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Population biology of late spider orchid *Ophrys fuciflora* - a study at Wye National Nature Reserve 1987 -98

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Population biology of late spider orchid *Ophrys fuciflora* - A study at Wye National Nature Reserve 1987-1998

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Abstract

Wild orchids are considered both beautiful and rare, and in many ways their conservation has come to be symbolic of the maintenance of biodiversity in Britain. The maintenance and or increase of populations of orchid species is desirable for many reasons. This may best be achieved through management based on an understanding of the ecology of the species. This study of the late spider orchid *Ophrys fuciflora* aimed to:

- add to the autecological knowledge base about the species;
- determine something of its environmental preferences; and
- develop appropriate practical management strategies for the species based on the acquired autecological knowledge.

The field research focussed on a population of *O. fuciflora* growing at Wye National Nature Reserve in Kent. A census of this population was carried out for a 12 year period. These data were supplemented by phytosociological data taken from heterogeneous areas of chalk grassland both within and without the orchid colonies. These data were subjected to analyses using statistical, matrix modelling, classification and ordination techniques.

The results showed *O. fuciflora*:

- to be reliant on seed for reproduction;
- to be sensitive to the mortality of flowering plants in respect of its population dynamics;
- to exhibit a preference for disturbed soils of low fertility; and
- to be demonstrating characteristic behaviour of an adventive species.

Proposals for appropriate management are put forward, they include the deliberate mechanical disturbance of chalk grassland. Proposals for further work include experimental management studies, revised census studies and pedological work.

Some of the implications of the study findings for wider conservation management of chalk grassland are also discussed.

1. Background to the study

1.1 Introduction

This study explored aspects of the ecology of the late spider orchid *Ophrys fuciflora*; the management of the species at Wye National Nature Reserve; and the relationship between species above ground performance, land management and vegetation community structure. Due to its rarity and legal protection in the United Kingdom, and previous incidences of vandalism, references to the exact location of the study plots have been withheld from the text. These are available to *bona fide* researchers. Nomenclature follows Stace 1997.

1.2 Background

1.2.1 Annual counts of late spider orchid *Ophrys fuciflora* flower spikes were started in the later 1960s by J Duffield, the then warden of Wye National Nature Reserve. There was also an attempt to establish an annual census but this met with only limited success. Nevertheless, these early attempts to study the species generated sufficient anecdotal evidence to indicate that life history of the plant wasn't as straightforward as described in the literature, and that variations in management had differing impacts.

1.2.2 In 1987 a systematic census of the known colonies of *Ophrys fuciflora* was established as a means of monitoring the effects of management on the species. The concern at that time was the increasing dominance of tor grass *Brachypodium pinnatum* in the chalk grassland sward, which was leading to a depauporite flora. The challenge facing the warden was to manage the grassland in such a way as to reduce the dominance of *B. pinnatum* without destroying the rich chalk grassland flora. The census was set up as one of the management monitoring measures.

1.2.3 The task of the census in respect of management was completed some years ago but its value as a tool for improving the ecological understanding of one of Britain's rarest plants was recognised, thus it continued. It is now one of very few long-term species studies, providing a unique and valuable insight into the ecology of this rare and attractive plant.

1.2.4 This report presents a summary of the published ecology of *O. fuciflora*; the physical and management background of Wye National Nature Reserve; the study methods; the results of the study from 1987 to 1998; analyses of those results; and discussion and conclusions about the autecology and management of the species at the study site.

1.3 Orchid management

1.3.1 Many of Britain's orchids are most abundant in the semi-natural habitats of the British landscape, for instance chalk downs and upland hill meadows (Lang 1989). These plagio-climatic habitats were created by the removal of Atlantic forest and subsequent land use practices over many centuries. Conservation of species that persist in such habitats requires that the natural successional processes are interfered with in order to maintain the appropriate seral state. Many British orchids are examples of such species. The process of interference, referred to as management, intends to maintain semi-natural habitats which offer appropriate conditions for orchid growth, where orchids are a feature of interest.

1.3.2 Through management, nature conservation bodies attempt to recreate and sustain optimum conditions for the growth of orchid species; therefore the growth requirements of the species need to be understood. Traditionally, Conservation management techniques have, to a large extent, replicated historical agricultural practices that created and maintained semi-natural habitats, for example sheep grazing, hay cutting and coppicing. These practices do not necessarily create optimum conditions for species of particular interest.

1.3.3 The effects of a traditional sheep grazing regime on a population of *Gymnadenia conopsea* (fragrant orchid) at a downland site in Sussex have been studied. The study established that population recruitment was mainly by seed and that traditional sheep grazing regimes affected the ability of the orchid to reproduce sexually. Experimental plots were used to establish the effects of grazing on the inflorescence. From the data it was apparent that appropriate management of the orchid entailed reducing grazing pressure during the early above ground development stages of the plant. This resulted in increased inflorescence length and therefore increased the level of potentially viable seed produced (Hutchings 1989). Two important points may be drawn from this example. Firstly, that traditional conservation management techniques may not create optimum conditions for the survival of a particular species. Secondly, that a greater understanding of the species ecology can lead to the development of more appropriate management.

1.3.4 A scientific approach to the management of orchids (or any species) must recognise three important principles:

i. "Each species of orchid has its' own special requirement which must be met for it to flourish" and survive (Lang 1989).

ii. In order that management practices employed to ensure the survival of a species are appropriate, it is important that management is based on a thorough knowledge of the species ecology Hutchings 1987).

iii. That the physical, practical and financial restraints of an individual site are borne in mind.

These principles need to be successfully integrated in order to achieve effective and sustainable management of an orchid population.

1.3.5 It can be argued that each species of orchid, or any other plant for that matter, has its own particular ecological requirements. These ecological requirements define the 'niche' of the species, its stress tolerances, and inter and intra specific competitiveness. Because of the differing particular ecological requirements of orchid species no standard management technique can be applied. Each species must be individually considered when developing management approaches for their conservation. The paucity of detailed ecological information about individual species hinders the development of appropriate management practices, though as available 8information is supplemented by further research it becomes possible to develop increasingly appropriate techniques, within the constraints of individual sites.

1.4 Aims of this investigation

1.4.1 This investigation focused on a population of late spider orchid *Ophrys fuciflora* growing on Wye National Nature Reserve, owned and managed by English Nature, the statutory agency responsible for nature conservation. The aims of this investigation were:

- to add to the autecological knowledge base of the species;
- to determine something of the 'special requirement' of *Ophrys fuciflora*;
- to describe the most appropriate management regime within the physical, practical and financial constraints of the site.

2. What is known about *Ophrys fuciflora*

2.1 Genus *Ophrys*

2.1.1 A large proportion of the European orchid flora is comprised of the tribe *Orchideae*. The genus *Ophrys* makes a large contribution to this tribe with as many as 140 species being recognised (IUCN/SCC 1996). Only four members of the genus occur naturally in Britain; the fly orchid *Ophrys insectifera*, the bee orchid *O. apifera*, the early spider orchid *O. sphegodes*, and the late spider orchid *O. fuciflora*.

2.1.2 *O. fuciflora* is the scarcest of the genus in Britain. Little is directly known about the species, particularly in Britain where it reaches the northern limits of its distribution. Some, if not all, European orchids vary in their 'behaviour' as they approach the limits of their distributional range (IUCN/SSC 1996). It is likely that *O. fuciflora* in Britain may differ in aspects of its phenology, demography and ecology from individuals growing in the Mediterranean which is more central to its distributional range. However, other members of the genus have been studied and it is considered that *O. fuciflora* shares many of the characteristics of these (van der Cingel 1995; Summerhayes 1968; Dressler 1981). Extrapolation of such characteristics enables a picture of the life cycle and ecology of the species to be built, at least in part.

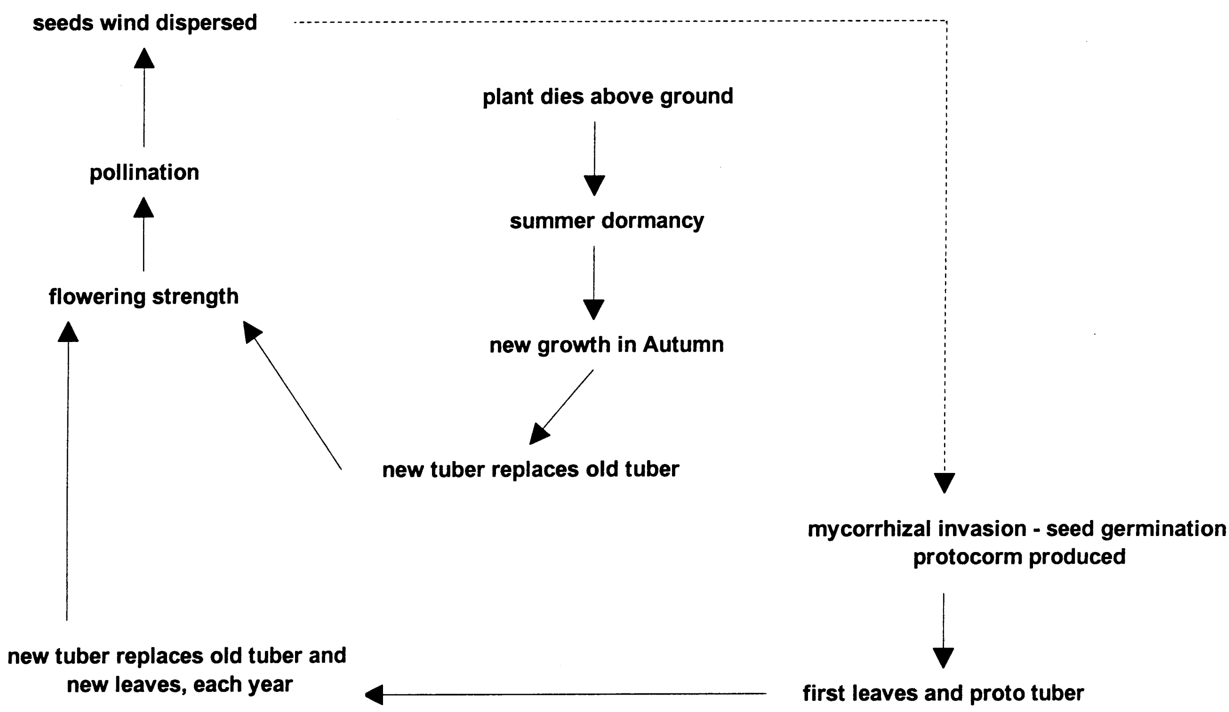


Figure 2.1 Typical life cycle of an orchid of the genus *Ophrys* (after Davies *et al* 1988)

2.2 The life cycle

2.2.1 Figure 2.1 shows the typical life cycle for an orchid of the genus (Davies *et al* 1988). The seeds of *Ophrys* are minute consisting of an embryo composed of a few cells covered by a flattened ingument which aids wind dispersal. Unlike the seeds of many plants, orchid seeds contain no nourishment and cannot germinate unassisted (Blackmore 1985; Davies *et al* 1988; Summerhayes 1968). For an orchid seed to germinate its immediate microclimate must have the correct combination of environmental factors, for instance light, moisture and soil pH (Land 1989). Whilst these factors are important, inoculation of the seed by a fungus of the genus *Rhizoctonia* is a prerequisite to germination (Dressler 1981; Summerhayes 1968). Fungal penetration of the ingument is thought to be the stimulus for germination. The fungus then forms intercellular coils or irregular hyphal aggregates within the host tissue. Fungal mycelium then spread through the embryo cells stimulating orchid growth (Jackson & Mason 1984; Dressler 1981).

2.2.2 The mycorrhizal relationship between the orchid and fungus is a complex symbiosis, in which the developing orchid is both host of and parasite of the fungus, while the fungus in turn is both parasite of the orchid and saprophytic upon organic matter within the soil (Jackson & Mason 1984). For the saprophytic part of the mycorrhizal fungus nutrition is obtained through the breakdown of organic matter by the secretion of enzymes, them amides are formed and converted to soluble sugars (Griffin 1972). The sugars pass through the part of the fungus within the soil (the ectotrophic part) to the part within the orchid itself. In this way the plant receives the energy required for gemination and development (Jackson & Mason 1984; Summerhayes 1968). Lang (1989) suggests that the dominance within the mycorrhizal relationship alternates from the orchid during the Spring and Summer, to the fungus during the Autumn and Winter, such that orchid cells are ingested by the fungus during the Winter period and vice versa during the Summer. This may or may not be the case, but the work of Smith (1966), Stribley *et al* (1980) and Alexander & Hadley (1985) indicates that there is a net nutritional gain by the orchid.

2.2.3 After germination *Ophrys* develop as a protocorm, a horizontal structure without roots or photosynthetic parts. The protocorm develops underground during which time the plant is totally dependent on the mycorrhizal fungus for nutrition. Estimates for the duration of this phase vary from 18 months to three years, though the exact duration in the wild is not known (Blackmore 1985; Davies *et al* 1988). At the next stage, roots and a proto tuber develop along with leaves which enable the plant to photosynthesize thus reducing its dependence on the mycorrhizal fungus for nutrition. At this time the protocorm withers away (Davies *et al* 1988; Summerhayes 1968). The leaves of some *Ophrys* species persist through the Winter and Spring forming a basal rosette, though whether *O. fuciflora* exhibits this characteristic is unknown (Wells & Cox 1985). The proto tuber develops into a spheroid tuber, which is not infected with the mycorrhizal fungus, feeding the growth of new leaves and flowering parts. The tuber becomes exhausted during the Spring and Summer growth and then decays. It is replaced by a new tuber which develops during Spring and Summer growth (Dressley 1981; Wells & Cox 1985; Davies *et al* 1988). The spheroid tuber of *Ophrys* is not rhizomatous, serving only as a food store for the plant. Though it is considered that vegetative reproduction may take place via the development of an additional lateral bud causing an additional 'new' tuber to grow. This would then separate forming a new plant (Summerhayes 1968).

2.2.4 In Britain *O. fuciflora* flowers from mid May through to late July, and has occasionally been observed flowering as late as August (Pers ob). The flowers of most orchids are adapted for pollination by a particular kind or even species of insect, *O. fuciflora* is no exception to this. The flowers of *O. fuciflora* are zygomorphic. It has three pink broad prominent sepals much as *O. apifera*. The two upper petals are short, hairy and orange pink in colour. Whilst the labellum is larger and squarer than that of *O. apifera* (see Figures 2.2 and 2.3) (Land 1989). Like all *Ophrys* the emerging flowers of *O. fuciflora* turn 180° in relation to the bract, a process known as resupination. This turning presents the colourful labellum as a landing platform for insect pollinators. *Ophrys* flowers also produce scents containing monoterpenes and fatty acid derivatives which are thought to play a role in the long distance attraction of male bees (van der Cingel 1995). The process whereby the pollinia of the flower attach themselves to the pollinator by pads called viscidia during psuedocopulation was described by Blackmore (1985) and Dressler (1981).

2.2.5 On the continent *O. fuciflora* is pollinated by male bees of the species *Eucera tuberculata* and *E. longicornis*, which do not occur in Britain (van der Cingel 1995). No insect pollinators of the orchid have been noted in Britain, but it is assumed that a\t least one species of insect must pollinate the orchid since viable seed occurs and hybrids with *O. apifera* have been observed (Lang 1989). Whilst the bees may not occur, van der Cingel (1995) noted *O. fuciflora* being pollinated by beetles.

2.2.6 Summerhayes (1968) suggests that British orchids, including *Ophrys*, behave monocarpically, expending all the energy of their tubers during flowering. Wells & Cox (1985) and Hutchings (1987) have shown this not to be the case for *O. apifera* and *O. sphegodes*. Work on other species has also shown that British species are not generically monocarpic (Lang 1989). It is probable the *O. fuciflora* displays the same perennial tendencies as other members of the genus in Britain.

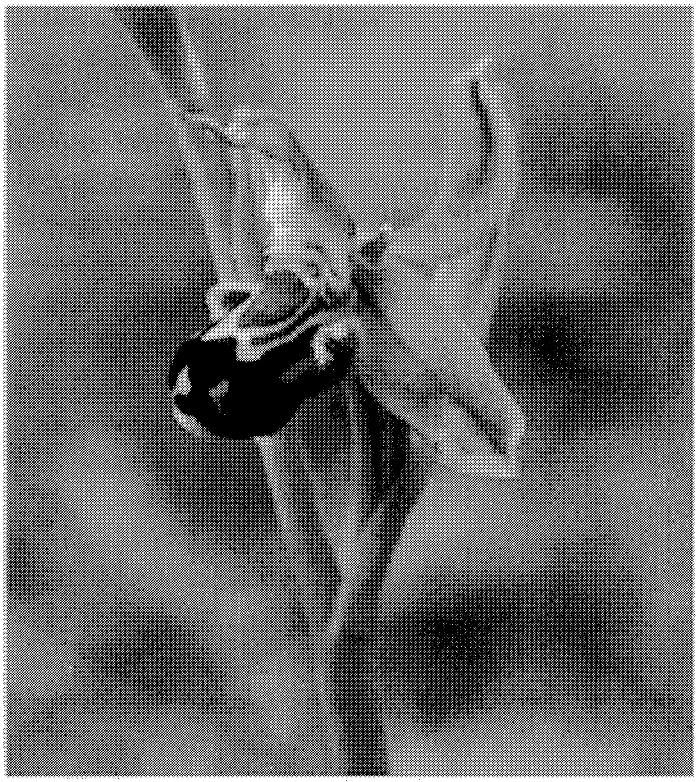


Figure 2.2 Bee orchid *O. apifera*

Figure 2.3 Late spider orchid *O. fuciflora*

2.3 Ecology

2.3.1 Dressler (1981) indicates that orchids of the genus *Ophrys* prefer soil with drainage and air movement. The consistent occurrence of *O. fuciflora* on the shallow free draining soils of the North Downs would support this hypothesis.

2.3.2 The soils of the North Downs escarpment on which *O. fuciflora* occurs are derived from the Senonian (Upper) and Turonian (Middle) Chalk. This is composed of 97%-98% calcium carbonate ($CaCO_3$) with traces of other oxidized minerals (see Table 2.1) (Clough & Hanifi 1979). These soils are low in plant nutrients creating conditions for physiological stress within plants. Dressler (1981) suggests that orchids tend to be stress tolerators enabling them to thrive in the depauperate rendzina soils of the chalk. He also suggests that orchids exhibit a number of physiological characteristics associated with 'weedy' species, for example high seed production. The work of Hutchings (1987) and Grime *et al* (1988) would tend to support the analysis by Dressler.

Table 2.1 Chemical composition of Senonian Chalk (after Clough & Hanifi 1979)

Oxide	% weight
SiO_2	0.47
Al_2O_3	0.08
FeO	0.02
MgO	0.63
CaO	54.44
K_2O	0.03
CO_2	43.38

2.4 Distribution

2.4.1 *O. fuciflora* grows throughout central southern Europe through to Asia Minor (Summerhayes 1968). Within its range it is sufficiently common place that it is not considered at risk (IUCN/SSC 1996). Within Britain though the species is very limited in its distribution. Godfrey (1933) refers to it as a speciality of the East Kent chalk, something echoed by Summerhayes (1968) and Lang (1989). The later authors do, however, make reference to unconfirmed records from the counties of Dorset, Surrey, Suffolk and Gloucestershire. There remains some doubt as to the authenticity of these records.

2.4.2 In essence, though, the species is restricted in distribution to the escarpment of the North Downs in East Kent (see Figure 2.4). Its rarity in Britain warrants its inclusion in the British Red Data Book of vascular plants (Perring & Farrell 1983; Wiggington 1999) and protection under Schedule 8 of the Wildlife and Countryside Act (1981).

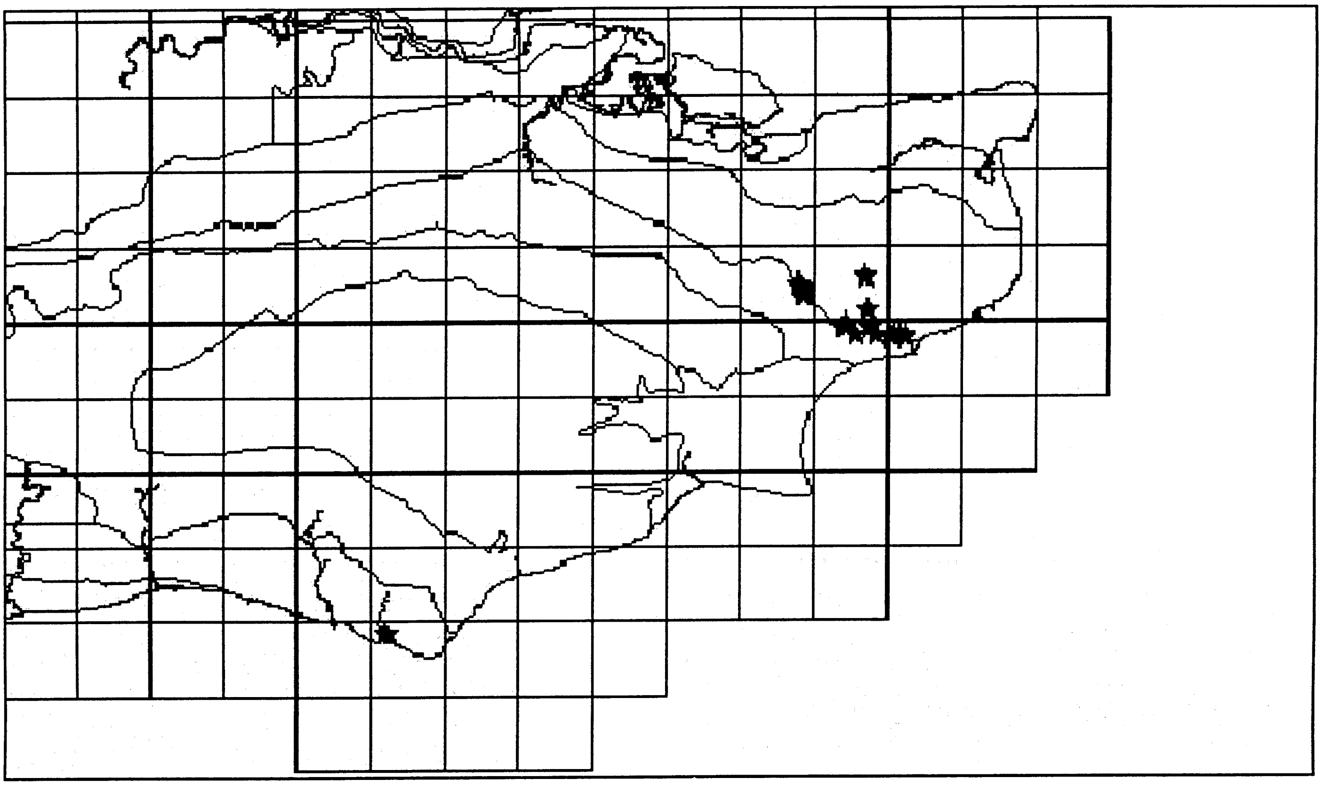


Figure 2.4 UK distribution of *O. fuciflora*: with Natural Areas and 10km sq overlay (location data supplied by JNCC)

2.4.3 Review of the literature indicates that the species has always been restricted in its British distribution. Comparison of the current distribution and that cited in the Atlas of the British Flora (Perring & Walters 1962) shows a decline in the number of j10 km squares occupied by the species. The decline of *O. fuciflora*, and other chalk grassland orchids, over the last 40 to 50 years has been attributed to loss of suitable habitat. The loss of chalk grassland being mainly due to agricultural improvement, loss of livestock grazing, and reduced rabbit grazing as a consequence of myxomatosis (Keymer & Leach 1990).

3. Study site - Wye National Nature Reserve

3.1 Location and description

3.1.1 Wye National Nature Reserve (NNR) is part of Wye and Crundale Site of Special Scientific Interest (SSSI). The site is in East Kent, the main part of the NNR known as Wye Downs, being some 6 km north east of Ashford in the parishes of Wye and Hastingleigh (see Figure 3.1).

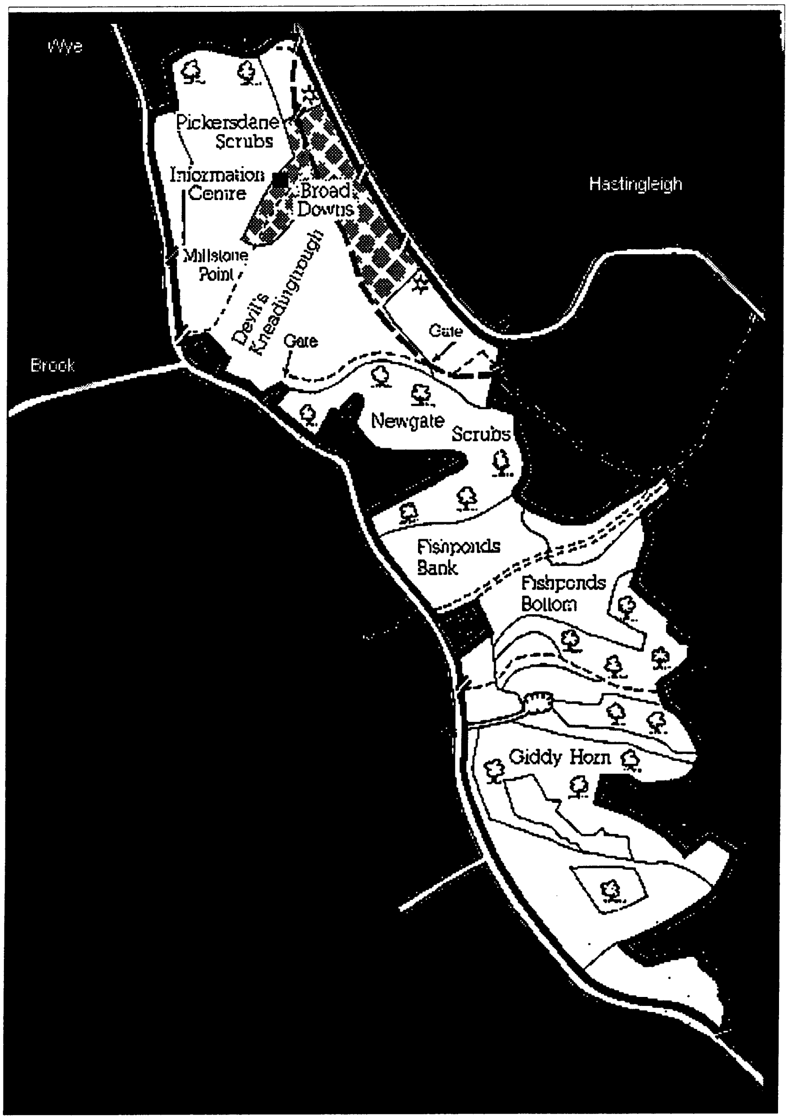


Figure 3.1 Location of Wye NNR (source NCC 1985)

3.1.2 Wye Downs was acquired by the Nature Conservancy in 1961 and 1965, with a small extension in 1978 increasing its total size to 104 ha. The major reasons for acquisition being extensive areas of herb rich *Brachypodium pinnatum* grassland and a rich invertebrate fauna boasting several rare species such as the Black-veined moth (*Siona lineata).* The site lies on the steep chalk escarpment of the North Downs and hosts a number of coombes which fret the scarp face, the Devils Kneading Trough being the best known of these.

3.1.3 The west-south-west facing scarp face of the NNR rises from 71 m to 178 m above OD, yielding impressive views to the English Channel 16 km away, and across the Weald of Kent to Ashdown Forest in Sussex some 60 km away (Russell 1993).

3.2 Geology and soils

3.2.1 The solid geology of Wye Downs is simple. The majority of the site overlies the Middle or Turonian Chalk, which was laid down during the Upper Cretaceous. Much like the Upper or Senonian Chalk this material is dominated by $CaCO_3$ which accounts for about 97% of mass (Clough & Hanifi 1979; Russell 1993).

3.2.2 On the lower reaches of the site there are exposures of Lower or Cenomanian Chalk, also known as Chalk Marl. This is a less pure material containing two antipathetic clay-grade assemblages, montmorillonite and illite (Clough & Hanifi 1979; Russel 1993).

3.2.3 The soils of Wye Downs are typical of the chalk downs. The top of the escarpment is capped periglacial deposits of clay-with-flints which give rise to Brown Earths. Whilst the floors of the coombes give rise to chalk loam known as Coombe Deposits. Adjacent to this on the toe-slopes of the escarpment are Brown Calcareous soils. These vary in composition due to topographical fluctuations and historic land use patterns, but are calcareous and moderately free draining. The steep face of the scarp gives rise to the formation of rendzina soils, often associated with areas of floristic richness (Russell 1993).

3.3 General vegetation of the site

3.3.1 The Wye Downs escarpment is characterized by a mosaic of secondary woodland, scrub and grassland. The woodland is dominated by either *Fagus sylvatica* or *Fraxinus excelsior* and is classified as W12a or W8a respectively, according to the National Vegetation Classification (NVC) (Rodwell 1991). Both woodland communities support an understorey rich in shrub species on this site, as well as a varied ground flora which boasts species such as *Orchis purpurea, Ophrys insectifera* and *Lathraea squamaria.*

3.3.2 The scrub areas provide valuable habitat for a range of vertebrate and invertebrate fauna. Locally the scrub is of mixed calcicolous shrub, more extensive areas are dominated *Cratocegus monogyna* (NVCW21a), *Prunus spinosa* (NVC W22) and *Corylus avenula.*

3.3.3 The calcareous grassland of the escarpment face is mainly dominated by *Brachypodium pinnatum* (NVC CG4). This is generally a species poor community where *B. pinnatum* forms extensive tussocks and a tall sward. Herb rich variants do occur when management suppresses dominance of *B. pinnatum*, opens the turf and reduces sward height. This is the case on Wye Downs. Interspersed within the CG4 community are areas of *Festuca ovina* dominated grassland (NVC CG2). This is a floristically rich community occurring on the thinnest of rendzina soils along the escarpment.

3.4 Wye NNR and grassland management

3.4.1 Wye NNR is divided into management compartments. These resulted from a mixture of previous tenure, habitat and pragmatism. The management compartments of Wye Downs are shown in Figure 3.2

3.4.2 The calcareous grassland is managed by employing a range of traditional land management techniques. Generally the calcareous grasslands are subject to light grazing during the Winter either by heifers or sheep. The bulk of the grassland is also summer grazed though grazing stock are excluded from orchid areas, but these areas continue to be grazed by natural herbivores. In addition hand removal of hawthorn scrub followed by treatment of the stumps with herbicide takes place as necessary. To prevent the sward becoming too rank, leading to selective grazing, some localized areas in and around *O. fuciflora* colonies are occasionally mown or 'strimmed' and the litter removed (Russell 1993).

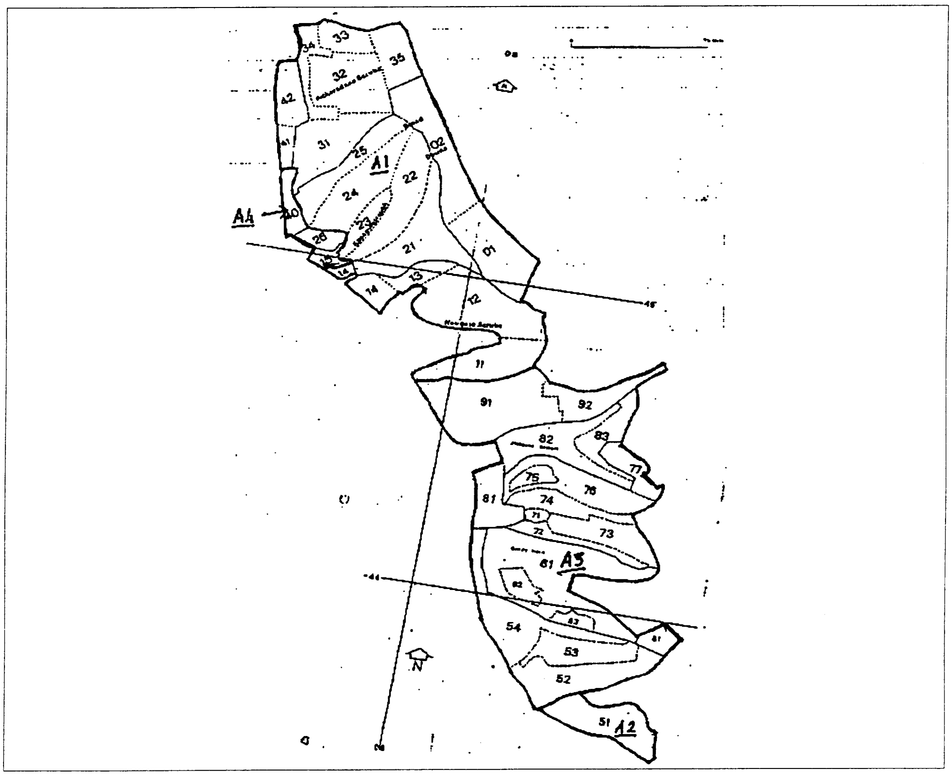


Figure 3.2 Wye Downs NNR Management Compartments (source Russell 1993)

3.5 Wye NNR and *O. fuciflora*

3.5.1 *Ophrys fuciflora* was first recorded on Wye Downs in 1889 by Rev B Malden (Fitzgerald 1985). Within the site it occurs on the herb rich calcareous grasslands on the rendzina soils of the scarp slope.

3.5.2 Six recognised colonies of the species grow on Wye Downs, within four separate management compartments. It was these six colonies that formed the basis of this study. The orchid population of the colonies accounts for over 50% of the UK population (Stone & Taylor 1999), making the site very significant for the protection and management of this Red Data Book plant within Britain.

3.6 Management of *O. fuciflora*

3.6.1 The recent land management practices during the period of the study have been reasonably consistent. Since 1991 all four compartments have been subject to a consistent Winter grazing regimes using sheep, cattle or a mixture of stock, and occasional supplementary technical intervention. (see Table 3.1).

3.6.2 Research also revealed other pieces of information about the land use of the compartments. The site of colony 5 is a stabilized spoil heap from a chalk quarry, date unknown. This was probably associated with the manufacture of agricultural lime at the end of the last century. The area containing colony 4 was very heavily disturbed by a large rabbit population until the advent of myxomatosis in the 1950s. It was noted by Francis Rose that the colony of *O. fuciflora* disappeared in the 1960s, probably due to increasingly rank vegetation (Fitzgerald 1985). In the early 1980s heavy cattle grazing was employed to reduce the dominance of *Brachypodium pinnatum* and in 1987 the colony was 'rediscovered'. In 1958, the previous owner bulldozed a tumulus which supported over 100 plants of *O. fuciflora*. The area occupied by Colonies 2 and 3 is below that site and was disturbed when the spoil was spread. Around the same time the area adjacent to colonies 1 and 1A was ploughed, though the land was not improved.

4. Methods

4.1 *Ophrys fuciflora* grows in six visually distinct colonies. It was noted that areas containing colonies appeared to be visually similar to other areas of grassland within the site. The aims of this investigation prompt three basic questions to be asked. First, what are the autecological characteristics of the species? Second, what can be determined about the 'special requirements' of the species that are capable of being manipulated by land management? finally, do different management treatments induce different population responses within the colonies? By determining the answers to these questions a framework for appropriate sustainable management of the species may be arrived at.

Table 3.1 Management regimes affecting *O. fuciflora* during study

Years	Colonies 1 & 1a	Colony 2	Colony 3	Colony 4	Colony 5
1987	<u>Mown and raked</u> Cattle - Winter	Cattle - periodic Sheep - Winter	As for colony two	Cattle - spring and Autumn	Sheep - periodic all year
1988	Cattle and Sheep periodic - all seasons	as 1987		Cattle - Winter	As 1987
1989	<u>Mown and raked</u> Cattle - Winter	<u>Mown and raked</u> Cattle/Sheep Winter		<u>Mown and raked</u> Cattle - Winter	<u>Strimmed</u> Sheep - spring only
1990	Cattle - Winter	Cattle and Sheep Winter		as 1988	Sheep - first and last quarters
1991	As 1991	As 1990		Cattle - spring and autumn	Sheep November-March
1992	<u>Strimmed</u> Cattle - Winter	as 1990		<u>Strimmed</u> Cattle spring/autumn	As 1991
1993	As 1991	As 1990		As 1991	As 1991
1994	As 1991	As 1990		As 1991	As 1991
1995	As 1991	As 1990		As 1991	Sheep and Cattle November-March
1996	<u>Strimmed</u> Cattle - Winter	As 1990		<u>Strimmed</u> Cattle - Winter	As 1995
1997	As 1991	As 1990		As 1991	As 1995
1998	As 1991	Cattle - Winter		As 1991	As 1995
	Cattle - 2/ha Sheep - 7-9/ha	Cattle - 2/ha Sheep - 7-8/ha		Cattle - 3-4/ha	Cattle - Sheep - 4-6/ha

1: Winter grazing refers to the period from September to March inclusive

4.2 Field methods - vegetation sampling

4.2.1 To address the above questions visually similar areas approximately 20 m x 20 m were considered as the basis for sampling along with colonies of *O. fuciflora*. The term 'visually similar' refers to areas apparently exhibiting the same vegetative, topographical and physical characteristics as the colonies but without the recorded presence of *O. fuciflora*. These areas were within the same management compartments as the colonies. This stratified approach to sampling was adopted to enable comparison of data from areas with and without the study species, potentially revealing differences between the relative values of ecological variables or phytosociological structure that may affect the establishment and survival of *O. fuciflora.*

4.2.2 Five areas were identified and marked on the ground. Within each of the visually similar areas and the colonies 25 cm x 25 cm quadrats were placed. Generated random numbers were used to locate the southern corner of the quadrat within the areas. It was then orientated North-South (see Figure 4.1). The size of quadrats was determined using the species-area curve method after goldsmith *et al* (1986). Within each quadrat the plant species were recorded. Species cover was used as an estimated measure of abundance (Kershaw & Looney 1885). Percentage cover for each species was estimated and a Domin score assigned (Goldsmith *et al* 1986). Two further pieces of data were recorded within each quadrat, vegetation height and bare ground. Vegetation height was measured by means of a simple hardboard drop-disk 20 cm in diameter. Bare ground was assessed in the same manner as species cover.

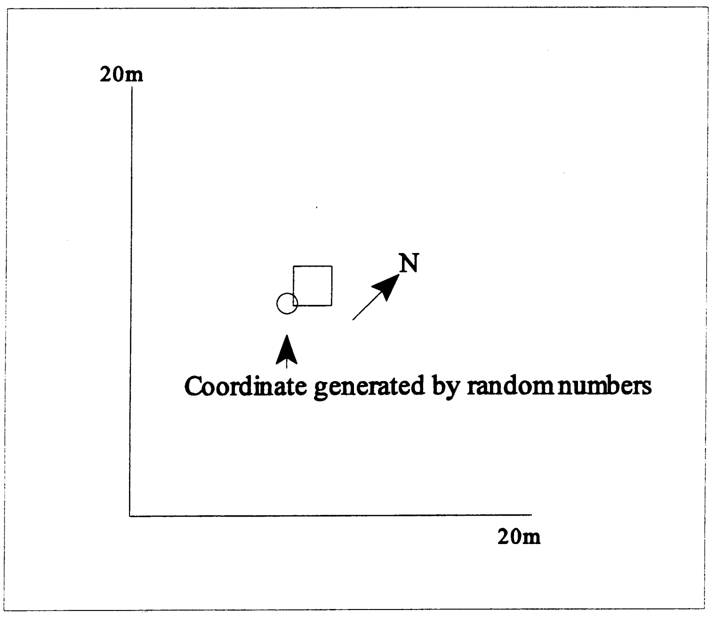


Figure 4.1 Placement of quadrats in colonies & 'visually similar areas'

4.3 Field methods - census data

4.3.1 From 1987 census of all individuals of *O. fuciflora* was done within each identified colony. For each colony a 'base line' of numbered Fenol Markers® was put in place at 2 m intervals. The location of individual plants was identified by measuring the distances from the nearest two markers (see Figure 4.2). Once located each plant was marked by means of a numbered coloured tag attached to a metal spike. The areas of each colony were thoroughly searched for individuals of *O. fuciflora* in late March/early April. Summer census work took place from mid-May to early August with visits at an 8-10 day interval. Individuals were re-identified each year along with new emergent plants. The presence of absence of an individual was recorded in any year. The developmental state vegetative, flowering or dormant was recorded during the Summer visits. Flowering specimens were re-surveyed towards the end of census period in order to ascertain if they had set capsules.

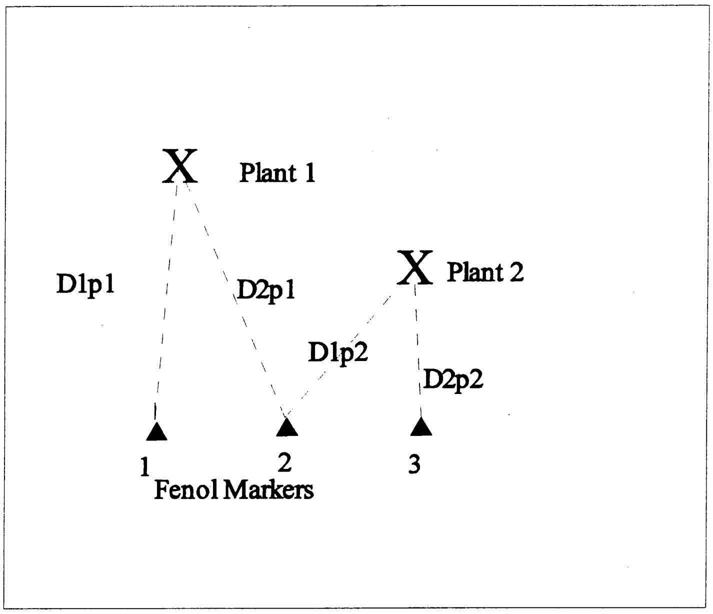


Figure 4.2 Identifying individual plants in a colony

5. Results and analyses of *O. fuciflora* census data

5.1 Basic census data

5.1.1 The census data was collected for all six known colonies for 12 years, 1987 to 1998 inclusive. Each individual was assigned an identifying marker in the field along with its coordinates. During the census 267 unique occurrences of *O. fuciflora* were noted. Zero (0) in the year column indicates that the plant was recorded as dormant; one (1) in a vegetative state; and two (2) as flowering.

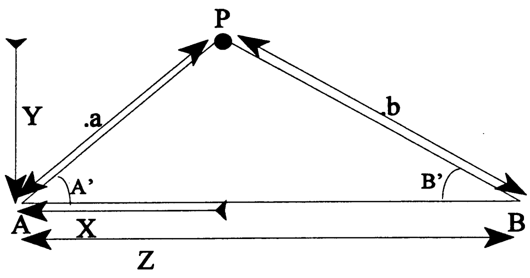
5.1.2 There are a number of 'unknowns', eg longevity about the autecology of *O. fuciflora*. The census data was subjected to a number of analyses to attempt to identify as many of the gaps as possible, for example degrees of vegetative reproduction, dormancy and population flux.

5.2 Spatial distribution of *O. fuciflora*

5.2.1 To what degree does the species in Britain depend on vegetative reproduction for its survival? In order to address this question the spatial distribution of individuals within the colonies was considered.

5.2.2 The triangulated coordinate data presented in Appendix A was transformed to rectangular coordinates using the Cosine rule and corrected to a common origin (Fenol Marker 0) within each colony (see text box). Figures 5.1 to 5.6 show the distribution of unique occurrences within each colony.

Where X, Y are rectangular coordinates of the plant P; a and b are the measurements taken from the markers A and B respectively



$$\cos A' = (z^2 + a^2 - b^2/2az);x = a \cos A';y = \sqrt{a^2 - x^2}.$$

5.2.3 Using Pythagorus's theorem, the distance between each occurrence of an orchid and every other occurrence within a colony was calculated. Each calculated distance was assigned to a category; 0-5 cm; 5.1-10 cm; 10.1-15 cm; 15.1-20 cm; 20.1-30 cm; >30 cm. Tables 5.1A and B show the results of the assignment for each colony in absolute and percentage terms.

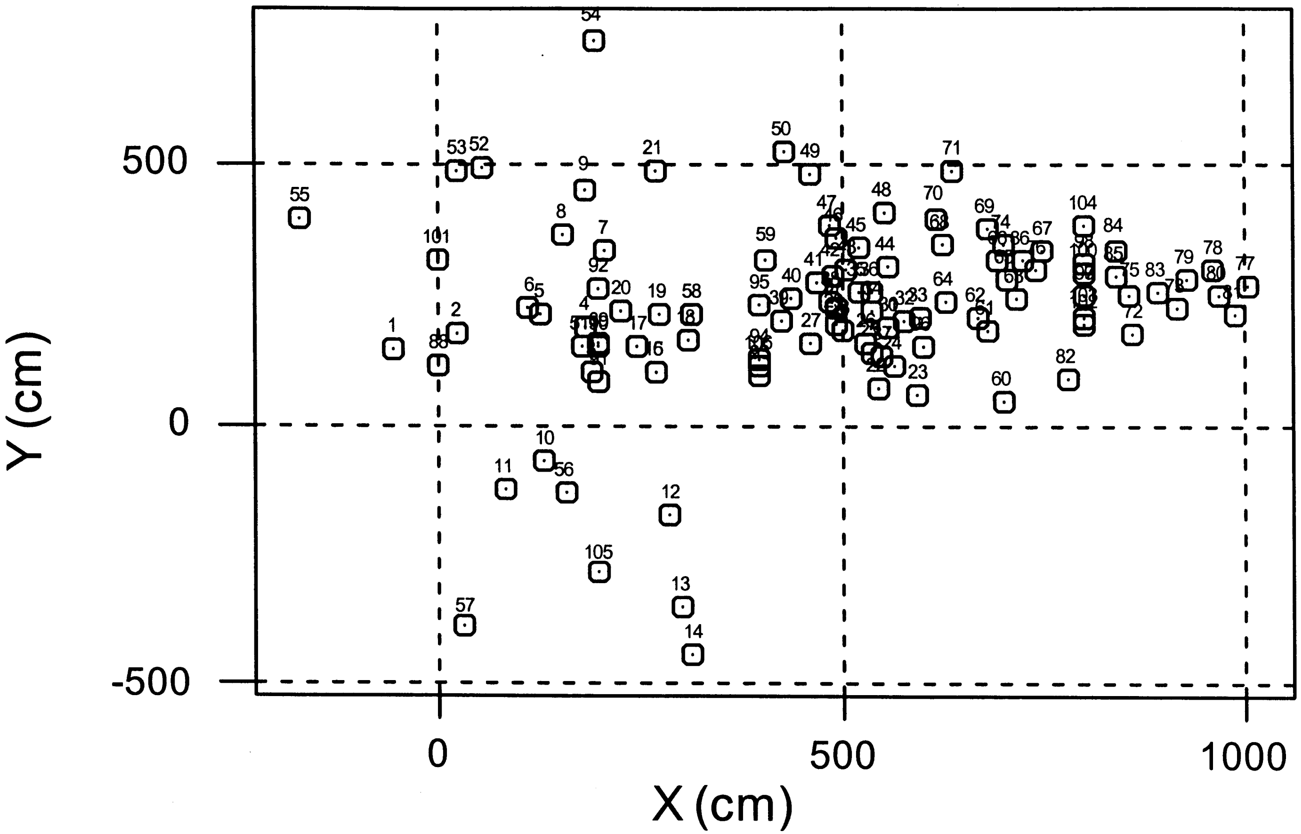


Figure 5.1: Distribution within Colony One

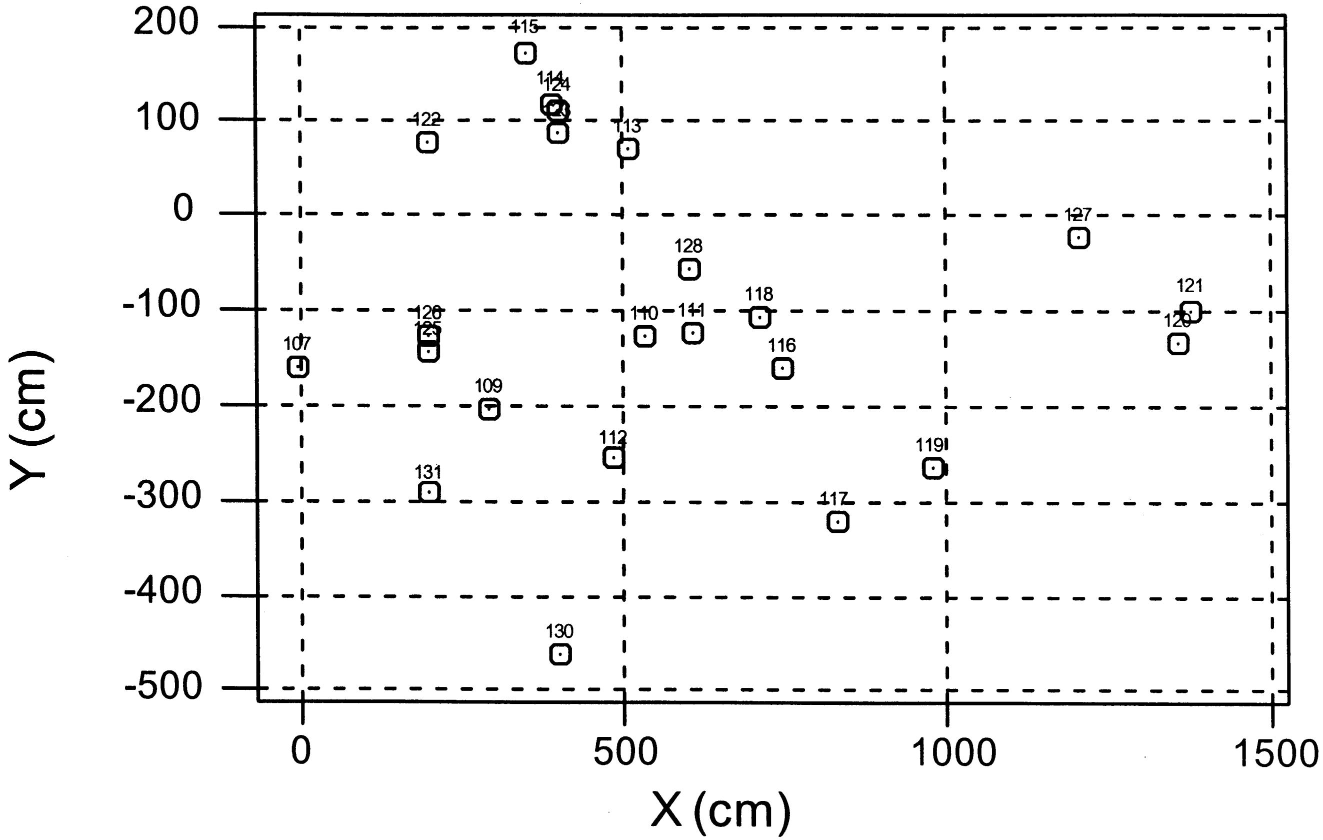


Figure 5.2: Distribution within Colony One A

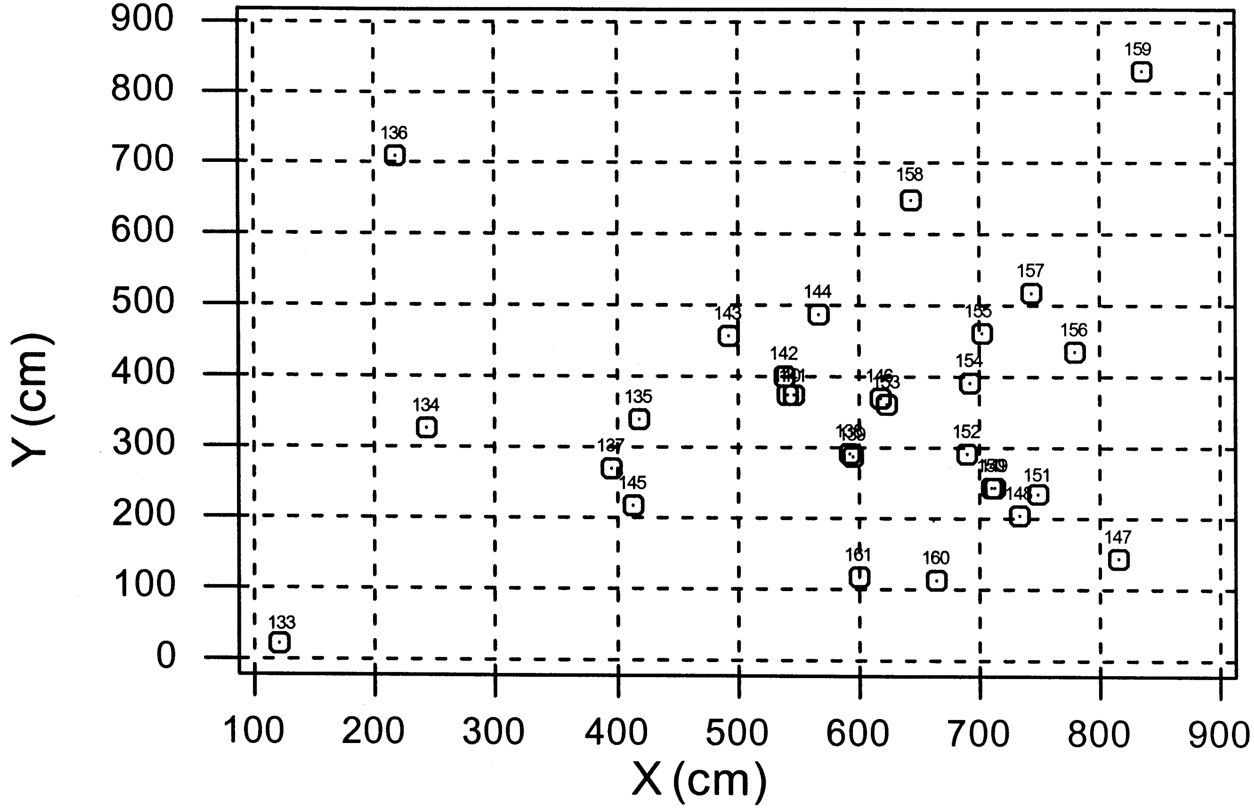


Figure 5.3: Distribution within Colony Two

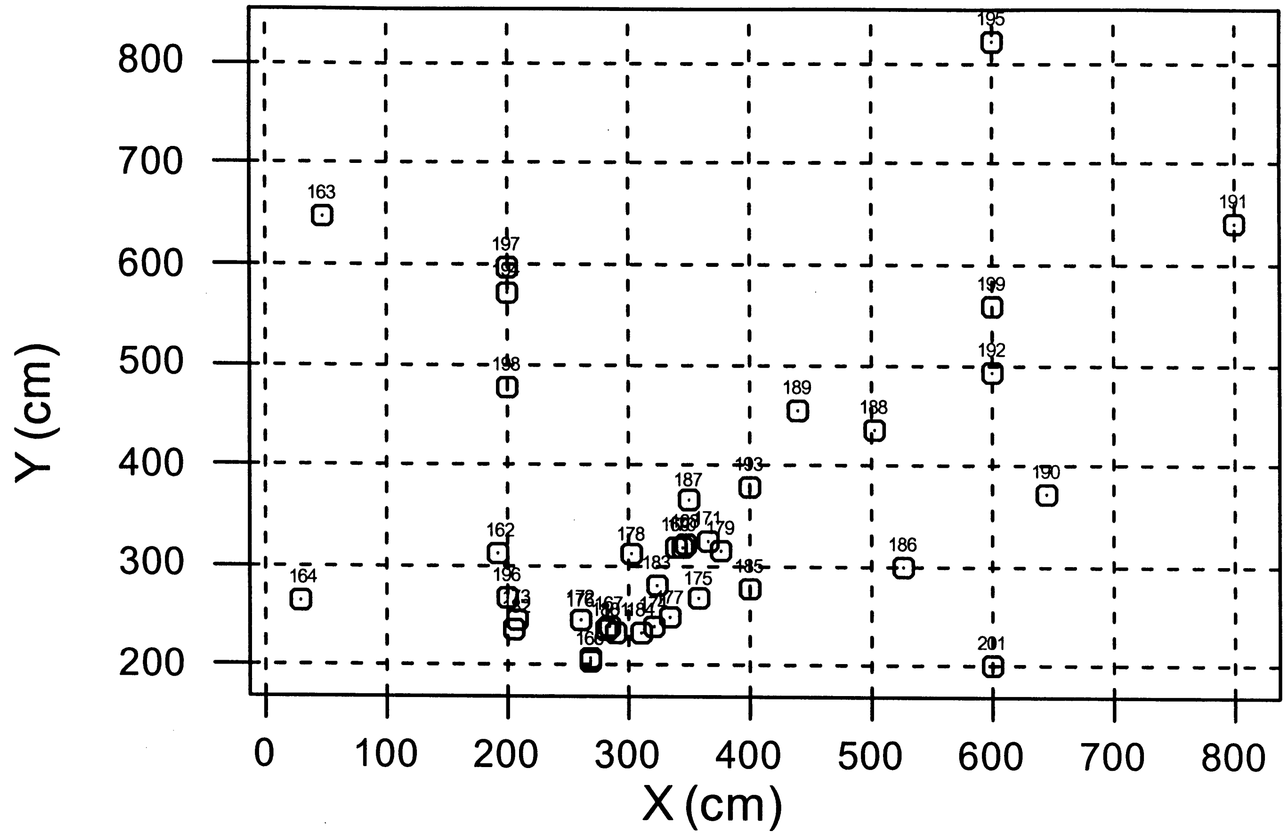


Figure 5.4: Distribution within Colony Three

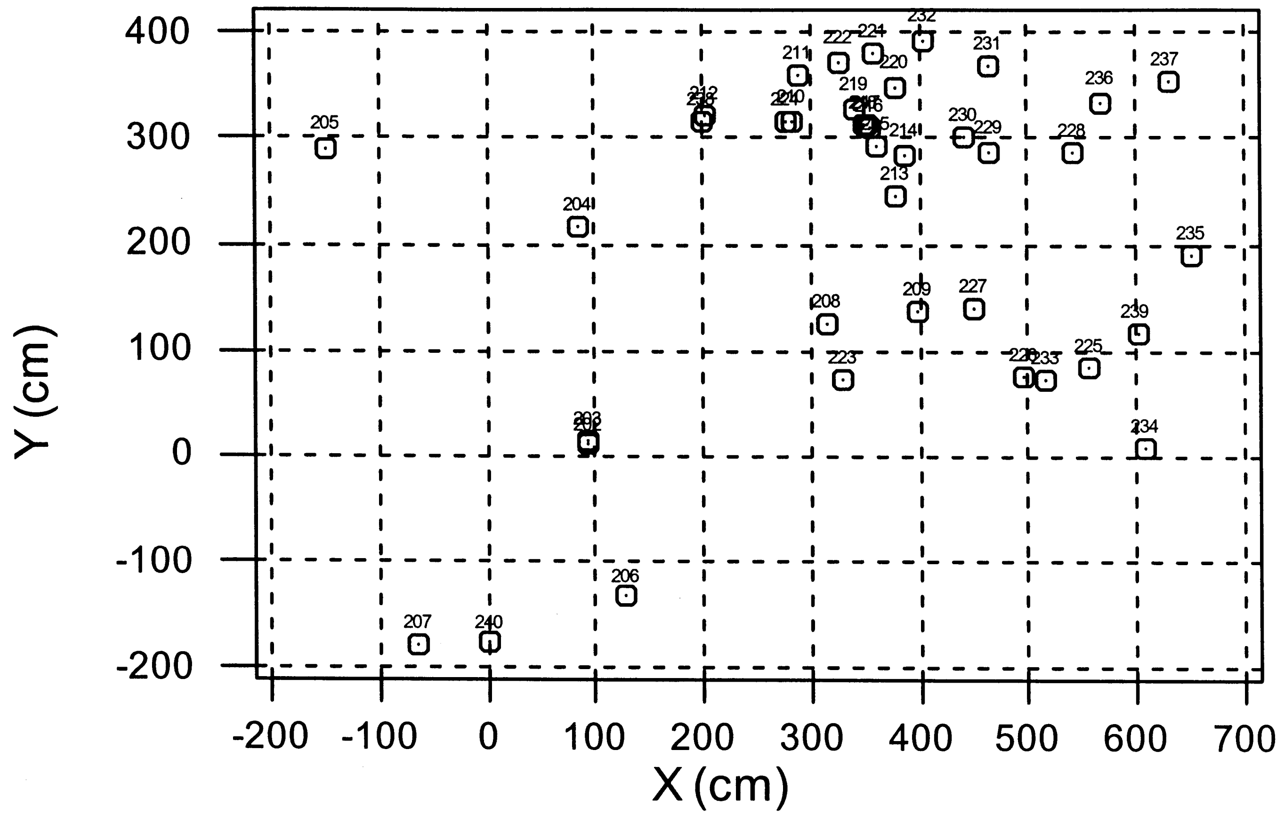


Figure 5.5: Distribution within Colony Four

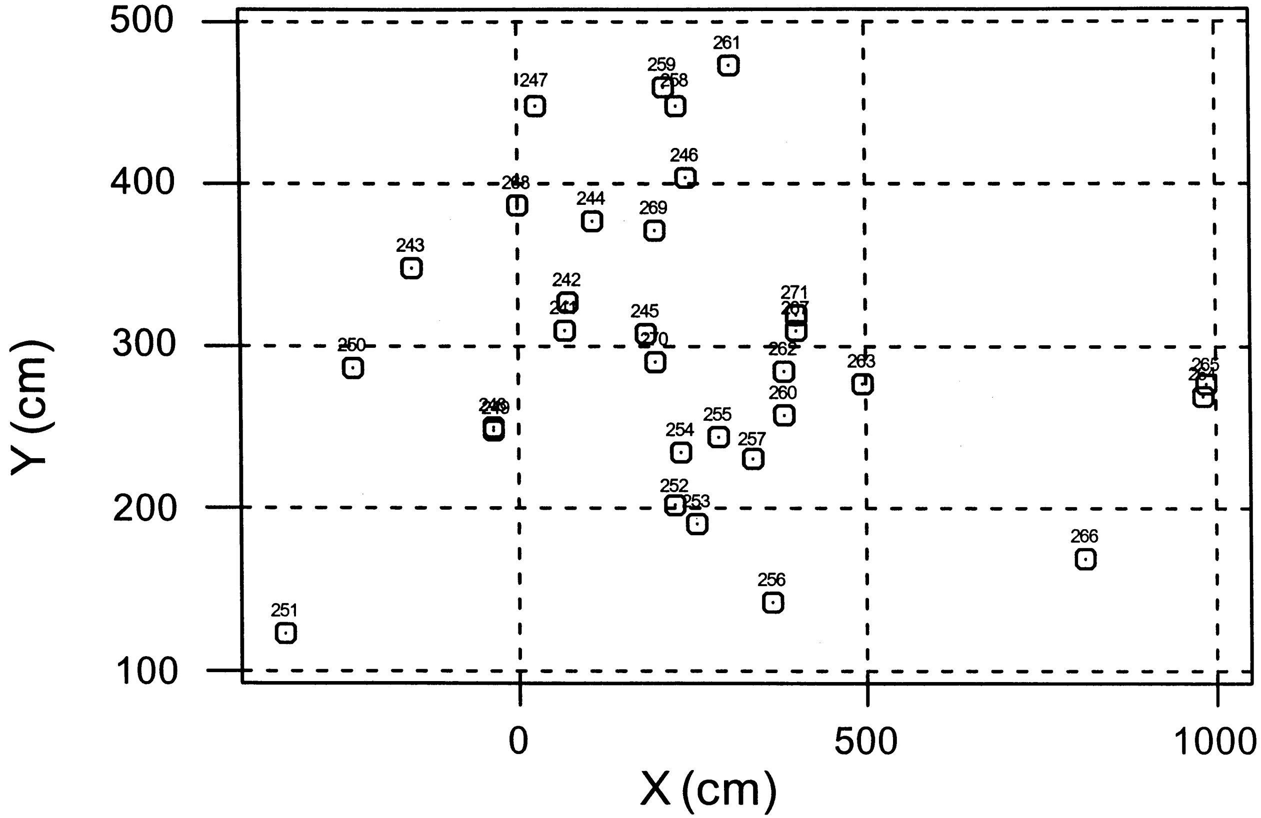


Figure 5.6: Distribution within Colony Five

Table 5.1A Absolute number of distance measures between orchids by category per colony

	Distance Class (cm)						
Colony	**0-5**	**5.1-10**	**10.1-15**	**15.1-20**	**20.1-30**	**>30**	**Total measures**
One	3	1	0	10	11	5540	5565
One A	0	0	2	0	1	250	253
Two	4	0	0	0	0	374	378
Three	4	5	3	1	11	756	780
Four	3	2	0	4	4	728	741
Five	1	1	0	1	0	432	435
Total	**15**	**9**	**5**	**16**	**27**	**8080**	**8152**

Table 5.1B Number of distance measures between orchids by category as a percentage of colony total

Colony	**0-5**	**5.1-10**	**10.1-15**	**15.1-20**	**20.1-30**	**>30**
One	0.05%	0.02%	0.00%	0.18%	0.20%	99.55%
One A	0.00%	0.00%	0.79%	0.00%	0.40%	98.81%
Two	1.06%	0.00%	0.0%	0.00%	0.00%	98.94%
Three	0.51%	0.64%	0.38%	0.13%	1.41%	96.92%
Four	0.40%	0.27%	0.00%	0.54%	0.54%	98.25%
Five	0.23%	0.23%	0.00%	0.23%	0.00%	99.31%
Total	**0.18%**	**0.11%**	**0.06%**	**0.20%**	**0.33%**	**99.12%**

5.2.4 Table 5.1A shows a total of 8,152 distance measures resulting from the total number of orchids recorded during the census. Colony One, the largest of the colonies, contributes 5,565 occurrence measures to the total. The number of measures less than 30 cm was 72 (0.88%) in total. Distances 10 cm or less between occurrences of *O. fuciflora* only account for 0.29% (24) of the measures. Tables 5.1A and B show the spatial patterns of the individual colonies to be broadly in line with the metapopulation pattern. However, Colonies Two and Three appear to exhibit a greater degree of clumping in their spatial distribution although this is not significant ($p>0.1$).

5.3 Dormancy

5.3.1 Many species of orchid are known to have periods of dormancy when they do not produce above group parts for a number of years, then re-appear. How long can *O. fuciflora* remain in this state after above ground appearance has been recorded?

5.3.2 In order to address this question the mean of all absence durations for individuals later re-appearing was calculated. The duration was determined by counting the number of consecutive years where an individual was recorded as absent before being recorded as present again. Such absences are recorded as a '0' in Annex A.

5.3.3 179 absences of this type were recorded. The mean of absences was 2.49 ± 0.15 ($p<0.05$). Using the upper confidence limit mean dormancy was calculated as 2.64 years. Therefore if an individual is recorded as absent for three years consecutively it can be assumed to be dead. Any subsequent individual recorded at the same ordinate reference was therefore considered to be a new plant.

5.4 Population size

5.4.1 The calculation of a dormancy period for the species enabled the census data to be recalibrated to determine the population size at the study site. Table 5.2 shows the population sizes for each of the colonies and the study site as a whole. The populations for 1987-88 are estimated as the figure will not include individuals in a dormant state as the start of the study. Conversely, the figures for 1996-1998 are estimated as they will include individuals that are dead but could not be discounted.

5.4.2 The total estimated population in 1998 was 220. This represents a population increase of 164 individuals (approximately 300% during the study period. All the colonies have shown an increase in population except Colony Two. Given the potential dormancy of individuals the data for 1995 is the last that can be regarded as absolute, since data from 1996 onwards may contain records of individuals that are dead but not yet determined as such because of the potential for dormancy. The population for 1995 shows a total population increase of 242.8% with Colonies One, One A, Four and Five contributing to this variously. In 1995 Colony Two showed no change in its population, whilst Colony Three had declined by 7.2%. These later colonies are geographically close and subject to the same management regime within a single compartment (see Figures 5.7 to 5.13).

Table 5.2 Population of colonies and total

Colony name		Year												
		1987	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**
One	Flowering	14	1	5	3	18	20	39	35	16	28	35		
One	Vegetative	1	12	6	12	1	15	5	6	40	26	34		
One	Dormant		1	1	1	10	4	1	7	3	14	13		
One	**Total**	**16**	**15**	**12**	**16**	**29**	**39**	**45**	**48**	**59**	**68**	**82**	**0**	**0**
One a	Def - flower					3	2	2	7		4	5		
One a	Def - veg						1	5		8	3	4		
One a	Def - no show								2	1	2	2		
One a	Prob													
One a	**Total**	**0**	**0**	**0**	**0**	**3**	**3**	**7**	**9**	**9**	**9**	**11**	**0**	**0**
Two	Def - flower	7	9	5	11	9	8	12	5	6		2		
Two	Def - veg	1	1	8	6	7	7	7	10	9	12	11		
Two	Def - no show		4	3	1	3	5	2	4	1	4	2		
Two	Prob	8	2											
Two	**Total**	**16**	**16**	**16**	**18**	**19**	**20**	**21**	**19**	**16**	**16**	**15**	**0**	**0**
Three	Def - flower	2	7	3	9	11	12	5	1	4	4	8		
Three	Def - veg		5	10	4	2	11	7	6	7	10	9		
Three	Def - no show			1	2	2	1	5	6	2	5	3		
Three	Prob	12	2											
Three	**Total**	**14**	**14**	**14**	**15**	**15**	**24**	**17**	**13**	**13**	**19**	**20**	**0**	**0**

Colony name		Year												
		1987	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**
Four	Def - flower	7	1	2	4	6	8	16	17	6	6	6		
Four	Def - veg		3		5	5	6	6	5	15	14	13		
Four	Def - no show		3	5		4	6	2	5	4	8	11		
Four	Prob													
Four	**Total**	**7**	**7**	**7**	**9**	**15**	**20**	**24**	**27**	**25**	**28**	**30**	**0**	**0**
Five	Def - flower	1	1	1	2	3	2	6	8	10	8	5		
Five	Def - veg			1	4	7	4	5	4	4	11	15		
Five	Def - no show		1	1		0	3	0	1	0	2	3		
Five	Prob	2	1											
Five	**Total**	**3**	**3**	**3**	**6**	**10**	**9**	**11**	**13**	**14**	**21**	**23**	**0**	**0**
ALL	Def - flower	31	19	16	29	50	52	80	73	42	50	61	0	0
ALL	DEF - veg	2	21	25	31	22	44	35	31	83	76	86	0	0
ALL	DEF - no show	0	9	11	4	19	19	10	25	11	35	34	0	0
ALL	DEF 0 prob	23	6	0	0	0	0	0	0	0	0	0	0	0
ALL	**Total**	**56**	**55**	**52**	**64**	**91**	**115**	**125**	**129**	**136**	**161**	**181**	**0**	**0**

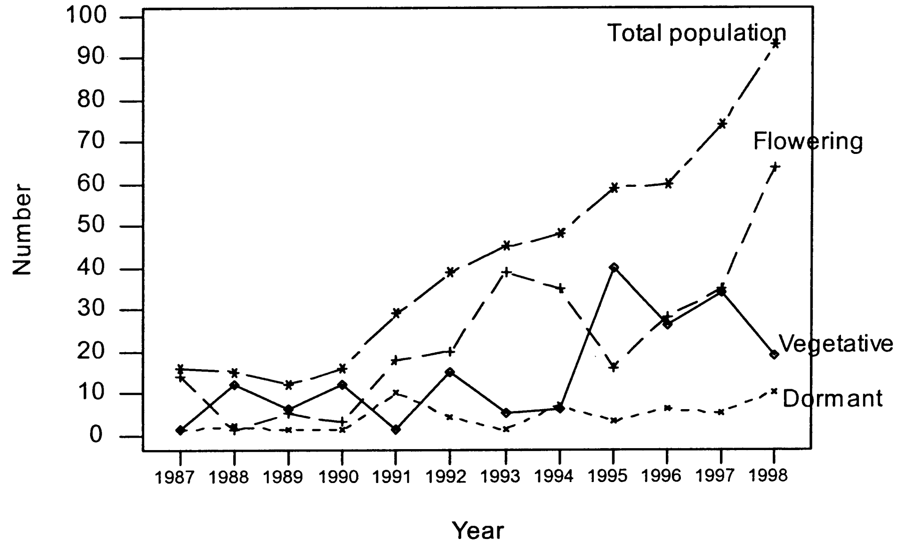


Figure 5.7 Colony One population

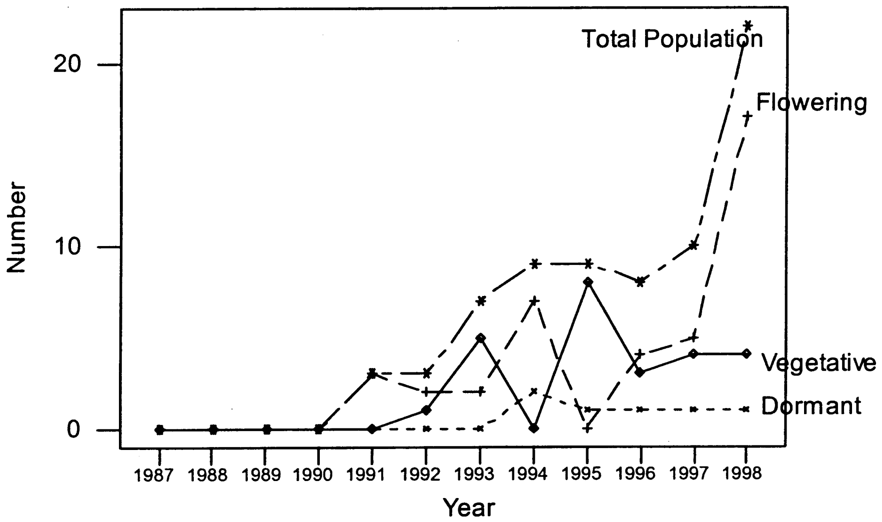


Figure 5.8 Colony One A population

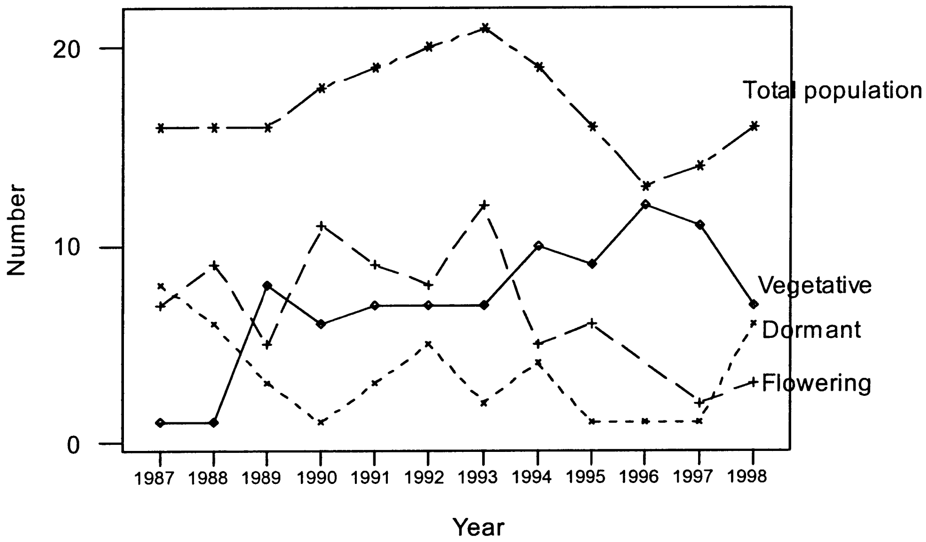


Figure 5.9 Colony Two population

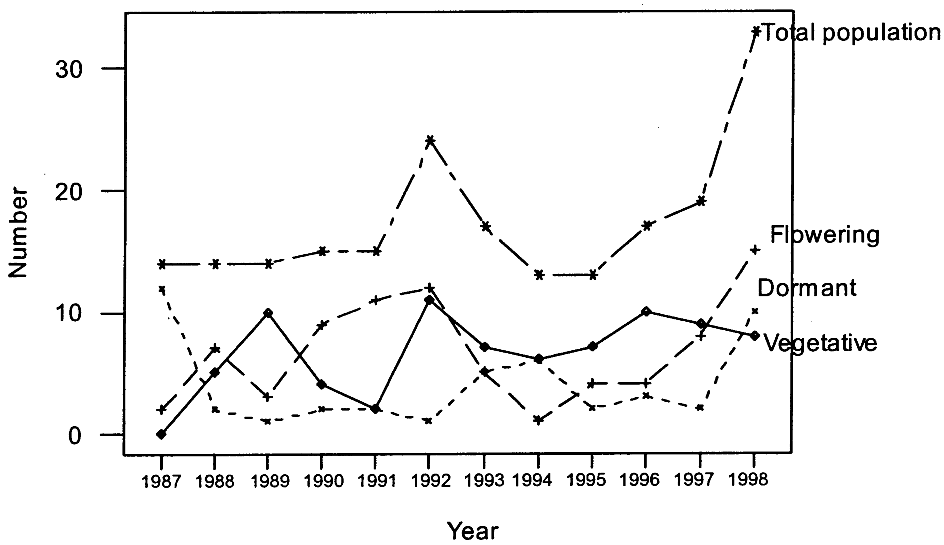


Figure 5.10 Colony Three population

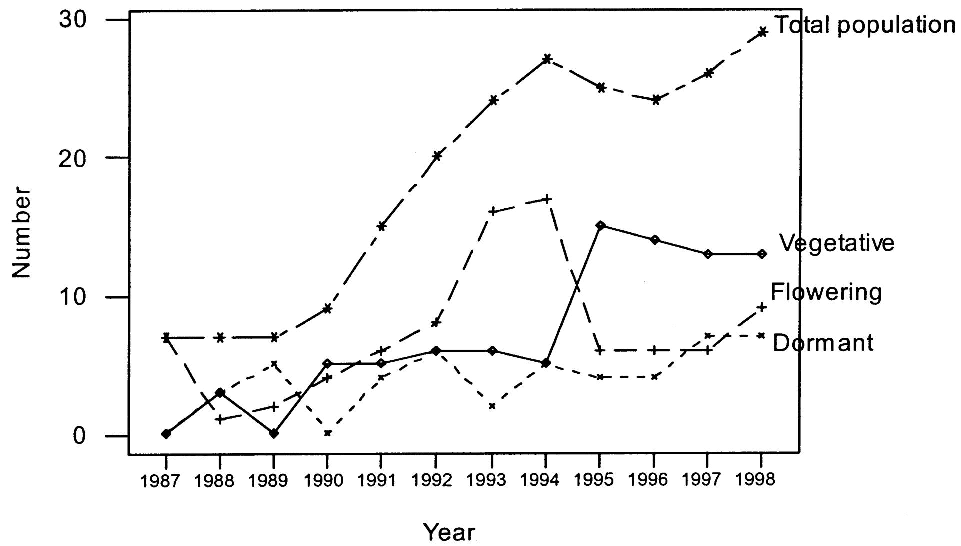


Figure 5.11 Colony Four population

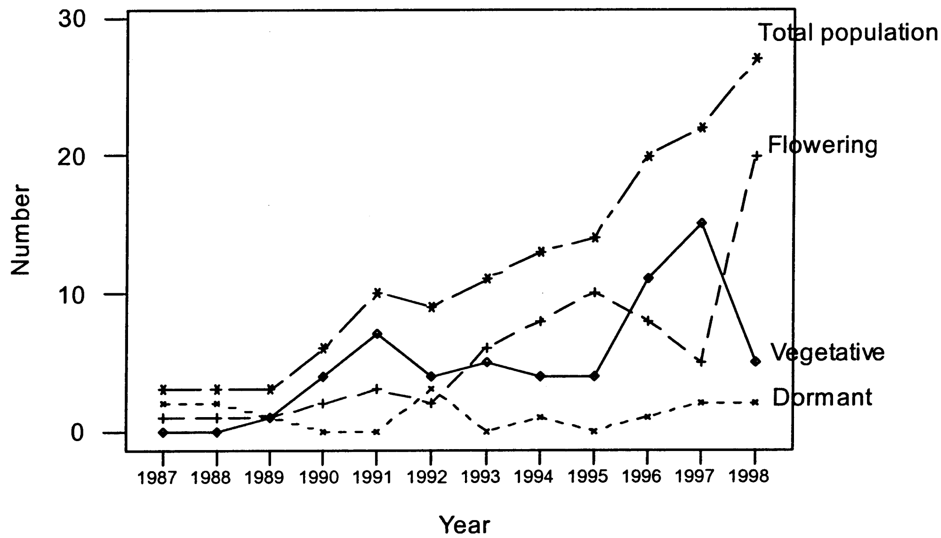


Figure 5.12 Colony Five population

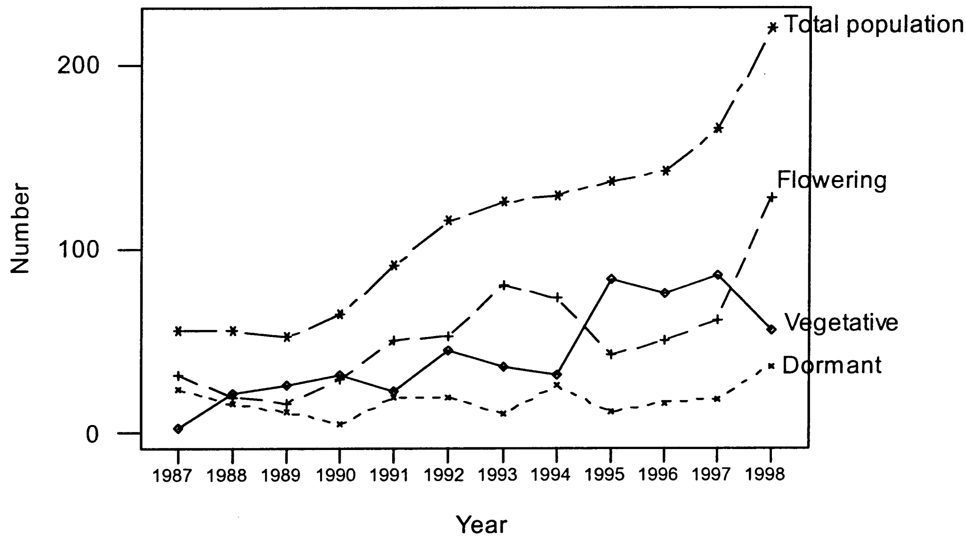


Figure 5.13 Study site population (all colonies)

5.4.3 Table 5.3 also shows the composition of the population within colonies. Three states are used to describe the composition; plants recorded as flowering; vegetative or dormant (after Wells & Cox 1991). The mean percentage of the population flowering was 45.67%, though this varied from 30.77% in 1989 to 64% in 1993. The variation within individual colonies was even greater, from 0% in 1996 for Colony Two, to 86.67% in 1993 for Colony One. All colonies show a mean >40% for percentage of individuals flowering, except colonies Two and Three which are 36.14% and 37.33% respectively. The mean percentage of the population in a vegetative state is 37.07%, though there is a high degree of variation between years and between colonies. The mean percentage of the total population in a dormant state is 12.93%, excluding the figures for 1987 and 1988 when dormancy state was uncertain. Again there is a great deal of variation between years and colonies. Figures 5.7 to 5.13 show the variation between states in absolute terms for all colonies.

5.5 Population flux

5.5.1 Figure 5.14 illustrates the changes in the population of *O. fuciflora* from 1987 to 1998, calculations are based on the numbers of plants. Again the data for 1987-88 and from 1996 onwards represents estimates due to the dormancy of the species limiting the ability to predict mortality.

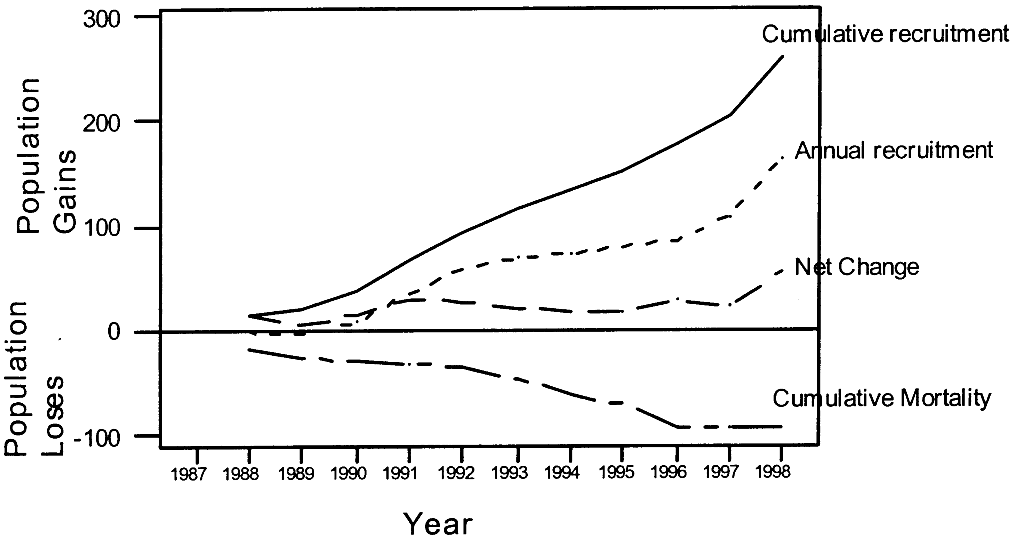
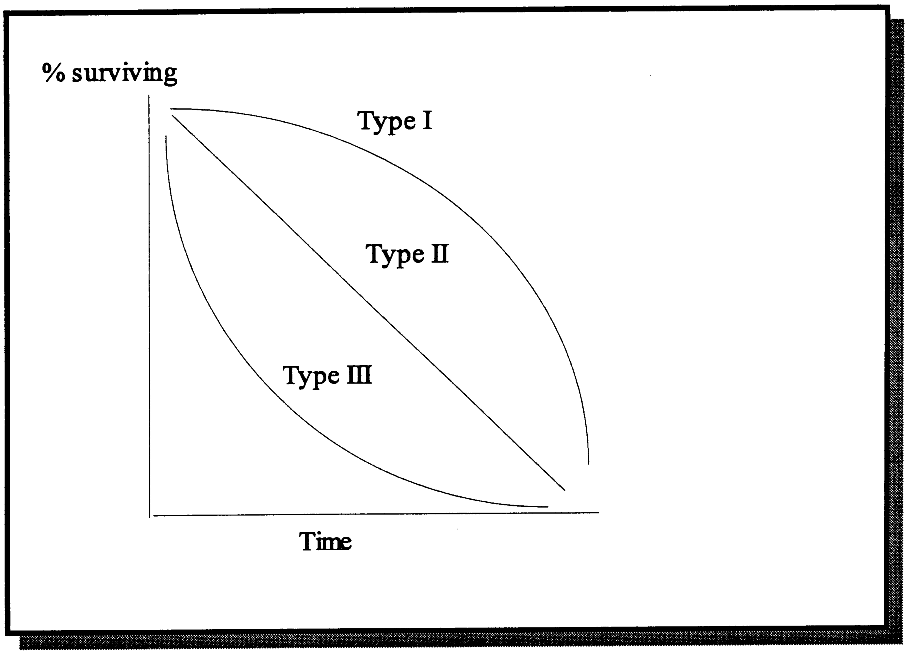


Figure 5.14 Analysis of *O. fuciflora* population flux (after Wells & Cox 1991)

5.5.2 Despite the limitations, the general trends of the population are clear. Recruitment since 1991 has been substantial, outweighing mortality. Up to 1990 there was a slight decline in the population which can be attributed solely to mortality within Colony One. All colonies, with the exception of Two and Three, mimic the recruitment pattern of the total population to a greater or lesser degree. Colonies Two and Three both show periods of reduction during 1995 to 1998, and 1994 to 1995 respectively. These two colonies also display low levels of recruitment in comparison to the other colonies.

5.6 Depletion and survivorship curves

5.6.1 'Harper (1977) distinguishes between depletion-curves, in which the number of survivors from multi-aged population is plotted against time, and survivorship curves in which the number of survivors from an even aged population is plotted against time' (Wells & Cox 1991). Deevey (1947) described three standard survivorship curves (see text box).



5.6.2 Figure 5.15 shows the depletion and survivorship curves for cohorts arising from 1987 to 1995. The curves for 1987 to 1989 are of the type described as depletion by Harper (1977). The curves are all of the Type II where there is a constant age independent mortality risk as described by Deevey (1947). The linear regression for each set of data is significant ($p<0.05$ to $p<0.01$). The linear regression model of the Type II curve (see Equation 5.1) provides a good fit ($R>0.8$) to the logarithmically transformed survival data, confirming the survivorship curve type. Type II survivorship and depletion curves are not unusual amongst plant populations (Hutchings 1986).

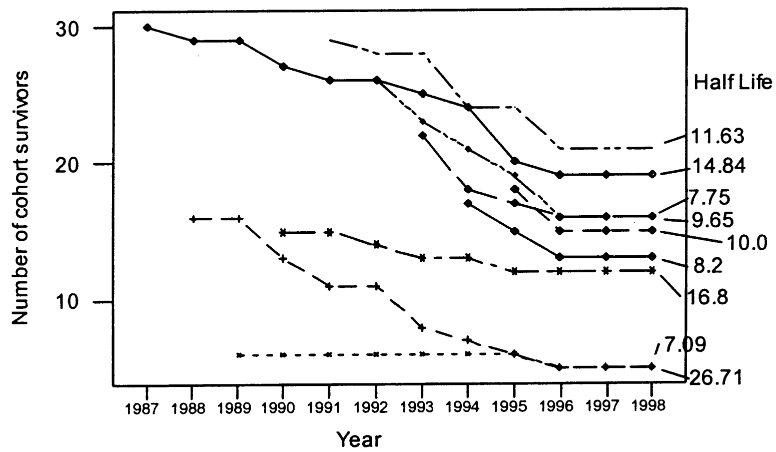


Figure 5.15 Depletion and survivorship curves for *O. fuciflora* population

$$\log_e Y_t = \log_e Y_0 - b'X$$

Equation 5.1 Linear regression model for Type II curve

5.6.3 The calculated half-lives of each cohort are indicated in Figure 5.15. These vary from 7.09 years for the 1988 cohort to 26.71 years for 1989 cohort. Even ignoring the 1989 cohort which may be distorted by a multi-aged population half lives are still as high at 16.80 years for the 1990 cohort. The data does display a good fit with the Type II curve and significance in regression. Therefore using the data the mean half-life for the *O. fuciflora* population was calculated at 12.52 years. Using this value b' within the transformed Type II model was calculated to be 0.0657 (see Equation 5.2).

$$\log_e Y_t = \log_e Y_0 - 0.0657X$$

Equation 5.2 Calculated regression model for *O. fuciflora* survivorship

5.6.4 The 1998 cohort was 50 individuals. Applying Equation 5.2 would take approximately 60 years for that cohort to be reduced to one individual. This does, of course, assume that environmental conditions remain constant and favourable for *O. fuciflora* for the duration.

5.7 Transition population matrix model of *O. fuciflora*

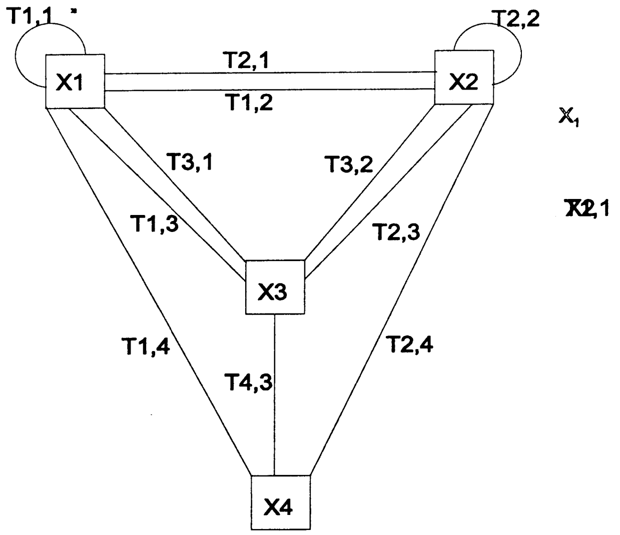
5.7.1 Emergent plants of *O. fuciflora* recorded in this study may be described as occurring in one of four states: flowering, vegetative, first year dormant and second year dormant. After three years of dormancy an individual is assumed to be dead (see section 5.3).

5.7.2 From the 1987 to 1997 census data the average probability of an individual being in one of the fours states at year 't+1' given its state in year 't' was calculated for the whole population and each colony (after Waite 1989). Mortality was attributed to the last observed state of an individual at 't-2'. Though some mortality probably occurs during the dormant phases this could not be discerned from the field data. Table 5.3 shows the results for the study site meta-population

Table 5.3 Mean state transition probabilities and mortality

Behaviour in t+t	**Behaviour in t**			
	Flowering	**Vegetative**	**Dormant Yr 1**	**Dormant Yr 2**
Flowering	0.460	0.365	0.213	0.538
Vegetative	0.374	0.382	0.472	0.462
Dormant Yr 1	0.109	0.180	0	0
Dormant Yr 2	0	0	0.315	0
Mortality	0.057	0.073	0	0

5.7.3 The year t state probability columns of the colonies were then compared to those of the whole population (see Table 5.4) using the Chi-squared test. By and large the transition behaviour of the colonies reflects the site population though some significant exceptions were identified. The transition behaviour of vegetative plants in Colony One was different in that the probability of an individual flowering in year 't+1' was significantly higher ($p = 0.05$). Whilst vegetative plants of Colony Two had a significantly higher chance of remaining vegetative in year t+1 ($p<0.05$). Plants of Colony Four in their first year of dormancy at 't' have a significantly higher probability of being dormant at 't+1' ($p<0.05$). Being dormant for two years the same individuals have a higher probability of flowering at 't+1', though this was not significantly higher.



$$T = \begin{bmatrix} t_{1,1} & t_{1,2} & t_{1,3} & t_{1,4} \\ t_{2,1} & t_{2,2} & t_{2,3} & t_{2,4} \\ t_{3,1} & t_{3,2} & t_{3,3} & t_{3,4} \\ t_{4,1} & t_{4,2} & t_{4,3} & t_{4,4} \end{bmatrix} \quad X = \begin{bmatrix} X_1 \\ X_2 \\ X_3 \\ X_4 \end{bmatrix}$$

Basic transition model for *O.fuciflora*

T = transition Matrix **X**= column vector, where X1 is number of flowering plants, x2 = vegetative plants, X3 = first year dormant plants, X4 = second year dormant plants.
[After Waite, 1989].

5.7.4 Waite (1989) describes a model and transition matrix (**T**) that can be derived from transition probability values (see text box). For example using the figures in Table 5.4 the probability that a flowering plant will survive to the next year is equal to 1-0.057 (1 - mortality rate), and the probability that it will flower the next year equals 0.460. The combined probability of the plant surviving and flowering is equal to (1- 0.057) X 0.460 = 0.433. Therefore the value of $t_{1,1}$ in the matrix **T** equals 0.433. Using this approach transitions matrices were calculated for the study site population and individual colonies (see Equations 5.3 to 5.9).

$$T = \begin{matrix} 0.495 & 0.457 & 0.333 & 0.400 \\ 0.350 & 0.302 & 0.455 & 0.600 \\ 0.098 & 0.119 & 0 & 0 \\ 0 & 0 & 0.212 & 0 \end{matrix}$$

Equation 5.3 Transition matrix T for Colony One

$$T = \begin{matrix} 0.349 & 0.453 & 0 & 0.500 \\ 0.548 & 0.272 & 0 & 0.500 \\ 0.113 & 0.163 & 0 & 0 \\ 0 & 0 & 0.333 & 0 \end{matrix}$$

Equation 5.4 Transition matrix for Colony One A

$$T = \begin{matrix} 0.416 & 0.163 & 0.222 & 0.400 \\ 0.340 & 0.477 & 0.444 & 0.600 \\ 0.113 & 0.163 & 0 & 0 \\ 0 & 0 & 0.333 & 0 \end{matrix}$$

Equation 5.5 Transition matrix T for Colony Two

$$T = \begin{matrix} 0.373 & 0.216 & 0.263 & 0 \\ 0.306 & 0.335 & 0.526 & 1.00 \\ 0.093 & 0.241 & 0 & 0 \\ 0 & 0 & 0.211 & 0 \end{matrix}$$

Equation 5.6 Transition matrix for Colony Three

$$T = \begin{matrix} 0.375 & 0.281 & 0.036 & 0.727 \\ 0.340 & 0.357 & 0.464 & 0.273 \\ 0.164 & 0.230 & 0 & 0 \\ 0 & 0 & 0.500 & 0 \end{matrix}$$

Equation 5.7 Transition matrix for Colony Four

$$T = \begin{matrix} 0.418 & 0.456 & 0.250 & 1.00 \\ 0.398 & 0.351 & 0.625 & 0 \\ 0.060 & 0.123 & 0 & 0 \\ 0 & 0 & 0.125 & 0 \end{matrix}$$

Equation 5.8 Transition matrix for Colony Five

$$T = \begin{matrix} 0.433 & 0.338 & 0.213 & 0.538 \\ 0.353 & 0.355 & 0.472 & 0.462 \\ 0.103 & 0.167 & 0.315 & 0.0 \\ 0 & 0 & & \end{matrix}$$

Equation 5.9 Transition matrix T for study site population

5.7.5 The site population matrix **T** (see Equation 5.9) was tested using a matrix **X** composed from the 1998 population. Since this model assumes no recruitment it was iterated until only one individual survived. This test showed it would take approximately 62 years for the population to be reduced to one plant. An outcome similar to that of the half-life model test (see Section 5.6).

5.7.6 Waite (1989) describes an approach for refining the basic transition matrix **T** so that a reproduction coefficient R can be ascribed to flowering plants. R is equal to the number of recruits in year t, divided by the number of flowering plants in year t-n. The results of R for the study site population are shown in Table 5.4.

Table 5.4 Calculated mean reproductive values (R) for flowering plants of *O. fuciflora*

n	Mean	Lowest value	Highest value
1	0.239	0.109	0.469
2	0.269	0.107	0.577
3	0.315	0.157	0.545
4	0.347	0.192	0.536
5	0.350	0.209	0.482
6	0.371	0.264	0.478
7	0.430	0.304	0.604
8	2.905	2.492	3.438
9	0.665	0.436	1.058
10	0.714	0.429	1.000
11	0.982	0.982	0.982

5.7.7 The mean values of R range from 0.239 to 2.905. The significant variation in R does not enable it to be easily incorporated into **T** without incorporating a time delay factor 'α'. 'α' could not be determined from the available field data. However, the proportion of recruits joining the vegetative and flowering states was calculated a 0.37R and 0.63R respectively. Recruitment to the dormant state could not be determined but could be ascribed a factor P. Using these values a separate model of recruitment **B** can be derived (see Equation 5.10).

$$B_t = \begin{bmatrix} 0.63R \\ 0.37R \\ RP \\ 0 \end{bmatrix} [X1_t]$$

Equation 5.10 Recruitment matrix model B

Matrix **B** can be incorporated to give a final transition matrix model **M** (see equation 5.11).

$$M = (X_t + B_{t-a})T$$

Equation 5.11 General transition matrix model M.

5.8 Classification analysis of quadrat data

5.8.1 In addition to *O. fuciflora* census data, data from 41 quadrats was collected from the colonies and 'visually' similar areas using the method outlined in section 4.2 (see Appendix B). The samples were attributed a National Vegetation Classification (Rodwell 1992). Collectively they can be considered as *Brachypodium pinnatum* grassland (CG4), though 15 of the samples could be classified as *Festuca-Avenula* grassland (CG2) and 15 were intermediate exhibiting many CG2 characteristics but with a high abundance of *Brachypodium pinnatum* present.

5.8.2 These data were analysed using the Two-way Indicator Species Analysis (TWINSPAN) method of divisive polythetic classification (after Hill 1979a). TWINSPAN utilises both species presence and abundance to establish variation in the data and employs the concept of indicator species to divide the data set (Hill 1979a). The end result of the analysis is the classification of both samples and species into distinguishable groups based on the original data. These groupings must be interpreted to establish whether or not a meaningful classification has been achieved.

5.8.3 Figure 5.16 shows the results of the species classification. The 52 species were classified into 20 end groups. Four of the end groups contained only a single species indicating that these species may be ecologically distinct and not readily associated with the vegetation type sampled. whilst the classification groups containing two or more species may represent a distinct vegetative association within the samples. To assess the ecological significance of the species classification the known ecology of the species was considered in relation to the following criteria:

i. habitat preference;
ii. bare soil preference;
iii. establishment strategy;
iv. hydrological tolerance;
v. soil pH tolerance;
vi. soil disturbance and fertility preferences.

(Grime *et al* 1988; Stace 1997; Hubbard 1984; Jermy *et al* 1982).

5.8.4 The TWINSPAN species groups were assessed in respect of these criteria. It was observed that:

a. the species preferences fell within the known ranges of ecological variables at the study site;

b. the dichotomy at the first level generally divided species with a preference for disturbed soil into group n = 29, though a number of generalist species capable of establishment and survival on disturbed soils appear in group n = 23, ie *Plantago media*;

c. at the second division group n = 29 species were generally divided in:

i. species associated with waste places and/or 'immature' grassland of low fertility (n = 15);

ii. species associated with established grassland of intermediate fertility (n = 14).

5.8.5 *O. fuciflora* was classified in a group along with *Dactylorhiza fuchsii, Hypericum perforatum, Rubus fruticosus* agg, and *Trifolium pratense* at the sixth level of division. These species exhibit common characteristics:

a. a preference for places of moderate disturbance and low fertility;

b. a competitive - ruderal regeneration strategy;

c. habitat preference for lightly grazed grasslands and waste places such as spoil heaps and quarry waste.

(Grime *et al* 1988).

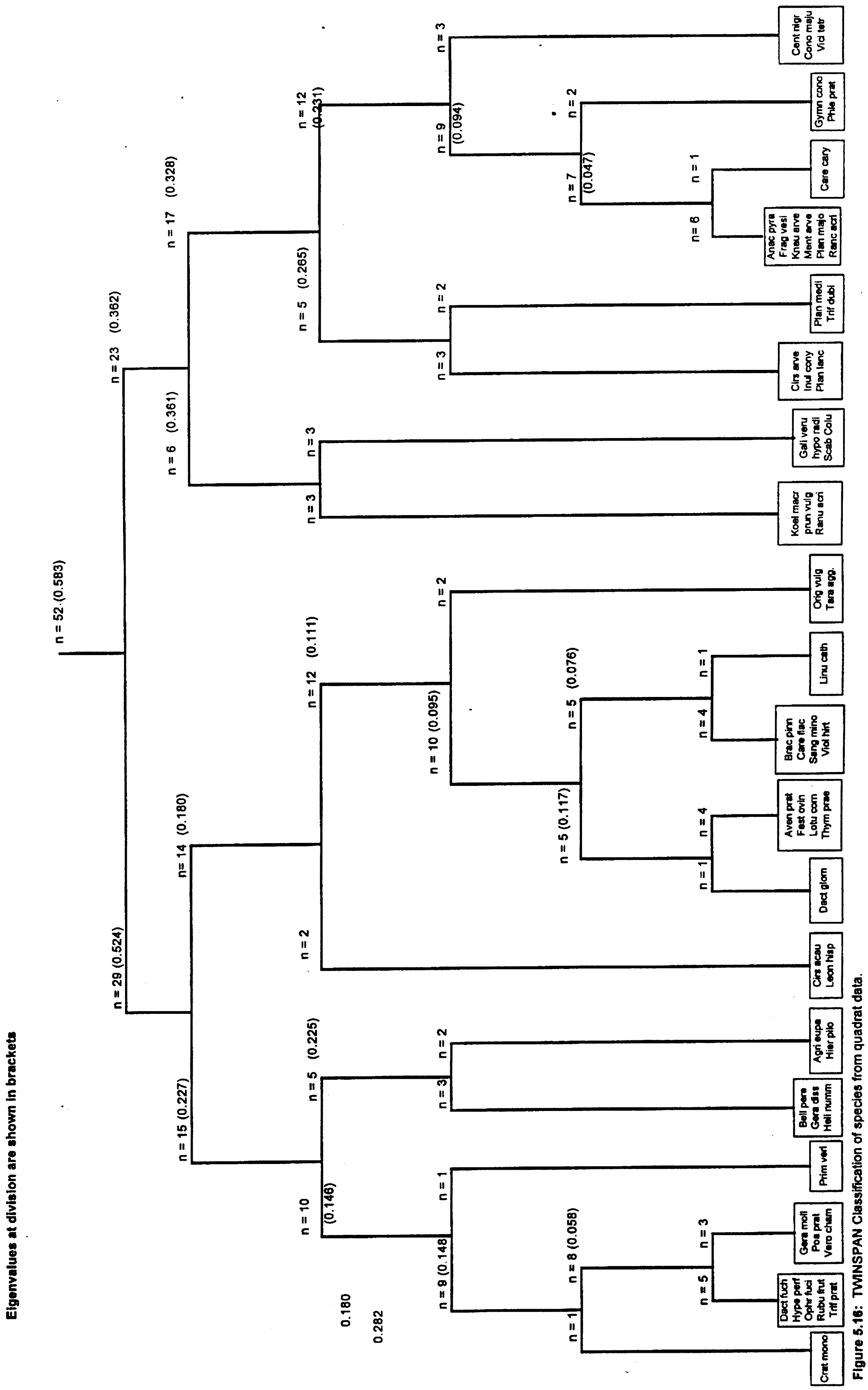


Figure 5.16 TWINSPAN Classification of species from quadrat data

5.8.6 When groups containing several member species were considered it was found that the range of ecological variables preferred by a species often exhibited equal or greater similarity with a member of another group. For instance *Hypericum perforatum* exhibits a requirement similarity of 81% with *Brachypodium pinnatum* which appears on the same side of the original dichotomy. Conversely, *H. perforatum* also exhibits a similarity requirement of 82% with *Centaurea nigra* and 73% with *Inula conyza*, which appear on the opposite side of the original dichotomy. Likewise, *Koeleria macrantha* exhibits a similarity requirement of 89% with *Carex caryophyllea* and 87% with *Helianthemum nummularium*, which appear on the same side of the dichotomy, but 95% with *Sanguisorba minor* which is on the opposite side (Grime *et al* 1988).

5.8.7 The assessment of the species classification failed to show categorical trends in the data. It was concluded that the TWINSPAN species classification could not be attributed significant meaning.

5.8.8 Figure 5.17 shows the results of the sample classification. The 41 samples were classified into 15 end groups. Five groups contain only a single sample indicating that they may be vegetatively distinct from the remainder of the samples. Whilst the classification of groups containing two or more samples may indicate that samples within a group may possess vegetatively similar characteristics. It was observed that positive preferential species used at the first level of the dichotomy, *Carex caryophyllea, Cirsium arvense, Centaurea nigra, Koeleria macrantha* and *Plantago lanceolata*, are species with a preference for situations with intermediate fertility and low levels of soil disturbance (Grime *et al* 1988). Therefore implying that samples in group n = 13 are those with a vegetation that may be described as mesophilic representative of a 'mature' grassland. However, the Eigenvalue at the first division equals 0.165, indicating a uniformity to the samples that did not enable them to be strongly differentiated.

5.8.9 Samples containing *O. fuciflora* appear on both sides of the initial dichotomy. The end groups with these samples also contain samples of 'visually' similar areas. These facts suggest that within the visually heterogeneous areas sampled a no distinct vegetation types occur to which *O. fuciflora* is affiliated. The classification of samples therefore confirms the initial interpretation of the species classification.

5.8.10 The ecology of indicator species used to define the end groups was considered in light of the criteria list (see 5.7.3). The divisions were either on the basis of a single species presence, ie juvenile *Crataegus monogyna* in samples Q9, 19, 20 and 21 (n = 4); or differences in abundance of a group of species common to all samples within the division. In summary, TWINSPAN classification of the samples did not extract groups possessing distinctive vegetative characteristics.

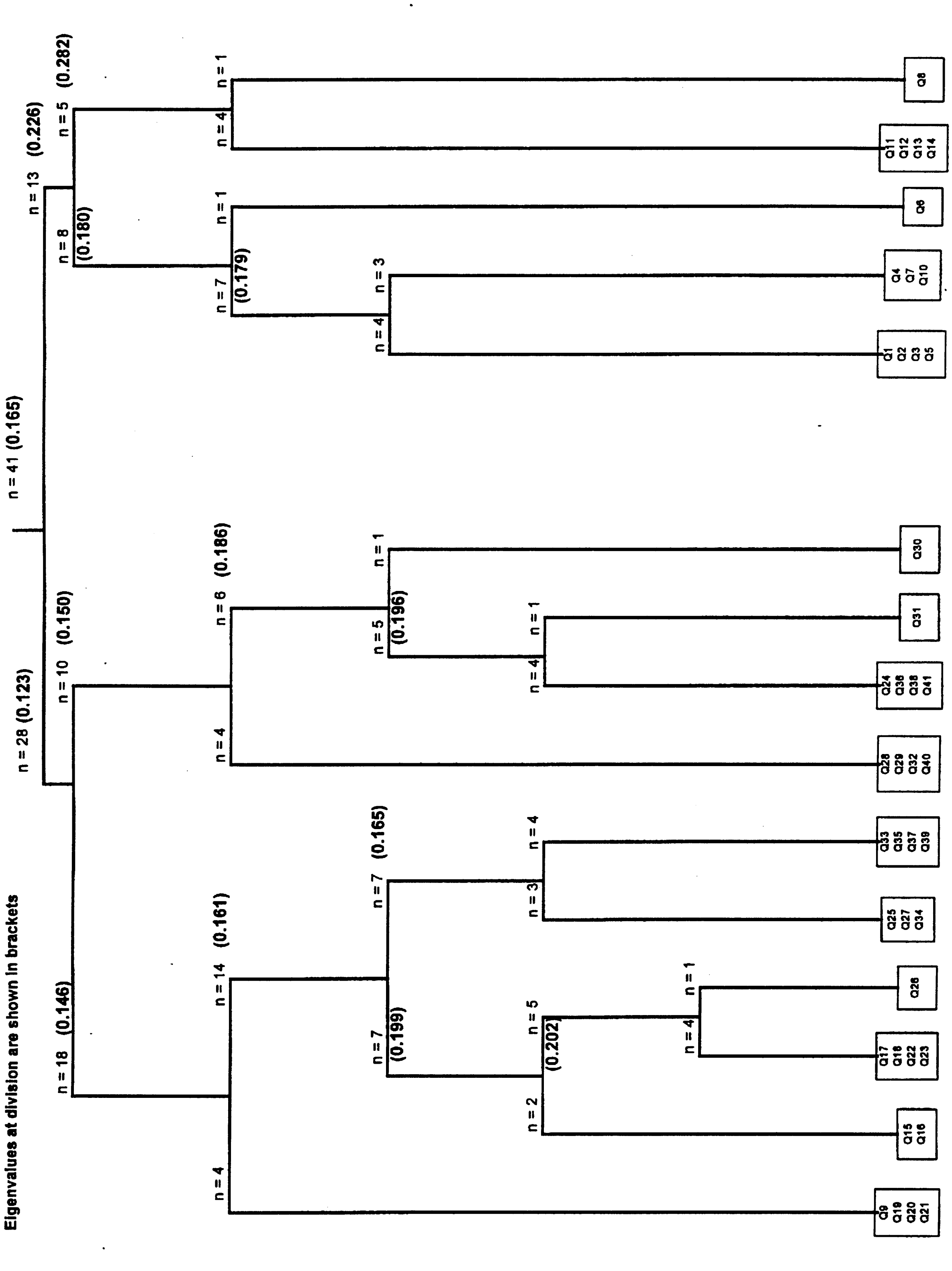


Figure 5.17: TWINSPAN classification of samples from quadrat data.

Figure 5.17 TWINSPAN classification of samples from quadrat data

5.9 Ordination analysis of quadrat data

5.9.1 Three variables manipulable by straightforward management were measured in each quadrat; litter cover, bare ground and vegetation height. To ascertain if any of these influenced the apparent distribution of *O. fuciflora* ordination of the quadrat data was performed. Ordination is an objective numerical technique that produces a spatial arrangement of samples such that their relative position along an axis reflects their degree of similarity (Goldsmith *et al* 1986). The position along the axes provides a framework onto which the variables can be overlaid in order to establish if the spatial distribution of samples correlates to a gradient exhibited by the variables (Goldsmith *et al* 1986). The position along the axes provides a framework onto which the variables can be overlaid in order to establish if the spatial distribution of samples correlates to a gradient exhibited by the variables (Goldsmith *et al* 1986; Kershaw & Looney 1985; Hill & Gough 1980). In this instance a phytosociological ordination was used where the axes are constructed from the vegetation data. Detrended Correspondence Analysis (DCA) was the ordination method employed via the DECORANA program (Hill 1979b).

5.9.2 A single run of DECORANA was performed:

a. using all 41 samples and 52 species;

b. without linear transformation of abundance values;

c. without down weighting rare species.

Table 5.5 showed the Eigenvalues derived for the generated four axes. The Eigenvalues of axes 3 and 4 were low, explaining only 8.2% and 5.5% of data variation respectively. The axes 3 and 4 were not considered for further analysis.

Table 5.5 Eigenvalues for ordination axes

Axis	Eigenvalue
1	0.134
2	0.099
3	0.082
4	0.055

5.9.3 Axes 1 and 2 were considered for further analysis. Three stages of analysis were performed:

i.. Plotting of the DCA axes from the species ordination to establish if *O. fuciflora* was grouped with other species to form a visually distinct cluster within the plot. A cluster may be considered a visually distinct grouping of data points exhibiting a similar spatial distribution on the plot of two axes.

ii. Plotting of the DCA axes from the samples ordination to establish if samples from colonies and/or containing *O. fuciflora* form a visually distinct cluster.

iii. Calculation of the correlation coefficients between the DCA axes and measured variables, in order to establish if these variables influenced the spatial distribution of samples along the individual axes.

5.9.4 Figure 5.18 shows the species plot of DCA axes 1 and 2, and two visually distinct clusters are indicated. Cluster 1 contains *O. fuciflora*, placing it with species, such as *Dactylorhiza fuchsii* and *Trifolium pratense*, which exhibit a preference for habitats characterized by moderate disturbance and low fertility (Grime *et al* 1988). Thus the species ordination confirms the results indicated by the TWINSPAN species classification. The second cluster contains species that exhibit characteristically mesophilic preferences and a preference for low levels of disturbance. The general trends exhibited by the spatial arrangement of species along the axes were interpreted as:

a. Axis 1, species with mesophilic preferences ordered to the right of Figure 5.18;

b. Axis 2, preferred levels of disturbance being ordered with 'low' at the bottom and 'high' at the top of Figure 5.18.

5.9.5 Figure 5.19 shows the sample plots of DCA axes 1 and 2. The points are labelled with the sample name (see Table 5.6). The data points exhibit some spatial similarity though no clustering or pattern was considered obvious.

5.9.6 Figure 5.20 shows a plot of the same sample DCA axes. The data are labelled either C or V depending on whether they were taken in a colony or visually similar area respectively, and with the number associated with the colony, ie C1 refers to a sample taken in Colony One, whilst V1 refers to a sample taken in visually similar area near Colony 1. What emerged from this overlay of the DCA plot was an apparent spatial separation of the colonies based on the phytosociological characteristics (see clusters indicated on Figure 5.20).

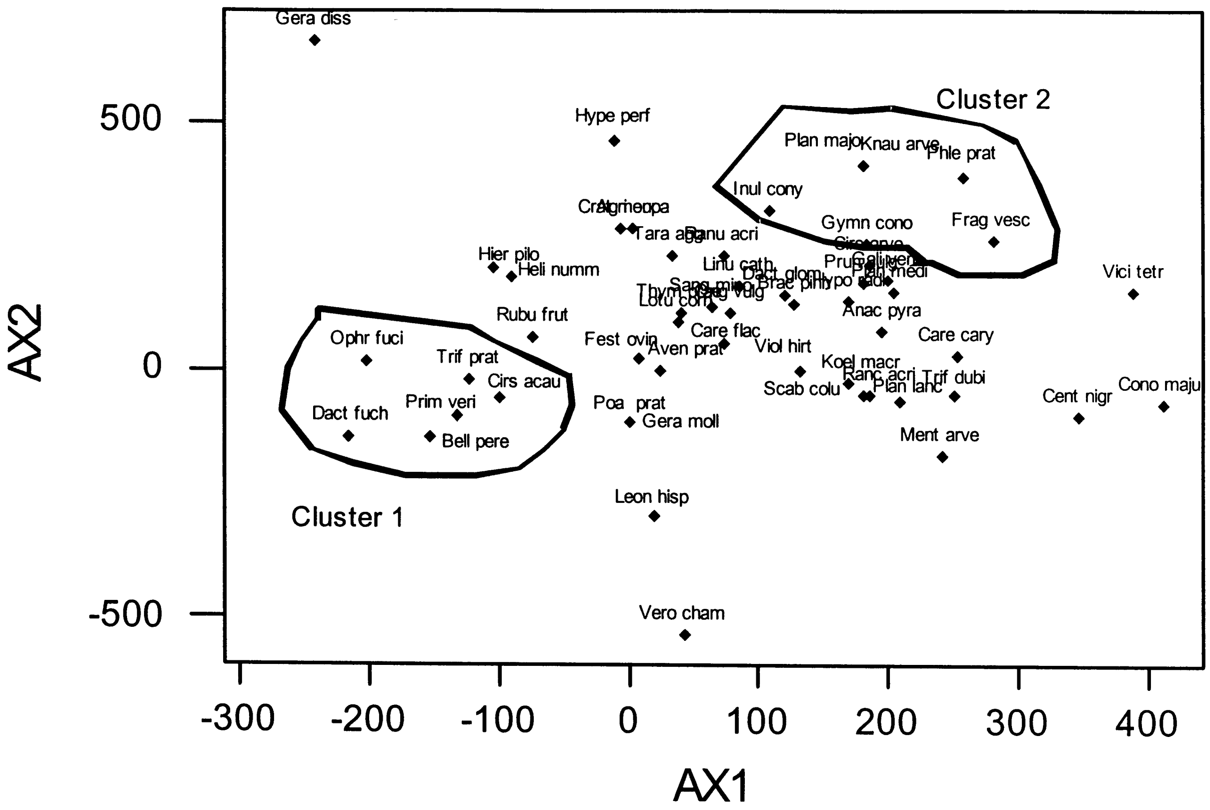


Figure 5.18 Species ordination plot (DCA Axes 1 & 2)

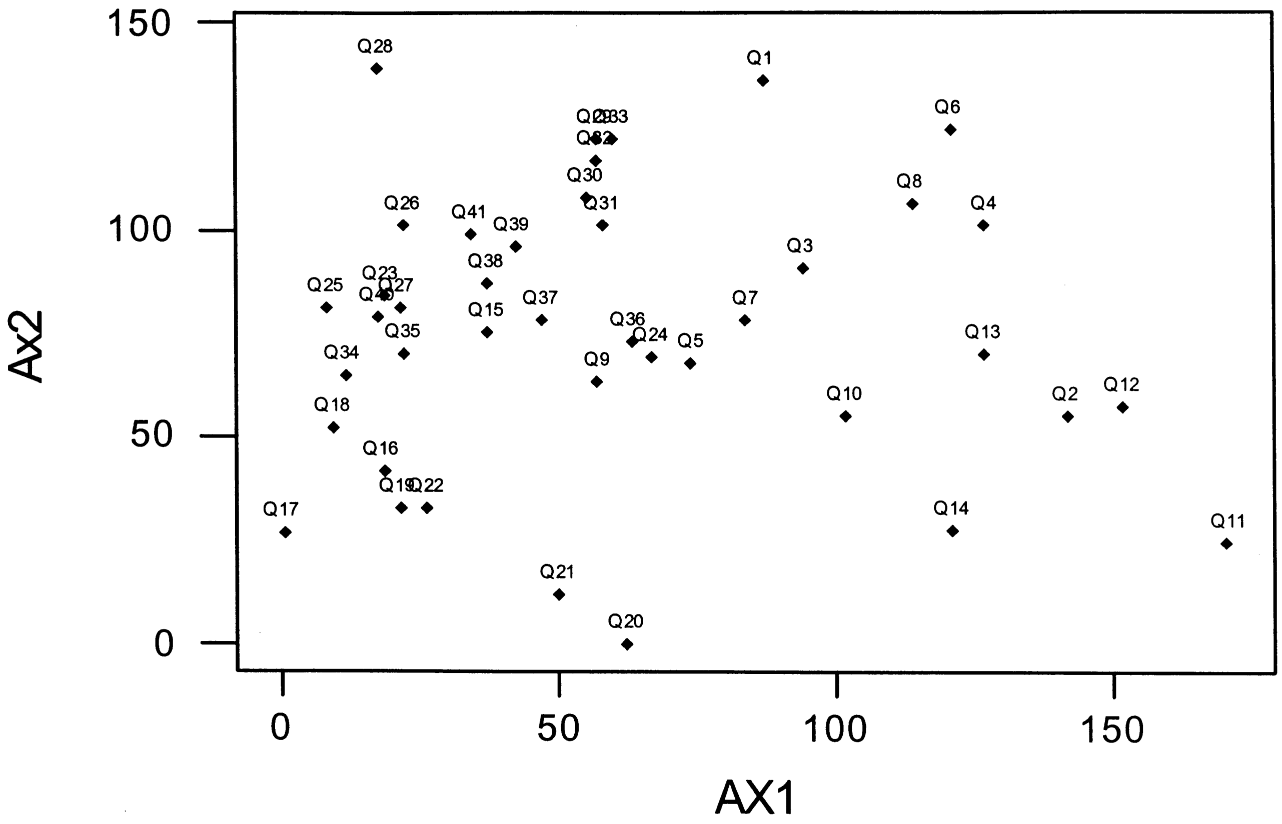


Figure 5.19 Sample ordination plot (DCA Axes 1 & 2) with sample names overlaid

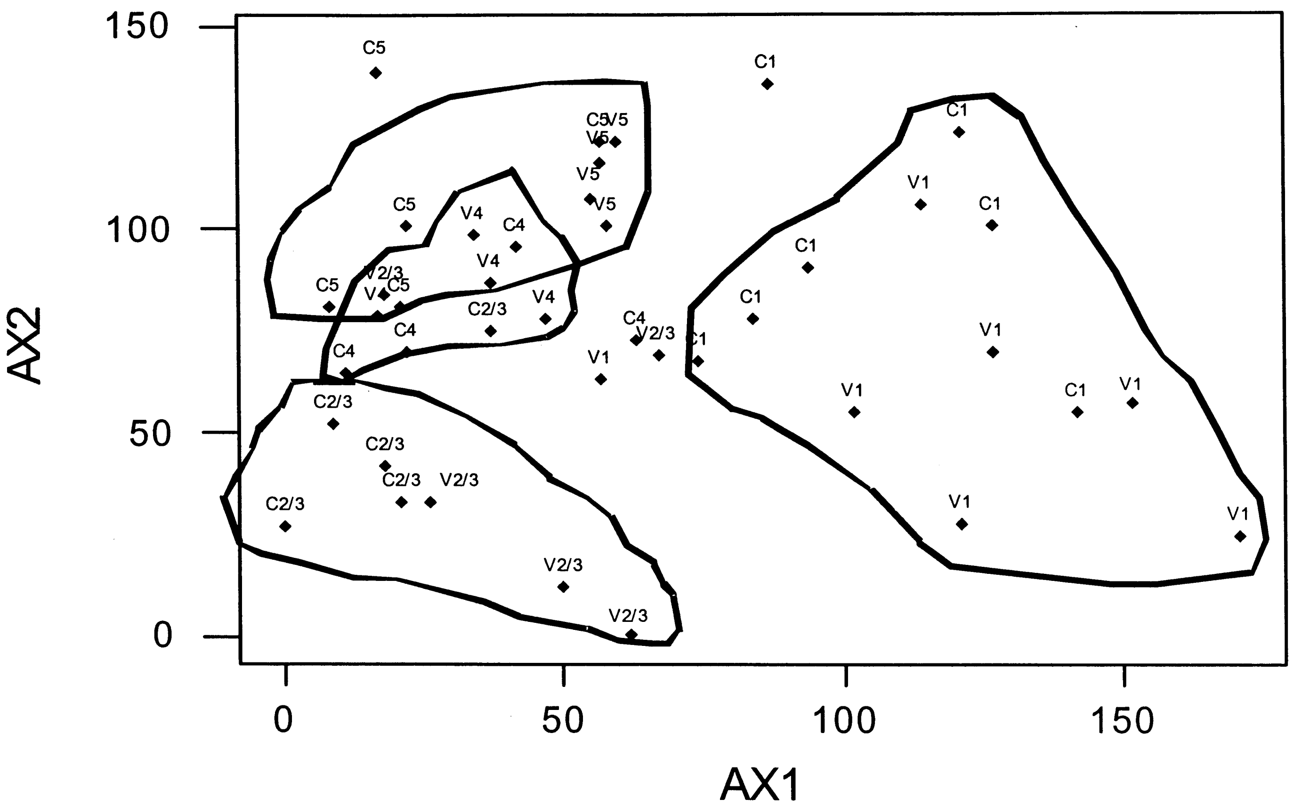


Figure 5.20 Sample ordination plot (DCA Axes 1 & 2) with colony association overlay

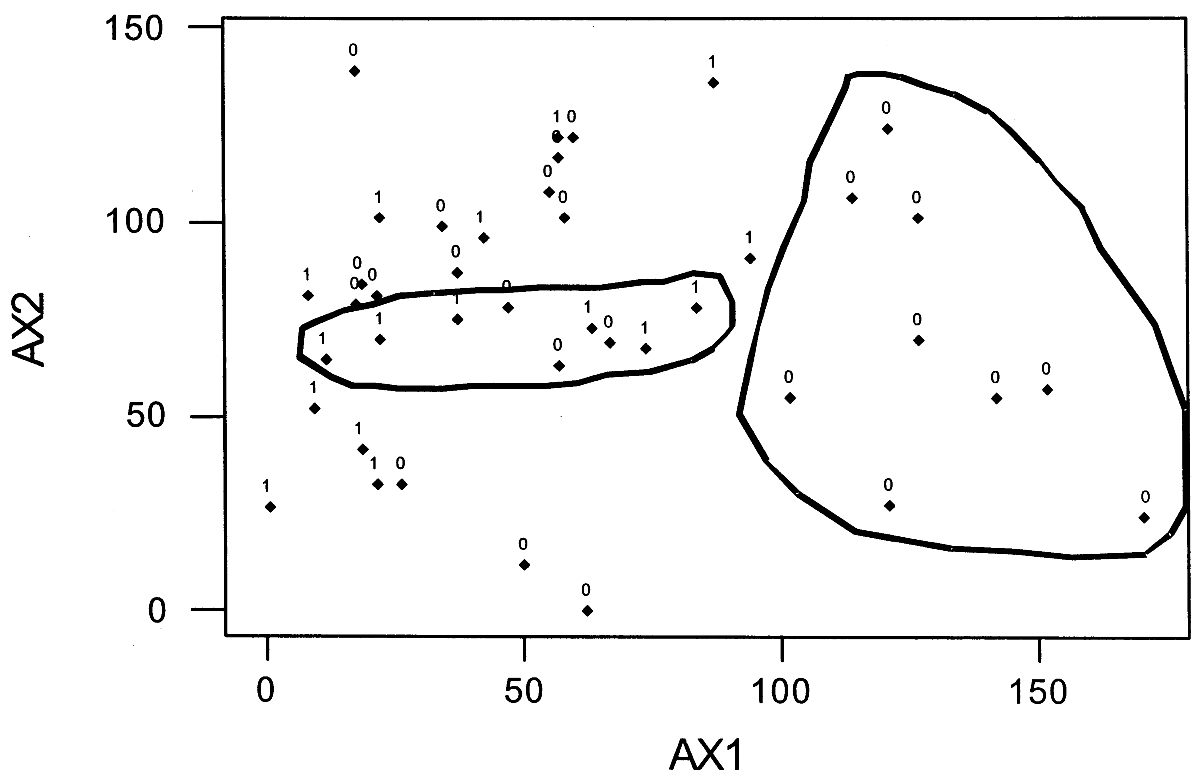


Figure 5.21 Sample ordination plot (DCA Axes 1 & 2) with *O. fuciflora* overlay

5.9.7 Figure 5.21 shows a further data point overlay of the sample DCA axes. The data points are labelled either 1 to indicate *O. fuciflora* recorded as present in the quadrat, or 0 to indicate it was not found. Samples with *O. fuciflora* recorded as present occur across the spatial range of the plot, but appear to concentrate into a cluster in the centre (see Figure 5.21). A distinctive cluster of samples without *O. fuciflora* is also indicated. The spatial arrangement of these clusters suggests that the presence and/or absence of *O. fuciflora* may be influenced by environmental variables, eg bare ground, exchangeable ions or soil moisture reflected along the ordination axes.

5.9.8 To test the influence of environmental variables hypothesis, the correlation coefficients of the measured variables within each sample were calculated against the DCA axes (see Table 5.6).

Table 5.6 Correlation coefficients for DCA axes and measured variables

DCA Axis	**Variable**		
	Veg. height	**Bare ground**	**Litter**
DCA 1	0.536 ($p<0.001$)	0.06 (NS)	0.18 (NS)
DCA 2	0.236	0.393 ($p<0.05$)	0.02 (NS)

Two significant correlations were identified. Firstly between DCA axis 1 and vegetation height **r** = 0.536, $p<0.001$), and secondly between DCA axis 2 and bare ground **r** = 0.393, $p<0.05$). These correlations confirm the influence of the measured environmental variables on the spatial arrangement of samples alluded to in section 5.9.7. Figures 5.22 and 5.23 show the plots of the correlation relationships with an indicative regression line.

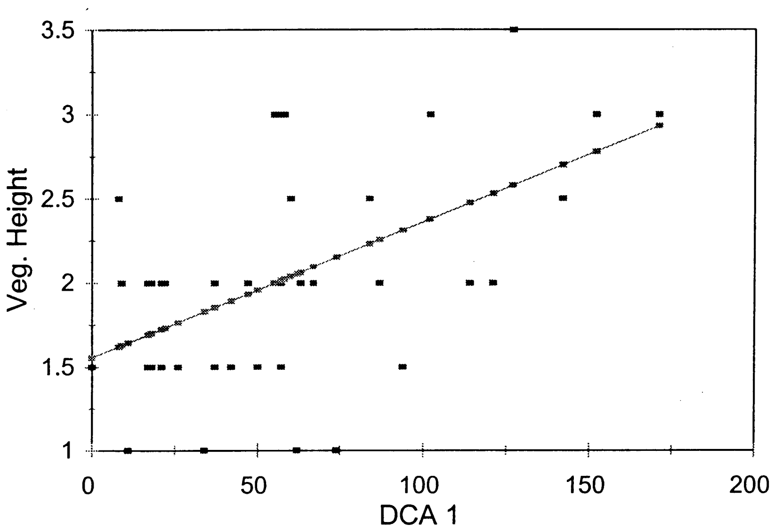


Figure 5.22 Correlation plot of DCA 1 and vegetation height

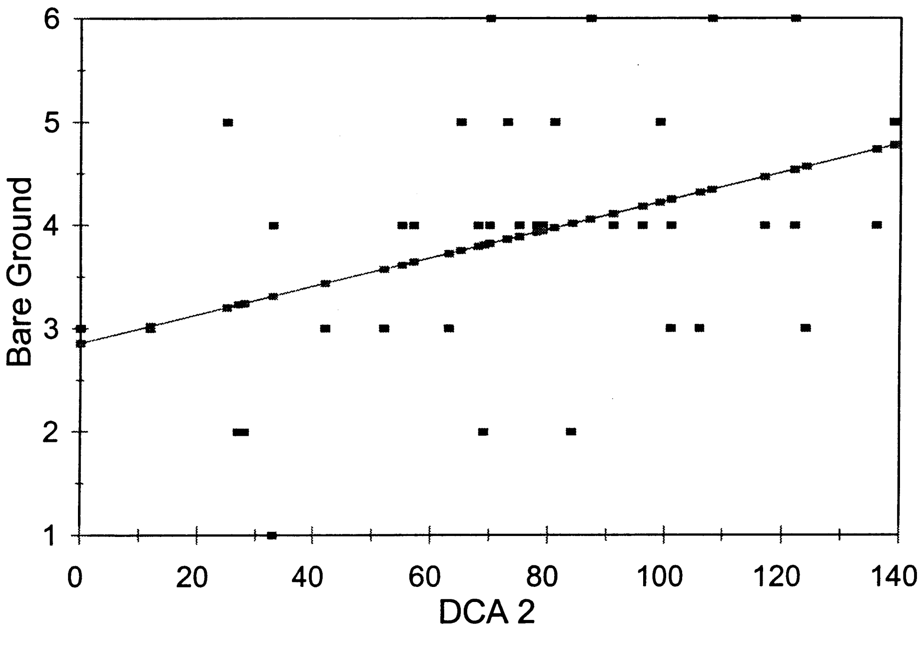


Figure 5.23 Correlation plot of DCA 2 and bare ground

6. Discussion

6.1 This investigation focused on the population of *O. fuciflora* at Wye NNR. In embarking on the investigation it was hoped to add to the autecological knowledge base of the species; identify some of the critical requirements of the species that determine its ability to perform; and using this information focus on practical modifications of land management that would improve the survivorship and performance of *O. fuciflora.*

6.2 Ecology of *O. fuciflora*

6.2.1 Chapter 2 describes the published known biology and ecology of *O. fuciflora*. A generic account of the underground life of orchids of the genus *Ophrys* was given and this investigation can shed no further light on that, since it was a non-destructive study focused on aerial stages of the species life cycle.

O. fuciflora, a perennial

6.2.2 Summerhayes (1968) asserted that British orchids behave monocarpically. This has been shown not to be the case for *O. apifera* and *O. sphegodes* (Wells & Cox 1991; Hutchings 1987). The census data and the practical relocation of individuals on the ground through the duration of the study confirm that *O. fuciflora* is perennial and not monocarpic.

Observations of the O. fuciflora life cycle

6.2.3 The forming of a basal rosette is a characteristic of the *genus ophrys* which was unconfirmed in *O. fuciflora.* Personal observation by the authors can confirm that *O. fuciflora* does form an over-Wintering basal rosette, usually in October. Further observations have shown that rosettes of flowering plants wither quickly, even on those forming capsules, and have disappeared before flowering is complete, usually by early July. The actual duration of flowering, form the opening of the first floret to the last, lasts 3-4 weeks. Numerous small pollen-beetles (species unknown) have been noted on *O. fuciflora* florets supporting the observations by van der Cingel (1995).

Dormancy in *O. fuciflora*

6.2.4 In stating that *O. fuciflora* is perennial, it is not to infer that plants appear above ground and flower every year. Of the 267 individuals recorded during the study only three plants wee recorded in either a vegetative or flowering state for all 12 years. Periods of dormancy were frequent amongst individuals, varying in duration from one to two growing seasons, the mean duration being 2.49 years. It was calculated that there was a >95% probability of any plant not recorded above ground for three consecutive years being dead. This suggests some physiological limitation to the ability of the underground parts of the plant to survive without photosynthetic nutrition. A 'two growing season' limit to dormancy for *O. fuciflora* is the same as that found for *O. apifera* and *O. sphegodes* in Britain (Wells & Cos 1991; Hutchings 1989). This limit on the ability of the plant to survive in an underground state can only be assumed to apply to plants once they have produced aerial parts. The data and observations provide no real evidence of the duration of the developmental underground phase; although it might be intimated that it is not a significantly longer period than that of the dormancy limit, eg in excess of 3-4 years, if one assumes similar physiological and ecological factors to dormancy are at play. The recording of *O. sphegodes* on spoil from Channel Tunnel excavations only four years after the spoil was deposited might suggest such an intimation to be reasonable (Gay & Philp 1999).

Half-life and survivorship of *O. fuciflora*

6.2.5 Tamm (1972) showed that the half-life of orchid species varied considerably, identifying the half-lives of *Listera ovata* and *Orchis mascula* as 83.6 and 4.3 years respectively. From the depletion and survivorship curves for *O. fuciflora* a range of half-lives (7.09 to 26.71 years) were calculated for the cohorts (see section 5.6). The calculated mean half-life of *O. fuciflora* was 12.52 years, well within the range described by Tamm (1972). It is of the same magnitude as the half-life of *O. apifera*, calculated to 11.18 years by Wells & Cox (1991), though the half-life of *O. sphegodes* was calculated as being only 1.5 to 2.3 years (Hutchings 1989).

6.2.6 The depletion and survivorship curves of *O. fuciflora* were found to be of the Type II (R>0.8) (Deevey 1947). Plant with this type of survivorship display a constant age independent mortality rate. It is typical though for many plants to experience a high mortality rate during early stages of their life, with the risk decreasing with maturity (Crawley 1986). This is represented by a type III survivorship curve (see section 5.6) (Deevey 1947). The survivorship curves of *O. sphegodes* conform to the Type III (Hutchings 1987). Type III species would be expected to demonstrate a shorter mean half-life than others within their genus with Type II curves since they invest in recruitment rather than longevity, a behaviour quite typical of weedy species (Hutchings 1989; Crawley 1986). However, it cannot be concluded that *O. fuciflora* does not possess this recruitment characteristic.

6.2.7 Clearly, *O. fuciflora* is a long lived plant at the study site, but the Type II curves were generated from data for aerial plants. From the known biology of genus *Ophrys* it may be concluded that aerial plants are already 'mature' since they have completed an underground life stage of unknown duration, and many (176 individuals in this study) flower during their first aerial year. Thus the calculated survivorship curves and mean half-life are for mature plants. Having reached this life stage it is clear that they are long lived as demonstrated by the 60 year calculated survivorship of the 1998 cohort. This does not preclude investment in recruitment and a high mortality rate during the subterranean life stage. If these rates were known the survivorship curve of *O. fuciflora* may better fit Type III, possibly leading one to think of it as 'weedy'.

Vegetative reproduction and spatial distribution

6.2.8 It is often thought that vegetative reproduction is common place amongst the British orchids (Summerhayes 1968). Whilst this is certainly the case for a number of species, notably *Listera ovata* (Tamm 1991), it is by no means true for all species. Willems and Bik (1991) showed this to be a 'rather rare phenomenon' in their studies of *Orchis simia*. Whilst

Hutchings (1987) concluded that vegetative reproduction did not make a significant contribution (<5%) to the reproductive strategy of *O. sphegodes*. In the case of *O. fuciflora* the results of the spatial analysis (see Table 5.2) suggest that vegetative reproduction is not a part of the species survival strategy. This conclusion is based on the assumption that an arbitrary distance of 10 cm between parent and daughter rosettes would be the maximum distance for vegetative offspring (after Hutchings 1987). Using this assumption the results show only 24 (0.29%) of the possible 8,152 distance measures between recorded plants to be 10 cm or less. Even if one assumed 30 cm to be the maximum distance for vegetative reproduction, only 0.88% of the measured distances would be accounted for. Thus it is reasonable to conclude that *O. fuciflora* does not regularly employ a vegetative reproduction strategy.

6.2.9 Having drawn that conclusion, it is striking that 99.12% of the measured distances between plants of *O. fuciflora* were greater than 30 cm. Whilst undoubtedly at a study site scale it can be argued that the spatial distribution of species is aggregated or clumped, hence the ease with which discrete colonies are identified, at a colony scale one might argue that the spatial distribution tends towards regular (Crawly 1986). The spatial distribution of *O. fuciflora* may be demonstrating influence of inta-specific competition at the juvenile stage. Clearly this is an area that warrants further investigation, beyond the scope of this study.

Population size and flux

6.2.10 A casual count of flower spikes as a means of monitoring *O. fuciflora* could readily deceive the observer into thinking that the population of the species fluctuates wildly. Certainly this was thought to be the case for *O. apifera* (Lang 1989), though Wells and Cox (1991) showed this not to be so. For *O. fuciflora*, as with *O. apifera*, what is being observed through a count of flowering spikes is transition between flowering, vegetative and dormant life stages. At the study site the mean percentage of the population in flowering, vegetative or a dormant state was 45.67%, 37.07% and 12.93% respectively. There was significant variation around the means, which could lead one to conclude from casual observation that the population fluctuates. Analysis of the population flux over the study period actually shows there to have been a steady increase in the population size with recruitment consistently out-weighing mortality.

6.2.11 Inghe (1990) hypothesized that the irregular life histories of perennials, such as orchids, were in response to resource dependent reproductive investment. However, Kindlemann (1999) concluded that Inghes' hypothesis did not satisfactorily account for the life history irregularities of the orchid *Epipactis albensis*. The argument proffered by Kindlemann (1999) would apply equally to the case of *O. fuciflora* though the data is inadequate to test the resource dependency hypothesis. Alternatively it may be proffered that fluctuations in percentage of population flowering is in response to environmental variables such as rainfall or temperature. This hypothesis remains to be tested.

Population matrix model

6.2.12 The modelling of *O. fuciflora* provides a predictive tool for establishing future population trends in circumstances where the opportunity for experimental management trials is limited.

In section 5.7 a simple model **T** of the population behaviour of *O. fuciflora* was developed (see Table 5.11). Further development of **T** identified significant variance in the recruitment coefficient **R** leading to the model **M**. The conclusion from this process is that the model suggests there is an undetermined time delay in the recruitment of aerial plants. This conclusion is consistent with the known biology of the genus *Ophrys*, though the model does not help to narrow down the band width of that time delay. Alternatively one might interpret the variation in **R** (see Table 5.5) as reflecting typical characteristics of an adventive species with recruitment fluctuation determined by environmental factors.

6.2.13 Whilst **M** remains untested, elements of **T** were altered in a systematic manner to learn more about the predicted behaviour of the orchids. Within the matrices this behaviour is characterized by the dominant eigenvalue and corresponding eigenvector (Gillman & Hails 1997).

6.2.14 So what was learnt from the population model of *O. fuciflora?* In the absence of recruitment the orchid population will slowly decline, confirming the predictions of the half-life model. The matrix model predicts a period of 62 years for the 1998 cohort to be reduced to a single individual. This is in stark contrast to the predictions for *O. sphegodes* which showed rapid declines in population levels over a three year period (Waite 1989).

6.2.15 The outputs of the model arrived at by systematically altering the mortality rates of flowering and vegetative plants suggest that populations of *O. fuciflora* are more sensitive to changes in flowering plant mortality, and less sensitive to changes in vegetative plant mortality (see Figure 6.1). The model outputs arrived at by systematically altering the recruitment rates to favour different state recruitment, also suggest that the population is sensitive to increased levels of recruitment and that this is mostly influenced by the level of flowering plant recruitment (see Figure 6.2). The sensitivity of *O. fuciflora* to flowering plant mortality is a characteristic shared with *O. sphegodes* (Waite 1989). However, *O. fuciflora* differs in being sensitive to flowering plant recruitment as opposed to dormant plant recruitment like *O. sphegodes* (Waite 1989).

6.2.16 The matrix model of *O. fuciflora* leads to an unsurprising but important conclusion. The population is sensitive to flowering plant mortality and reproduction, a probable consequence of the virtual absence of vegetative reproduction in the species. The model also highlights that low rates of recruitment (<5% of the annual population) are necessary to sustain the population. Given the potential for thousands of viable seeds to be produced by one mature ripened capsule, low reproduction rates mean that few capsules need to be produced. This goes a long way to explaining why the population at Wye NNR continues to thrive when very few ripe capsules have been observed by reserve staff or the author; and in the absence of its preferred pollinator.

6.3 Requirements of *O. fuciflora*

6.3.1 The analysis of census data revealed a number of autecological characteristics of the species at Wye NNR. The analysis of the quadrat data using classification and ordination techniques provided some insight into the ecological requirements of the species.

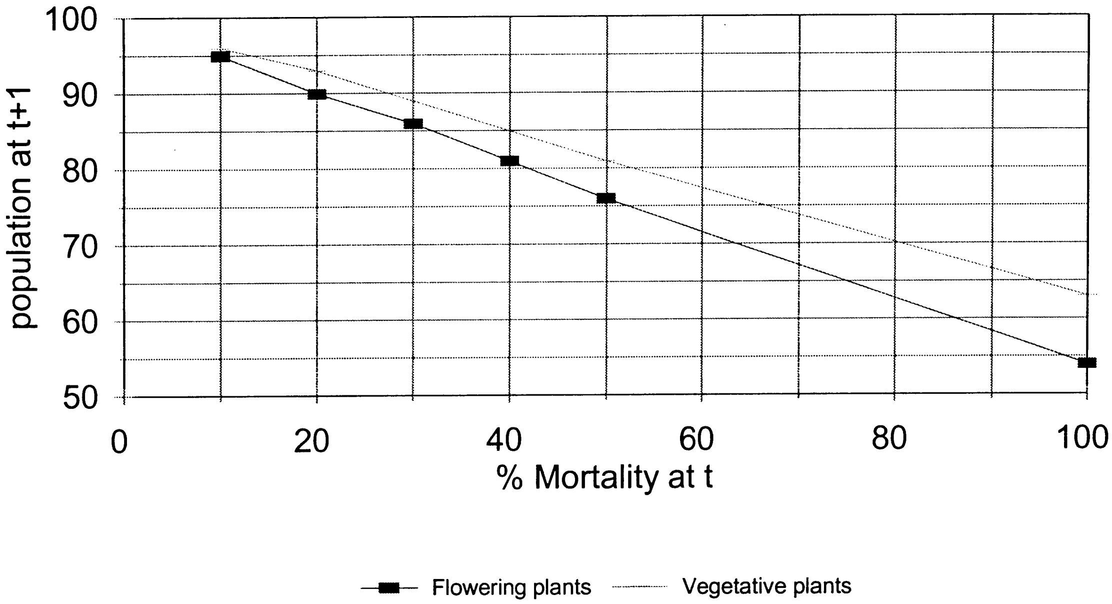


Figure 6.1 Population responses to alteration of mortality rates for flowering and vegetative plants

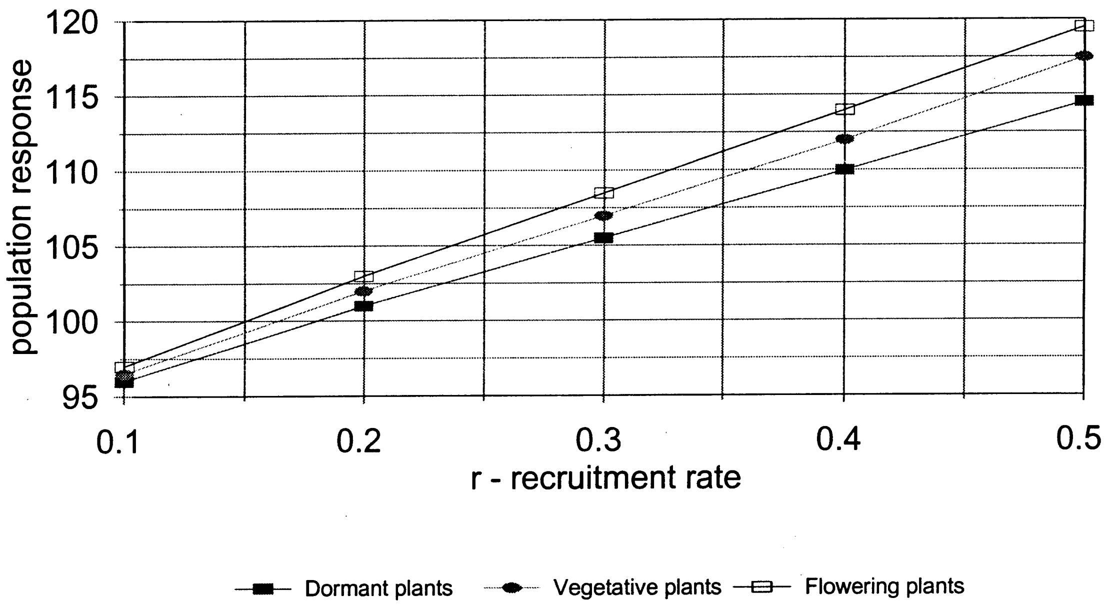


Figure 6.2 Population response to alteration of recruitment 'r' to favour different states

6.3.2 The TWINSPAN analyses of the quadrat data was not wholly conclusive, nevertheless some ecological preferences of *O. fuciflora* were indicated by the results. The species analysis associated *O. fuciflora* with *Dactylorhiza fuchsii, Hypericum perforatum, Rubus fruticosus* and *Trifolium pratense*. These species exhibit preferences for moderately disturbed places of low soil fertility j(Grime *et al* 1988). The work of Ingram and Ingram (1981) analysing the soils of Wye NNR confirms the low nutrient status of the soils. Whilst it could be argued that disturbance preferences are consistent with habitats such as waste places and lightly grazed grassland such as the unimproved calcareous grassland of the study site. The associated species also exhibit a preference for a competitive-ruderal regeneration strategy (Grime *et al* 1988). The lack of a clear distinction in the end groups of the species analysis is perhaps unsurprising since samples were taken from within a single habitat and visually heterogeneous stands.

6.3.3 The TWINSPAN analysis of the samples went some way to confirming the preferences highlighted by the species analysis with an initial division based on species more representative of mesophilic grassland and those with a distinct preference for low fertility disturbance. However, *O. fuciflora* occurred on both sides of this initial dichotomy. Why might this be the case? It could be argued that this mixed picture of preference is reflective of the longevity of the species and or different life stages. For instance, low fertility and disturbance may be a pre-requisite for establishment of young plants, a facet consistent with a ruderal regenerative strategy, whilst more mesophilic conditions may be tolerable to established plants. The longevity of *O. fuciflora* may also mean that a 'mature' grassland state develops around the plant during its life span.

6.3.4 The ordination analyses of the species and samples provided further evidence of the ecological preferences or requirements of *O. fuciflora*. The species ordination placed *O. fuciflora* together with species exhibiting a moderate disturbance and low fertility preference, whilst there was also a distinct spatial cluster of species with mesophilic preferences. The samples ordination initially gave a somewhat mixed picture with no clear distinction between samples taken in colonies or 'visually' similar areas. However, the overlay of actual orchid presence in the sample (see Figure 5.21) did reveal a spatial distinction between samples with and without *O. fuciflora*. The axes of this analysis were significantly correlated to two of the sample variables measured during the study. DCA Axis 1 correlated to vegetation height ($p<0.001$) and DCA Axis 2 to bare ground ($p<0.05$). One might consider these variables as surrogates or vegetative attributes indicating the ecological conditions or state within the calcareous grassland. Bare ground can be considered indicative of a localized level of disturbance, and vegetation height indicative of the 'maturity' of the grassland. It can therefore be concluded from the sample ordination that *O. fuciflora* exhibits a preference for moderately disturbed soil conditions and low vegetation height.

6.3.5 The NVC descriptions of the samples further support this conclusion. Two distinct phytosociological communities were identified, *Brachypodium pinnatum* grassland (CG4) and *Festuca-Avenula* grassland (CG2), along with some intermediate samples. CG4 grassland includes vegetative characteristics of CG2 but is ranker and its floristics indicate a shift towards mesotrophic grassland (Rodwell 1992). Because of the unpalability of *B. pinnatum* these grassland swards tend to be taller than CG2. CG2 grassland tend to occur on free draining rendzina soils which are oligotrophic but with high levels of free calcium. They are characterised by intimate mixtures of diminutive herbaceous dicotyledons and grasses, usually closely grazed. Grazing is critical to maintaining the balance of the sward. Relaxation leads to dominance by ranker grasses. On the North Downs of Kent this usually means that *B. pinnatum* becomes dominant and the community type shifts to CG4 (Rodwell 1992). Therefore one can conclude that within the samples one is observing variation in grazing pressure reflected by the vegetative response.

6.3.6 It could also be argued that the preference of *O. fuciflora* for low fertility and moderately disturbed conditions is reflected by the physiology of the species. Crawley (1986) suggests that the type of environmental conditions described above may be manifested in physiological plant features such as:

a. reduced size;

b. a tendency for the development of long-lived leathery leaves;

c. the reabsorption of foliar nutrients;

d. the development of storage tissues;

e. failure to respond to fertilizer application; and

f. investment in mycorrhizal development.

O. fuciflora exhibits several of these features. For instance mycorrhizal development, storage tissues and leathery long-lived leaves. Again this supports the conclusion regarding the environmental preference of the species.

6.4 *O. fuciflora* autecology: reprise

6.4.1 In summing up what has been learnt about the autecology of *O. fuciflora* it must be remembered that this study has focused on a population at the very north of the species distributional range. Therefore one can only tentatively extrapolate these conclusions to specimens occurring more centrally in the species range.

6.4.2 From this study it can be concluded that *O. fuciflora*:

a. is perennial and not monocarpic;

b. has a limited below ground dormancy life of two years once the aerial life stage has started;

c. has a long half-life of 12.52 years;

d. aerial plants demonstrate Type II survivorship, though Type III is probable if subterranean life stages were considered;

e. it does not readily reproduce vegetatively;

f. at Wye NNR the population has steadily increased but flowering and vegetative performance fluctuate significantly for unknown reasons, though it is not in response to reproductive resource investment;

g. flowering plant mortality and reproduction are the key factors influencing long-term population levels;

h. mortality rates are low (approximately 5%);

i. that the species exhibits preferences for habitats with oligotrophic free draining soils and moderate levels of disturbance; and

j. it exhibits the characteristics of a stress tolerant species using a competitive-ruderal regeneration strategy.

6.4.3 It was previously stated that orchids are considered to be amongst the most sensitive of British plants (see section 1). The results of this study suggest that far from being sensitive *O. fuciflora* is a robust long-lived plant physiologically adapted to survival in a stressful environment. Though this is not to say that the species does not have ecological limitations. Rather one might tentatively suggest that *O. fuciflora* is an opportunistic species that is easily out-competed for resources by more rigorous plants and as a consequence has evolved such that its physiology and biology is adapted for environmental conditions where interspecific competition is reduced.

6.4.4 The suggestion that the species is opportunistic is substantiated by its high level of seed production, a characteristic of opportunistic or adventive species that are generally considered weeds, for instance *Capsella bursa-pastoris*. Such species are also characterised by short term peaks in population which dwindle as conditions become more mesotrophic. Whilst *O. fuciflora* does not behave in this way in the aerial stage, it is characterised by peaks and troughs of flowering performance, and localised decline in mesotrophic areas. Furthermore, it might be suggested that as an opportunistic species *O. fuciflora*, in common with other orchid species such as *O. sphegodes*, exhibits a preference for colonisation of early seral stages of vegetational development, such as disused quarries, disturbed ground and *Festuca-Avenula* grassland (Hutchings 1989; Gay & Philp 1999). Dressler (1991) argued that orchids of the genus *Ophrys* are adventive, the evidence of this study adds further weight to that argument. This characteristic does not appear explicit within UK populations of *O. fuciflora*, though it may be confounded by occurrence in mature grassland which develops past establishment.

6.5 Behaviour of the colonies

6.5.1 Thus far the discussion has focused on the behaviour of *O. fuciflora* as an individual. The results also provide some information about differences in the behaviour of the individual colonies giving a further insight into the species and its management.

6.5.2 Taking the colonies as a whole the general picture of *O. fuciflora* at Wye NNR is of a healthy expanding population. It is notable that the rate of population growth increased markedly around 1991-1992 with the introduction of Winter cattle grazing and periodic strimming of rank vegetation (see Table 3.1 and Figure 5.13). However, there are a couple of exceptions to the general picture; notably Colonies Two and Three.

6.5.3 Colonies Two and Three have been subject to the same management as the other colonies. In 1995, the last certain date for assessment of population size, Colony Two had neither increased or decreased in size, whilst Colony Three showed a decrease of 7.2%. All other colonies had increased in population size at this time. Colonies Two and Three have respective means of 36.14% and 37.33% of the populations in flower compared to >40% for all other colonies. The transition matrices of these two colonies incorporate higher probabilities for first year dormant plants to either be dormant for a second year or reappear as vegetative plants (see Tables 5.7 and 5.8). The spatial analyses of the colonies indicated a higher degree of clumping in these two colonies (1.06% <5.1 cm for Colony Two, and 3.08% <30 cm for Colony Three) possibly indicating a greater propensity for vegetative reproduction. The DCA ordination placed samples from these colonies in a spatially distinct cluster towards the bottom left of the plot (see Figure 5.20) indicating low levels of bare ground/disturbance and low vegetation height, suggesting a closely grazed but tight sward. However, the phytosociological classification did not distinguish the samples from the other colonies, and they appear visually similar in the field.

6.5.4 Clearly Colonies Two and Three are behaving differently to the others, even those within the same management block. The only distinguishing factor of these colonies emerging from the analysis is the lower level of bare ground, suggesting less disturbance. Though it could be argued that the spatial differentiation in the DCA analysis is not sufficiently strong to explain the differences in population behaviour. Reflection upon the early history of the colonies provides no explanation either. It was noted during the census that these colonies exhibit a tendency to flower 3-4 weeks later than the others.

6.5.5 From the available information one difference does stand out. The aspect of Colonies Two and Three is different from the other four colonies. Colonies Two and Three face west-southwest, whilst the others face more or less due south. The local topography causes three sites to be very exposed from south-east to north-west. What is the significance of this? Remembering that the central distributional range of *O. fuciflora* is the Mediterranean, one might conclude that the difference in aspect coupled with short sward would lead to lower soil temperatures in the area around these colonies at various times of the year. Thus the difference in the population behaviour of Colonies Two and Three may be a response to these conditions. One might reasonably conclude that *O. fuciflora*, at the northern limits of its distributional range is likely to be thermophilic, and the observed behaviour of Colonies Two and Three is a result of thermal stress.

6.6 Management of *O. fuciflora*

6.6.1 One of the aims of the investigation was, using autecological knowledge, to guide the appropriate management of extant *O. fuciflora* colonies within the study site, and within the physical, practical and financial constraints of Wye NNR.

6.6.2 Before considering management the constraints of the site should be highlighted. Financially resources are limited, therefore management proposals that significantly increase costs are unrealistic. Physically the site is well fenced with good water supplies, offering limited stock shelter, and good accessibility. The steep incline of the scarp makes the soils vulnerable to poaching when wet. With the exception of 7 Sussex heffers used to graze areas outside the main grazing blocks English Nature no longer owns stock at the site, therefore grazing regimes are reliant upon agricultural graziers. There are a range of other scientific interest features on the reserve, therefore specific management for *O. fuciflora* should involve only localized modification.

6.6.3 The management of *O. fuciflora* can be considered in two parts. Firstly management of extant colonies in order to maintain their viability. Secondly enhancement to increase the extent of existing colonies, create new ones or significantly increase population size.

6.6.4 Realistically only two factors of the grassland can be controlled at Wye NNR, vegetation structure and nutrient status. Other factors such as climate, adjacent land use and atmospheric deposition may be influential upon *O. fuciflora* but they are uncontrollable [Crofts & Jefferson, 1999]. The most practical approach to managing vegetation structure and nutrient status is through grazing.

6.6.5 In exploring the autecology of *O. fuciflora* key attributes were identified of relevance to the management. The preference of the species for disturbed ground of low fertility, the importance of flowering plant mortality and its thermophilic tendency.

Managing extant colonies

6.6.6 In considering the management of extant colonies at Wye NNR the success of the existing regime must be acknowledged. The Winter grazing of cattle with periodic strimming to reduce rank vegetation appears to have been successful in increasing the population of *O. fuciflora* within the site.

6.6.7 The Winter grazing regime at Wye NNR extends from September to March. The advantages of this grazing regime are:

a. it does not directly affect most herbs;

b. it can weaken vigorous grasses;

c. at moderate levels it can break up litter exposing ground for colonization.

[Crofts & Jefferson, 1999]. The disadvantages of the grazing regime are that;

a. it does not remove many nutrients;

b. because of declining palatability competitive grasses can become dominant in the sward.

[Crofts & Jefferson, 1999]. The palatability issues partly overcome by grazing with cattle which are less selective than sheep.

6.6.8 Given the sensitivity of *O. fuciflora* to flowering plant mortality management regimes that reduce this are most likely to be successful in conserving the species, thus the timing of management practices is an issue. Low Winter soil temperatures may be reduced if site vegetation is not reduced excessively by Winter grazing [Waite, 1989], thus the intensity of grazing is an issue. Levels of bare ground, soil disturbance and of vigorous grasses may also be controlled by a balance of intensity and timing of grazing.

6.6.9 The current management regime at Wye does not take full account of the requirements of *O. fuciflora*. It would also appear from the data that it has only moderate success in suppressing *B. pinnatum* grassland, hence the patchwork revealed by the sample data. Rich [1997] recommends that *O. fuciflora* should be managed by grazing from September to May using cattle (2/ha) and/or sheep (5-10 ewes/ha) with occasional mowing in August to control rank swards. We would argue that this regime would adversely affect any population of *O. fuciflora* in the long term. *O. fuciflora* has been observed flowering as late as August, and seed maturation would generally occur in this month also, if not early September. The regime suggested by Rich [1997] would increase flowering plant mortality and directly reduce recruitment leading to rapid population decline. Moreover the grazing intensity is inadequate to maintain a CG2 type grassland with adequate levels of localized disturbance.

6.6.10 It has been shown that rosettes of *O. fuciflora* appear in October. These are susceptible to damage by Winter grazing-stock, especially if conditions are wet. The rosettes of flowering plants wither by late July and capsule maturation is reached in mid-August. Taking onboard the constraints of the site and the ecological requirements of *O. fuciflora* it would be reasonable to argue that extant colonies might be managed as follows:

a. sward conditions to be assessed in late July/early August ie depth of thatch or litter, sward height.

b. i.. if rank with an underlying mat of dead material: mow or strim and rake-off cut material between late August and end of September: Do not graze

ii. if sward has little underlying material and average vegetation height > 10 cm: graze with cattle at 2-3/ha from mid-August to end of September.

iii) if sward height <10 cm: graze with sheep 8-10/ha from mid-August to end of September.

c. In mild years when sward growth is vigorous during the Winter period repeat cattle grazing for a 2-3 week period between mid-March and early April.

d. Exclude grazing-stock from October through to August (see C above).

NB This regime assumes stock may be readily excluded and that protective cages will be retained as necessary over late flowering specimens or plants with capsules.

6.6.11 Such a regime should minimize flowering plant mortality; maintain Winter vegetation cove; weaken vigorous species. The aim of the regime is to maintain nutrient removal, and achieve uniform sward type with 5% - 10% bare ground. Given the scarcity of pollinators in the UK hand pollination during July might be considered as a means of increasing recruitment.

Enhancement of the colonies

6.6.12 The adventive character of *O. fuciflora* has already been discussed. It can be argued that this characteristic holds the key to enhancement either through extension of extant colonies or local establishment of new colonies. Historic evidence (see section 3.6) indicates that *O. fuciflora* tends to occur in areas of heavily disturbed ground. This is consistent with the preferences highlighted by the ordination and classification analyses.

6.6.13 Given the autecological and historical evidence it can be argued that enhancement would be best achieved through deliberate soil disturbance. Such a disturbance regime should not be regular but rather episodic, and should be on a small scale so as not to disturb the grassland structure too radically. The following regime is suggested for enhancement:

a. Shallow rotivation of an area no greater than 0.01ha at the end of May. This area should not be re-disturbed within a 20 year period;

b. as for management of extant colonies (see section 6.6.10).

6.6.14 In choosing an area to disturb some things should be taken into account, for example aspect, availability of seed, continuance of management. Therefore, unless seed is to be artificially introduced, it is suggested that areas adjacent to, but not contiguous with, *O. fuciflora* colonies would be priority candidates for such a regime. It is suggested that amongst candidate areas those dominated by *B. pinnatum* grassland should be targeted.

6.7 Wider implications of this research

6.7.1 This investigation has focused on *O. fuciflora* at Wye NNR. Conclusions have been drawn about aspects of its autecology and management at the site. These conclusions do however have wider implications for the management of the species in Britain, and perhaps for the management of chalk grasslands.

6.7.2 The other persistent localities for *O. fuciflora* are also on the North Downs of Kent, in very similar situations, geographically close to Wye NNR. Some of these localities are subject to grazing, whilst others are small, isolated and discrete making grazing difficult, if not impossible. Many historical locations for the species fall into the later category and grazing ceased a number of decades ago. The evidence provided by this investigation showed that for *O. fuciflora* to thrive nutrient removal and low level disturbance are critical. The species almost appears to depend upon colonization of early seral phases of chalk grassland development. The wider conservation of the species at extant sites is likely to depend on the recreation or maintenance of these habitat conditions. Grazing can clearly play an important part in achieving an environment suitable to sustain populations of *O. fuciflora*. Alternatively, mechanical scrub clearance and mowing may be a practical option when stock are not available. In places where these management tools are not practical conservationists may need to consider more radical alternatives such as shallow rotivation.

6.7.3 What can we learn about chalk grassland management from this investigation? It can be argued that British conservation is very much about preservation, placing value on certain habitats and species and seeking to maintain them in a static state. *O. fuciflora* is a valued species, but this study shows that far from benefiting from a static seral state such preservation could lead to its decline, if not extinction.

6.7.4 *O. fuciflora* has been shown to have preferences for disturbed places of low fertility. It has associations with species that exhibit similar preferences. The approaches employed to manage chalk grassland at the end of the twentieth century tend to maintain constant and relatively even sward cover over areas of land for prolonged periods. The evidence here suggests that a more destructive approach to chalk grassland management would benefit *O. fuciflora* and associated species. In essence dynamism should be re-introduced to chalk grassland systems. As part of the management of chalk grassland the conservation community should consider deliberate disturbance. Whilst this may initially seem to be a radical approach to chalk grassland management it can be argued that it is merely replicating the chalk grassland habitat that would have developed in the canopy gaps left by storms in the days of the 'wild woods'.

6.7.5 We should make clear that I am not advocating the mass destruction of calcareous grasslands, rather the introduction of areas of localized disturbance within sites subject to traditional grazing management. Not only would such an approach benefit plants but the structural and micro-climate variation created by disturbed areas may be beneficial to other organisms, such as invertebrates, leading to an overall increase in the biodiversity of the grassland habitat.

6.8 Discussion of methods

6.8.1 This investigation yielded a considerable amount of information about *O. fuciflora* that was previously unknown or unproven. Yet it also raised a number of questions about the autecology of the species and occasionally the methods were too imprecise to enable definite conclusions to be drawn from the data.

6.8.2 The methods employed during this investigation (see section 4) were to a great extent standard methods used in other similar studies, for instance Hutchings [1989] and Wells and Cox [1991]. Indeed Hutchings [1989], whilst recognizing the time consuming and laborious nature of census techniques, expounds their virtue as the most appropriate non-destructive means of gathering population data for plants in the field. However this is not to say that with some additional effort the methods employed in this investigation could not be improved.

6.8.3 With some additional effort the census data could be improved to provide a more complete picture of *O. fuciflora* population behaviour. At present census data is collected during two periods in a year and amalgamated into a single annualized view. In doing this data about in-year changes are lost. A standardized pro-forma would enable such detail to be retained. To the same end recording the state of individuals later in the year may yield valuable information, for example the number of capsules formed. Conducting a late census in October, just after rosettes emerge would provide valuable data about Winter changes to the population, perhaps revealing a very different dynamic controlling population structure. Though locating these minute rosettes is time consuming so such an approach should perhaps be restricted to 2 or 3 of the smaller colonies.

6.8.4 The other method employed in the investigation was the use of quadrats for collection of phytosociological and ecological variable data. Whilst a large data set was collected it may be considered that the methods employed did not supply sufficiently detailed measures of the variables to determine any trends between ecologically similar samples. In retrospect it was concluded that more detailed measurements of certain variables may have provided results from which trends could have perhaps been determined. For example, the measurement of species abundance using a Domin score essentially categorizes species into abundance groups. It was considered that the use of point quadrats may have provided sufficient detail about species abundance within samples to enable dissimilarity of samples and association of species to be more clearly indicated by the classification and ordination methods used to analyse the data. The range of variables measured was deliberately limited to those that might be manipulated by management. In retrospect the measure of bare ground would also have been improved by the use of point quadrats. The measurement of a range of non-manipulable variables, for example aspect, gradient and exchangeable ions within soils, may also have enabled trends, patterns and attributes of *O. fuciflora* to have been determined.

6.8.5 It must be considered though that one of the aims of the investigation was to propose appropriate management of *O. fuciflora*. Whilst more detailed measures may have yielded more specific and subtle information about the ecological requirements of the species such requirements may well have proved beyond the practical scope of conservation management. For instance, if more detailed results had shown that a mean vegetation height of 3.5cm was critical in determining the survival and establishment of *O. fuciflora*, one must then question the practicability of ensuring that vegetation could be maintained at that height by conservation management techniques.

6.8.6 It was concluded therefore that the methodology was appropriate to the aims of the investigation bearing in mind the limited resources of field work and sample analysis.

6.9 Suggestions for further research

6.9.1 As previously stated this investigation raises a number of questions about *O. fuciflora*, and to a lesser degree orchids in general. As previously stated orchids are an advantageous political and publicity tool for nature conservationists. Many are also legally protected or the focus of conservation conventions eg Habitats Directive (92/43/EEC) and UK Biodiversity Action Plan, which enshrine duties to maintain or enhance populations. Equally, many orchid species remain an enigma to the ecologist, and as such it is difficult to propose appropriate management. This investigation suggested a more appropriate regime for *O. fuciflora* based on improved, but still incomplete, ecological knowledge of the species. This regime remains untested. In light of these factors suggestions for further research of *O. fuciflora* were considered to fall into two broad categories;

a. Research with the primary aim of enhancing knowledge about the ecology of the species;

b. research with the primary aim of testing the appropriateness of the management proposals.

Ecological research of *O. fuciflora*

6.9.2 First a pedological study to examine the relationship, if any, between *O. fuciflora* occurrence and exchangeable ions within the soil. Accompanying this work should be measurement of soil compaction and structure in order to substantiate or otherwise the phytosociological conclusions drawn during this study of the importance of soil disturbance.

6.9.3 Second research examining climatological links to *O. fuciflora* performance should be undertaken in order to test the conclusion regarding thermophilic preference of the species and other linkages. This could be undertaken at a detailed level through measurement of soil temperature over a prolonged period. Alternatively, or additionally, census data could be tested for correspondence with meteorological data, such as rainfall, temperature minima and maxima, from the nearest available source.

6.9.4 Third, a study of plant performance in relation to size might be undertaken using an approach similar to that of Wells and Cox [1989]. Such a study, combined with census data would clarify the relationship of vigour and chronological age to the transitional behaviour of *O. fuciflora*.

6.9.5 Fourth, an observational study and taxonomic determination of the pollen beetles seen exploiting the flower may shed light on the pollination performance and invertebrate relationships of *O. fuciflora*.

6.9.6 Finally regarding pure ecological research, it is suggested that the census of *O. fuciflora* be continued to extend the data set. Though, as suggested in section 6.7, the method should be modified to take account of year-in-year changes within the population using multiple recording events. Given the increased effort required for this approach the number of colonies being studied should be reduced, but to no fewer than two.

Research for management of *O. fuciflora*

6.9.7 Modifications to the existing management regime have been proposed. The appropriateness of these remains to be tested. It is suggested that two experimental management studies be established.

6.9.8 First a differential study maintaining the existing regime on three of the colonies and imposing the modified regime on the remainder. Data on the phytosociological composition and orchid population and behavioural responses should be systematically collected.

6.9.9 Finally, experimental disturbance plots should be established. A range of plots might be tried with varied degrees of disturbance. Data on vegetative colonization should be collected. Such a study will give information of variable quality without the ability to control conditions with laboratory precision. However it can be argued that such an experiment is representative management conditions and as such would yield applied information for the enhancement of *O. fuciflora* populations.

7. Conclusion

7.1 This investigation focused on a population of Late Spider orchids growing at Wye NNR in Kent. This population constitutes over 50% of the UK population. This investigation set out with the following aims:

- to add to the autecological knowledge base of the species;
- to determine something of the 'special requirement' of *Ophrys fuciflora*;
- to describe the most appropriate management regime within the physical, practical and financial constraints of the site.

In so far as the study went it was successful in meeting these aims.

7.2 In respect of the autecological knowledge of the species it was concluded that *O. fuciflora*;

- is perennial and not monocarpic;
- produces over-wintering rosettes;
- has a limited below ground dormancy life of two years once the aerial life stage has started;
- has a long half-life of 12.52 years;
- aerial plants demonstrate Type II survivorship, though Type III may be probable in subterranean life stages and should be considered;
- it does not readily reproduce vegetatively in the UK;
- at Wye NNR the population has steadily increased but flowering and vegetative performance fluctuate significantly for unknown reasons, though it is not in response to reproductive resource investment;
- flowering plant mortality and reproduction are the key factors influencing long-term population levels;
- mortality rates are low (approximately 5%).

7.3 In respect of the 'special requirement' of *O. fuciflora* in the UK a number of conclusions can be drawn from this study:

- *O. fuciflora* exhibits a preference for habitats with oligothrophic free draining soils;
- *O. fuciflora* exhibits a preference for areas with moderate levels of soil disturbance;

- the species exhibits a thermophilic preference for warm Winter soils within the UK;

- the species exhibits a preference for a short broken grass sward within the chalk grassland habitat.

7.4 Extrapolation of the study results indicated that *O. fuciflora* is a stress tolerant species. It exhibits a number of characteristics that may lead one to conclude that it can and should be considered as an opportunistic or adventive species. Though one may also conclude that this part of its character is somewhat suppressed by being at the northern extreme of its distributional range in the UK.

7.5 Using this additional information about the autecology of the species the management practices at Wye NNR were reviewed. Two proposals were put forward. First modification of the existing regime for extant colonies primarily through alteration of the grazing period and intensity of grazing. Second the introduction of a mechanical disturbance regime with grazing to establish new colonies or enhance extant ones.

7.6 Finally whilst this study has added to the autecological knowledge of the late spider orchid several questions still remain to be answered. This study should improve our ability to conserve *O. fuciflora* ensuring that it remains a feature of the biodiversity of the UK. Further information may help us manage the species yet better and allow its continued existence if the environment changes significantly as predicted by many climate scientists.

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Appendix A Colony census data

Colony Name	Plant ID	Plant Marker	Post No	Post No	Coordinate 1	Coordinate 2	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
One	1	GN1	0	1	157	296					2	2	2	2	1	2	2	2
One	2	GN2	0	1	177	250					2	1	2	0	1	0	1	1
One	3	GN3	0	1	215	100	2	1	0	1	2	2	2	0	0	2	0	0
One	4	GN4	0	1	260	185					2	2	2	2	2	1	2	2
One	5	GN5	0	1	248	225					2	1	2	2	1	2	0	2
One	6	GN6	0	1	250	239								2	0	0	0	0
One	7	GN7	0	1	395	336						2	2	2	2	2	1	2
One	8	GN8	0	1	397	368							2	0	1	1	1	0
One	9	GN9	0	1	488	453									1	0	1	0
One	10	GN10	0	1	-149	-97								2	1	1	1	2
One	11	GN11	0	1	-150	-172									1	2	2	2
One	12	GN12	1	2	-196	-209						2	1	2	2	1	1	2
One	13	GN13	1	2	-368	-367				1	0	1	2	2	1	2	1	2
One	14	GN14	1	2	-460	-453						2	1	2	0	0	0	0
One	15	GN15	1	2	122	165					2	2	2	2	1	2	1	2
One	16	GN16	1	2	124	165				1	0	1	2	0	1	1	2	1
One	17	GN17	1	2	156	212	2	1	0	0	0	0	0	0	0	0	0	0
One	18	GN18	1	2	195	186									2	2	1	2
One	19	GN19	1	2	221	244						2	2	2	1	2	2	2
One	20	GN20	1	2	222	280								2	2	1	1	2
One	21	GN21	1	2	493	505						2	2	2	2	2	2	2
One	22	GN22	2	3	161	88	2	1	2	1	2	2	2	2	1	0	1	0
One	23	GN23	2	3	202	58	2	1	2	1	2	2	0	2	2	2	2	1
One	24	GN24	2	3	200	118	2	1	1	1	2	2	2	1	2	1	2	2

Colony Name	Plant ID	Plant Marker	Post No	Post No	Coordinate 1	Coordinate 2	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
One	25	GN25	2	3	195	153					2	0	2	0	0	0	0	0
One	26	GN26	2	3	203	170						1	2	2	1	0	0	0
One	27	GN27	2	3	168	207				1	2	0	2	2	2	1	1	0
One	28	GN28	2	3	204	204									1	2	1	1
One	29	GN29	2	3	215	221							2	2	1	1	2	2
One	30	GN30	2	3	247	193									1	1	2	1
One	31	GN31	2	3	246	193					2	2	2	2	1	0	0	0
One	32	GN32	2	3	266	199	2	2	2	1	0	2	2	2	1	2	2	1
One	33	GN33	2	3	285	206							2	2	1	2	1	2
One	34	GN34	2	3	260	228								2	1	0	2	0
One	35	GN35	2	3	283	268	2	1	0	0	0	0	2	0	1	0	2	0
One	36	GN36	2	3	288	262	2	1	1	0	0	0	0	0	1	1	1	1
One	37	GN37	2	3	244	250	1	0	1	2	0	2	2	0	1	2	2	2
One	38	GN38	2	3	253	263									1	1	2	1
One	39	GN39	2	3	200	265	2	1	0	0	0	0	0	0	0	0	0	0
One	40	GN40	2	3	244	290					1	2	2	0	2	1	2	2
One	41	GN41	2	3	282	304	2	1	1	1	0	1	2	2	1	2	2	1
One	42	GN42	2	3	302	309						1	2	2	2	2	1	2
One	43	GN43	2	3	316	312					2	1	2	0	0	1	2	0
One	44	GN44	2	3	339	304			2	2	2	2	1	2	1	1	0	2
One	45	GN45	2	3	363	351	2	1	1	1	0	1	2	2	2	2	2	2
One	46	GN46	2	3	371	375							2	2	1	2	1	2
One	47	GN47	2	3	392	400						1	1	1	1	0	0	1
One	48	GN48	2	3	437	412							2	2	1	2	1	2
One	49	GN49	2	3	483	498					2	1	2	2	1	1	2	2
One	50	GN50	2	3	523	550								2	1	2	1	2
One	51	WT30	0	1	231	149											1	2

Colony Name	Plant ID	Plant Marker	Post No	Post No	Coordinate 1	Coordinate 2	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
One	52	WH31	0	1	495	513											1	1
One	53	WH32	0	1	489	519											2	2
One	54	WH33	0	1	765	740										1	2	2
One	55	WH34	0	1	430	542										2	2	2
One	56	WH35	0	1	-206	-138											2	2
One	57	WH36	0	1	-392	-425											2	2
One	58	WH28	1	2	241	228											1	2
One	59	WH29	1	2	380	318											1	1
One	60	WH1	3	4	111	111							2	2	2	0	0	0
One	61	WH2	3	4	196	217						2	1	1	1	1	1	1
One	62	WH3	3	4	218	245				1	2	2	2	1	1	1	1	1
One	63	WH4	3	4	268	255	2	1	0	0	0	2	2	0	0	0	0	0
One	64	WH5	3	4	237	292	2	1	1	1	0	1	2	1	2	0	0	0
One	65	WH6	3	4	296	294						1	2	2	1	1	1	1
One	66	WH7	3	4	330	334									1	0	0	0
One	67	WH8	3	4	363	335	2	0	2	2	0	0	2	2	2	2	0	0
One	68	WH9	3	4	345	387					2	1			1	2	1	2
One	69	WH10	3	4	383	394							2	1	2	2	1	2
One	70	WH11	3	4	398	438					2	1	2	2	1	0	0	0
One	71	WH12	3	4	488	513								2	1	0	0	0
One	72	WH13	3	4	314	184									1	1	1	1
One	73	WH14	3	4	385	250									1	1	1	2
One	74	WH15	3	4	358	359									1	2	2	0
One	75	WH16	3	4	359	257										1	2	2
One	76	WH17	3	4	331	305										1	2	2
One	77	WH18	3	4	484	335										2	2	2
One	78	WH19	3	4	467	337										1	1	2

Colony Name	Plant ID	Plant Marker	Post No	Post No	Coordinate 1	Coordinate 2	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
One	79	WH20	3	4	430	306										1	2	2
One	80	WH21	3	4	442	297										2	1	1
One	81	WH22	3	4	441	281											2	2
One	82	WH23	3	4	201	94											1	2
One	83	WH24	3	4	386	269											2	2
One	84	WH25	3	4	413	339											2	2
One	85	WH26	3	4	373	288											2	2
One	86	WH27	3	4	338	323											1	1
One	87	WH37	2	3	200	141											2	2
One	88	WH38	0	1	207	115												2
One	89	WH39	1	2	156	235												2
One	90	WH40	1	2	154	233												2
One	91	WH41	1	2	130	126												2
One	92	WH42	1	2	325	258												2
One	93	WH43	2	3	102	190												2
One	94	WH44	2	3	210	126												1
One	95	WH45	2	3	284	233												2
One	96	WH46	3	4	160	210												2
One	97	WH47	4	5	257	286												2
One	98	WH48	4	5	311	376												2
One	99	WH49	4	5	271	268												2
One	100	WH50	4	5	310	306												2
One	101	BL1	0	1	335	327												2
One	102	BL19	4	5	195	245												2
One	103	BL26	4	5	287	206												2
One	104	BL32	4	5	404	390												2
One	105	BL47	1	2	-335	-290												2

Colony Name	Plant ID	Plant Marker	Post No	Post No	Coordinate 1	Coordinate 2	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
One	106	BL49	2	3	171	135												2
One(a)	107	WH	JD1	JD2	-220	-385					2	2	2	0	0	0	0	0
One(a)	108	WH	JD1	JD2	-685	-445							2	0	0	0	0	0
One(a)	109	MV31	1	2	-225	-232							1	2	0	0	0	0
One(a)	110	MV32	2	3	-184	-144								2	1	1	2	2
One(a)	111	MV33	2	3	-241	-123								2	1	2	2	2
One(a)	112	MV34	2	3	-270	-281								2	1	2	1	2
One(a)	113	MV35	2	3	130	117								2	1	0	0	2
One(a)	114	MV42	2	3	120	243											2	2
One(a)	115	MV43	2	3	181	305											2	1
One(a)	116	MV36	3	4	-216	-169									1	2	1	2
One(a)	117	MV37	3	4	-393	-323					2	1	1	2	1	1	1	1
One(a)	118	MV41	3	4	-152	-140												2
One(a)	119	MV40	4	5	-315	-265					2	2	1	0	0	1	1	0
One(a)	120	MV38	6	7	-202	-141							1	2	1	2	2	2
One(a)	121	MV39	6	7	-198	-102							1	0	1	0	0	0
One(a)	122	MV44	1	2	175	91												2
One(a)	123	MV45	2	3	90	206												1
One(a)	124	MV46	2	3	155	149												2
One(a)	125	MV47	1	2	-237	-142												1
One(a)	126	MV48	1	2	-222	-130												2
One(a)	127	MV49	6	7	-61	-146												2
One(a)	128	MV50	3	4	-169	-70												2
One(a)	129	BL36	2	3														2
One(a)	130	BL42	2	3	-528	-466												2
One(a)	131	BL45	1	2	-395	-300												2
One(a)	132	BL49																2

Colony Name	Plant ID	Plant Marker	Post No	Post No	Coordinate 1	Coordinate 2	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
Two	133	MV1	0	1	122	81		2	2	2	0	0	1	2	1	0	0	0
Two	134	MV2	0	1	405	327	2	0	1	0	0	0	0	0	0	0	0	0
Two	135	MV3	1	2	402	337		2	1	2	0	0	0	0	0	0	0	0
Two	136	MV4	1	2	709	732							2	0	2	1	0	0
Two	137	MV5	2	3	269	338				1	1	1	2	0	1	1	1	1
Two	138	MV6	2	3	347	289					2	2	1	0	1	0	0	0
Two	139	MV7	2	3	346	286					2	2	1	0	0	0	0	0
Two	140	MV8	2	3	396	374	2	2	1	2	2	2	2	1	2	1	1	0
Two	141	MV9	2	3	398	374			1	1	1	1	1	1	1	1	1	0
Two	142	MV10	2	3	424	405	2	0	0	1	1	1	2	2	1	1	1	0
Two	143	MV11	2	3	465	468				2	2	0	0	0	0	0	0	0
Two	144	MV12	2	3	514	487						2	1	1	1	0	1	1
Two	145	MV13	2	3	217	285	2	0	0	2	0	0	0	0	0	0	0	0
Two	146	MV14	2	3	428	368		2	2	2	1	0	1	2	2	1	1	1
Two	147	MV15	3	4	258	143	2	1	1	2	2	2	0	1	0	0	0	0
Two	148	MV16	3	4	243	212		2	1	0	0	0	0	0	0	0	0	0
Two	149	MV17	3	4	266	255	2	2	1	2	2	2	2	1	1	1	1	1
Two	150	MV18	3	4	265	257			1	1	1	1	0	1	2	1	2	2
Two	151	MV19	3	4	275	236	bee orchid											
Two	152	MV20	3	4	303	309		2	2	0	0	0	2	0	0	0	0	1
Two	153	MV	3	4	362	402		2	2	2	2	2	2	1	0	0	0	0
Two	154	MV21	3	4	399	403	1	0	0	2	1	2	2	2	1	1	1	1
Two	155	MV22	3	4	472	471						1	1	0	2	1	2	2
Two	156	MV23	3	4	470	435									2	1	1	1
Two	157	MV24	3	4	537	520	2	2	2	1	3	1	2	2	0	0	0	0
Two	158	MV27	3	4	650	667					2	0	2	1	0	0	1	0

Colony Name	Plant ID	Plant Marker	Post No	Post No	Coordinate 1	Coordinate 2	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
Two	159	MV28	3	4	862	830				2	0	1	2	1	1	1	1	0
Two	160	MV30	3	4	130	175				1	1	0	2	1	0	0	0	0
Two	161	GR10	3	4	222	116												2
Three	162	BK31	0	1	366	311						2	0	0	0	2	1	0
Three	163	BK32	0	1	650	666		2	2	2	2	1	0	0	0	2	2	2
Three	164	BK40	0	1	266	314										1	2	1
Three	165	BK21	1	2	216	243	2	1	2	2	2	2	1	2	2	0	2	2
Three	166	BK22	1	2	217	245						2	1	0	2	1	2	2
Three	167	BK23	1	2	254	266		2	2	2	2	2	1	0	1	1	1	1
Three	168	BK24	1	2	353	325			1	2	1	1	1	0	1	0	0	0
Three	169	BK25	1	2	347	323				1	1	1	2	1	1	0	1	1
Three	170	BK26	1	2	349	323		2	0	2	2	1	2	1	1	1	1	1
Three	171	BK27	1	2	364	326						1	1	0	1	1	1	0
Three	172	BK29	1	2	252	283						1	0	1	2	0	0	0
Three	173	BK35	1	2	245	312		1	1	1	2	2	0	0	0	2	1	1
Three	174	BK36	1	2	268	252		1	1	0	0	1	0	0	1	1	0	0
Three	175	BK37	1	2	309	270										1	1	0
Three	176	BK38	1	2	251	282										2	2	0
Three	177	3	1	2	281	256		2	1	2	2	2	0	0	0	0	0	1
Three	178	BL3	1	2	326	325						2	0	1	0	0	0	0
Three	179	BL7	1	2	361	316		2	1	0	2	1	1	0	0	0	0	0
Three	180	BL9	1	2	248	262	2	2	1	2	2	0	1	0	0	0	0	2
Three	181	BL11	1	2	248	257						1	2	0	0	0	0	0
Three	182	BL12	1	2	235	305		1	1	2	2	1	0	0	0	0	0	2
Three	183	BL15	1	2	307	291						2	0	0	0	0	0	0
Three	184	BL17	1	2	256	249		1	1	0	0	0	0	0	0	0	0	0
Three	185	BK28	2	3	277	342						1	2	1	1	0	1	0

Colony Name	Plant ID	Plant Marker	Post No	Post No	Coordinate 1	Coordinate 2	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
Three	186	BK30	2	3	323	307			1	1	2	2	0	1	2	1	2	1
Three	187	BK39	2	3	368	443										1	0	0
Three	188	BK41	2	3	448	447				1	0	2	0	0	0	0	2	0
Three	189	BK42	2	3	455	481											2	2
Three	190	BK33	3	4	374	403		2	1	2	2	2	2	1	0	1	1	0
Three	191	BK34	3	4	672	642						2	0	0	0	0	0	0
Three	192	BL13	3	4	497	508												2
Three	193	BL18	2	3	383	403												1
Three	194	BL22	1	2	585	578												2
Three	195	BL27	3	4	825	837												2
Three	196	BL28	1	2	268	323												2
Three	197	BL35	1	2	603	610												2
Three	198	BL38	1	2	505	480												2
Three	199	BL31	3	4	564	575												2
Three	200	RD38	1	2														2
Three	201	BL45	3	4	200	281												2
Four	202	O1	0	1	93	109					2	1	2	2	1	1	1	1
Four	203	O2	0	1	93	110					2	2	2	2	1	2	1	0
Four	204	O3	0	1	232	245					1	0	1	1	1	1	2	1
Four	205	O4	0	1	327	455	2	0	0	2	0	0	2	0	1	0	0	1
Four	206	O5	0	1	-185	-153				2	1	1	2	2	0	0	0	0
Four	207	O6	0	1	-190	-320						1	0	0	0	0	0	0
Four	208	O7	1	2	164	158	2	2	0	1	2	2	2	1	0	0	0	0
Four	209	O8	1	2	233	138							1	2	0	0	0	0
Four	210	O9	1	2	325	342							2	2	2	2	2	2
Four	211	O10	1	2	367	379							2	0	1	1	0	0
Four	212	O11	1	2	322	383	2	1	0	1	0	0	1	1	0	1	0	0

Colony Name	Plant ID	Plant Marker	Post No	Post No	Coordinate 1	Coordinate 2	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
Four	213	O12	1	2	297	248									1	2	1	1
Four	214	O13	1	2	335	286	2	0	0	1	2	2	1	2	1	1	0	1
Four	215	O14	1	2	330	297								2	1	0	0	0
Four	216	O15	1	2	343	315						1	2	2	1	0	0	0
Four	217	O16	1	2	343	317								2	1	0	0	1
Four	218	O17	1	2	341	318						1	1	2	1	1	1	1
Four	219	O18	1	2	354	336									2	1	1	1
Four	220	O19	1	2	388	351									2	0	0	0
Four	221	O20	1	2	408	384					2	2	2	0	2	1	2	1
Four	222	O21	1	2	390	382							2	2	1	1	1	1
Four	223	O34	1	2	140	109										2	1	1
Four	224	O36	1	2	323	342											2	2
Four	225	O22	2	3	178	97	2	1	2	2	2	2	2	1	0	0	0	0
Four	226	O23	2	3	122	128	2	0	0	2	1	2	0	0	0	0	0	0
Four	227	O24	2	3	147	205	2	1	2	1	0	0	2	2	0	1	1	1
Four	228	O25	2	3	320	293						2	0	1	0	1	1	2
Four	229	O26	2	3	295	319					1	2	2	2	2	1	0	0
Four	230	O27	2	3	305	342				1	0	0	2	2	0	0	0	0
Four	231	O28	2	3	374	393								2	2	0	0	2
Four	232	O29	2	3	393	440							2	0	1	0	1	0
Four	233	O30	2	3	135	112					1	0	0	2	1	2	2	2
Four	234	O31	3	4	10	194						1	1	2	2	1	2	0
Four	235	O32	3	4	198	243							2	0	1	2	1	0
Four	236	O33	3	4	337	408										1	1	2
Four	237	O35	3	4	355	393											1	1
Four	238	O37	1	2	324	341												2
Four	239	O38	3	4	118	225												2

Colony Name	Plant ID	Plant Marker	Post No	Post No	Coordinate 1	Coordinate 2	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
Four	240	O39	0	1	-220	-192												2
Five	241	BK1	0	1	318	336				1	1	1	1	0	2	2	1	2
Five	242	BK2	0	1	335	351					2	0	0	0	0	0	0	0
Five	243	BK3	0	1	379	492								2	2	1	1	0
Five	244	BK4	0	1	392	388					1	1	2	1	1	1	1	2
Five	245	BK5	0	1	359	308	2	0	0	2	2	2	1	2	1	2	1	2
Five	246	BK6	0	1	470	406								2	2	1	1	2
Five	247	BK7	0	1	450	481									2	2	0	1
Five	248	BK45	0	1	252	341											1	1
Five	249	BK46	0	1	250	339											1	0
Five	250	BK49	0	1	371	520										1	1	2
Five	251	BK50	0	1	358	548										2	1	2
Five	252	BK8	1	2	203	265					1	1	2	2	2	2	1	2
Five	253	BK9	1	2	199	238			1	2	1	1	2	2	1	2	1	2
Five	254	BK10	1	2	236	288					1	0	1	0	0	0	0	0
Five	255	BK11	1	2	260	270		2	2	1	0	0	0	2	0	0	0	0
Five	256	BK12	1	2	220	147				1	1	0	1	2	1	1	1	1
Five	257	BK18	1	2	268	239										1	2	2
Five	258	BK19	1	2	450	480										2	2	2
Five	259	BK20	1	2	459	496										1	2	2
Five	260	BK47	1	2	316	258										1	1	2
Five	261	BK48	1	2	485	482										1	1	2
Five	262	BK13	2	3	286	360							2	1	2	2	2	2
Five	263	BK14	2	3	293	297				1	1	0	2	1	2	1	0	1
Five	264	BK15	3	4	470	325					2	2	1	2	2	0	1	2
Five	265	BK16	3	4	476	332							2	1	2	1	2	2
Five	266	BK17	3	4	270	169									2	0	0	0

Colony Name	Plant ID	Plant Marker	Post No	Post No	Coordinate 1	Coordinate 2	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
Five	267	BL3	2	3	325	327												2
Five	268	BL7	0	1	387	438												1
Five	269	BL42	1	2	398	375												2
Five	270	BL48	1	2	352	290												2
Five	271	BL49	2	3	319	367												2