PII: S0006-3207(96)00130-9

Biological Conservation **80** (1997) 135–145

0006-3207/97 $17.00+.00

CONSERVATION IN RELATION TO MATING SYSTEM IN *Nesohedyotis arborea* (RUBIACEAE), A RARE ENDEMIC TREE FROM ST HELENA

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(Received 28 November 1995; accepted 27 September 1996)

Abstract

A field survey of Nesohedyotis arborea *reveals that there are 132 adult trees in the wild, making it one of the commoner endemic plants of St Helena. The trees exhibit leaky dioecy: females are entirely male-sterile, but 'males' do set a small amount of seed. The floral differences between the two morphs are marked: the female is long-styled with large, smooth stigmatic papillae and vestigial anthers, while the male is short-styled with small, rugose stigmatic papillae and large anthers overarching the style. The dioecy probably evolved autochthonously on the island from an ancestral heterostylous condition. The partial loss of female function in males is associated with the production of smaller ovules: approximately a third of the volume of the female ovules. The sex ratio of adult trees is 3:2 in favour of males, due to greater allocation of resources in vegetative survival by males. Pollination is by small syrphid flies and is highly efficient up to distances of 50 m, and most of the gene flow in the population is contributed by pollen transport rather than seed dispersal. Although the population has been fragmented by human land-use patterns, rather few individuals are completely reproductively isolated. An assessment is given of the implications for conservation of the patterns of gene flow and spatial distribution of individuals. The mating system of* Nesohedyotis *reduces the effective population size, but this is likely to be more than outweighed by the effective outbreeding that it promotes. However, subpopulations should be monitored to assure co-sexuality, with, if appropriate, supplementary planting of opposite sex individuals. © 1997 Elsevier Science Ltd. All rights reserved*

Keywords: dioecy, gene flow, island biology, endemic flora and breeding system.

INTRODUCTION

St Helena

St Helena (Lat. 15° 56′S, Long. 5° 42′W) is a small (122 km^2) island in the South Atlantic Ocean with an extraordinary flora including many taxonomically isolated endemic plant species (Cronk, 1992). The highest point is Diana's Peak (826 m) on the sickle-shaped central ridge which forms the backbone of the island. Massive destruction of the indigenous vegetation followed the island's discovery by humans in 1502 (Cronk, 1989), and the small relict patches of tree-fern thicket on the summits of the central ridge are almost all that remains of the original forest. These relict patches are of great importance for conservation with nearly 100% plant endemism. The relict tree-fern thickets are, however, too small to have preserved all the constituent species and several have become extinct, such as *Nesiota elliptica* (Roxb.) Hook. f., *Acalypha rubrinervis* Cronk and *Trochetiopsis erythroxylon* (Forst.) Marais (while the *Acalypha* is entirely extinct, fortunately both *Nesiota* and *Trochetiopsis* are preserved in cultivation). It is in these damp tree-fern thickets of the central ridge, above 700 m, that *Nesohedyotis arborea* (Roxb.) Bremek. grows.

Nesohedyotis

Nesohedyotis is an endemic genus of the Rubiaceae: Hedyotideae. *N. arborea*, the only species, is a small glabrous tree, up to 7 m tall with terete, erect branches. The leaves are opposite, lanceolate and entire, with an acuminate down-curved drip-tip and cylindrical stipular sheath at the base. The inflorescence is a terminal, subglobular compound cyme with small white flowers, 3–4 mm across. The fruit is a subglobular capsule, dark brown or black when mature. The seeds are small (0·75 mm) and angular.

First described as *Hedyotis arborea* Roxburgh (1816), Bremekamp (1952) created the new monotypic endemic genus *Nesohedyotis*, after his revision of *Hedyotis* in Africa removed other members, restricting *Hedyotis* to Asian species alone. *Nesohedyotis* shows at least a superficial similarity to *Hedythyrsus* (two species) and *Pseudonesohedyotis* (one species), all rare tropical African shrubs (Tennant, 1965). The vernacular name on St Helena is 'dogwood' from a fancied resemblance to the European dogwood, *Cornus sanguinea* L., Cornaceae, based on the opposite leaves, white flower heads and tetramerous flowers.

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Dogwood is a keystone species in the threatened ecosystem of the St Helena tree-fern thicket. First, it is the most efficient mist-interceptor (Cronk, 1989) by virtue of its drip tip and upright habit, in a community that depends to a large extent on fog drip to provide the high precipitation to which most plants in this vegetation are adapted. Secondly, it is part of a guild of white-flowered and small-flowered endemics that flower in succession and are all pollinated by an endemic syrphid fly. The species involved are *Melanodendron integrifolium* (Roxb.) DC. (flowers November–January), *Nesohedyotis arborea* (flowers January–March), *Petrobium arborea* (flowers March–June) and *Commidendrum robustum* (Roxb.) DC. (flowers June–August). All are endemic genera. This temporal organisation of flowering at the community level is evidence of competition for pollinators and high selective pressure for efficient pollination and outbreeding. However, the temporal organisation of flowering also provides an almost continual year-round nectar and pollen supply to maintain high populations of syrphids. Thirdly, its vigorous growth and longevity make it an ideal potential species for habitat restoration when attempts are made to rehabilitate abandoned *Phormium tenax* plantations as endemic thicket, so expanding the fragmented and threatened habitat.

Hooker (1868) was the first to notice that *Nesohedyotis arborea* exhibited marked floral dimorphism. He interpreted the morphs as male and female forms, noting the 'very minute and quite sterile' stamens in the female flowers. Dioecy is unusual in the Rubiaceae, but other dioecious species occur, such as species of *Conostomium, Coprosma, Coussarea, Genipa, Mussaenda, Psychotria* (Hawaiian spp.), *Randia* and *Kadua* sect. Wiegmannia from Polynesia. *Nesohedyotis* and *Petrobium arboreum* R.Br. (Compositae) are the only native angiosperms in St Helena that are not fully co-sexual (hermaphrodite or monoecious), and as neither of these two species appears to be fully dioecious, true dioecy does not occur in St Helena. Although there is no fossil evidence for *Nesohedyotis* on St Helena, the St Helena flora is an ancient one (Cronk, 1990), and the genus is likely to have arrived in the Tertiary (Miocene or Pliocene).

Mating system and islands

Carlquist (1965) suggested that the incidence of dioecy is greater in island floras than in continental ones. Underlying this observation was what was termed 'Baker's Law' by Stebbins (1957)—that taxa successfully establishing seed-reproducing populations after long-distance dispersal will usually be self-compatible (Baker, 1955). Selective pressures for an outbreeding system would then result in autochthonous development of dioecy (Baker, 1967; Carlquist, 1965, 1966, 1974).

Baker and Cox (1984) pointed out that figures for dioecy on ocean islands were biased by the exceptional cases of Hawaii (28% dioecious-Mayer and Charlesworth, 1992) and New Zealand (14·5% dioecious-Carlquist, 1966). They showed that low islands in the tropics and dry islands in the subtropics and tropics have few dioecious species. They conclude that latitude and altitude of islands together account for 82% of the variation in dioecy and that the degree of dioecy in an island flora appears to be related to its frequency in a probable source flora in a comparable climatic zone.

Only more detailed study, on a case by case basis, can determine the amount of island dioecy which is autochthonous in origin. However, where autochthonous dioecy can be demonstrated it would be clear evidence for strong selective pressure for outcrossing in restricted oceanic island plant populations. A completely pollen-sterile mutant can establish in a population of co-sexuals if its seed output is more than doubled to compensate for the loss of pollen (Lewis, 1941), but if the population displays inbreeding depression, such a mutant can be established even if it has the same seed output as the hermaphrodite, because all its progeny would be outcrossed and therefore fitter (Bawa, 1980; Thomson & Barrett, 1981).

Mating system and conservation

Although dioecy has the effect of ensuring outcrossing, it also reduces the effective population size (N_e), in comparison to a multiple-allelic self-incompatibility (SI) system, as only half the population are available for any plant to exchange genes with (assuming a 1:1 sex ratio). In this respect it is the same as heterostyly and this lowering of the effective population size is one reason often given for the rarity of heterostyly (di-allelic SI) in comparison to multiple-allelic SI. Furthermore, in small or fragmented populations, chance factors in subpopulations may lead to small groups of same-sex plants becoming isolated from plants of the opposite sex, with disastrous results for the subpopulation. It is clear that where floral dimorphism exists in populations of very rare plants, fully informed conservation decisions cannot be taken without: (1) knowledge of the nature of the dimorphism and the mating system; (2) the ratio of the two morphs in the population; (3) the spatial distribution of the morphs, and (4) the gene flow between morphs. This paper is an attempt to answer these questions for *Nesohedyotis*.

METHODS

Field survey

During a six-week period in February and March 1995 nearly all the *Nesohedyotis* plants on St Helena were visited to determine their precise position, height, stem diameter at base, sex, number of inflorescences, evidence of regeneration and other details. Eight plants proved too inaccessible to be approached closely enough to sex, and a further nine plants could not be sexed as they were not flowering. Reaching all the plants

Table 1. Summary of differences between *Nesohedyotis* morphotypes

Character	Male morph	Female morph
Vegetative growth	Vigorous; long-lived; clonally reproducing from fallen trunks	Main resource allocation into fruit production: trees tending to be smaller; rarely sprouting from fallen trunks
Inflorescence	Less crowded in appearance but tending to have more flowers	Inflorescence with a tighter, globose appearance, though tending to have fewer flowers
Flowers	Corolla lobes tending to be slightly larger	Corolla lobes slightly smaller
Stamens	Filaments long, overarching the style; anthers large, functional; pollen abundant	Filaments more or less absent; anthers small, vestigial with no expanded loculus; pollen entirely absent
Style	Stylar column more or less absent; stigmatic lobes sessile on disk	Stylar column long; stigmatic lobes large
Stigmatic papillae	Small, globose and with a rugose-textured surface	Large, somewhat elongated, and with a smooth surface
Ovary	Ovules small; ovary rarely swelling after anthesis	Ovules larger even before anthesis; ovary rapidly swelling after anthesis
Proportion	60% of population male	40% of population female

proved difficult and time-consuming: many grow in inaccessible places far from paths, on cliffs or very steep (> 60°) slopes, surrounded by dense thicket, native or exotic, that is difficult to penetrate, such as abandoned New Zealand flax *Phormium tenax* Forst. plantations, or thickets of elderberry *Solanum mauritianum* Ait. and blackberry *Rubus pinnatus* Willd. In almost all cases rope had to be used on the steep slopes and cliffs and often a day or so had to be spent cutting a path with a machete before a particular site could be visited. All the trees, whether sexed or not, were mapped by direct determination of the distances and directions between trees in subpopulations, and the accurate positioning of the subpopulation (by triangulation if appropriate).

Floral structure

Bud and flower material was fixed and preserved in formalin–acetic acid–alcohol (FAA). Material was collected from five female plants (located under Diana's Peak, above Cole's Rock, Taylor's and Grapevine Gut), and from six male plants (located at Grapevine Gut and above Cole's Rock). For scanning electron microscope (SEM) examination the material was critical-point dried, sputter-coated with gold/palladium and examined at an accelerating voltage of 5 kV using a digital SEM (Carl Zeiss, Oberkochen, Germany: DSM 962). For light microscopy (LM), material was prepared for wax-embedding and microtoming by dehydration with either a tertiary butyl alcohol (TBA) series (Johansen, 1940) or an alcohol: histoclear series. The material was embedded in 'parawax' and cut in 10 μm sections using a rotary micotome. The sections were stained in safranin and alcian blue, mounted in Euparal and examined under a Zeiss Axiophot microscope. Image analysis to calculate ovule volume was carried out using a Zeiss Axiophot microscope coupled to a video camera and Optimas digital image analyser. For each ovule (serially sectioned at 10 μm) the area of each successive section was obtained by digital analysis and the summed areas used as a volume comparison. For this comparison 12 ovules of each morph were used, sampled from three flowers representing two plants of each morph.

RESULTS

Floral dimorphism

We found very marked floral dimorphism (Table 1, Figs 1–3) with no intermediate or equivocal morphs in any flowers examined.

Inflorescence

The male inflorescence tends to have marginally more flowers than the female, but the slightly longer peduncle and pedicels of the male give the inflorescence a less crowded appearance. In the female, the rapid swelling of the gynoecium after flowering coupled with the compact inflorescence gives rise to a tight globose head of developing fruits.

Perianth

No sexual differences were discernible in the calyx, but the corolla lobes appear to be slightly larger in males (*c.*2·4×1·8–2 mm as opposed to 1·8–2×*c.*1·5 mm).

Stamens

In females the stamens are vestigial (Fig. 1). The filament is very short (0·1 mm) and the diminutive anthers (0·5×0·2 mm) appear almost sessile on the disk. The anther cells are unexpanded (LM). Although the anther slits open partially (SEM) this is probably due to shrivelling of the anther rather than to any operative dehiscence. No pollen is formed and the locules do not expand. In contrast, the male stamens are well developed, with long overarching filaments (1·5×0·3 mm) that hold the anthers (0·9–1×0·7–0·8 mm) above the diminutive stigma with the ventral surface and anther slits facing downwards. They are initially connivent at the tips. Pollen in the male form is abundant.

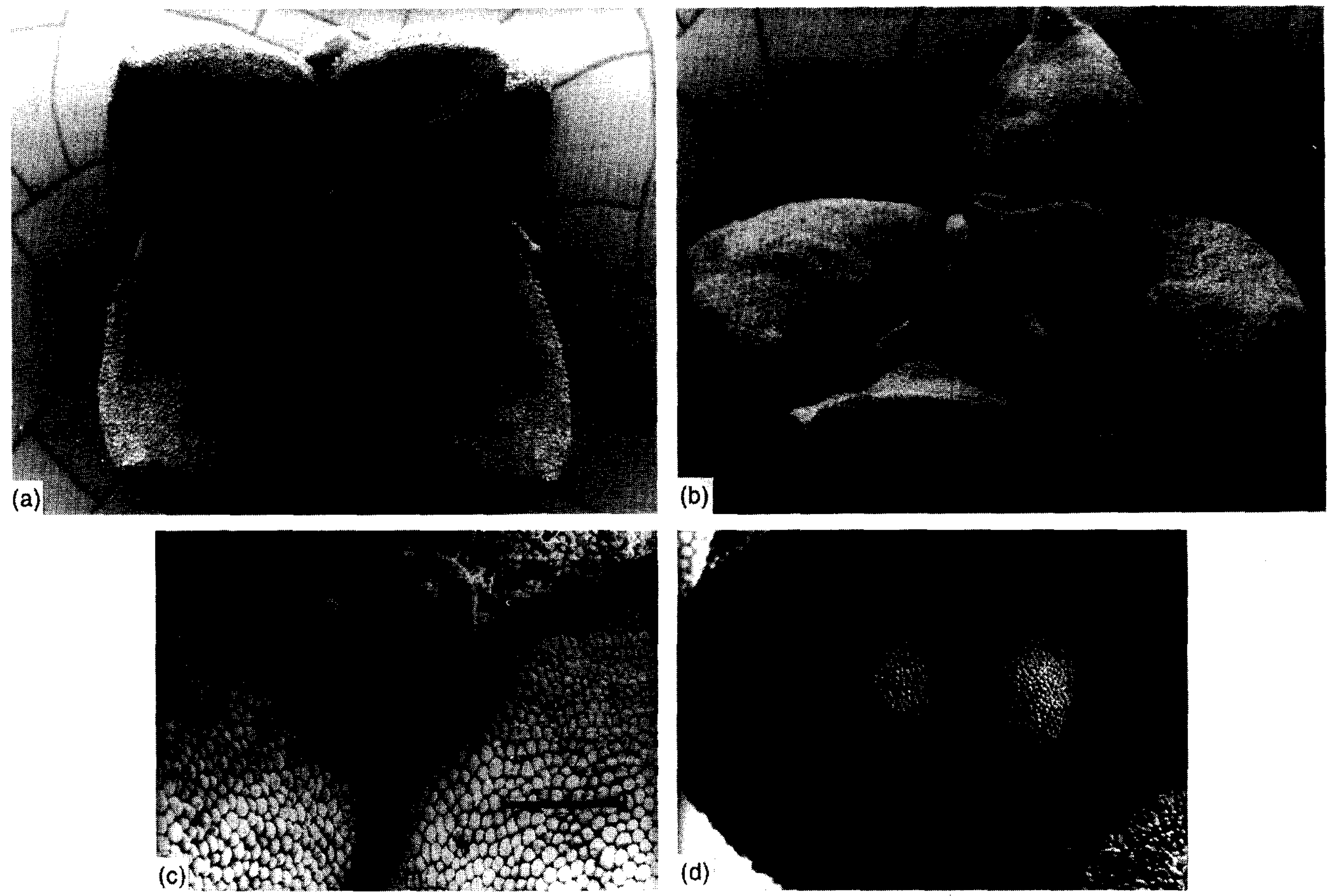

Fig. 1. SEM photographs of *Nesohedyotis* flowers. (a) female, showing the enlarged stigmatic lobes and vestigial anthers; (b) male, showing the four stamens overarching the short style; (c) vestigial anther of female showing the irregular fissuring along the locule (pseudodehiscence); (d) short style of male, pollen grains are adhering to the surface. Scale: (a) and (b), bar = 1 mm; (c) and (d), bar = 20 μm.

Style and stigma

The female morph (Fig. 2) is long-styled (*c.* 0·7 mm) with fully developed stigma lobes (0·4–0·5 mm). The stigmatic papillae of the female (Fig. 2(c)) are large, elongated and smooth (SEM). The male morph is short-styled with smaller stigma lobes. In fact the stigma lobes in males are virtually sessile on the top of the ovary with a scarcely discernible style. The stigmatic papillae in the male (Fig. 2(d)) are small, globose and with a rugose surface (SEM). The difference in style length between the two morphs is due in part to the failure of the cells in the male to elongate (LM).

Ovary and ovules

The ovaries of male and female morphs are more or less identical in bud, but after pollination the female ovaries undergo a rapid increase in size, which rarely happens in the male and, if it does, is usually less marked. The males and females do not differ markedly in ovule number (25–31 per locule): if anything there is a very slight tendency for the males to have more ovules (LM). However, there is a very marked and general difference in the size of the hemitropous ovules (Fig. 3), even in bud (LM). Male ovules (0·1–0·23×0·08–0·13 mm) are notably smaller than female (0·25–0·3×0·14–0·18 mm). Consequently female ovule volumes are up to five times greater than male (LM + Optimas image analyser). The female ovules have a mean volume of 0·051 mm^3 (range 0·028–0·121; SE 0·007). In contrast the male ovules have a mean volume of 0·013 mm^3 (range 0·007–0·020; SE 0·001). The difference in ovule volume is due both to a difference in number of cells and cell expansion (LM). Embryosac development was seen in both morphs but the embryosac of the male is smaller, in line with the difference in ovule size. The difference in ovule size appears to indicate a loss of female function in the 'male' gynoecium.

Sexuality of the morphs

The sexuality of the 'female' morph is unproblematic. No pollen is ever produced and the anthers are in all cases purely vestigial. All females produce abundant seed if adequately pollinated. Thus the female morph is absolutely female and fecund. The 'male' morph is more difficult to characterise sexually as it does produce some seed, as well as abundant pollen. The evidence for the production of viable seed by the male morph is threefold: (1) the Conservation Section of the St Helena

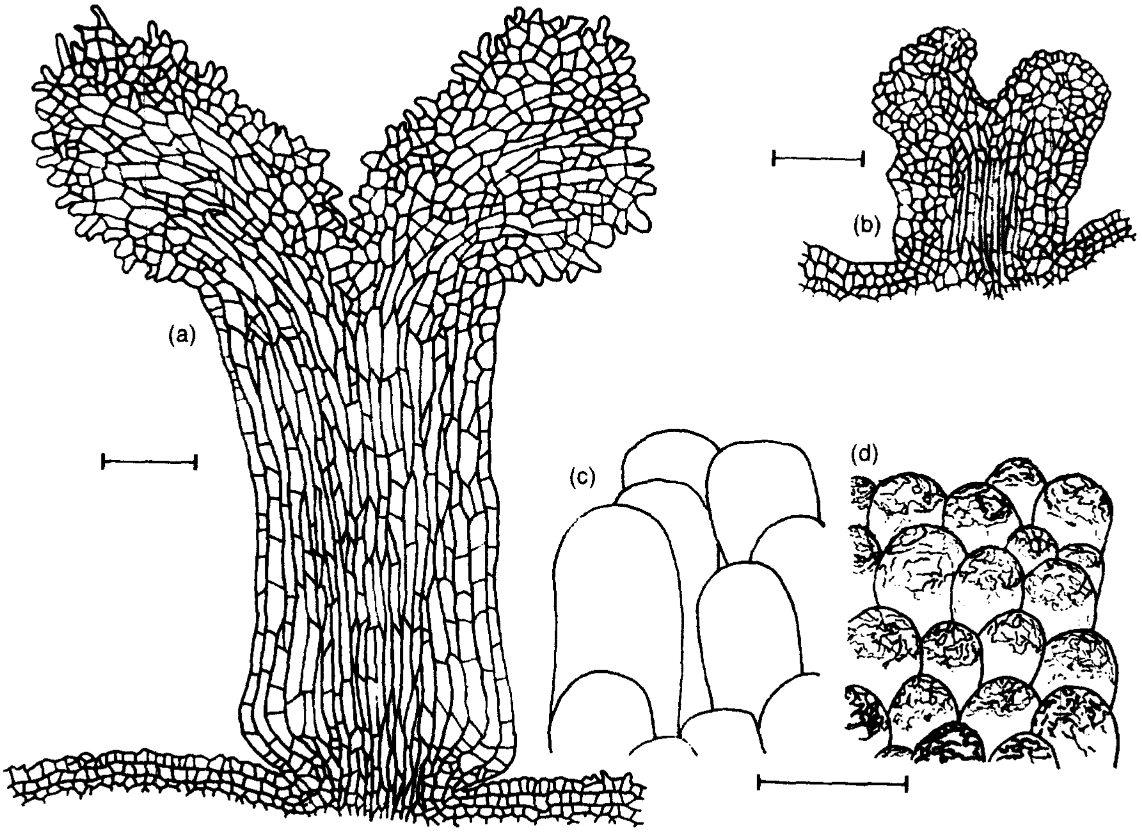

Fig. 2. Drawings of *Nesohedyotis* styles and stigmatic surfaces, showing the evidence for evolution from heterostyly: (a) female (long styled) morph; (b) male (short styled) morph; (c) stigmatic papillae from female showing the elongated, smooth papillae; (d) rounded stigmatic papillae from male showing the smaller size and rugose surface texturing. Scale: upper bars, (a) and (b), = 0·5 mm; lower bar, (c) and (d), = 20 μm. Note that the long style results both from a greater number of cells and greater elongation of those cells.

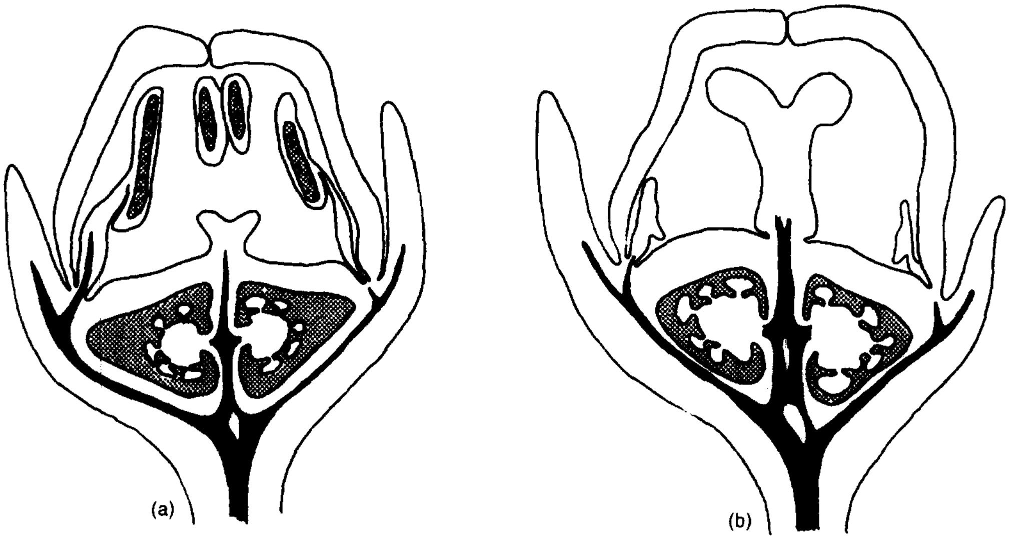

Fig. 3. Ovaries of the two morphs, as longitudinal sections of the two ovary locules and the large placentas, showing the ovule dimorphism between males and females characteristic of subdioecy in this *Nesohedyotis*: (a) male, showing also the bisected anthers; (b) female showing the larger ovules and long style.

Agriculture and Forestry Department has raised seedling dogwoods from seed collected from a male tree at High Peak (G. Benjamin, pers. comm.); (2) field observations of occasional swelling ovaries on male trees after pollination; (3) three seedlings were observed under a male tree that had obviously originated as seed from that tree. However, the amount of seed set by males is very low: estimates from ovary development in the field indicating fruit set rates of 0–1(–2)% of female rates per inflorescence. There appears to be some tree-to-tree variation in fruit set, and some males apparently do not mature any seed at all. This level of seed set seems to be nearly negligible in ecosystem terms: of 76 dogwood seedlings observed only three were associated with a male tree. However, it may be highly significant for long-term metapopulation dynamics as isolated trees could potentially set seed. The male morphs are probably self-compatible as one isolated male at the Depot (the most western dogwood) seemed to be maturing some seed.

Vegetative dimorphism

There is a slight tendency for female plants to be smaller (both in terms of trunk diameter and overall height) and to have fewer inflorescences: a mean of 87 in males (range 2–600; $n = 63$) and a mean of 68 in females (range 1–400; $n = 42$). However, this is merely due to the fact that there are some very large, floriferous males while in the main female plants are smaller. In general the males appear to have more vigorous vegetative growth and more vigorous shoot regeneration when old trunks fall over on the steep and unstable slopes. Very old male trees have a red heartwood which is never seen in female trees, leading to the vernacular island term of 'red dogwood' for these.

Numbers and distribution of *Nesohedyotis* morphs

All *Nesohedyotis* adults (> 1 m in height) were located. The total world population for this species is 132 plants, of which 69 are males, 46 are females and 17 not determined (the nine that were not flowering tended to be smaller plants). The morphs are shown mapped on a 1 ha grid square basis (Fig. 4). The population is clearly fragmented along the central ridge but good concentrations remain north west of Cuckholds Point and Diana's Peak and south west of Mt Actaeon as well as at High Peak. The plants at High Peak tend to be small and many flower poorly as the south-facing cliffs of High Peak are extremely exposed to wind. The 3:2 ratio of male to female morphs may well be due to the greater vigour, longevity and clonal reproduction of the males. In places dogwoods occur in a line where regeneration from successive trunk-falls had led to new trees being produced when the connecting trunk had rotted away (Fig. 5). These groups were almost always all male (rarely all female). The greater vegetative vigour of the males seems to be due to lower resource allocation in seed production, and consequent greater resource allocation to vegetative growth.

Gene flow and seed regeneration

The bilocular capsules dehisce when ripe by means of apical slits and the small seeds are shaken out by wind and dispersed by wind and gravity, for which they have no special adaptations. It appears that seed dispersal is not very efficient. Of 76 seedlings observed during field work 59 (78%) were within 2 m of the trunk of the presumed parent tree, and the furthest seedling was 6 m away. The seedlings regenerate mainly on the horizontal trunks of the endemic tree fern *Dicksonia arborescens* L'Hér., but occasionally seedlings may be found on moss or damp humus on banks or cliffs.

In contrast, pollination is by small syrphid flies which are highly efficient vectors up to a distance of around 50 m. Few species of syrphid fly occur on St Helena and two species are responsible for most of the insect visits. The main species is the yellow-faced and yellow-legged *Loveridgeana beattiei* Doesb. and Doesb., which is distinguished by the conspicuous black marking on the first tergite and has a body length of 8–11 mm. The second species is the dark-bodied *Syritta stigmatica* Loew, which is distinguished by the yellow markings on the abdomen and the very swollen hind femora, and has a body length of 7–9·5 mm. *Loveridgeana* is an endemic genus (van Doesburg & van Doesburg, 1976) and there may have been considerable co-evolution between this generalist pollinator, which seems especially attracted to small white flowers, and the endemic trees. The *S. stigmatica* is a South African species and while it may be native, it could equally well be a recent introduction.

Isolated female trees of *Nesohedyotis* had a low percentage of developing fruits, implying that they are pollination-limited (Fig. 6). The most distant tree (over 500 m from the nearest male) was effectively isolated from gene flow. A sharp decline in pollination efficiency is indicated at distances greater than 50 m. These data suggest (1) that cross pollination is mainly responsible for gene flow within the population; and (2) up to distances of 50 m this gene flow is highly efficient. As all members of the population were accurately mapped it was possible to ascertain the distance from all female plants to the nearest male and vice versa (Fig. 7(a), (b)). Taking 50 m as an arbitrary, but reasonable, cut-off point, it can be shown that of the 69 males only 11 (16%) are over 50 m from the nearest female and hence may be seriously under-contributing to the gene pool. For females, out of a total of 46, only eight (17·4%) are isolated from the nearest male by over 50 m (Fig. 7(a), (b)).

DISCUSSION

Implication of the mating system and gene flow for conservation

As the female function of the males is so poor the mating system is best considered as dioecy or more specifically 'leaky dioecy', and the polliniferous morph is certainly, in ecosystem terms, most accurately described as male rather than hermaphrodite. Lloyd (1981) characterised plant sexuality as categories on a 'gender value' continuum. However, polliniferous *Nesohedyotis* plants appear to have the quantitative features of his 'males' category, rather than the next category 'inconstant males'. Nevertheless, if the term 'inconstant males'

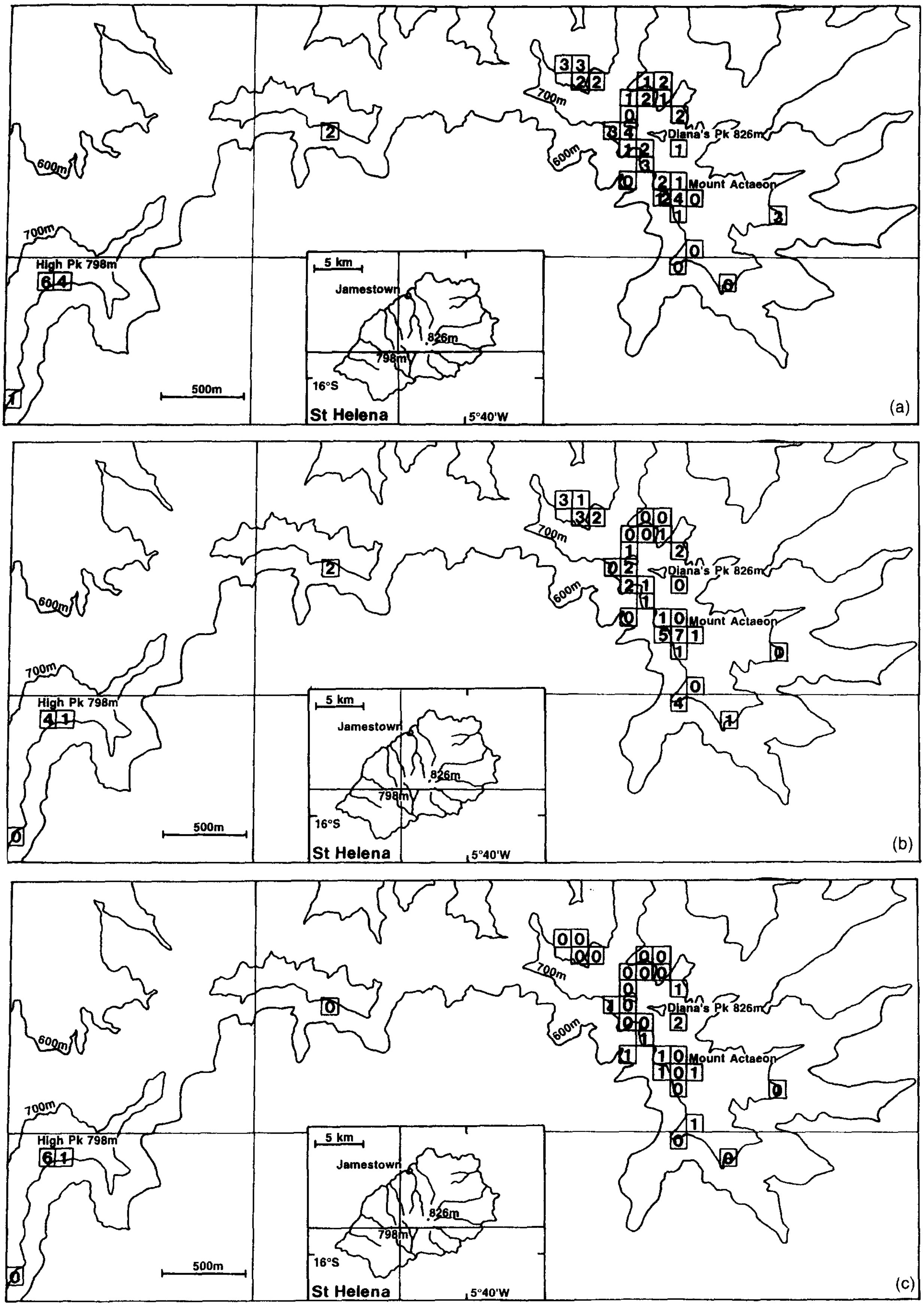

Fig. 4. Maps of the distribution of (a) males; (b) females; (c) indeterminate, mapped on a 1 ha grid square basis. Indeterminate individuals were either not flowering or too inaccessible to be sexed. The inset map shows the position of high Peak (798 m) and Diana's Peak (826 m) relative to the island as a whole. The main map covers the central ridge. The Depot is the site south east of High Peak. Cuckhold's Point is just west of Diana's Peak.

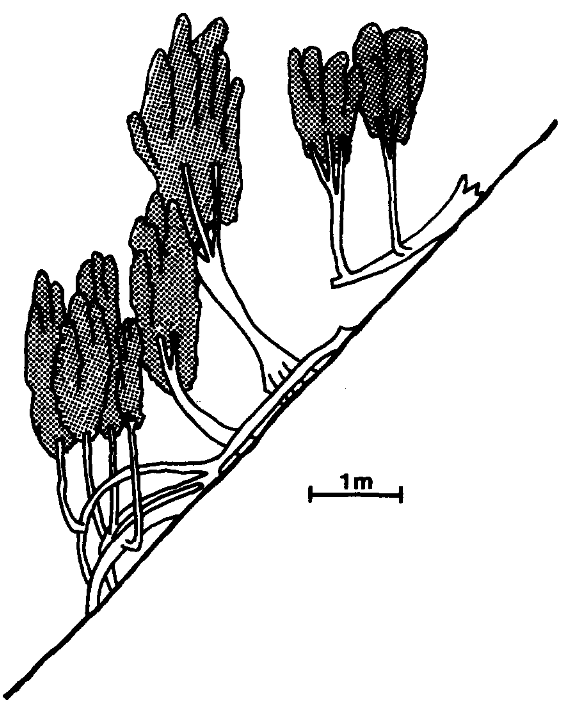

Fig. 5. Sketch of a group of male *Nesohedyotis* plants showing the phenomenon of downslope collapse. This group is interpreted as one ancient clone. Vegetative reproduction of this sort appears to be largely restricted to males and has a potentially important effect on the sexual- and age-structure of the populations.

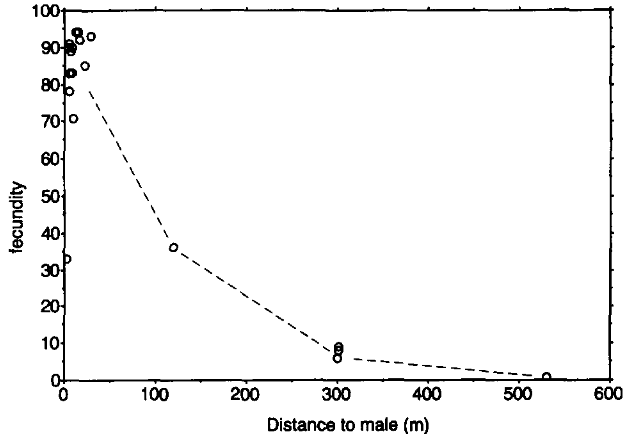

Fig. 6. Graph of pollen transport as indicated by the declining fecundity (% of ovaries swelling) with distance from the nearest pollen donor. The lines are intended as a visual guide to the trend. No attempt has been made to fit a curve to the data.

is interpreted loosely, it is a useful one to apply in this case. Self-compatibility in male morphs is important for two reasons: first, it suggests that any possible ancestral self-incompatibility system has been lost, and secondly it raises the possibility that all, or almost all, the seed collected from male trees may be selfed. The mating system of *Nesohedyotis* (with its 3:2 ratio of males to females) will reduce the effective population size as on average any plant will only have half the population available for mating (40% for males, 60% for females).

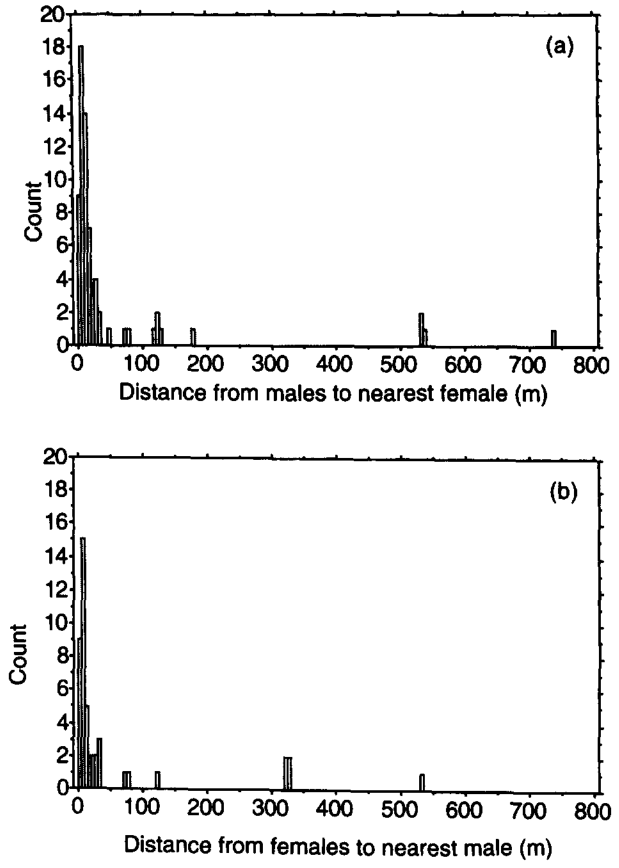

Fig. 7. Frequency of interplant distances between: (a) males and the nearest female; (b) females and the nearest male. Class interval = 5 m.

However, the reduction of inbreeding through avoidance of selfing compensates for this. There is no striking evidence of poor growth that can be interpreted as inbreeding depression in *Nesohedyotis*. This is contrary to the situation with some other, rarer, endemics such as the St Helena redwood *Trochetiopsis erythroxylon* (Cronk, 1983) which is now extinct in the wild and very difficult to cultivate because of its poor growth and high mortality. Redwood is hermaphrodite and fully self-compatible and has been selfed for many years. The mating system of *Nesohedyotis*, by preventing selfing, may improve its chances of successful conservation.

Nevertheless, the population is small and fragmented. The total population was divided into 24 subpopulations, on a criterion of 50 m separation, for mapping purposes. The mean number of trees per subpopulation is 5·5, and the dogwood thus has a clumped distribution. However, the size of these clumps is small and inbreeding is likely to be occurring even though selfing is avoided. Six of the subpopulations consisted of single, isolated trees. The other subpopulations ranged in size up to nine, except for one of 35. These figures suggest that population fragmentation is not yet critical for the population as a whole, but that a significant impact on gene flow and effective population size could be made by judicious planting of opposite sex individuals into unisexual, isolated subpopulations. Habitat loss in the past, mainly caused by clearing native vegetation for New Zealand flax plantations, will have affected chances of the future survival of *Nesohedyotis* both by reducing total numbers and by adversely affecting the genetic structure of the population. Gene flow operates mainly through pollination rather than seed dispersal, thus it is the syrphid flies that maintain the genetic integrity of the population. However, pollination efficiency appears to drop rapidly at distances of greater than 50 m, and thus some 16–18% of the population (isolated from the opposite sex by more than 50 m) may be under-contributing to the gene pool—another loss of effective population size. Males can rescue themselves from isolation by selfing, but females must wait for a male to arrive by dispersal of seed from another population. The inefficient seed dispersal makes this a slow process. *Nesohedyotis* does appear to be quite long lived and Baker and Cox (1984) point out that the correlation between dioecy and a woody, perennial, iteroparous habit may mitigate this potentially deleterious effect of dioecy on islands, since a single plant may simply 'wait' for a propagule of the opposite sex to grow to maturity nearby. In the main, then, the mating system still serves to promote efficient outbreeding and this has probably been the major driving force behind the evolution of the system. To put the relationship between mating system and conservation into context it is interesting to consider the likely selective forces that have led to its evolution.

Evolution of mating system

The pronounced herkogamy and style-length dimorphism, together with the differences in size and texturing of the stigmatic papillae, are all features strongly suggestive of an original heterostylous condition. Darwin (1877) wrote that the family Rubiaceae 'contains a much larger number of heterostyled genera than any other one, as yet known'. This still stands, and Ganders (1979) lists 155 genera in which heterostyly has been reported, of which 91 belong to the Rubiaceae. Furthermore, Muenchow and Grebus (1989) list a number of genera of the Rubiaceae where heterostyly and dioecy co-occur, and where 'it seems clear that distyly is ancestral'.

If we assume a heterostylous ancestor for *Nesohedyotis* the following course of events may plausibly have led to the present condition: (a) colonisation by a distylous and largely self-incompatible ancestor; (b) breakdown of incompatibility associated with colonisation event; (c) gynodioecy established as an outbreeding mechanism; (d) further sexual differentiation to leaky dioecy.

This scheme raises a number of questions. First, what was the cause of the breakdown of incompatibility? Secondly, why was gynodioecy established? Thirdly, why did the putative gynodioecious population evolve towards dioecy? Further, why did the population not become fully dioecious?

The breakdown of self-incompatibility (SI)

SI is an unsuitable and unusual strategy for a colonising plant (Baker's Law). In such situations it is assumed that reproductive assurance will be selected for, and there are a number of examples of SI breaking down in colonising populations of otherwise SI species (Baker, 1955, 1966; Barrett, 1988, 1989*a*,*b*; Cox, 1989). We therefore propose that the breakdown of SI in *Nesohedyotis* occurred synchronously with the colonisation event that brought it to St Helena, and that founding populations on St Helena quickly evolved self-compatibility from an incompletely SI heterostylous ancestor. If this is accepted then the implication is that dioecy arose autochthonously on St Helena.

The establishment of gynodioecy

The next likely step is that the di- or homostylous intermediate became gynodioecious (i.e. with populations of hermaphrodites and females) in order to re-establish outbreeding. A male sterile mutant can only establish in a formerly co-sexual population if its seed-reproductive fitness is more than doubled to compensate for the loss of pollen (Lewis, 1941). However, Bawa (1980) points out that, under conditions of inbreeding, the increased fitness produced by the restoration of outbreeding would allow such a mutant to become established (even if it had only the same seed-reproductive fertility as the hermaphrodite). It is easy to see how in a small but stable population on an oceanic island the need for outbreeding might be re-established (Bawa, 1982). Indeed, selection for outcrossing seems to have led to the evolution of dioecy more than once in the Hawaiian genus *Wikstroemia* (Mayer & Charlesworth, 1992). If outbreeding is to be restored, it might seem likely that the original SI system (in this case heterostyly) would be restored rather than a new system. A possible explanation for the evolution of gynodioecy in such cases is that a single male-sterile mutation is easier to evolve than a complex di-allelic or multiple-allelic system such as SI (Baker, 1967) Furthermore, the absence of specialist pollinators on oceanic islands and the shift to generalist syrphid fly pollination may render dioecy more suitable (Beach & Bawa, 1980; Beach, 1981; Bawa, 1994).

Evolution towards dioecy

The evolution of dioecy from gynodioecy is assumed to be characteristically gradual (Bawa, 1980). The modifiers (female sterility mutations) appear generally to increase pollen production of hermaphrodites at the expense of ovule production, converting them first into subhermaphrodites, and then after further selection into males. The modifier genes are assumed to spread rapidly in the presence of male-steriles (females) in an inbreeding population because the subhermaphrodites (males) contribute more genes via pollen than via ovules (Charlesworth & Charlesworth, 1978). In the *Wikstroemia* case (Mayer & Charlesworth, 1992) one or both populations studied appeared to be genetically variable for modifiers controlling the degree of unisexuality. This might also be the case in *Nesohedyotis*, which would explain the apparent variability in fruit set among males.

Failure to become completely dioecious

In terms of metapopulation dynamics, the ability of isolated males to undergo occasional sexual reproduction may be important and heavily selected for, preventing the extinction of subpopulations that have become unisexual through drift. An alternative explanation is that when full dioecy is approached the selective pressure for further loss of female function might be negligible (J. Pannell, pers. comm.).

Conservation of *Nesohedyotis*

We suggested in the Introduction that dogwood is potentially a good species for habitat restoration-if attempts are to be made to restore abandoned *Phormium tenax* plantations as endemic thicket, so expanding the fragmented and threatened habitat. Plants for this purpose could be obtained from seed orchards formed from equal numbers of male and female plants propagated from cuttings. The number of genotypes should be maximised and they should be drawn from different parts of the eastern ridge and from large populations (such as the south face of Actaeon) to minimise the use of inbred stock. Plants so derived could also form the basis for judicious supplementation planting of opposite-sex individuals into single-sex subpopulations, to prevent subpopulation extinction. Supplementation planting to link subpopulations and provide corridors for gene flow would also be advantageous.

There is a conservation trade-off between either keeping plants from different subpopulations genetically separate to avoid obscuring patterns of microevolution and infraspecific diversity, or genetically manipulating subpopulations to maximise outbreeding and fitness. In the case of *Nesohedyotis* there is no morphological evidence for any population differentiation, and before human clearance on the central ridge it is unlikely that any population would have been entirely isolated. However, it would certainly be wise for the present to keep the western (High Peak) populations discrete from the eastern (Diana's Peak etc.) populations as it is here that the greatest disjunction occurs. Generally, however, the survival of the genus without genetic collapse from inbreeding, in a fragmented population of 132 individuals, may be more important than other considerations.

The former IUCN conservation status of *Nesohedyotis* was 'endangered' (E), and under the new categories (IUCN, 1994) it falls into the category of 'critically endangered' (CR), as the population is under 250 individuals and fragmented (i.e. no subpopulation is estimated to contain more than 50 mature individuals). As such it is deserving of conservation action even though the population appears to be stable at present. Indeed, the fact that it has not yet become very rare may make it a good target for conservation. The St Helena redwood *Trochetiopsis erythroxylon*, now extinct in the wild (EW), may not be savable from extinction because of the inbreeding damage it has sustained and its consequent depauperate gene pool (Cronk, 1993; R. Rowe, pers. comm.). However, given a knowledge of the mating system and an appropriate genetic core, there is a good prospect of effective conservation allowing *Nesohedyotis* to survive indefinitely.

ACKNOWLEDGEMENTS

We thank the many people in St Helena who helped, directly or indirectly, with the field-work, particularly: George Benjamin, Glenville Henry, Leslie Benjamin, Colin Richards, Nicholas Williams, Mark Williams and Chris Lomas. Particular tribute is paid to the fieldcraft of George Benjamin. We also thank the staff of the Royal Botanic Garden, Edinburgh for advice on technical matters, particularly Frieda Christie, Mark Watson and Stephen Droop. We also thank Graham Rothery for advice on syrphid flies. Deborah Charlesworth and Philip and Myrtle Ashmole kindly commented on an earlier draft of the manuscript. The field-work was carried out under a Royal Society Research Grant to Q.C.B.C., which is gratefully acknowledged.

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