

# **Vegetation changes under influence of management and weather in the Taarlo brook area**



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### **Notice**

Due to an error occurring during the printing proces, figure 2 on page 8 has been smudged. In order to make it clear, I'll give the result of the clustering in groups:

Dehydrated Calthion: plots 43, 48, 50, 51, 61-69

Intermediary Calthion: plots 40, 45, 46, 49, 52, 53

Well developed Calthion: plots 41, 42, 44, 47, 54, 55-60.

## 1. Introduction

The Taarlo brook area is a part of the Drentse Aa Valley, which has been a nature reserve since the end of the 1960's. In time more areas have been acquired by the National Forestry Commission (SBB). This nature reserve was formed in order to preserve and restore the half-natural grasslands that existed in the area before farmers started to fertilise and drain the land. As a consequence of the modern agricultural use of the area, especially the wet meadows disappeared or became rare. *Calthion palustris* meadows are rich in species and used to be widespread in North-western Europe on wet soils with a relatively good nutrient availability. In the Drentse Aa area extensive *Calthion* vegetations can still be found (Grootjans, 1985). But even in preserved areas these vegetations may be threatened by drainage or contamination of the groundwater. Because of some characteristics of the valley, damage by drainage was relatively small and therefore the conditions for restoration were good (Everts et.al., 1984). Goal of the management was to maintain and development of the biological and landscape diversity. To preserve these remnant vegetations, the National Forestry Commission started to diminish the nutrient status of the soil by ceasing the application of fertiliser. In addition to that, a management of haycutting once a year (in July) was initiated. Within a fairly short time (4-8 years) after the management has started species-poor grasslands have developed into more species-rich half-natural grasslands (Bakker, 1989).

At present, well developed *Calthion palustris* meadows can be found. This vegetation type is characteristic for upwelling, calcareous groundwater and medium-rich nutrient conditions. The *Calthion palustris* vegetation may degenerate by drainage or fertilising of the soil. Except for the management and the hydrology, other factors may play an important role. The amount of precipitation for instance, may influence the characteristics of the groundwater (both quality and quantity).

This research will focus on the relations between characteristic species of the *Calthion palustris* vegetation and environmental factors such as precipitation and temperature. Such relationships are difficult to tackle because many factors may have an influence. Therefore it is necessary to quantify the fluctuations of both species and weather factors. Statistical analysis may then be applied to find any relations of importance. Former research on the effects of weather, in particular rainfall, on vegetation and species (biomass) has been done in more extreme environments, like California (Pitt & Heady, 1978), Southwest Spain (Figueroa & Davy, 1991) and the Dutch salt-marsh (Bakker & Olff, 1991).

In Pitt & Heady (1991) also several authors, who studied weather effects on vegetation or species, are mentioned. Also effects of temperature have been studied before, but mainly in relation to nutrient (nitrogen) contents of the soil (Whitehead, 1995). Vogel (1986) also tried to find relations between *Calthion* species and weather factors, but found that specification of weather factors and more powerful statistical test were needed to find better results.

Annual changes can occur in the vegetation because species disappear, appear or become dominant. Afore mentioned analysis of long term vegetation changes can be important to management because it can give an answer to the question whether or not the management has been successful and if not what other factors (hydrology) were likely to have caused the changes.

### Research questions

- What is the vegetation change that can be observed in the Taarlo brook area?
- What is the effect of management on individual Calthion-species?
- How are individual Calthion-species influenced by weather conditions (precipitation and temperature)?

## 2. Method

### 2.1 Area description

The “Taarlose diep” is situated in the nature reserve “the Drentse Aa” (53° 01'N, 6° 40'E) (see figure 1) and is a tributary of the Drentse Aa brook. This area is characterised by a strong influence of upwelling groundwater and therefore, in the past, peat has developed. Due to the strong upward direction of the ground water flow the peat has been formed in a curved way (Grootjans, 1985). The top of the peat layer can be locally dehydrated because of lowered groundwater tables (Everts et.al., 1984). The four transects are situated closely together. Since the last century, farmers used the area for agriculture. Because of the hydrological characteristics of the middle course, this area was not used intensively. Fields 422 and 431 were acquired in 1972; 419 in 1965 and 424 in 1967 (Vogel, 1987) and fertiliser has stopped since then.

The Drentse Aa brook originates on the Drenthian Plateau, from which it finds its way down to the sea. Its valley system can be divided into three parts: the upper, middle and lower part. In the middle part, upwelling of groundwater is caused by infiltration of precipitation on the higher course. During its course underground, the nutrient poor water is enriched with  $\text{Ca}^{2+}$ . The Taarlo brook is a tributary of the Drentse Aa and is situated in the middle part of the valley system (Everts et.al., 1984; Grootjans, 1985).

### 2.1 Vegetation

The permanent plots used in this study were established in 1972 and are situated in transects. The transects are situated along a small height gradient towards the brook. Each relevée was recorded once a year (permanent quadrates) in the beginning of June. The number of plots differs between transects. Transects 431 and 424 both have 9 plots, 422 and 419 both have 6. The total number of quadrates is 30. Later on (in 1988) a plot 0 was added to transect 431, though hasn't been used for the analysis. From 1972 to 1974 the vegetation was recorded with the scale of Braun-Blanquet; from 1976 on the scale of Londo (see Appendix I) was used. In some of the years, no recording of the vegetation took place: 1975, 1982 (only

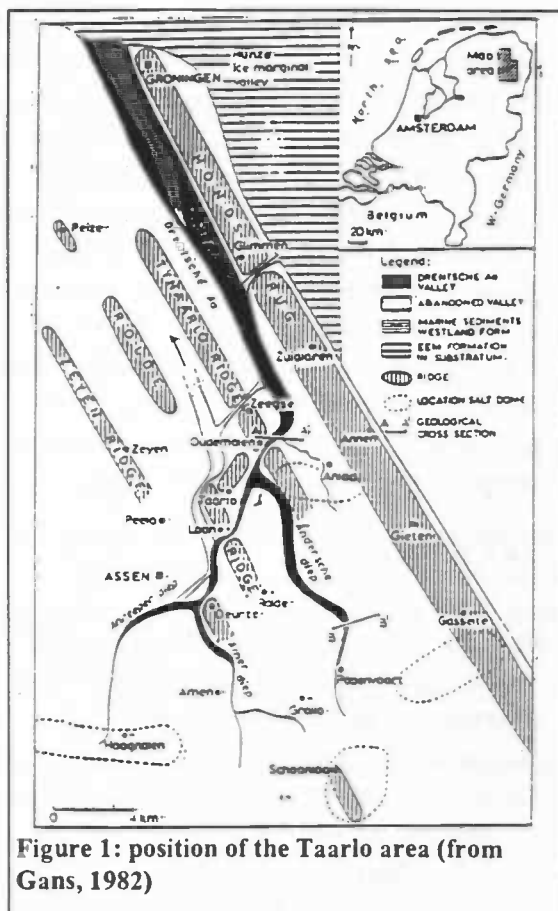


Figure 1: position of the Taarlo area (from Gans, 1982)

transect 431 was not recorded), 1985 and 1989. The vegetation data (Draa\_3) were stored in a database (Turboveg9.40).

### 2.3 Weather data

Data about weather conditions were obtained from the Royal Dutch Meteorological Institute (KNMI). These data originated from the closest weather station (Eelde Airport) and consisted of monthly means of precipitation, calculated (Makkink) evaporation and mean minimum temperature. The precipitation data were given in tens of millimetres, but were recalculated to millimetres. Averages over December-February (winter) and March-May (spring) were calculated using the program Excel 5.0a (Eelde.xls). The precipitation surplus/deficit was calculated by diminishing the averaged actual precipitation by the averaged evaporation. Then, (standardised) residuals were calculated in order to make a comparison with the species residuals. A residual of 0 (zero) represents the average value. Thus, a value above zero reflects a value which exceeds average (wet, warm); a value below zero reflects a value which is lower than average (dry, cold). The weather conditions that were considered: mean precipitation over two periods of three months (winter and spring) and mean minimum spring temperature. The following formula was used:  $(x - x_{\text{mean}})/SD$ .

### 2.4 Clustering

In order to evaluate what the changes in the permanent plots between 1972-1997 have been, a clustering of the relevés was carried out. All the separate plots were compared with three reference community (Grootjans et al., 1996) types, which contained the regionally occurring characteristic species on the alliance level (see table 1). The types used were *Calthion palustris*, *Cynosurion cristati* and *Arrhenatherion*. The references of these types were based on the vegetation typology of the Drentse Aa area as by Everts, De Vries & Grootjans (1980, deel 2: tables 2.6, 2a<sub>1</sub>, 2.9, 2b<sub>1</sub> and 2.10, 1b<sub>2</sub>). Some adjustments were made to fit the references better to the Taarlo brook area. The references differed from each other in species composition and cover. As a measure for similarity with the references, the Present Percentage index (PP) was used, which was calculated using a Pascal computer program (Types2). The PP was calculated by dividing the number of species which were both present in the vegetation and in the reference, by the total number of species in the reference. This was done in a quantitative way: both presence/absence and cover were taken into account.

The results are shown in figures (see Appendix IVa-c). Each graph for each plot (pq\*.wp) consists of three lines. The patterns of these graphs, the mean coverage and the mean change (increase/decrease) over the whole period (pqclean.wpd), were used to divide the 30 plots in three groups, which had a comparable vegetation development.

Table 1: References of vegetation-types used for the clustering

Calthion palustris n = 10		Cynosurion cristati n = 8		Arrhenaterion n = 10	
species	cover	species	cover	species	cover
Caltha palustris	10%	Agrostis tenuis	1%	Heracleum sphondylium	5%
Lychnis flos-cuculi	1%	Festuca rubra	10%	Anthriscus sylvestris	5%
Crepis paludosa	10%	Holcus lanatus	5%	Glechoma hederata	1%
Myosotis palustris	1%	Anthoxanthum odoratum	5%	Veronica chamaedrys	1%
Carex acutiformis	10%	Rhinanthus angustifolius	2%	Phalaris arundinacea	1%
Lotus uliginosus	10%	Plantago lanceolata	3%	Equisetum fluviatile	1%
Filipendula ulmaria	1%	Ranunculus repens	5%	Phyteuma nigrum	1%
Plantago lanceolata	1%	Cirsium palustre	1%	Viccia cracca	1%
Equisetum fluviatile	1%	Cirsium palustre	2%		
Equisetum palustre	1%	Filipendula ulmaria	3%		

2.5 Ordination

An indirect ordination was executed in order to obtain the most important factor for vegetation change. The ordination was carried out using a Detrended Canonical Correspondence Analysis (Ter Braak, 1987) in Canoco (version 3.10). Using OPLOT from the shell-program VEGROWv.5 (Fresco, 1991), the results of the ordination could be graphically presented in a two-dimensional diagram. The relevees were put in a diagram which consists of two axes. The position of a point is determined by the first axis and by the second axis. The meaning of both axes can be interpreted by looking at the relative position of the points. Points which are closely related in vegetation composition are also close to each other in the diagram. The extreme positions of the species in these types of diagram can be used to interpret the meaning of the axes. An indirect ordination is used here because no information was available about any directly measured (a)biotic factors.

2.6 Regression analysis

In order to detect successional trends for species, species response to time was calculated (Grootjans et.al., 1996). Deviations from this trend may be ascribed to weather fluctuations (Huisman, Olff & Fresco, 1993). A selection of 13 characteristic Calthion species (see table 2) was analysed separately using a third-order polynomial regression analysis technique. This technique is used to find the simplest possible model explaining the observed patterns. An additional parameter is incorporated only if it can explain a significant part of the remaining variation (Huisman, Olff & Fresco, 1993). The fit was continued to the third degree; an extra factor was added in case of statistical improvement of the fit. Here, a step forward regression was applied. That is, first a linear (1st degree) function was tested, then a secondary function and - if it gave a significant improvement of the description- a tertiary factor (third degree) was added. This significance can be given by  $R^2$ , which is a measure for the proportion of the variance that can be explained by the model.



Form of the function is:  $Y_t = a_0 + a_1t + a_2t^2 + a_3t^3$ , where  $Y_t$  is the estimated abundance and  $t$  is the time in years (Zar, 1996). In Excel, a spreadsheet was prepared to be used by the statistical computer program SPSS. In this spreadsheet the cover percentages from all the relevés from the group were averaged for each of the selected species for each year. This spreadsheet was exported as a Dbase-file (groep\*.dbf). For the commands used in SPSS see Appendix II.

This analysis (see Appendix II) was carried out within each group for each of the thirteen selected species. SPSS could carry out both the regression analysis and the statistical analysis (t-test). For the species that gave a significant reaction, a regression line based on the residuals calculated by SPSS, could be drawn using the graphical presentation program Sigmaplot 4.0 (resid1.jnb). For the species without successional trend, the residuals were calculated using the formula  $(x - x_{\text{mean}})/SD$ .

<i>Caltha palustris</i>
<i>Carex acutiformis</i>
<i>Crepis paludosa</i>
<i>Cynosurus cristatus</i>
<i>Equisetum fluviatile</i>
<i>Equisetum palustre</i>
<i>Filipendula ulmaria</i>
<i>Holcus lanatus</i>
<i>Lotus uliginosus</i>
<i>Lychnis flos-cuculi</i>
<i>Myosotis palustris</i>
<i>Phyteuma nigrum</i>
<i>Plantago lanceolata</i>

**Table 2: Species used for analysis**

## 2.7 Residual analysis

The next step was to correct the vegetation response for the successional trend. In order to relate weather conditions to changes in the vegetation composition it is best to look at extreme reactions from species which are important characteristic of the vegetation type. Those extremes could be derived from the residuals that remained after the correction for the successional trend. For species that showed a trend in succession, the residuals were calculated by SPSS; for the remaining species this was done manually. To find relations, the weather conditions were plotted in graphs in order to detect the extremes. When drawing these graphs, missing values were interpolated.

Two approaches were used to look for relations between species and weather residuals. First, regression coefficients (regres.xls) were calculated between the species residuals and the residuals of each of the three weather factors. This was done for each species from each group. Relations were assumed to be relevant if the value of the regression coefficient exceeded (+/-) 0,20. However, the correlation coefficient may not always be of any importance. This is caused by the fact that all residual values are used for the calculation and, consequently, values that do not deviate much from the mean are also taken into account. Therefore, a second approach was used. This approach was to look for extreme residual values of both species and weather factors in the same year.

### 3. RESULTS

#### 3.1 Vegetation changes

Three major response patterns could be recognised from the cluster analysis: (1) plots which showed Cynosurion as being the dominant vegetation type during most of the period '72-'97; (2) plots with Calthion as the dominant vegetation type and (3) plots with dominance for Calthion in one year and Cynosurion in another year. This resulted in three groups (see figure x). One group which could be characterised as a dehydrated Calthion (group 1, 8 plots), one group with equal aspects of Cynosurion and Calthion (group 2: intermediate Calthion, 6 plots) and one group consisting of well-developed Calthion palustris stands (group 3, 16 plots). The position of the groups within the transects is shown in figure x. In the first few years, larger fluctuations can be seen than later. The reference for Arrhenaterion resulted in very low PP's in all the plots and was therefore not considered. PP's varied in time and sometimes even reached values of 100%. For an overview of the reaction patterns of the separate plots, see Appendix IVa-c.

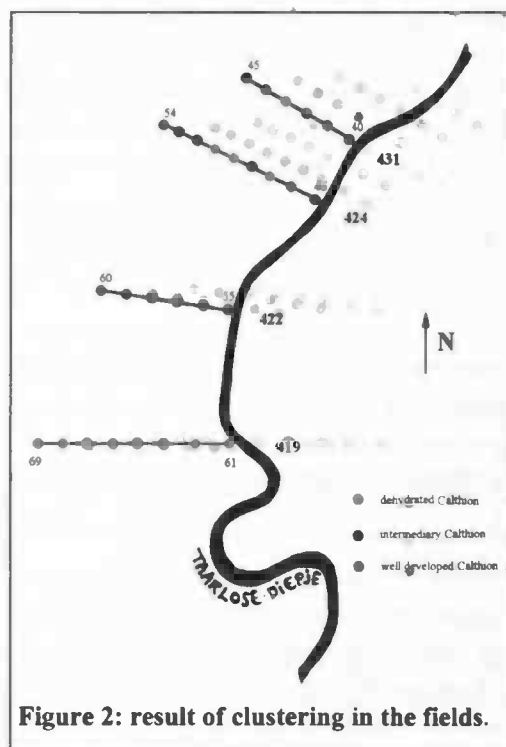


Figure 2: result of clustering in the fields.

#### 3.2 Successional trend

Not all the species showed a successional trend (see Appendix Va-d). Some showed no trend at all (*Cynosurus cristatus*, *Holcus lanatus*); some showed a trend in only one group out of the three groups (*Carex acutiformis*, *Equisetum fluv.*, *E. pal.*, *Filipendula ulmaria*, *Lotus uliginosus*, *Lychnis flos-cuculi*) or two groups (*Caltha palustris*, *Crepis paludosa*, *Myosotis palustris*, *Plantago lanceolata*, *Phyteuma nigrum*). Some species showed a (large) positive trend (*Crepis paludosa*, *Caltha palustris*, *Carex acutiformis*, *Myosotis palustris*, *Filipendula ulmaria*), some species showed negative trends (*Equisetum fluviatile*, *Lychnis flos-cuculi*, *Myosotis palustris*, *Plantago lanceolata*). Some of the negative trends (*Equisetum palustre*, *Lotus uliginosus*, *Phyteuma nigrum*) may be too small to be considered. Significance of the trends could be derived from  $R^2$ , the coefficient of determination. This value was on average higher in groups 2 and 3 ( $> 0.4$ ) as in group 1 (on  $< 0.2$ ).

In group 2 more species (8 in number) showed a successional trend in comparison to groups 1 (4) and 3 (4). *Plantago* in group 1 and *Filipendula* in group 2 were the only species that showed a fluctuating trend.

### 3.3 Range of cover values

The ranges of the cover values are extreme low for some species in some groups (see table 3). This is probably a result of averaging the cover value of several plots per group, because some species are only present in one of the plots. The high cover values of most species (*Carex acutiformis*, *Caltha palustris*, *Holcus lanatus*, *Crepis paludosa*) are a confirmation of dividing the plots into different groups. Group 3 is the average of well-developed *Calthion palustris* plots and accordingly has high cover values for this community-specific species like *Crepis*, *Caltha* and *Lychnis*. The group of the drier *Cynosurion cristati* has a higher percentage of *Holcus lanatus* and *Plantago lanceolata*. Group 2 has characteristics of both communities and is therefore intermediate for almost all species considered. Low cover values often give rise to no successional trend (*Caltha palustris*, *Crepis paludosa*) or a negative one *Lychnis flos-cuculi*, *Plantago lanceolata*). For *Myosotis palustris* the successional trend does not seem to be related to its cover value.

**Table 3: species reactions (real cover range & successional trend) per group (+(+)) = (strong) positive trend, (-(-)) = (strong) negative trend,  $\pm$  = fluctuating trend.**

Species	group	range cover (%)	successional trend	Species	group	range cover (%)	successional trend
<b>CALTHPAL</b>	1	0 - 0.3		<b>HOLCULAN</b>	1	1 - 35	
	2	0.5 - 5.5	+		2	1 - 12	
	3	0.5 - 7	+		3	0.5 - 9	
<b>CAREXACT</b>	1	3 - 25	+	<b>LOTUSULI</b>	1	0 - 0.016	
	2	0.1 - 11			2	1 - 5	
	3	6 - 18			3	1 - 4	
<b>CREPIPAL</b>	1	0 - 0.6		<b>LYCHNFLO</b>	1	0 - 0.8	-
	2	2 - 10	+		2	0.01 - 1.5	
	2	3 - 16	+		3	0.25 - 1.5	
<b>CYNOSCRI</b>	1	0 - 0.016		<b>MYOSOPAL</b>	1	0 - 0.06	
	2	0.25 - 5			2	0.025 - 0.45	+
	3	0 - 3			3	0 - 0.45	-
<b>EQUISFLU</b>	1	0.1 - 1		<b>PHYTEUMS</b>	1	0 - 0.06	
	2	0.5 - 7	-		2	0 - 0.25	-
	3	0.25 - 3.5			3	0 - 0.14	
<b>EQUISPAL</b>	1	ABSENT		<b>PLANTLAN</b>	1	3 - 24	$\pm$
	2	0.75 - 2.5			2	2 - 10	
	3	0.2 - 1			3	1.5 - 9	-
<b>FILIPULM</b>	1	1 - 6.5					
	2	3 - 35	$\pm$				
	3	5 - 33					

3.4 Weather patterns

The three weather factors fluctuate enormously over the years (see tables 4 and 5). These figures are shown in Appendix VIa-b. Effective precipitation in winter has been high in '88 and '95; low in '96. Moderate high precipitation fell in winters '77, '80, '84, '87, '90 and '94. Moderate low precipitation in '79, '82, '85, '89, '91 , '92 and '97. During the spring period much precipitation fell in '79, '83 and '94; moderate high precipitation in '81 and '85. Little precipitation in spring fell in '76, and '96. Table 3 contains actual precipitation values for winter and spring.

Extreme low spring temperatures occurred in '76, '86 and '96; high spring temperatures in '83, '85 and '94.

Table 4: Weather factors residual characteristics (P=precipitation, T=temperature, 0 between +0,5 and -0,5, + and - between +0,5 and -0,5, + and - = between 0,5 and 1, ++ and -- = between 1 and 1,5, +++ and - - = beyond a value of 1,5).

Year	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97
Pwinter	0	+	0	-	+	0	-	0	+	-	0	+	++	-	+	-	-	0	+	+++	- -	-
Pspring	- -	0	0	++	-	+	0	+++	0	0	-	0	-	0	-	-	0	-	+++	+	- -	0
Tspring	- - -	-	+	0	0	0	0	+++	0	++	- - -	-	0	+	+	0	0	0	+++	+	- -	0

Table 5: Actual precipitation (in millimetres) in winter and spring in 1976-1997.

year	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97
winter	193	219	143	172	222	209	130	203	245	119	182	241	271	140	220	156	124	177	141	361	77	157
spring	69	176	131	229	129	203	148	329	125	160	120	164	139	173	122	109	204	126	272	206	52	240

3.5 Ordination diagrams

The diagrams (see Appendix VIIa-c) show the changes of the separate plots for each group over the period '76-'97. The plots within each of the three ordination diagrams, showed changes in the same direction. The direction differed between the three groups, which means the plots were grouped according to a similar development.

It is clear that within the groups the changes are more or less the same and therefore the arrangement into three different groups can be justified. The dehydrated group shows a change mostly along the first axis from the right to the left. The change along the second axis is very small. In the intermediary group the plots show a change along the first axis from both directions (left and right) to a certain common point. The change along the second axis is directed downwards. In the well-developed group the distance over which the plots change is not very large. Overall do they show a development into the same direction.

Although the variance of both the axes in all diagrams is very low, it can be expected that the change pattern does not change much when the variance increases.

3.6 Correlation coefficients

Species correlation coefficients (see table 6) gave different results both within species and within groups. Some species had highest values for precipitation in spring (*Equisetum fluv.*, *Lychnis*, *Lotus*, *Crepis paludosa*, *Cynosurus cristatus*, *Plantago lanceolata*), others for precipitation in winter (*Carex acutiformis*) or mean minimum temperature in spring (*Holcus lanatus*, *Filipendula ulmaria*, *Carex acutiformis*, *Myosotis palustris*, *Phyteuma nigrum*). Also, the type of relation (positive or negative) differs within species (*Holcus lanatus*, *Crepis paludosa*) and within groups (*Lotus uliginosus*, *Lychnis flos-cuculi*, *Plantago lanceolata*). Few species showed a correlation for the same weather factor in each group (*Holcus lanatus*, *Lychnis flos-cuculi*, *Phyteuma nigrum*).

Table 6: Species-weather correlation coefficients of Dehydrated (1), Intermediary (2) and Well-developed Calthion (3).

dehydrated	CALTHP	CAREXA	CREPIPA	CYNOSC	EQUISFL	EQUISPA	FILIPULM	HOLCUL	LOTUSUL	LYCHNIS	MYOSOP	PHYTEU	PLANTL
R <sup>2</sup> (P winter)	-0.30	0.03	-0.06	x	-0.35	x	-0.18	0.16	0.11	0.01	-0.28	-0.17	-0.0
R <sup>2</sup> (P spring)	0.11	0.20	0.06	x	-0.04	x	-0.15	0.39	-0.17	-0.27	0.10	-0.14	0.0
R <sup>2</sup> (T spring)	0.31	0.37	-0.33	x	0.05	x	-0.41	0.51	-0.37	-0.14	-0.13	-0.34	0.0
intermediary	CALTHP	CAREXA	CREPIPA	CYNOSC	EQUISFL	EQUISPA	FILIPULM	HOLCUL	LOTUSUL	LYCHNIS	MYOSOP	PHYTEU	PLANTL
R <sup>2</sup> (P winter)	0.45	0.25	0.07	-0.11	0.01	-0.18	0.32	-0.03	0.03	-0.15	-0.27	-0.04	0.0
R <sup>2</sup> (P spring)	-0.18	-0.15	-0.23	0.36	0.64	0.02	-0.06	-0.01	0.36	0.29	-0.20	-0.20	-0.0
R <sup>2</sup> (T spring)	0.12	-0.04	-0.50	0.33	0.50	0.20	-0.19	0.25	0.26	0.06	0.00	-0.51	-0.0
well developed	CALTHP	CAREXA	CREPIPA	CYNOSC	EQUISFL	EQUISPA	FILIPULM	HOLCUL	LOTUSUL	LYCHNIS	MYOSOP	PHYTEU	PLANTL
R <sup>2</sup> (P winter)	0.22	0.31	-0.10	0.11	-0.07	-0.05	0.18	0.13	0.21	-0.06	0.09	-0.09	-0.0
R <sup>2</sup> (P spring)	-0.04	0.03	-0.33	0.39	0.52	0.17	-0.13	0.15	0.05	0.33	0.05	-0.27	-0.0
R <sup>2</sup> (T spring)	-0.05	0.08	-0.24	0.64	0.27	0.09	0.13	0.35	0.40	0.18	-0.24	-0.39	-0.0

3.7 Species residual reactions

The residual reaction patterns (see Appendix VIIIa-m) of the species can be different, within and between groups and in time. The species do not always react according to the same pattern or to the same extent within the different groups. Depending on the group of descent, the reaction can be very diverse. Some species do not show extreme reactions at all (*Plantago lanceolata*). Other species only show extreme responses in one or two groups. This is most often the case for the group in which the species is present, on average, with a certain minimum cover. Each species seems to have a minimum cover below which other than weather factors become more important.

Some species fluctuate between extreme values from year to year (*Carex acutiformis*), others show fluctuations over longer periods (*Filipendula ulmaria*). Some species reacted stronger in the beginning than later in the observation period (*Equisetum fluviatile*). This can be seen in particular for species with high cover values. Other species which do not respond to any of the weather factors, but instead are mainly influenced by management (*Caltha*, *Crepis*).

### ***Caltha palustris***

1. Only present in '78, '79, '94, '96 and '97 (<0.3%).
2. Constant level until '87. Large peak in '88-'90 (>5%), peaks in '93 (>2%) and '95 (>2%).
3. Declining trend towards '91 (peaks in '78 and '80); then increasing trend (peak in '95, low in '96). Steep increase in '94. Increase continues.

### ***Carex acutiformis***

1. No extreme deviation from 0 till '86, then decrease in '87. Then strong increasing trend (towards 25% in '94), followed by a decline in '97 (below 10%).
2. Fluctuating over the whole period (1-11%). Largest declines in '77, '79, '80, and '90-'91; largest increase in '84 and '88, high in '94/'95.
3. Strong decline in '77 towards lowest point in '80. From '81 on increase (6-18%). Cover and residuals stay at high level until '95, except for declines (below 0) in '87 and '90.

### ***Crepis paludosa***

1. Declining trend till below 1,5 in '90 (except two peaks in '77 and '79); later ('91) stable but below a cover value of 0.2%.
2. Decline in '77/'78, then stepwise increase ('79, '84), declining trend from '87 on, followed by a peak in '93 with decline in '94. Around average towards '97.
3. Strong fluctuating residuals without trend. Positive extremes in '80, '84, '87/'88, '92/'93 and '96. Negative extremes in '79, '81, '86, '90/'91 and '94/'95. Strong increase (16%) till 1988 (peaks at '82, '83 and '87), slight decrease (12-14%), then stable.

### ***Cynosurus cristatus***

1. Only present in '77 and '92 (high positive extremes) with very low cover (<0.016).
2. Extreme large peak (5%) in '77, declining trend (extreme low in '86, high in '88) until '90 (0.1%). Then in '93 a rise to a high positive extreme (3.5%), with a decline in '95-'96, after which recovery.
3. Most obvious residual declines in '76, '86 and '96 (<0.5%) and small ones in '80 and '90. Peaks in '77, '83/'84 and '93/'94 (>1%).

### ***Equisetum fluviatile***

1. Lowest cover in '84-'89 (<0.5%). Period before and after, cover values are more or less stable, but low (0.5-1%). Residuals show only extremes below 0 ('86/'87 and '93/'94).
2. Steep increase in '78, '83 and '94 (3-7%). Low cover value in '76, declines in '80/'81, '86-'93 and '96/'97 (<2%). Residuals show increasing trend, with remarking extremes in '83 (7%), '86 (5%) and '94 (3%).
3. Strong increase in '79 and '83, then decline until '93 (<1%) after which a small (to 1%) increase follows. Peaks in '79 and '83 (2.5-3.5%).

### ***Equisetum palustre***

1. Not present in this group.
2. Peaks in '78, '87 and '92 (increasing trend of residuals).

3. Lowest cover value in '78 (0.2%), after which an increase with steep peaks in '81 and '93. Recovers from low residual values from '76-'80 to high in '83-'86. The small fluctuations, positive in '90 and '92; negative in '94 and '96. Very high positive residual in '97.

#### **Filipendula ulmaria**

1. In '78 low residuals, also from '81-'84, then positive peak in '96 then stable around 2 %, then a peak in '86 (>5%). Decline to 1% till '93, then increase, strongest in '96.
2. From '77 to '90 a major increase (5-35%), with peaks in '79, '87 and '90, followed by a decline which is extreme in '93, then recovery.
3. From '76 (5%) on increasing, with a negative extreme in '78 and peaks in '82 and '88-'90 (>25%). Steep decline towards '93 (<10%).

#### **Holcus lanatus:**

1. Not stable. Large peaks in '77, '83 and '90 (20-35%). Decline in '78-'81, '84-'87, '93 and '96 (<5%).
2. Cover values not stable. Major peaks in '77, '83 and '90 (6-12%). Steep declines in '79, '87, '93 and '96 (<2%).
3. Unstable cover values. Peaks in '77 (9%), '83 and '90 and lowest values in '79-'82, '86-'87 and '93-'96 (<2%).

#### **Lotus uliginosus**

1. Only present in '76-'77 and '80-'81 (<0.05%).
2. Over '76-'97 reasonably stable (2-3%), large peaks in '82 and '88 ( $\pm 5\%$ ).
3. Small increasing trend. Some peaks in '77, '82, '84, '88 and '93. Decline in '76, '85-'87, '86, '91 and '96.

#### **Lychnis flos-cuculi**

1. Overall decline from '76 till '88. Low cover in '79 (<0.5%), peaks in '81(>0.5%) and '87. From '89 on absent.
2. Slight decline over '76-'88; lowest in '88, with peak in '79 (1.5%). After that recovery to former level ( $\pm 0.5\%$ ).
3. '76 - '88 decline, peak in '87, following '88 (<0.5%) increase to 1% level.

#### **Myosotis palustris**

1. Most of the period absent. Peaks in '79, '81, and '84. Absent between '76-'78, '83, '85-'95; reappears in '96 with very low cover (<0.02%).
2. Strong fluctuation. Peaks in '78, '81, '84 and '92 (>0.4%). Declines in '77, '79, '80, '83, '86-'88 and '96.
3. Decline to low level in '76 (<0.4%), peak in '79 (0.4%), then till '97 very low cover (0.2%), especially during '83-'86 (0.02%).

#### **Phyteuma nigrum**

1. Only present in '76-'81 and '86 with very low cover values (<0.04%).
2. Present in '76, '79-'81, '85/'86, '95 and '96 with low cover values (<0.25%).

3. High cover in '78, '80 and '97 (0.06-0.14%), but decline in '77 and '82. Absent in '83, '90, '91 and '94.

#### **Plantago lanceolata**

1. High cover in '76, '90 and '93 (>20%). Between '76-'88 U-shaped decline.
2. Peaks in '76, '80, '82 and '93. Steep declines in '77, '79, '81 '86 and '96.
3. Decline from '76-'79, from then on fairly stable cover values (2-3%).

## **4. Discussion**

### **4.1 Vegetation changes**

The vegetation changes within the area can obviously be very different on a relative small scale, due to locally differing situations. The fact that there are plots which show a year to year fluctuation in dominance to either Cynosurion or Calthion, means that after 20 years of management there are still plots in development. Results from Olff & Bakker (1991) indicate that productivity fluctuations can be determined by year to year variation in weather conditions. Though Arrhenaterion has been left out in the clustering, in some plots it reaches a fairly high PP. It may be that characteristic species from this vegetation in practice have more influence than expected.

### **4.2 Successional trend**

*Cynosurus cristatus* and *Holcus lanatus* may be much more influenced by precipitation or low temperature than by management (Keatington et.al. in: Whitehead, 1995). Drought may cause mineralisation of the peat, as a result of which more nitrogen is available for the plants (Grootjans, 1985). The growth of grasses from the more nutrient rich conditions will be stimulated by this. Species in the Intermediary Calthion are probably more influenced by management because the succession towards a Calthion vegetation is still in progress. In contrast to the Dehydrated Calthion group, the Intermediate group has, still the potential to become a well developed Calthion palustris. Soil and water conditions are good and, considering the increase of some of the important Calthion-species under the influence of the management (*Caltha palustris*, *Crepis paludosa*, *Myosotis palustris*), the prospects for this group are good.

Considering that the Dehydrated group is situated in a part of the area which is influenced by drainage, it is unlikely that it will develop into a Calthion vegetation. Here only *Carex acutiformis* is stimulated by the management, while *Lychnis* and *Plantago* decrease. Grootjans et.al. (1996) found an initial positive reaction of these species to drainage but a very distinct decrease afterwards. Why *Plantago* decreases is unclear. *Lychnis*, a typical Calthion palustris-species, could also be hindered by grasses. In the calculations for the polynomial regression, the period before 1976 was also used. Because of the use of the Braun-Blanquet scale instead of the Londo-scale in the period before 1976, this may have



caused unreal differences. The Braun-Blanquet-scale is less differentiated and gives overestimated percentages when transformed from Turboveg to Cornell condensed file. In order to omit any possible artefacts from this period it is left out in other presentations of data.

The particular pattern shown by *P. lanceolata* was also found by Olff & Bakker (1991). This pattern is even more pronounced in *Filipendula ulmaria*.

#### 4.3 Ordination diagrams

Changes along the axes of the ordination diagrams are very nicely uniform within all groups. Although the axes, however, can explain for only less than 10% of the variance, the changes must mean something. The changes are probably a result of appearing and disappearing of species caused by an underlying environmental factor. In the drained group time will play the most important role in the changes. For the other two groups, the change in time is displayed along the second axis.

It is actually not clear why the percentages are so low, although some explanations may be given. One explanation might be that too many species were left in the records when carrying out the DCA. The presence of rare species may blur the outcome of the DCA and cause the low percentage of explanation of the first axis.

Although it appears to be a very exact result, the outcome is influenced by the relevés themselves; they are not independent from one another. Though, it can be useful to get an idea about the changes that have taken place and the factors which caused these changes.

#### 4.4 Response of species residuals

Species relations to weather characteristics differ per species because of the differences in ecological and physiological adaptations. This relation may also differ if the species is present in different conditions (dry/moist), which can be seen clearly looking at the response of a species in the different groups. Both precipitation and temperature seem to have different effects under different soil conditions. The relationship between species and weather may also change in the course of the successional stage. In the following we will describe the response of individual species under different conditions

##### ***Caltha palustris***

Management has only effects on *Caltha* in the well developed situation. When soil conditions are too dry for the species to sustain, management cannot stimulate an increase of *Caltha*. The strong increases in '88 and '94 for the intermediate group may be due to relative wet winters; the residual decrease in '96 may be due to a dry winter. *Caltha* does not react to precipitation characteristics in the well developed group as would be expected from the correlation coefficients. The extremes show no consistent relation with winter precipitation. It may be that only under conditions of relative drought in previous years, *Caltha* reacts to a precipitation surplus after a recovery of the groundwater level. It has a wide moisture range (but with preference for wet conditions) in which it can survive, due to its thick roots. In the field probably an effect can be seen on the quality of the plant individuals (brown leaves). No effect of low spring temperatures can be seen, probably because *Caltha* regenerates very

quickly after dying back due to night frost (pers. obs.). Seeds of *Caltha* are mostly short-term persistent (Thompson et.al., 1997).

Concluding, management may have the largest influence in the beginning (10 years). Then, winter precipitation becomes more important due to the influence on the upwelling of groundwater. This is particularly true for the drained situation.

### **Carex acutiformis**

*Carex acutiformis* appears to remain stable in all the groups, and shows fluctuations which seem to be caused by winter precipitation. Extreme high residuals in '88, '94 and the lesser extreme in '84, can be related to extreme high winter precipitation in those years. This can be seen for both the intermediate and the well developed group. Strangely though, in these groups, *Carex* seems first to be (negatively) related to low or high spring temperature, but later on positively: the relation switches sign. What may cause this 'switch' reaction pattern of *Carex*, is not clear. It may also be that this 'switch' is just caused by the successional stadium. Then the reaction on precipitation must be related to the nutrient status of the soil, which is related to the management. In the dehydrated group, *Carex* at first doesn't seem to be influenced. But the strong decreases in '87 and '97 may be caused by an extreme low temperature; the opposite relation seems to be present in '94.

*Carex* is only influenced by management in the dehydrated group. A precipitation surplus or deficit does not influence the cover of *Carex* here, but temperature is more important. *Carex acutiformis* has an ill developed seedbank (Thompson et.al., 1997), but good opportunities to extend their root system, which it may utilise in drained conditions.

### **Crepis paludosa**

Except the large influence of management in the intermediate and well developed groups, temperature adds to the fluctuations. In both groups the species is (negatively) correlated to temperature in spring, which can also be found clearly by looking at the extremes of '76, '83, '86, '94 and '96. This may be an effect of open spaces caused by dying back of species in years with low spring temperatures. Indirectly, this means a correlation to dominance of *Holcus*. This relation is less important for the well developed group, in which *Holcus* has only a low cover. *Crepis* does seem to be capable of reappearing in the vegetation after one year of absence. This could be an artefact of not finding individual plants in the vegetation, considering the low cover of past years. According to findings of Bakker and Olff (1995) *Crepis* does replicate vegetatively, but seems to fail to colonise other fields. If conditions are bad for a few years in succession, recovery by seed is not very likely, because the seed bank is short-persistent (Thompson et.al., 1997). Fluctuations in the dehydrated group are only of importance in '77, '79 and '90. The first two can be related to the precipitation deficit in the previous years, but for '90 it is more likely that dominance of *Holcus* was responsible.

### **Cynosurus cristatus**

The abundance of *Cynosurus* can be related to spring precipitation and temperature for both the Intermediate as the well developed group. Only in the well developed group the relation to spring temperature is stronger. This can clearly be seen in the residual extremes. *Cynosurus* is the dominant grass species in the well developed group, while *Holcus* is

dominant in the dehydrated group. Turkington et al. (1979, in Bakker et al., 1980) demonstrated that the sward dominated by *Holcus* was more competitive than *Cynosurus*.

### ***Equisetum fluviatile***

Both the intermediate and well developed group are very well correlated to spring precipitation. This can be confirmed by the extremes from '76, '96 (dry) and '79, '83 and '94 (wet). The extremes become weaker in time. Apparently, the successional stadium interact with this effect. *Equisetum* can flourish in anaerobic conditions. During a year with a high precipitation surplus therefore it has an advantage over species that do not grow well under anaerobic conditions. Only in the drained group there is no relation with spring precipitation. *Equisetum* is already present with a very low cover value because the soil conditions on average are too dry. The negative correlation with winter precipitation, may point out an opposite effect in respect to the other groups, because of both the low cover values and the dry soil conditions. In the dehydrated group *E. fluviatile* seems only to be positively affected by the negative effect of low spring temperature on other plant species. It can then colonise open spaces.

In the dehydrated group the competition with grassy species appears to be important. For the well developed group *E. fluviatile* reacts negatively in '93 when *Cynosurus* is very dominant. Since both species are very positively correlated to precipitation in spring in this group, the positive effect on *E. fluviatile* is most likely diminished by the larger effect (and thus large dominance) on *Cynosurus*.

### ***Equisetum palustre***

It would be expected that cover of *Equisetum palustre* is related to precipitation, since it is sensitive to moisture conditions, like *E. fluviatile*. The species shows the most eminent decrease in groups 2 and 3 in '76 and '96, which both had a dry spring and summer. *E. palustre* has possibly a better capacity to survive in dry conditions than *E. fluviatile*. Total absence in group 1 occurs, probably because of the long-term dry soil conditions. All these reactions, however, cannot be explained by correlation, because the coefficient values are too low in all groups.

### ***Filipendula ulmaria***

*Filipendula* in the dehydrated group is negatively correlated to spring temperature, which can clearly be confirmed by the extremes of '83 (warm), '86 and '96 (cold). In '76 drought must have decreased the positive reaction. The positive correlation of the intermediate group to winter precipitation cannot be confirmed by the extremes present.

In the period '86-'93 all groups show a certain decline, which may be caused by the overall extreme precipitation surplus of '88. A very negative reaction for *Filipendula* in all the groups can be seen in '93. No extreme precipitation or temperature can be pointed out to explain this. It could be that, because of the large increase over the previous period, a negative effect of mown biomass has taken place. Mown material may have been left behind, which after several years created open spots. Other species such as *E. fluviatile* and *palustre*, *Holcus lanatus* and *Plantago lanceolata* show a negative effect in '93 or '94. In '95 and '96 in almost all plots an average of 10% dead material can be found (3-75%). If in '93 much

mown material has remained on the site, it could have shown an effect in '94. This is, however, hard to trace because recording of dead material has not been done consequently.

### **Holcus lanatus**

This species reacts strongly negative to the low spring temperatures in '76, '86 and '96 in all three groups. This is also what De Vries & 'T Hart found (in Watt, 1978). A high spring temperature gives a positive effect. This relation is stronger for the dehydrated than for the intermediate and well developed group. Although '89 and '90 have reasonable, but not extreme, spring temperatures, *Holcus* does react very positively.

Bakker (1980) suggests that in 1979 the wet spring could have lowered the N-mineralisation rate resulting in a low  $\text{NO}_3^-$  content and a low *Holcus* cover. A decrease of availability of mineral N or other growth-limiting factors, causes a decrease in *Holcus lanatus*, because this species responds both to direct availability of mineral N applied as N fertiliser in a *Holcus/Agrostis* community (Elliott et al. in: Watt, 1978) and to indirect availability if N, resulting from lowering of the groundwater table in a *Calthion palustris* (Grootjans, 1985).

Overall, *Holcus* is a strong competitive species, which will according to Bakker (1980) keep species number low. Bakker and Olff (1995) also found that the cumulative nitrogen balance is probably a better explanation for the variation in cover and frequency of *Holcus lanatus* than the number of years of management.

### **Lotus uliginosus**

In the Intermediary group *Lotus* is positively correlated to precipitation in spring, which can be confirmed by the extremes of '76, '79, '84 and '90. The disappearance of *Lotus* in group 1 is probably caused by severe drought conditions of the soil. *Lotus* is capable of vegetative replication, but in this case the conditions are too dry to survive. It's negative correlation has no meaning due to absence in years of extreme spring temperatures. Maybe due to the mineralisation of the peat in dry conditions, *Lotus* is outcompeted by better competitors of higher nutrient conditions (*Holcus*). In the other two groups, *Lotus* shows a large increase in '83 and '88, which both might be related to the extreme total precipitation. Only in groups 2 and 3 both the cover and the exfiltration potential are high enough to keep *Lotus* present in the vegetation. After 1976, which was an overall extreme dry year, a slow recovery towards higher cover can be seen.

A wet spring slows down the N-mineralisation. *Lotus* is capable of fixating nitrogen with the help of underground root nodules. So it should be expected to be a better competitor in conditions of low N-availability, like a precipitation surplus. Correlation to minimum spring temperature could be explained by the relation of temperature to nitrogen mineralisation of the soil. When temperature is high, N-mineralisation is high too and *Lotus* is outcompeted by other species, like grasses. This cannot be found for groups 2 and 3 in which the grasses are much less dominant. Here, the correlation is positive (to precipitation and temperature, respectively), which means that *Lotus* can profit from the available N-pool.

### **Lychnis flos-cuculi**

The disappearance of *Lychnis* in group 1 is probably a combination of low cover and soil conditions being too dry for seedlings to survive. From the negative correlation to spring

precipitation one can see that if a precipitation surplus is present, it probably has a negative effect on the scarce seedlings that are present. This is true for the extremes in '76, '79 and '83, but not for the remaining because of total absence in the vegetation. Bakker et al. (1980) conclude from their results that a dense canopy hinders seedlings to become juveniles. This and bad seed dispersal may play a role in the decreasing trend of *Lychnis*. In this case *Lychnis* can be spread by mowing machines, which may delay the disappearing of it from the vegetation. Although the number of viable seeds found on mowing machines is low, it is likely that *Lychnis* can be dispersed in this way (Bakker & De Vries, 1988). Grootjans et al. (1996) noticed that *Lychnis* showed a strong decrease before *Myosotis* disappeared. Here, the low initial frequency and the development of a closed sward of grasses caused the decline. New establishments however occurred in a few plots after drainage because open gaps appeared in which seedlings germinated.

### ***Myosotis palustris***

*Myosotis* is negatively correlated to winter precipitation in the dehydrated and intermediary group. This relation can clearly be seen for the extremes. Apparently after ten years, *Myosotis* can return in the vegetation, likely due to spreading by mowing machines.

*Myosotis* is negatively correlated to winter precipitation in both the drained and intermediate group; in the well developed group to spring minimum temperature. Seedlings of *Myosotis* as well as of *Lychnis* are very small and delicate and may be killed by freezing. Whether or not the relation to spring temperature is real, can be doubted. No confirmation can be given by the residual pattern: only a few extremes are present. The negative relation to spring temperature could be a result of appearing of open spaces, in which *Myosotis* can establish. Due to extreme weather (frost) open spaces in the vegetation may occur because of the negative effect it has on certain (dominant) species. In this way seedlings of less dominant species, like *Myosotis*, can establish.

### ***Phyteuma nigrum***

*Phyteuma* is negatively correlated to spring temperature in all groups. This is, however, a weak relation, due to periods of absence in all groups. Although cover values are low, *Phyteuma* is capable of reappearing in the vegetation after several years of absence. It could be that, because *Phyteuma* individuals can become fairly old in some cases *Phyteuma* was actually present but didn't flower or formed only few or no leaves and consequently wasn't noticed.

Boerrigter (1995) found a decline of *P. nigrum* in the Drentse Aa area, possibly caused by acidification, impoverishment and decreasing wetness. She mentions that superficial acidification might therefore be an important cause of decline in the shallow rooting *P. nigrum* in this area. This may explain why *Phyteuma* reacts positively in the well developed group after years with a precipitation surplus. The explanation Boerrigter (1995) gives is that a surplus of (acid) precipitation would cause a lowering of the soil pH, for which *Phyteuma* is sensitive. Superficial acidification of the peat soil (Grootjans & van Duren, 1995) in the dehydrated group may already have had a negative influence on *Phyteuma*. Another remark is that in case of a precipitation deficit, pH is also lowered because of the mineralisation of the peat.

Reitsema (1974, in Boerrigter, 1995) considers the poor dispersal ability accountable for its rarity in the Drentse Aa. Bakker (1989) and Everts & De Vries (1991) found that meadow populations of *P. nigrum* are restricted to plant communities of the *Calthion palustris* with *Carex acutiformis*. These communities are found in superficially drained meadows with a strong influence of discharging  $\text{Ca}^{2+}$ -rich groundwater and are restricted to the middle course of the Drentse Aa. In the Taarlo area there is a strong influence of upwelling  $\text{Ca}^{2+}$ -rich increase in cover of *Phyteuma* in the vegetation.

In all groups, *P. nigrum*, is decreasing to a certain extent. This can, however, not be explained by any of the weather factors.

### ***Plantago lanceolata***

Everts, Grootjans & De Vries (1984) suggest that *Plantago* may increase due to superficial drying out of the peat layer. This may be the reason that the successional trend of *Plantago* is curved. But, here the fluctuations of *Plantago* show no spectacular changes and actually not big enough to be related to precipitation or temperature.

### **4.5 Concluding remarks**

The effect of management on species of the *Calthion* community in general is more profound in the areas where the community is well developed (that is moist-wet conditions). Here, more species do react (positively) compared to the dehydrated situation, where more negative reactions can be found. This may be related to cover values of species, which are mostly lower in the dehydrated situations. Moreover, the amplitude of the effect diminishes later onwards in the successional stadium. Beside the management, weather (both precipitation as temperature) can have very diverse effects on the *Calthion* species by very different causes. In this case too, species reaction is dependent on cover. Not only can this determine whether or not an effect can be seen, but also what the amplitude and sign (positively or negatively correlated) of the reaction looks like. Only few species show no relation to either precipitation or temperature. Afterwards, with ecological knowledge and insight, explanations can be found and understood for the way species reacted in combined situations. Figueroa and Davy (1991) conclude for their Spanish grasslands that rainfall might affect individual species directly; or indirectly through biotic interactions. Some of their results suggest some sort of direct effect of water availability on plant performance. In the wet *Calthion* vegetation this will probably not be the case, because moisture conditions are not limiting plant growth but indirectly determine nutrient conditions. Only in extreme situations (drought) or by other influences (drainage) species may be affected. As mentioned by Grootjans et.al. (1996) population dynamic processes are likely to be responsible for changes in species composition.

## **Further Research**

Perhaps in future investigations it will be interesting to look for accelerating or delaying effects of weather on the vegetation succession. Will a certain vegetation succession be influenced by extreme patterns of weather factors and what will be the role of management in such a situation? To improve on the methods, searching for coincidental relations may be done using a MonteCarlo test. It will also be interesting to look for relations between rainfall in summer and autumn and species cover in the following years. More data about groundwater level and its (immediate) reaction to precipitation will give more detailed insight into the processes.

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## APPENDIX I : Londo vegetation recording scale:

r = 1 or 2 individuals (rare)	p/a/m1 = 1%	1- = 7 %
p = 3 - 20 individuals	p/a/m2 = 2%	1+ = 13 %
a = 20 - 100 individuals	p/a/m4 = 4%	
m = more than 100 individuals	1 = 10 % (2 = 20, 3 = 30 etc.)	

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## APPENDIX II : Commands used in SPSS for the polynomial regression:

```
translate from' g:\windows.311\ploec\groep*.dbf/FIELDNAMES
LIST.
REGRESSION/VARIABLES Tijd1 Tijd2 Tijd3 CALTHPAL /DEPENDENT
CALTHPAL/METHOD /FORWARD /RESIDUALS /CASEWISE DEFAULTS RESID
ZRESID /SAVE ZRESID.
TRANSLATE TO' g:\windows.311\ploec\'CALTH*.WK1' /KEEP Tijd1 /ZRE_1
/FIELDNAMES.
```

---

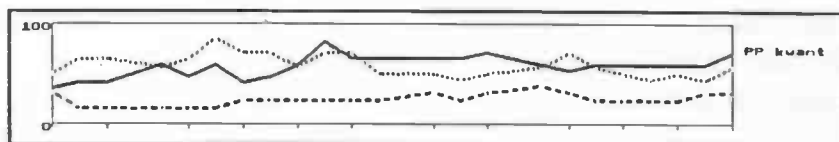
## APPENDIX III : Files prepared and used

<i>Turboveg files:</i>	<i>Word Perfect files:</i>	realrel4.xls
Draa_3	pq1.wp	Eelde.xls
	pq2.wp	
groep2.txt	pq3.wp	<i>Pascal program:</i>
groep3.txt	oplot2.wpd	types2.pal
groep14.txt	oplot3.wpd	
	oplot14.wpd	<i>Cornel Condensed files:</i>
groep2.dbf		Calthion.cc!
groep3.dbf	<i>Excel files:</i>	Arrhena.cc!
groep14.dbf	residu1.xls	Cynosuri.cc!
	sd2.xls	Taarlo40.cc! -
<i>SPSS files</i>	sd3.xls	Taarlo69.cc!
groep2.lis	sd14.xls	
groep3.lis	correl.xls	
groep14.lis	tektab.xls	Eelde.dat
	realrel2.xls	Leesmij.doc
<i>Sigmaplot files:</i>	realrel3.xls	
regres1.jnb		

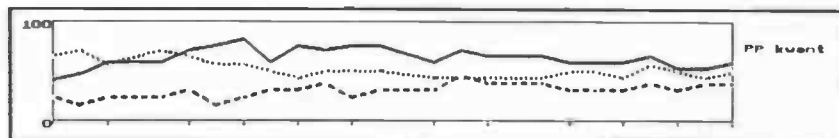
# APPENDIX IV a: PP-reaction patterns of separate plots (40-49).

————— *Calthion palustris*  
 ..... *Cynosurion cristati*  
 - - - - - *Arrhenaterion*

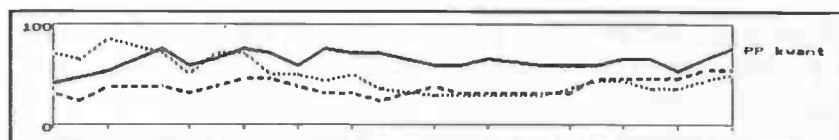
Pq 40



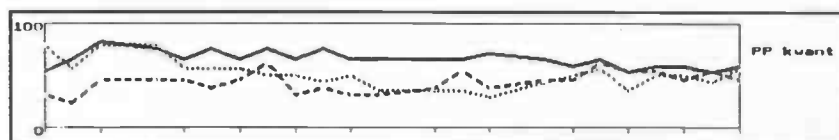
Pq 41



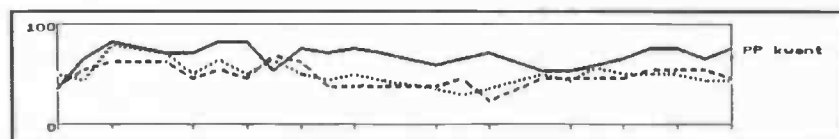
Pq 42



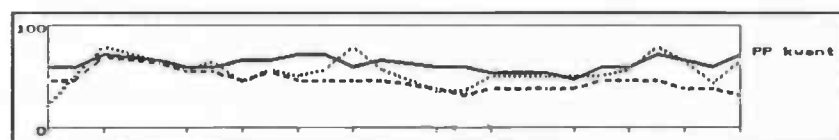
Pq 43



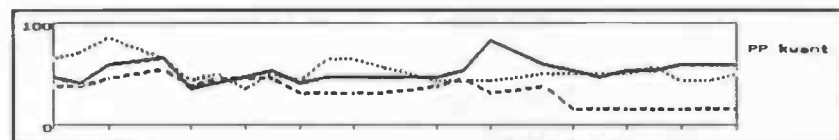
Pq 44



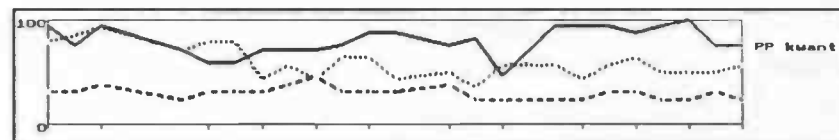
Pq 45



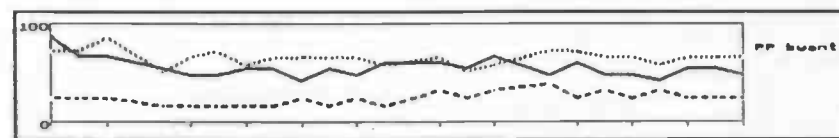
Pq 46



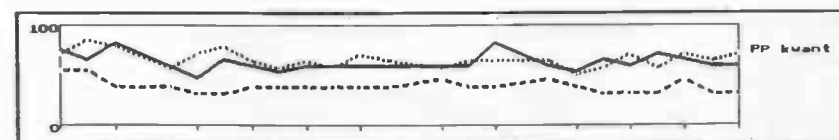
Pq 47



Pq 48



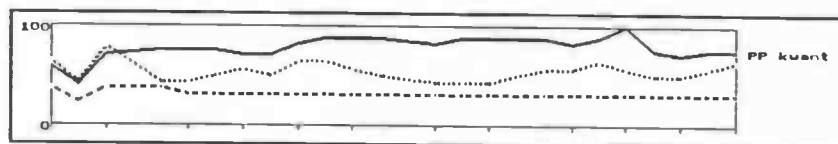
Pq 49



# APPENDIX IV b: PP-reaction patterns of separate plots (50-59).

————— *Calthion palustris*  
 ..... *Cynosurion cristati*  
 - - - - - *Arrhenaterion*

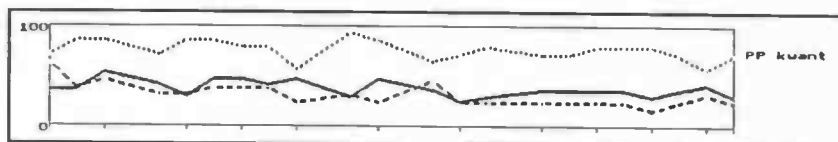
Pq 60



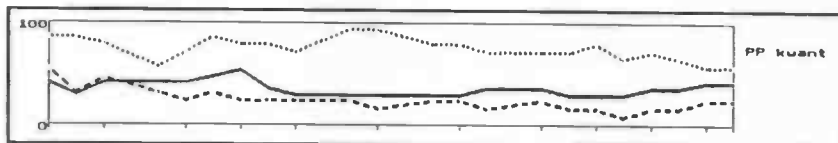
Pq 61



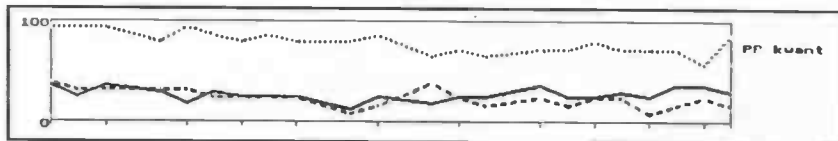
Pq 62



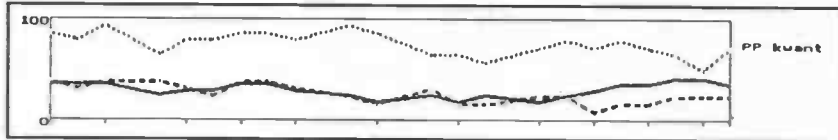
Pq 63



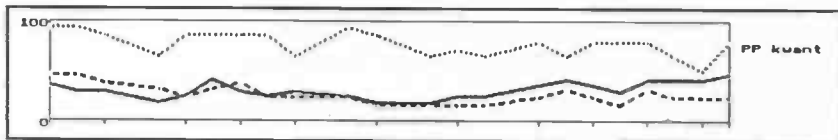
Pq 64



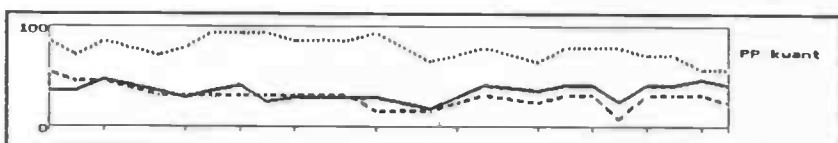
Pq 65



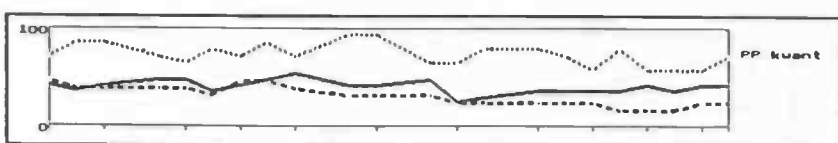
Pq 66



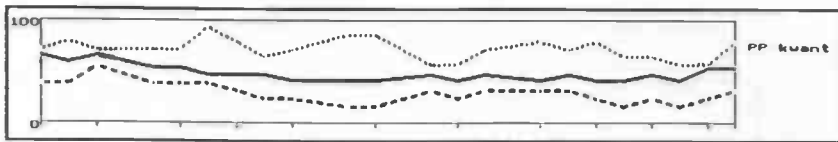
Pq 67



Pq 68

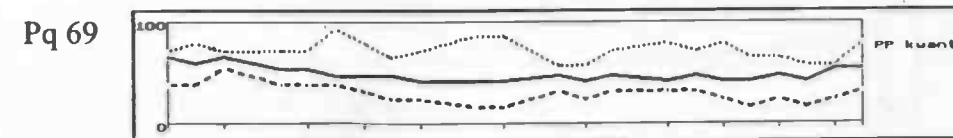
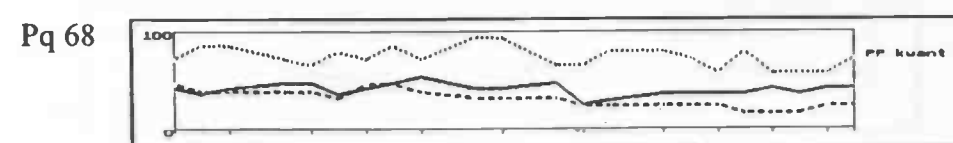
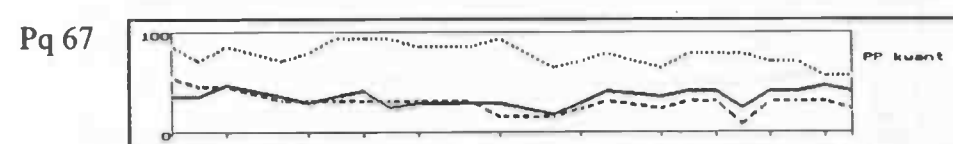
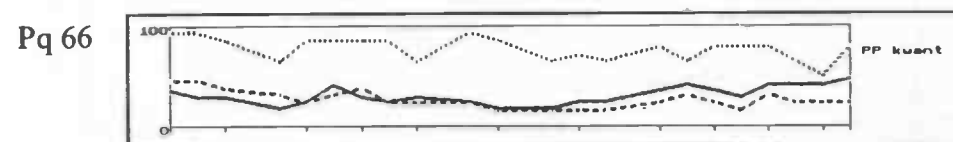
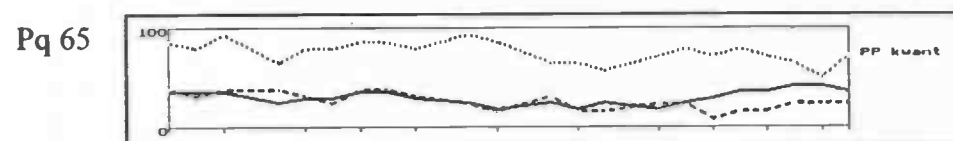
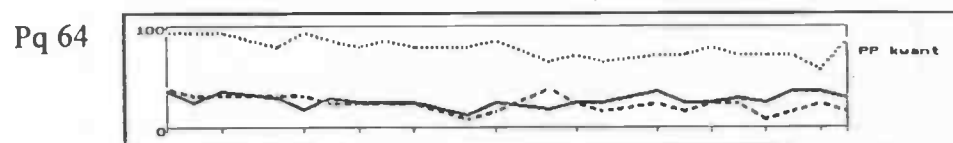
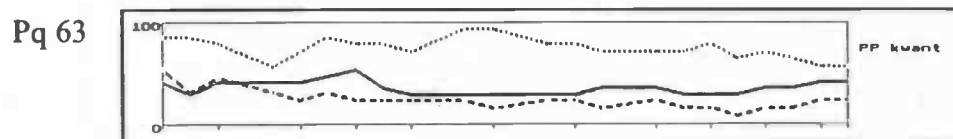
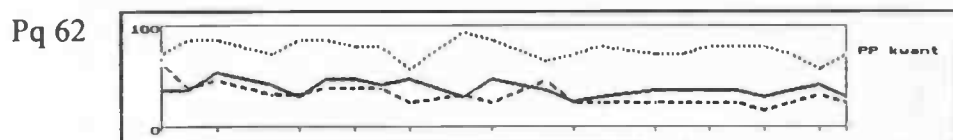
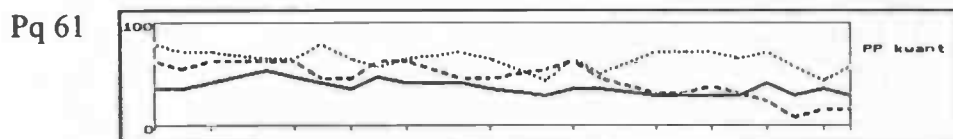
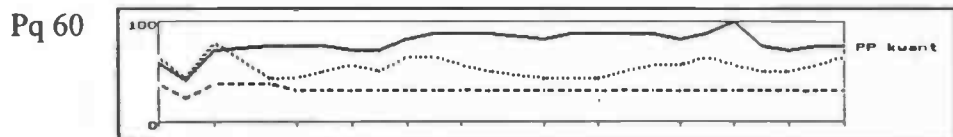


Pq 69

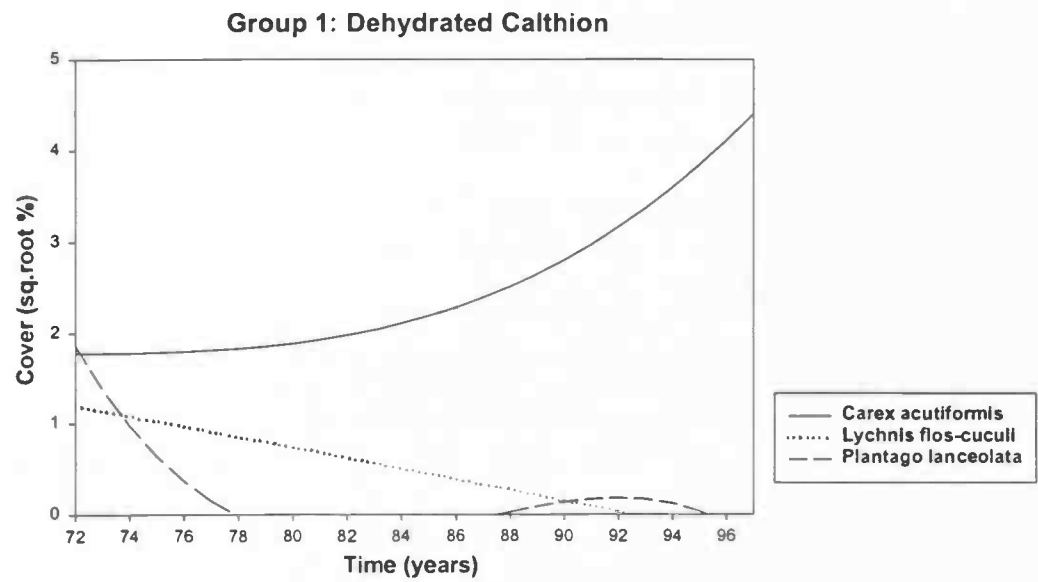


# **APPENDIX IV c: PP-reaction patterns of separate plots (60-69).**

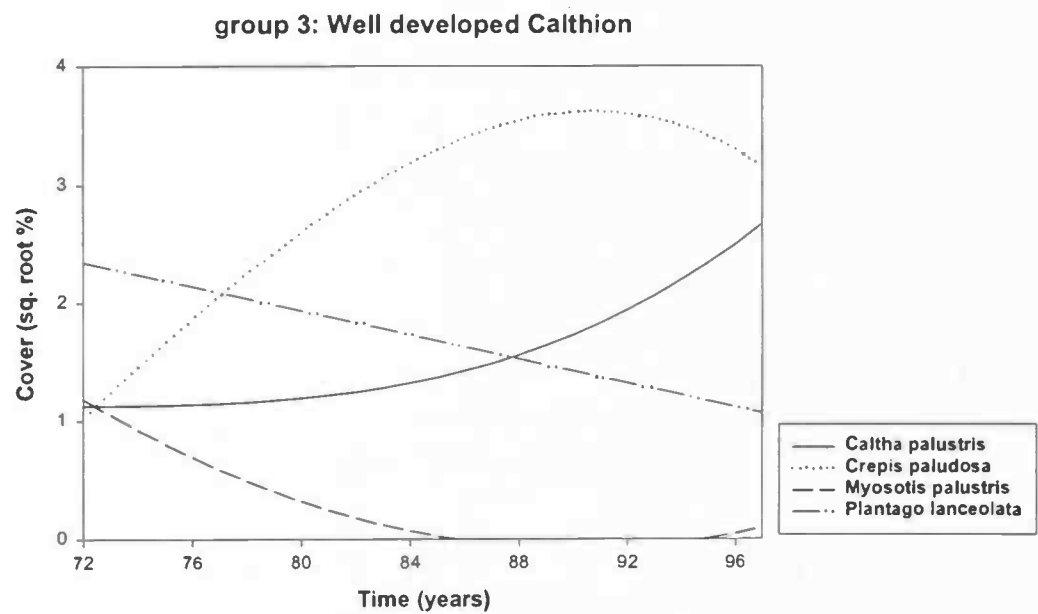
————— *Calthion palustris*  
 ..... *Cynosurion cristati*  
 - - - - - *Arrhenaterion*



APPENDIX V: Successional trend

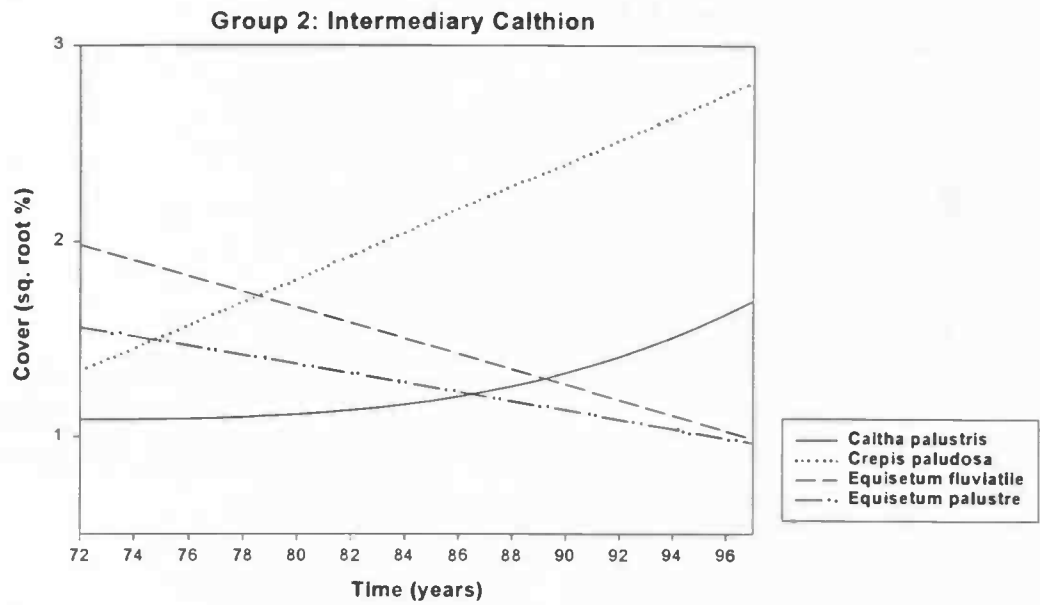


V a

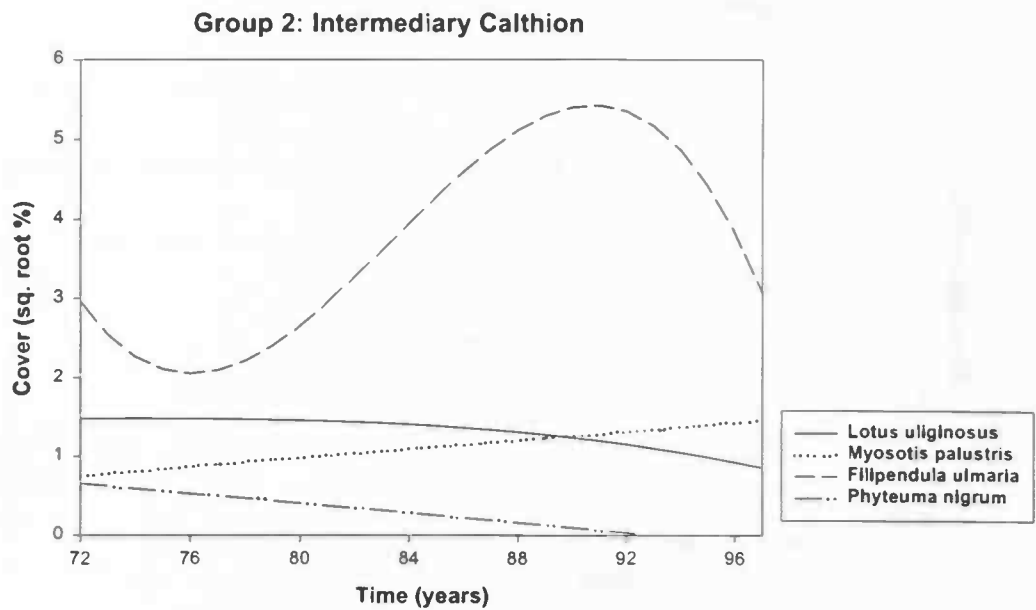


V b

APPENDIX V: Successional trend

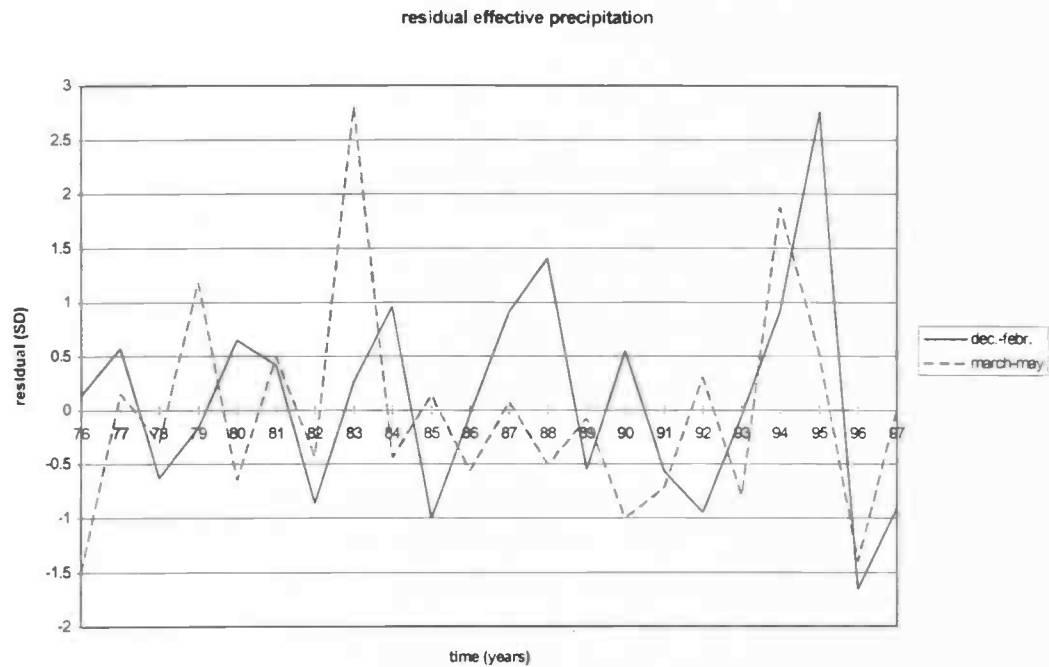


V c

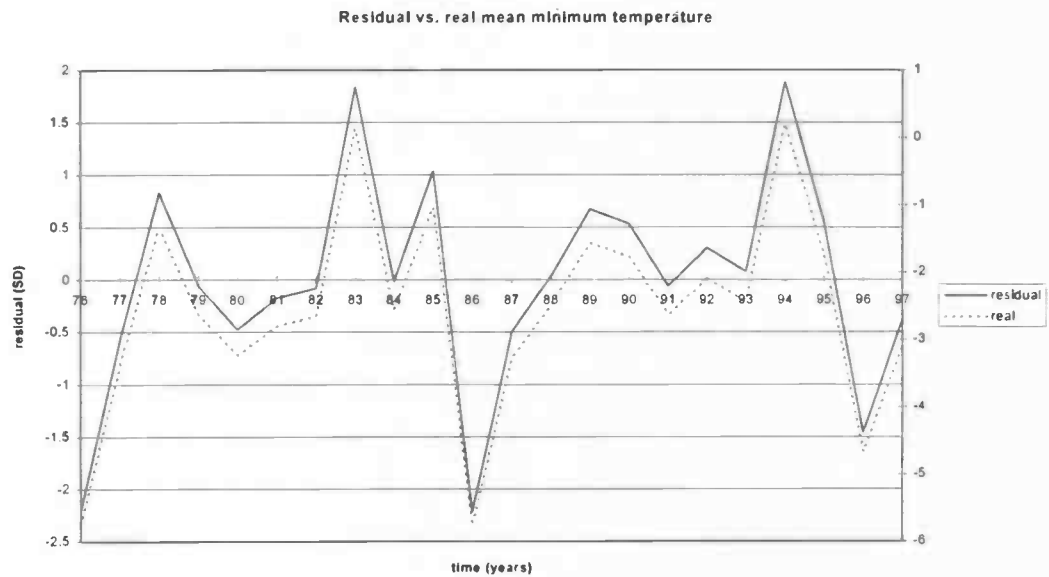


V d

APPENDIX VI: Weather factors residual patterns



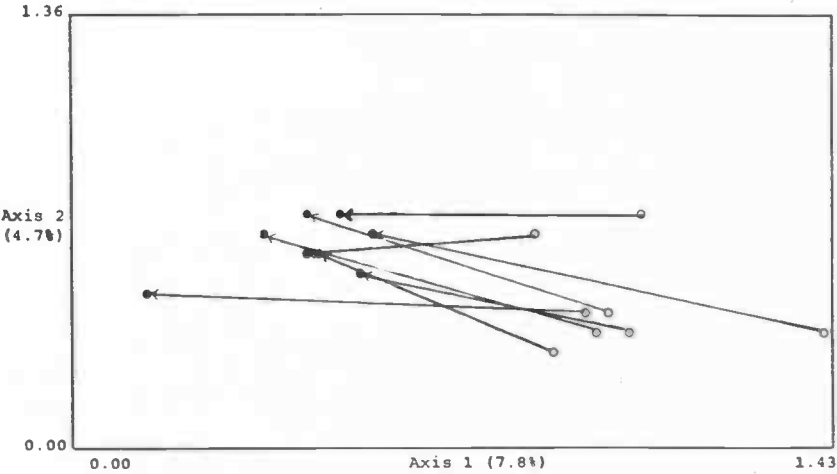
VI a



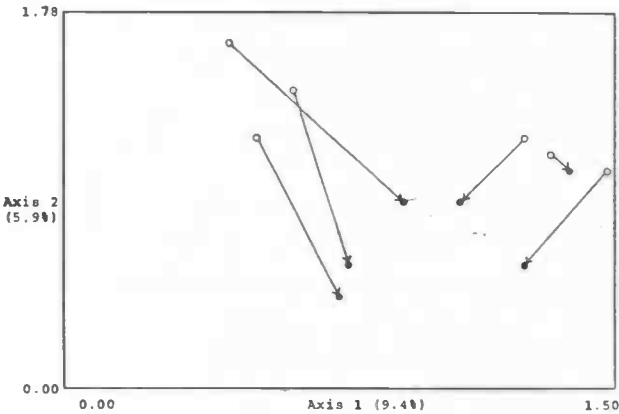
VI b



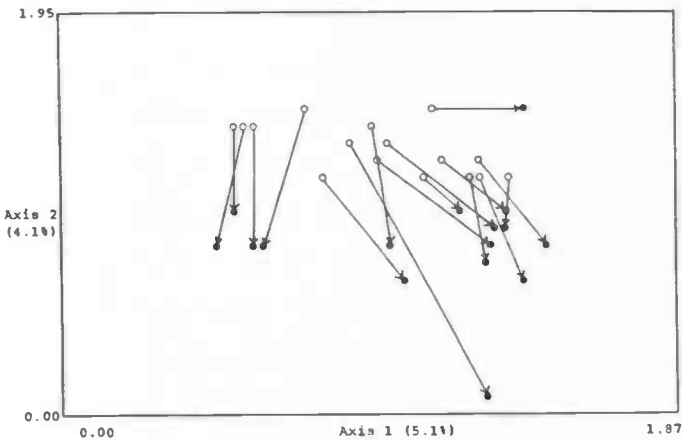
**APPENDIX VII: Ordination diagrams**



**a: group 1 (Dehydrated Calthion) 1976 (●) → 1997 (○)**

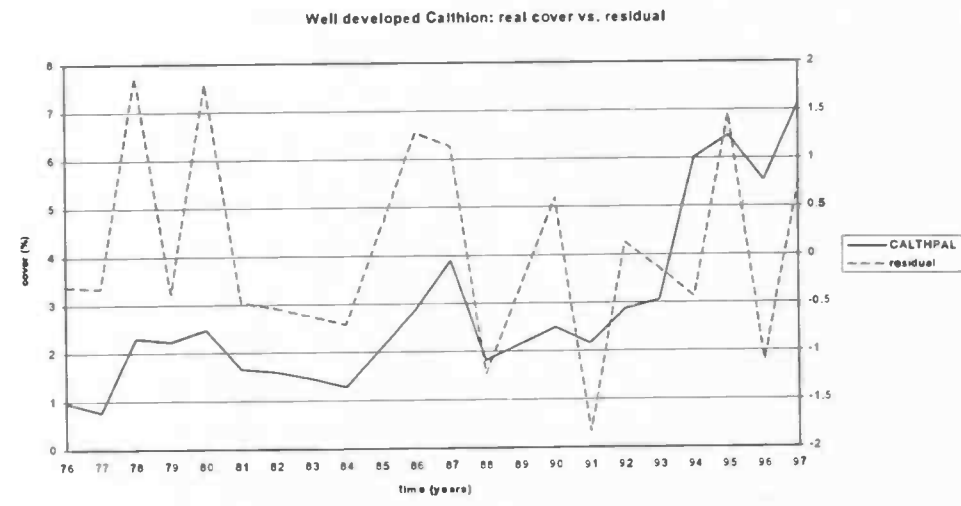
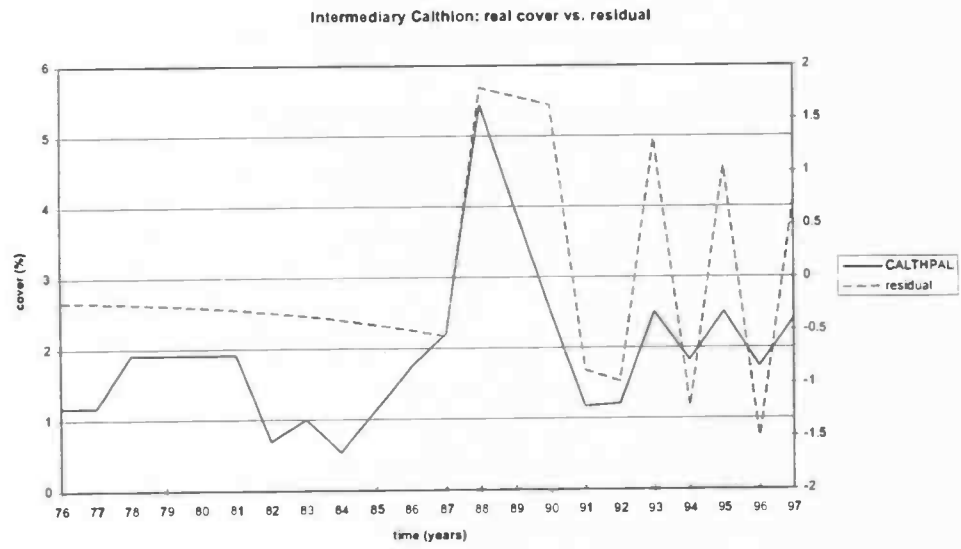
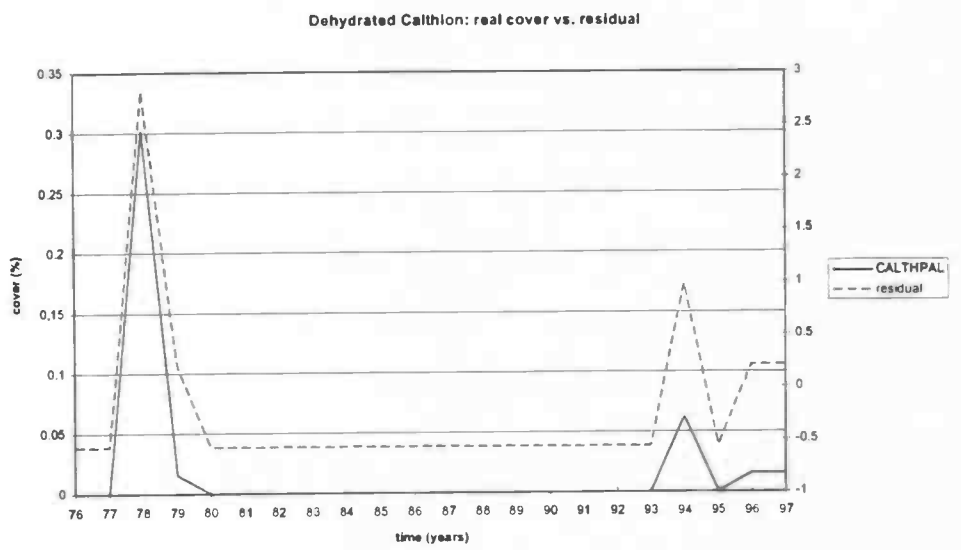


**b: group 2: (Intermediary Calthion) 1976 (●) → 1997 (○)**



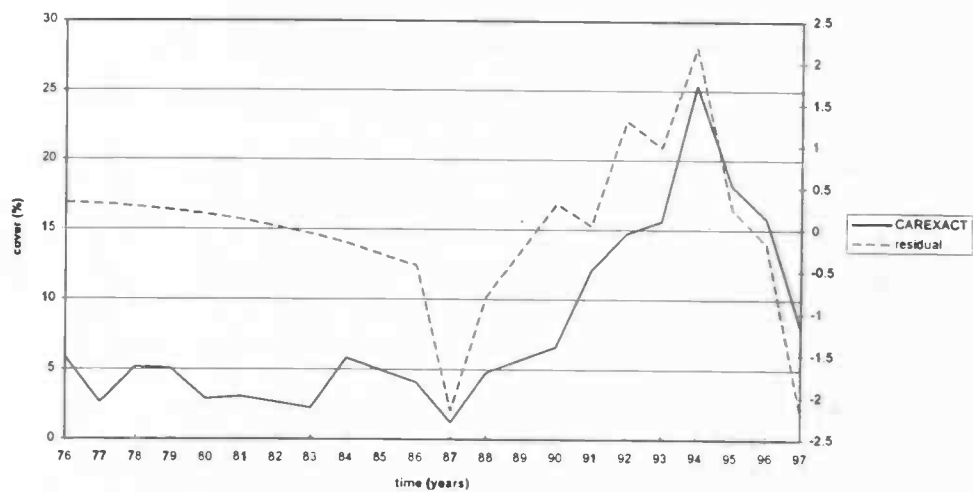
**c: group 3 (Well developed Calthion) 1976 (●) → 1997 (○)**

APPENDIX VIII a: residual reaction *Caltha palustris*

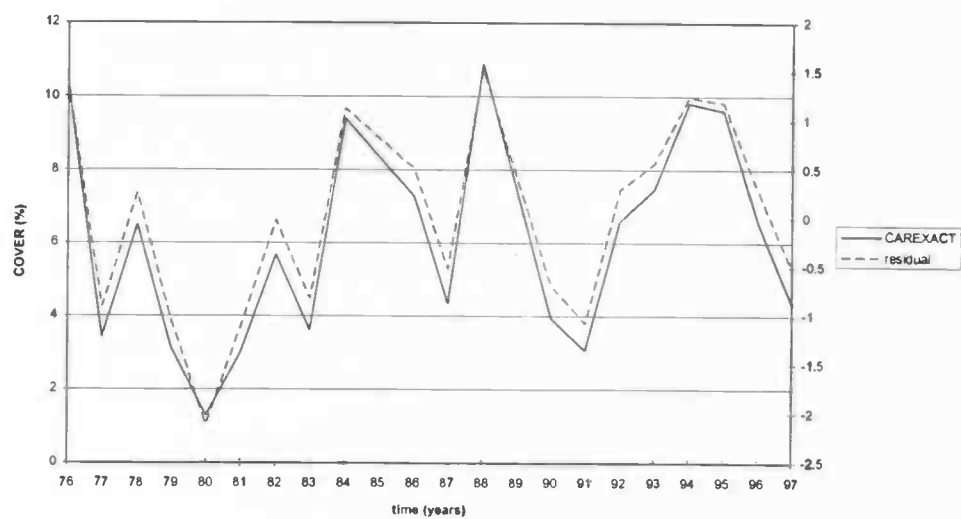


## APPENDIX VIII b: residual reaction *Carex acutiformis*

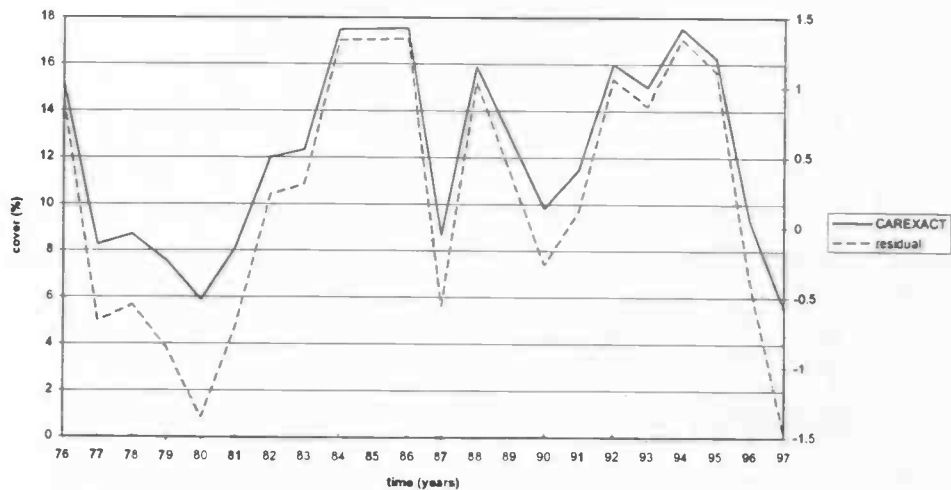
Dehydrated Calthion: real cover vs. residual



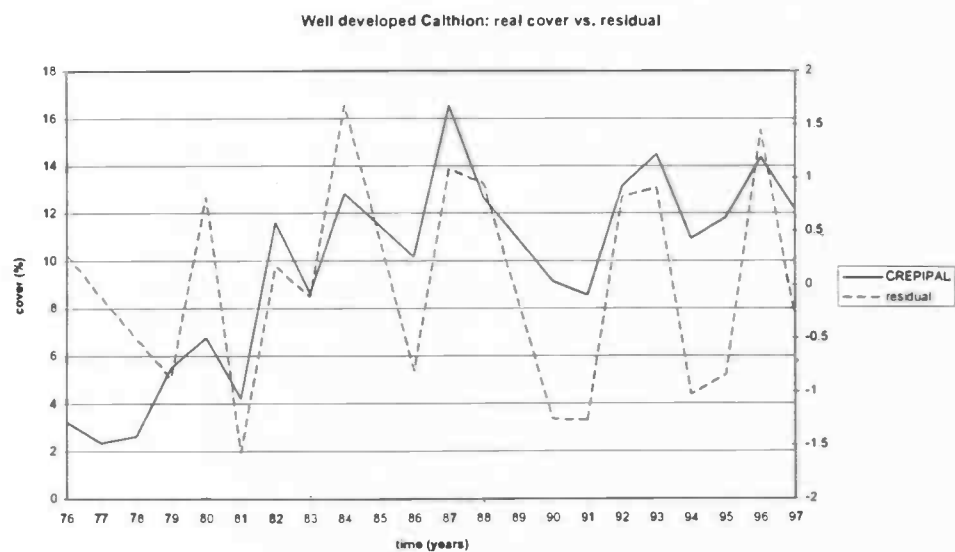
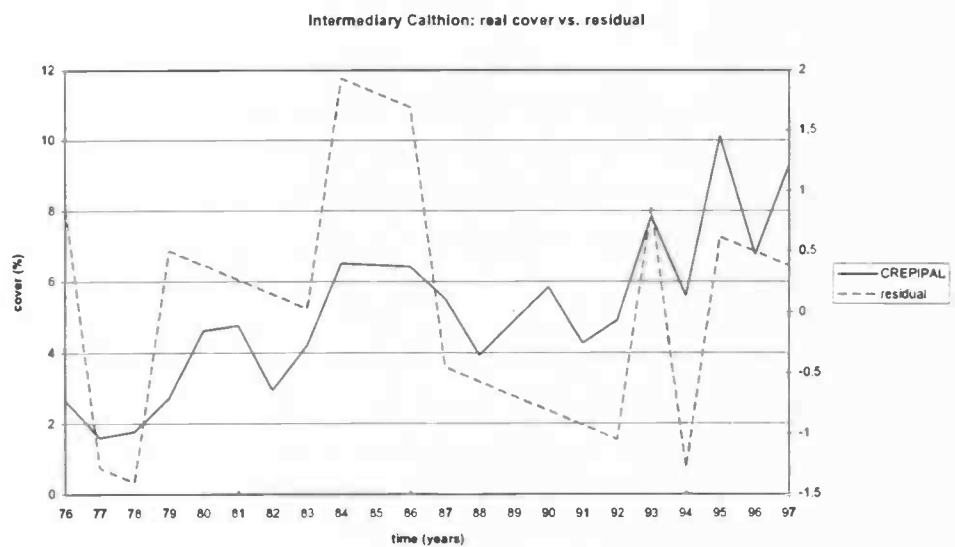
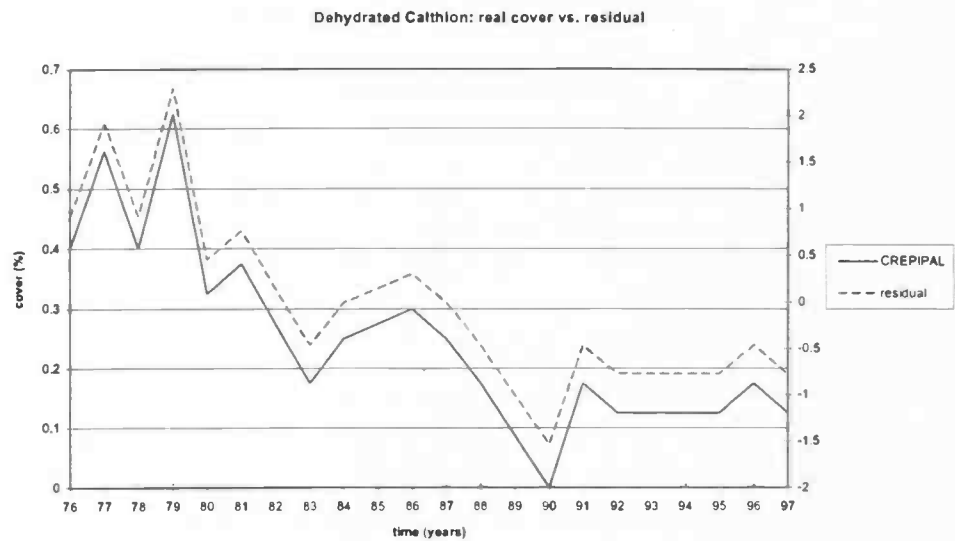
Intermediary Calthion: real cover vs. residual



Well developed Calthion: real cover vs. residual

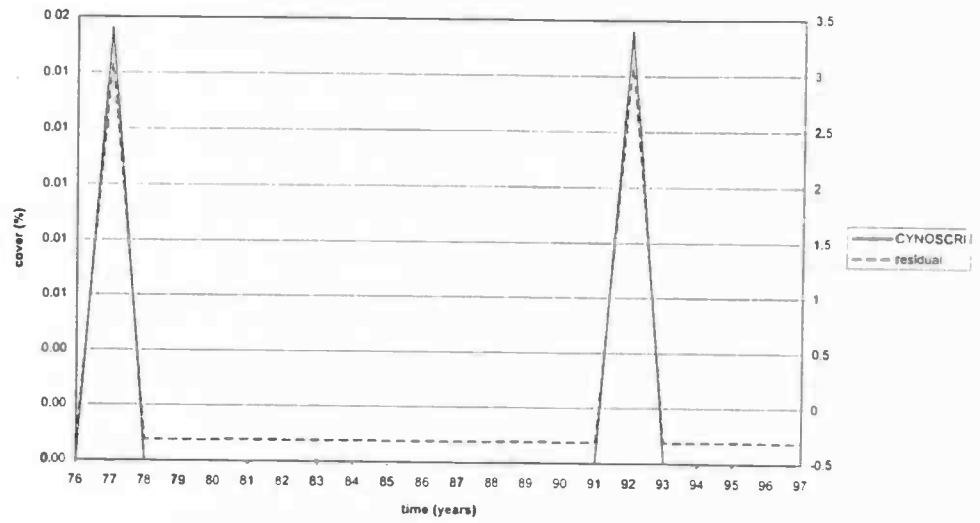


APPENDIX VIII c: residual reaction *Crepis paludosa*

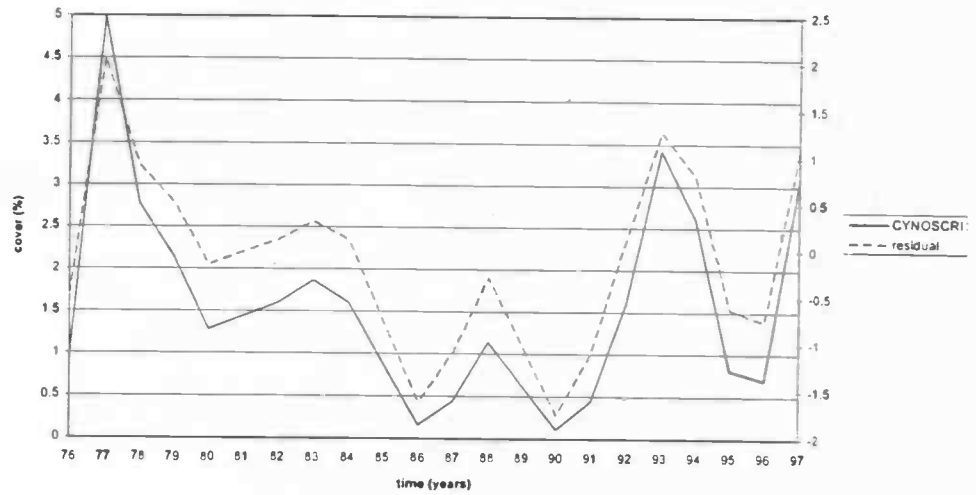


# APPENDIX VIII d: residual reaction *Cynosurus cristatus*

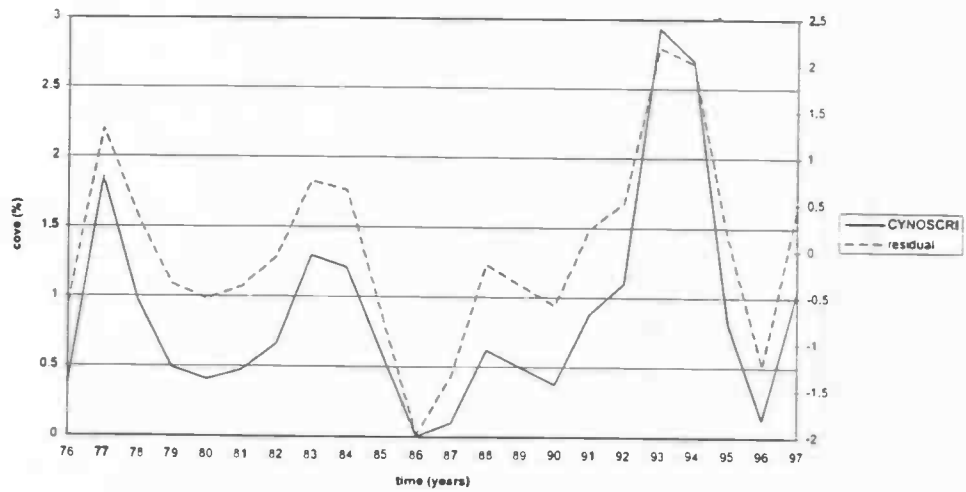
Dehydrated Calthion: real cover vs. residual



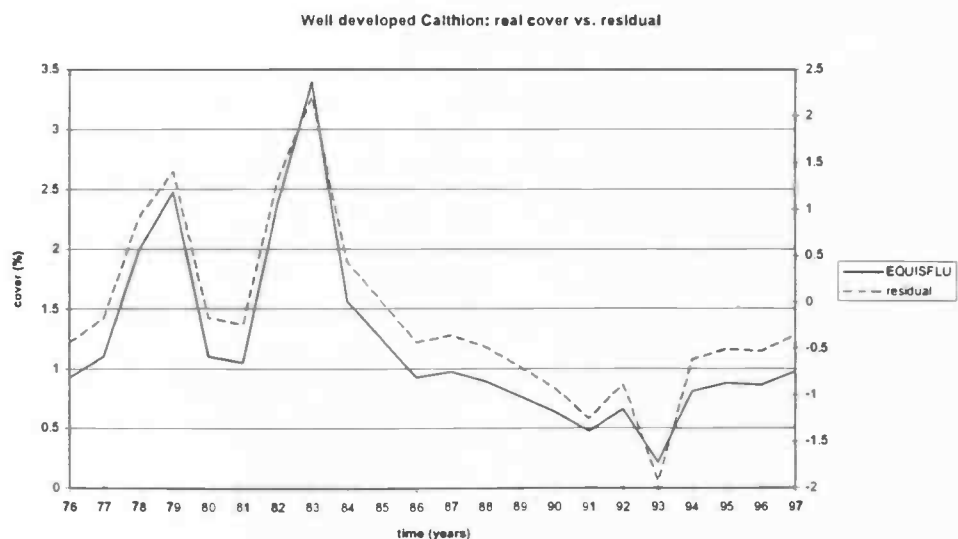
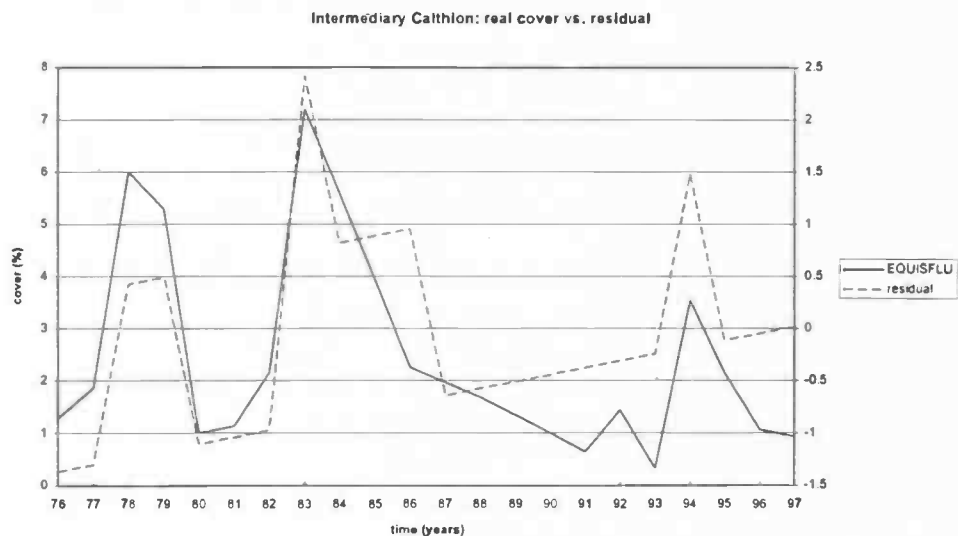
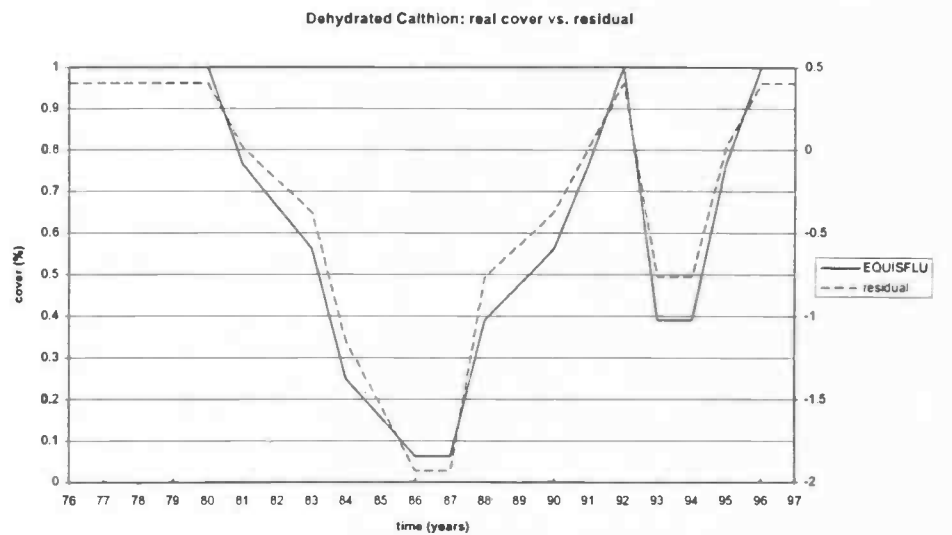
Intermediary Calthion: real cover vs. residual



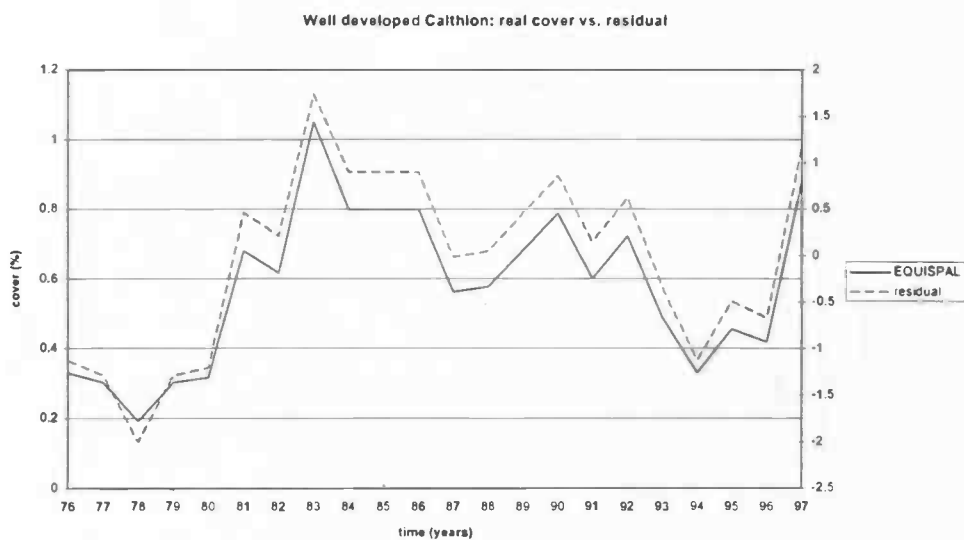
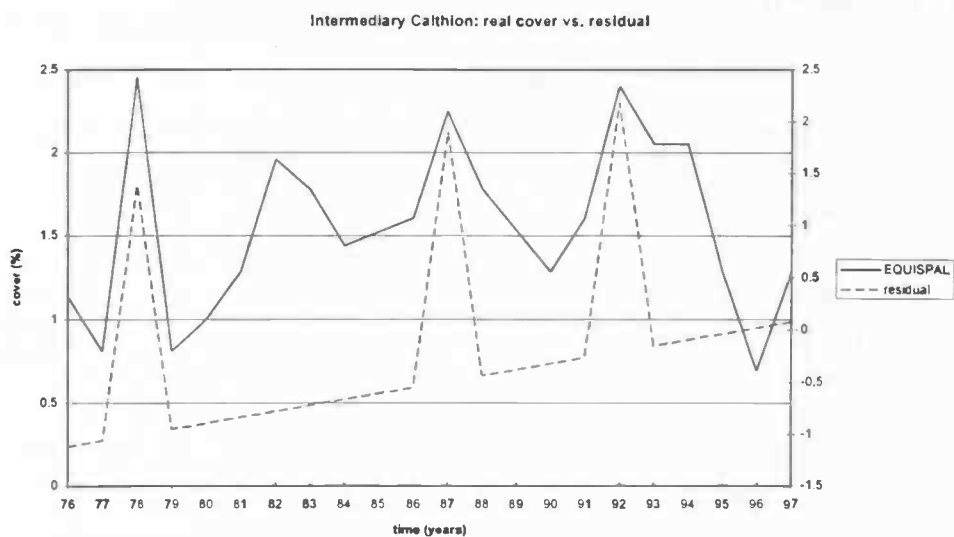
Well developed Calthion: real cover vs. residual



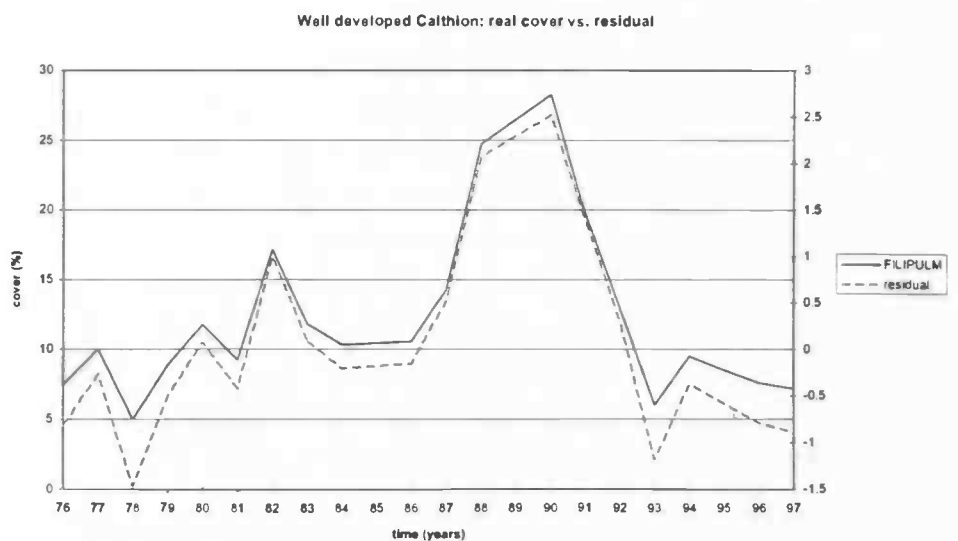
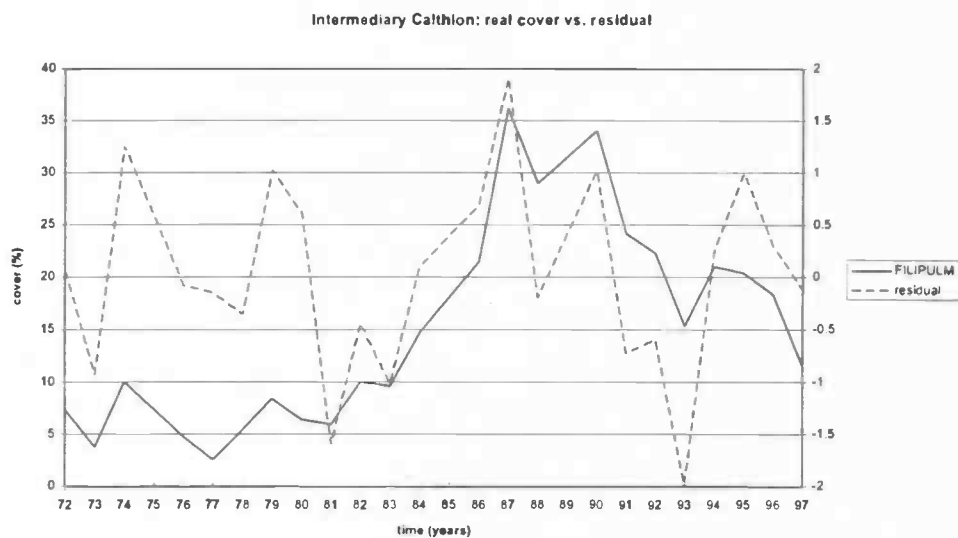
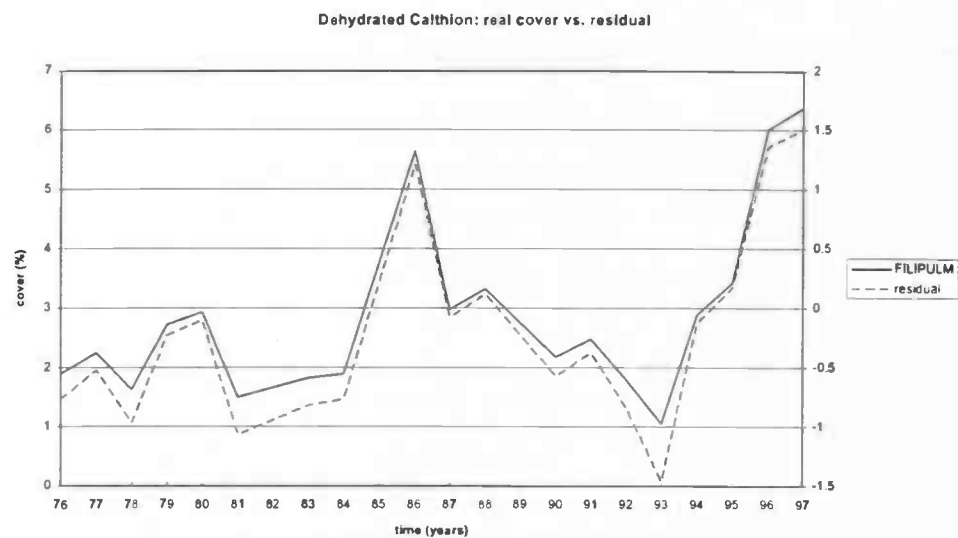
APPENDIX VIII e: residual reaction *Equisetum fluvitatile*



## APPENDIX VIII f: residual reaction *Equisetum palustre*

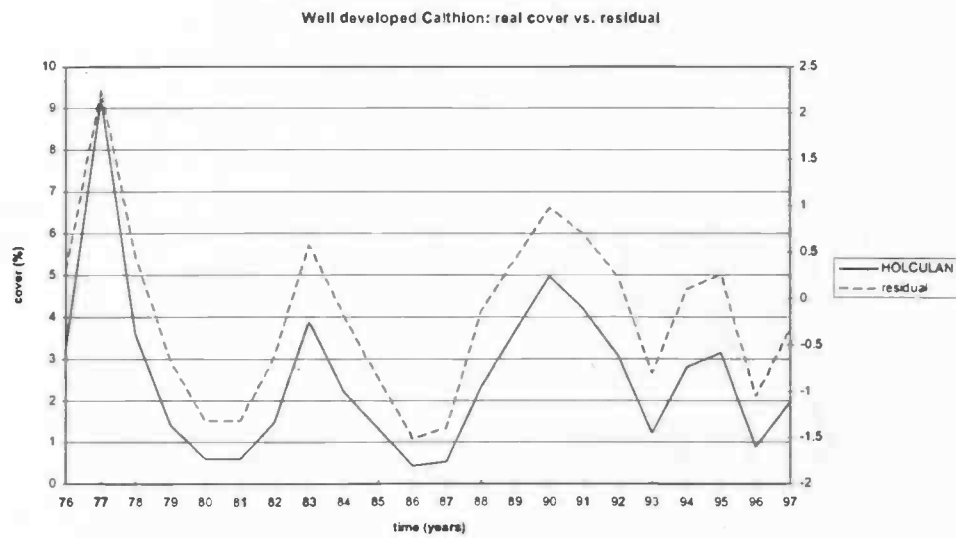
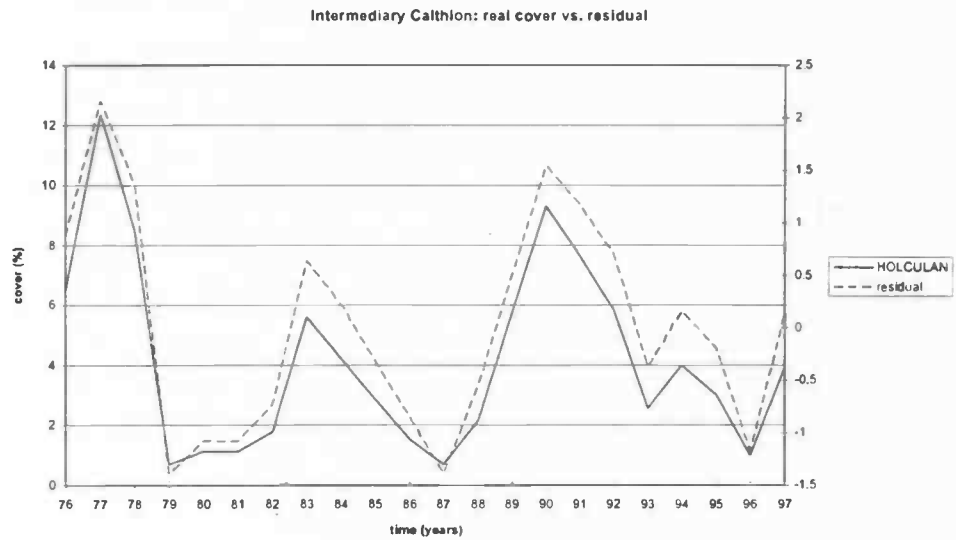
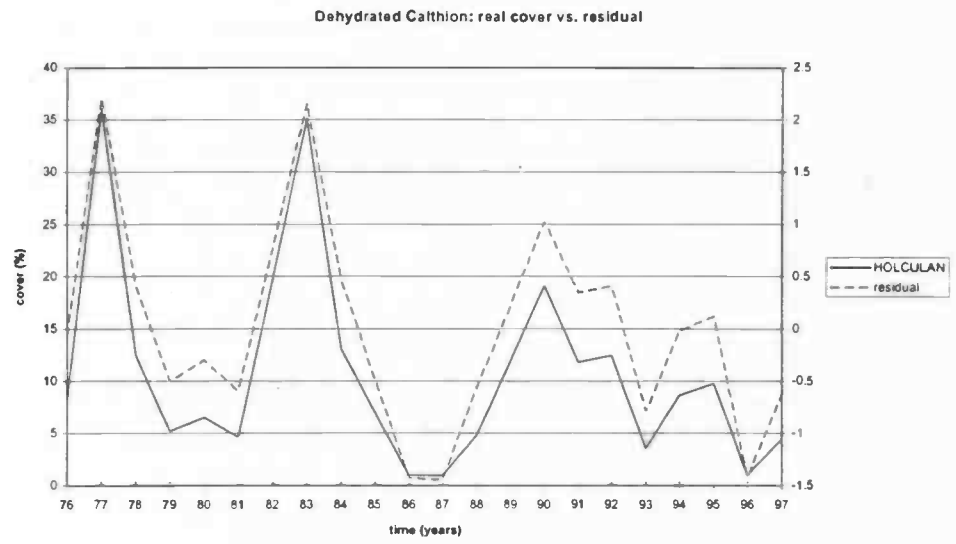


APPENDIX VIII g: residual reaction *Filipendula ulmaria*

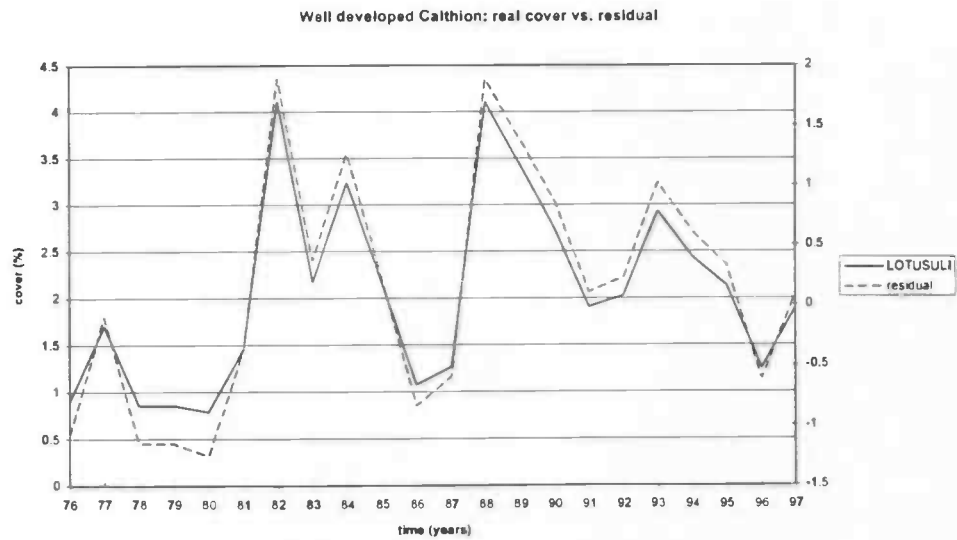
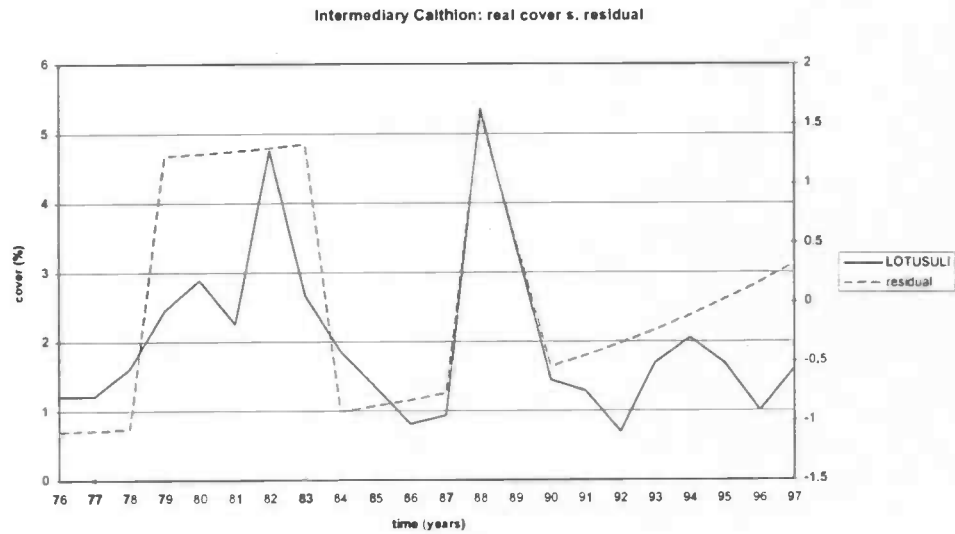
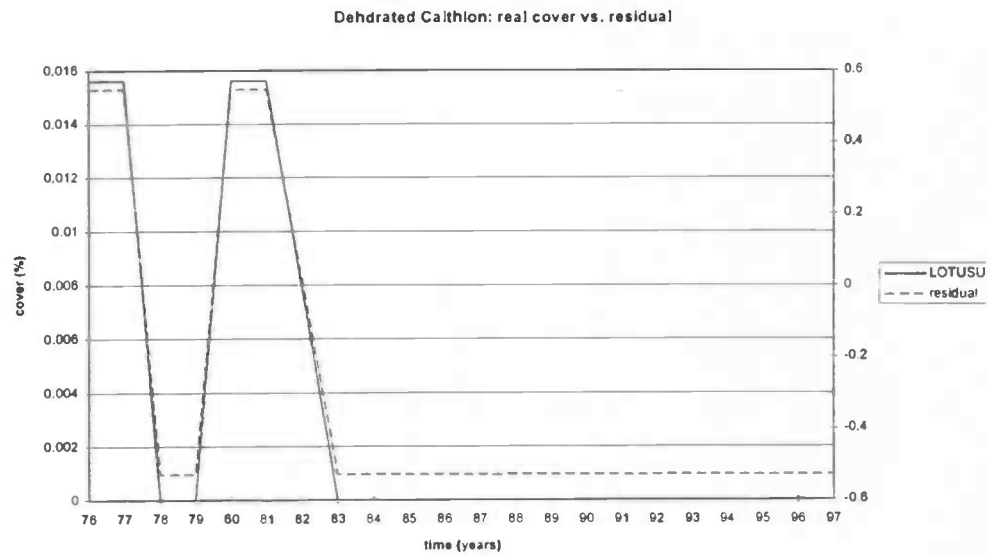




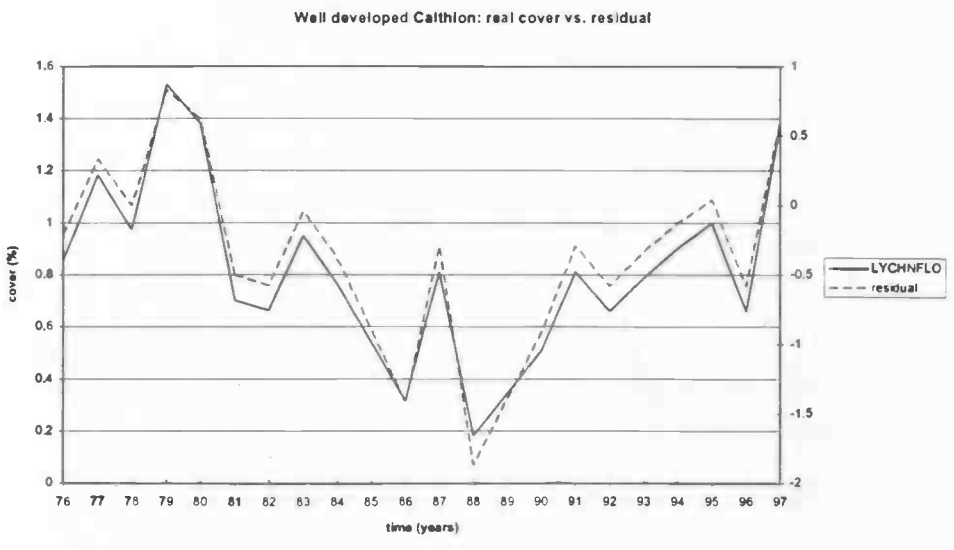
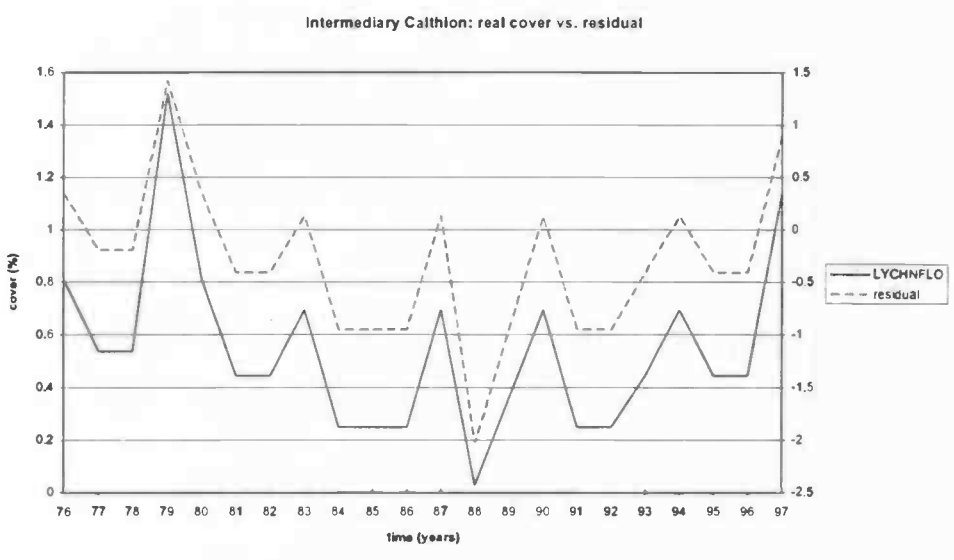
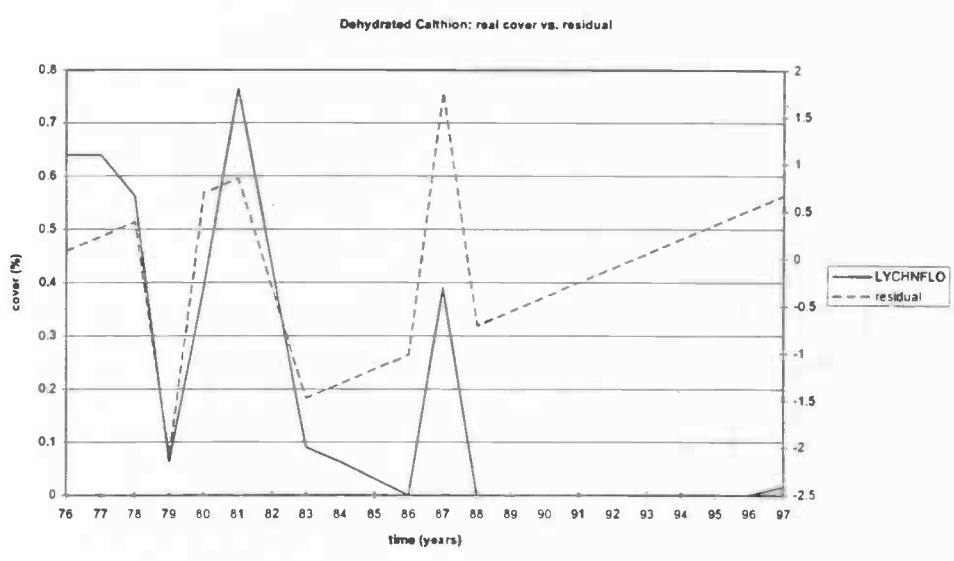
**APPENDIX VIII h: residual reaction *Holcus lanatus***



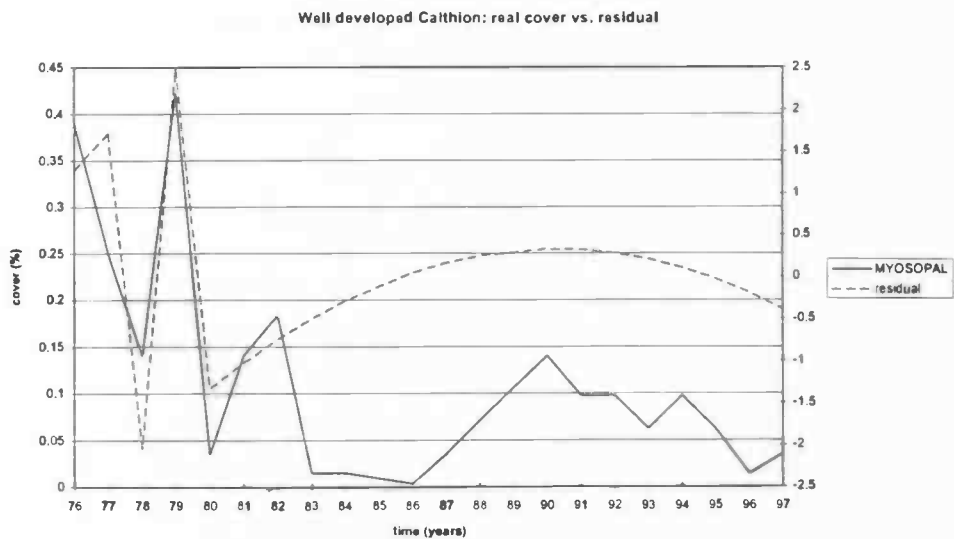
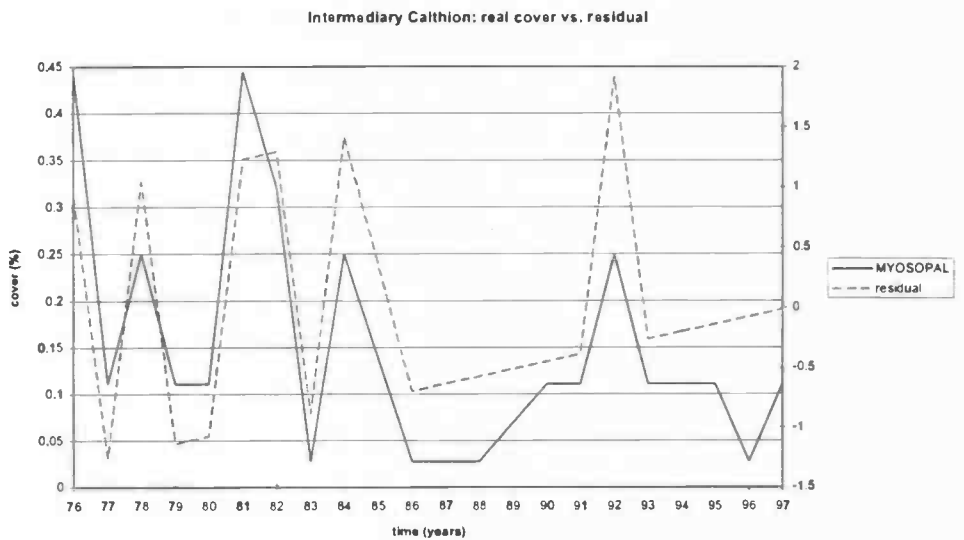
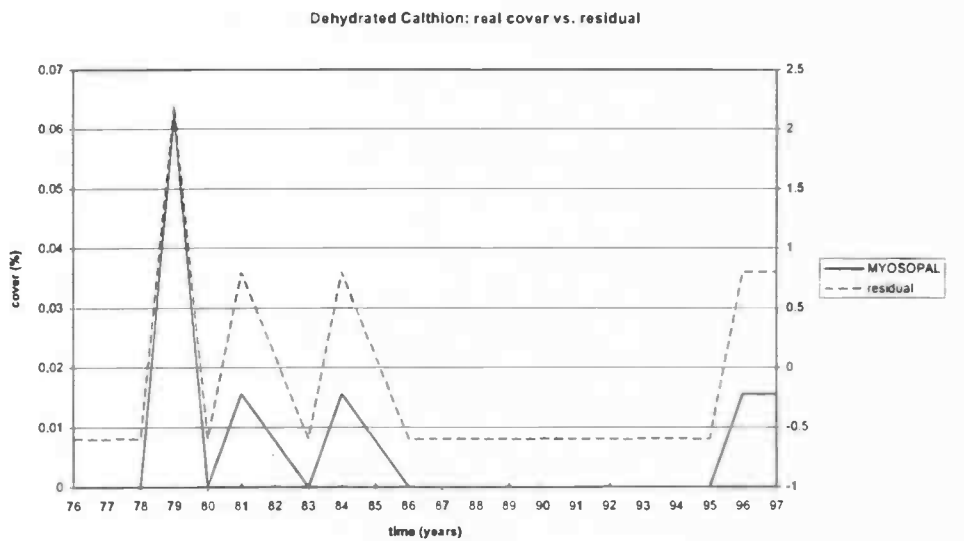
**APPENDIX VIII i: residual reaction Lotus uliginosus**



# APPENDIX VIII j: residual reaction *Lychnis flos-cuculi*

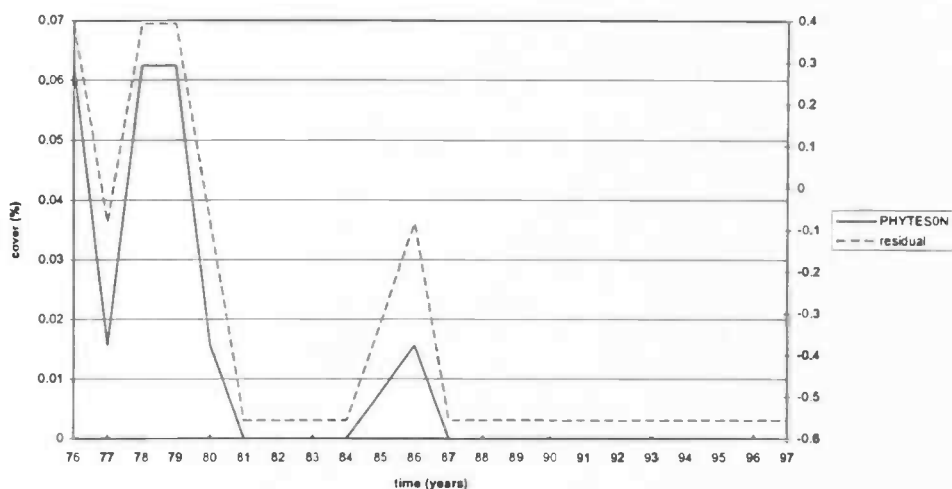


APPENDIX VIII k: residual reaction *Myosotis palustris*

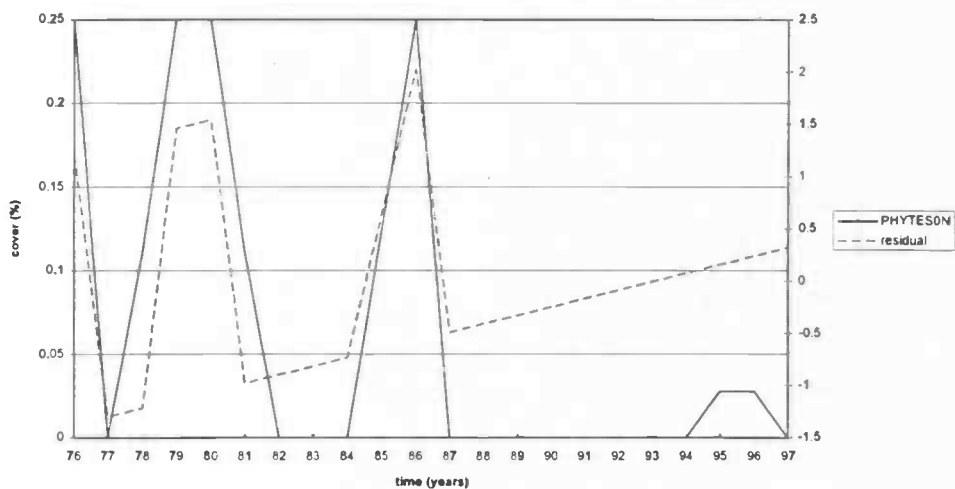


## APPENDIX VIII I: residual reaction *Phyteuma nigrum*

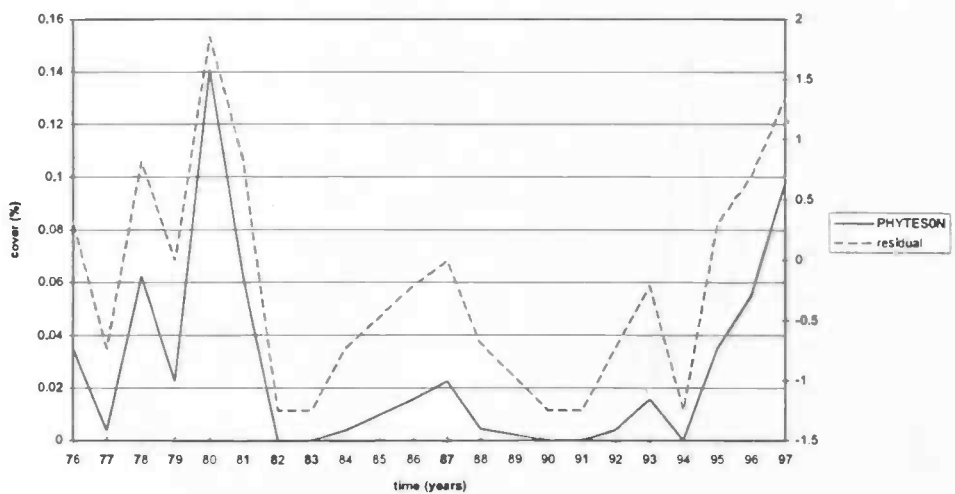
Dehydrated Calthion: real cover vs. residual



Intermediary Calthion: real cover vs. residual



Well developed Calthion: real cover vs. residual



APPENDIX VIII m: residual reaction *Plantago lanceolata*

