80	?	AKL 80	N109/2	outdoors	Pukekura Park	New Plymouth	Apr 1983	Yes (11)	P. Matthews, G. Puller pers. comm. 1983
AKL 81	?	AKL 81	N109/2	outdoors	Pukekura Park	New Plymouth	Apr 1983		P. Matthews, G. Fuller pers. comm. 1983
AKL 81	N109/2	AKL 81 AKL 12		Outside, potted	Botany Dept	Auckland	Dec 1983		P. Matthews
Tonga Sea	DSIR Rarotonga	AKL 12		Glasshouse, potted	Botany Dept	Auckland	Apr 1983	Yes (12)	P. Matthews
Niukini Ava'ava	DSIR Rarotonga	AKL 15		Glasshouse, potted	Botany Dept	Auckland	Apr 1983	Yes (13)	P. Matthews
Malahu	DSIR Rarotonga	AKL 16		Glasshouse, potted	Botany Dept	Auck land	Apr 1983	Yes (14)	P. Matthews

1) See R.C. Cooper (1969). 2) See New Zealand Archaeological Association Site Record Form (NZMS 1) N11/300.

Variant RR, potted in the glasshouse (Figure 5.5) and outside, has been seen to flower and shed pollen. Prolific flowering in patches, as with variant GP, was not observed. Flowers have not been observed for variant GR. This may be partly due to chance: fewer accessions of this variant were collected than of variant RR. Formation of a flag leaf, however, was seen on one occasion in the field. In all instances of the other variants flowering, each inflorescence was preceded by emergence of a flag leaf. Ghani (1982) described the flag leaf as a 'morphological indicator' for flower emergence within the following twelve days. Coarse dissection of variant GR with a flag leaf, however, revealed only young vegetative shoots. Very young or retarded inflorescences may have been missed in this dissection.

Records and measurements of flowering by other taro variants collected are given in Appendix 8.

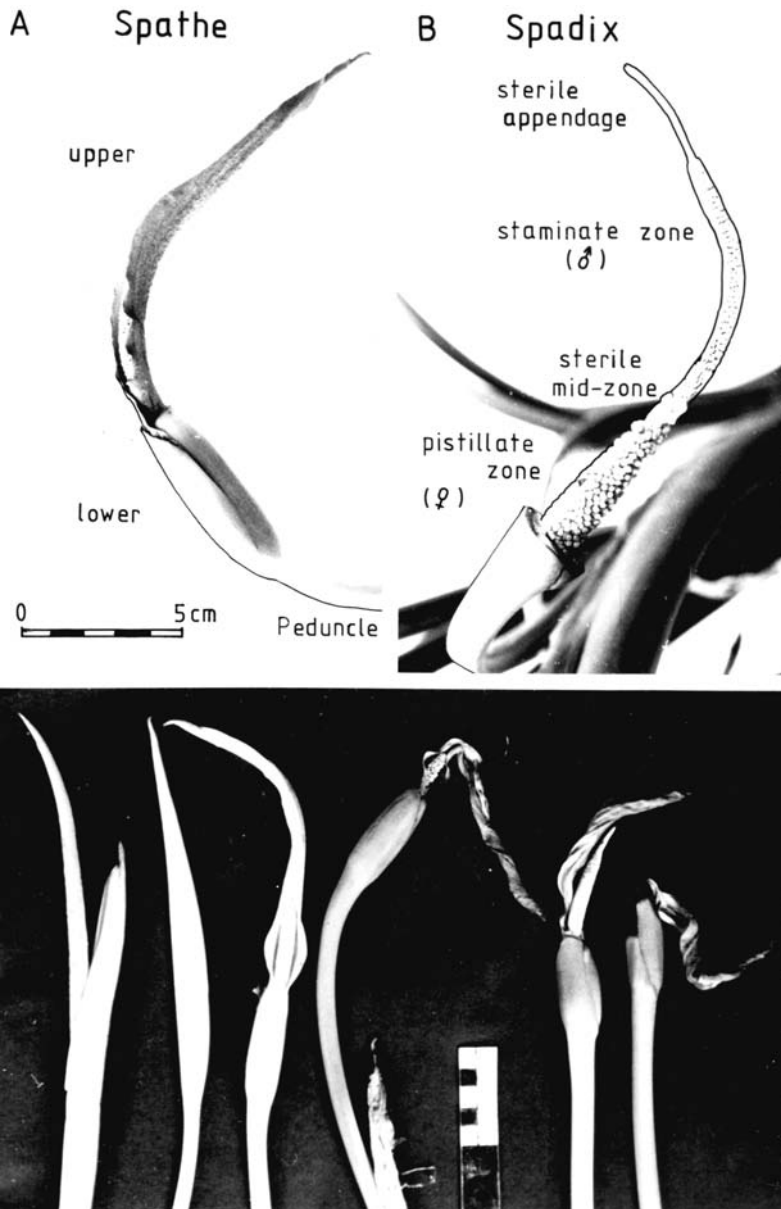


Figure 5.5 Flowering of *C. esculenta* variant RR, in New Zealand. (A) Spathe and peduncle with parts labelled. (B) Spadix with parts labelled. A and B: Accession AKL 2 from Little Huia, Auckland, potted in glasshouse, March 1982. Lower: A full set of four inflorescences from one plant, with the first formed inflorescence at far right. The flag leaves are not shown except for one between the second and third inflorescences, and one before the young leaf (rolled) at far left. The return to vegetative growth is accompanied here by the formation of a pseudo-spathe containing no spadix, and an aberrant flag leaf with a small growth of lamina tissue at its tip (far left). The spadix of the second inflorescence has become free of the spathe, while that of the third inflorescence remains bound within. Accession AKL 1 from Little Barrier Island, Hauraki Gulf, growing outside at Mount Albert, Auckland. March 1983

Table 5.2 Floral morphology of *C. esculenta*. Summary statistics for observations in New Zealand (variants RR and GP, 1982–83; var. *esculenta* and var. *antiquorum* from Cooper 1969) and Hawai’i (field-station varietal collection, Whitney et al. 1939). Data: Appendix 8. Note: Some rounding error is apparent in the calculation of means.

		Spathe (cm)			Spadix (cm)					Ratios				
		Total Length	Lower Part	Upper Part	Total Length	Pistillate Zone	Sterile mid-zone			Staminate Zone	Sterile Appendage	Spathe	Spadix	
												Lower/Upper	Sterile Append./Spadix	Sterile Append./Staminate
Variant RR	n	6	6	6	5	5	6	6	6	6	5	6		
	X	25.6	5.2	20.5	13.5	3.0	1.8	5.7	3.4	0.24	0.23	0.59		
	s.d.	3.5	0.7	2.9	3.6	1.0	0.5	1.1	1.2	0.03	0.06	0.17		
Variant GP	n				21	21	21	21	21		21	21		
	X				10.9	3.7	1.7	2.9	2.6		0.24	0.96		
	s.d.				1.5	0.6	0.7	0.7	0.5		0.03	0.23		
var. <i>esculenta</i>	n	6			6	6	3	6	6		6	6		
	X	23.6			9.3	3.9	1.9	3.0	1.4		0.14	0.53		
	s.d.	3.8			2.5	1.9	0.7	1.7	0.9		0.08	0.43		
var. <i>antiquorum</i>	n	2			2	2	2	2	2		2	2		
	X	20.3			13.4	3.5	1.7	4.3	3.9		0.29	0.90		
	s.d.	3.1			2.2	0.5	0.8	0.8	1.0		0.03	0.06		
Hawai'i n=No. of varieties	n	35	34	35	31				31	34	31			
	X	23.3	4.0	19.2	8.3				0.81	0.21	0.10			
	s.d.	5.5	1.0	4.7	2.6				0.31	0.03	0.03			



Figure 5.6 Flowering of *C. esculenta* variant GP, in New Zealand. Left: Whole plant with the first-formed inflorescence (outer-most) withered, and the second at the stage marked by yellow colour of the upper spathe. The spadix of the first inflorescence remains bound within the spathe. Plants in a derelict, non-cultivated garden, northern Hokianga (site N14/3). February 1983. Scale bar with centimetres. Right: Spadix revealed by partial dissection of the spathe. The upper spathe is yellow and pollen is being shed (apparent in roughness at surface of the staminate zone). Gynoecia (green) and stigmas are visible in the pistillate zone.

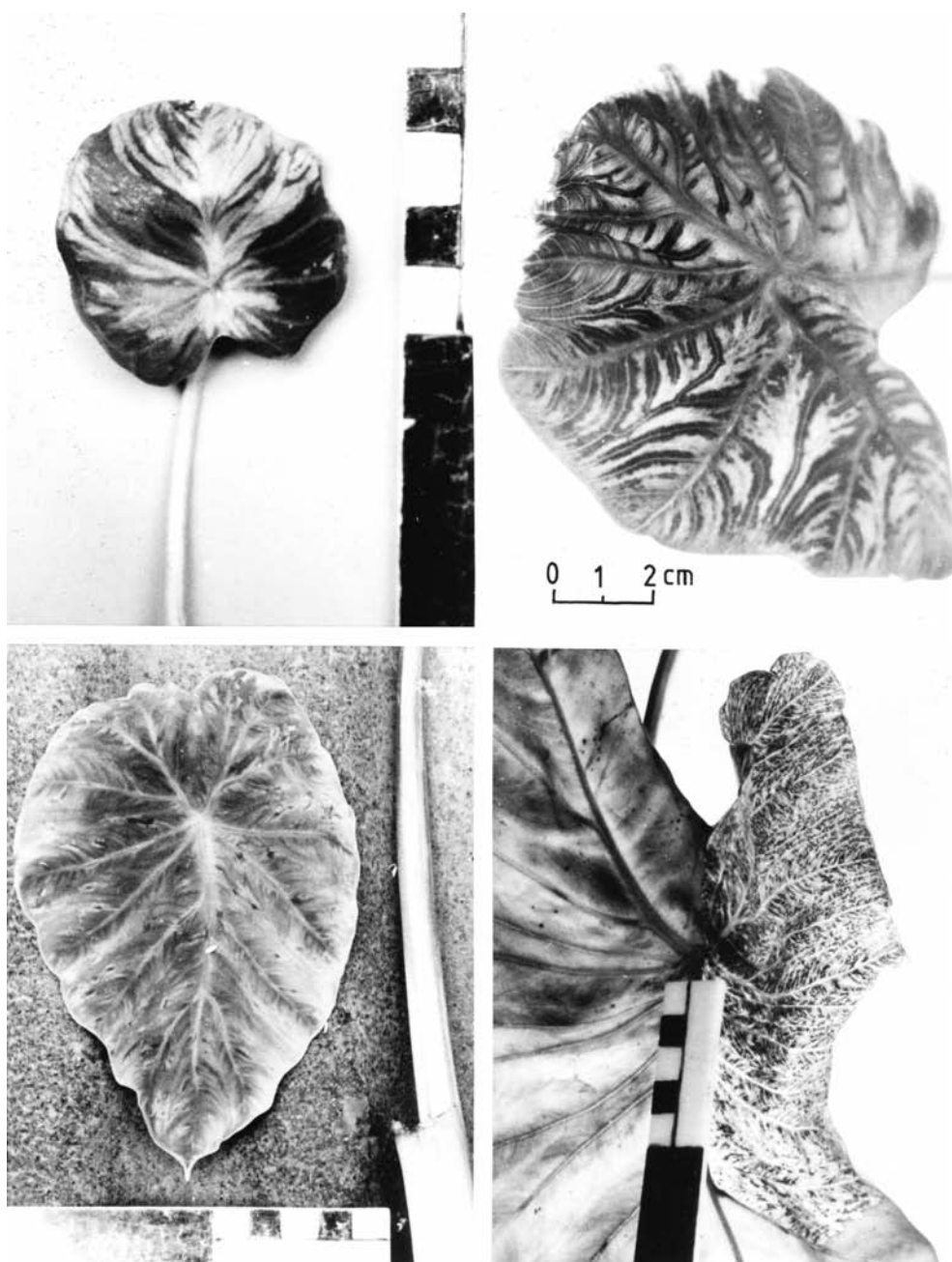


Figure 5.7 Leaf blades of *C. esculenta* with symptoms suggesting virus infection. Upper: Variant RR, AKL 2. Leaves taken at two times during August 1982, from a potted plant in the Department of Botany collection, Auckland. Lower left: Variant GP. Single diseased leaf in a wild patch at Omaio, East Cape (site N70/4), January 1983. Lower right: Variant GP. One of two diseased leaves observed in a wild patch at Herekino, Northland (site N9+13/5), February 1983.

Measurements

A summary of previously published data and the present observations is given in Table 5.2. Generally, the observations are very scanty and incomplete. While Whitney et al. (1939) state that their descriptions are based on turgid material, Cooper (1969) reports observations on dried herbarium specimens and the withered samples brought to him. In withered inflorescences disproportionate shrinkage of the male and sterile parts has been observed (Figure 5.5, lower).

5.3.4 Leaf shape analysis

Leaves of the variants RR, GR, and GP were classified prior to the analysis on the basis of leaf shape and colour, as described in the key above. The observations presented here quantify the characteristics of shape upon which the key is partially based.

Univariate statistics

Descriptive statistics for each of the observed leaf characters and some derived characters are given in Appendix 6.

Means and standard deviations for the blade characters used for canonical discriminant analysis are shown in Table 5.3. These statistics are summarised as the mean blade outlines shown in Figure 5.8. The visually most striking features of the outlines are:

- (1) the attenuation and spread of the rear lobes in variant GP; and
- (2) the similarity between RR and GR.

Multivariate statistics

Canonical discriminant analysis creates axes in the multidimensional space defined by the observed characters. The created axes (canonical variates) provide maximal discrimination between the centroid means of each group (taro variant). In this analysis the number of canonical variates that might provide discrimination is limited to two, one less than the number of taro variants, since the number of observed characters is greater than the number of groups (variants). Two canonical variates are sufficient for discrimination between three groups, assuming that all three are different with respect to characters included in the analysis.

With analysis of \log_{10} transformed blade measurements (Figure 5.9) only canonical variate 1 (CV 1) provides discrimination between the three taro variants. Scores for variant GP are clearly distributed lower on CV 1 than are scores for variants RR and GR, while no discrimination is apparent between the latter.

The largest standardised canonical coefficients (Table 5.3) for CV 1 are found with $\log_{10}B$ and $\log_{10}D$, showing that the characters B and D contribute most to between-group variation along the discriminant function (CV 1).

The reversed signs of these two coefficients show that maximum discrimination is obtained by contrast of large B and small D values with small B and large D values.

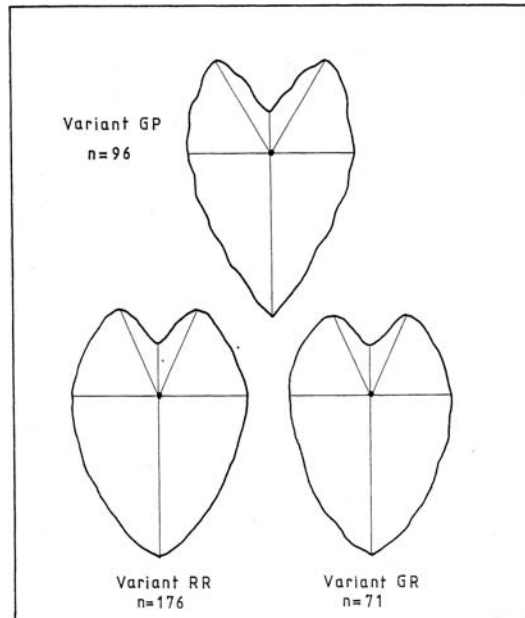


Figure 5.8 Leaf blades of three New Zealand variants of *C. esculenta*. Outlines based on mean values of the linear dimensions shown, depicted relative to the largest dimension of each. The real-size means of the largest dimension range from 20 to 26 cm approximately. Undulation in the margin of variant GP is a characteristic of that variant. The central circle represents the point of petiole insertion.

Close inspection of the blade outlines in Figure 5.8 confirms this interpretation: Variant GP has both longer rear lobes and a shorter sinus-to-petiole distance than variants RR and GR.

Although the spread between rear lobes is noticeably greater for variant GP than the other variants (Figure 5.8), the character (G) proved of minor importance in this analysis. This may reflect relatively low correlation between measurements of characters G and D (Table 5.4) resulting from the relatively high measurement error associated with G. In the field, difficulty was met in measuring G due to the flexibility of the lobes, while other, internal blade dimensions were more easily measured. On the obtuse rear lobes, the absence of a clear point of maximum lobe extension also contributes to error in measurement of G, and also to the derived character, sinus angle.

The blade sinus-angle, $2 \cdot \sin^{-1} \left(\frac{G}{B+C} \right)$, is a further quality which distinguishes variant GP from variants RR and GR, (Figure 5.8, Appendix 6).

However, because it is composed of linear leaf-blade characters related in a non-additive fashion, sinus-angle cannot contribute to the discriminant functions (canonical variates) — the present analysis is based only on the raw measurements of linear characters.

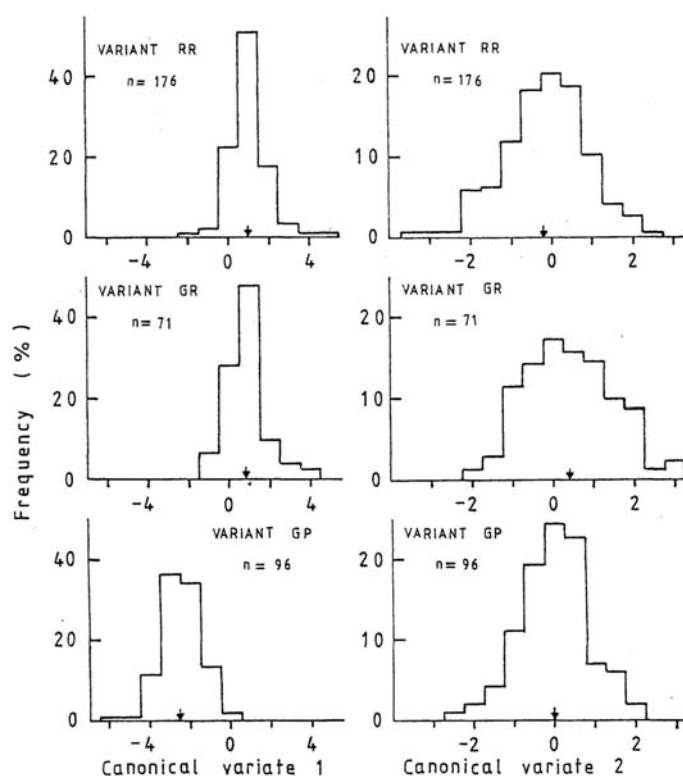


Figure 5.9 Canonical discriminant analysis of leaf shape in *C. esculenta*. Frequency histograms of the canonical scores for the New Zealand variants RR, GR, and GP. Arrows indicate mean scores.

Table 5.3 Canonical discriminant analysis of leaf shape in *C. esculenta*, New Zealand variants RR, GR and GP. Standardised canonical coefficients for canonical variates CV 1 and CV 2. The analysis was performed on \log_{10} transformed measurements of leaf blade characters (means and standard deviations of untransformed and transformed data given). Canonical r-squared shows the proportion of variance, in the canonical variate scores, explained by groups.

Units	Variant	n	Character Means and Standard Deviations.					
			A	B	D	E	G	
cm	RR	176	20.9 \pm 11.3	12.1 \pm 6.5	6.7 \pm 3.8	11.1 \pm 5.9	8.9 \pm 4.8	Canonical r-squared (%)
	GR	71	24.0 \pm 10.2	12.9 \pm 4.9	7.3 \pm 3.4	12.0 \pm 4.7	10.5 \pm 4.6	
	GP	96	25.5 \pm 10.3	16.8 \pm 6.8	6.6 \pm 3.1	12.9 \pm 5.5	16.3 \pm 7.6	
\log_{10} (cm)	RR	176	1.25 \pm 0.26	1.00 \pm 0.29	0.74 \pm 0.3	0.98 \pm 0.26	0.88 \pm 0.28	
	GR	71	1.34 \pm 0.18	1.08 \pm 0.17	0.82 \pm 0.19	1.05 \pm 0.17	0.97 \pm 0.21	
	GP	96	1.37 \pm 0.19	1.19 \pm 0.20	0.77 \pm 0.22	1.07 \pm 0.20	1.18 \pm 0.21	
Standard canonical coefficients	CV1		-0.12	-4.4	3.9	1.4	-1.1	70.3
	CV2		2.3	-4.4	1.5	-0.7	2.1	5.1

Table 5.4 Correlations between blade characters in *C. esculenta*. These were calculated as part of a principal components analysis (SAS command PRINCOMP) of 343 observed leaves (data for taro variants RR, GR, and GP, pooled after \log_{10} transformation; analysis not presented).

	log						
	A	B	C	D	E	F	G
log D	0.92	0.94	0.94	1	0.94	0.95	0.83

5.4 Discussion

5.4.1 Taxonomy

Floral Morphology

Despite the paucity of observations on flowering, possible differences can be seen between variants RR and GP in both the absolute and relative sizes of the staminate zones and sterile appendages (Table 5.2). Variant GP, with a mean ratio of sterile appendage to staminate zone length of 0.96, may represent what Cooper (1969) regards as var. *antiquorum* (Table 5.2) despite the fact that his specimens (mean ratio = 0.90) do not fit his stated criterion of a ratio equal to or greater than one. Further, both variants RR and GP were observed in the present study to retain the sterile appendage in the terminal part of the spathe (Figure 5.5, 5.6), a stated characteristic of var. *antiquorum* (Massal and Barrau 1956; Barrau 1957; Cooper 1969). Variant RR however, with a mean ratio of sterile appendage to staminate zone length of 0.59, clearly does not fit the stated criterion for var. *antiquorum*.

Comparison of the New Zealand variants with the observations of Whitney et al. (1939; and Table 5.2) indicates that varieties in the Hawai'ian collection have, in general, a much shorter sterile appendage which is also shorter relative to the overall length of the spadix. An inflorescence of such proportions is used by Massal and Barrau (1956) to illustrate *C. esculenta* in distinction from *C. antiquorum* (Figure 5.10).²⁾

From the above it appears likely that variant RR (with a sterile appendage of large size but shorter in length than the staminate zone) is like neither *esculenta* nor *antiquorum* according to the definitions of these (as either species or varieties) by authors outside New Zealand. On the basis of flower measurements it is not clear that variant GP is of *antiquorum* kind, and it certainly is not like *esculenta*. It seems likely that Cooper (1969) attempted to apply criteria developed by previous authors working with examples which did not include flowering types similar to the New Zealand variants.

Variation in floral characters may be greater than previously indicated by their use in the identification of two varieties of *C. esculenta*, and might have future use in identifying additional varieties. Gross floral morphology may however prove no more stable or useful than vegetative characters. Further, as Plucknett (1983) points out, floral characters are often not useful as many *Colocasia* cultivars rarely flower.

General Morphology

While only leaf shape and colour appear sufficient to consistently distinguish three New Zealand variants in the field, a much greater range of vegetative characters was required by Whitney et al. (1939) to classify a large collection of varieties. A greater range of characters has not been described for the New Zealand variants as little practical benefit would result. The variants RR, GR, and GP have been described on the basis of observations over a wide range of non-cultivated habitats in a temperate climate. Descriptions made outside New Zealand generally apply to plants under various forms of cultivation in tropical climates (Whitney et al. 1939; Purseglove 1972; Plucknett 1983). These environmental differences do not allow any clear comparisons of growth habit or individual leaf characters.

Leaf shape, rather than size, has been useful in the present study for discriminating between variants. However the shapes cannot be compared usefully with previous descriptions of leaves since these are based on insufficient numbers of characters to describe shape well. Whitney et al. (1939) present only ranges of blade length and width, while Strauss et al. (1979) measure numerous characters but omit the lobe length B (or

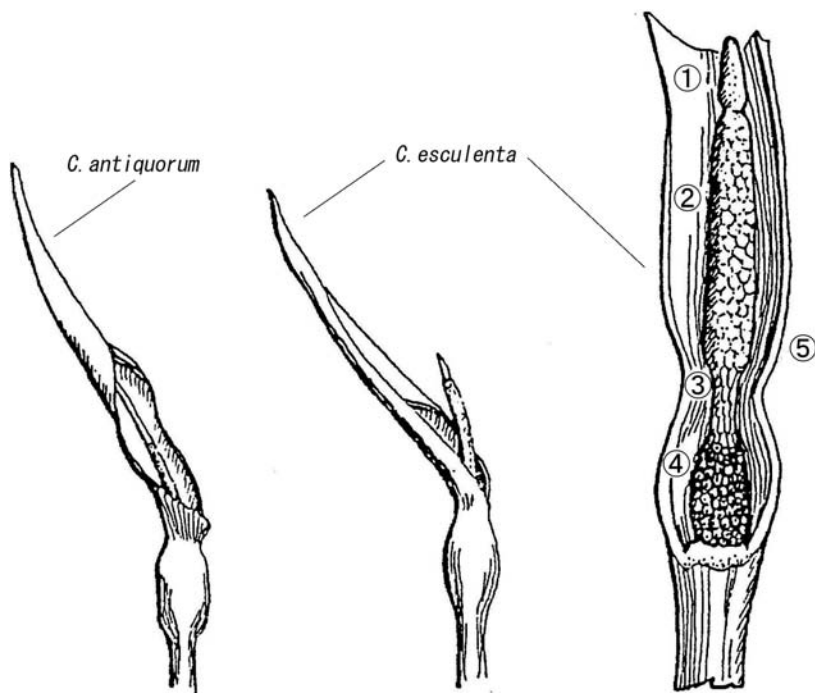


Figure 5.10 Two kinds of inflorescence in *C. esculenta*. The *esculenta* kind (right) has the following proportions: sterile appendage/staminate zone = 0.27; sterile appendage/total spadix = 0.13. Floral parts: (1) sterile appendage, (2) male flowers, (3) abortive flowers, (4) female flowers, (5) spathe cut lengthwise to show inflorescence. Illustrations and naming from Massal and Barrau (1956).

its equivalent, C) found important for best discrimination between the New Zealand variants.

In any event, leaf shape alone is insufficient to fully identify variants, cultivars, or varieties. Even comparisons using complete raw data sets and multivariate statistical techniques would probably, at best, show only very broad groupings in such an apparently polymorphic genus as *Colocasia*.

Using Field Keys for Recognition and Comparison

Classification keys based on vegetative characters, whether few or many, appear to have most use for the local recognition (for example, New Zealand or Hawai'i) of variants, cultivars, or varieties. Nevertheless, even crude comparisons between areas may be useful.

In applying the key of Whitney et al. (1939) to the New Zealand variants RR and GR, no progress could be made due to uncertainties in comparisons with corm size, production of side-corms, and petiole colour. Many variations of these characters appear in the key. However, one variety (*Aweu*) is reported with slender rhizomes which sometimes 'appear like creeping stolons' close to the surface, similar to the growth habit of variant GP. *Aweu* also resembles variant GP in leaf shape and possibly colour (Appendix 7). Although it is not possible to claim identity, the similarity may warrant an attempt to obtain living material from Hawai'i for a side-by-side comparison.

5.4.2 Natural dispersal

The distribution of taro in New Zealand is the outcome of both natural dispersal and transfer by people. The dispersal of corms and side-corms in watersheds (variants RR and GR), and by close side-shoots or spreading stolons (variant GP) has been described.

Cooper (1969), summing up observations of seven spadices from New Zealand sources (variants not identifiable), notes that they have small fruit and white ovules when fresh, but when spathes and stalks wither the fruit fail to ripen seed. Similar observations were made during the summer of 1982–83 for both variants RR and GP. All observations made to date indicate that there is no seed production in New Zealand.

The records of flowering in winter and summer suggest that seasonal control of flowering is poor, though this may differ for different variants. The number of records suggests that flowering is quite common.

Outside New Zealand, seedlings or germinating taro seed have not been observed in areas where the crop is cultivated and it is generally believed that seed rarely or never germinate.³ Seedlings if formed may perish due to fungal attacks or damping off (Sunell and Arditti 1983). Seed have germinated under a wide variety of controlled conditions (Ghani 1982; Strauss 1983; Sunell and Arditti 1983). Seed production after artificial self-pollination varied from much to little in different varieties (Sunell and Arditti 1983). Mass flowering may be a general characteristic of stolon-producing *Colocasia* such as variant GP, since Wilson (1982) notes from casual observations that natural flowering in *Colocasia* appears associated with a tendency towards stolon production.

5.4.3 Archaeology

Finally, good and bad news for archaeologists: taro pollen certainly is produced in New Zealand swamp sites but apparently, in Highland Papua New Guinea, it has proved impossible or extremely difficult to distinguish claimed fossil taro pollen from the pollen of other genera (Spriggs 1982). Encouragingly, the seed is hard and may have useful diagnostic characters. It remains to be tested how easily the seed rots.

5.5 Conclusion

Three major variants of New Zealand taro are readily recognised in the field. These have only been informally named as variants in order to stress that nothing should be assumed about their phylogenetic relationships. The taxonomic descriptions that have been made here, and elsewhere, are inadequate for positive identification of genetically similar taro outside New Zealand.

The present field observations indicate that taro is readily able to survive and self-propagate vegetatively in New Zealand, without human intervention.

Notes

- 1) Not all attempts to analyse chromosomes were successful. The standard method — described in Appendix 10 — works best when the plants are growing rapidly, eg. in warm conditions with increasing day-length. For tropical cultivars, the day length condition may not be important.
- 2) While describing a new species of *Colocasia* in Borneo, Hay (1996) provides a useful review of the naming of *C. esculenta* and its varieties.
- 3) A first indication that this view is wrong was provided by Barrau (1959), who found wild taro with fruit and seeds in Papua New Guinea. See also Figure 9.3, this volume.

Chapter Six Cytology

6.1 Introduction

Here, the chromosome numbers of New Zealand taro are investigated and the observations of previous authors are confirmed. The variants identified on morphological grounds (Chapter Five) are characterised further by chromosome number and karyotype. Observation of the karyotypes provides a further means for distinguishing the variants and allows limited speculation about the evolution of the nuclear genomes.

Rattenbury (1956, 1957) reported the somatic cell chromosome number of $2n = 42$ for untended taro from the Cavalli Islands. Further counts made by Rattenbury for New Zealand taro were reported by Yen and Wheeler (1968). ‘Apparently wild’ taro from Great Barrier Island and Spirits Bay also gave counts of $2n = 42$, and the specimen from Great Barrier Island was morphologically similar to that from the Cavallis (Yen and Wheeler 1968). A variety cultivated by the Māori of Northland, and called ‘island taro’, shared some morphological likenesses as well as the 42-chromosome complement with a wild specimen called *taro hoia* in the same area. Two other cultivated varieties from this district called *makatiti* and *pongu* gave counts of $2n = 28$. A reputedly Chinese variety grown by a Chinese market gardener in Auckland had the same chromosome number ($2n = 42$, implied by Yen and Wheeler 1968) as morphologically identical plants collected from two untended situations near Māori settlements in North Auckland and the Bay of Plenty. In their Pacific-wide study, ‘no obvious morphological correlates were noted in the field during the periods of collection or during the experimental growing in New Zealand of varieties of known chromosome number’ (Yen and Wheeler 1968).

As a consequence of the confusion surrounding the Linnaean nomenclature of *Colocasia* species and varieties, little significance can be placed on the correspondence between reported species/variety and chromosome number in lists such as presented by Plucknett et al. (1970), Marchant (1971), and Ramachandran (1978). In a particular instance, Rattenbury (1957) reported the New Zealand chromosome number under the name *C. antiquorum* Schott, while both he (Rattenbury 1956) and Yen and Wheeler (1968) regarded this name as synonymous with *C. esculenta* (L.) Schott, the name used by the latter authors when reporting the New Zealand chromosome numbers.

As part of a stated attempt to resolve conflicting results among chromosome studies of the Araceae, Marchant (1971), noted the range of counts previously reported for *C. antiquorum* (L.) Schott. Summarily, and without discussion, *C. antiquorum* is identified as a hexaploid ($2n = 42$) and *C. esculenta* as diploid [sic] ($2n = 28$), both with a basic number of $x = 7$.

Given the confused state of affairs outlined, I will simply present here all the previously reported $2n$ chromosome numbers under the genus name *Colocasia* Schott. The reports may be found cited in the lists of Plucknett et al. (1970), Marchant (1971) and Ramachandran (1978). Chromosome numbers reported for *Colocasia* Schott are $2n = 14, 22, 26, 28, 36, 38$, and 42 . Darlington and Wylie (1955) also report counts of $2n = 24$ and 48 . For the Pacific region, from Japan through Southeast Asia and out to Eastern Polynesia, Yen and Wheeler (1968) report only $2n = 28$ and 42 .

Two polyploid number series have been recognised for *Colocasia*, founded on the basic chromosome numbers $x = 12$, and $x = 7$ or 14 . Although Mookerjee (1955) reports an individual with $2n = 14$ as a probable diploid, that is with a basic number of $x = 7$, Yen and Wheeler (1968) note as an alternative explanation that Mookerjee's find may be a rare natural haploid. However, Plucknett et al. (1970), citing Sharma (1956), list a count of $2n = 14$ for a hybrid plant, thus implying a diploid with the basic number of $x = 7$. More recent authors also differ in what they regard as the basic chromosome number for the $2n = 28$ and 42 series. Marchant (1971) gives the basic number as $x = 7$, while Pursglove (1972) regards it as $x = 14$. Ramachandran's report (1978) of irregular meiotic pairing behaviour in pollen mother cells is good evidence of triploidy in a variety with 42 chromosomes. It seems quite possible that in fact both $x = 7$ and $x = 14$ occur as basic chromosome numbers in the genus *Colocasia*.¹⁾

6.2 Materials and Methods

All plants investigated were obtained from within New Zealand. Material used for cytological analysis came from potted plants of the living plant collection in Auckland. Shoots were removed from the pots and stripped of leaves and roots before export to Australia, where the investigation was made. The shoots were repotted in a loam and peat potting mix and grown in a glasshouse at the Research School of Biological Sciences, Australian National University, Canberra. Root tips 1–2 cm long were harvested from young roots 1–10 cm long, 1–2 weeks after repotting, at times during morning or afternoon.

Pre-treatment, fixation, staining, and squash of root tips were performed as described in Appendix 10. Feulgen staining, using a modified formula after Darlington and La Cour (1969) was followed by lacto-propionic orcein.

Chromosome counts of cells at mitotic metaphase, and photographs, were made using a Zeiss photomicroscope with either a Neofluar 100x/1.3 aperture/oil immersion objective for bright field optics or a Ph 3 oil immersion lens for phase-contrast. Photographs were taken with green light on panchromatic, black and white film rated at ASA 25 for bright field exposure and ASA 15 for phase-contrast. Varying magnification was used depending on the spread of chromosomes on the slide. For the preparation of karyotypes enlargements of photomicrographs were traced, the tracings enlarged and then reduced to similar scale by Xerox. Chromosome outlines were cut out, sorted, and retraced. Sorting was carried out by the following routine: outlines were first sized against two ruled divergent lines, then roughly grouped according to centromere position.

Closer matching was then made largely on the basis of shape and centromere position as judged subjectively by eye. Grouping by centromere position followed the definitions provided by Dyer (1979) for median centromeres (arm length ratio 1:1), sub-median (arm ratio $> 1:1$, $< 3:1$), and sub-terminal (arm ratio 3:1 or greater). Since accurate and repeated measurements are lacking, the groupings must be regarded only as approximate and tentative. Other terminology used follows Dyer (1979).

6.3 Observations

Details of reliably observed chromosome counts are presented in Appendix 10. Somatic cell chromosome counts were all $2n = 42$ for the variants RR, GR, and GP, represented by plants from sites spanning the distributional ranges (Chapter Seven) of each of these variants (Figure 6.1; Appendix 10). Two accessions of variants known only from single sites have the number $2n = 28$ (AKL 34 and AKL 79, Figure 6.1). Unreliable counts previously made by the author in Auckland also indicated the number $2n = 42$ for variant RR (accessions AKL 2, 50, 84, and 86), variant GR (AKL 67), and variant GP (AKL 25 and 29).

Outline drawings for the karyotypes of variants RR, GR, GP, AKL 34, and AKL 79 are presented in Figure 6.2. Two examples of each are given, with the chromosomes grouped according to centromere position, size, and general shape. Features of the karyotypes of each variant are outlined below. Note that where little size range is apparent within a numbered group, allocation to pairs as shown in Figure 6.2 is highly speculative.

6.3.1 Variants RR and GR

Chromosomes with sub-terminal centromeres: (1) Three pairs of larger chromosomes. A slight range of size between pairs. (2) Three pairs of smaller chromosomes, centromeres approaching sub-median position. A slight range of size between pairs.

Chromosomes with sub-median centromeres: (3) Three pairs of larger chromosomes, centromeres approaching sub-terminal position. Some range in size apparent between pairs. (4) Three pairs of larger chromosomes, similar in size to group three. No obvious range in size. (5) Three pairs of smaller chromosomes. No obvious range in size. (6) Three pairs of chromosomes smaller than those in group five. No obvious range in size.

Chromosomes with median centromeres: (7) Three pairs with possibly a slight range in size.

6.3.2 Variant GP

Chromosomes with sub-terminal centromeres: (1) Three unpaired chromosomes ranging in size.

Chromosomes with sub-median centromeres: (2) Three unpaired chromosomes with centromeres approaching sub-terminal position. No obvious range in size. (3)–(7) Five groups of six chromosomes, with groups ranging in size from large to small. No obvious range in size within groups.

Chromosomes with median centromeres: (8) Three pairs with no obvious range in size.

6.3.3 Variants AKL 34 and AXL 79

Chromosomes with sub-median centromeres: (1)–(6) Six groups of four chromosomes, with groups ranging in size from large to small. No obvious size range within groups.

Chromosomes with median centromeres: (7) Two pairs of chromosomes with possibly a slight difference in size.

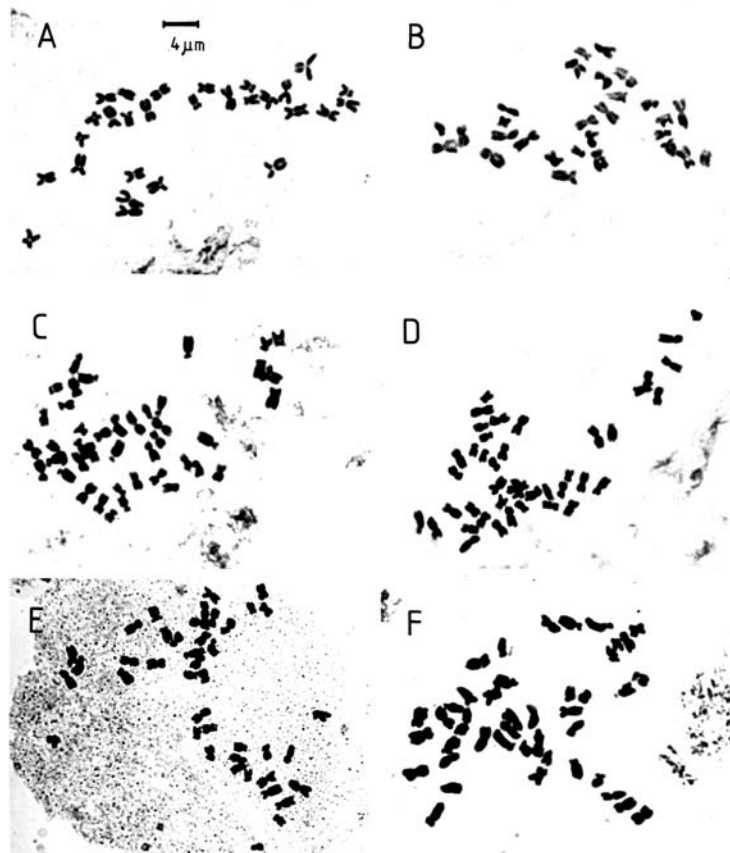












































































































































Figure 6.1 *C. esculenta*–root-tip metaphase chromosomes from single cells of: (A) AKL 34, $2n=28$; (B) AKL 79, $2n=28$; (C) Variant GR, AKL 83, $2n = 42$ (photo collage); (D) Variant GP, AKL 30, $2n = 42$; (E) Variant RR, AKL 48, $2n = 42$; (F) Variant RR, AKL 27, $2n = 42$. Scale: highly approximate, for A–E.















Centromere	Colocalize	esculento	AKL 69 Variant GR
sub-terminal			
sub-medial			
medial			

Centromere	Colocasia	esculenta	AKL 93	Varian ⁹	GR
sub-terminal					
sub-medial					
medial					

Centromere	Coloagasic esclerótica	AKL 17 Variant GP
sub-terminal	  	sub-medial   
sub-medial	 	 
 	 	 
 	 	 
 	 	 
 	 missing	 
medial	 	 

Centromere	<i>Colocasia esculenta</i>	AKL 30	Variant GP
sub-terminal			
sub-medial			
sub-terminal			
sub-terminal			
sub-terminal			
sub-terminal			
sub-terminal			
sub-terminal			
sub-terminal			
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Centromere	Colocasia esculenta	AKL 34 cell 1
sub-median		
		
		
		
		
		
median		

Centromere	<i>Calceolaria esculenta</i>	AKL 34 cell 2
sub-median		
		
		
		
		
		
median		

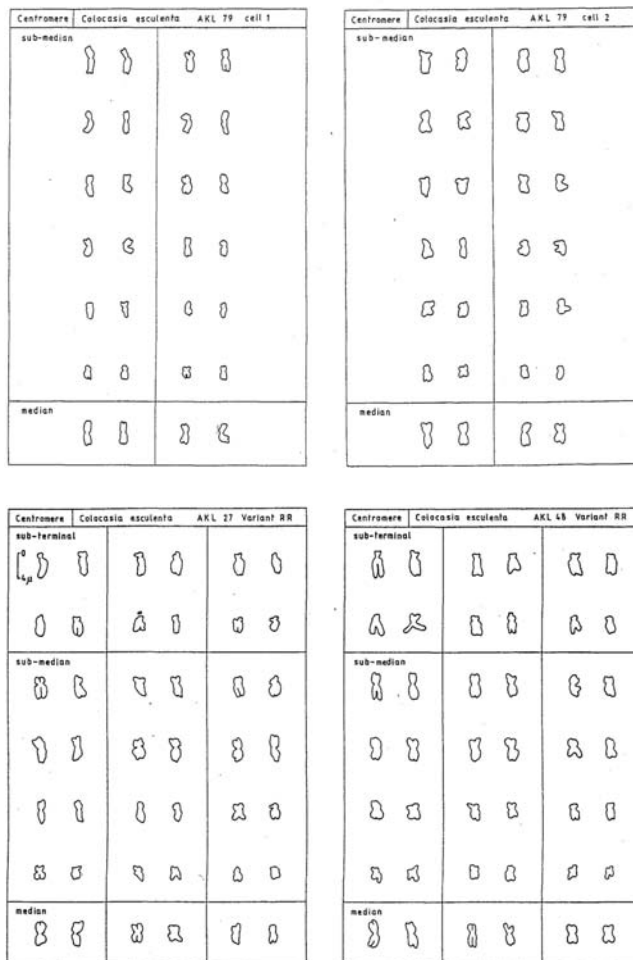


Figure 6.2 Tentative karyotypes of five variants of New Zealand taro. Variant RR: $2n = 42$ (accessions AKL 27 and 48); Variant GR: $2n = 42$ (accessions AKL 69 and 83); Variant GP: $2n = 42$ (accessions AKL 17 and 30). Variant AKL 34: $2n = 28$ (two cells from one root tip); Variant AKL 79: $2n = 28$ (two cells from one root tip). Scale similar but not identical for each accession. A highly approximate indication of scale is shown for AKL 27.

6.4 Concluding Discussion

6.4.1 Chromosome numbers

The repeated observation of the chromosome number $2n = 42$ has firmly established this as a characteristic of each of the three variants RR, GR, and GP. The observations also confirm the previous reports of $2n = 42$ for taro at Spirits Bay, the Cavalli Islands, Great Barrier Island, North Auckland, and the Bay of Plenty. In contrast to the report of Yen and Wheeler (1968), no taro with the number $2n = 28$ were observed in accessions from in or around Māori communities of Northland. However, the variant AKL 34 ($2n = 28$) is said to have arrived at its present single known site in Whangarei hand-to-hand from a Māori source in the central inland Bay of Islands (K. Reynolds pers. comm. 1981, 1982; T. Chamberlain pers. comm. 1982). The variant AKL 79 ($2n = 28$) is also known from a Māori source (M. Rau-Kupa pers. comm. 1983), but in Taranaki. This is an area where no field exploration has been made, and from where other as yet untested variants (AKL 80, 81, and 82) have been received.

6.4.2 Karyotypes

Variants RR and GR

Initial observation of karyotypes in the tentatively proposed arrangement shown in Figure 6.2 indicates that the variants RR and GR are similar. One possible interpretation of the arrangement, assuming variation along rows (Figure 6.2) between chromosome pairs, is that it represents an amphidiploid allohexaploid ($2n = 6x = 42$) of a form such as AABBC. The possible routes of origin for such a combination of genomes are varied and complex, and do not warrant discussion here in the absence of a definite karyotype.

Variant GP

While the karyotypes of variants RR and GR quite clearly suggest a basic chromosome number of $x = 7$, the karyotype of GP may reflect a basic number of $x = 14$. Although in variant GP few distinctions are apparent among the large number of sub-median chromosomes, the presence of three unpaired sub-terminal chromosomes of varying size could reflect an allotriploid arrangement ($2n = 3x = 42$) of the form ABC. A basic number of $x = 14$ could have evolved by differentiation between pairs of homologous complements of $x = 7$ present in an amphidiploid allopolyploid ancestor (for example AABBC, AABB) or autotetraploid ancestors (for example AAAA); or between the diploid genomes ($2n = 2x = 14$) of different ancestral parent populations prior to hybridisation events and amphidiploidy. The degree to which such differentiated complements $x = 7$ might behave in non-homologous fashion would be an important determinant of chromosome pairing behaviour during meiosis.²⁾

It is unfortunate that reports of seed production and germination have not generally been accompanied by the observation of karyotypes or chromosome number (for example, Strauss et al. 1980; Ghani 1982; Shaw 1982). It can only be hoped that in future, greater attention will be given to combining observations of cytology with breeding trials and observations of natural seed production.

Approximately 2500 seed per inflorescence were harvested by Strauss et al. (1980) after hand pollination of *C. esculenta* var. *antiquorum* cv. UCI Runner, grown under greenhouse conditions.

Mookerjea (1955) describes an Indian 42-chromosome karyotype, but the absence of a clear pictorial presentation prevents useful comparison.

Secondary constrictions and chromosome satellites observed by Mookerjea (1955) may or not be present in the New Zealand karyotypes. The observations made so far are insufficient for further comment on the potential of constrictions and satellites as genomic markers.

Other Variants

The karyotypes of AKL 34 and AKL 79 appear similar, with a possible arrangement of 28 chromosomes into seven groups of four indicating a basic number of $x = 7$. The uniformity within each of the seven groups suggests an autotetraploid arrangement of the form AAAA.

However, in the absence of any knowledge of intrachromosomal structure or meiotic pairing behaviour, allotetraploid (AABB) or even diploid ($2n = 2x = 28$) arrangements must be regarded as possible interpretations. The regular meiosis and high pollen fertility reported by Ramachandran (1978) for two South Indian 28-chromosome varieties could reflect either amphidiploid tetraploid (AABB) behaviour, or the fertility of a non-hybrid diploid (AA) (Dyer 1979). Thus Ramachandran's interpretation of the South Indian varieties as diploid ($2n = 2x = 28$) must be treated as tentative. This example illustrates the caution required should further study of the New Zealand variants be made.

6.4.3 Cytological correlations with phenotypes

An interesting aspect of the present observations is that there seems to be a correlation between morphological phenotype and karyotype. Variants RR and GR, of similar growth habit, share similar karyotypes, while variant GP is dissimilar in both growth habit and karyotype. Variants AKL 34 and 79 share a third kind of growth habit and a third form of karyotype. It would be of considerable evolutionary interest to verify this suggestion with both the present variants and a wider selection of cultivars and wild forms. Verification would require better definitions than are presently available for both phenotypes and karyotypes.

The observation of marked morphological differences between the variants, RR, GR, and GP, all with the chromosome number $2n = 42$, confirms the lack of correlation between morphology and chromosome number, as noted by Yen and Wheeler (1968).

6.4.4 Future investigation

Future investigation of meiotic pairing behaviour is possible for at least the variants RR and GP, since both of these have been observed flowering quite commonly (Table 5.1). During the formation of pollen, varying genomic arrangements may result in similar meiotic pairing behaviour, so observation of meiosis should be accompanied by the investigation of intrachromosomal structure. This is needed to test for variation between

putatively identical genomes, or for homologies between putatively dissimilar genomes.

A large range of techniques are available for such an investigation including, in addition to the traditional cytological stains: Geimsa stain, DNA-specific fluorescent dyes, and radioactive DNA probes made from cloned genes or fragments of genes (see Chapter Twelve).

Notes

- 1) Cusimano et al. (2012) demonstrate that $2n = 28$ is the common diploid number for genus *Colocasia*, and that the ancestral haploid chromosome number for Araceae is $n = 16$, with chromosome loss leading to the haploid number $n = 14$.
- 2) The discussion up to here follows the observed variation in karyotypes. In the original MSc thesis, discussion continued based on a misidentification of fruit and seeds (which suggested that var. GP was a fertile hexaploid, not a sterile triploid). A recent study by Cusimano et al. (2012) indicates that a haploid chromosome of $n = 9$ is ancestral deep in the evolutionary past of all Araceae, that this doubled to $n = 18$ in early history of Araceae, and that a haploid chromosome number of $n = 14$ (diploid number of $2n = 28$) arose by reduction among distant ancestors of the genus *Colocasia*, within the Araceae (these authors reject the use of 'x' basic number terminology).

Chapter Seven Distribution

7.1 Introduction

Observations are presented here from fieldwork conducted in 1982 and 1983. Intensive fieldwork was carried out in widely separate areas of the North Island, establishing something of both the general range and local distribution pattern of the three taro variants already described (Chapter Five). In order to gain insight into the possible historical basis of distribution, records also were made of cultural practices related to taro.

The observations provide limited and circumstantial evidence of when taro introductions to New Zealand may have been made. Consideration is given to the possibility, raised by Rattenbury (1956) and Yen and Wheeler (1968), that taro present on the Cavalli Islands, at Spirits Bay, and on Great Barrier Island are remnants from pre-European times.

Early written records indicate that taro was once widespread in Māori cultivations of the North Island (Nicholas 1817; Wade 1842; Best 1976). In 1769, Captain Cook and his companions observed taro in plantations around the East Cape and in the Bay of Islands (Best 1976). Colenso (1880) listed Māori names for taro in two groups, according to the geographic origin of each name:

- (1) the North, including the Bay of Islands, Hokianga, and Kaitia districts; and
- (2) Hawkes Bay and the East Coast, south of East Cape.

European crops in Māori cultivations were commonly observed by the early writers after Captain Cook. Hargreaves (1959) stated that by the time the first European settlers arrived in the North Island (between 1800 and 1850), Māori agriculture had developed to such an extent that it was able to provide the settlers with regular supplies of pigs, and crops of European origin: potatoes, maize, and wheat.

Taro appears to have been quickly displaced after the introduction of European crop plants. Cheeseman (1900) notes that fifty years previously ‘taro was seen in every Māori cultivation of any size’ but had by 1900 fallen into almost total disuse. Kirk (1868) briefly described, amongst naturalised plants of the Auckland Province, ‘*Colocasia antiquorum*’ as remnant or escaped from field cultivation, found growing on waste places or by roadsides, and in wet soil or water.

Taro also was observed last century in South Island cultivations. Dieffenbach (1843) found taro growing alongside potatoes by the village of Mokupeka, on Arapawa Island, Queen Charlotte Sound, about 1839, while Brunner (1952) observed taro plantations ‘of former days’ near a deserted *paa* (hill forts) at the mouth of the Hokitika River, in 1847. It is not clear from these and other reports whether taro was a pre-European crop in the

South Island.

A fuller outline of records and events during the early period of European contact is presented by Leach (1984).

Details of site location, or descriptions which allow direct identification of variants, have not generally been presented. Recently, taro chromosome numbers were reported for unspecified sites on the Cavalli Islands (Rattenbury 1956, 1957), Great Barrier Island, Spirits Bay and near settlements (unspecified) of Northland and the Bay of Plenty (Yen and Wheeler 1968).

Hayward et al. (1979) did report specific locations for taro sites seen during an archaeological survey of Motukawanui Island of the Cavalli's group.

7.2 Methods

7.2.1 Botanical exploration: strategy

Because of cost and time limitations, fieldwork was conducted in areas where taro was already known to exist. Initial information came from correspondence (Appendix 1), site records of the New Zealand Archaeological Association, historical references, and through personal contacts with a number of archaeological and botanical fieldworkers.

In an exploratory field trip (Matthews 1982b) it appeared that taro was common in rural Māori communities. Subsequent field surveys were generally directed through such communities.

Surveys were made by observation from the road, interviewing farmers and other residents, and exploration by foot. Taro sites were recorded on archaeological site record forms of the New Zealand Archaeological Association (Appendix 2). These provided a convenient recording format. Map grid references were obtained from maps of the NZMS 1, one inch to the mile, series. The new NZMS 260 metric map series was not used as its coverage was incomplete.

7.2.2 Cultural observations

Observations and information on cultural practices were recorded as opportunity arose, and depending on the inclination and knowledge of informants.

7.2.3 Coverage

During field survey, coverage of local areas was never complete. The subjective decision to leave a locality was made when either it was felt that too little new information could be obtained by interview or observation, or when the effort of finding people or visiting possible sites was too time-consuming.

A limited knowledge of local absences of taro was obtained in interviews with farmers familiar with large areas of land, or with people familiar with a local community. Constraints on time were exerted by the day-to-day necessities of living and by the overall time allotted to the field trip. Legal restraints on access also limited observation.

Because of these limitations on coverage in the field, only the known positive extent of distribution can be presented here.

7.3 Observations

7.3.1 Taro sites

For areas and dates of fieldwork (1981–1983), see Chapter Five.

Records and definitions of site categories

The records of sites are filed in the Department of Botany Herbarium, University of Auckland, and a duplicate set is held at the Auckland office of the New Zealand Archaeological Association. A list of the sites with tabulated descriptions is presented in Appendix 2 and summarised here in Table 7.1. Explanations of the terms used are as follows:

Botany Department (B.D.) Site Number Map Number for the N.Z.M.S. 1 map series (unless otherwise indicated) followed by a serial number for each site.

Variant Botanical variants (informal nomenclature, see Chapter Five) found at each site.

Cultivated Garden The plants are found in soil which is presently cultivated. Plants may or may not form a clumped growth habit depending on the attention given to them.

Non-cultivated Garden The plants are found in soil which is not presently cultivated. Plants of each of the variants typically form clumps by natural vegetative propagation. Varying intervention in the natural growth of the plants may occur depending on how people use them.

While cultivation of the soil clearly identifies a garden, non-cultivation may make it difficult to identify the plants as a garden component rather than as wild plants. If information from a local resident is not available, two kinds of circumstantial evidence can indicate plants as a non-cultivated garden component: (1) the immediate proximity of structural evidence for human settlement (house or other building of the European architectural tradition), and (2) the presence of other exotic plants characteristic of gardens: for example, the garden ornamentals *Alocasia macrorrhizos* (elephant's ear) and *Zantedeschia aethiopica* (arum lily).

Non-derelict: non-cultivated garden sites are considered non-derelict if they are in the immediate proximity of an inhabited or clearly habitable house.

Derelict: non-cultivated garden sites are considered derelict if they are in the immediate proximity of only ruined or clearly uninhabitable structures, or are apparently garden sites only because of the presence of other exotic plants.

Wild: Non-cultivated plants are classed as wild if no evidence of settlement (of European design) is seen or visible in the immediate proximity. Non-cultivated plants are also classed as wild if the circumstantial evidence of association with settlement (of European design) seems unclear. This requires subjective evaluation of the field evidence, so that the site categories of 'non-cultivated garden' and 'wild' overlap to an unmeasurable extent.

This classification of sites depends upon the thoroughness of field exploration, which for practical reasons can never be complete and consistent. Relevant field evidence of settlement also may have been destroyed.

Criteria for recording sites as separate

Generally, each site-record represents taro in a local watershed (stream, gully, rivulet, etc.) separate from other local watersheds. Exceptions to this rule were sometimes made where taro in a larger confluence is found below taro in a tributary or tributaries some distance away. A site on the larger confluence is separately recorded in this situation because it is not possible to identify a particular tributary as the only likely upstream source of taro (because more than one tributary is known with taro, or because not all the tributaries have been searched). Exceptions to the rule also were made where taro were found near each other, but in different site environments.

Non-cultivated and cultivated taro near a house may be recorded as separate sites if one group does not appear immediately derived from the other.

Summary of site records

A total of 300 sites were recorded in the file, including 243 sites reported by the present author. Three sites containing only taro other than the variants RR, GR, and GP are not represented in the summary (Table 7.1). The distributions of variants other than variants RR, GR, and GP (AKL 34, AKL 79, AKL 80, AKL 81, AKL 82, and AKL 87) are limited to single sites and are not considered further here.

The oldest site recorded was observed in 1930 or 1931 (N41/1), and the oldest site seen again in the present study was first recorded twenty-six years previously, in 1957 (N70/4, with variant GP).

The majority of sites recorded before 1981, and of sites recently observed only by persons other than the author, fall in the 'not known' categories shown in Table 7.1. Because of this, the frequencies of identified variants and of known site description largely represent the present-day distribution of taro.

Photographs of sites in each of the categories defined for site description are shown in Figures 7.1 and 7.2.

Geographic distribution of C. esculenta variants

The distribution of the three variants RR, GR, and GP in the areas of intensive fieldwork (Figure 7.3) are shown in Figures 7.4, 7.5, and 7.6. These areas are North Auckland, the Hauraki Gulf, and East Cape, and represent respectively the northern, middle, and southern areas of the explored distribution range. Inland East Cape (Figure 7.6) was not searched since it is largely uninhabited, unroaded, steep hill-country, rising to the Raukumara Ranges.

Other areas which are known through correspondence and archaeological site records to have taro have not been explored. These areas are the Kaipara Harbour district, Tauranga, Taranaki, and the northern West Coast of the South Island.

The South Island distribution does not seem likely to be important (J. Eyles pers. comm. 1982; G. Walls pers. comm. 1982), and A. Sheward (pers. comm. 1984) reports no success at finding 'pre-European' taro in the western Waikato area.

The northern and southern extremes of observed distribution are shown in Table 7.2 for each of the three major variants. Variant RR was overall the most commonly found,

Table 7.1 Occurrence of *C. esculenta* variants RR, GR, and GP in different site categories

VARIANT	SITE DESCRIPTION					Total	% Known Variants
	Garden			Not Known			
	Cultiv.	Non-cultivated					
		Non-derelict	Derelict		Wild		
RR	21	49	12	55	28	165	75
GR	1	18	1	6	2	28	13
GP	0	3	1	21	2	27	12
Not Known	2	1	2	8	76	89	
TOTAL	24	71	16	90	108	309	
Corrected Total	23	65	16	85	108	297	
Known Sites (%)	12	34.5	8.5	45			100

Note¹: site numbers corrected to account for twelve sites where two variants were recorded within each site.

Table 7.2 Observed ranges of *C. esculenta* variants RR, GR, and GP

		longitude	latitude
Variant RR	N	172°53'	34°28'
	S	175°00'	39°20'
Variant GR	N	172°52'	34°26'
	S	178°22'	37°40'
Variant GP	N	172°52'	34°23'
	S	177°37'	37°49'

while variants GR and GP were found with almost equal, lower frequency (Table 7.1). In all areas searched, variant RR predominated in frequency, while variants GR and GP appeared largely restricted to the Northland area. Variant GR is also known from one site close to the southern head of the Hokianga Harbour, but not shown in Figure 7.4, and variant GP is known from one site at the southern head of the Manukau Harbour, South Auckland, not shown in the figures. Variant RR was also the most common variant found with scattered observations outside the areas of intensive fieldwork.

The local distributions of taro (variant RR) on two offshore islands, North Auckland, are shown in Figures 7.7 and 7.8. These correspond to two of the three clusters of sites indicated in Figure 7.4.

The first cluster indicated in Figure 7.4, northeast of Tauroa Point, consists of eight recorded sites. These may be derived from at least four different plantings in the presently forested tributaries of two farmed valleys, above what was once the Whangatane swamp. Four of the recorded sites contain variant RR; the other sites were not visited but were reported by the farmer.



Figure 7.1 *C. esculenta* sites, North Island, New Zealand.

Above: Variant GP growing wild at Ngawha, Bay of Islands (site N15/4) May 1982.

Lower: Kikipaku Stream on Motukawanui, of the Cavalli Islands, Northland (site N8/12). December 1982. Established plants and loose corms of variant RR were found wild and scattered along the streambed, which was dry at the time of visit. This site was previously recorded by Hayward et al. (1979) for taro downstream (towards left of photo) from the upper region shown here.



Figure 7.1 cont'd.

Variant RR (centre) cultivated in a mixed-crop, family garden at Waima, southern Hokianga (site NI4/17). February 1983. Other crops are, from left: *Zea mays* (corn), *Solanum tuberosum* (potato), and at immediate right of the taro: *Ipomoea batatas* (kumara). Māori gardens of similar composition were recorded early in the nineteenth century.



Figure 7.2 Further sites with *C. esculenta*, North Island, New Zealand. *Upper left*: Variant RR (arrow), wild, mixed with *Alocasia* sp. (see Figure 2.1). Plants reaching 1–2 metres height, growing on a supralittoral beach flat, by the outlet of a small stream. Near Te Kaha, East Cape (site N61&60/5). January 1983. *Upper right*: Variant RR, wild. Clumps in and beside a stream. The patch is about ten years old, according to the farm owner who originally transferred plants here from Motairehe nearby. Northern Great Barrier Island, Hauraki Gulf (site NZMS 259/6). January 1983. *Middle left*: Variant RR, wild. Clumps in level area beside a small stream. This patch is a locally recognised source of food, and evidence was found of very recent harvesting of corms. Tikitiki, East Cape (site N72/5). January 1983. *Middle right*: Variant RR, in derelict, non-cultivated garden (now paddock). Stunted plants in hard, dry ground. Tikitiki, East Cape (site N72/4). January 1983. *Lower left*: Variant RR, in non-derelict, non-cultivated garden. Plants formerly in the backyard of the house were dug up and thrown over the fence, and now survive in the adjacent ditch. The source of the plants isn't known in the homeowner's family history, but they were possibly brought here as long ago as 1902, when the house was built. Port Charles, Coromandel Peninsula, Hauraki Gulf (site N35/1). August 1983. *Lower right*: Variant GP, in non-derelict, non-cultivated garden. Plants reaching between 1 and 2 metres height, shaded, in a boggy ditch adjacent to a house. Southern Hokianga, Northland (site N14/14). February 1983.

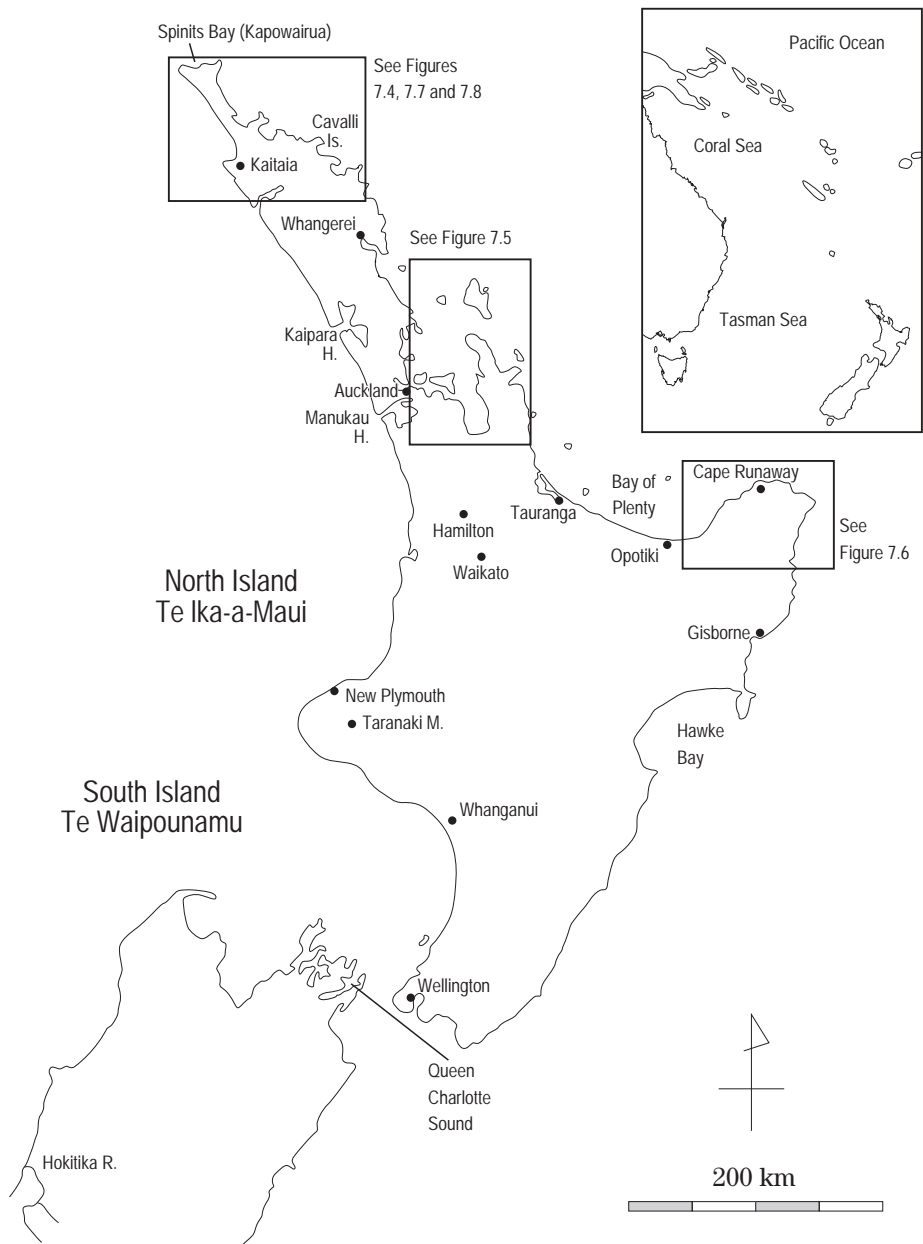


Figure 7.3 New Zealand locations mentioned in text, and areas of intensive fieldwork (rectangles)

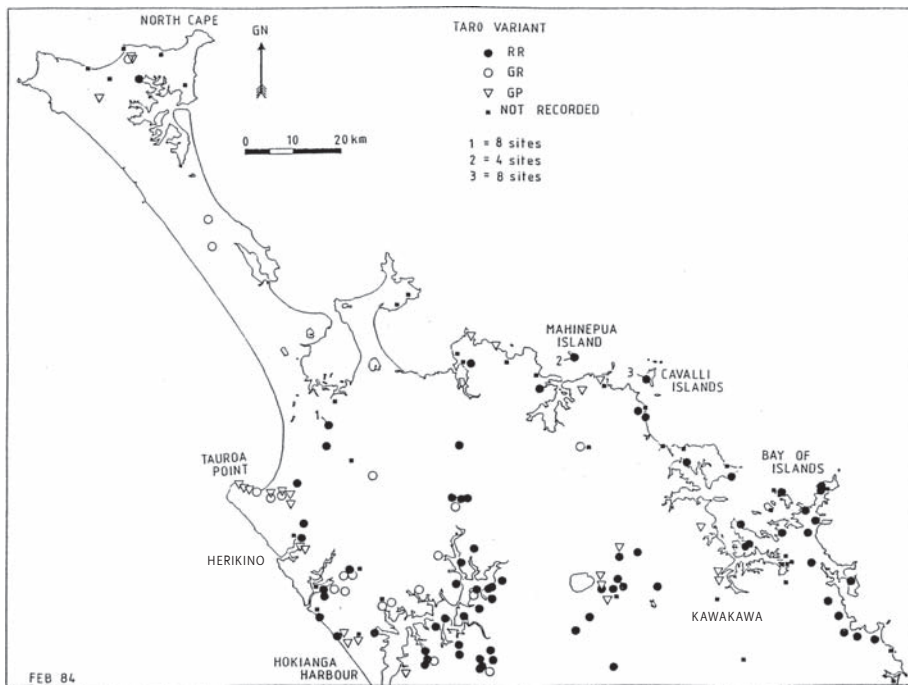


Figure 7.4 *C. esculenta* in Northland: observed distributions of variants RR, GR, and GP
Site clusters 2 and 3 are shown in Figures 7.7 and 7.8 respectively

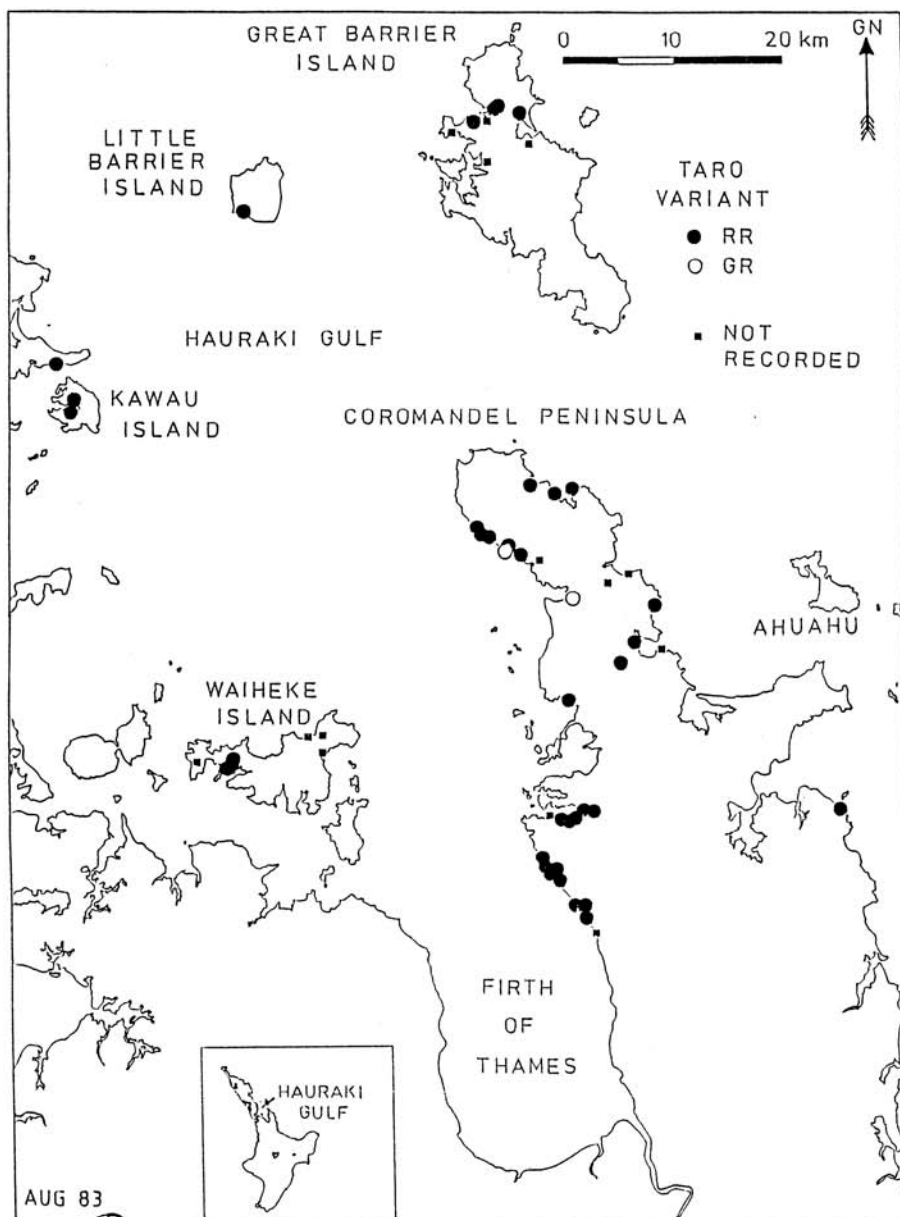


Figure 7.5 *C. esculenta* in or near the Hauraki Gulf, Auckland: observed distributions of variants RR and GR. Variant GP has not been observed here

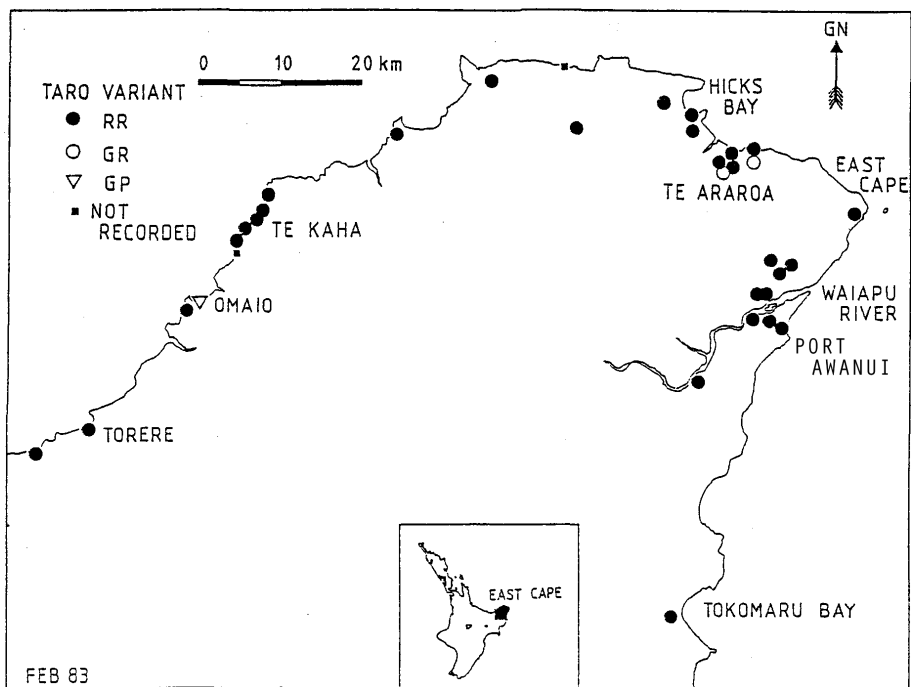


Figure 7.6 *C. esculenta* around East Cape: observed distributions of variants RR, GR, and GP

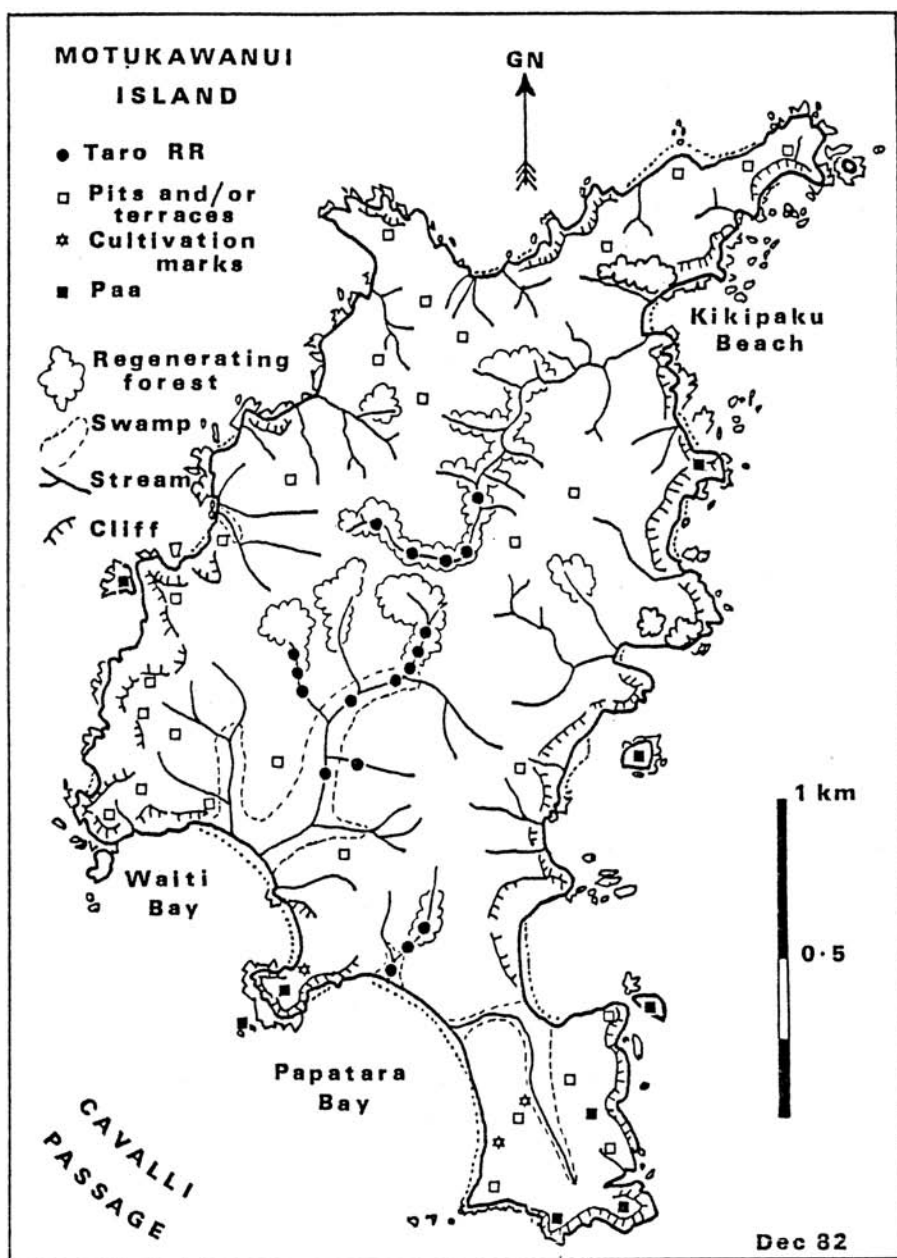


Figure 7.7 Distribution of taro (variant RR) and archaeological sites on Motukawauni, Cavalli Islands, Northland. Eight taro sites have been recorded although only five separate tributaries are populated. Map adapted from Hayward et al. 1979. See area map, Figure 7.3.

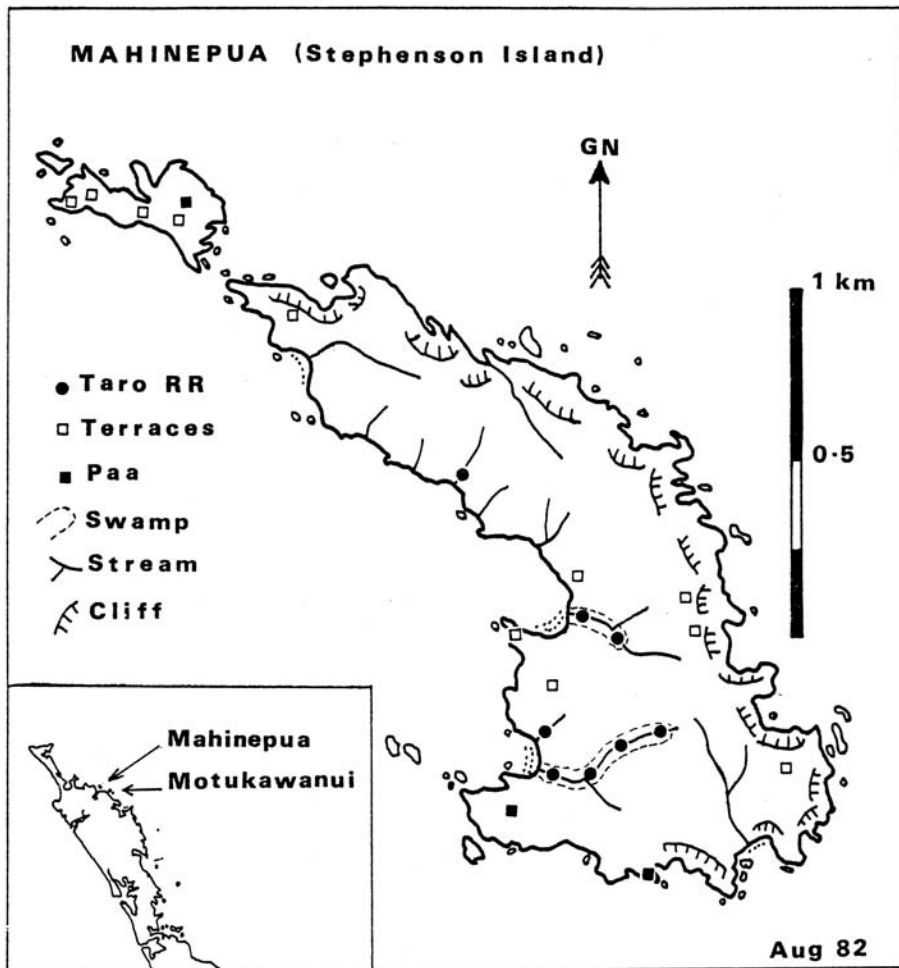


Figure 7.8 Distribution of taro (variant RR) and archaeological sites on Mahinepua, Northland. Four taro sites have been recorded, one for each populated water-course. Survey by A.E. Wright, Auckland Institute and Museum (pers. comm. 1982)

7.3.2 Cultural practices

The following observations were recorded while travelling through rural Māori communities. The records are extremely fragmentary since they were more or less incidental to the botanical survey rather than a serious attempt at full ethnographic description. The original field notes and a partially edited typescript of them are held by the Herbarium, Department of Botany, University of Auckland.

Unless specifically stated otherwise, the observations are best taken as applying to the variant RR, which predominates in both gardens and in the wild, and to which informants directly referred in many instances.

Use

The use of leaves (blades) was infrequently mentioned. Younger leaves are preferred for eating, but one informant said that leaves could be deribbed (central and side-veins of blade removed) to get rid of poisons. Contrary to the general opinion that variant GP is inedible, even after cooking, one informant said it is good but needs longer cooking. Recent influences on cultural practices were indicated when two Māori informants gave Pacific Island methods of cooking leaves, involving canned coconut milk, and when informants recalled, on perhaps two or three occasions, that Islanders had harvested leaves from local taro.

Another culinary use for leaves, mentioned only once, is for covering *hangi* (earth oven) stones to stop food burning on. Other uses are noted in the description of cultivation methods, below.

Use of petioles was never mentioned. Corms are the part generally eaten, after cooking by either boiling or roasting to remove poisons. One informant described splitting corms length-ways in half and letting them dry for half an hour in the sun until mucilage from the cut surfaces has dried off, prior to cooking and as a method for making them non-poisonous (the corms harvested by this informant come from a non-cultivated clump in a ditch by his house). Peeling the thick skin layer off corms is general practice prior to cooking.

Almost no information was gleaned regarding consumption of the variant GR. One informant whose plants came from a Māori cultivator some twenty years ago recollected that the 'small green' (variant GR) had been regarded then as sweeter and better than 'the red' (variant RR), although not as big. This statement may be presumed to refer to the quality of the corm.

Both the central corm and the larger side-corms from cultivated and non-cultivated plants were variously mentioned as the part consumed. Even the larger side-corms may be quite small (for example, approximately 5 x 3 cm, from a cultivated plant) but are recognised as best for eating by their dense or firm texture, pure and opaque white colour, and their non-coarseness. 'Coarseness' is a term which appears to describe more than just how fibrous corms are. Old corms or parts of corms which have become less dense, less opaque, and more fibrous, are described as 'coarse'. The small amount of food to be obtained from the smaller side-corms makes the effort of peeling them not worthwhile.

Feeding taro to pigs was frequently mentioned, particularly in Northland where variant GP was pointed out as inedible and good only for pigs. In one instance, poor, dry clay ground had resulted in corms of the variant RR that were unpleasant for eating ('fibrous and starchy') but which were cooked for pigs.

Many people mentioned *tangi* (funeral ceremonies) as occasions at which taro is served. One very old woman continued to cultivate taro in case (her daughter thought) it is requested as a food for a tangi at the *marae* (community meeting house) maintained by the family.

In the East Cape area, one particular locality, Torere (Figure 7.6), was remembered by many informants as the place where taro had been grown and served at tangi.

Although tangi were most frequently mentioned as occasions for use, taro also appears to be used for any large, temporary gathering requiring large amounts of food (for example, *hui* (community meetings), Christmas reunions, and when a large number of visitors stay at a marae). For some families with many rows of taro in their cultivations, use of the plant as a starchy staple may be of some economic importance. A number of informants and correspondents have said that there has been an upsurge of interest in cultivation and use of the plant, in recent years, or have expressed an increased interest themselves. Generally though, taro appears regarded with disfavour or disinterest, particularly by younger people. Older women with families recollect eating taro when they were children, and may now cultivate just one or two plants, or have non-cultivated clumps in their garden, to taste for themselves or to give to an older relative.

Cultivation

Of the areas surveyed, Northland was where cultivations or plantings of more than just one or two plants were most frequently encountered (Figures 7.1 and 7.2). Despite this, more recollections of past cultivation methods were recorded in the East Cape area. Taro is presently cultivated as a summer root crop, although in some cultivations clumps of more than one year in age had been allowed to form, possibly deliberately. In the Hokianga, informants regarded October as the time to plant and March the time to harvest, after the tops had died off. These dates are just a general rule. Late frosts have to be avoided in October; later plantings in November and December were reported. One informant gave March or April as harvesting times, and a harvesting in May was observed in the Bay of Islands. Southwards, in the East Cape area, planting is said to be in November, after the late frosts. M. Rau-Kupa (pers. comm. 1983) wrote from New Plymouth that planting is done when the weather is warm and frost-free, and harvesting is about March.

P. Tangiwai (pers. comm. 1983) wrote that leaves of two kinds of cultivated taro (*taro hoia* and *taro Tonga*) are harvested and eaten during the winter months.

Side-corms and the cut tops from corms were both mentioned as planting material or 'seed'. Planting material is initially obtainable from a wide range of sources: from locally known wild taro, from non-cultivated derelict or non-derelict gardens, and from the gardens of friends and relatives.

Once in cultivation, cut tops or smaller side-corms are obtained at the time of harvesting.

Planting itself was not observed, but methods currently used appear from reports to include or combine aspects of both traditional methods with methods common to kumara, potato, and other vegetable crops. One method of planting described, which appears to reflect tradition, is to place 'seed' (side-corms) in holes mulched with hay until the shoots appear (soil is presumably added for subsequent growth). During the hot summer weather, watering appears particularly important for taro.

M. Rau-Kupa (pers. comm. 1983) recommended cultivating taro in rich loam with compost. The larger taro cultivations of the Hokianga area were found in areas with rich alluvial loams.

For the over-wintering of planting material, a practice described twice in the field and once in correspondence is that of placing 'seed' on the ground outside with some sort of covering. Elaborations mentioned were placing the 'seed' on a matting of plant material, or in a shallow pit, and covering with taro leaves, or bracken fern and other plants, or sheet iron. The lattermost is valued for the warmth it gives the plants (M. Rau-Kupa pers. comm. 1983). This practice of sheltered but not dry storage indicates a need to maintain meristematic activity, during storage, as a guard against rotting. Another practice mentioned once is that of planting shoots during the winter and replanting them out in spring.

The statements of many informants about the original source of their plants indicated that the transfer of planting material about the North Island occurs over long distances between friends and relatives. Most reports described transfer within the three general areas surveyed, for example, between Kawakawa and Herekino Gorge (Northland, Figure 7.4), from one side of the Coromandel Peninsula to the other (Hauraki Gulf, Figure 7.5), and from Opotiki to Te Kaha, and Torere to Port Awanui (East Cape, Figure 7.6). Possibly the greatest distance reported was from Hamilton to Cape Runaway, East Cape (240km, straight line distance), from a daughter to a mother. At Motairehe, northern Great Barrier Island, an informant indicated that taro was quite possibly brought in from the eastern Bay of Islands (part of the same tribal district) during resettlement of the Island after World War I.

During the field surveys, it became apparent from the statements of informants that a major part of the transfer and cultivation of taro, as well as its cooking, is carried out by Māori women. However, the involvement of men was probably less fully recorded since most interviews were at houses and on weekdays, places and times at which encounters with men were less likely.

The fullest recollections of traditional cultivation were given by the Reverend Davis and his wife at Torere, East Cape, 19 January 1983. They described nearby taro gardens that existed some time ago (unspecified), on alluvial river soil by the river, and above the beach. There were several gardens, with fencing to keep stock out, and each garden had approximately twenty holes in which the taro were planted. The holes were scraped out using a piece of barrel-hoop iron which was also used to determine the spacing between each hole.

After digging the holes, sand was put over the whole patch and in the holes. The small side-shoots used as planting material were then placed on the sand in the holes. Clean, fine river gravel also was spread around the plants to the thickness of a hand. As the plants grew, the gravel was pushed up around them to attract moisture and keep the ground temperature up. Silty river gravel wasn't suitable because it gave weed problems, and beach gravel was too salty.

Plantings and later attentions were made at special times, and in wet weather like that 'at present' (19 January, a steady drizzle). The aim of cultivation and all the effort was to get just one large central corm.

As it grew the small side-corms were pulled off, 'like breaking off tomatoes', and older leaves and dry leaves were cut off and put on as a mulch, together with earth.

Shoots had to be sorted out and the leaves 'feeding' the desired corm preserved.

For storage after harvest, *tutu* (a common wild herb) was laid down as a mat and all the taro including 'seed' pieces were placed on this, followed by leaves from the taro plants.

The Reverend Davis also recalled that when young, he and his family lived in a village on the flat behind Okahau Bay, Auckland, where they also had gardens of maize, corn, kumara, and taro. This lasted up to the late 1930s, until they were ordered by the borough council to shift onto the hill.

The former gardens at Torere were mentioned or described by many people at other places around East Cape, as far as Port Awanui, just south of the Waiapu River. Torere is renowned both for these gardens and the serving of taro at tangi, while Te Kaha, nearby along the coast, is known for its kumara. Taro was not actually seen at Torere, but plants of variant RR at other sites were said to have come from Torere.

In the later descriptions it was further established that the gardens by the river at Torere had lasted up until twenty-five or thirty years ago (i.e. 1953–1958), and were communal gardens in an overall oblong area consisting of family plots, with boundary markers of round stones for each plot. An aerial photo taken in a 1948 mapping survey (Figure 7.9) shows what may have been among the last taro gardens in New Zealand cultivated by traditional methods. (It is possible that by 1948 the traditional methods were superceded even though taro cultivation continued).

The aspect of the traditional methods described by the Reverend Davis which seemed most often and clearly recalled by other informants, was that of mulching each plant individually by wrapping each successive, old outer leaf around the base of the plant, with or without first breaking off the leaf (informants varied on this point). Pushing gravel or soil up around the growing plant was also mentioned, though very rarely. The most common opinion of the old methods was that they had required a lot of care and effort. One very old man in the East Cape area recalled how potatoes had seemed a better proposition when he was young, while the old people then still had big patches of taro.

Non-cultivated sites

The occurrence of non-cultivated taro is frequently the result of neglect, either because a house and its associated garden have been abandoned (Figure 7.2, middle right), or because the taro has been discarded or has naturally escaped from a cultivated area and now propagates itself in an adjacent area of swampy ground, a stream, or a ditch (Figure 7.2, lower left).

It can be easily imagined that many wild sites have arisen by such a gradual transition of taro out of cultivations into natural watercourses, though this cannot be observed in a short-term study such as this. The statements of informants show, however, that plants may be moved by one of many routes between different types of site. A non-cultivated clump of taro may be planted and kept in a garden as an ornamental, as a reminder of the past and for an occasional taste, or as a potential source of planting material for future cultivation. One informant suggested that presently-wild taro had



Figure 7.9 The settlement Torere, East Cape, in September, 1948. Reconstructing from recorded oral history, the gardens visible by the upper arrow were probably used for taro cultivation over the following summer, and possibly for as many as ten more seasons. From these gardens taro were supplied for occasions at the nearby marae (lower arrow). Scale approximate only. Crown Copyright, Survey No. 371, Run No. 1753/6. New Zealand Aerial Mapping Ltd.

originally been planted in streams to preserve planting stocks, noting that they produce too much leaf and not a good 'root' (corm) in streams. Planting in the wild was reported by other informants also (Figure 7.2, upper right).

The harvesting of corms from non-cultivated sites can be at any time of year, though there are said to be times of year when the corms are less poisonous, a state which can be recognised by the amount of mucilage expressed at the surface of a cut corm (whether by more, or by less, was unfortunately not learned).

A number of informants lamented the fact that people had recently been digging up local non-cultivated patches (either in derelict gardens or wild) without replanting. Despite this problem, it appears generally acceptable in rural communities for anyone to use such sites when access is readily made from the road, or if permission is sought, and assuming care is taken to replant unwanted side-corms or cut tops. In a few sites the smoothly-cut ends of petioles were discovered, indicating recent harvests of the inner tender leaves. Although these observations were made in both summer and winter months, it seems likely that most harvesting of leaves occurs during the burst of leaf production over the warmer months.

Chapter Eight

Historical Implications and Future Research

This chapter has three main parts: (1) discussion of the present evidence, (2) a statement of the main conclusions, and (3) consideration of broader historical implications and future research on crop genetic resources and *Colocasia*.

8.1 Present Evidence

8.1.1 General distribution

The general geographic distribution of each variant provides, in itself, little evidence regarding history. The variant GR, for example, with a distribution apparently centred in Northland (Figure 7.4) could be a relic from the distant past, or it could have been of such recent origin that only limited dispersal has taken place. It is apparent that almost any explanation can be proposed for any geographic distribution in the absence of other kinds of evidence.

8.1.2 Site categories and plant transferral

The classification of New Zealand taro sites into cultivated and a range of non-cultivated categories, though necessarily loose, was made in the hope that some degree of historical perspective could be added to the observed distributions of each variant. An initial reaction to these categories is to suggest that they represent different points on a simple, linear historical sequence: cultivated sites becoming non-cultivated through neglect, then derelict, and finally the taro appearing in a wild setting.

Though such a sequence or route has undoubtedly often been followed, the cultural practices described above make it obvious that many alternative routes can lead to the creation of a taro site. Even with a good description of present day practices, speculating by analogy on the relative importance of different routes in the past would be hazardous. The present observations of geographic distribution, of occurrence in different types of site, and of cultural practices, therefore allow only two general, definite suggestions regarding history:

(1) the general history of each variant is different, since each variant can be distinguished by the combination of its general geographic distribution and its occurrence in different types of sites: variant RR is the most common overall (75% of identified taro), is common to all areas, and is found most commonly in non-derelict, non-cultivated gardens and in the wild; variant GR is less common overall (13% of identified taro), is most common in Northland, and is found most commonly in non-derelict, non-cultivated gardens; and variant GP is also less common overall (12% of identified taro), is also

most common in Northland, but is most commonly found in the wild (Figures 7.4, 7.5, 7.6, and Table 7.1).

(2) the transfer and planting of taro by people have been important mechanisms for its dispersal over long distances and into both cultivated and non-cultivated sites.

8.1.3 Site density and survey method

The highest density of sites appears to be in North Auckland and is the outcome of the interactions between land and climate, people, and the plant. The absolute frequency of taro per square kilometre in North Auckland may be high because of both a warm climate suited to its natural survival and because the same area attracts a greater density of people than other areas. The factors involved are complex and interdependent, and further discussion would require detailed geographic and demographic data from which quantities such as the per capita frequency of taro could be calculated. Such a detailed analysis could not be sustained with the present information which has been obtained in a rapid botanical survey.

Although the rapid survey methods used to find taro were undoubtedly biased in favour of sites near roads and around settlements, the use of these methods was justified by the practical limitations on time and finance. These limitations arose directly from the belief that a wide geographic coverage would give a less biased and more general view of the New Zealand taro population than detailed surveys of a few small areas or localities.

8.1.4 Archaeological sites

Exceptions to the rule of rapid survey were made for the surveys of Motukawanui, in the Cavalli Islands, and on northern Great Barrier Island. Rattenbury (1956) suggested that taro from the Cavalli Islands may have survived there 'since earliest known settlement', while Yen and Wheeler (1968) noted that specimens from Great Barrier Island and from Spirits Bay 'cannot be ascribed confidently to transfer in European times'. Following these suggestions and the report of taro sites on Motukawanui by Hayward et al. (1979), opportunities were taken to visit the islands in hope that detailed surveys would establish whether or not their taro can be regarded as 'archaeological'.

Samples of taro have been obtained from Spirits Bay, but a detailed survey was not made there. The settlement at Kapowairua, at the eastern end of Spirits Bay, was occupied earlier this century according to former residents now living at Te Hapua, nearby (O. Sutherland, DSIR, pers. comm. 1982), so it is quite possible that recent introductions have been made to the area. Taro often has been recorded in the New Zealand Archaeological Association site recording scheme as comprising all or part of an archaeological site. Archaeological sites are legally defined as more than one hundred years old (*Historic Places Act 1980*) but it is generally impossible to establish such antiquity for taro sites, since recent or present settlement is also commonly found associated with the archaeological landscape of paa, pits, terraces, and middens. This problem is particularly apparent along the western coast of Coromandel Peninsula (Figure 7.5) where wild taro is found at the entrances to a number of coastal gullies in possible

association with archaeological sites, but also only a few metres from the coastal road. The plantings could pre-date the road, they might represent plantings on a number of occasions distant or recent in time, or one person on one day may have driven along the road planting taro in gullies.

Motukawanui is the largest member of the Cavalli Islands (Figures 7.4 and 7.7), which were home to numerous Māori from pre-European times up to about 1900, with the first European encounter being made by Captain Cook in 1769 (Hayward 1979). Cruise (1824) recorded Cavalli Islanders offering vegetables for sale to his ship the *Dromedary* in 1820, and photographs at the Auckland Institute and Museum Library (Hayward et al. 1979) show in about 1900 a small village of Māori-owned huts behind the southern part of Papatara Bay. The island was farmed from the latter part of the nineteenth century up until 1974, and a homestead at the northern end of Papatara Bay was last permanently occupied about 1953 (Hayward 1979). Since 1978 the island has been part of the Bay of Islands Maritime and Historic Park.

On Motukawanui, taro (variant RR) was found in five tributaries and may therefore represent five separate plantings. Archaeological pit and/or terrace sites are distributed along the ridges, and the distribution of taro high in tributaries among remnant patches of native bush (Figure 7.1) suggests an association with past Māori occupation of the archaeological landscape. This occupation may have continued for some time after the encounter by Cruise in 1820.

The history of occupation of Mahinepua (Figure 7.7) is not known, though it has been farmed until recently without occupation, and is largely vegetated with ungrazed grass (A. Wright pers. comm. 1982). The distribution of taro (variant RR) here in four separate streams is suggestive of an association with past occupation of the archaeological landscape. Even without recent occupation, however, it is possible that plantings were made on both Motukawanui and Mahinepua in recent times by the Māori living nearby, on the mainland, and visiting the islands for various purposes (D. Simmons, Auckland Institute and Museum, pers. comm. 1983).

On Great Barrier Island, taro was not found in the unsettled, forested areas of the islands' northern end, despite an intensive search and the presence of a rich archaeological landscape. Although taro (variant RR) was found in settled areas nearby (Figure 7.5), this may be of recent post-World War I introduction from the eastern Bay of Islands according to a Māori informant at Motairehe, northern Great Barrier Island. Taro was present on the island in earlier times, since Kirk (1868) recorded it (as *C. antiquorum*) in a species list for the island. The present absence of wild taro in an unfarmed and presently unsettled part of the island is possibly due to the dense populations of pigs and goats inhabiting the native forest. Neither of these herbivores has been mentioned as past inhabitants of Motukawanui, where taro survives, although other islands in the Cavalli group have had pigs or goats (Hayward 1979). The survival of taro in the wild may require protection from dense populations of these herbivores, while pasture-fed stock probably pose little threat.

8.1.5 Cultural practices

Further interpretation of the distributions of the taro variants, beyond the two suggestions already enumerated, becomes speculative and involves further consideration of the cultural practices.

(1) Variant RR: This is clearly the most important variant as a food crop, and its dominance in both cultivated and non-cultivated sites does suggest that it has been more important in the past than the other variants, whatever the routes of plants into these sites. The range of sites indicated in the above statement is important — occurrence of the numerically dominant variant only in cultivations would strongly suggest something different, namely, recent adoption of a very popular cultivar.

(2) Variant GR: Speculation regarding variant GR is more difficult since almost no information about its cultural importance was obtained. This lack of information might not simply be due to a small chance of encountering both informants and the plant at the same time, since variant GP, with a similar low overall frequency, was quite often spoken about. It is quite possible that there is no common awareness of variant GR as a distinct type, since it is almost identical to variant RR in leaf shape and corm morphology (Chapter Five). The distinctive petiole colours of these variants may be generally ignored if, perhaps, there is little or no difference in the cooking and eating qualities of the two variants.

This discussion however does not lead to any favoured suggestion regarding history. Variant GR could be of old origin or introduction but may have been only slowly dispersed for some (not obvious) reason. Alternatively, variant GR could be young historically, without having had time to become widely dispersed. Factors affecting the rate and extent of dispersal may have included: (1) the close morphological resemblance to variant RR (Chapter Five); (2) arrival at a time after the introduction of European crops, when interest in trying a new taro cultivar may have been low; (3) a poor food quality not noted with the present limited observations; and (4) local cultural barriers to its dispersal from the point of origin or introduction. The restricted distribution of variant GR could be a relic of a formerly greater distribution if, for example, variant RR had been a more recent and popular introduction that displaced variant GR from cultivation, and if variant GR is incapable of surviving outside gardens (since it is mostly found in gardens). However, the one report of eating quality suggests that variant GR may be better than variant RR, and observations of the growth of variant GR (Chapter Five) give no indication that it is incapable of surviving without human intervention.

Historically, therefore, it seems likely that variant GR has always had a distribution limited to Northland since its appearance there. Whether this appearance was before or after the arrival of Europeans is not known.

c. Variant GP: The general absence of variant GP from garden sites undoubtedly reflects its poor eating qualities. Another reason for exclusion from gardens is suggested by the observation that stolon-producing taro, such as variant GP, are unpopular as cultivars in areas outside New Zealand because they require laborious repeated removal of the stolons to promote the growth of the central corm (Wilson 1982). A similar observation was made by Whitney et al. (1939), who noted that the two rhizome-

producing taro varieties in Hawai'i are commercially the least important of all the taros because the rhizomes increase the difficulty of cultivation and harvesting. It is more difficult to explain why variant GP has become dispersed in numerous wild sites. Two suggestions can be made which are not mutually exclusive: (1) that variant GP has been planted outside garden areas as a cheap source of pig food; and (2) that since its introduction the curiosity of people in a potential new food source has been sufficient reason for them to plant it in handy waterways, where no further care is required for it. They might also try it in gardens, but then soon discard it when the taste and growth habit prove undesirable.

The present general absence of variant GP from gardens makes it seem unlikely that its present distribution is relict from a formerly wider geographic distribution resulting from dispersal by people among gardens. Further, the good ability of variant GP to survive in the wild (Chapter Five) makes it seem unlikely that its present distribution is relict from a formerly wider distribution in the wild.

Variant GP may have become dispersed during the early nineteenth century as a food source for pigs, since pigs were raised by the Māori as an item of trade with the early European settlers (Hargreaves 1959).

Even if pig rearing was the main reason for the dispersal of this variant, the original introduction could have preceded the arrival of pigs. There is some suggestion from historical records that the variant GP was introduced by an early American whaling ship (Appendix 9), but no conclusive evidence exists regarding when this variant was introduced.

8.1.6 Site categories: analogy from the present to the past.

The different categories of taro site have been defined here partly on the basis of their present relationship to settlement of European design, to help distinguish between 'garden' and 'wild' sites. The attempt at a direct classification of historical status using such evidence (Matthews 1982) was not made here. It seems quite likely that a similar range of site categories existed in pre-European times in relation to Māori settlement. The relative importance of the different kinds of site would have been quite different though, since the cultivation of taro before the arrival of European crops was undoubtedly of much greater importance than afterwards. Non-cultivated taro in a variety of settings, garden or wild, could have had similar uses in the past as less labour-demanding, less controlled sources of food, and as sources of planting material.

8.1.7 The definition of cultivation

The observations of cultural practices make it apparent that cultivation is not the only way in which people aid the survival of taro in New Zealand. Deliberate dispersal of taro into non-cultivated sites is also important, though not the only means by which it may arrive in such sites. The replanting associated with the harvesting of taro from non-cultivated sites may well be necessary to the plant's perpetuation in the more frequently harvested sites (Figure 7.2, middle left, for example).

It is with the practice of replanting that the distinction between cultivated and

non-cultivated sites becomes unclear, since planting to some extent alters the immediate environment of the plants. As Zeven and de Wet (1982) note, people maintain cultivated plants in an artificial habitat if the plants are of sufficient value, while cultivation includes all kinds of agricultural practices, from merely protecting individual plants to actual planting or sowing, and tending of planted populations. The definition of a cultivated site used in the present study has been deliberately restricted to sites in which the soil appears cultivated, since consistent observation of the cultural practices attendant to the plants, over time, was not possible for every site. Even this restricted definition fails when the effects of people on the soil are indiscernable, though possibly important to the plants.

8.1.8 Traditional cultivation methods

Traditional cultivation methods similar to those recorded here were reported by Best (1976), who visited the Waiapu district near East Cape sometime before 1925, although in one respect the accounts differ. Best (1976) wrote that, in at least some cases, the innermost immature leaves were pinched off with the effect, reputedly, of increasing the size of the edible part. This seems an unlikely practice if the aim of cultivation was to produce a large central corm, as reported here for Torere. The expected effect of retarding apical growth in plants is to stimulate lateral growth (meaning, in the case of taro, the growth of side-corms). It is quite possible that this was the aim of cultivators in Waiapu district.

Since the cultivations at Torere appear to have been closely associated with the production of food for tangi, it is possible that especially large corms were desirable for public presentation. Methods for stimulating the growth of central corms may have been appropriate for publicly presented food, at special occasions, while the cultivation of side-corms may have been appropriate to mundane food production for ordinary consumption.

These suggestions need substantiation by people with traditional knowledge, and by further study of ethnographic records.

8.2 Main Conclusions

8.2.1 A taro variant of pre-European introduction?

The wide search for taro revealed only three taro variants of major geographic distribution. The distribution patterns of the variants RR, GR, and GP differ, but are not readily interpreted regarding two questions of history:

- (1) Which, if any, of the three variants are of pre-European origin or introduction?
- (2) Have pre-European distribution patterns of taro been perpetuated to the present, or have they been totally obscured by recent dispersal and loss?

Since the distributions of these three variants together span a wide geographic range in which other taro appear almost completely absent, perhaps one of them – at least – is of pre-European origin. Variant RR is predominant numerically, in the range of settings it occupies (including possibly archaeological sites), and in cultural importance. It therefore

seems the most likely taro variant to have been introduced in pre-European times (if any of them were so introduced).

This argument requires two suppositions; namely that taro was introduced in pre-European times (as indicated by first-eyewitness European records, and Māori tradition), and that not all pre-European taro was lost from cultivation, or was unable to survive without cultivation, after recent introduction of the taro varieties found now.

If the first argument is correct and taro of pre-European introduction is still present, it seems unlikely that its pre-European distribution pattern has been totally obscured. To identify a particular distribution pattern as pre-European would, unfortunately, entail a circular argument. The suggestion that variant RR is the most likely taro to have been introduced in pre-European times is largely based on its present abundance, without assuming that its present distribution reflects a pre-European pattern.

8.2.2 A taro variant originating in New Zealand?

Whitney et al. (1939) described varieties of the group *Lauloa* previously reported (Hawai'i Agricultural Experiment Station 1937) to have arisen by vegetative mutation in the varietal collection. The new mutants resembled already established varieties (Hawai'i Agricultural Experiment Station 1937). The *Lauloa* varieties are all distinguished by differences in the colouration of various parts of the petiole. (Whitney et al. 1939).

These reports suggest another explanation for the distribution of variant GR: this variant may have only recently dispersed after origin as a colour mutant of variant RR (although another explanation, perhaps less likely, is that variant RR originated a long time ago as a colour mutant of variant GR). This is consistent with the observations of similar leaf shape and corm morphology (Chapter Five) and similar karyotypes (Chapter Six) for variants RR and GR. However, the suggestions must remain tentative pending definitive cytological observations and investigation of the basis for the colour difference (green versus red) in the petioles.¹⁾

8.3 Wider Implications

8.3.1 Historical interpretations

Three taro variants with a chromosome number of $2n = 42$ appear predominant in New Zealand today. The present field evidence and records of cultural practices provide circumstantial evidence that taro of $2n = 42$ could have persisted since pre-European times in two ways:

(1) Naturally. The taro observed readily grow and self propagate vegetatively without human intervention.

(2) With human intervention. Taro has probably never fully ceased to be planted and cultivated as a food crop since its introduction to New Zealand.

Accepting this suggestion of persistence $2n = 42$ taro since pre-European times could lead to the suggestion of a pre-European transfer from the southwestern Pacific to Aotearoa, while the evidence from archaeology, physical anthropology, and language demonstrate Māori origins in the southeastern Pacific, in Polynesia (Bellwood 1978;

Davidson 1979). This interpretation is however not secure because it is just one of a wide range of possible explanations for the present predominance of taro with $2n = 42$, and the scarcity of taro with $2n = 28$:

(1) Plants with $2n = 42$ were introduced in pre-European times (and/or after European influx) from the southwestern Pacific, where this chromosome number has been recorded.

(2) Plants with $2n = 42$ were introduced — in pre-European times, and/or after European influx — from Polynesia, where extensive sampling may have yet failed to detect taro present with this chromosome number.

(3) Plants with $2n = 28$ were introduced in pre-European times, but failed to survive when the introduction of European crops and new cultivars of kumara led to the general neglect of taro.

(4) Plants of $2n = 28$ were introduced in pre-European times and still survive, but did not become dispersed in the areas searched during the surveys reported here.

(5) Plants with $2n = 28$ were never introduced in pre-European times, despite human colonisation from Polynesia.

(6) Plants of $2n = 28$ were introduced in pre-European times and gave rise to $2n = 42$ polyploids which somehow displaced the parental stocks.

These possible explanations and some implications for future studies are discussed next:

(1) and (2) Introduction of taro with $2n = 42$: An important aspect of the present observations is that taro of $2n = 42$ are not of uniform morphology or karyotype. Although chromosome numbers alone are suggestive of links between different regions of the Pacific, they are not sufficient to verify them. Presently, neither morphological nor genetic descriptions exist, which allow closer comparison of the New Zealand taro with taro of $2n = 42$ in the southwestern Pacific. The discovery of phenotypically and genetically close relatives of the New Zealand taro variants in overseas locations would indicate possible geographic origins and would allow more selective examination of historical records relevant to the issue of recent introductions (see Chapter 14).

It is difficult to judge how well the Polynesian region has been covered by sampling. Yen and Wheeler (1968) report counts of $2n = 28$ for 65 varieties from the Polynesian region outside New Zealand. Further varieties with chromosome counts of $2n = 28$ have been found in the area but have not appeared in published reports (D. Yen pers. comm. 1983). The number of varieties observed is on its own a poor basis to judge the quality of the data, since the spatial distribution of samples must in theory affect the chance of observing variation. Varieties sampled from one garden area would in general be less likely to exhibit variation than samples from a diverse range of natural and artificial habitats on one island. Yen and Wheeler (1968), in what was an exploratory study, used a Pacific-wide sampling approach with the aim of associating plants and people in theories of migration. Their descriptions of sample sources are minimal, but it is obvious that for such a general aim, the practical limitations imposed on the observation of local distributions are vastly greater than for the present study of taro within New Zealand.

According to the aims of these studies, Pacific-wide and within New Zealand (and

given the constraints of time and funding), compromises have been made between the ideals of wide sampling range and thorough sample description.

With the above considerations in mind, it appears that if a future study has the aim of identifying possible overseas origins of New Zealand taro then some effort will be justified for establishing the local distributions, and both natural and cultural associations, of taro found within the chromosome number $2n = 42$. This may be particularly important in the Polynesian region and other areas opened to modern shipping and road transport, because it is known that varieties held in the collections of agricultural field stations soon become dispersed amongst local cultivators (R. Fullerton, DSIR, pers. comm. 1982; D. Yen pers. comm. 1983).

The best initial strategy for future studies may be to look at existing, well-provenanced living-plant collections as well as in areas more or less isolated from recent wide-ranging transfer of taro cultivars. Long-established collections with material collected from what were, at the time, isolated locations may be an ideal starting point.

(3) Extinction of taro with $2n = 28$: The possibility that taro of $2n = 28$ are unable to survive in New Zealand without human intervention cannot be sensibly discussed until field trials are made with such taro in New Zealand, in a range of habitats.

(4) Insufficient sampling: Since two major variants are more or less restricted to Northland, it is quite possible that the variants with $2n = 28$ from New Plymouth have a wider and historically important distribution in the Taranaki area. A general field survey of the Taranaki area would be valuable if it established the extensive distribution (or otherwise) of such taro.

(5) Non-introduction of taro with $2n = 28$: Given the long-standing importance of aroid root-crops for Pacific horticulturalists (Bellwood 1980), it seems quite unlikely that taro of $2n = 28$ were never introduced from Polynesia in pre-European times. Nevertheless it should not be assumed that all voyagers brought taro with them.

(6) Diploids give rise to triploids in New Zealand: It is unlikely that polyploidisation and displacement led to the predominance of taro with $2n = 42$ chromosome numbers. The number $2n = 42$ cannot be derived from $2n = 28$ by a simple doubling of the somatic cell chromosome number in an apical meristem, in the absence of breeding and seed production.²⁾

The import of taro for a wide range of immigrant ethnic groups is significant for the present discussion. While it is estimated that 97% of present commercial imports are from Samoa and Tonga (J. Watson pers. comm. 1982), and are therefore probably of $2n = 28$ chromosome number, it is possible that taro has entered directly, or indirectly (Yen and Wheeler 1968), from Asian sources where the number $2n = 42$ is present. Any information about imports of vegetables for immigrants during the nineteenth century would be of interest.

8.3.2 The genetic evaluation of crop plants

In conclusion to a discussion of crop germplasm conservation and developing countries, Plucknett et al. (1983) state that 'currently, the phenotypic characters of accessions are noted rather than the genes of the plants; in the future, the usefulness of gene bank

records will depend on the relevant gene symbols being recorded for each accession'.

It is clear, however, that the evaluation of crop germplasm has generally been conducted on a sporadic basis depending on the particular interests of specialists in such fields as pathology, entomology, plant physiology, and agronomy. If gene banks are to be evaluated genetically prior to the investigations of such specialists, and in order to aid them, then the study of plant phylogeny is likely to be the most useful field of investigation, since it provides a general basis for understanding and predicting the occurrence of phenotypic attributes.

Within the study of phylogeny innumerable strategies may be adopted. Traditional taxonomic methods based on the analysis of morphology, and biochemical studies of protein phenotypes, may be used to identify genetic relationships indirectly. Both approaches suffer from developmental and environmental effects on gene expression and require verification using breeding and inheritance studies. Recent developments in molecular biology make it possible to directly identify and compare the nucleotide sequences of DNA. The occurrence of certain sequences of nucleotides also may in essence be phenotypic, since developmental and environmental effects on the replication and transcription of genes are now being revealed. Not all directly examinable aspects of genomes are suitable for phylogenetic analysis.

Given the large range of options available for studying phylogeny, particular aims must be made explicit to develop a rational strategy for the evaluation of crop plant gene pools.

The evolution and dispersal of crop plants is dependent in various ways upon their interaction with humans, so that the study of crop plant phylogeny is in effect a study also of human cultural history. A strategy of phylogenetic analysis aimed at clarifying the relationships between plants and humans must benefit the understanding of both.

During the present study, some consideration was given to developing a strategy for the genetic analysis of *C. esculenta*, and an initial attempt to characterise the leaf protein ribulose-1, 5-bisphosphate carboxylase-oxygenase (RuBP carboxylase) is described in Appendix 11.

The genetic basis of RuBP carboxylase is now particularly well understood, though by no means completely. The native protein consists of two kinds of subunit, a large one encoded by chloroplast genomes and a small one encoded by the nuclear genome. Genetic analyses of the modes of inheritance demonstrate maternal transmission of genes for the large subunit and biparental transmission of genes for the small subunit (Uchimiya et al. 1977; Miziorko and Lorimer 1983). The polypeptide banding patterns of the dissociated subunits (eight large and eight small subunits) after polyacrylamide gel electrophoresis and isoelectric focusing have been frequently used for studying plant phylogeny, although recent work has revealed a major methodological artefact (O'Connell and Brady 1981).

Studies of the polypeptide banding patterns of the large subunit reveal little variation within and between genera (for example, only four types within the entire genus *Nicotiana*, Uchimiya et al. 1977), while more variation is observed for the small subunit (Chen et al. 1976; Cammaerts and Jacobs 1981). Recent studies of chloroplast DNA

using restriction endonucleases have shown the nucleotide sequences of the large subunit genes of maize and spinach to be highly conserved with 84% homology, corresponding to an overall amino acid homology of about 90% due to silent nucleotide changes (Whitfield and Bottomley 1983). It is apparent that the small amount of genetic variation revealed by the large subunit of RuBP carboxylase severely limits its utility for phylogenetic analysis.

Gatenby and Cocking (1978) note, in conclusion to a study of RuBP carboxylase in *Solanum*, that the analysis of chloroplast DNA with restriction enzymes is a more sensitive method for identifying chloroplast genomes than analysis of the large subunit of RuBP carboxylase. Restriction endonuclease digestion of total chloroplast DNA has now been used to establish a phylogeny for species of *Lycopersicon* and *Solanum* (Palmer and Zamir 1982). Although an extremely limited amount of sequence divergence was observed among the DNAs, use of a moderate number (25) of different restriction endonucleases revealed sufficient variation to permit construction of a detailed chloroplast DNA phylogeny essentially free of ambiguity. Major sequence rearrangements are generally quite rare during chloroplast genome evolution, so changes in restriction fragment patterns can usually be interpreted as the consequence of base substitutions rather than DNA rearrangements (Palmer and Zamir 1982). The phylogeny obtained for mainly *Lycopersicon* and some closely related *Solanum* species is generally consistent with relationships based on morphology and crossability but provides more detailed resolution at several places (Palmer and Zamir 1982).

From the above studies it is apparent that a compromise must be made between two conflicting needs for the study of relationships between plants and people: (1) the need for the sampled part of the plant's genetic system to have been sufficiently variable to result in differentiation during the course of human history; and (2) the need for a sufficiently stable part of the plant's genetic system to allow a phylogeny to be established unambiguously.

Further, in order to relate phylogeny to geographic distribution and to dispersal by humans, consideration must be given to differences in the transmission of different components of the plant's genetic system. In theory, if natural geographic and genetic dispersal of a genetic component is limited, then the effects of dispersal by humans should be more clearly evident.

Chloroplast genomes appear to fit the criteria indicated above. They appear both genetically stable and sufficiently variable for their use in evaluating evolutionary relationships amongst plant species within a genus (Palmer and Zamir 1982).³⁾ In addition, the natural geographic dispersal of chloroplast genomes appears more limited than nuclear genomes because:

(1) Assuming strict maternal transmission, dispersal of chloroplast genomes depends on the dispersal of vegetative parts and seed. Pollen provides an additional mode of dispersal for nuclear genes. In some plants sexual reproduction may be rare or non-existent, so that dispersal of both plastid and nuclear genomes is either by relatively localised natural dispersal of vegetative parts, or by people who use vegetative parts for propagation.

(2) Assuming strict maternal transmission only, opportunity does not arise for a hybrid mixture of chloroplast populations within an individual plant, c.f. hybridisation and sexual recombination of nuclear genomes, and other mechanisms of molecular evolution in nuclear genomes.

In theory, these limitations on chloroplast dispersal will have resulted in more tightly defined boundaries of geographic distribution for variants of chloroplast genomes than for nuclear genomes. With plants in which mitochondria are also maternally transmitted, *Coffea* for example (Berthou et al. 1983), a similar argument may apply.

The primary purpose of this discussion has been to develop a strategy for the future study of *C. esculenta*. However, if the foremost aim in future is to clarify the cultural history of humans, the consideration of genetic transmission in plants may indicate more suitable genera for study. This will also depend of course on the plants present in the geographic region entered. To conclude the present discussion however, a number of questions are posed regarding the evolution of *Colocasia*:

(1) Where is the natural origin of this genus and to what extent have humans been responsible for its wide dispersal throughout the tropics and sub-tropics? The aroid genus *Xanthosoma* originates in South America, while *Colocasia* and other edible aroids are found in Asia and Australasia (Leon 1977). Does this indicate that the genus *Colocasia* may include endemic populations in the different continental areas, arising during the geological history of Gondwanaland?⁴⁾

(2) What has been the importance of sexual hybridisation in the evolution of cultivars and can the phylogeny of cultivars be related to the dispersal and mixing of cultivar populations by people?

(3) What combination of phenotypic and genetic characters is best observed to identify particular subspecies or cultivars, and to allow comparisons between them?

(4) Do plants that are phenotypically and genetically identical to the New Zealand variants of taro exist outside New Zealand, or has evolution obscured origins?⁵⁾

Notes

- 1) The ribosomal DNA (rDNA) patterns of var. RR and var. GR were subsequently found to be identical (see Chapter 14). They were also found to be similar to the rDNA patterns of certain Japanese and Chinese taro cultivars, lending support to the interpretation of historical introduction to New Zealand by Chinese immigrants in the 19th century.
- 2) Short, relatively cool summers and long cool winters in the North Island of New Zealand (latitude range approx. 34.5 – 45.5 degrees S) prevent fruit and seed development. In Okayama, Japan (approx. 34.5 degrees N), it has been possible to breed taro experimentally by using a hothouse to raise temperatures and extend the growing season (Yoshino pers. comm.; see Yoshino 2002). It may be possible to breed taro in the Far North of New Zealand, using hothouse conditions and artificial lighting to extend the growing period of taro.
- 3) The value of chloroplast DNA analysis has been recently confirmed for taro, through complete sequencing of the chloroplast genomes of var. RR and var. GP, and testing of a wide range of taro samples; see Ahmed et al. (2012, 2013).

- 4) There is currently no evidence that the natural range of genus *Colocasia* extends beyond the continental regions of Sunda and Sanul. The evolutionary diversification of Family Araceae is discussed in relation to Gondwanaland and continental drift by Nauheimer et al. (2012).
- 5) Plants that are phenotypically and genetically *similar* to the New Zealand triploid cultivars have since been found outside New Zealand (see Chapter 14); full-genome sequencing is now technically possible and could be used to confirm clonal identity with complete certainty. The term ‘evolution’ is more usually used in relation to long-term processes of genetic and phenotypic change; in the present context, it is better to consider the possibility that cultivar origins have been obscured by processes of selection, domestication, dispersal, and cultivar replacement over periods of thousands or hundreds of years (and possibly over periods of decades, given the speed with which devastating plant diseases can spread; see Chapter 17 comments on *Phytophthora colocasiae*).