ENGLISH NATURE

No. 340

The effect of shade and weather on daffodils *Narcissus pseudonarcissus* in West Dean Woods, West Sussex

Brian Hopkins

Lowlands Team

English Nature Research Reports

English Nature Research Reports

Number 340

The effect of shade and weather on daffodils *Narcissus pseudonarcissus* in West Dean Woods, West Sussex

Brian Hopkins

7 Highland Road
Chichester
West Sussex PO19 4QX

ISSN 0967-876X

Contents

Acknowledgements

I thank the Sussex Wildlife Trust and the West Dean Estate for permission and encouragement to carry out this work; Richard Williamson for marking and swiping the plots; the members of the Chichester Natural History Society who did the recording; Peter Collyer of the Institute of Horticultural Research, Littlehampton; the Met Office Archives and Stewart Palzeaird of Hazlewood VHB for weather data; the librarian, Institute of Horticultural Research for use of the library; and John Ferlon, Ian J.Odin, Dr Alan R. Rees and Richard Williamson for discussions.

Preface

A great deal of commitment is needed to maintain the recording necessary to study long-term changes in British woodland. While there has been quite a lot of work on tree and shrub dynamics since the 1940s, it is only in the last ten years that results from research on ground flora changes have become common. The study reported here is particularly unusual in that it involves experimental treatments directed at a quite specific management aim: maintaining the local daffodil populations.

Even when you have the results, however, they may not lend themselves to publication in the usual journals. English Nature was, therefore, pleased to provide the opportunity to publish the full account of Brian Hopkins' research at West Dean, to make it available to other conservation managers. We would, similarly, welcome data from other such studies where publication will help ensure that the results get used and not lost.

Keith Kirby

Summary

This Research Report describes a 12-year experiment on the effect of shade on wild daffodils *Narcissus pseudonarcissus* to determine the best management for their conservation in a woodland nature reserve.

Under dense woody-plant shade there was a slight increase in the density of mature bulbs during the experimental period. Daffodils increased considerably under light woody-plant shade with and without annual swiping in winter to remove the undergrowth. In the open, they also increased considerably with swiping, but without swiping the increase was only just statistically-significant due to dense bracken fern.

Compared to the effect of shade, other factors were of less importance in affecting the density of mature bulbs, although daffodil density did increase following years with few spring and many autumn frosts.

An average of 8-9% of mature daffodil bulbs produced flowers each year except under dense woody-plant shade where only 5% did.

The yearly means of the fraction of mature bulbs flowering varied from 1.4% to 16%. Flowering appeared to be a drain on a plant's resources so that the fraction flowering tended to alternate between high and low values in successive years. It also increased in the year following a warm dry spring. These variables were used to devise multiple regressions to forecast the amount of flowering which could be useful for informing potential visitors.

Germination and establishment were greatest under light total shade and following wet autumns and cold winters; they were least in the open.

Following the 12-year experiment, the management of the daffodil area of the reserve was changed to annual swiping during the summer. Monitoring the plots continued and some of them appeared to be approaching a sustainable maximum density of daffodils.

1. Introduction

West Dean Woods was created a nature reserve of what is now the Sussex Wildlife Trust in 1975, and was notified as an SSSI in 1980. One of the four main reasons for its reservation was the colony of wild daffodils *Narcissus pseudonarcissus.* (Nomenclature in this paper follows Stace (1991).)

The creation of this new, coppice-woodland, nature reserve posed the question of what would be the optimum shade treatment for the conservation of daffodil colony and the main section of this Research Report describes an experiment to determine the effects of shade - of both woody plants and of undergrowth - on daffodil density. The effects of weather were also investigated.

The flowering and sexual reproduction of these daffodils were studied in the same experiment. These aspects are relevant to the conservation of the daffodils both biologically and because, for many years, their flowering had attracted many human visitors.

After 12 years the optimum shade treatment for conserving the daffodils was clear and was put into practice. The experimental treatments were discontinued, but monitoring of the plots continued.

To avoid considerable repetition in this report, the word 'significant' is only used to mean 'statistically significant'.

2. The site

The experiment took place in West Dean Woods Nature Reserve on the South Downs in West Sussex, where the Upper Chalk rock is covered by up to 1 m of non-calcareous deposits. The area had been farmed but, secondary woodland developed during the Mediaeval period (Tittensor 1991) and woodland, coppice or shrub cover have been continuous since at least 1604 AD (Stewart 1976). Consequently, the wood is species-rich for many large taxa of plants, animals and fungi. Much of the reserve had been managed as coppice-with-standards, although this had been neglected sometime before 1975. On reservation, both coppicing and the felling and replanting of oak standards were re-established over most of the reserve. Most standards were oak *Quercus robur*, and most coppice was hazel *Corylus avellana* with some sweet chestnut *Castanea sativa*. According to growth-ring counts of felled trees, most of the mature oaks were planted *c*1870.

This study concerns the 1.65-ha wild daffodil colony at an altitude of 140-160 m above sea level on an ESE aspect in the north-western corner of the reserve, in Compartment 123 (National Grid reference SU 847159). Daffodils also occur in the adjacent compartments and, at very low densities, in a few other compartments in the northern part of the reserve. In Compartment 123, the standards and shrubs were older and more widely spaced than in most of the reserve. It appeared to have been less heavily coppiced, and some parts were probably parkland in the past. Coppicing and the felling and replanting of oak standards were not re-established here. The dead fronds of bracken *Pteridium aquilinum* and the tangles of bramble *Rubus fruticosus* agg. have been swiped using a tractor and a 'Bushhog' swipe (an approximately 1.4-m diameter rotatory blade at a height of 40-50 cm) during a dry period (when there was little danger of compressing the soil or the bulbs) each winter (except 1987-88) to allow more light to reach the daffodils.

The mean annual rainfall in West Dean village (4 km SSE and 110 m lower) is 971 mm; in the reserve it is about 1000 mm (Potts & Browne 1983). The nearest, most comparable, climatic data are for Rustington, near Littlehampton (24 km SE of West Dean Woods; 3 m altitude). On 27 September 1995, the site of this weather station was moved about 1 km and became known as Littlehampton (23 km SE; 2 m altitude). Allowing for lapse-rate cooling, these give a mean maximum temperature for the hottest month (normally July or August) of about 19 °C and a mean minimum temperature for the coldest month (normally January or February) of about 0 °C.

3. The plant

Narcissus pseudonarcissus is native in England, but has also been introduced by transplanting. It is a rather local, but gregarious, bulbous geophyte of lowland, damp woods and pastures. After flowering, two buds are formed which may eventually separate from the mother-bulb to form daughter-bulbs. This is its main method of increase.

Daffodils are prevernal species of English woodlands. The leaves emerge in January or February and increase slowly over four to six weeks to a maximum area which lasts for a very short time before senescence by May or June (Rees 1972). During the summer and autumn the plant has no aerial organs and appears dormant.

Little is known about wild daffodils apart from the review of Caldwell & Wallace (1955) and the work of Barkham (1980a, b, 1992b) and Barkham & Hance (1982) in Brigsteer Wood, Cumbria. The large amount of research on cultivated daffodils summarized in Rees (1972) was mainly designed to help the bulb trade, but it has yielded much basic information which is relevant to wild daffodils. Bulbs have to be above a certain size (which varies enormously between cultivars) in order to flower. The flowers are solitary and generally open in late March in southern England (Blanchard 1990). The flowers are self-fertile but a high proportion of capsules are seedless (Caldwell & Wallace 1955; Proctor & Yeo 1973; Barkham 1980a). Germination is low and variable and has a cold requirement, but the optimum temperatures are unknown (Rees 1972). During normal development the seeds are dormant for six months. Seedlings and young plants have a single leaf. Adult leaves are formed in the fourth year and, under ideal conditions, fifth-year plants have three leaves and a flower (Chan 1951-52). The long juvenile period is due to the slow increase in bulb weight.

4. Methods

4.1 Plots and treatments

In April 1977, five 30 x 20 m plots were selected to give three degrees of woody-plant shade: dense, light and open (virtually none). Two plots under both light shade and open conditions were chosen. One of each was swiped (as already described); the other was left un-swiped. Swiping was not possible under the dense shade as the closeness of the trees and shrubs prevented the use of a tractor. Care was taken to provide suitable differences in cover between the three shade categories and to make the paired plots as similar as possible. The daffodil colony occupied too small an area for the treatments to be replicated.

The total area containing the five plots was about 0.5 ha and had contained 18 standards. Each was large: >125 cm GBH and >1243 cm^2 trunk basal area. All were oak. The dense-shade plot had 0.5 woody plants (>2 cm dbh) m^{-2} - five times the density of each of the light-shade plots (0.1m^{-2}) and 17 times that of the open plots (0.03 m^{-2}) (Table 1). On the open plots all the trees and shrubs exceeded 20 cm GBH; under light shade just over one-third did so; and, on the dense-shade plot, only one-sixth. The main shrubs and small trees were ash *Fraxinus excelsior*, hazel *Corylus avellana*, birch *Betula pendula* and *B. pubescens*, and dogwood *Cornus sanguinea*. Most sycamore *Acer pseudoplatanus* were killed in 1979-80 in accordance with reserve management policy.

Table 1: Tree and shrub densities (in 1977); cover by bramble and bracken; and densities of mature daffodil bulbs (in 1979) at West Dean Woods

Plot	1	2	3	4	5
Shade treatment	dense	light	light	open	open
Swiped	no	yes	no	yes	no
Woody plants >2cm dbh (density per sq m)	0.49	0.1	0.1	0.02	0.04
Woody plants >20cm GBH (% of total)	17	38	34	100	100
Bramble cover	light	very sparse	sparse	sparse	light
Bracken cover	sparse	very sparse	sparse	light	dense
Daffodil density (per sq m)	98.9	77.2	76.5	10.4	6.1

The density of undergrowth of both bramble and bracken varied between the plots (Table 1) and bramble appears to have declined during the experiment probably due to the effects of fallow deer *Dama dama*. The great storm of October 1987 blew over a few trees on or near the plots and caused some increase in illumination to the northern edges of Plots 1, 2 and 3 due to the devastation of a beech *Fagus sylvatica* plantation immediately to the north of the reserve.

4.2 Numbers of daffodils

Following two years of observation and trials, the density of daffodils was determined between late March and late April each year from 1979 to 1987. By 1987 the trends on each plot were clear. However, to confirm these, the experiment was continued until 1991 but with density determinations in alternate years. For each assessment, quadrats (25 x 25 cm) were placed at 200 randomly-selected points on each plot. This process was repeated on each plot and in each year with a fresh randomization each time.

Following the completion of the experiment, the density in each plot continued to be monitored and all the figures which follow include the results for the years of monitoring after the completion of the experiment. These post-1991 results are discussed later.

In each quadrat, the number of daffodil individuals was recorded under four categories:

- 'seedlings': a single small leaf which was almost circular in transverse section;
- 'young': a single larger leaf which was flatter, with usually one flat and one convex side (Chan 1951-52);
- 'sterile': flat linear adult-type leaves, but with no flower; and
- 'flowering': flat linear adult-type leaves and a flower.

'Sterile' and 'flowering' plants were both termed 'mature'. Most of the recording was done by trained amateur volunteers under supervision.

There are four possible recording errors; all concern seedlings. First, difficulties in counting large numbers growing among dense brambles; normally, such quadrats were counted twice. Secondly, seedlings were not always easy to distinguish from young without excavation - which was not carried out. Thirdly, confusion between daffodil and bluebell *Hyacinthoides non-scripta* seedlings. Errors from all these sources were probably very small because volunteers in doubt sought advice before proceeding. Fourthly, in years when germination was late, seedlings could be missed in dense leaf litter; such occasional underestimates are the most likely errors.

4.3 Weather

The major weather factors affecting plants in British woodlands are temperature, precipitation and solar radiation. For a vernal plant, like the daffodil, they will probably mainly operate in the spring. However, it is known that low temperatures affect the flowering and germination of daffodils (Rees 1972). Consequently, the weather over the whole year was examined and five measures of temperature were employed.

The changes in density of all four plant categories were correlated with weather data for each of the fourteen calendar months from March of the year before recording to April of the year when the records were made. Seven variables were examined: mean maximum temperature; mean minimum temperature; mean temperature (average of the two previous variables); mean soil temperature at 10cm depth (most bulbs were near the surface); number of days (nights) of ground frost (recorded by a grass-minimum thermometer); total rainfall; and total hours of sunshine. All the correlation coefficients were calculated for the mean results of all five plots. When a factor showed significant correlations for two or more consecutive months, additional correlation coefficients were determined for the combined periods.

Owing to damaged instruments, there were no data for: maximum and mean temperatures in March and April 1978; soil temperature in September 1985; and sunshine for two days in April 1965. The sunshine data were replaced by those from Bognor Regis (19 km SSE of the site); the three months with missing temperature data were omitted from the analyses. The change of site in 1995 is most unlikely to affect these analyses.

5. Density of mature bulbs

5.1 Results

The initial (1979) densities were very similar on the three shaded plots (77-99 m^2); they were much less on the two open plots (6-10 m^2). During the 12-years, approximately linear increases in density occurred on all plots (Figures 1a to 1e) and regression lines were calculated for this period. The slopes of these regression lines of mean annual increase in density were all significantly different from zero (Table 2), with those on Plots 2, 3 (light shade) and 4 (open, swiped) having P values (for t tests) <0.001. The only significant differences among these rates were between Plot 2 (light shade, swiped), which had the highest rate of increase ($6m^2$ $year^{-1}$), and Plots 1, 4 and 5 (t values of 2.73-3.19 and P values of <0.02 or <0.01).

Table 2: Twelve-year means and increases in density of mature daffodils at West Dean Woods from 1979 to 1991

Plot	Woody-plant shade	Swiped	Mean density (per sq m)	Regression slope*	Density increase: Comparison with zero t	Density increase: Comparison with zero P	Density increase: Plot differences†	Proportional increase‡
1	dense	no	97.7	1.49	2.52	<0.02	a	1.53
2	light	yes	108.4	6.23	7.9	<0.001	a, b, c	5.9
3	light	no	97	2.94	4.35	<0.001		3.03
4	open	yes	27.2	1.93	3.51	<0.001	b	8.08
5	open	no	11.5	0.7	2.03	<0.05	c	6.25

* Increase per sq m per year.
† Plots with the same letter have significant differences in slope at P < 0.02 or < 0.01.
‡ Annual increase as a percentage of density.

Increases can also be considered in proportion to density, and the annual percentage increases (by compound interest) are shown in the last column of Table 2. These show the open plots (4 and 5) had values greater than 6%, whilst Plot 1 (dense shade) had the lowest increase of 1.5%. These values showed significant differences between all pairs of plots at P<0.001, except that between Plots 2 and 5 where P was < 0.01.

The significant correlations for the mean annual changes in density between 1979 and 1987 with the weather variables are presented in Table 3. There were 17 in two seasonal groups: positive with temperature in the previous spring; and negative with both temperature and rainfall, but positive with sunshine, in the late autumn.

Table 3: Significant (P <0.05) correlation coefficients (r) of annual changes in density of mature daffodils with weather factors at West Dean Woods during 1979-87

	Weather factors					
Months	**Temperature**				**Rain**	**Sun**
	Minimum	**Mean**	**Frost**	**Soil**		
April	0.743		-0.758			
Apr-May	0.904		-0.909			
May	0.799		-0.782			
October			0.813		-0.783	0.71
Oct-Nov	-0.833	-0.757	0.887	-0.778	-0.869	
November	-0.759	-0.762		-0.756		

Values for P < 0.01 in italics and underlined; there were none at P < 0.001.

5.2 Discussion

5.2.1 Aggregation

Daffodils can occur at very high densities. The plots with woody-plant shade averaged approximately 100 mature bulbs m^{-2} (Table 2) and counts equivalent to 500 bulbs m^{-2} were not uncommon within individual quadrats. Barkham (1980b) recorded similar densities.

The degree of aggregation was determined in both 1983 and 1995 by the variance/mean (V/m) method, and comparing the value of (V/m -1) with its standard error by a t test (Greig-Smith 1964). All the plots showed significant aggregation (P < 0.001). In both years there were significant differences (at P < 0.001) between all but one of the pairs of plots and the order of aggregation differed only slightly between the two years. The mean order was: Plot 5 (V/m = 15.1) > Plot 4 (14.9) > Plot 2 (8.8) > Plot 1 (5.7) > Plot 3 (5.6). This is similar to the order of their rates of percentage increase (Table 2) and probably indicates that the daffodils are more recent colonizers on the more open plots (4 and 5) in contrast with their more stable populations on the more wooded plots, particularly Plot 1.

5.2.2 Shade

Population increase may be measured either as density or in proportion to the population size (Table 2). Both measures show a considerable range. The highest increase in density (6m^{-2} $year^{-1}$) was on Plot 2 (light shade, swiped), followed by half that rate on Plot 3 (light shade, un-swiped), with Plot 5 (open, un-swiped) the lowest at 1 m^{-2} $year^{-1}$. Plot 5 had a dense undergrowth of partly-collapsed dead bracken fronds which overtopped many of the daffodil leaves. (New bracken fronds emerge and expand as the daffodil foliage senesces.) So, the dead bracken acted in a similar way to the dense trees and shrubs on Plot 1.

However, the two open plots are not really comparable with the others because of their very much lower densities. The highest proportional increases (6-8%) were in the open (Plots 4 and 5), with the least (1.5%) under dense shade (Plot 1). The high rates on Plots 4 and 5 are probably related to their recent colonization as suggested above.

As expected, woody-plant shade is very important for daffodils, but shade from the undergrowth also has a strong influence. This is clear from a comparison of the pairs of swiped and un-swiped plots (Table 2) where, in all cases, the swiped plots have the higher values. Thus, the plots with most total shade showed the least increases, whilst the greatest increases were on the swiped plots.

Research in Brigsteer Wood showed similar results, with a rapid increase in daffodil populations when the tree canopy was removed, so that their density increased slowly under coppice but they no more than persisted under continual shade (Barkham 1980a, b, 1992a, c; Barkham & Hance 1982). Brambles declined under almost all these treatments and, once this occurred, there was further daffodil increase.

Although light is the most obvious difference between the shade treatments it may not be the controlling factor. Shade also affects the temperature of the soil and just above the ground, and the shade plants exert root competition and affect soil-water availability - which Barkham (1980a, b) thought particularly important.

5.2.3 Weather

The annual changes in density were compared with seven weather variables for 14 months. This gives 98 correlations. By chance, one of these can be expected to be significant at $P = 0.01$ and five at $P = 0.05$. Except for the lack of autumn rainfall, all the significant correlations were related to temperature: positive in the spring and negative in the autumn. There were only 10 significant monthly correlations (Table 3). All were at $P < 0.05$ only. The only correlations at $P < 0.01$ were for two-month periods and (together with eight of the monthly correlations) strongly reinforce the idea that temperature is a key factor.

Spring is the growing season for daffodils and, clearly, it is the low temperatures which are restricting daffodil increase. In cultivation, daughter-bulb dry weight is correlated with soil temperature (Rees 1972). Autumn is part of the 'dormant' season when high temperatures would increase respiratory losses, and so decrease bulb weight, and a time when too much rain might cause bulb rot.

Barkham (1980b), found the main weather factor was summer sunshine - but his correlations were positive or negative according to site habitat factors. Also, some of his sites had negative correlations with spring rainfall. He did not consider minimum temperature or frost, nor did he investigate the weather of the autumn and winter. Brigsteer Wood is more than 4° north of West Dean and so has a different climate and, possibly, different daffodil populations. For example, Blackman & Rutter (1950) found significantly different relative growth rates between 'strains' of bluebells in three woodlands in SE England.

Whilst shade is the over-riding factor controlling daffodil density, there are many others. In view of this, it was decided to use just two weather variables for a multiple regression with the annual change in density. Only eight years of increase were available (1979-80 to 1986-87). There were four correlations at $P < 0.01$: spring frost and minimum temperature; and autumn frost and rainfall. Spring frost and minimum temperature will affect plants in the same way (although there was no significant correlation between these two weather variables during 1978-95). So, spring frost, which had the slightly higher correlation, was used as the first variable. Autumn frost, which had the highest autumn correlation, was employed as the second variable.

The regression is:

change in density = 1.30 x autumn frost - 1.84 x spring frost + 6.87

For this, the periods, variables and units are:

> annual change in density ($m^{-2} year^{-1}$) to spring of year n;
> mean monthly nights of ground frost during October-November of year n -1; and
> mean monthly nights of ground frost during April-May of year n -1.

For this, $R = 0.9341$ and $P < 0.01$.

5.2.4 Later changes

Following the conclusion of the shade experiment, the management of the daffodil area of the reserve was changed to annual swiping. In order to have maximum effect on the bracken and not to disturb the nesting birds, the season of swiping was changed to a dry period in mid-July (or as soon as possible afterwards). This policy (which affected all the plots except Plot 1 - where the density of trees and shrubs prevented the use of a tractor) came into effect in 1994. Monitoring continued but, from 1995 was scheduled for five-year intervals.

In general, the trends of density increase continued but at a slower rate, although the yearly means for Plot 1 (dense shade) stayed very close to the extrapolated regression line. Plots 2 and 3 were somewhat erratic, but showed signs of reaching stability from about 1987. If this is so, these plots will have a maximum sustainable density of about 130 mature bulbs m^{-2}. Plots 4 and 5 were even more erratic, and all their yearly means after 1987 were below the extrapolated regression line. If these two plots are reaching equilibrium, they are achieving it at extremely low maximum sustainable densities.

The major change due to the alteration of management was the enormous decrease of bracken and its replacement by grass. This was particularly noticeable on Plot 5 (open, un-swiped) which, together with its surrounding area, appeared like parkland - which it may well have been in the past.

It is very questionable if these changes in density were caused by the modification in management. The most likely cause is the great storm of 1987. There were a few wind-blown trees on the plots and a resulting increase in the microhabitats such as exposed root plates and hollows. This would account for both the death of bulbs and for the increase in variation both between and within plots.

Presumably, the daffodil densities must reach equilibrium in the near future, and Plots 1, 2 and 3 may be at, or approaching, this stage. Certainly, the rate of increase of the daffodil populations on some of the plots is declining. However, it is very doubtful if Plots 4 and 5 are nearing equilibrium. Their daffodils densities are very much less than those on Plots 1-3 (Table 2) and their degrees of aggregation are very much greater. Such highly-clumped bulbs produce fewer and smaller daughter bulbs (Rees & Turquand 1969; Barkham 1980a) and, so, increase in density slowly, if at all. Once the daffodils spread to other parts of these plots, their mean densities should again increase rapidly.

As the daffodil populations on some plots appear to be approaching stability, too much emphasis should not be placed on the predictive power of the multiple regression presented above.

6. Sexual reproduction

6.1 Results

All the plots showed large between-year fluctuations in the densities of flowers, seedlings and young (Figures 2a to 2e).

The means of flowering individuals, seedlings and young expressed as density, 'fraction of mature' bulbs and as quotients of each other, are given in Table 4, which also shows the mean densities of mature bulbs.

Table 4: Mean 1979-91 densities, fractions of mature bulbs, and quotients of daffodil flowers, seedlings and young at West Dean Woods.

Plot		1	2	3	4	5	Mean
Shade treatment		dense	light	light	open	open	
Swiped		no	yes	no	yes	no	
Density (per sq m):							
	Mature	97.7	108.4	97.1	27.2	11.5	68.4
	Flowers	4.7	9.5	8.4	2.5	0.7	5.1
	Seedlings	3.2	10.3	14.8	1.4	1.4	6.2
	Young	10.5	16.6	22.9	2.8	1.9	10.9
Fraction of mature (%):							
	Flowers	4.8	9	8.8	9.1	7.9	7.9
	Seedlings	3.3	10.5	15.7	5.5	10.4	9.1
	Young	11	16.7	24.7	11.7	15.1	15.9
Quotient:							
	Seedlings/Flowers	0.7	1.1	1.8	0.6	1.9	1.2
	Young/Seedlings	3.3	1.6	1.5	2	1.4	2
	Young/Flowers	2.2	1.7	2.7	1.2	2.6	2.1

For fraction of mature, Plot 3 (light shade, un-swiped) generally had the highest values, followed by Plot 2 (light shade, swiped), with Plot 1 (dense shade) the lowest. With the exception of Plot 1 (dense shade; 5%), an average of 8-9% of the mature bulbs flowered each year. Seedlings and young showed a similar pattern to each other, with the lowest fractions on Plots 1 and 4 (dense shade and open, swiped) and the highest on Plot 3 (light shade, un-swiped).

The quotients showed considerable variation between the plots. Those of seedlings and young in relation to flowers were highest on Plots 5 (open, un-swiped) and 3 (light shade, un-swiped), with Plot 4 (open, swiped) having the lowest values. The young/seedlings quotients were the opposite of these, with the highest value on Plot 1, followed by Plot 4.

Correlation coefficients were determined between the densities of flowers in year n and the densities of seedlings in years n+l and n+2 and of young in years n+2 and n+3 for the years 1979-89. They were also determined between the densities of seedlings in year n and of young in years n+l, n+2 and n+3. Five of these seven correlations were significant at $P < 0.01$ or $P<0.001$ (Table 5).

Table 5: Significant (P < 0.01) correlation coefficients of comparisons between the densities of flowering, seedling and young daffodils in successive years on the combined plots at West Dean Woods 1979-89

Comparison of flowering individuals in year n with:	
Seedlings in year n + 1	N.S.
Seedlings in year n + 2	0.587
Young in year n + 2	0.467
Young in year n + 3	0.492
Comparison of seedlings in year n with:	
Young in year n + 1	0.463
Young in year n + 2	0.679
Young in year n + 3	N.S.

N.S. = not significant at $P < 0.01$.

Coefficients for which $P < 0.001$ are shown in bold print.

N.B. none were significant at $P < 0.05$-0.01.

Despite the high aggregation of bulbs, there were rarely more than four flowering individuals in a quadrat. Nevertheless, flowers, seedlings and young were all significantly aggregated ($P<0.001$). On average, mature bulbs were the most aggregated category in both 1983 and 1995 (mean V/m for the five plots in both years = 10), followed by seedlings (8), flowering individuals (5) and young (4).

The significant correlations between flowers (as a quotient of mature bulbs) and weather factors for the combined plots are shown in (Table 6). The highest were for maximum temperature and lack-of-rain during the spring of the year prior to flowering.

Table 6: **Significant (P < 0.05) correlation coefficients of flowering daffodils (as fraction of mature) during 1979-93 with weather factors during the preceding year at West Dean Woods**

	Weather Factors				
Months	Temperature			Rain	Sun
	Maximum	Minimum	Frost		
March					0.577
Mar-Apr				-0.859	0.702
April	0.767			-0.745	0.65
Mar-May			0.578	-0.736	
Apr-May				-0.722	
May			0.59		
July		-0.607			
February*			0.625		

Values for P < 0.01 in italics and underlined.
Values for P < 0.001 in bold.
* In calendar year of daffodil density count.

The significant correlations between seedling density and weather factors are shown in Table 7. All but one were for the autumn or winter, with the most significant for autumn rainfall and low winter temperatures.

Table 7: **Significant (P <0.05) correlation coefficients of density of seedling daffodils during 1979-91 with weather factors during the previous year on the combined plots at West Dean Woods**

Months	Temperature					Rain	Sun
	Maximum	Minimum	Mean	Frost	Soil		
May				0.579			
September						0.761	
Sep-Oct						0.894	
October	0.793					0.854	
November							-0.735
December	-0.582	-0.828	-0.745	0.841	-0.691		
January*							-0.576

Values for P < 0.01 in italics and underlined; those for P values < 0.001 in bold.
* In calendar year of daffodil density count.

The significant correlations between the density of young daffodils and weather factors are shown in Table 8. Low temperatures in the spring of both years, together with low sunshine in the previous spring, were the main factors limiting density. Rainfall had a positive influence during the winter but a negative one during the autumn.

Table 8: Significant (P <0.05) correlation coefficients of density of young daffodils during 1979-91 with weather factors during the previous year on the combined plots at West Dean Woods

Months	Temperature					Rain	Sun
	Maximum	Minimum	Mean	Frost	Soil		
March			-0.737				
April			-0.752				-0.656
April-May	-0.743		-0.7				-0.711
May					-0.621		-0.722
October						-0.592	
December						0.832	
January*		-0.655	-0.61	0.668	-0.577		
February*						0.579	
March*	-0.69		-0.659		-0.613		
April*							

Values for P < 0.01 in italics and underlined; there were none at P < 0.001.
* In calendar year of daffodil density count.

6.2 Discussion

6.2.1 Flowering, germination and establishment

In contrast to the density of mature bulbs, the densities of flowers, seedlings and young showed large between-year variation (Figure 2) which suggests that weather (or other) factors were playing a much more important role in controlling sexual than vegetative reproduction.

Abundant flowering could be expected to result in abundant seedlings the following year and many young the year after that. Despite this, there was significant correlation between the densities of flowers one year and the densities of seedlings the next (Table 5). That there was a significant correlation between the densities of flowers with that of seedlings the following year (n + 2) suggests that germination might be delayed for 18 months - as may happen after summer drought (Barkham 1980a). However, West Dean seeds planted in a garden germinated after the normal six months dormancy.

All flowers produced capsules but a high proportion were empty due, apparently, to the absence of insect pollinators. Pollination is mainly by bumblebees (*Bombus* spp., especially *B. terrestris* queens) and is very dependent on the weather (Caldwell & Wallace 1955; Proctor & Yeo 1973; Barkham 1980a). In 1978, half the capsules at West Dean were empty. Those with seeds had a mean content of 27 (i.e. 13.5 seeds per flower) - values similar to those obtained by Caldwell

& Wallace (1955) and Barkham (1980a). As the mean seedling/flower quotient was 1.2 (calculated from Table 4), an average of about 10% of the seeds germinate and establish seedlings.

6.2.2 Flowering and shade

The lowest fraction flowering (Table 4) was 5% on Plot 1 (dense shade) and was significantly different from the mean of the other four plots ($P < 0.01$). It was also significantly different from Plots 2 and 3 individually, but not from Plots 4 and 5 which were more variable. There were no significant differences between Plots 2, 3, 4 and 5.

This low fraction flowering under dense shade is in agreement with earlier work (Salisbury 1924, Barkham 1980b and Peterken 1981).

6.2.3 Flowering and weather

The fraction-flowering for each plot and for the mean of all five plots have been plotted on the same axes (Figure 3). The mean had a large range from 1.2% (1984) to 16% (1983), and the years fall into four, fairly clear, fraction-flowering groups: high (1983, 1985, 1991); average (1986, 1995); low (1982, 1984, 1987,1989, 1993); and those with large between-plot differences (1979, 1980, 1981).

Figure 3 also shows a marked tendency, during the years of annual counts, for the mean fraction-flowering to increase and decrease in alternate years and there was a significant negative correlation between these two variables ($r = -0.756$; $P < 0.02$) suggesting that the resources expended in producing flowers and fruits decrease the plant's capacity to flower the following year.

For reasons given above, correlations with weather variables at only $P < 0.05$ will be ignored unless they corroborate those at higher probabilities. Those at $P < 0.01$ between the mean fraction-flowering and weather were positive for the mean maximum April temperature and negative for the March-May rainfall of the year prior to flowering (Table 6).

Warm weather is favourable to plant growth and, no doubt, enhances the formation of floral initials. Why spring rainfall should depress flowering the following year - as Barkham (1980b) also found in his shaded plots - is less clear. Whilst a negative correlation between temperature and rainfall could be expected, that for the mean maximum March temperature and the mean March-April rainfall for the years 1979-95 at West Dean was not significant.

There is no evidence for the photoperiodic control of flowering of bulbs (Rees 1972). In daffodils, nine stages of floral differentiation have been recognized (Hartsema 1961). For cv. 'King Alfred' in southern England, the first protuberance on the vegetative apex occurs in early May and the last initiation stage (the paracorolla) in July (Preece & Morrison 1963). Virtually nothing is known of the biochemistry of the processes involved (Rees 1972); the various stages may have different requirements, and the immediate and later effects of any treatment may differ. High temperatures followed by low temperatures are required for flower initiation and, in the field, these are satisfied by high summer and low winter soil temperatures.

The lack of any correlations with high summer or low winter temperatures at West Dean is probably because these criteria are supplied each year. For example, there were far more than 50 ground frosts each winter during the years of this study. In addition to spring rainfall, Barkham (1980b) found the main weather factor limiting daffodil flowering was summer drought but, as pointed out above, he considered only a limited range of weather variables.

6.2.4 Flowering and other factors

The flowering of cultivated daffodils is mainly controlled by bulb weight, and the proportion of small bulbs increased at high densities (Rees, Bleasdale & Wallis 1968; Rees, Wallis & Tompsett 1973). In wild populations, Barkham (1980a, 1992b) has shown that flowering is density-dependent. At West Dean, the mean V/m values were five for flowers compared with 10 for mature bulbs, suggesting that flowering is less in dense clumps. However, no significant correlations were found between the numbers of mature bulbs and of flowers in the over 500 occupied quadrats in both 1983 and 1995.

Daughter bulbs do not flower before their third year, so populations which are rapidly expanding would have a low fraction of bulbs capable of flowering. This probably explains the gradual relative-decline of the fraction flowering, but not of flower density, on Plot 4 (Figures 3 and 2d).

In view of these and other likely factors, it was decided to use just the two variables with the highest correlations for a multiple regression with the mean fraction flowering. There were three possible variables. They all concern the previous spring and were: spring rainfall, spring maximum temperature and fraction flowering. Although fraction flowering had the lowest of these correlation coefficients, it was based on the fewest years (1979-80 to 1986-87). So, it was decided to use it and, for these seven years, spring temperature gave the best regression, which was:

fraction flowering (n) =
3.96 x mean maximum temperature - 0.172 x fraction flowering (n-1) - 41.1

For this, the periods, variables and units are:

> fraction flowering (n) (% mature) in spring of year n;
> mean maximum temperature during April (°C) of year n -1; and
> fraction flowering (n-1) (% mature) in spring of year n -1.

For this, $R = 0.9413$ and $P < 0.05$. (P was almost 0.01.)

When monitoring is not carried out annually, the value for fraction flowering in the previous year will be unknown. Therefore, a second regression based entirely on weather factors is presented. This was for the years 1979-93 and is:

fraction flowering = 0.0691 x spring maximum temperature - 0.234 x spring rainfall + 19.9

For this, the periods, variables and units are:

fraction flowering (% mature) in spring of year n;
mean maximum temperature (°C) during April of year n -1; and
mean monthly rainfall (mm) during March-April of year n -1.

For this, $R = 0.8605$ and $P < 0.01$.

This formula permits the fraction flowering to be estimated a year in advance and enables potential visitors to be advised accordingly. It forecast the fraction flowering for 1995 as 5.6%; it was 3.8%. This was a good estimate, particularly when the total observed range of 1.2-16% taken into account. It forecast the fraction flowering as 0.3 % for 1999 - a year when monitoring was not undertaken, but when many regular visitors remarked how 'extremely poor' the daffodils were. For the year 2000, the forecast is 12.0 %.

6.2.5 Seedlings and young

Seeds fall near to parent plants (Caldwell & Wallace 1955; Barkham 1980a) and seedling clumps arise from capsules whose stalks have fallen over and, consequently, fall within about 40 cm of their parent bulb. At West Dean the seedlings were highly aggregated (V/m = 8); the maximum observed in a quadrat was 65 - equivalent to 1040 m^{-2}. Competitive thinning soon reduced such densities. As virtually all reproduction is by daughter bulbs and seed dispersal is so inefficient, it is very difficult for daffodils to spread to other suitable habitats and their distribution is very patchy within West Dean - as it is in other woodlands (Caldwell & Wallace 1955; Barkham 1980a, 1992b).

Barkham (1980a) found no significant differences between habitats in the proportion of capsules with seeds, nor in the number of seeds they contained. If this holds generally, then the different densities and fractions of seedlings and young on the West Dean plots are due to the effects of the habitat on germination or later stages. Table 4 suggests that germination and seedling establishment were greatest under light total shade (Plots 3 and 5) and least in open, swiped conditions (Plot 4) or under dense woody-plant shade (Plot 1), but that their survival to become young was greatest under dense woody-plant shade (Plot 1). The quotient of young to flowers is a combination of these two processes and is greatest on the three un-swiped plots. These results are very similar to those for Barkham's (1980a) 'juvenile' age-class (equivalent to seedlings plus young at West Dean).

The highest correlations ($P < 0.001$) of seedling density with weather factors (Table 7) were for autumn rainfall and winter frost. Others (at $P < 0.01$) were negative with winter temperatures (including little sunshine), and one for maximum temperature in October. Little is known about the germination requirements of daffodils beyond the necessity of a cold treatment (Rees 1972). No doubt, this explains the high correlation with frost and the others with low winter temperatures. Because of the lack of any correlation between the densities of flowers in one year and of seedlings the next (as noted above), these weather factors are particularly important in determining seedling abundance.

Of the 15 significant monthly correlations at $P < 0.05$ for young daffodils (Table 8), there were none at $P < 0.001$ and only four at $P < 0.01$. These were negative with mean temperature and sunshine during the previous spring and positive with winter rain. Not surprisingly, these were similar to those affecting mature bulbs (Table 3). The positive correlations with winter rain might be explained by the importance of such small bulbs not drying out. Thus seeds from experimental crossings are sown soon after harvest and, together with the resulting seedlings, kept moist (Chan 1951-52; Blanchard 1975).

7. Conclusions

At West Dean, as elsewhere, illumination was the overriding factor controlling daffodil density. Light woody-plant shade prevented the development of a dense ground flora of bracken or bramble and the daffodils increased considerably. The virtual absence of woody-plant shade permitted a dense ground flora of bracken to develop and the dead bracken fronds, like dense woody-plant cover, allowed the daffodils to increase only moderately. Without woody-plant shade, swiping to reduce the undergrowth was virtually essential in order for daffodil density to increase. Thus the effects of shade from both the woody plants and the ground flora need to be considered together.

Weather was of secondary importance, but daffodil density increased following years with few spring and many autumn frosts. Bulb density was also important, but is itself largely determined by shade and weather. After 15 years, there were signs, at least on some plots, that the daffodils were reaching a maximum sustainable density. Pests and diseases appear to be of minor importance, as noted by Caldwell & Wallace (1955) and Blanchard (1990).

The flowering of the wild daffodils at West Dean attract large numbers of human visitors each spring. There were large between-year differences in the proportion of mature bulbs flowering, and even when the woodland appeared to be carpeted in flowers, as in 1983, only one bulb in six was in bloom. In addition to a tendency for abundant flowering in alternate years, flowering was also controlled by the weather of the previous spring. Flowering was less under dense shade, but shade was definitely a secondary factor, and the fraction flowering could be predicted from the temperature and rainfall of the previous spring.

The mean density of seedlings was approximately one-eleventh that of mature bulbs and there were high mortalities of both seedlings and young plants. As expected, the main method of increase was vegetative by daughter-bulbs.

The wild daffodils were one of the main reasons for the establishment of the SSSI and the nature reserve in West Dean Woods. Following this experiment, no charge in management of the trees and shrubs was proposed - for most of the daffodil colony was covered by light woody-plant shade. Swiping of the undergrowth each summer was recommended and came into practice in 1994. This management modification and the great storm of 1987 caused some changes. Monitoring the original five plots is continuing.

References

BARKHAM, J.P. 1980a. Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*) I. Clonal growth, seed reproduction, mortality and the effects of density. *Journal of Ecology*. **68**, 607-633.

BARKHAM, J.P. 1980b. Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*) II. Changes in number of shoots and flowers, and the effects of bulb depth on growth and regeneration. *Journal of Ecology*, **68**, 635-664.

BARKHAM, J.P. 1992a. The effects of management on the ground flora of ancient woodland, Brigsteer Park Wood, Cumbria, England. *Biological Conservation*, **60**, 167-187.

BARKHAM, J.P. 1992b. Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*) IV. Clumps and gaps. Journal of Ecology, **80**, 757-808.

BARKHAM, J.P. 1992c. The effects of coppicing and neglect on the performance of the perennial ground flora. *In*: G. P. Buckley, ed. *The Ecology of Coppice Management*. London: Chapman & Hall, pp. 115-146.

BARKHAM, J.P. & HANCE, C.E. 1982. Population dynamics of the wild daffodil (Narcissus pseudonarcissus) III. Implications of a computer model of 1000 years of population change. *Journal of Ecology*, **70**, 323-344.

BLACKMAN, G.E. & RUTTER, A.J. 1950. Physiological and ecological studies in the analysis of the plant environment V. An assessment of the factors controlling the distribution of the bluebell (Scilla non-scripta) in different communities. *Annals of Botany, London*, **14**, 487-520.

BLANCHARD, J.W. 1975. Daffodils from seed. *Daffodils: An Annual For Amateurs and Specialists*, pp. 13-16. London: Royal Horticultural Society.

BLANCHARD, J.W. 1990. *Narcissus - A Guide to Wild Daffodils*. Woking: Alpine Garden Society.

CALDWELL, J. & WALLACE, T.J. 1955. Biological Flora of the British Isles. *Narcissus pseudonarcissus* L. *Journal of Ecology*, **43**, 331-341.

CHAN, T-T. 1951-52. The development of the Narcissus plant. *Royal Horticultural Society Daffodil and Tulip Yearbook 1951-52*, **17**, 72-100.

GREIG-SMITH, P. 1964. *Quantitative Plant Ecology*. London: Butterworths.

HARTSEMA, A.M. 1961. Influence of temperature on flower formation and flowering of bulbous and tuberous plants. *In:* W. Ruhland, ed. *Encyclopaedia of Plant Physiology, 16, External Factors Affecting Growth and Development*, pp. 123-167. Berlin: Springer.

PETERKEN, G.F. 1981. *Woodland Conservation and Management*. London: Chapman & Hall.

POTTS, A.S. & BROWNE, T.J. 1983. The climate of Sussex. *In*: University of Sussex Geography Editorial Committee, ed. *Sussex: Environment, Landscape and Society*. pp. 88-108. Gloucester: Alan Sutton.

PREECE, T.F. & MORRISON, J.R. 1963. Growth stages of the narcissus flower within the bulb. Illustrations of the Beyer scale. *Plant Pathology*, **12**, 145-146.

PROCTOR, M. & YEO, P. 1973. *The Pollination of Flowers*. London: Collins.

REES, A.R. 1972. *The Growth of Bulbs*. London: Academic Press.

REES, A.R., BLEASDALE, J. & WALLIS, L.W. 1968. Effects of spacing on bulb yield in the narcissus. *Journal of Horticultural Science*, **113**, 113-120.

REES, A.R. & TURQUAND, E.D. 1969. Effects of planting density on bulb yield in the tulip. *Journal of Applied Ecology*, **6**, 349-358.

REES, A.R., WALLIS, L.W. & TOMPSETT, A.A. 1973. Effects of planting density and frequency of lifting on flower and bulb production of narcissus in SW England. *Journal of Horticultural Science*, **48**, 59-73.

SALISBURY, E.J. 1924. The effects of coppicing as illustrated by the woods of Hertfordshire. *Transactions of the Hertfordshire Natural History Society and Field Club*. **18**, 1-21.

STACE, C. 1991. *New Flora of the British Isles*. Cambridge: Cambridge University Press.

STEWART, J.G. 1976. *West Dean Woods Nature Reserve. Management Plan*. Unpublished ms, Sussex Trust for Wildlife Conservation Ltd.

TITTENSOR, R.M. 1991. *West Dean: A History of Conservation on a Sussex Estate*. Bognor Regis, Sussex: Felpham Press.

Figure 1 (a) Mature bulb density

Plot 1: dense woody plants, unswiped

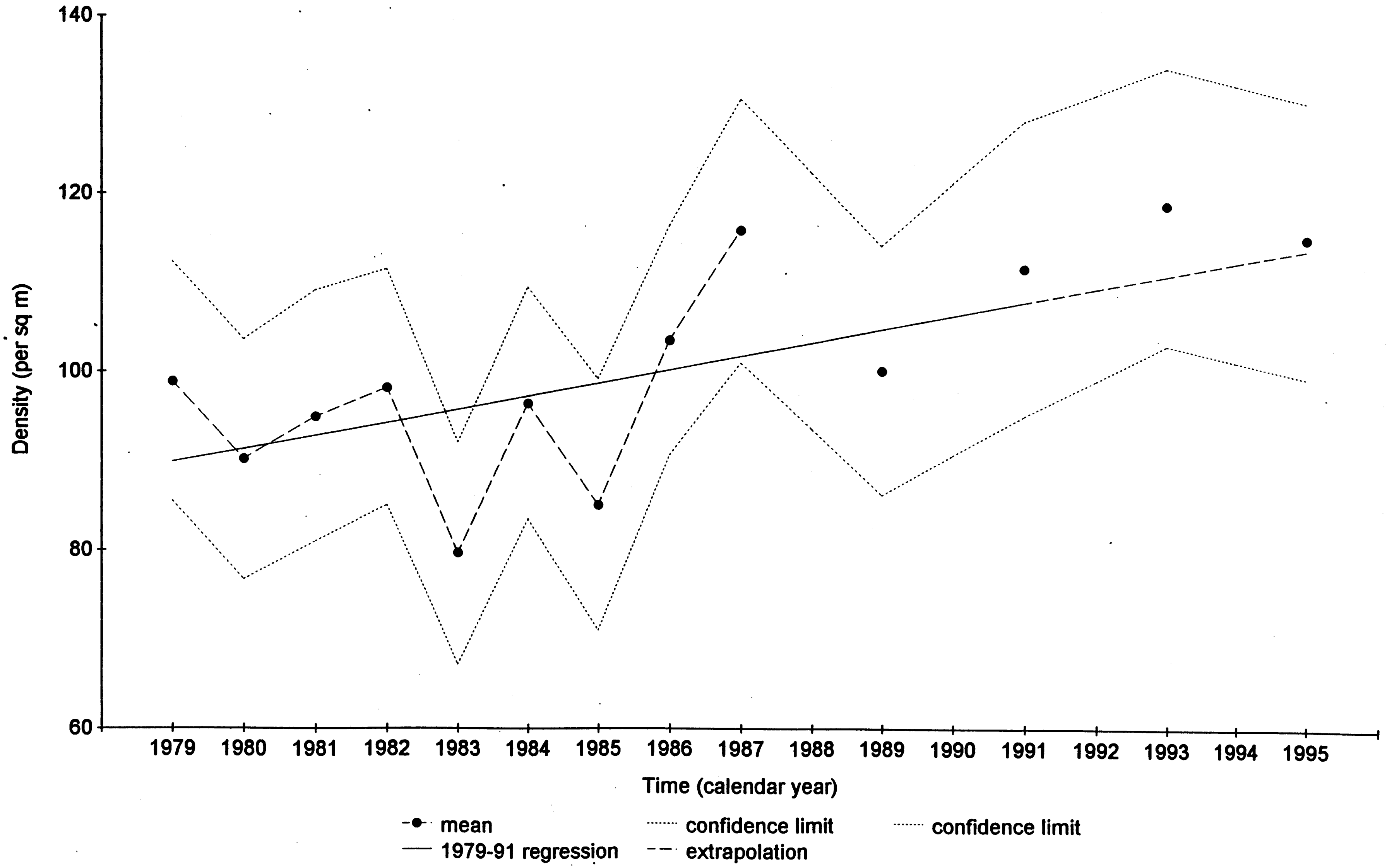

Figure 1 (b) Mature bulb density

Plot 2: light woody plants, swiped

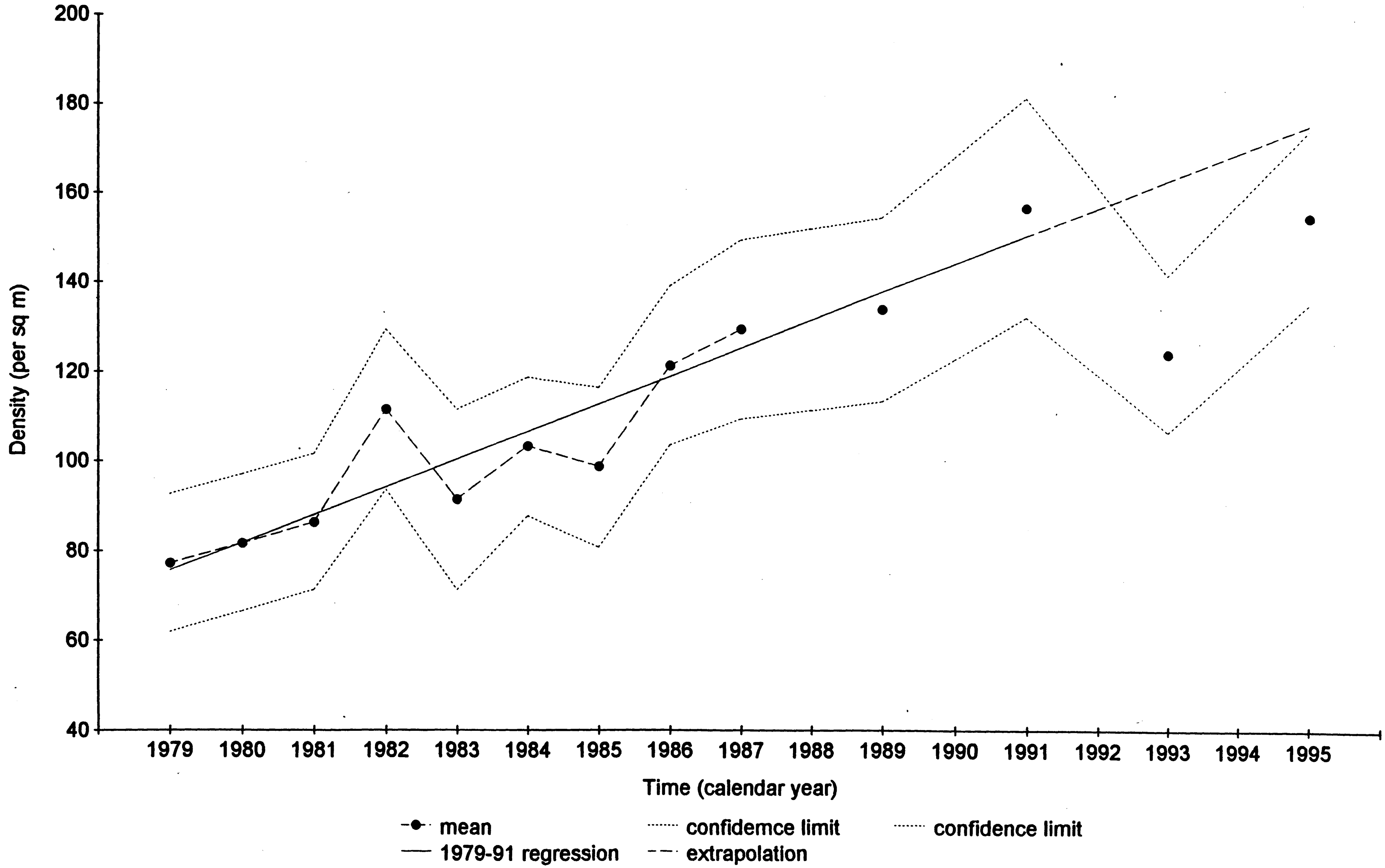

Figure 1 (c) Mature bulb density

Plot 3: light woody plants, unswiped

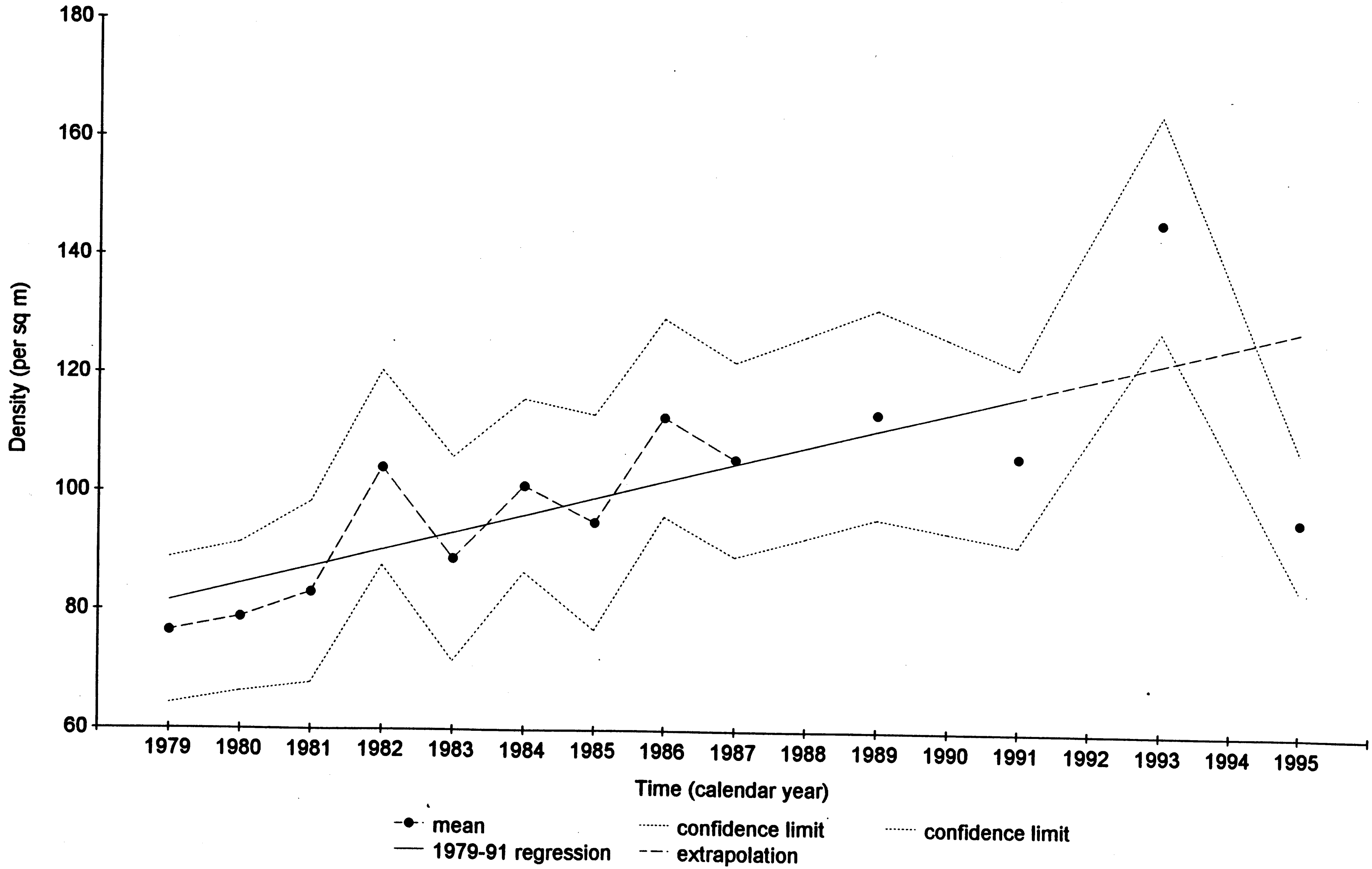

Figure 1 (d) Mature bulb density

Plot 4: open, swiped

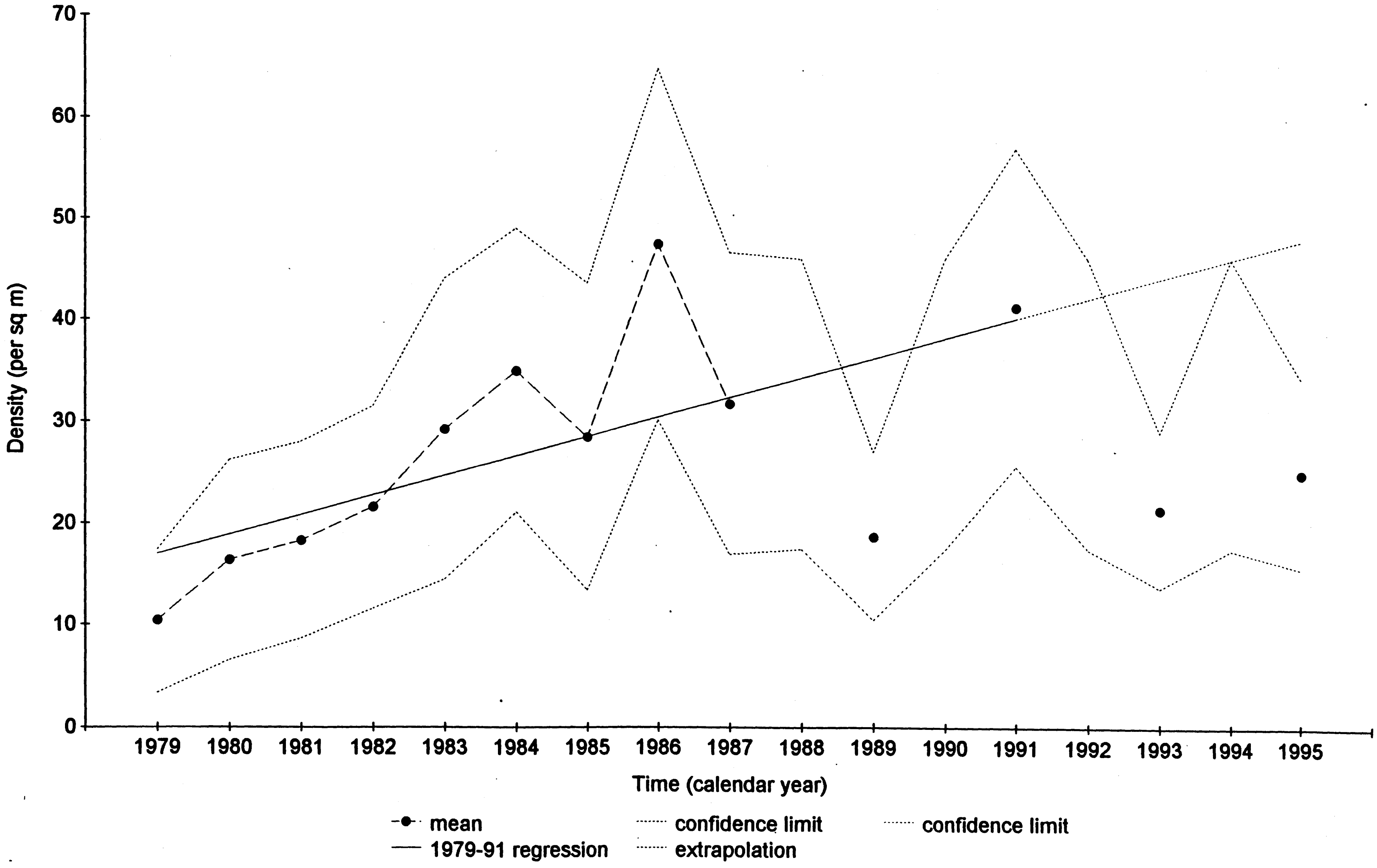

Figure 1 (e) Mature bulb density

Plot 5: open, unswiped

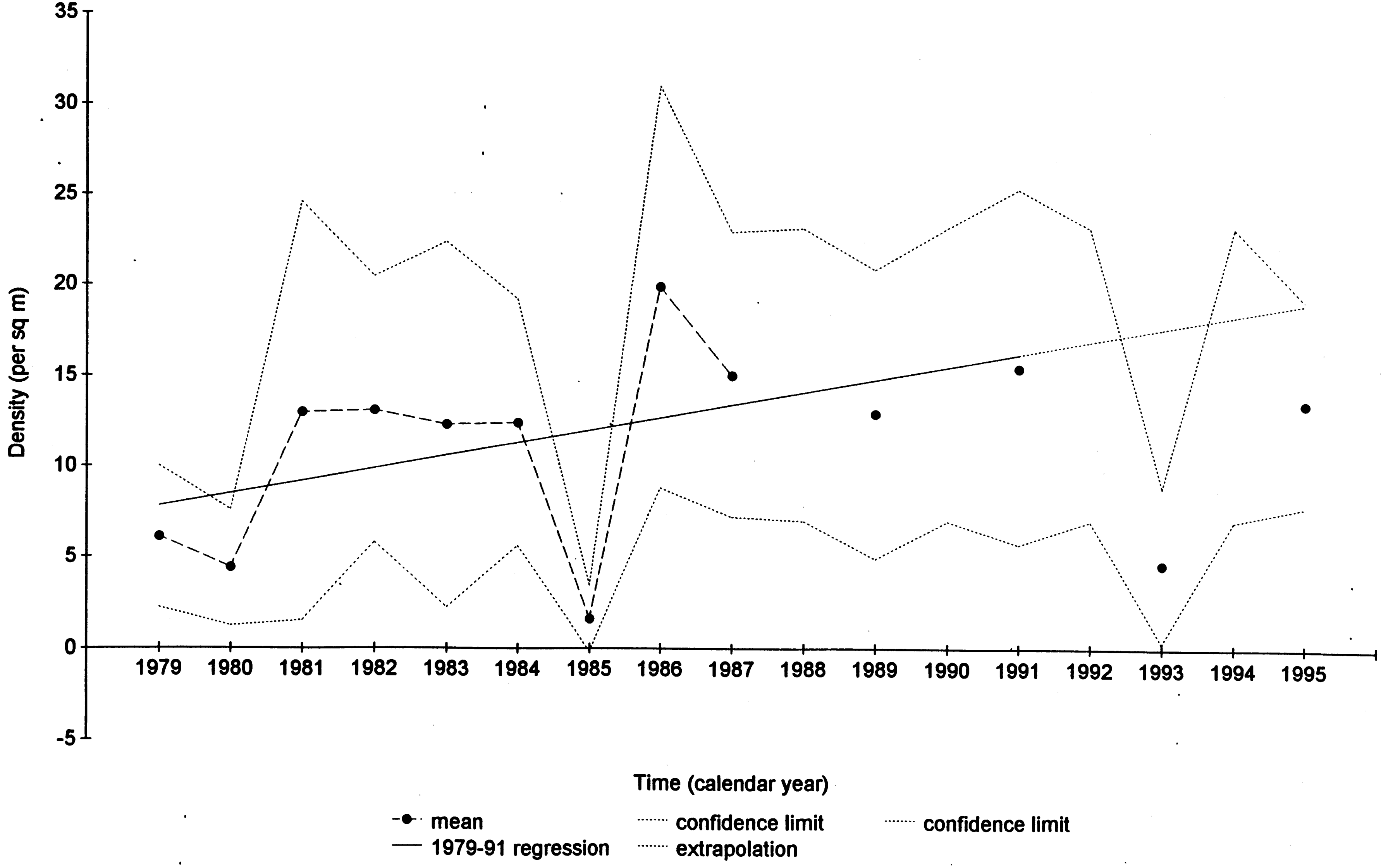

Figure 2 (a) Flowers, Seedlings & Young

Plot 1: dense woody plants, unswiped

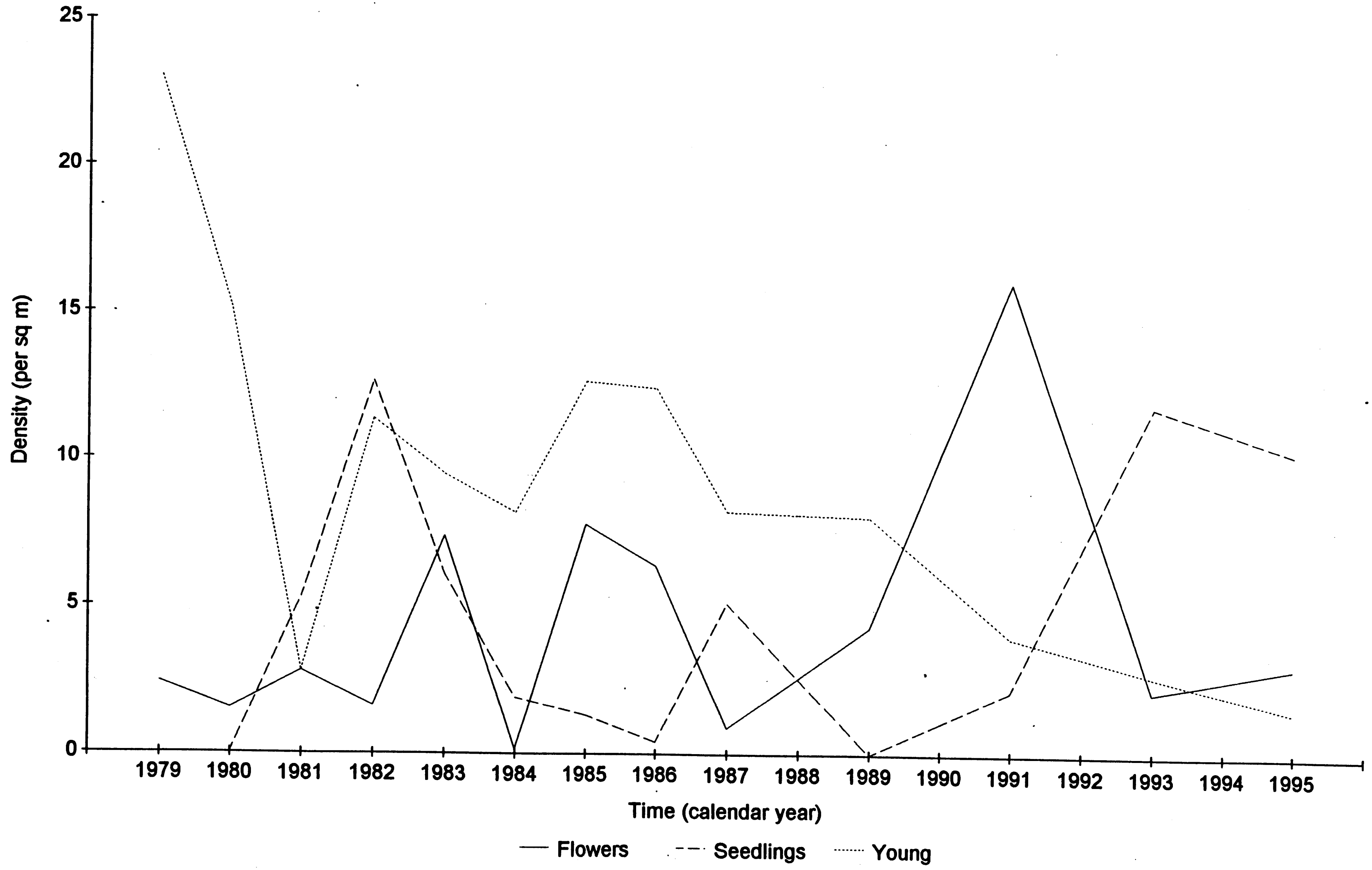

Figure 2 (b) Flowers, Seedlings & Young

Plot 2: light woody plants, swiped

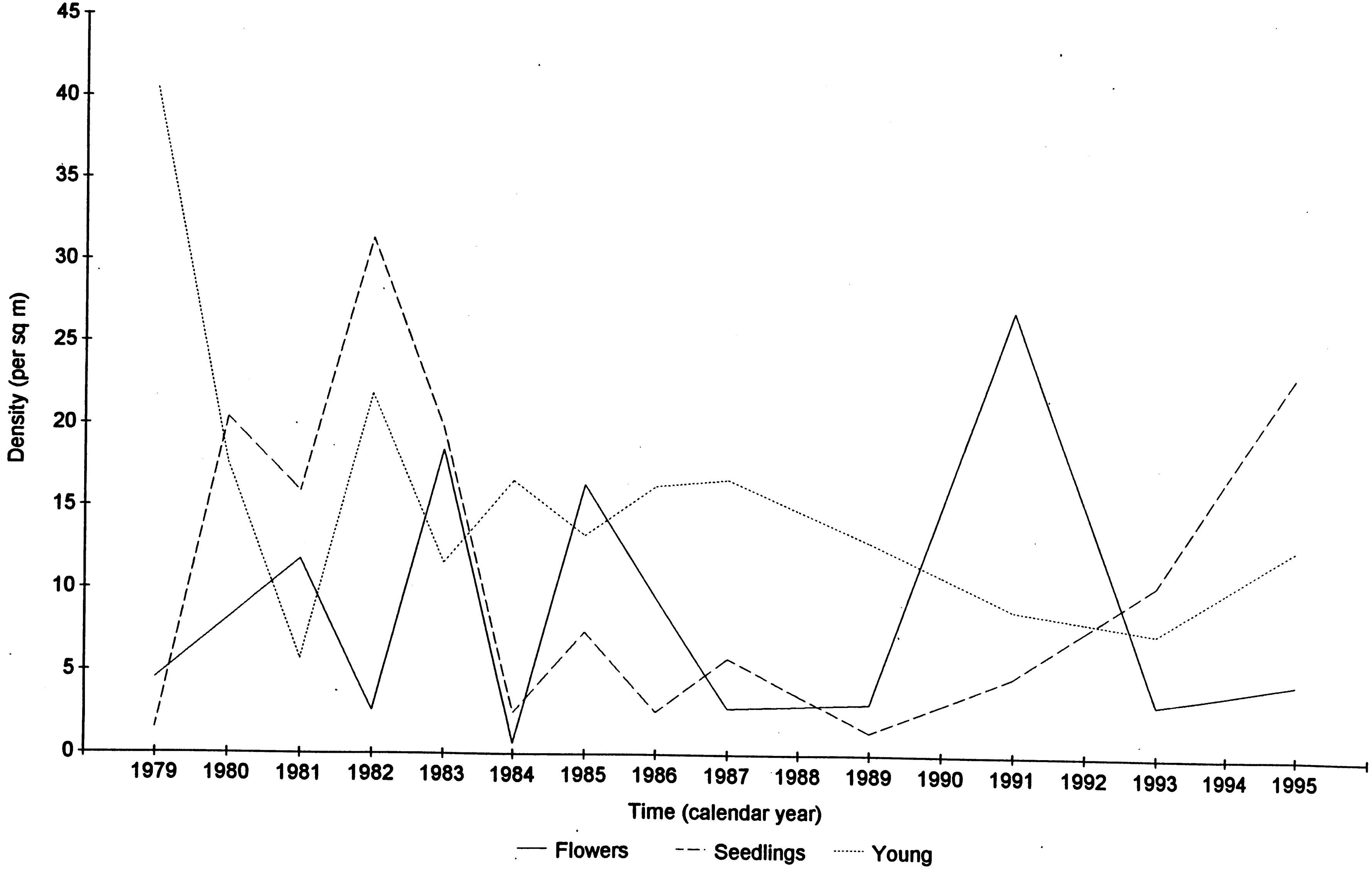

Figure 2 (c) Flowers, Seedlings & Young

Plot 3: light woody plants, unswiped

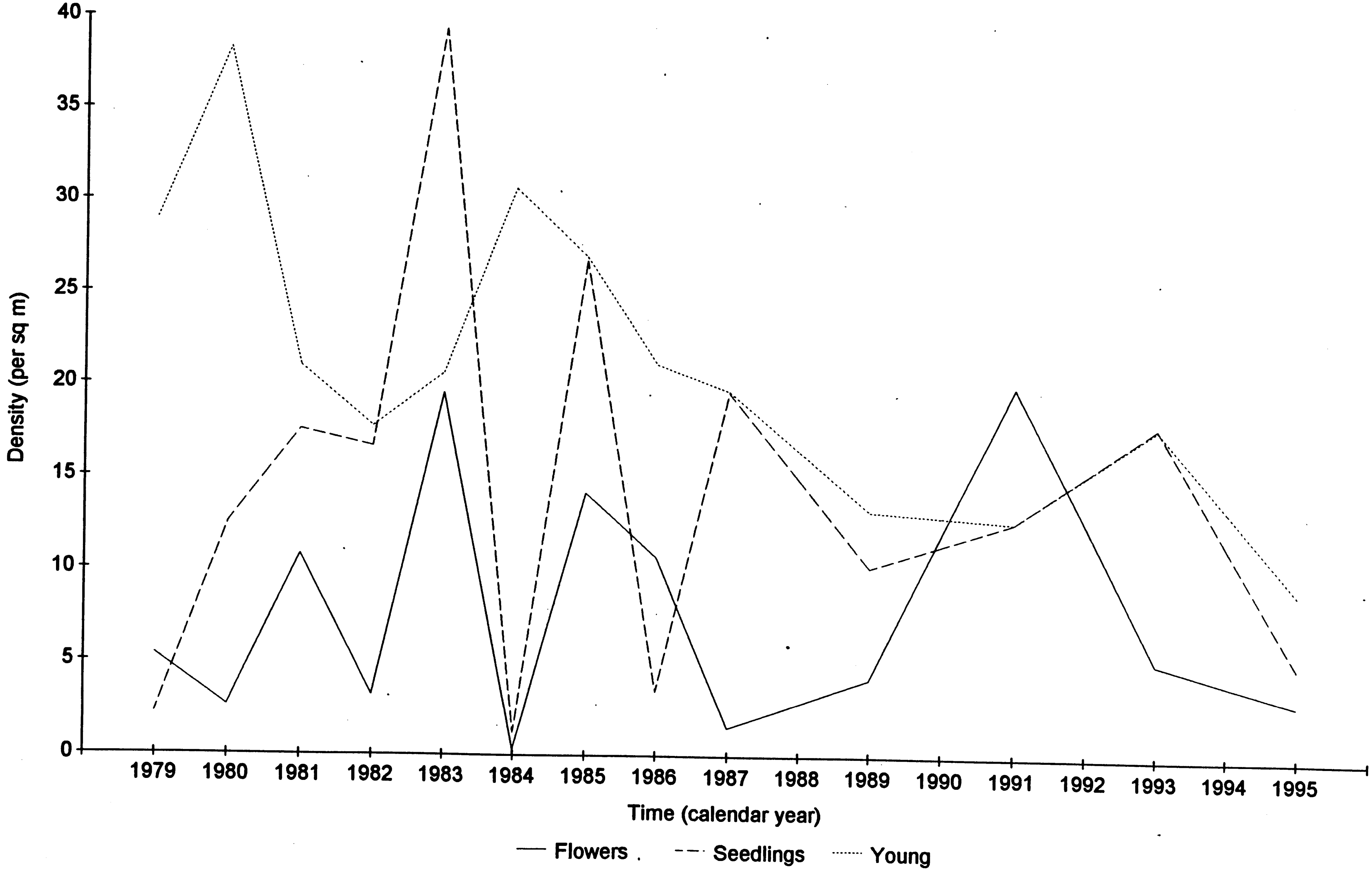

Figure 2 (d) Flowers, Seedlings & Young

Plot 4: open, swiped

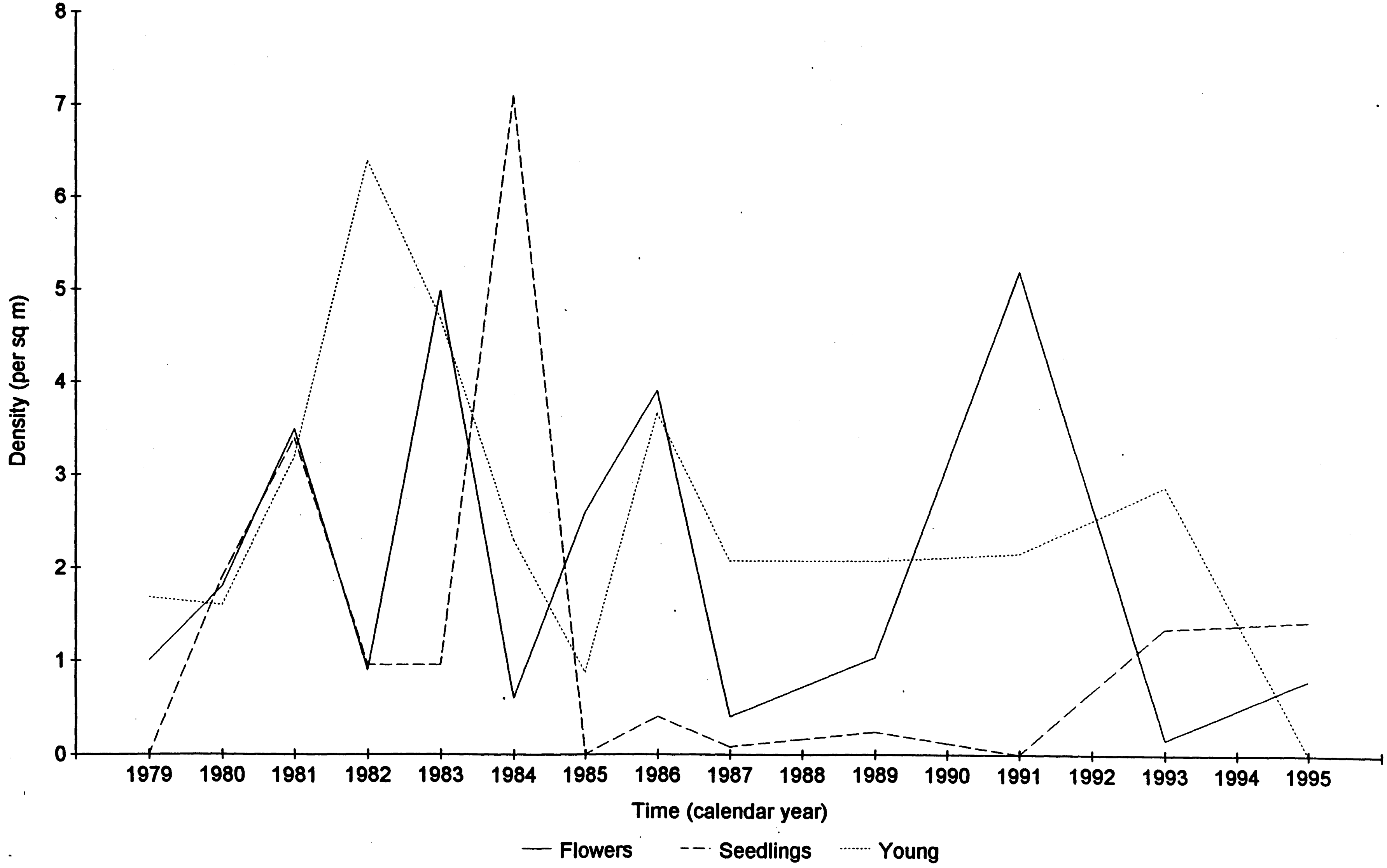

Figure 2 (e) Flowers, Seedlings & Young

Plot 5: open, unswiped

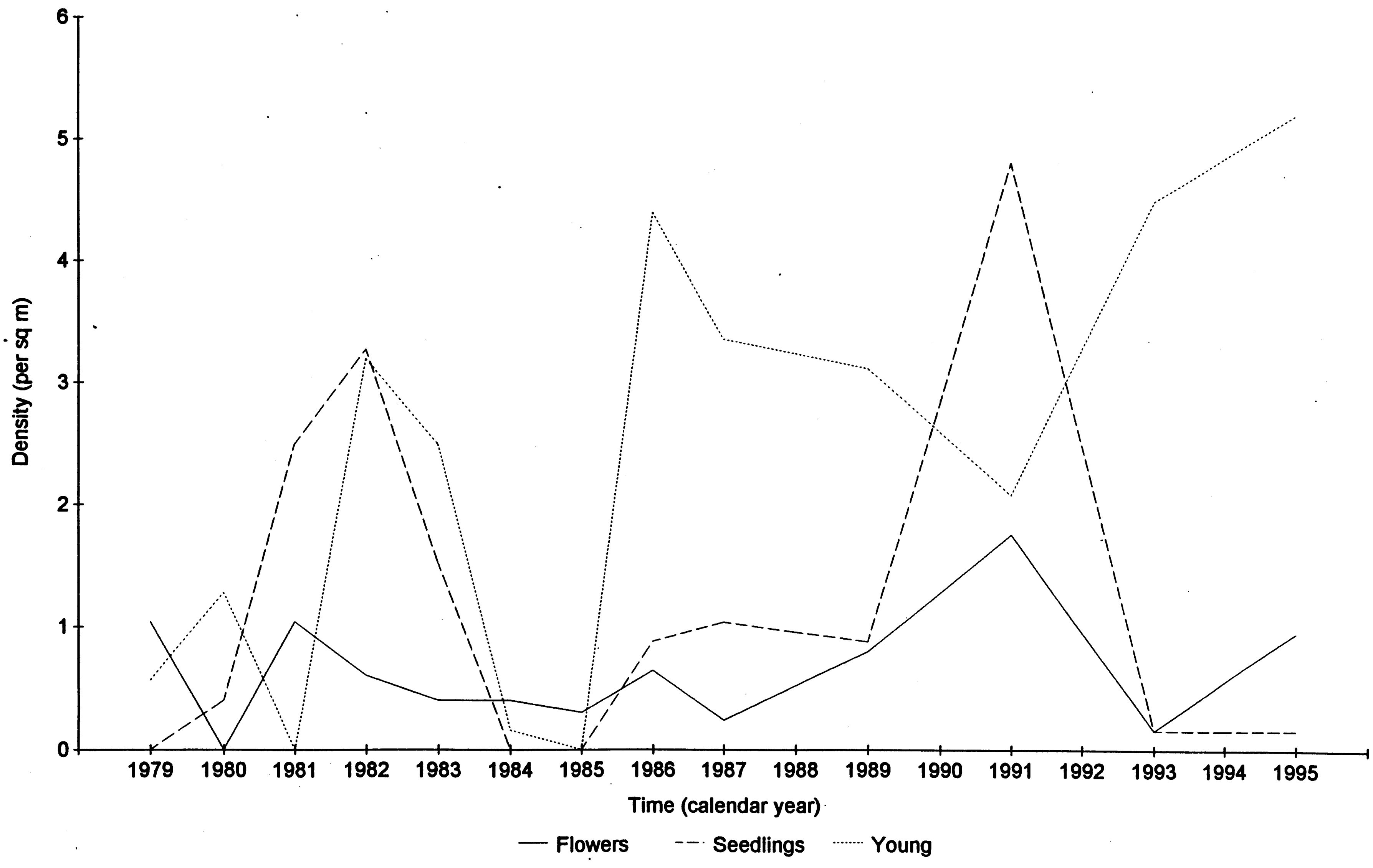

Figure 3 Flowering bulbs (% mature)
Note alternate year records from 1987