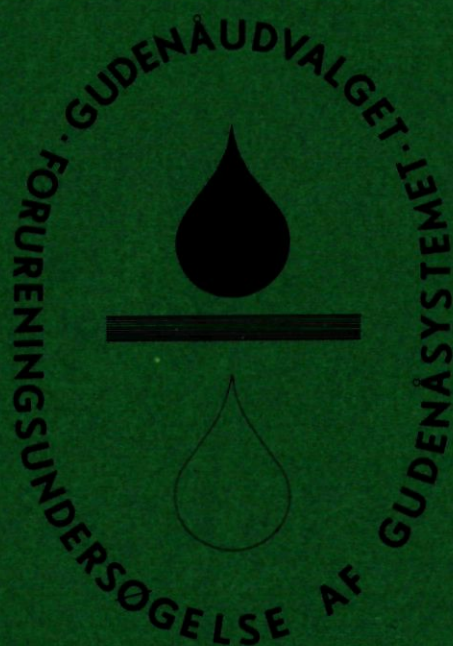

RAPPORT NR. 14



GUDENAUNDERSØGELSEN
Søundersøgelser Bilagsdel

G U D E N Å U N D E R S Ø G E L S E N

1973 - 1975

SØUNDERSØGELSER

B I L A G

VANDKVALITETSINSTITUTTET, ATV
Agern Allé 11, 2970 Hørsholm

Sagsnr.: 25.4.049
1977-09-26 - WWT-MK.

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civ.ing. Svend Dige Pedersen

SAGSBEHANDLERE:

cand.scient. Ebbe Lastein
civ.ing. Poul B. Heise

	side
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B I L A G 1

VANDKEMISKE OG BIOLOGISKE STØRRELSER
AFBILDET PÅ KURVEFORM

Bilaget indeholder målinger i følgende søer:

<u>NAVN</u>	<u>FORKORTEELSE</u>
Alling sø	ALL
Almind sø	ALM
Brassø	BRS og BRA
Hald sø	HLD og HAL
Hinge sø	HNG og HIN
Nørresø	NRS og NØR
Salten langsø	SAL
Silkeborg langsø	SIL
Slåen sø	SLA
Søndersø	SRS og SØN
Tange sø	TAN
Thor sø	THO
Ved sø	VED
Vessø	VES
Ørn sø	ØRN

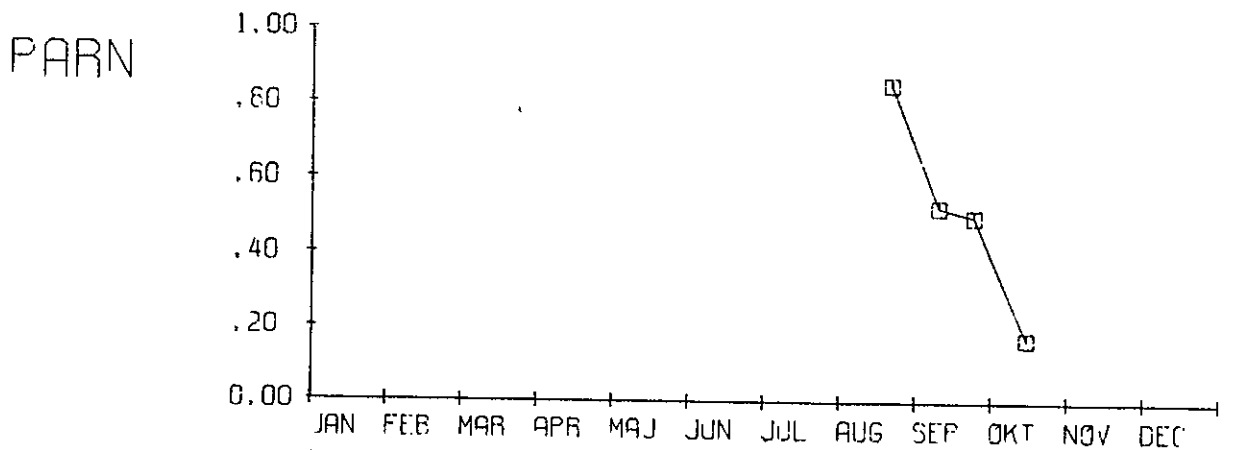
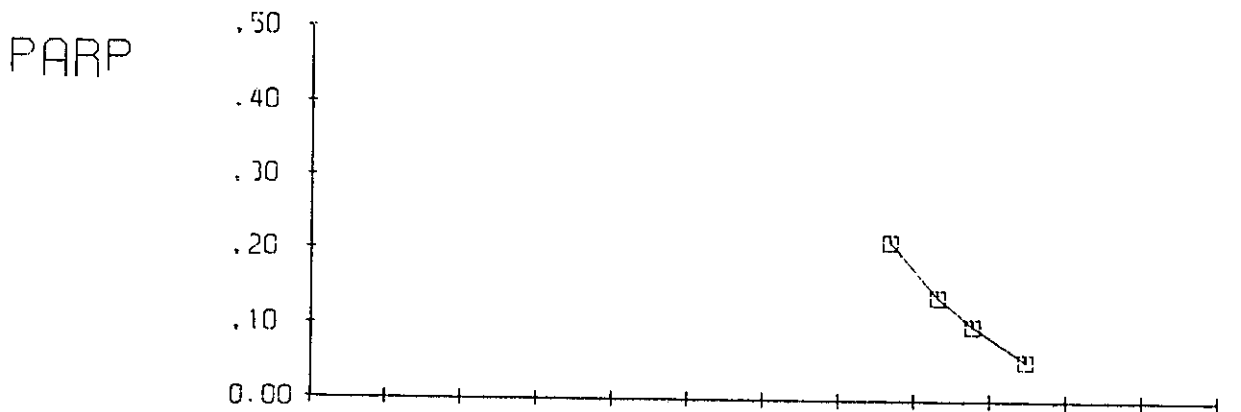
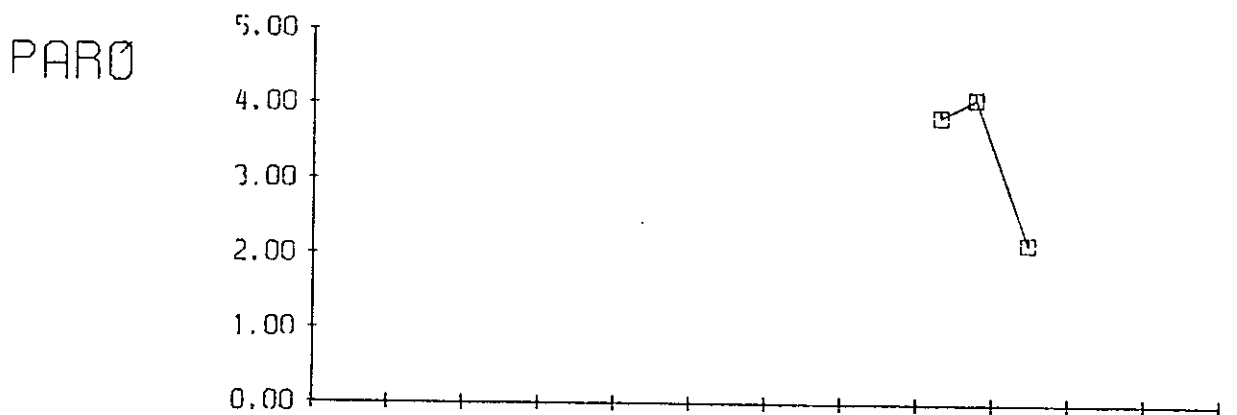
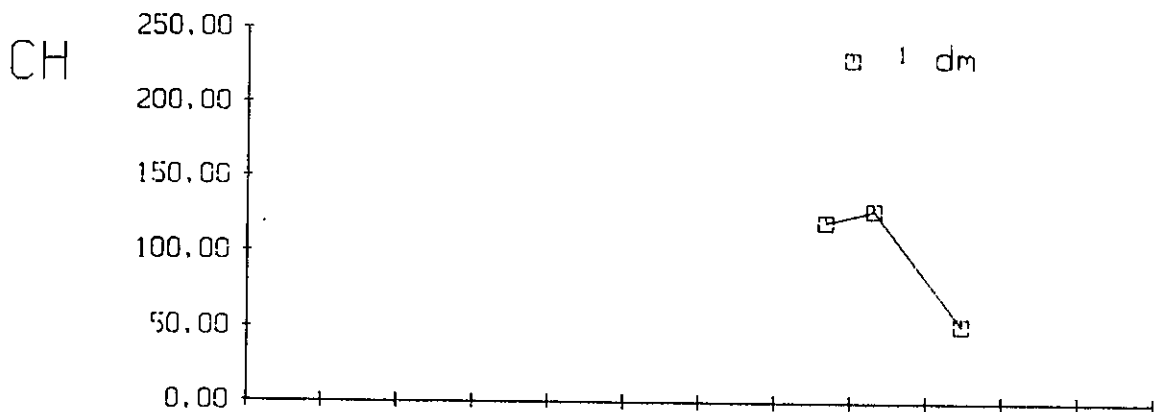
For hver sø er følgende parameter angivet:

CH	klorofyl-a
PAR Q	partikulært kulstof udtrykt ved COD-anal. (mg l^{-1})
PAR P	partikulært fosfor (mg l^{-1})
PAR N	partikulært kvælstof (mg l^{-1})
OO	opløst ilt (mg l^{-1})
PP	bruttoprimerproduktionen pr. m^2 ($\text{mg C m}^{-2} \text{ dg}$)
SI	siliciumkonc. (mg l^{-1})
TF	felttemp. ($^{\circ}\text{C}$)
PQ	opløst fosfor (mg l^{-1})

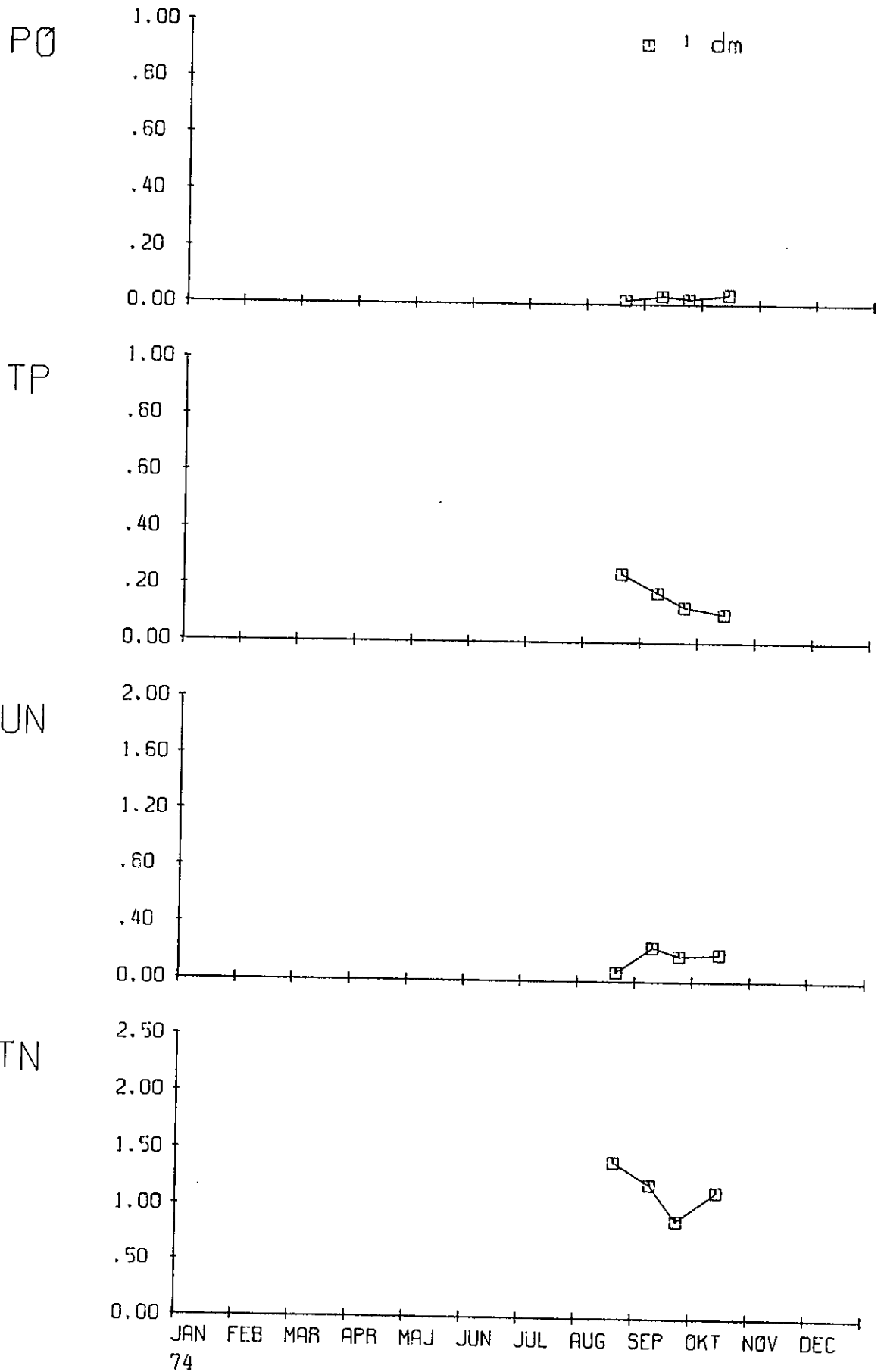
TP	total fosfor (mg l^{-1})
UN	summen af konc. af opløste kvælstofsalte (mg l^{-1})
TN	total kvælstof (mg l^{-1})
G-24-MAX	primærproduktionen i den mådedybde, hvor den største produktion beregnes
SY	den dybde (m), hvori resterer 10 % af belysningen umiddelbart under overfladen, målt med grønfilter
PROD	bruttoprimerproduktionen pr. m^2 ($\text{mg C m}^{-2} \text{ dg}^{-1}$) (PROD ~ PP)

På kurverne er anført dybdeangivelser i form af symboler. Symbolet for "overfladen" betyder altid 0,2 m. De øvrige symboler er relative dybdeangivelser. Den eksakte dm-angivelse passer altså ikke nødvendigvis.

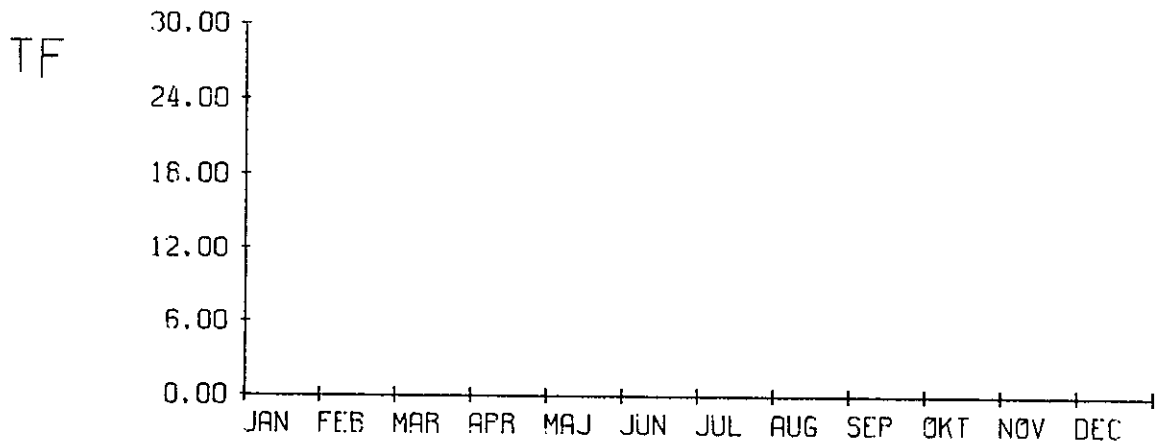
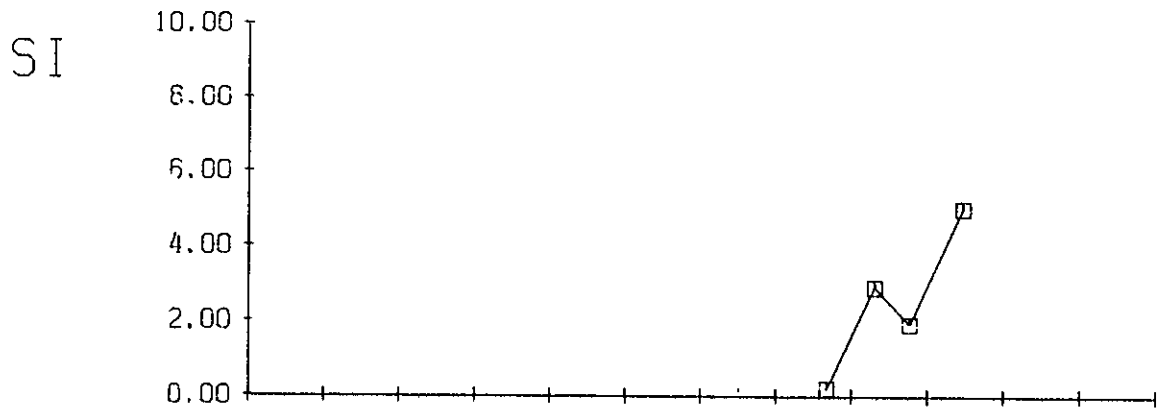
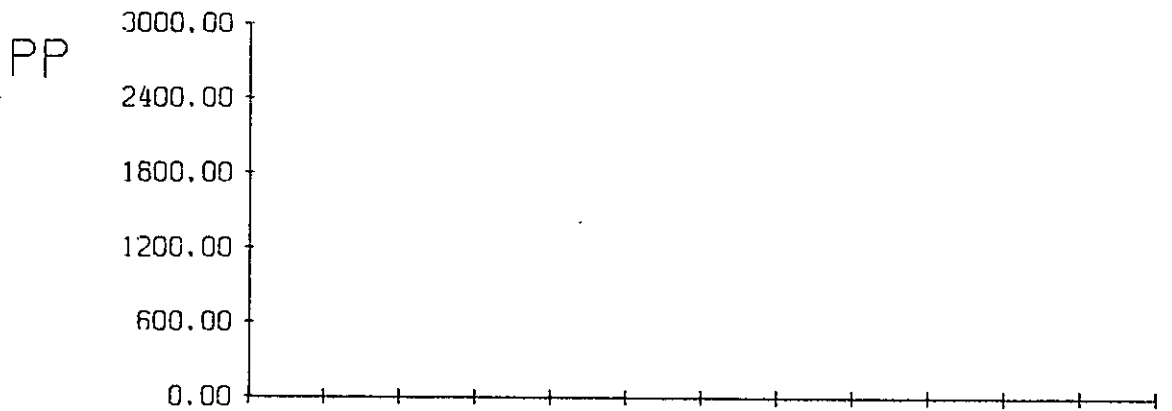
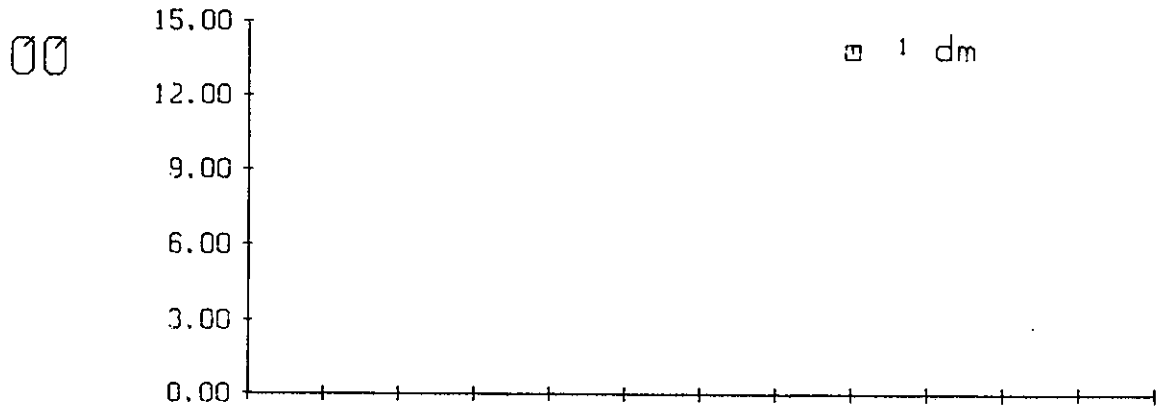
ALA 751



ALA 751

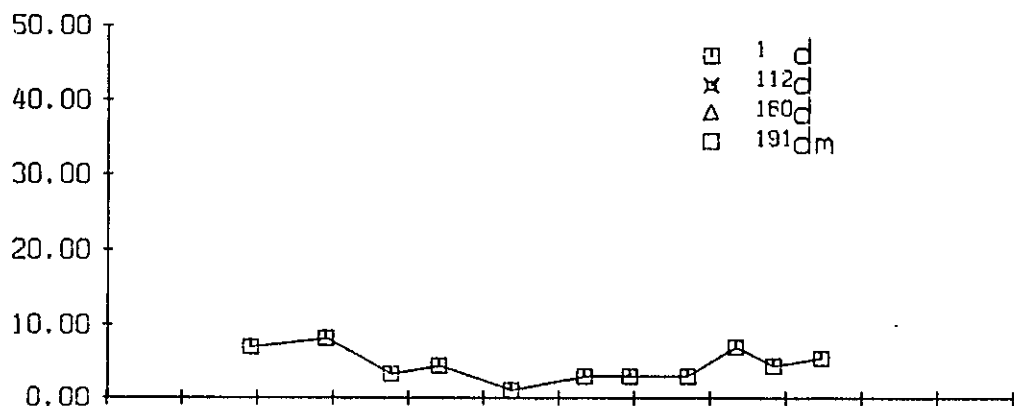


ALA 751

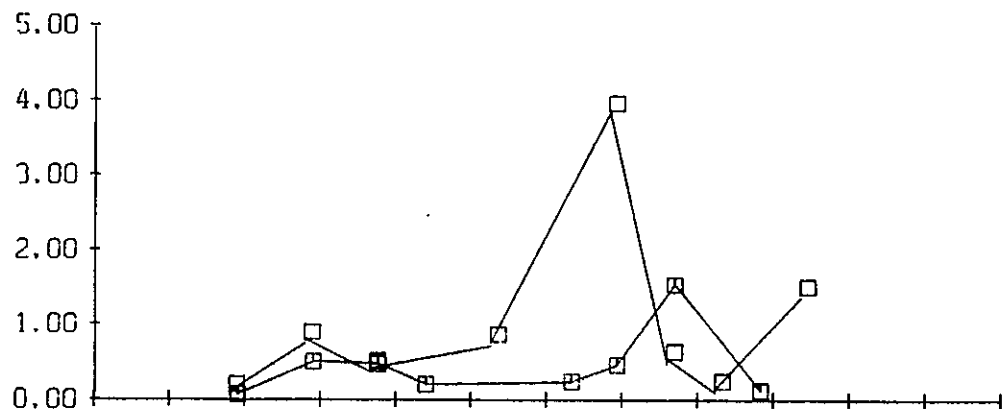


ALM 751

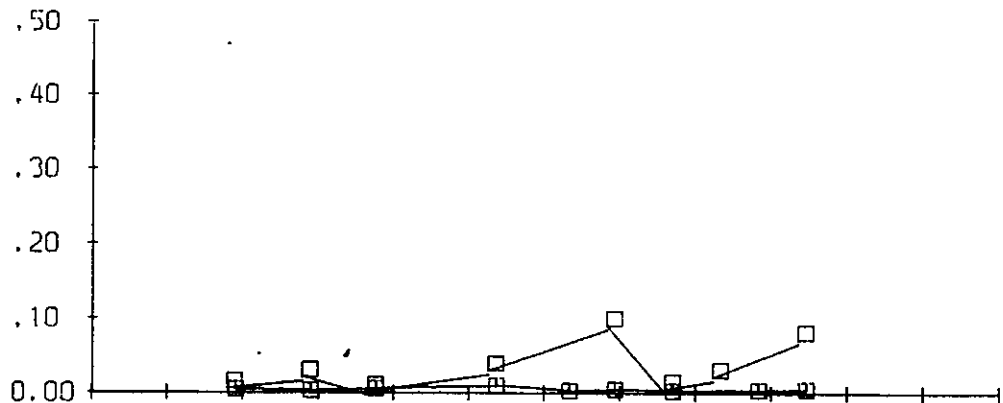
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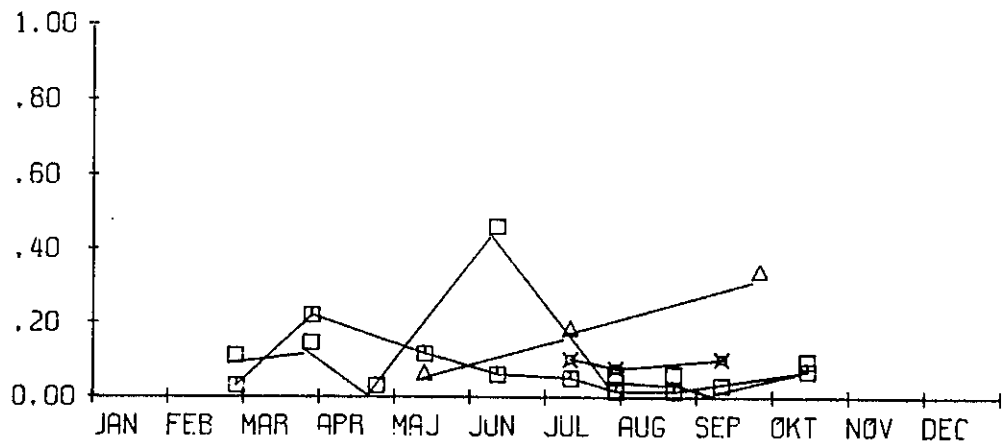
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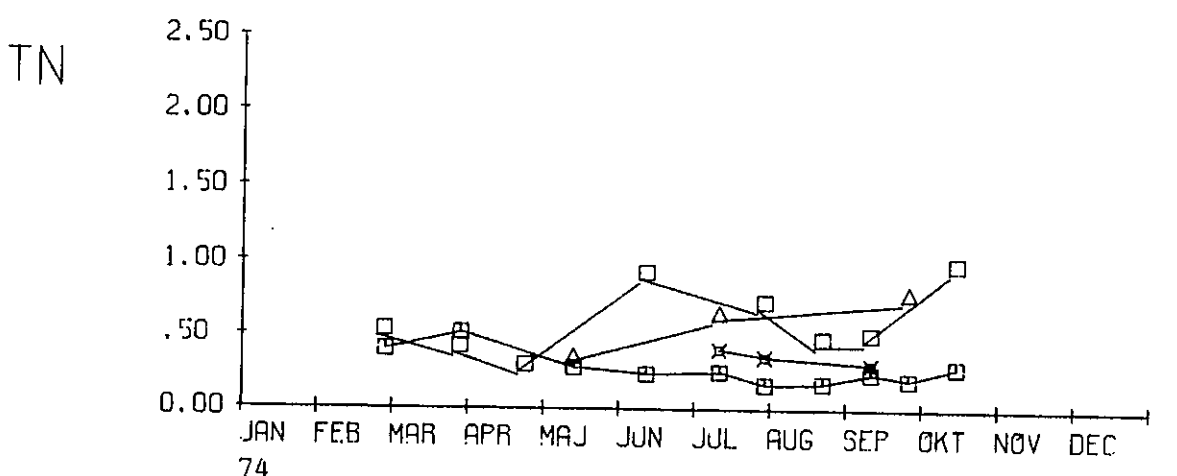
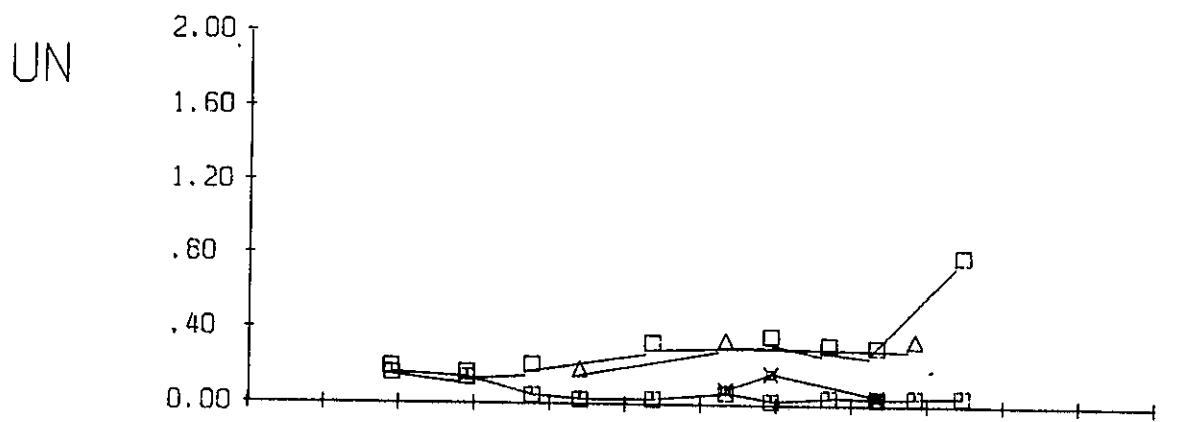
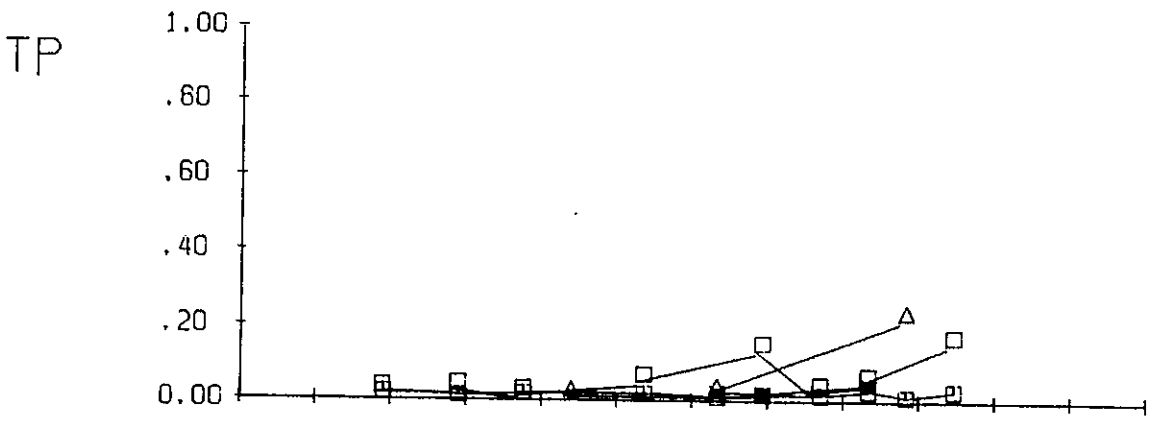
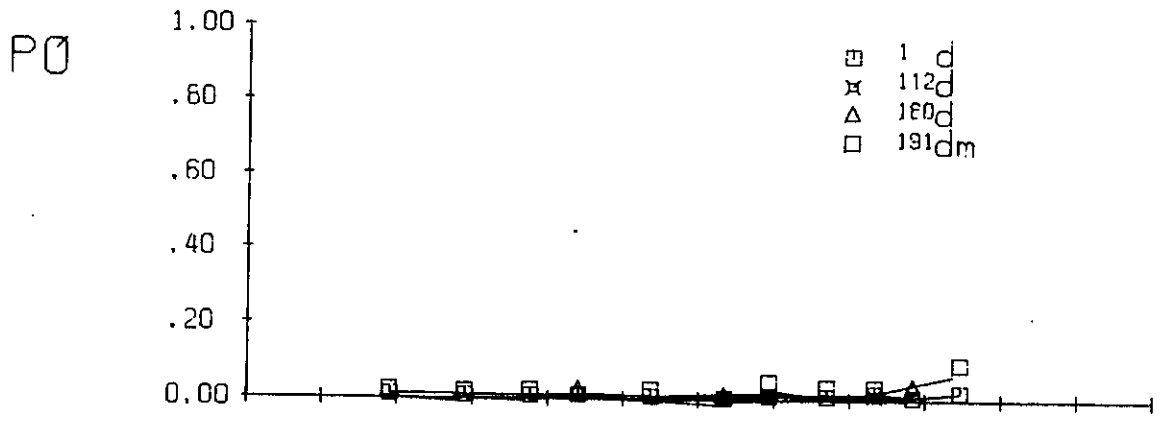
PARP



PARN

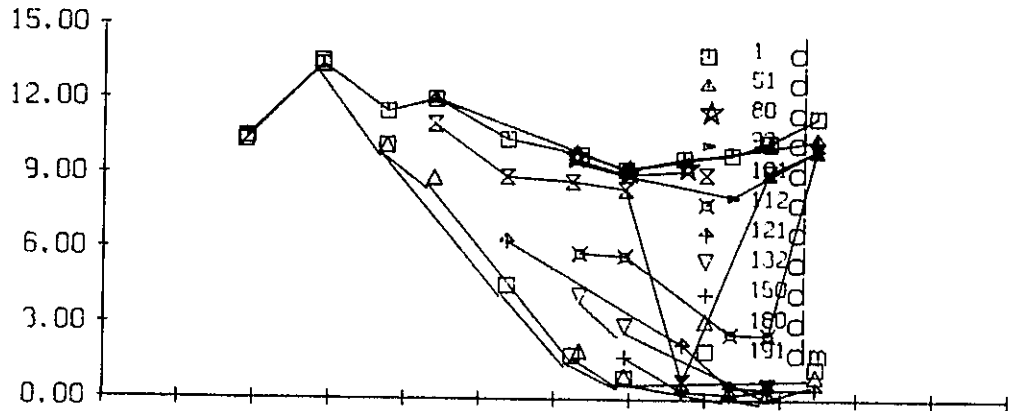


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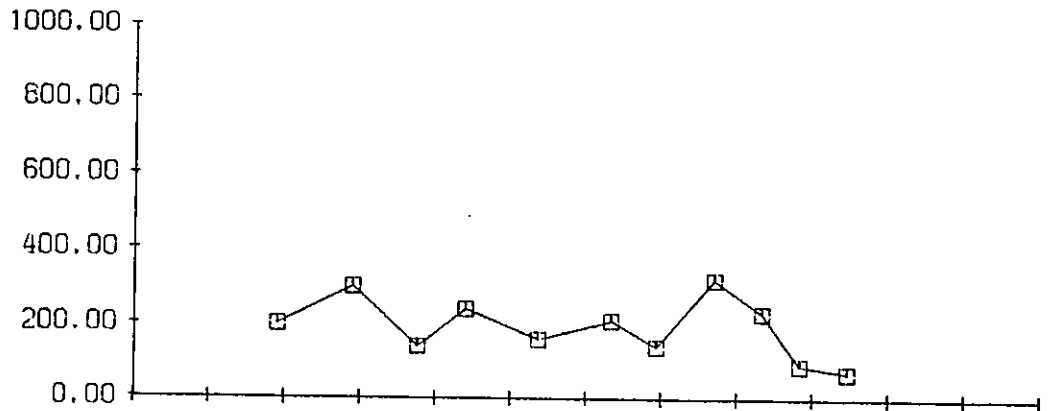


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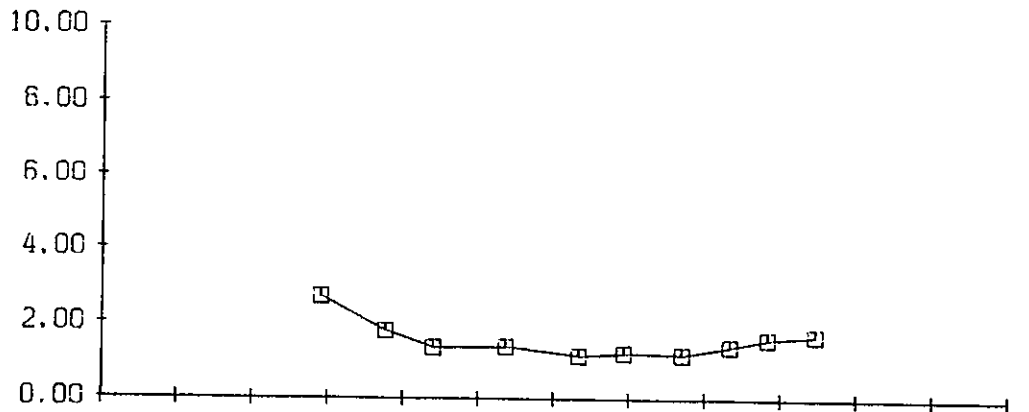
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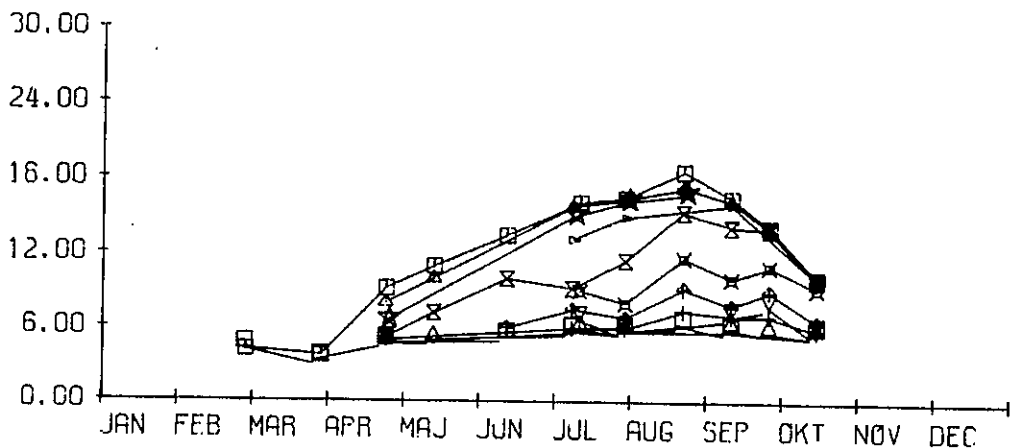
PP



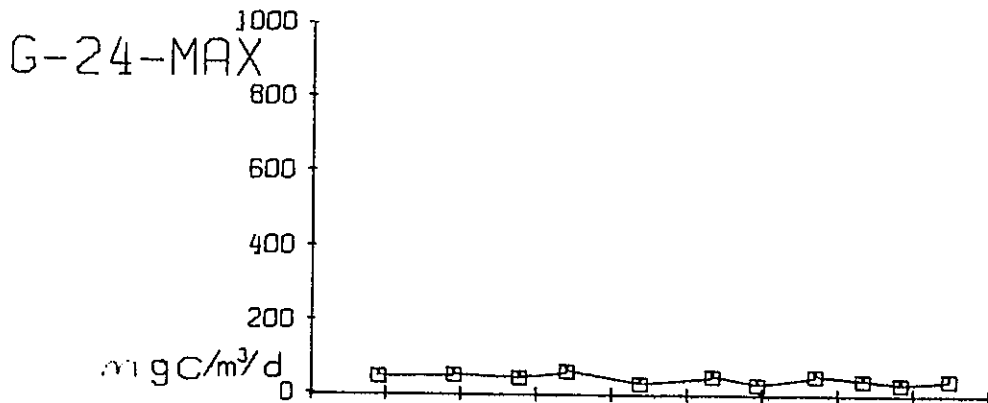
SI



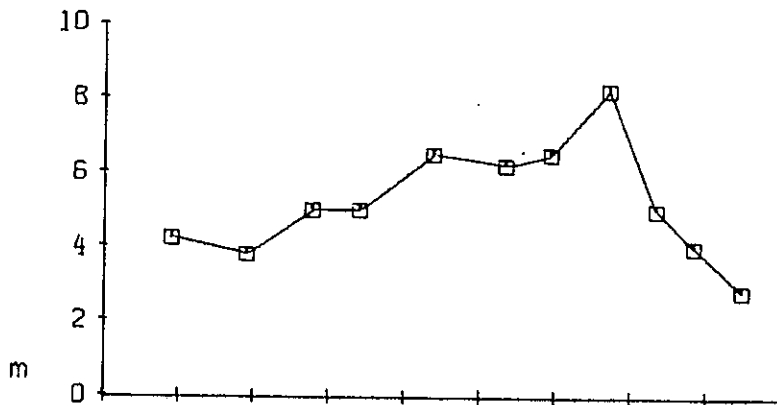
TF



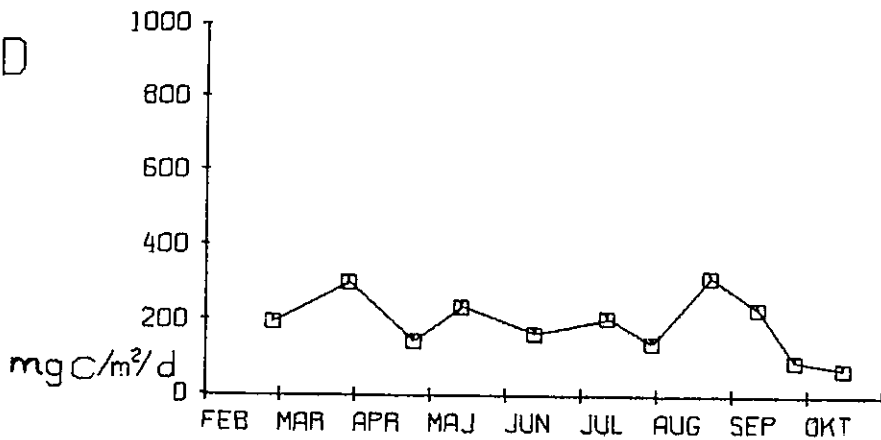
ALM 1



SY



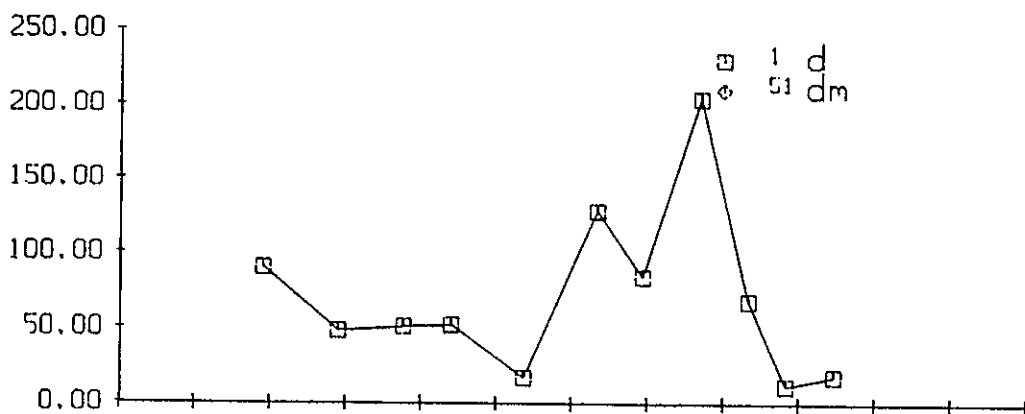
PROD



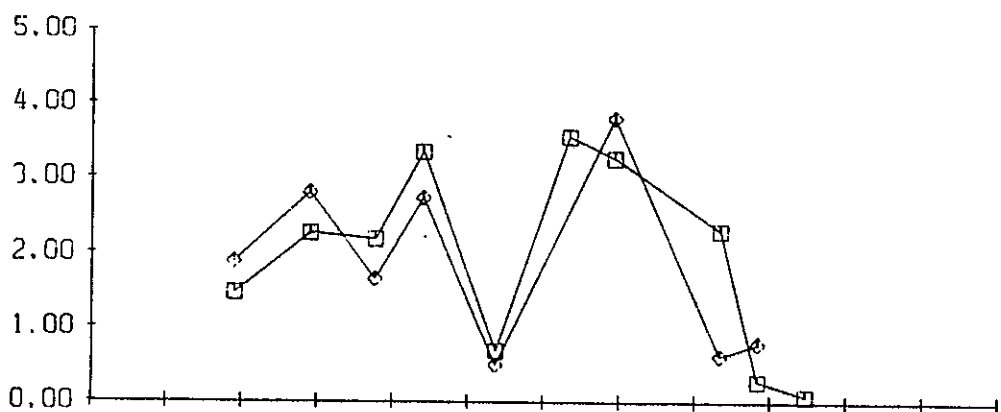
74
AIRSPKOD. 45 gCm⁻²år⁻¹

BRS 751

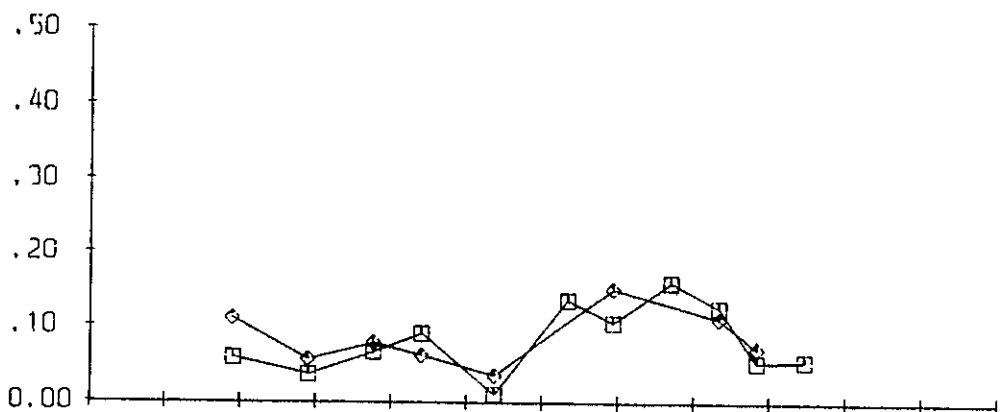
CH



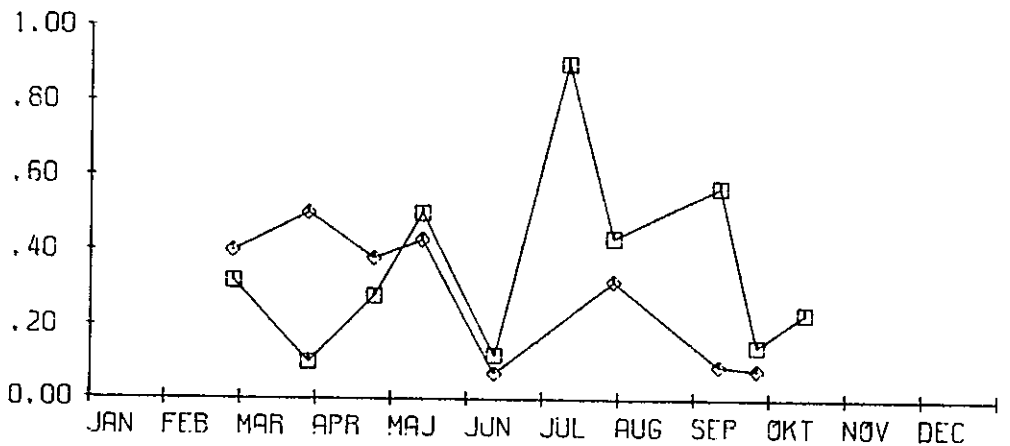
PARO



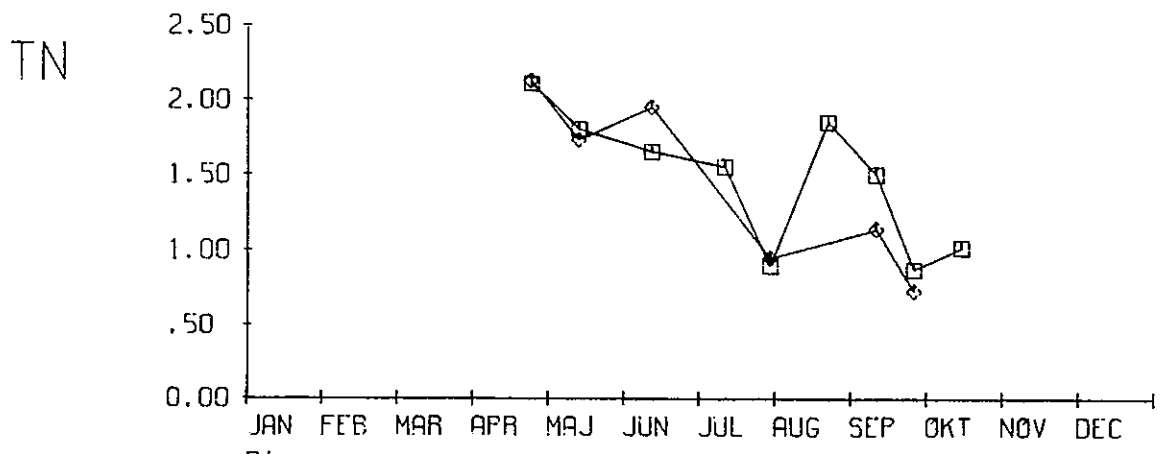
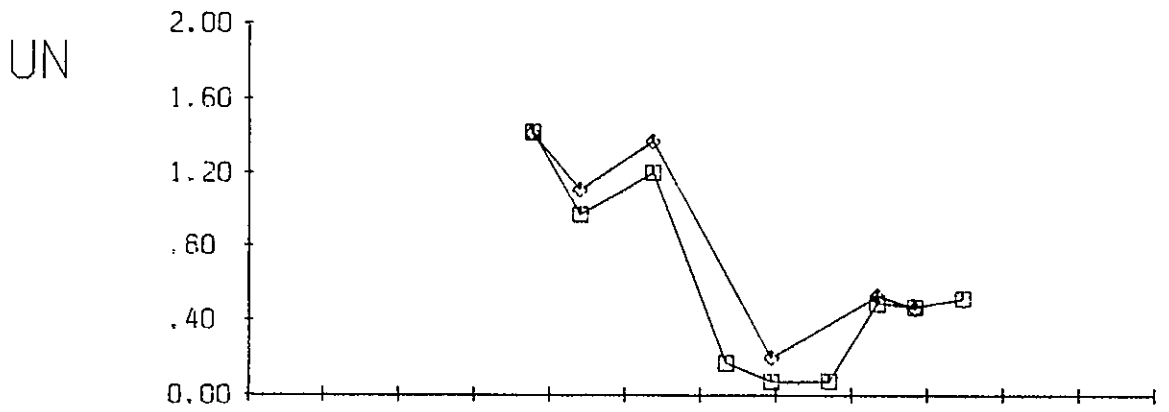
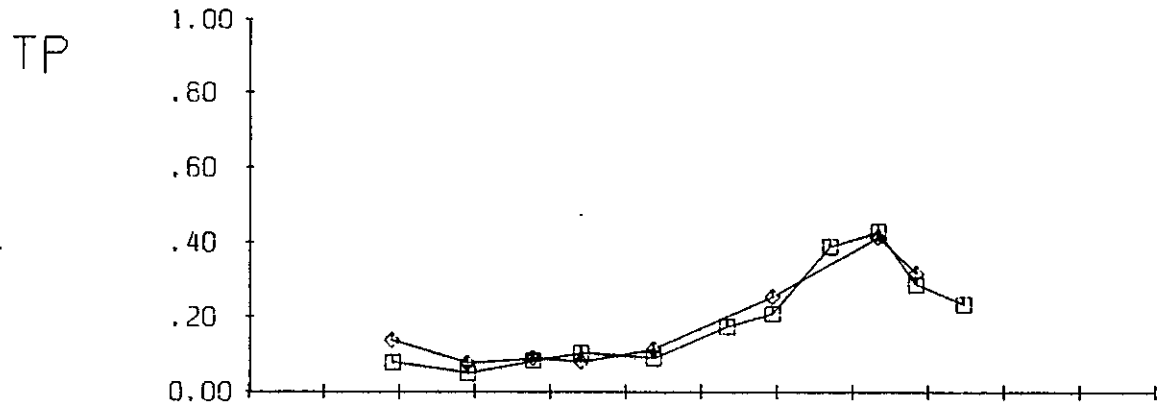
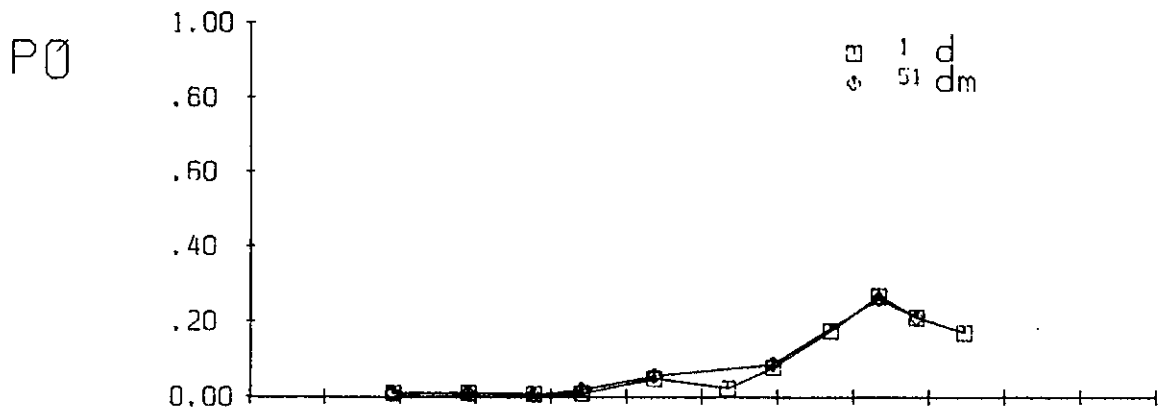
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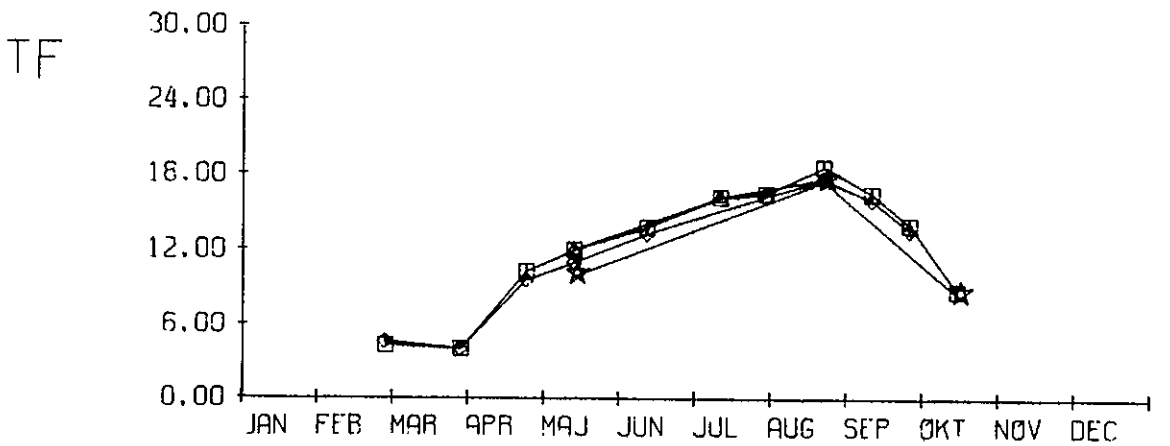
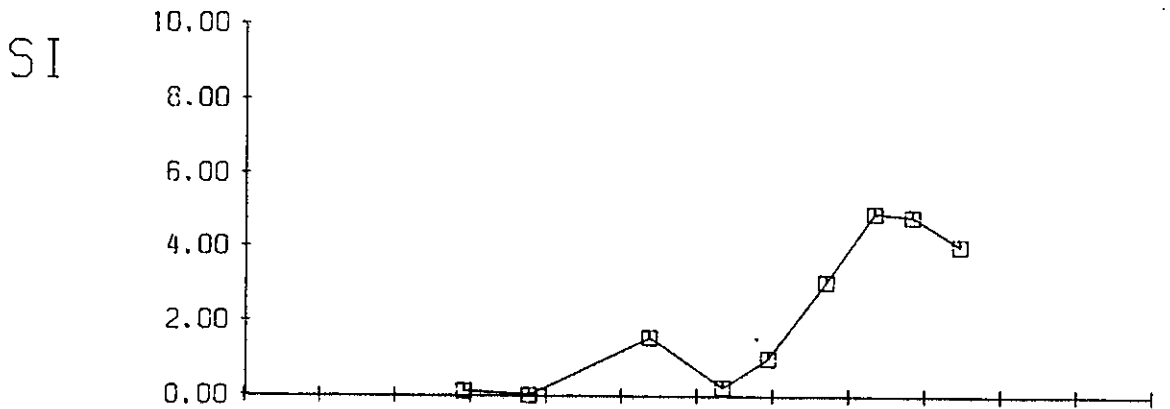
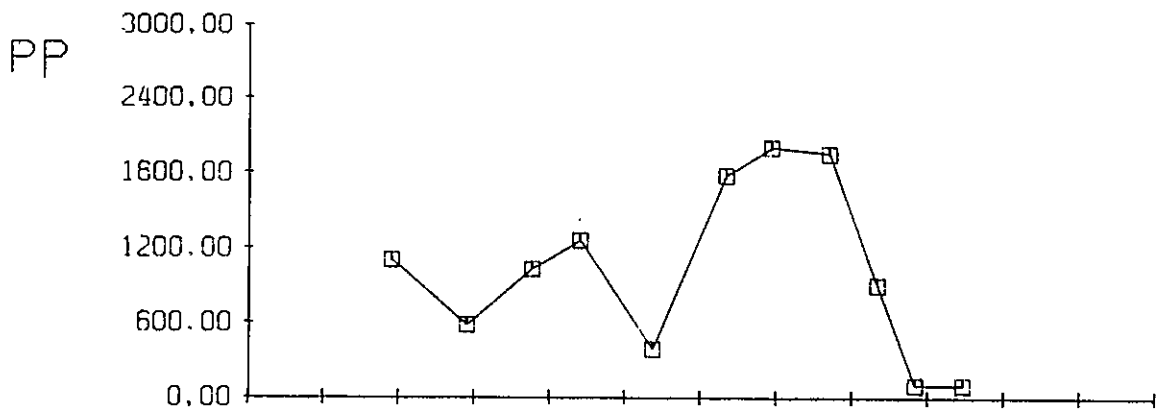
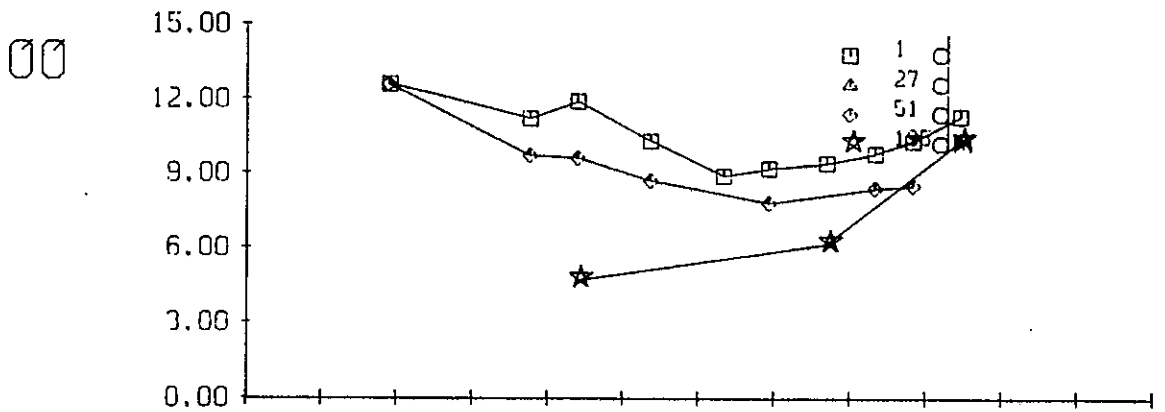
PARN



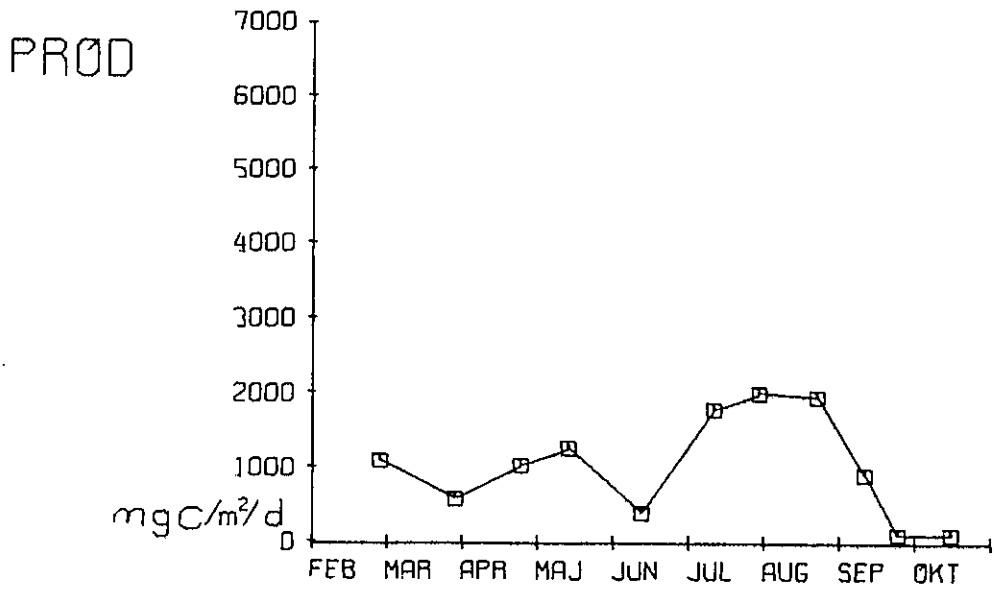
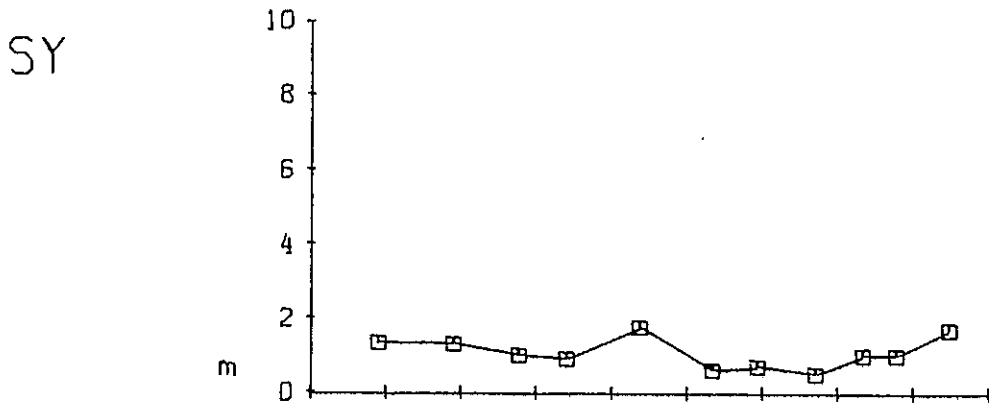
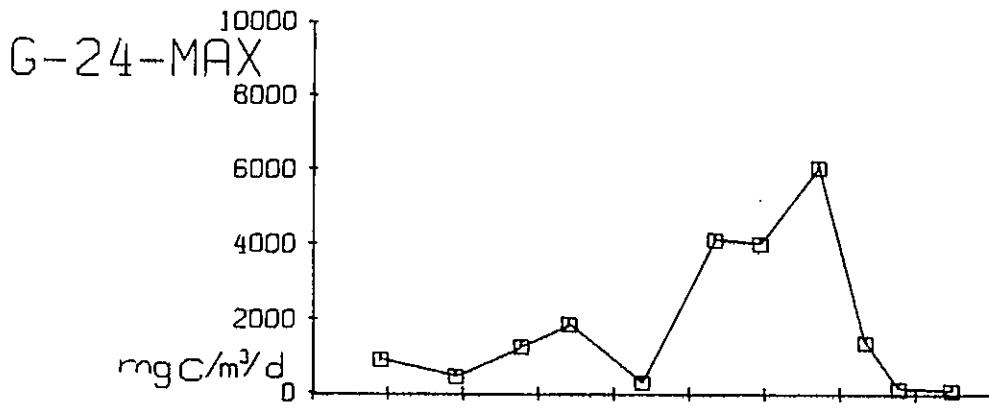
BRS 751



BRS 751

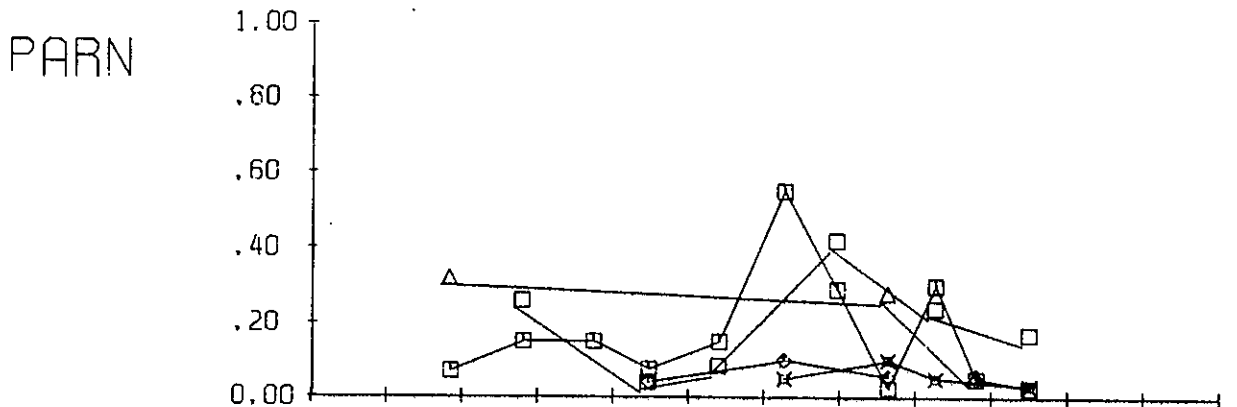
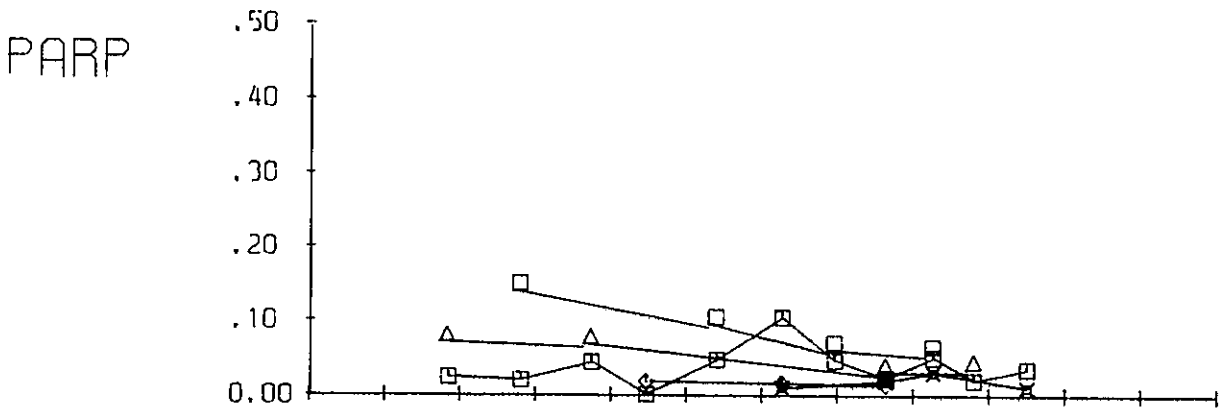
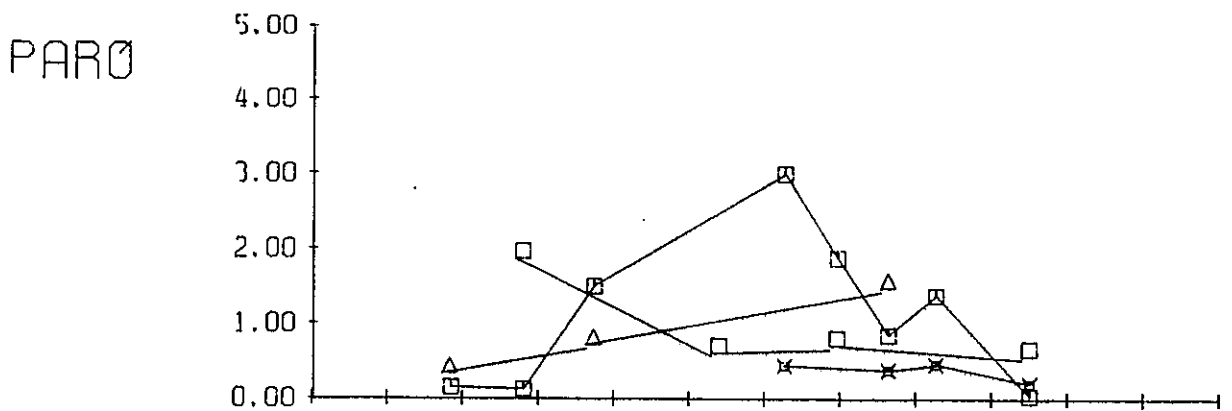
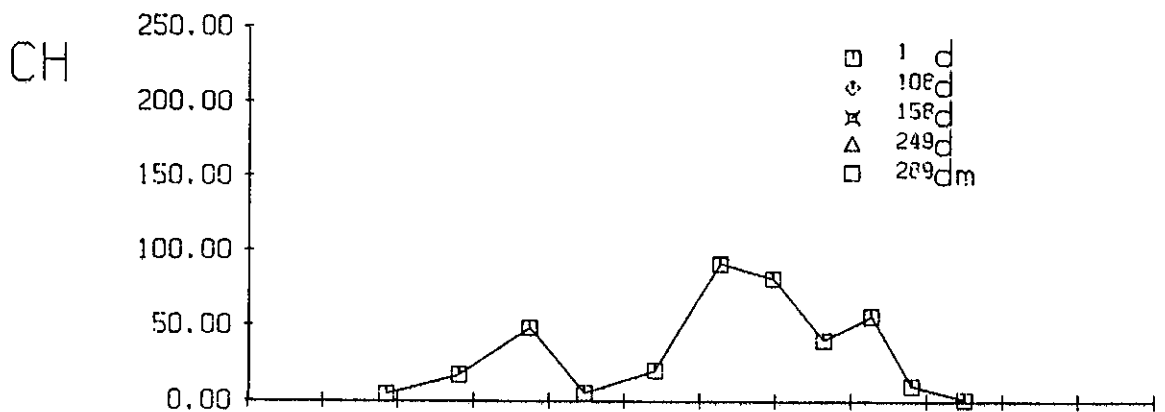


BRA 1



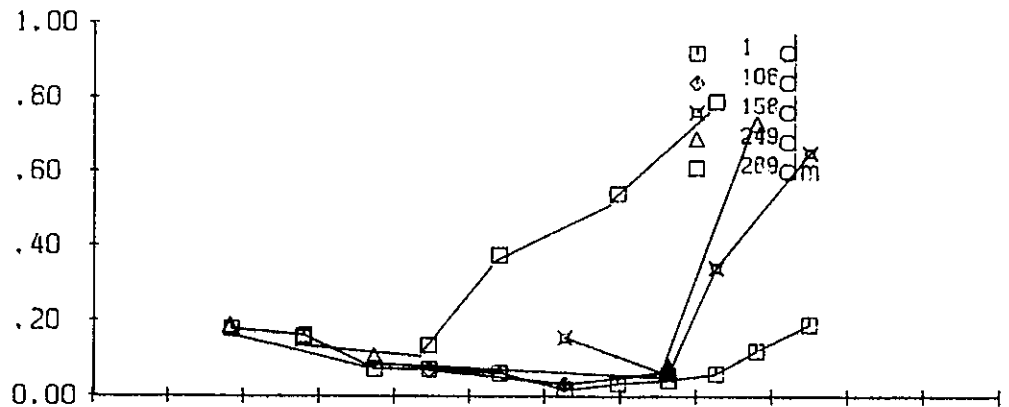
74
ÅRSPROD. 240 gCm⁻²år⁻¹

HLD 751

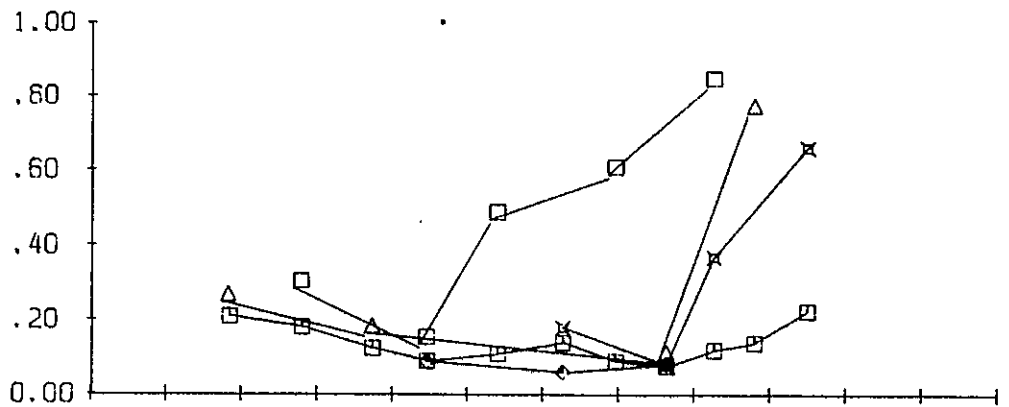


HLD 751

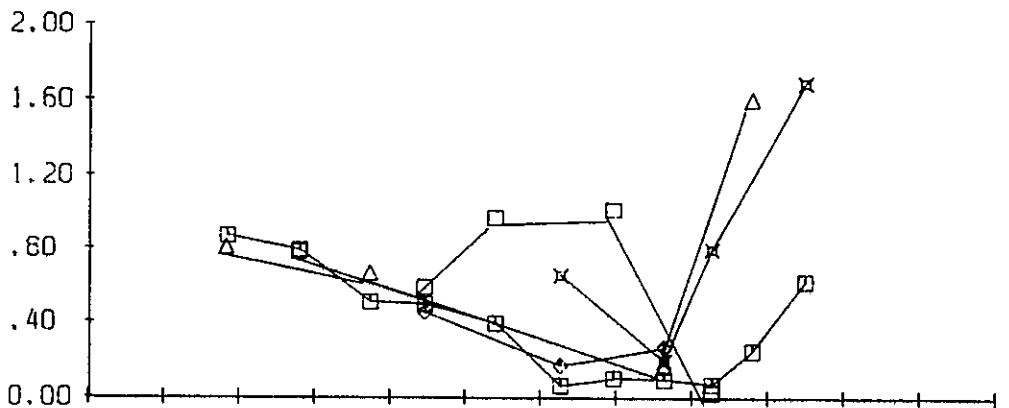
P0



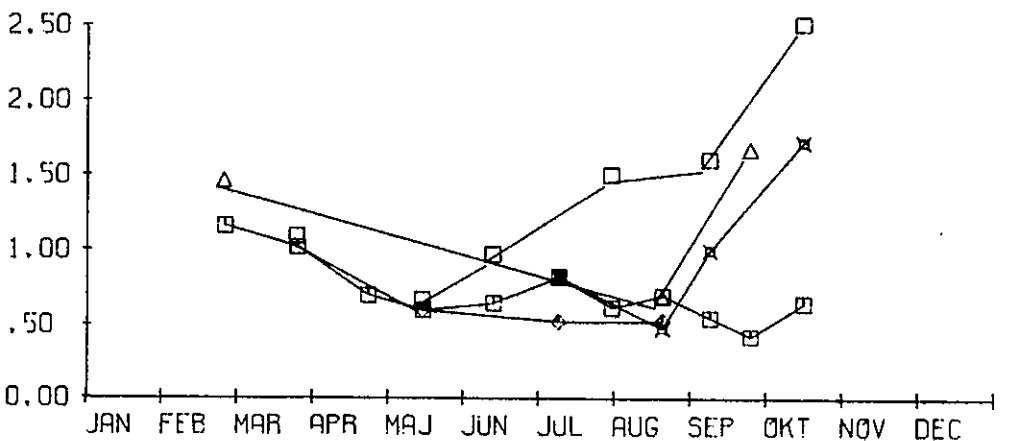
TP



UN

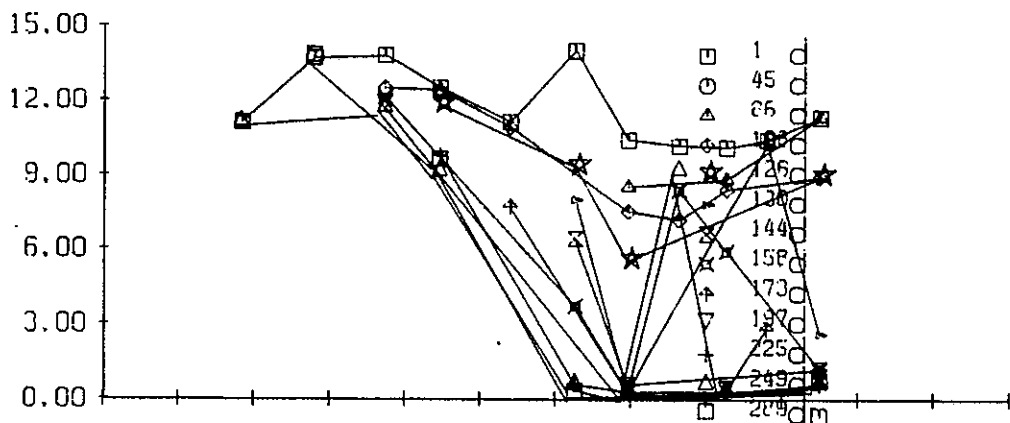


TN

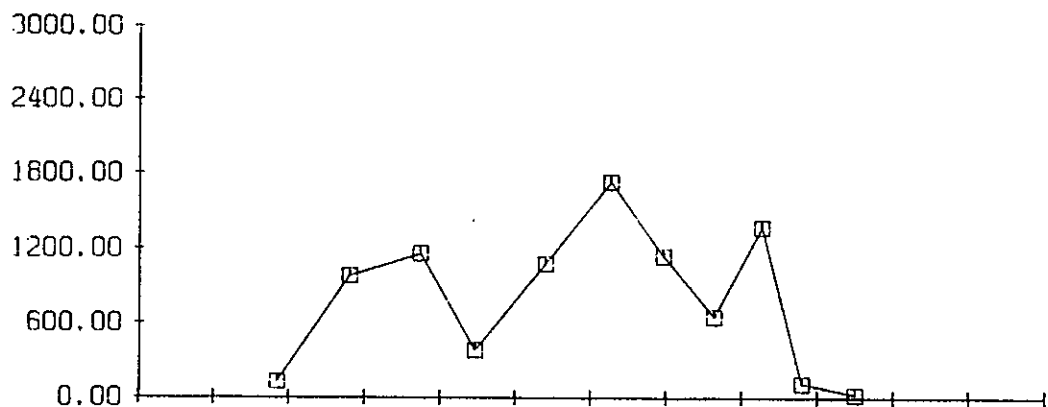


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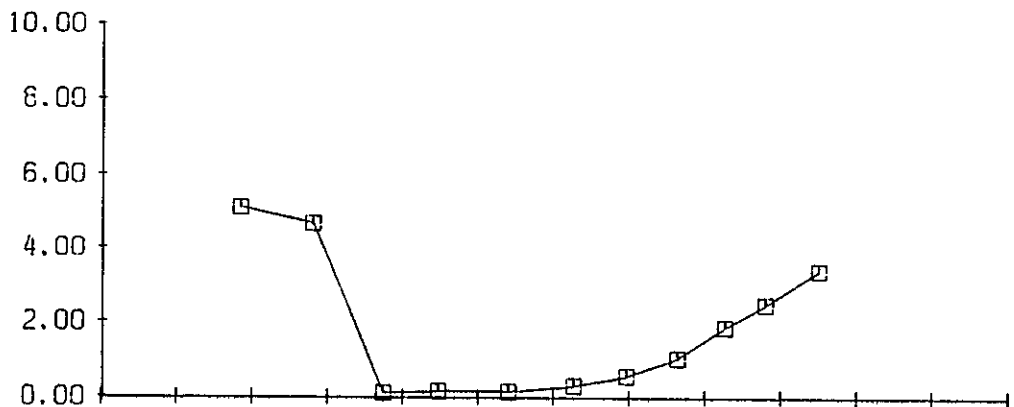
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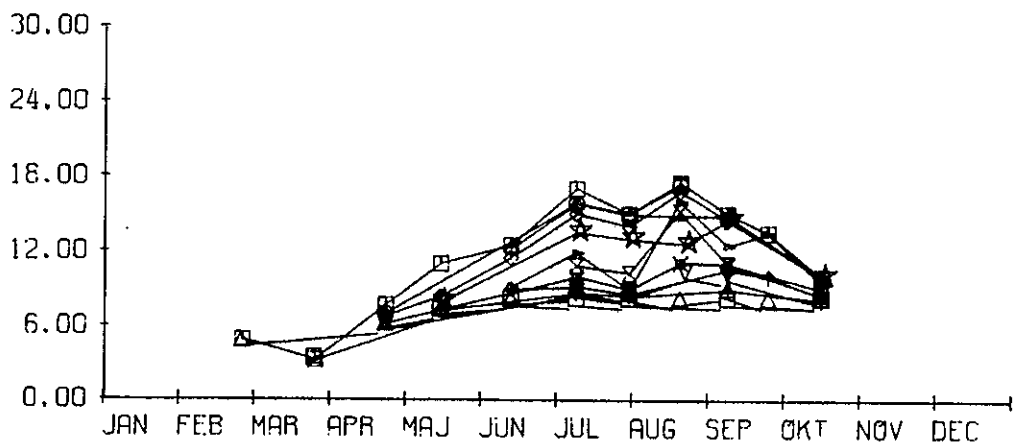
PP



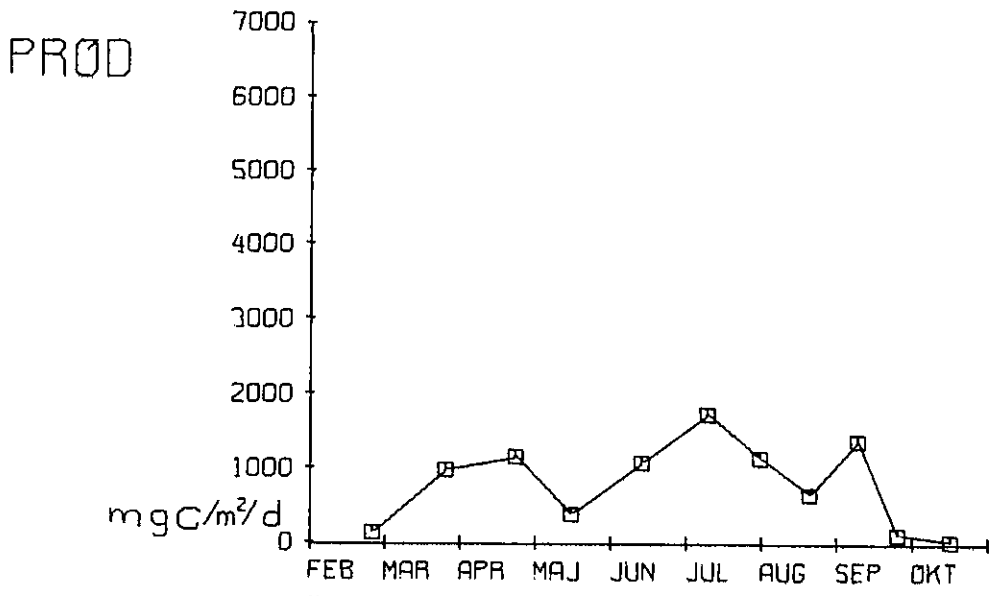
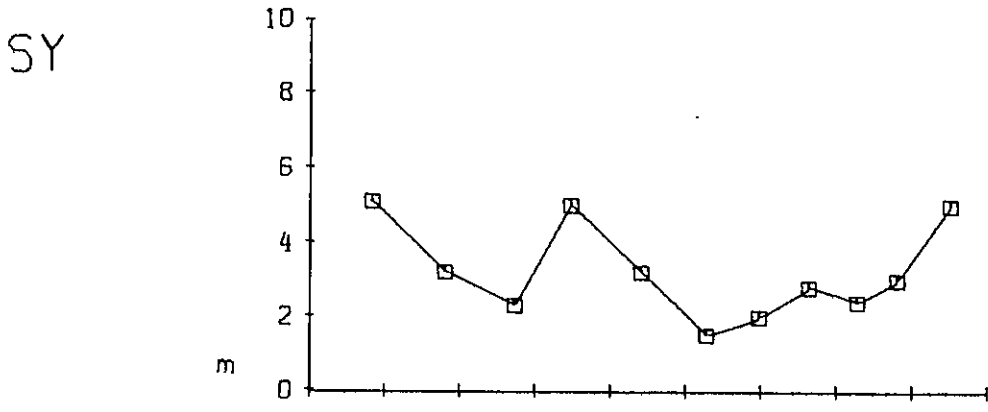
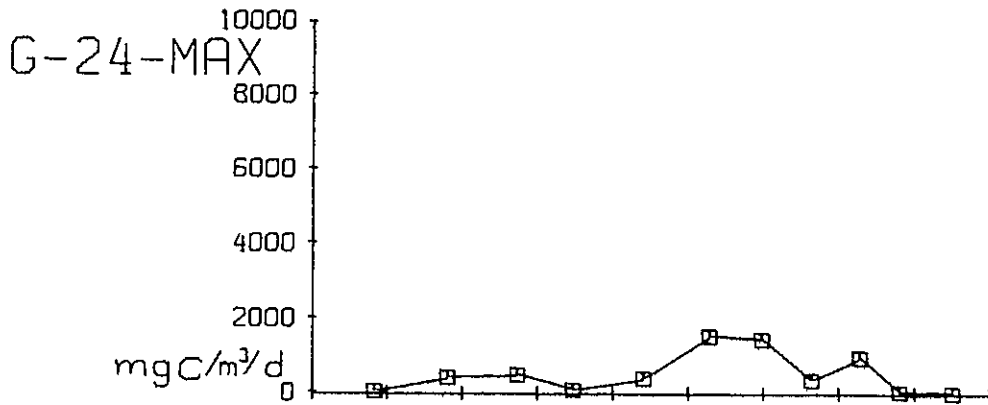
SI



TF



HAL 1



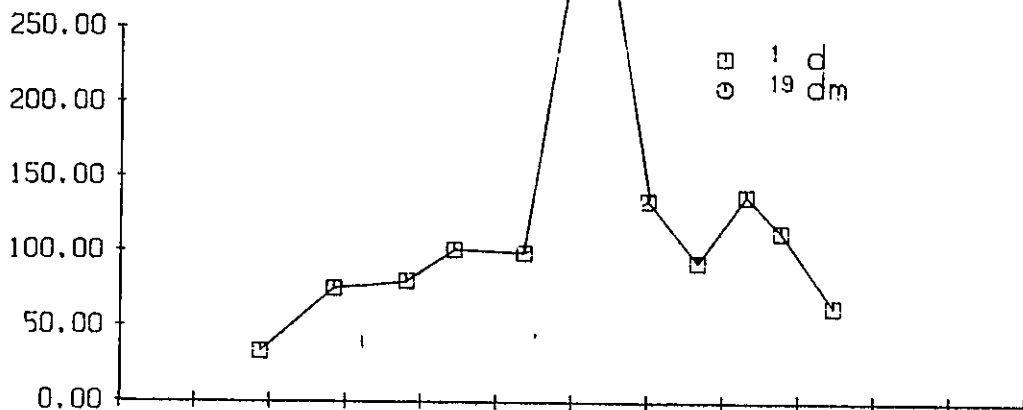
74
ÅRSPROD.

200 gC/m²/år

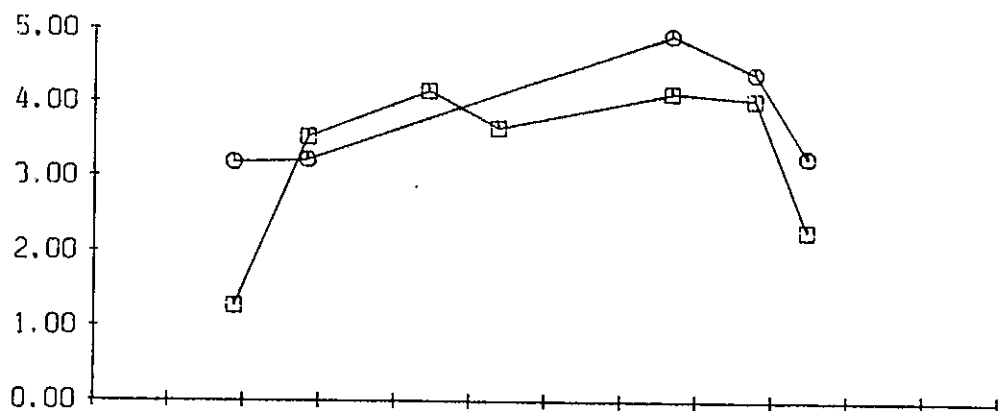
fig. 7.3.1

HNG 751

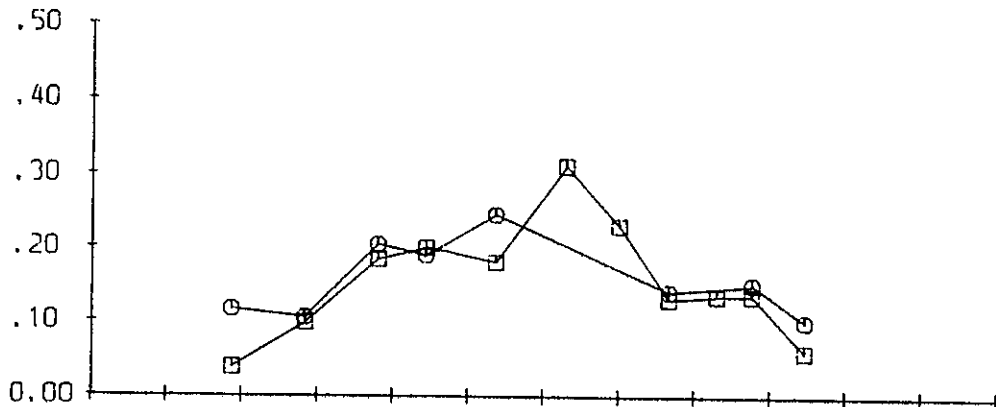
CH



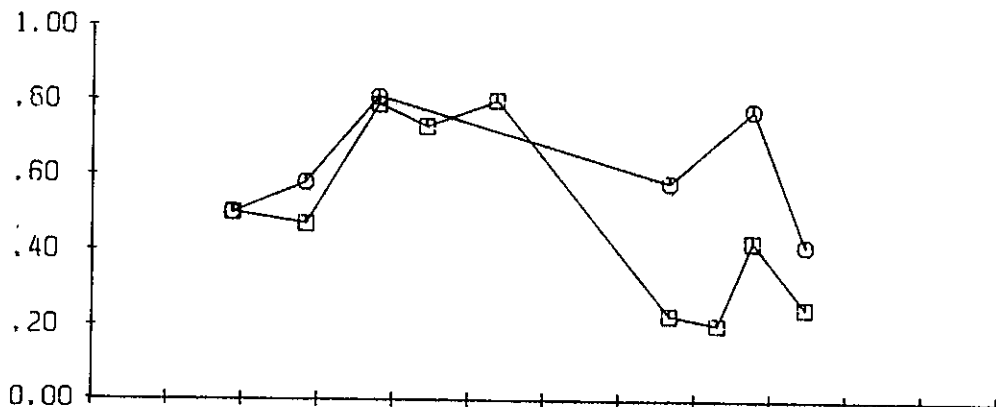
PARO



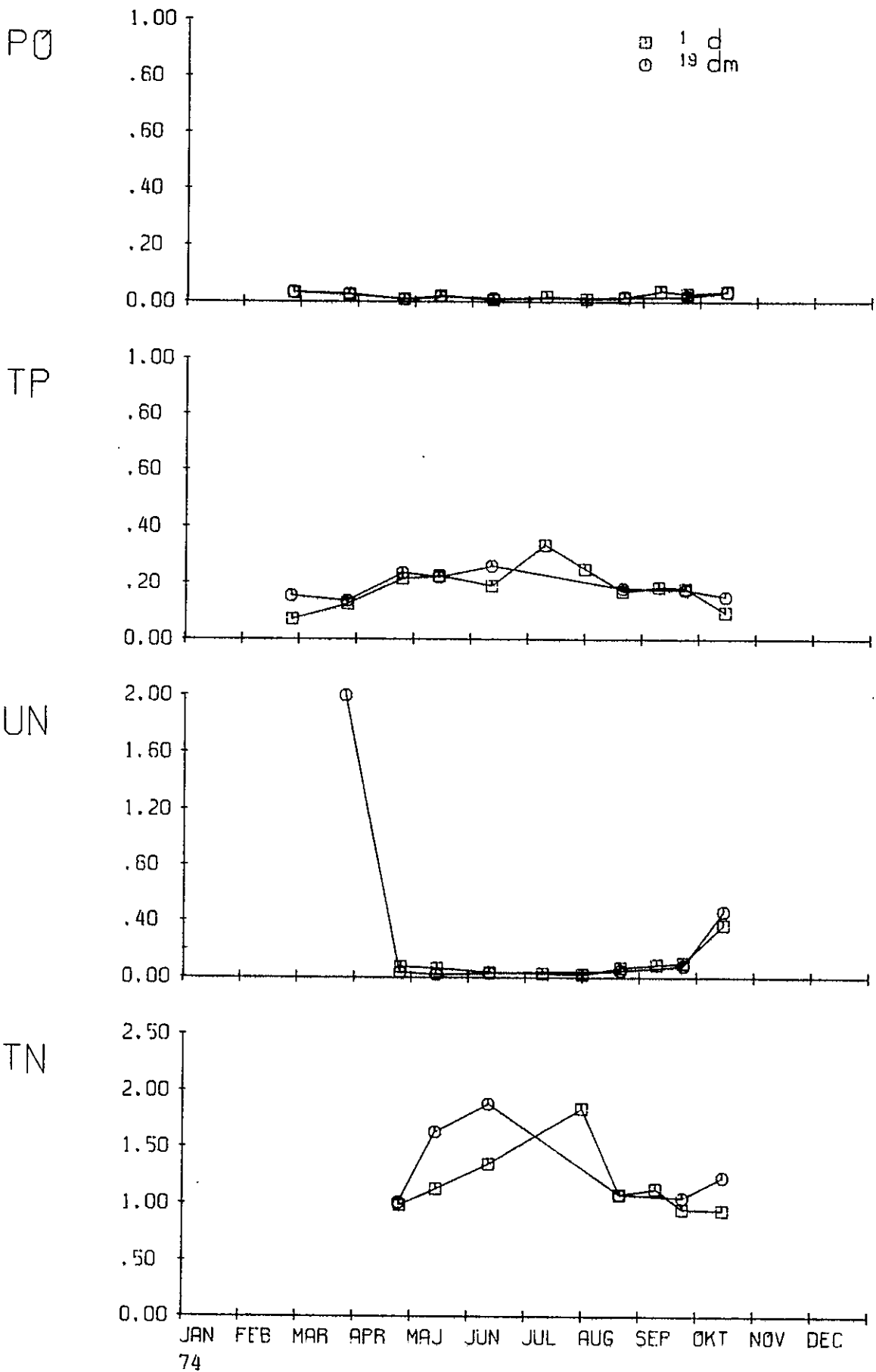
PARP



PARN

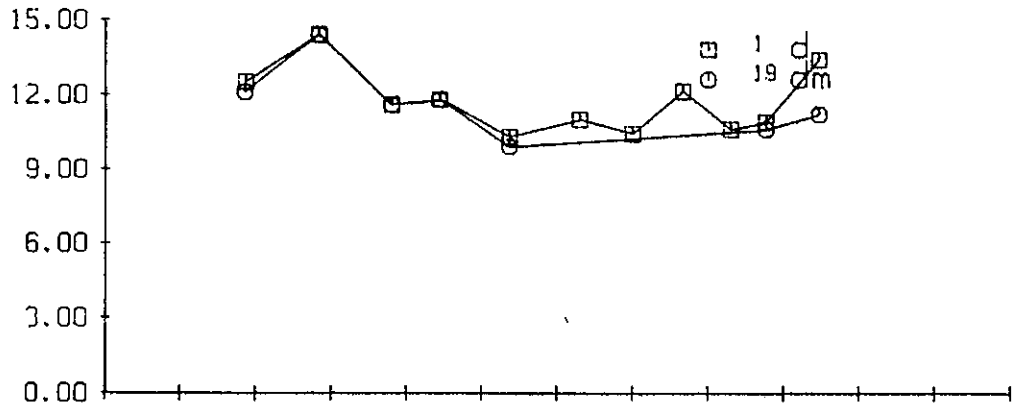


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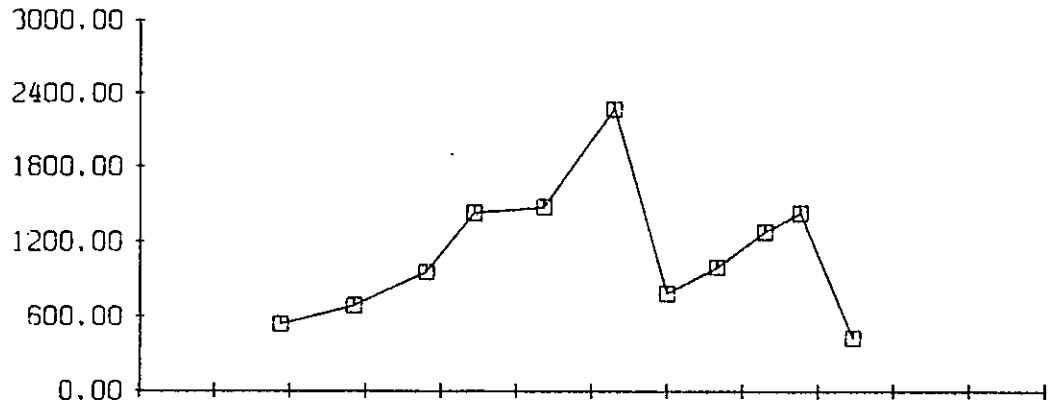


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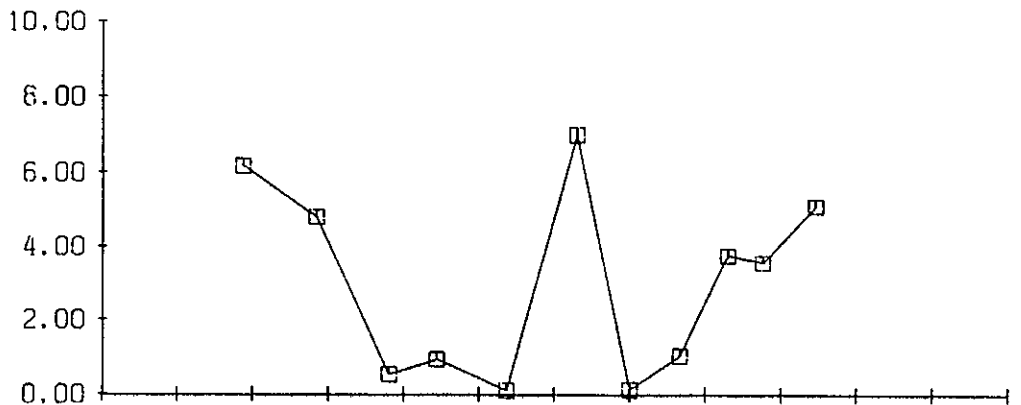
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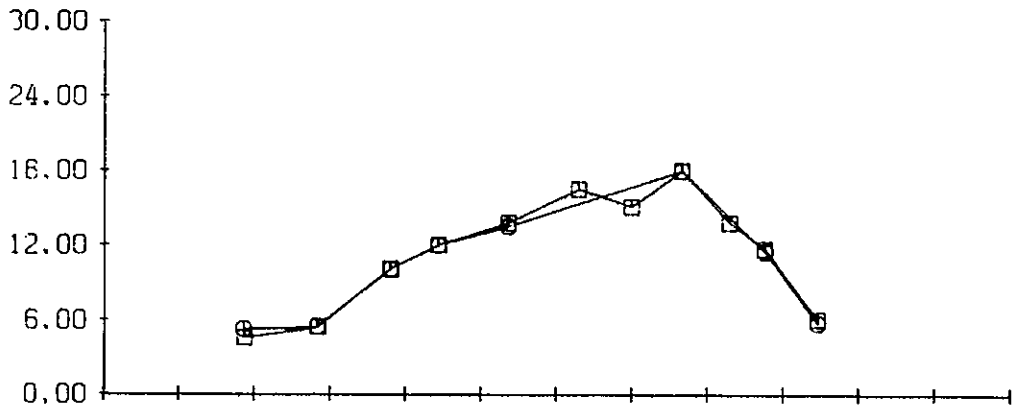
PP



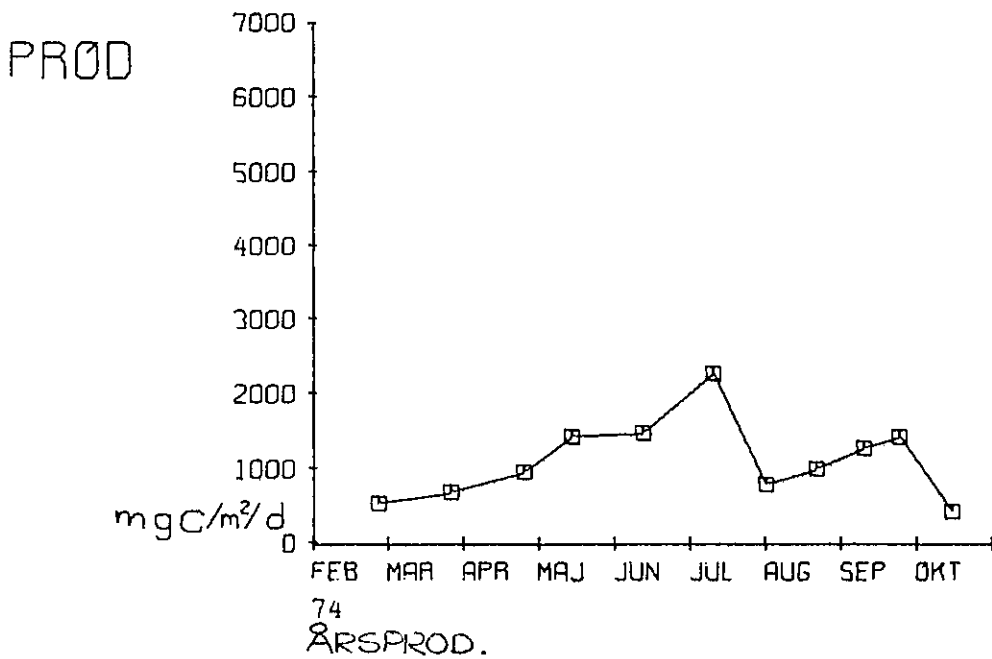
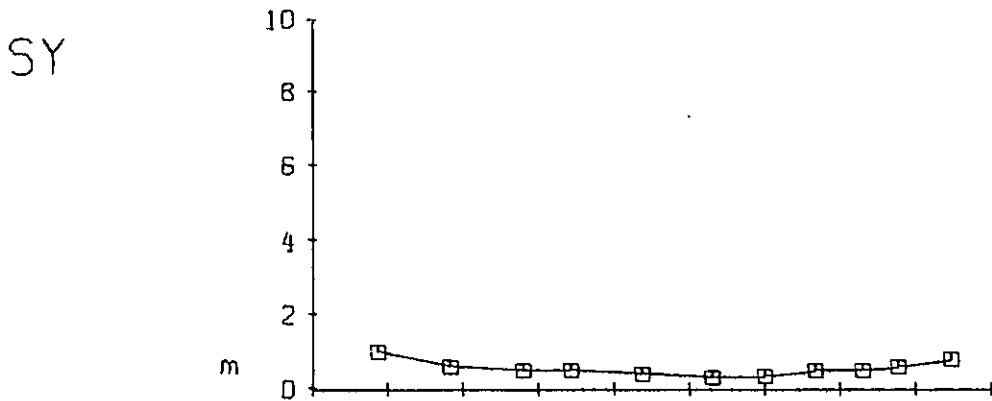
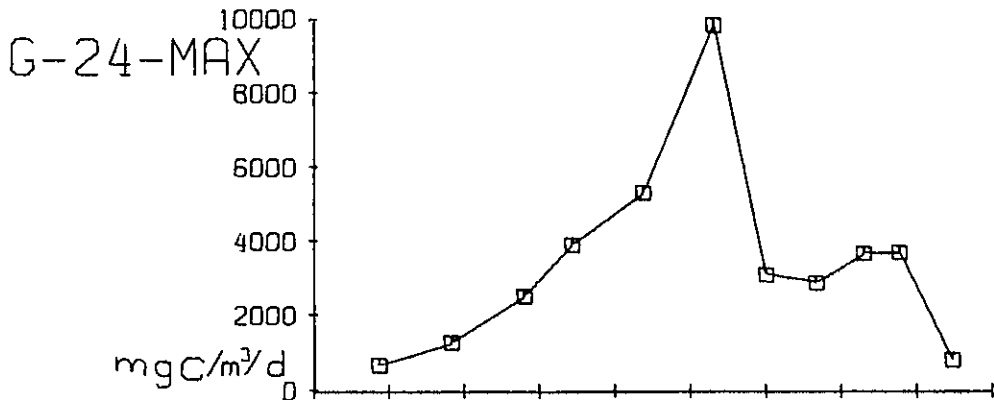
SI



TF

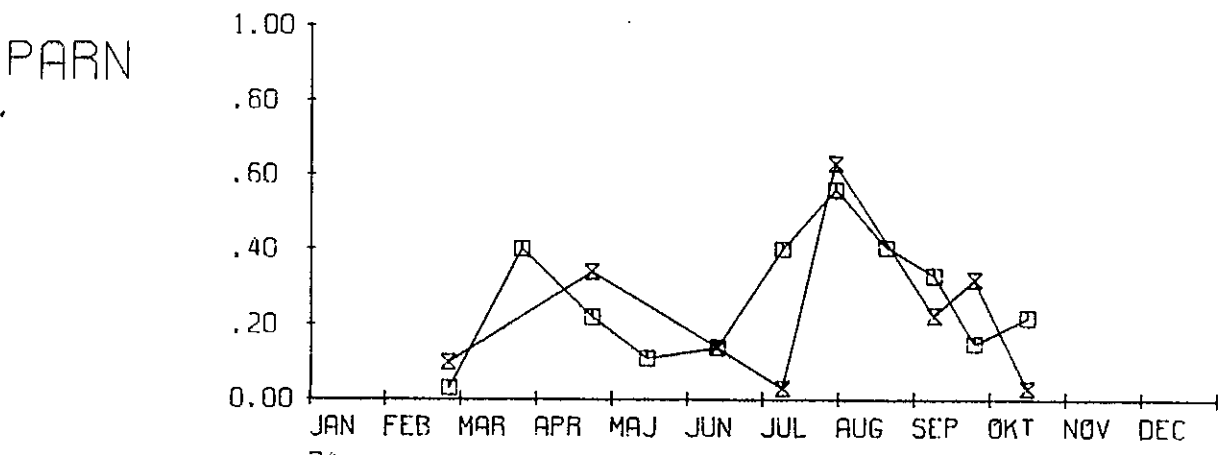
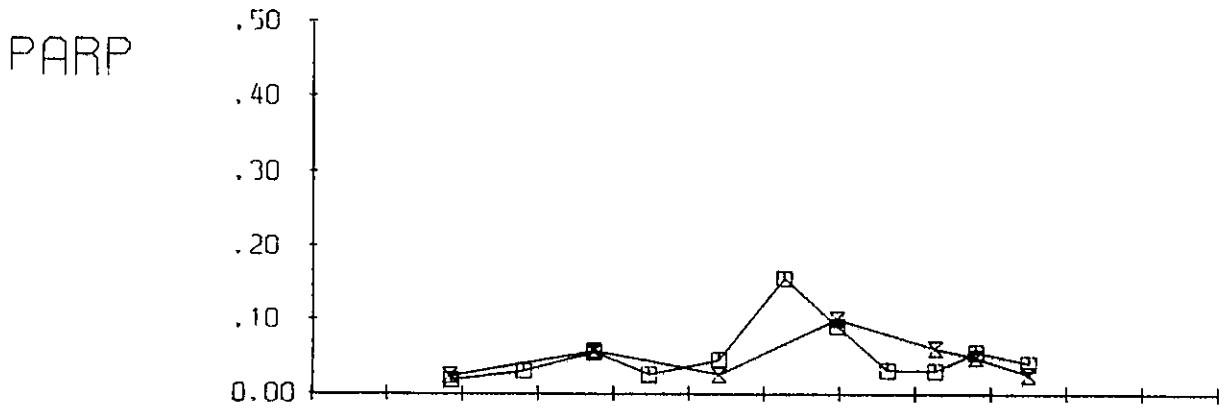
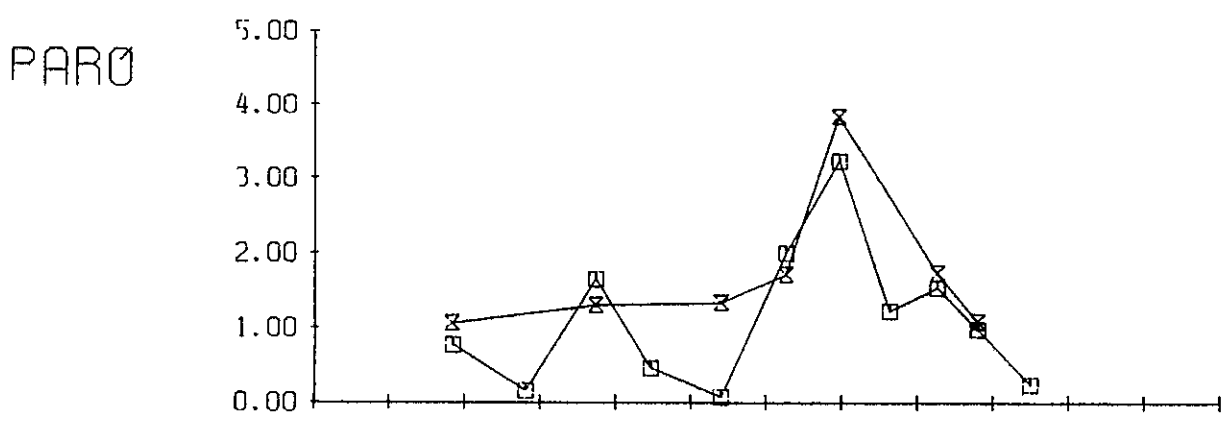
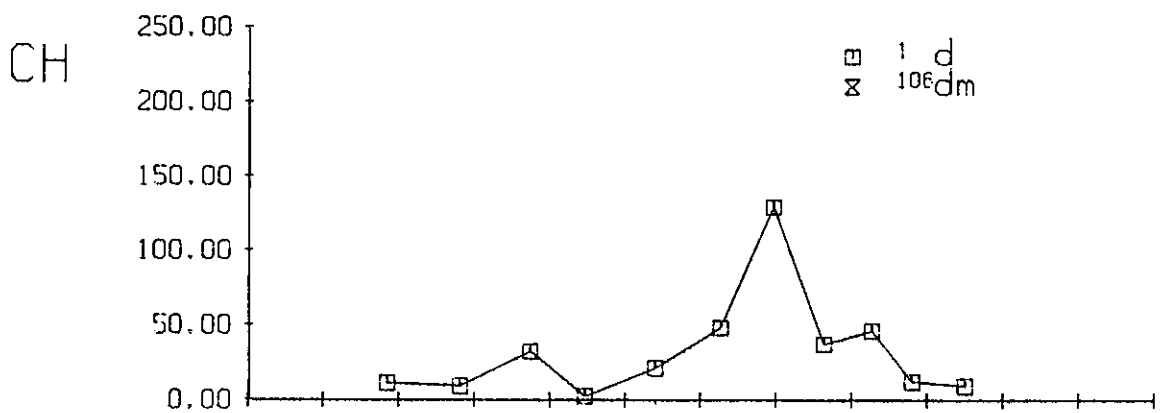


HIN 1

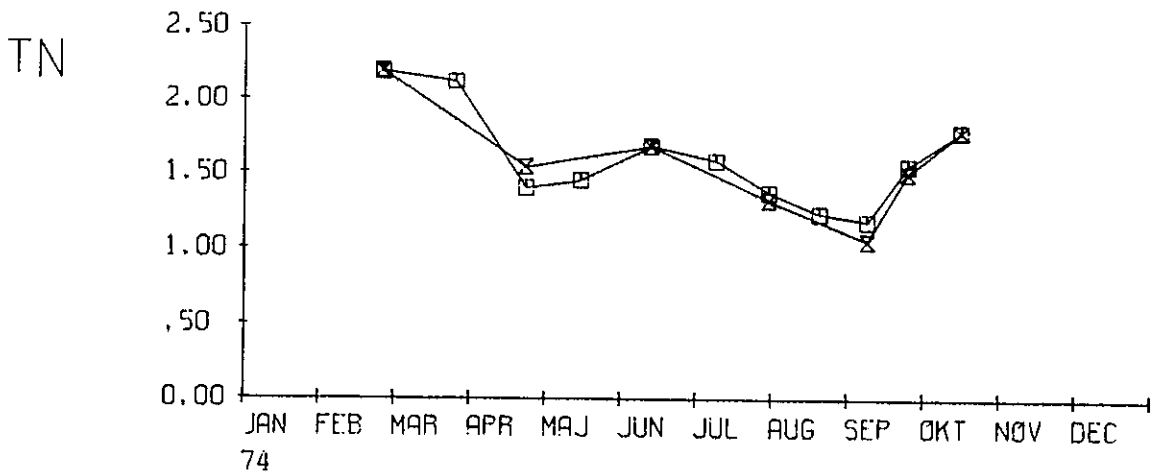
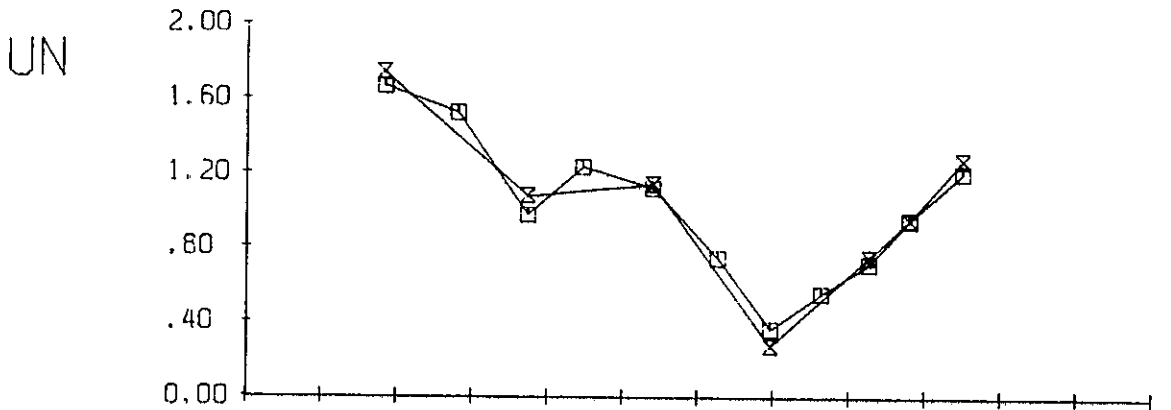
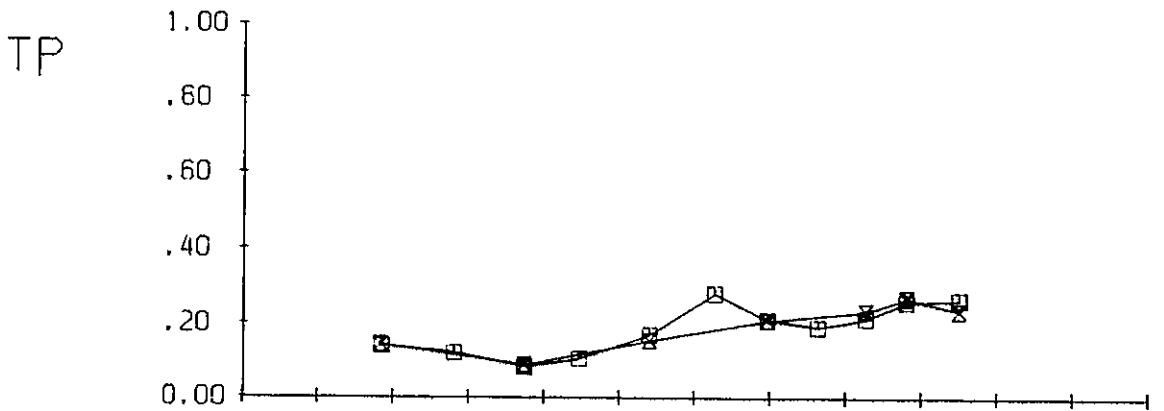
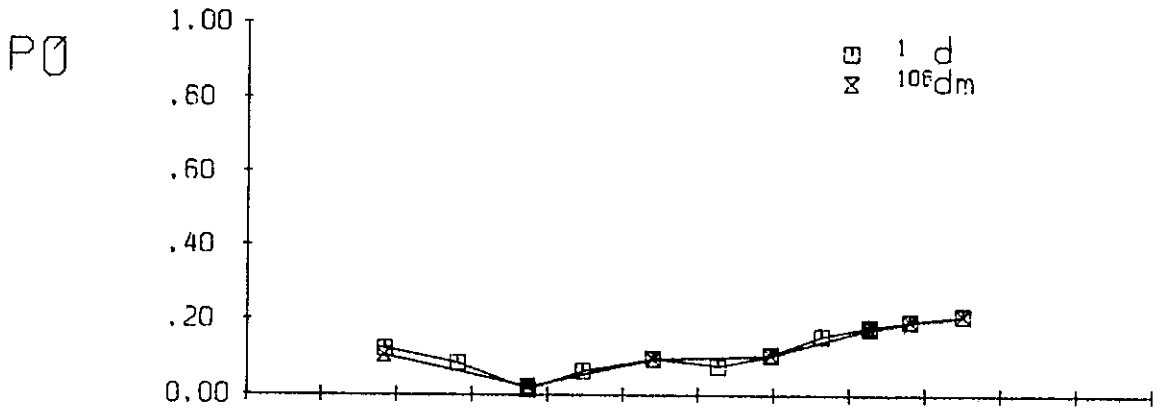


270 gC/m²/år

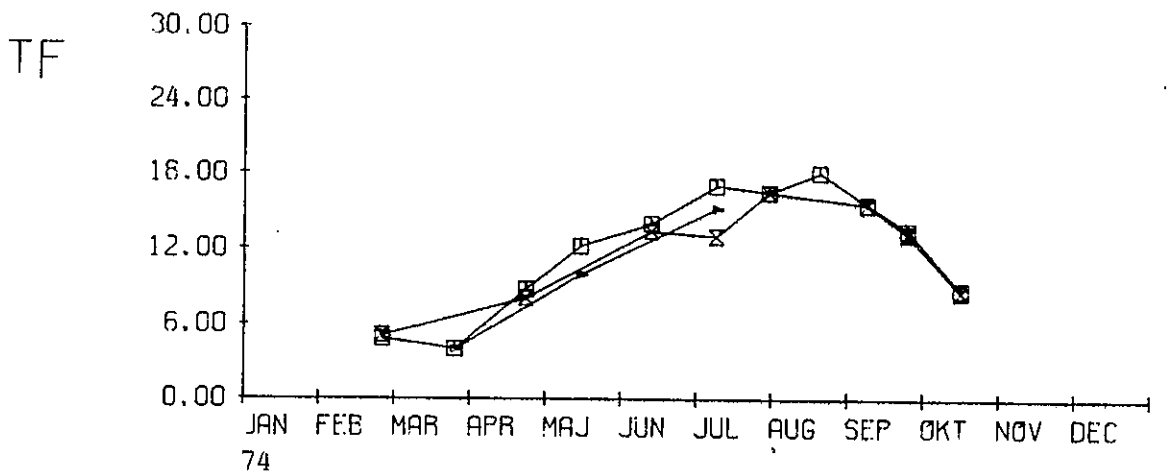
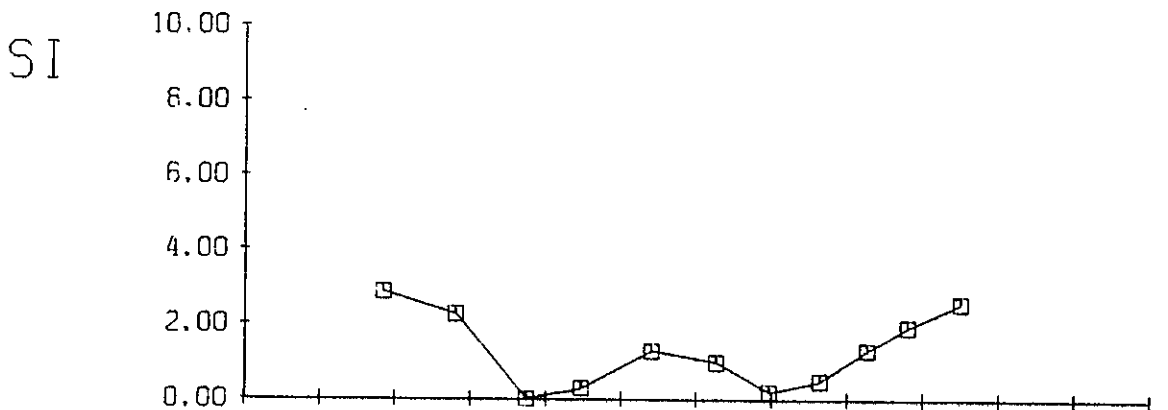
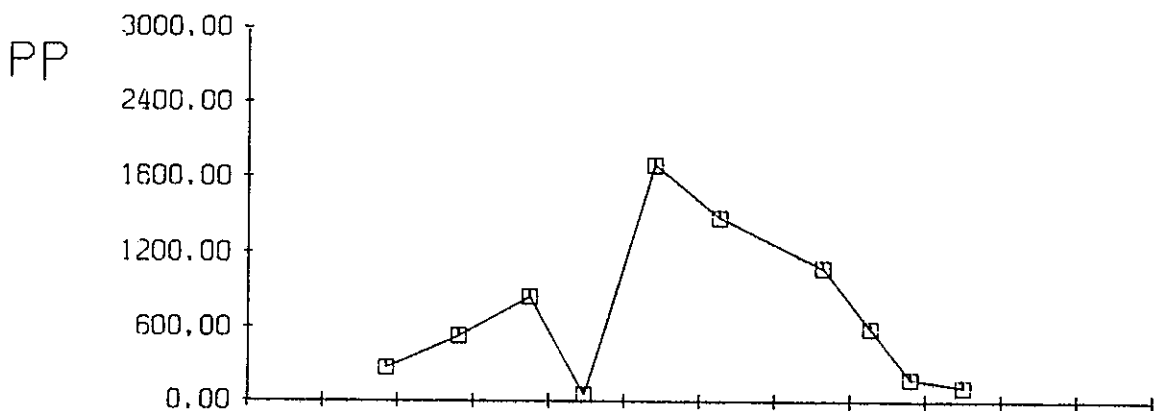
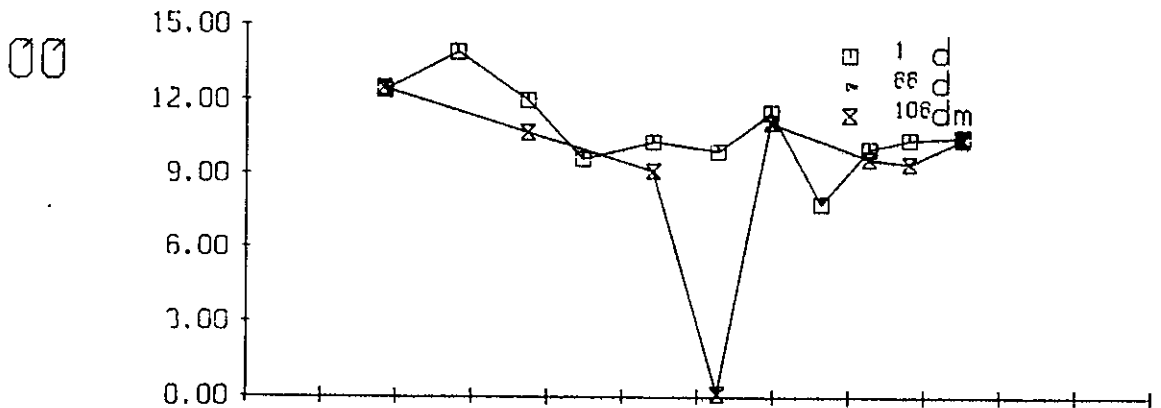
NRS 751



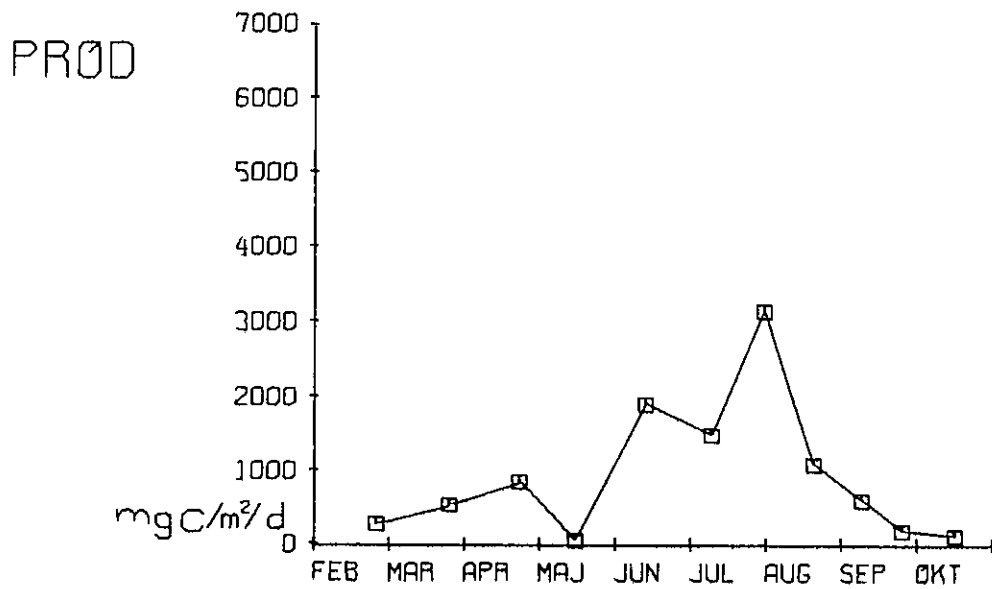
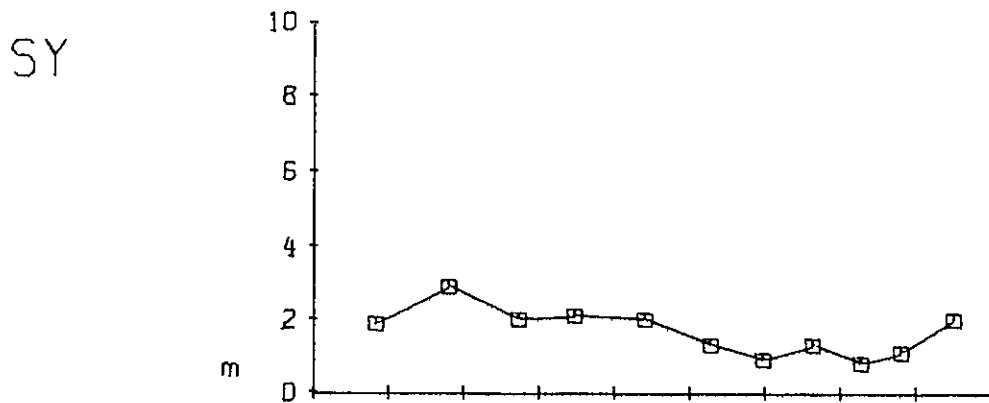
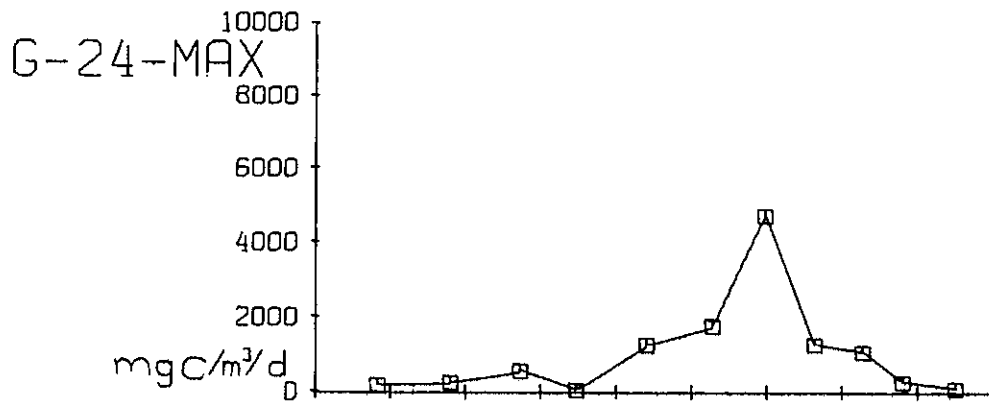
NRS 751



NRS 751



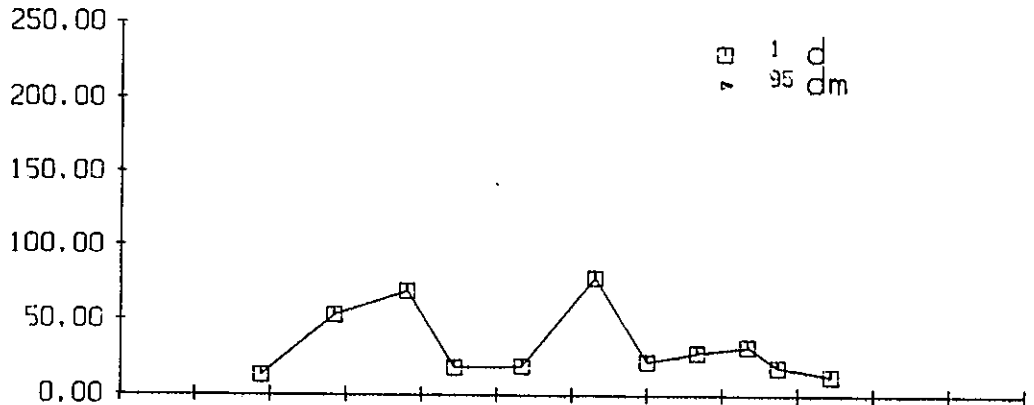
NOR 1



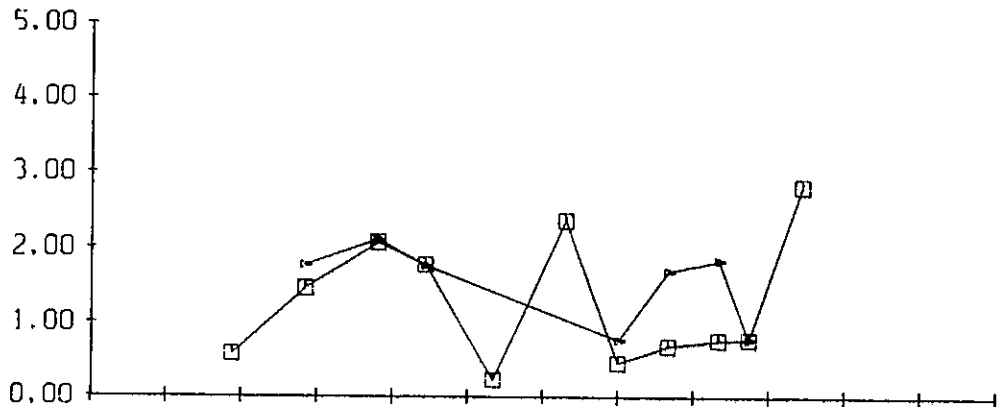
74
ARS PROD: 230 gCm²år⁻¹

SAL 751

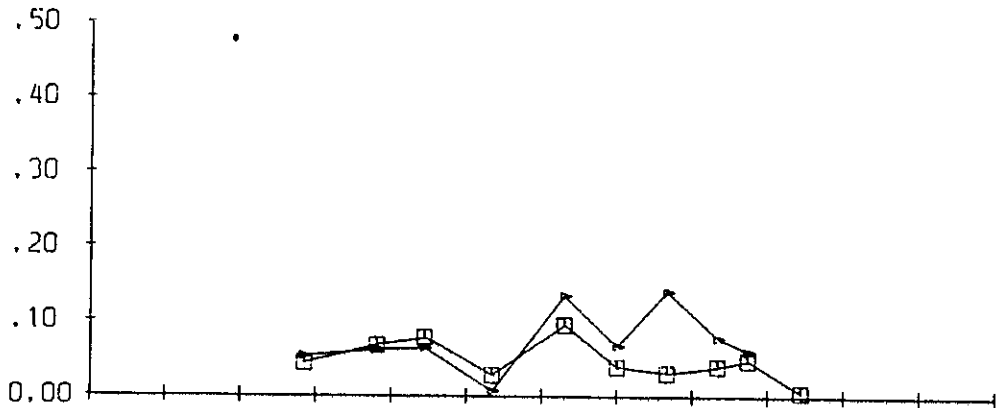
CH



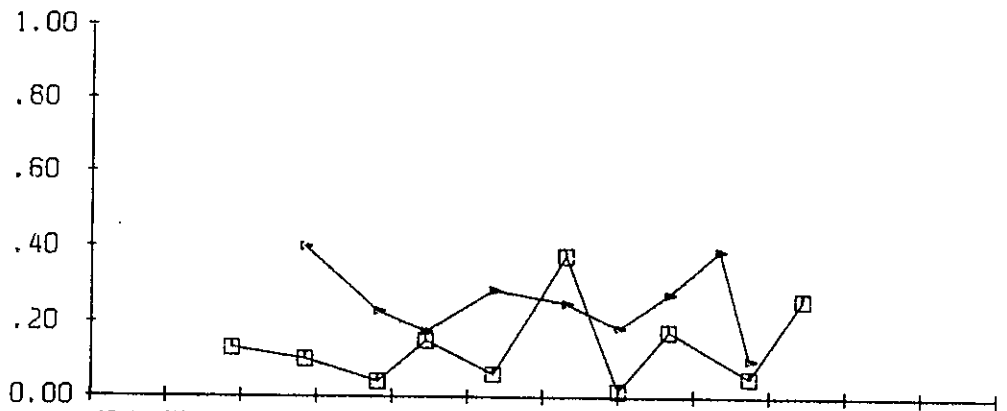
PAR0



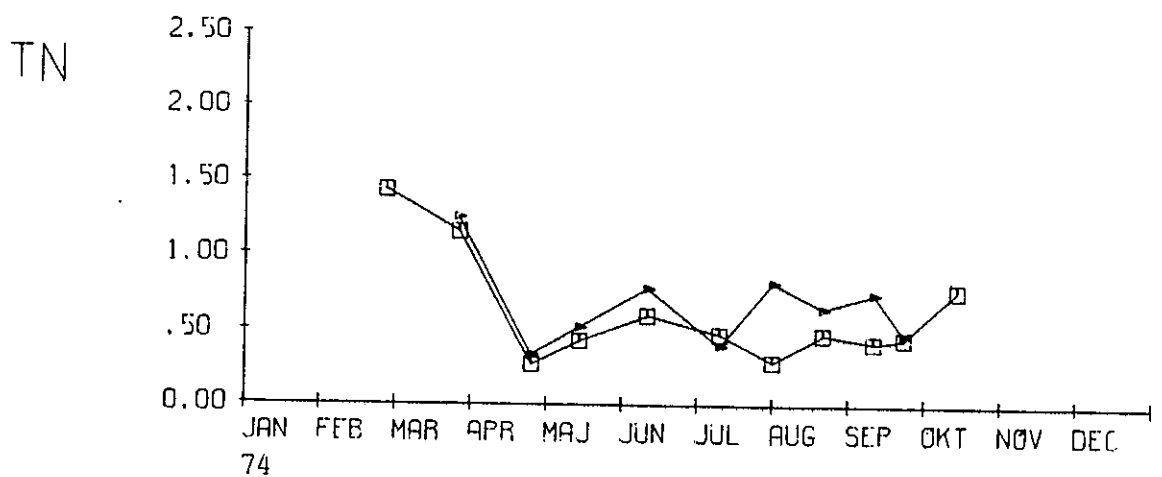
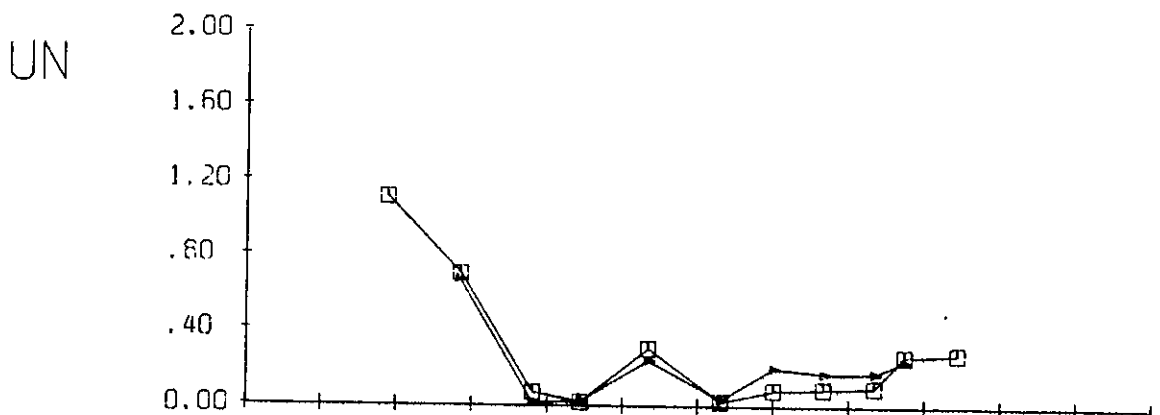
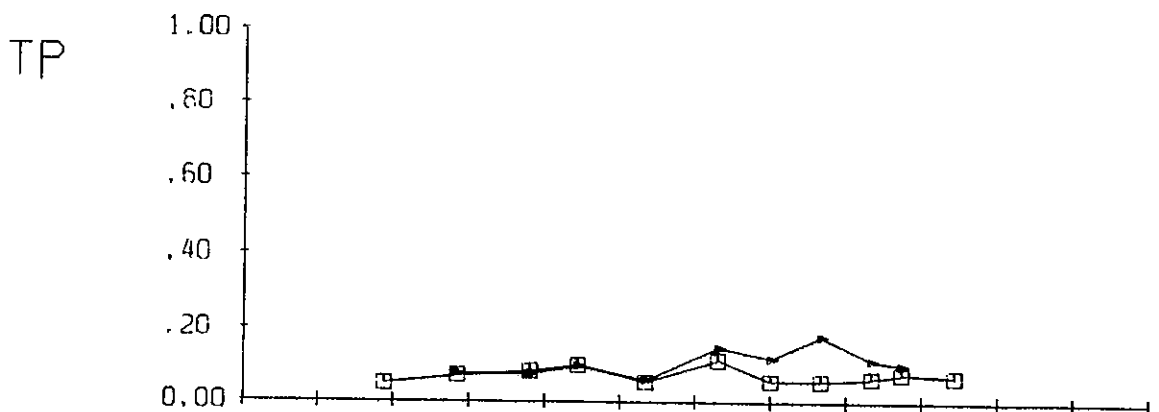
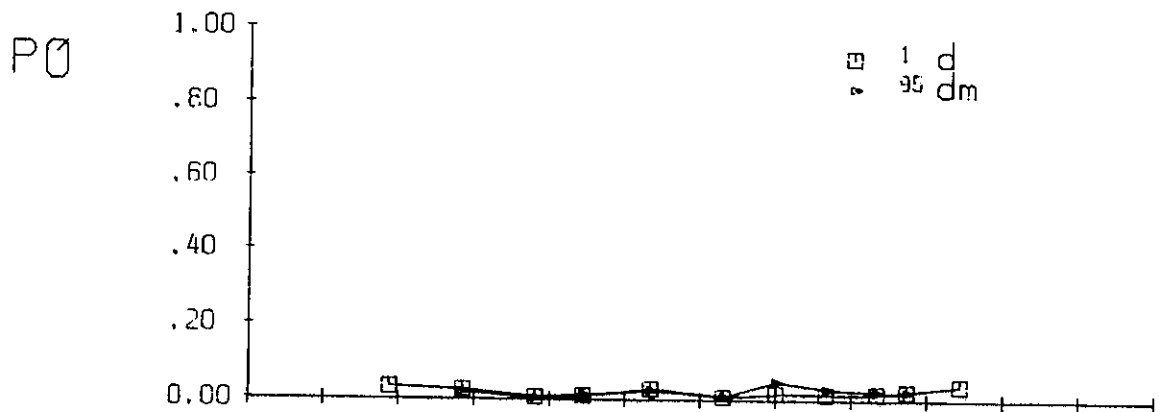
PARP



PARN

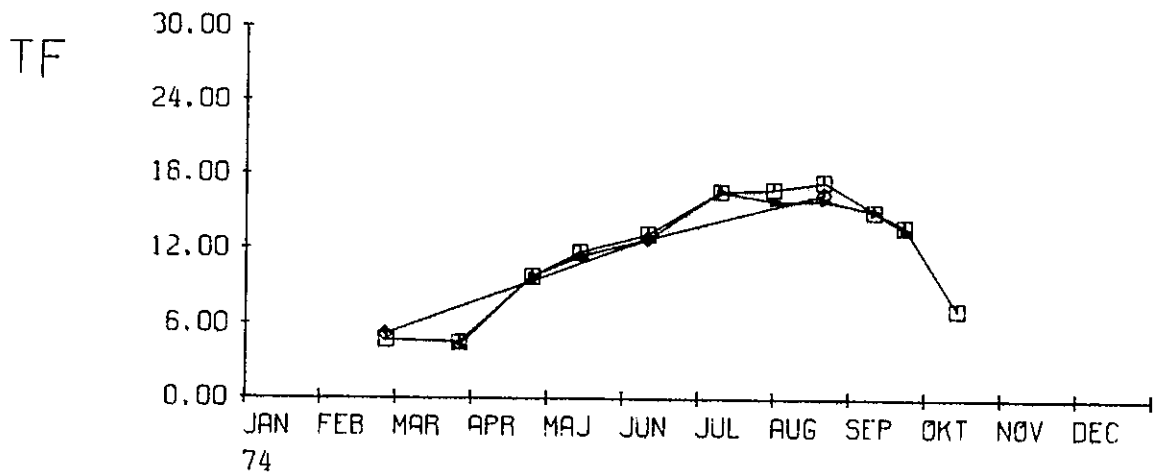
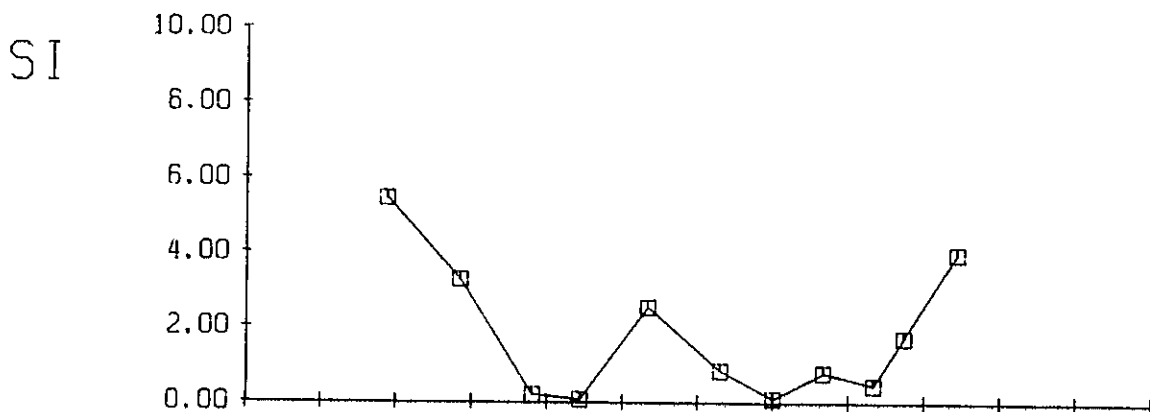
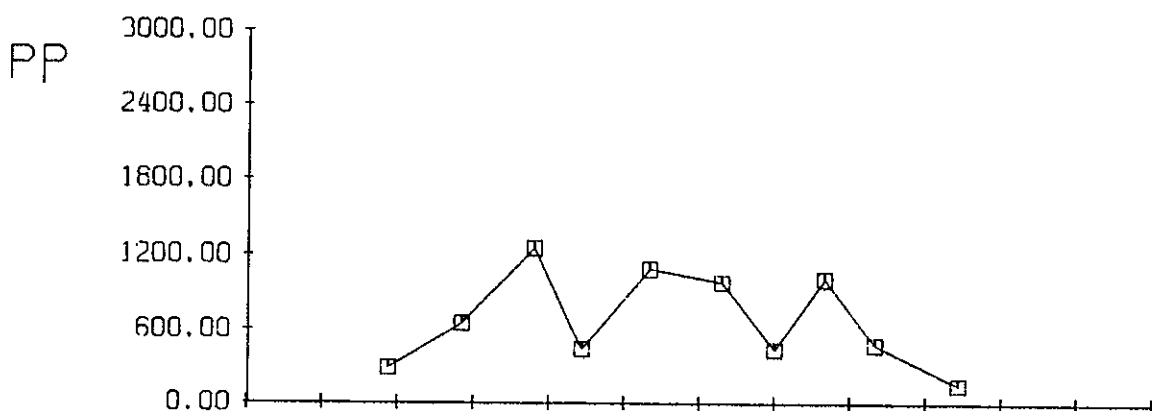
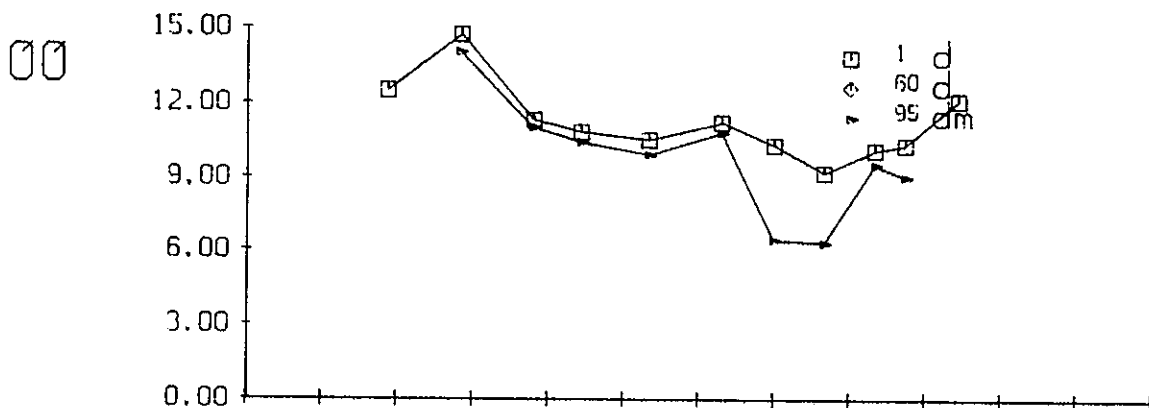


SAL 751



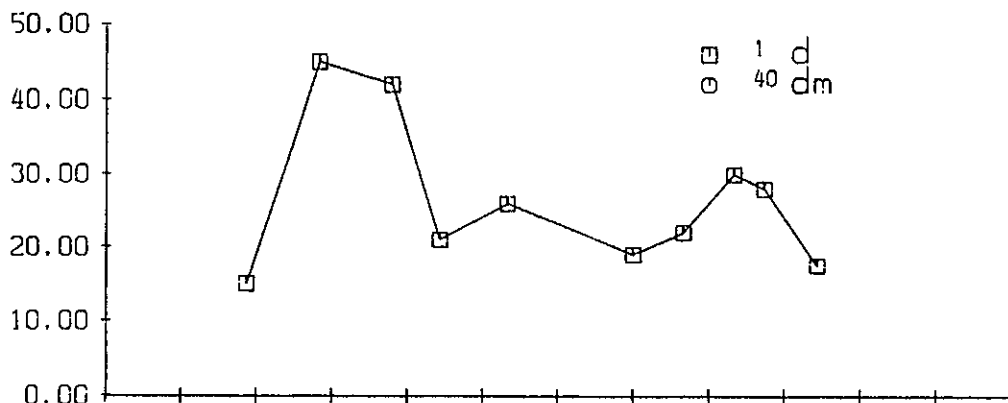
JAN FEB MAR APR MAJ JUN JUL AUG SEP OKT NOV DEC
74

SAL 751

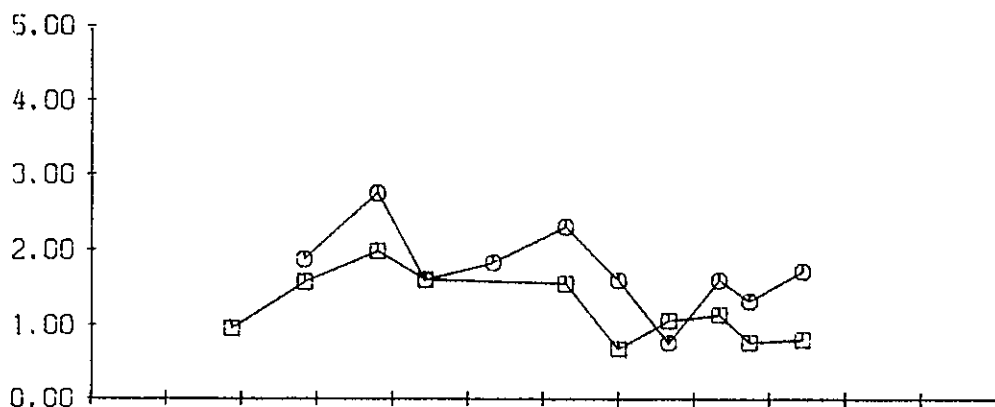


SAL 752

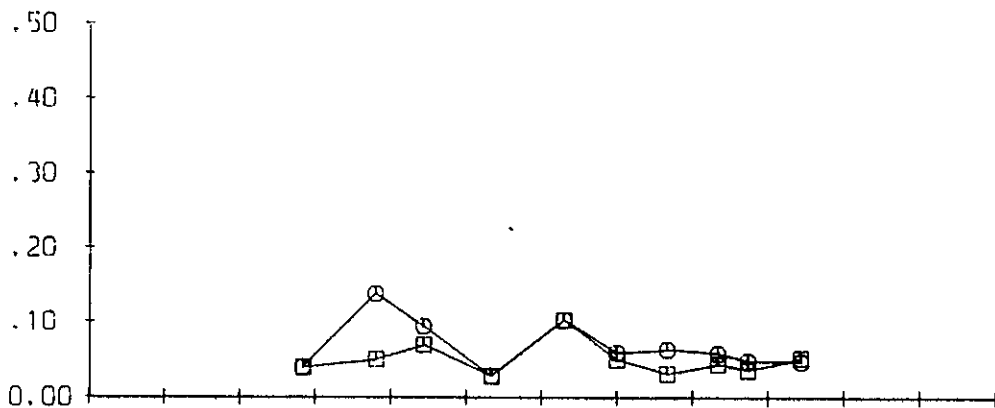
CH



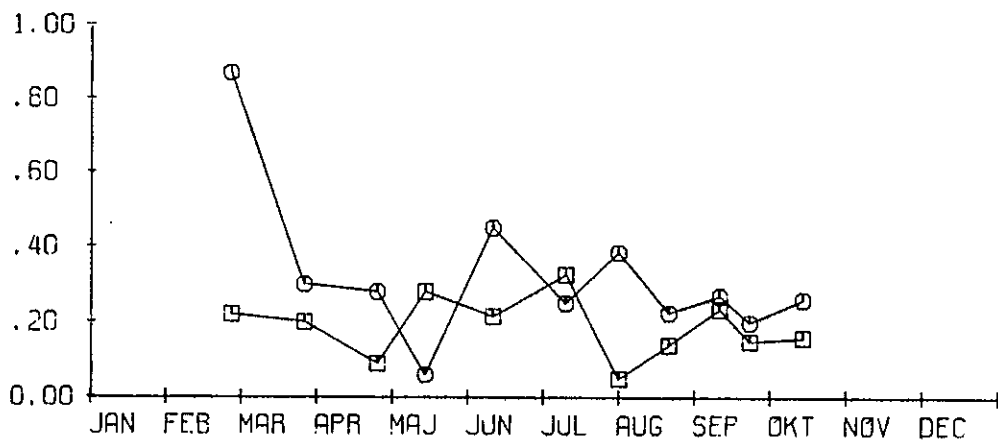
PARO



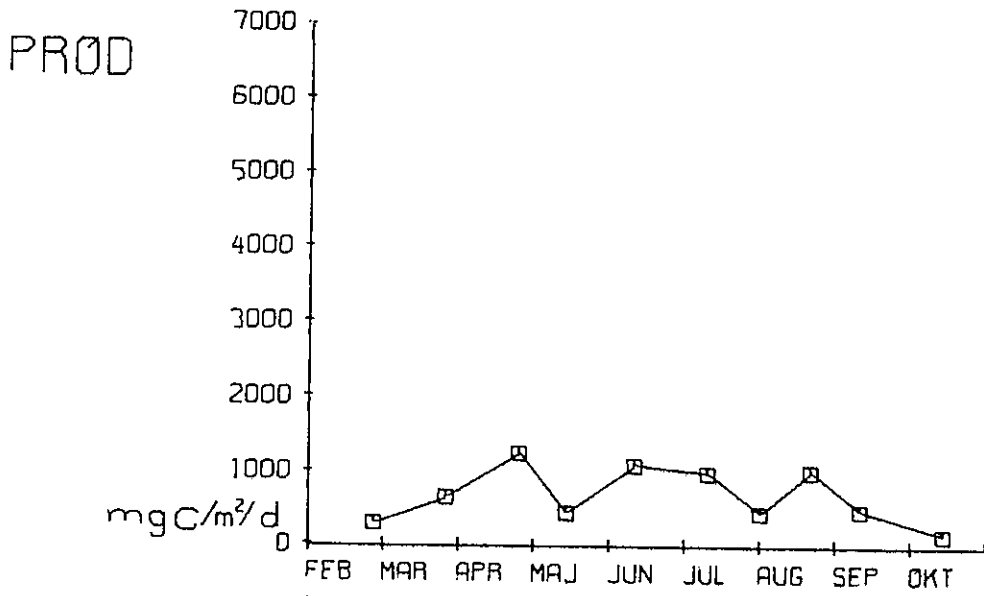
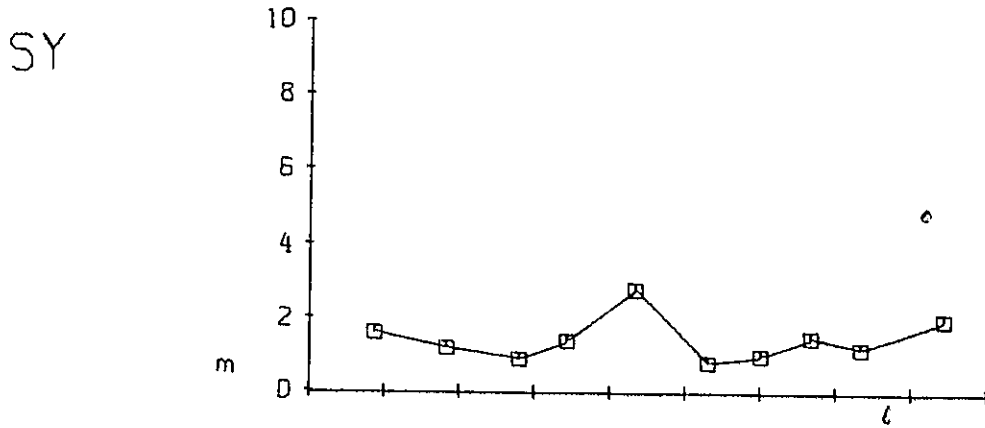
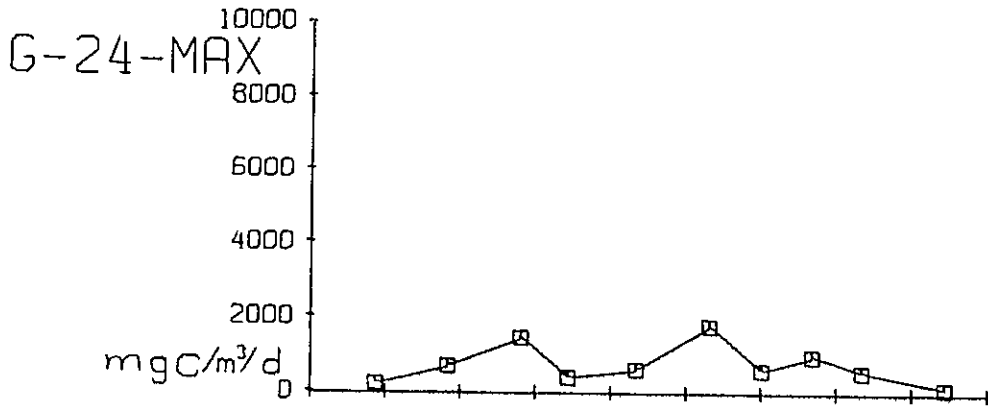
PARP



PARN

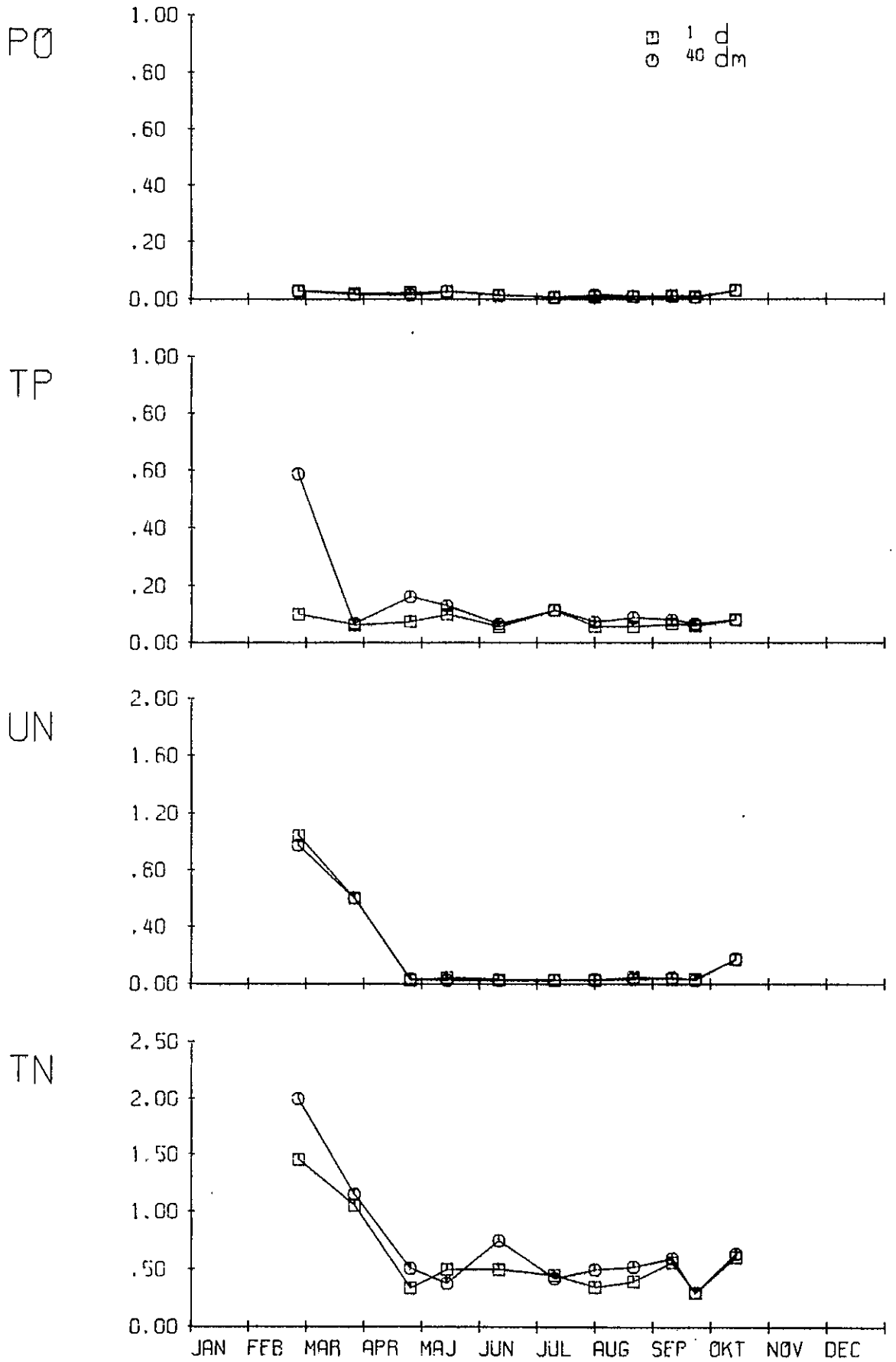


SAL 1

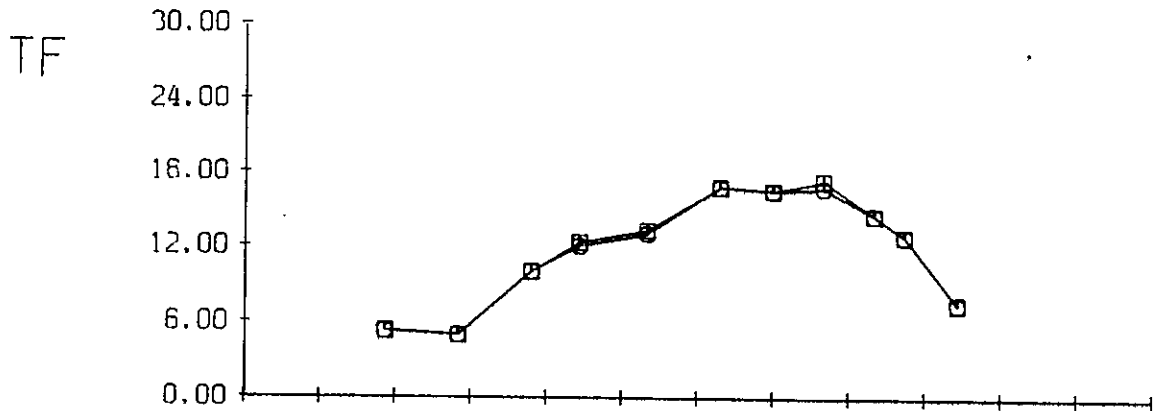
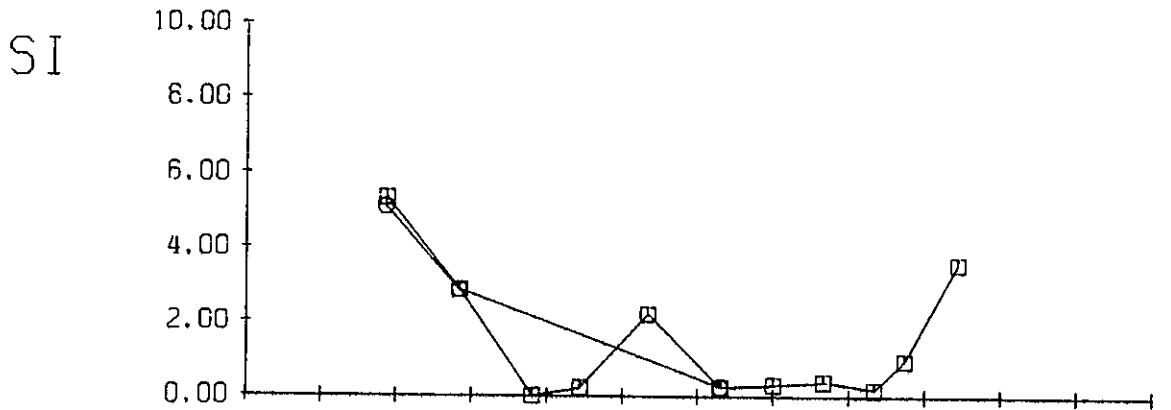
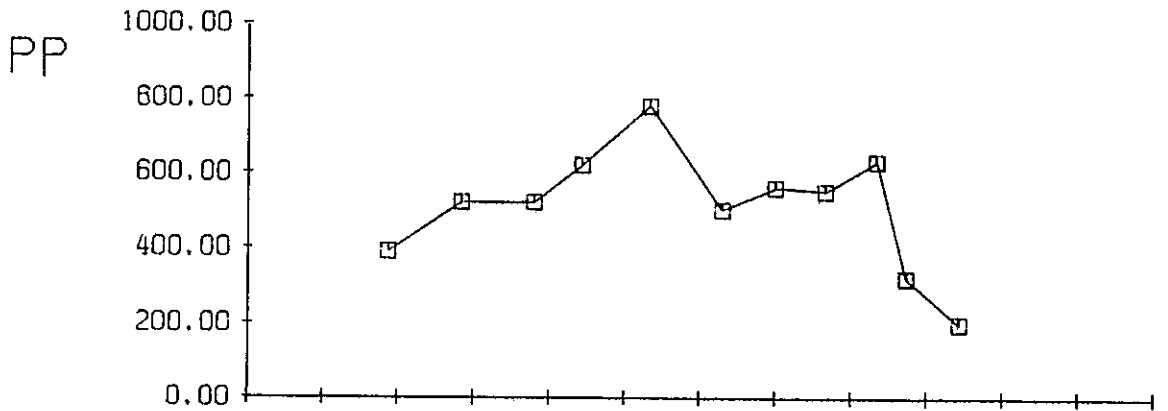
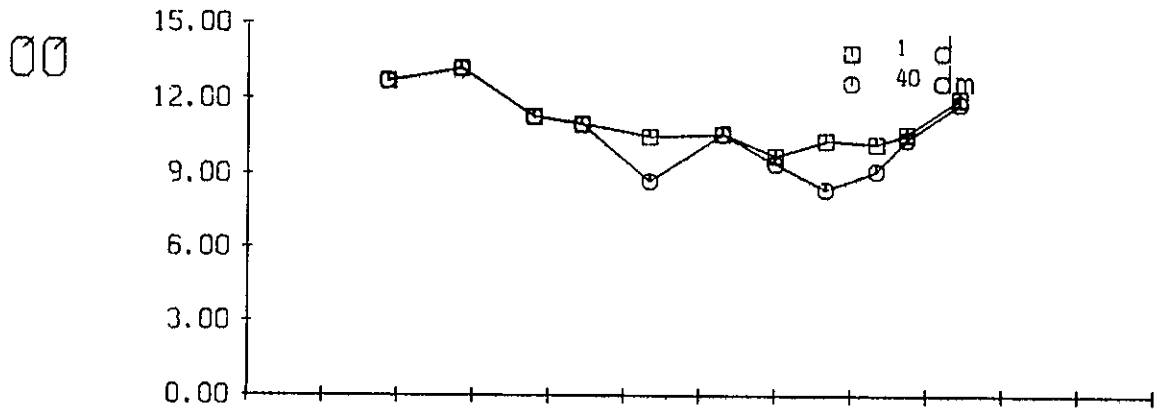


74
ARSPROD. 150 gCm⁻²ar⁻¹

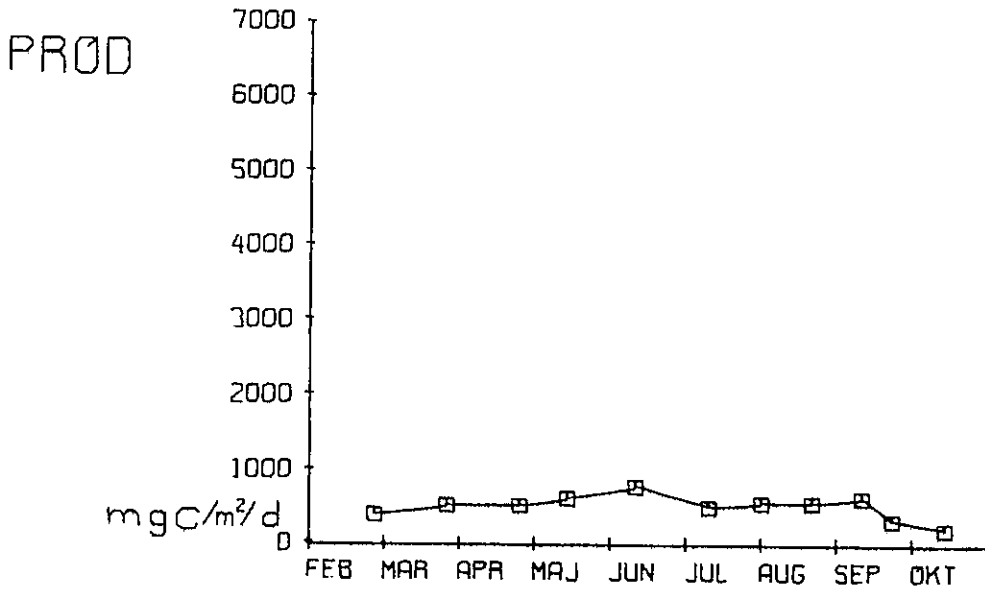
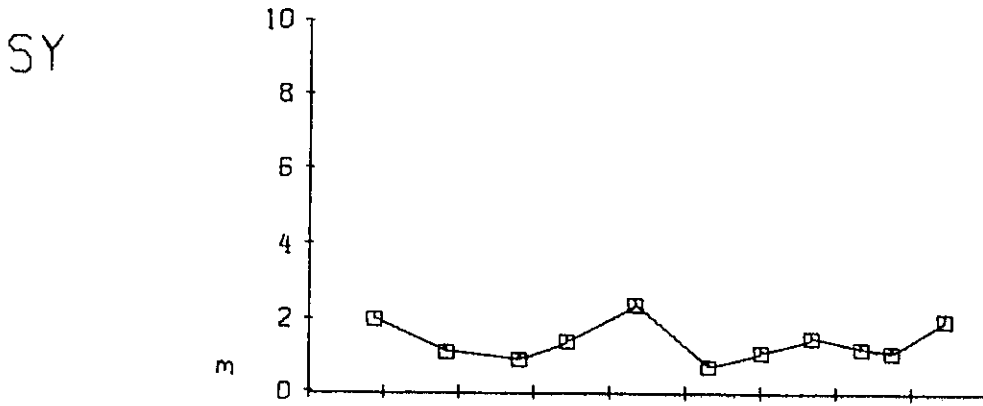
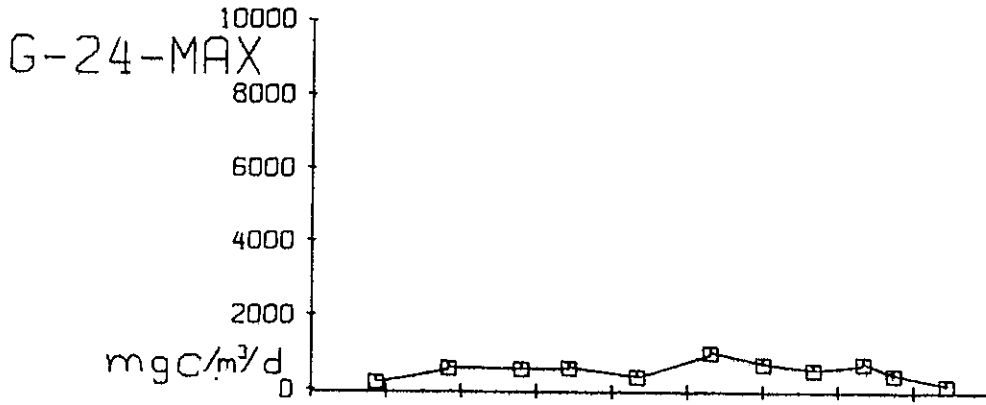
SAL 752



SAL 752



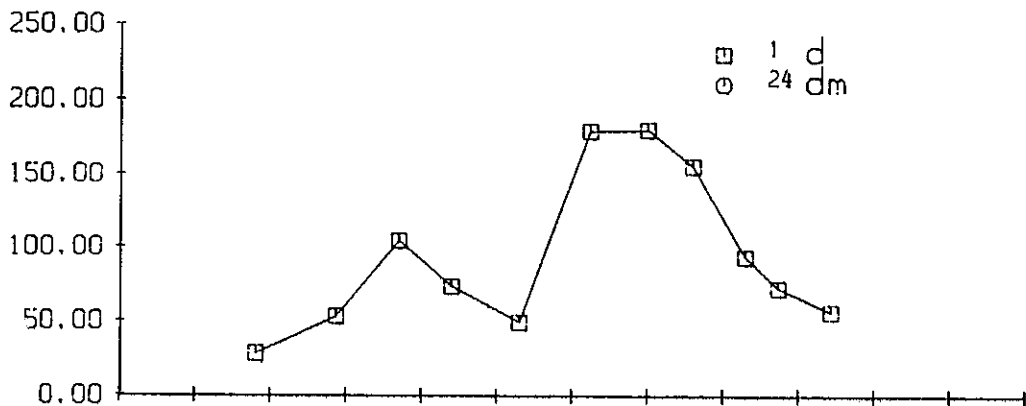
SAL 2



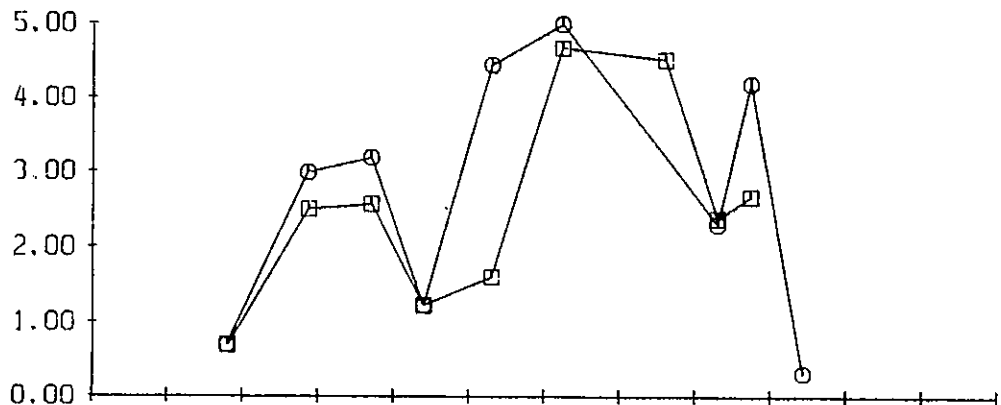
74
ÅRSPROD. 120 gCm²år⁻¹

SIL 751

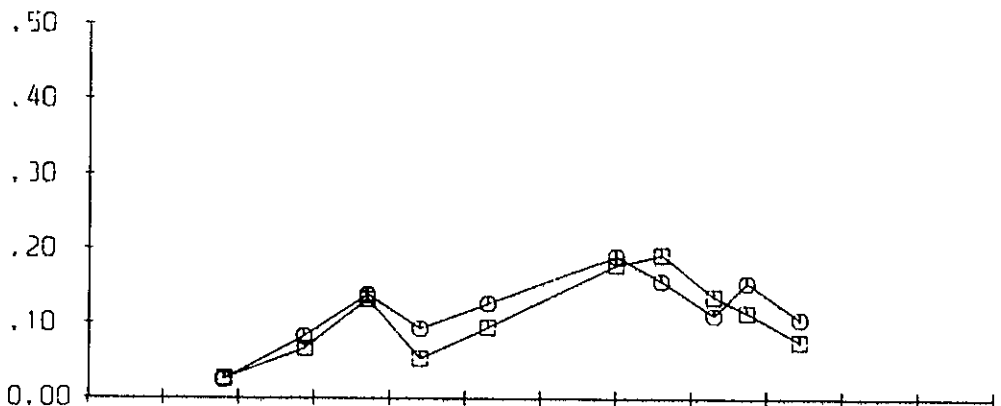
CH



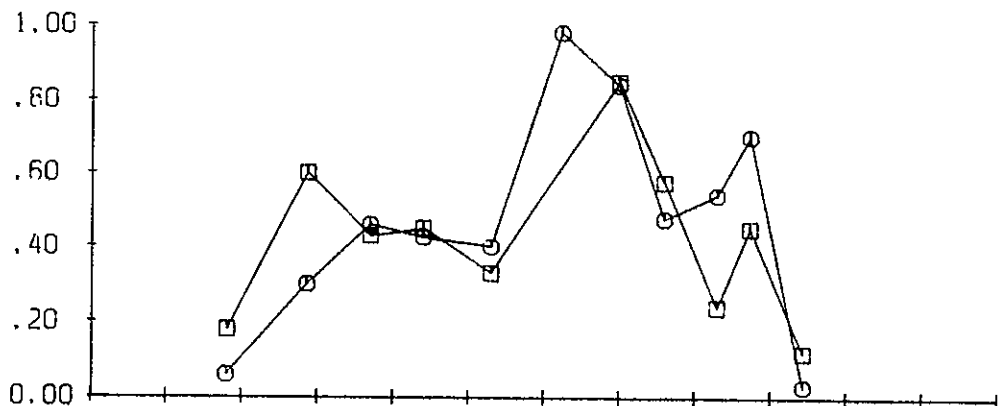
PARO



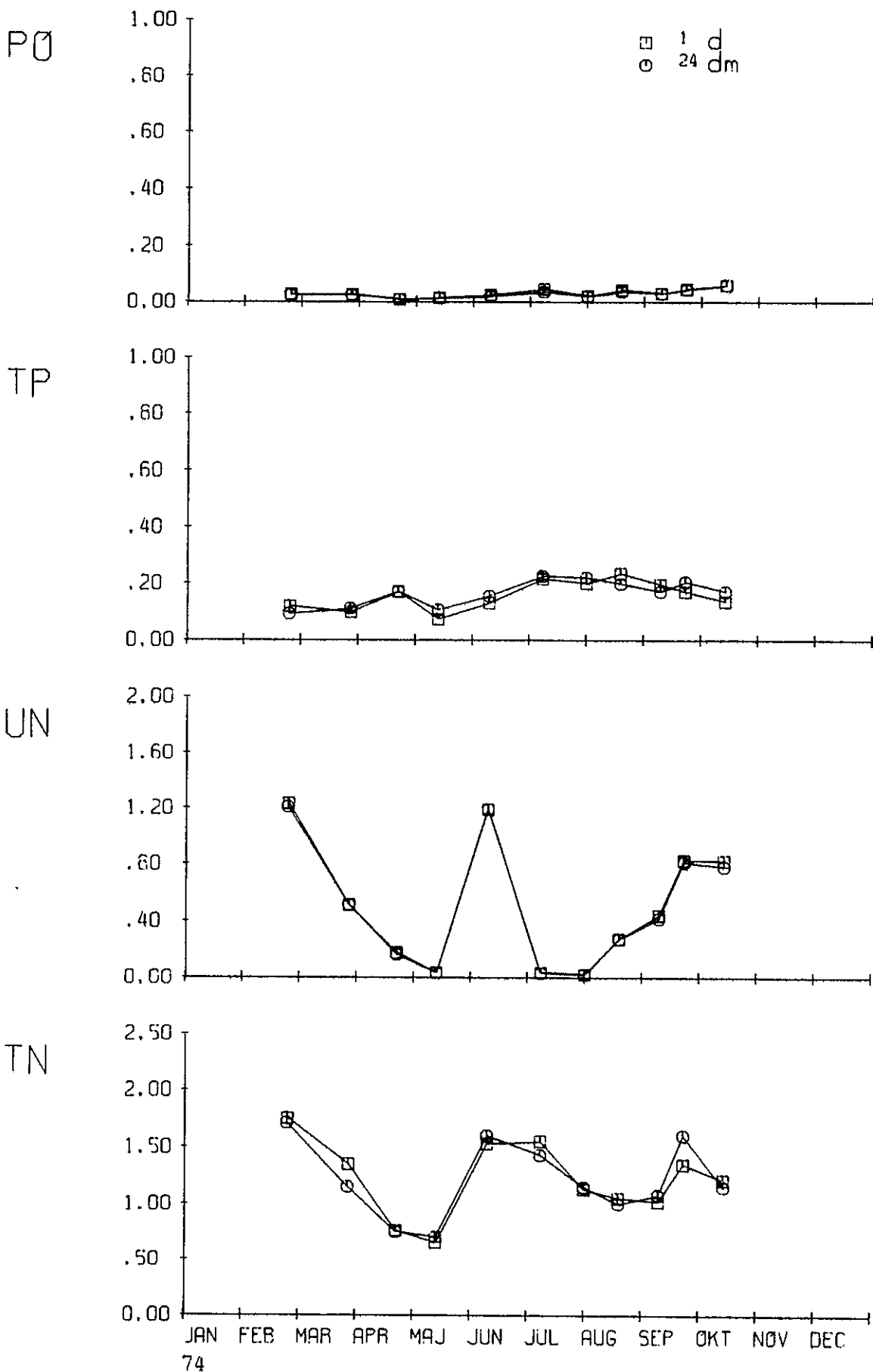
PARP



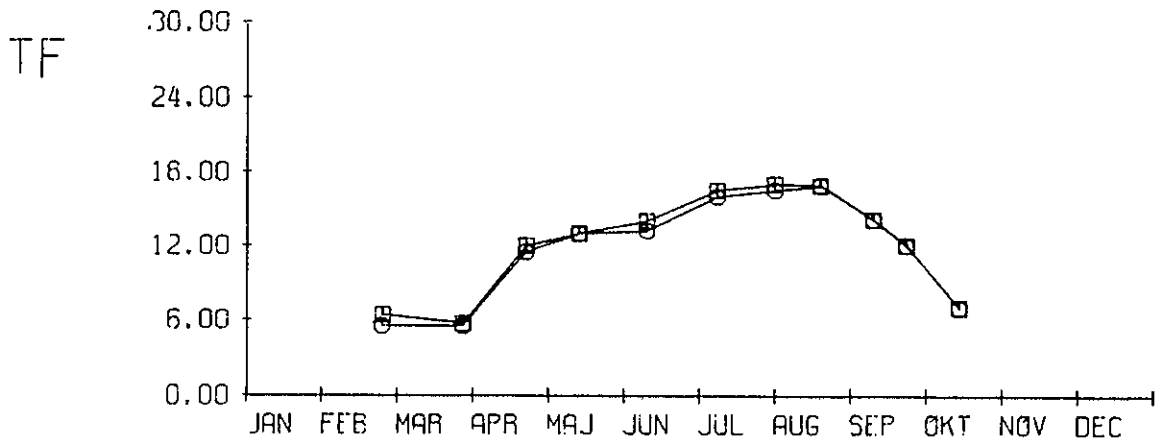
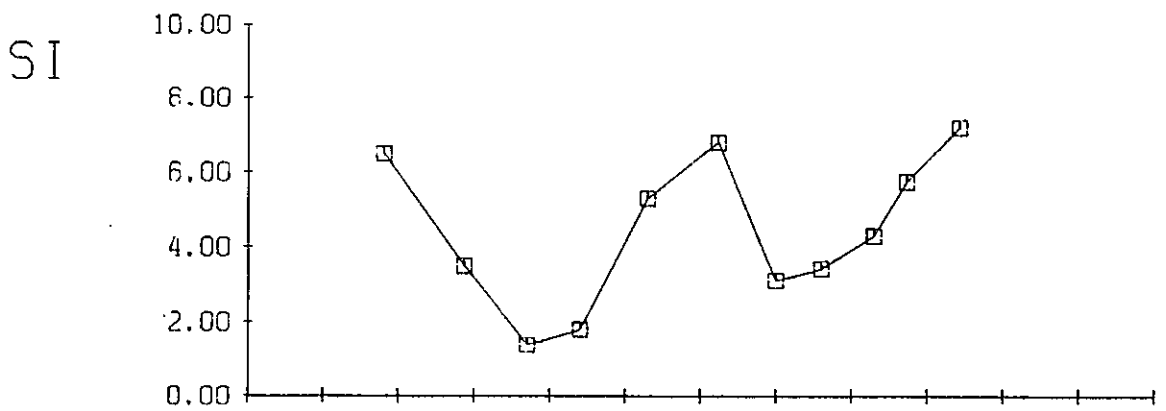
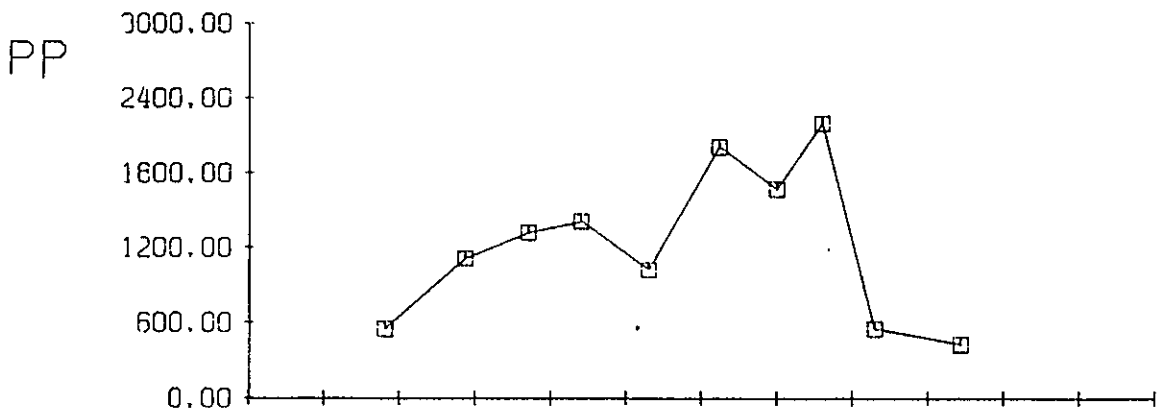
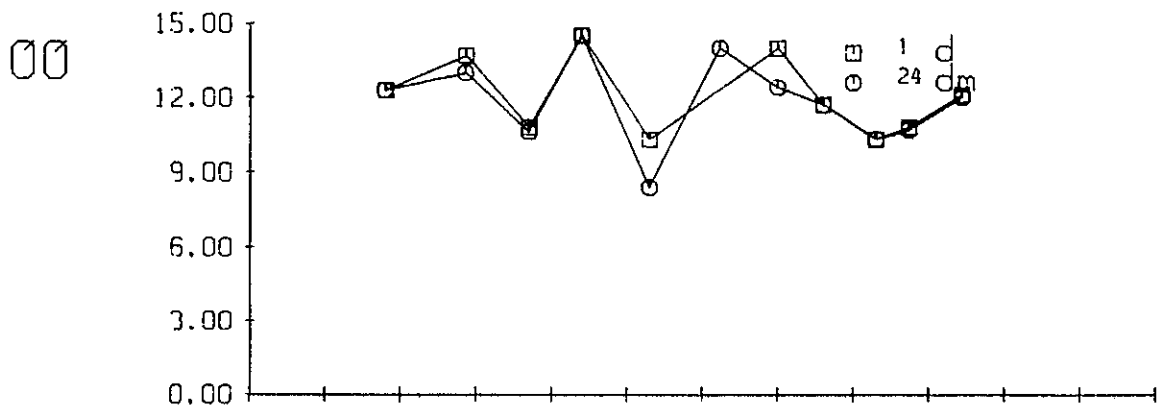
PARN



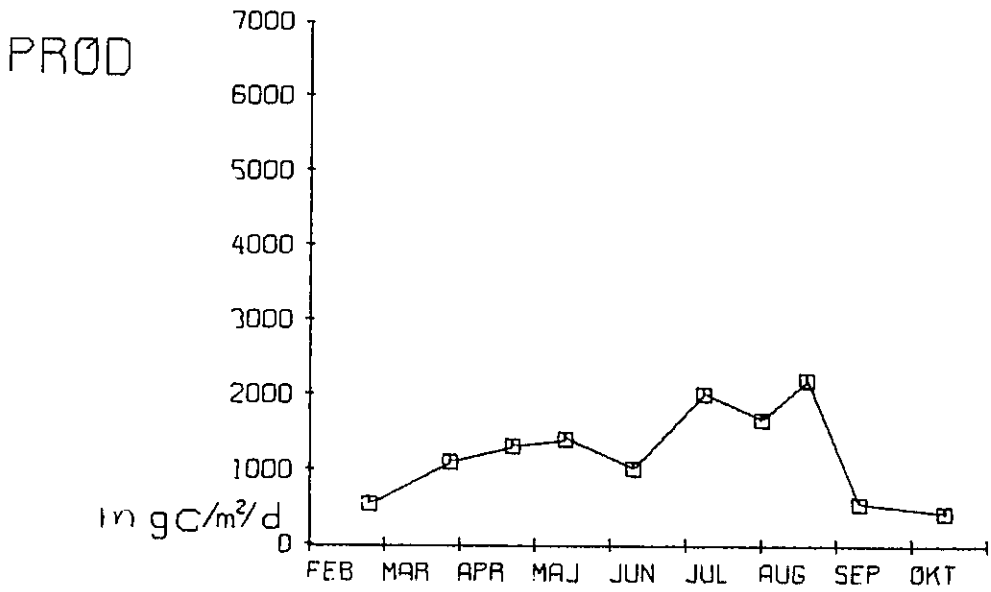
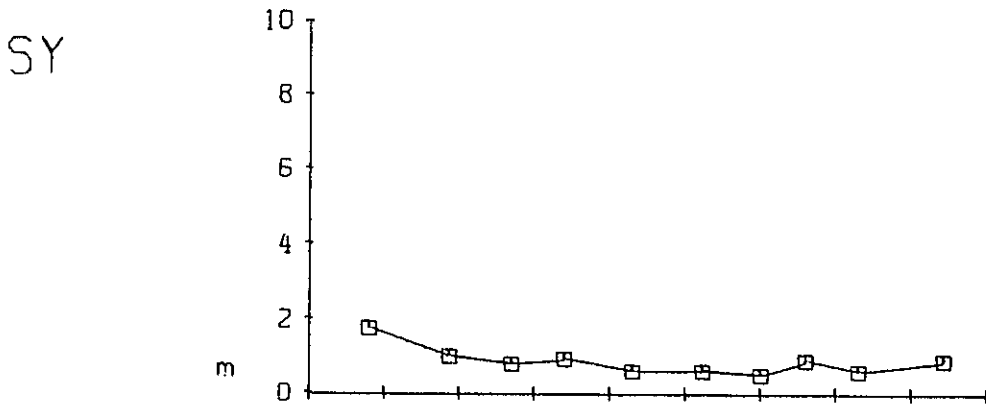
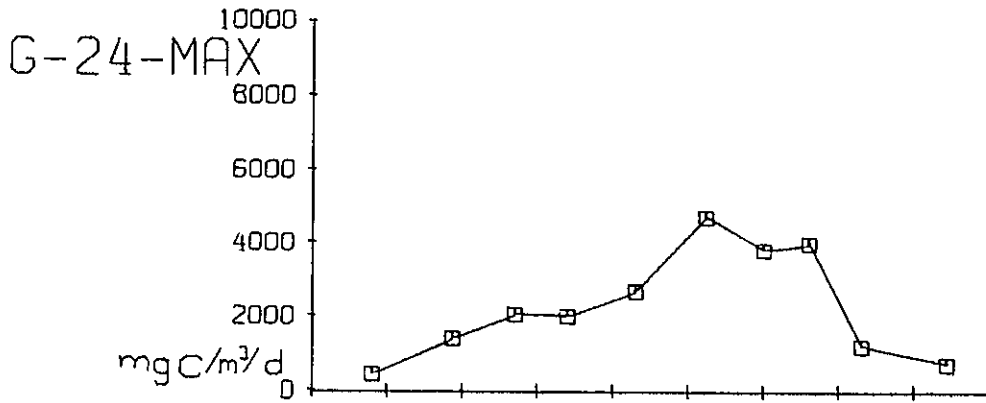
SIL 751



SIL 751



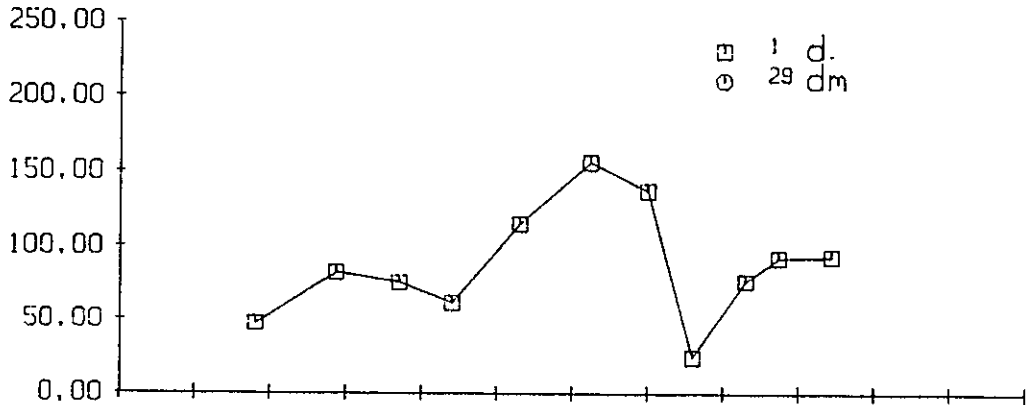
SIL 1



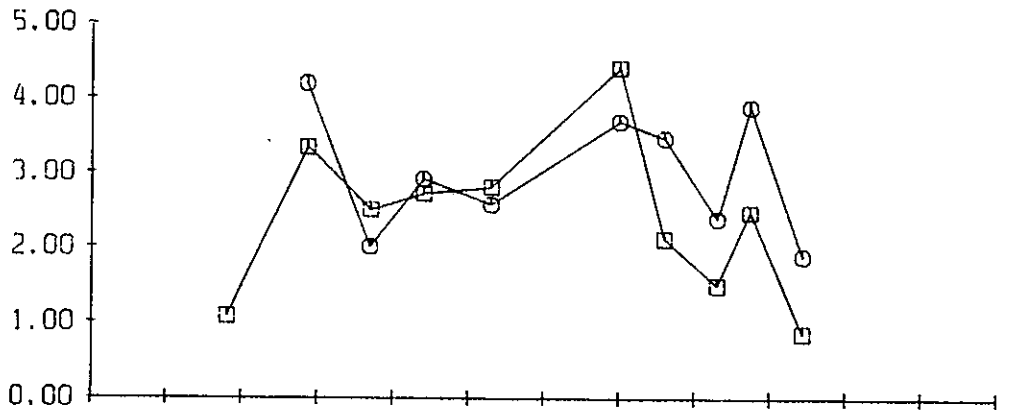
74
ÅRSPROD. 280 gCm⁻²år⁻¹

SIL 752

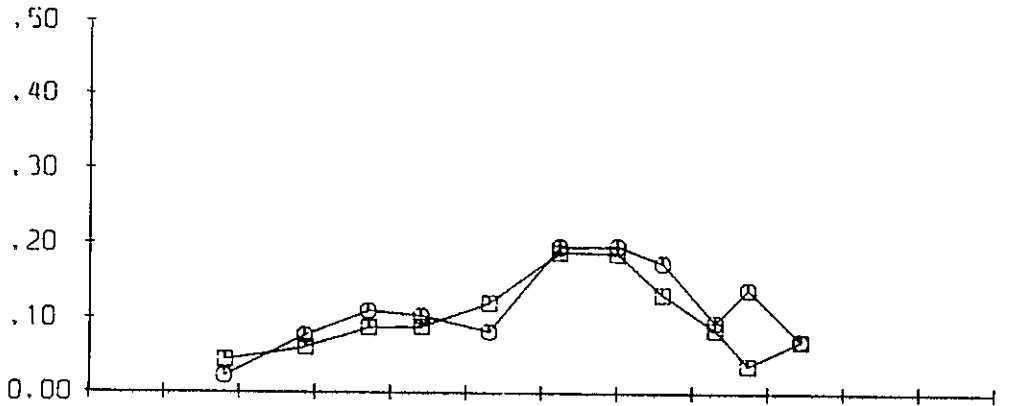
CH



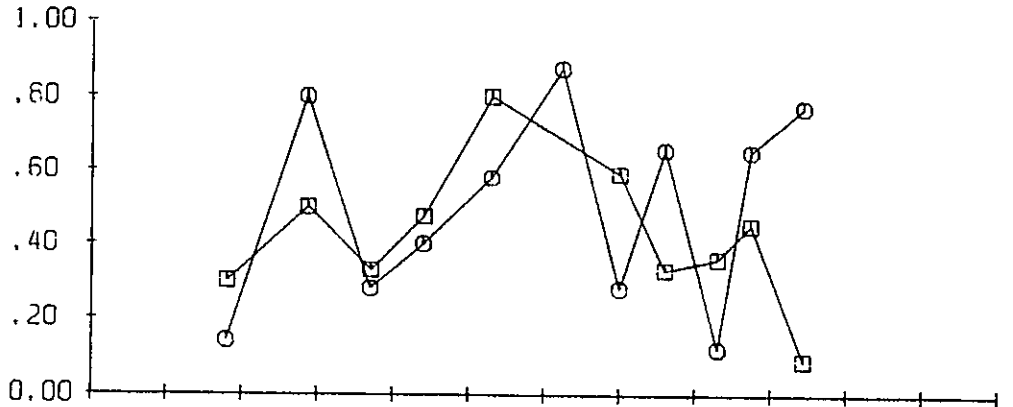
PARO



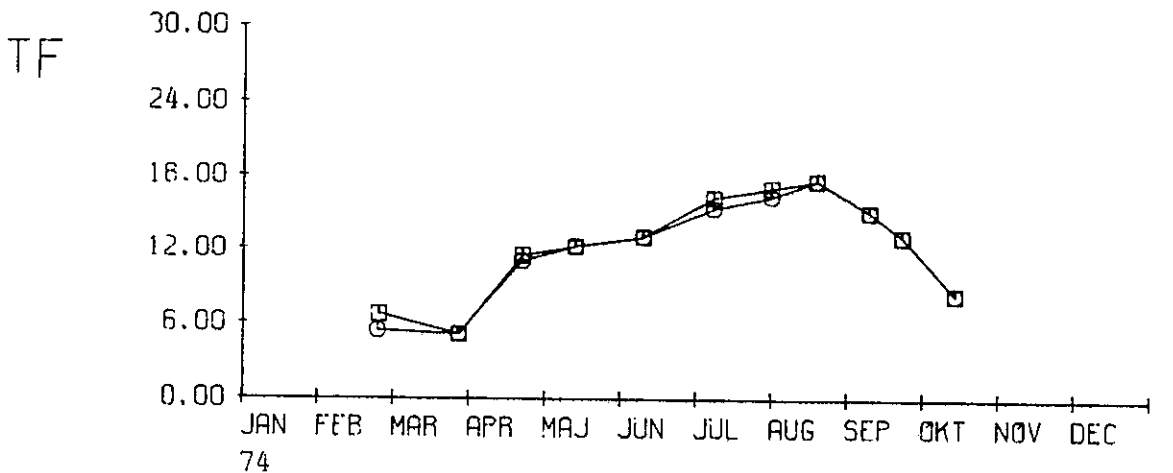
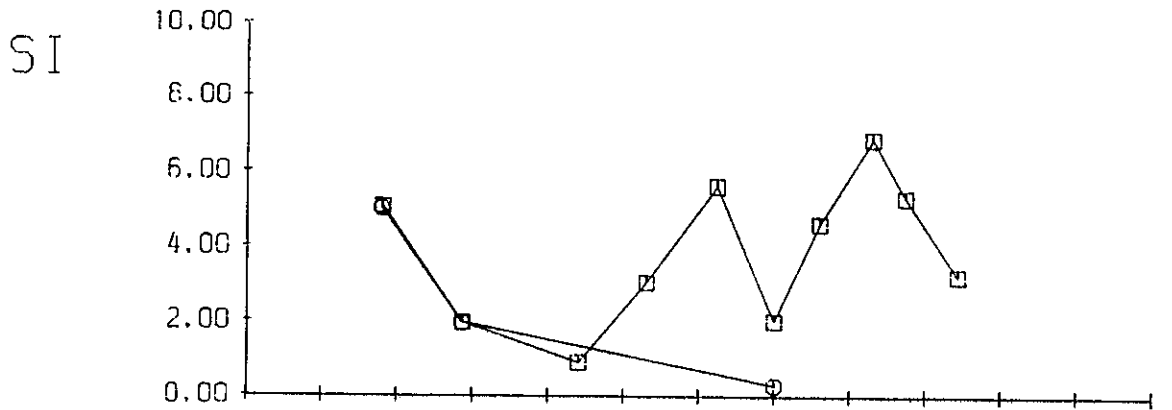
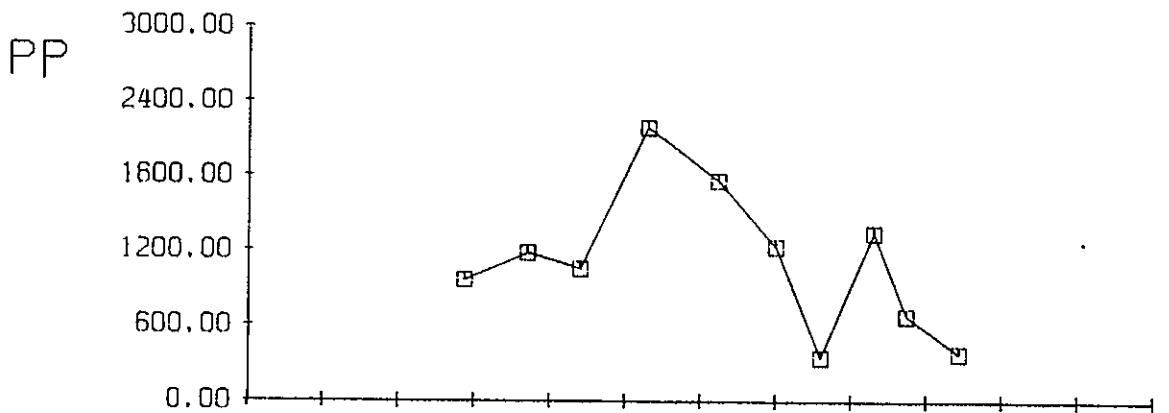
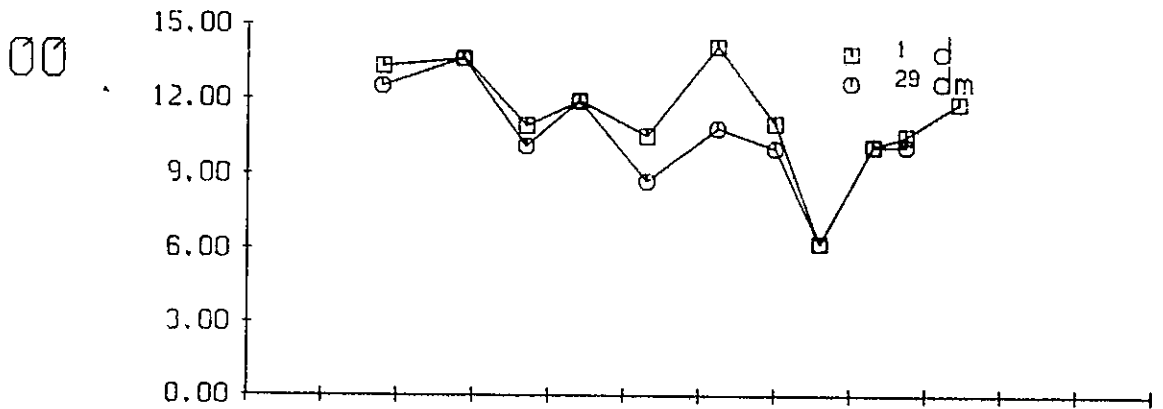
PARP



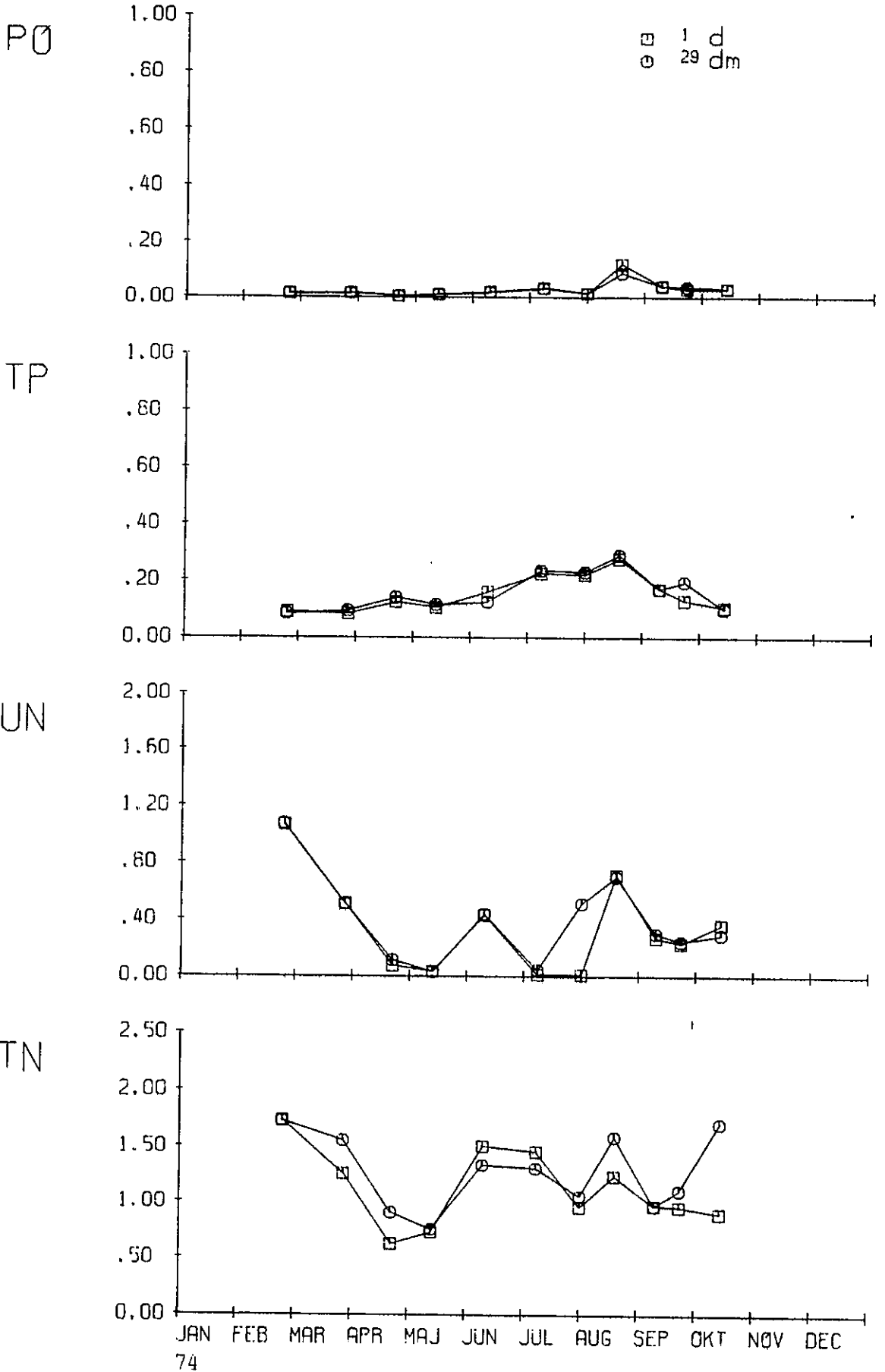
PARN



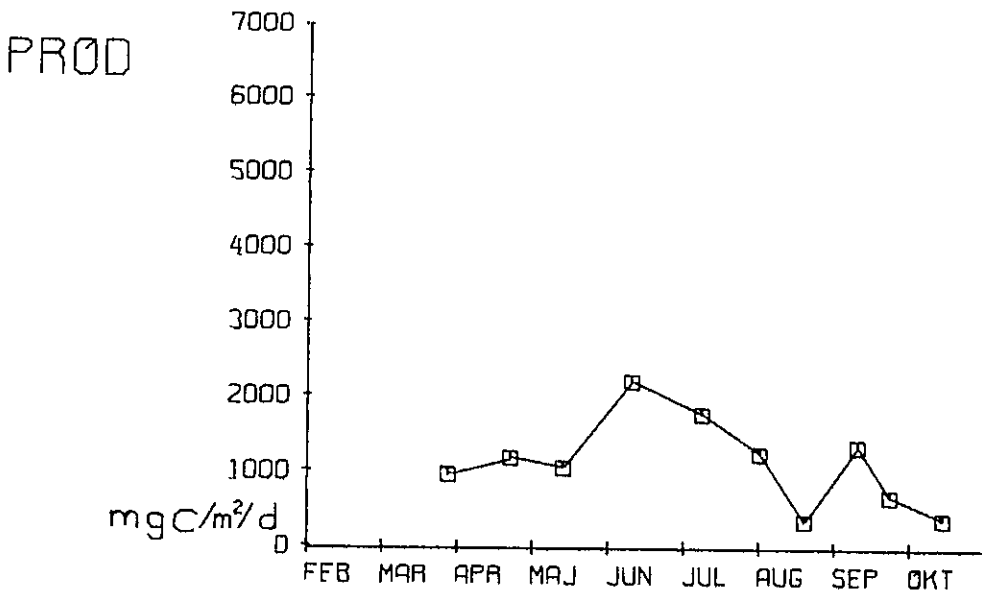
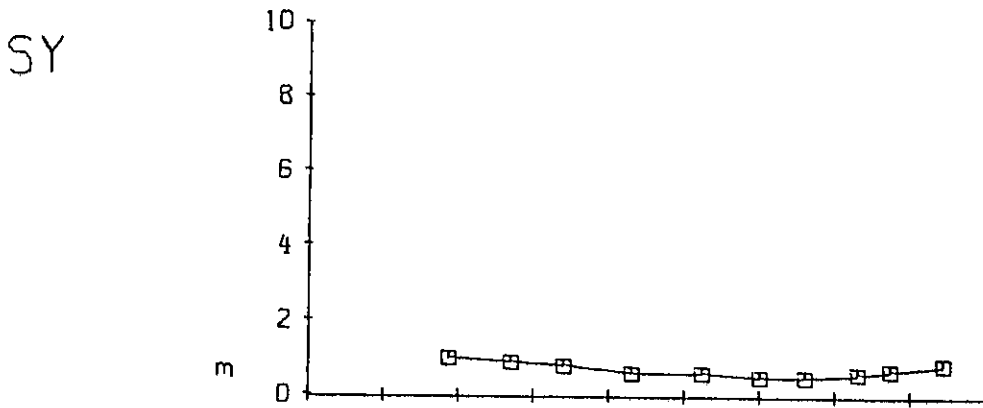
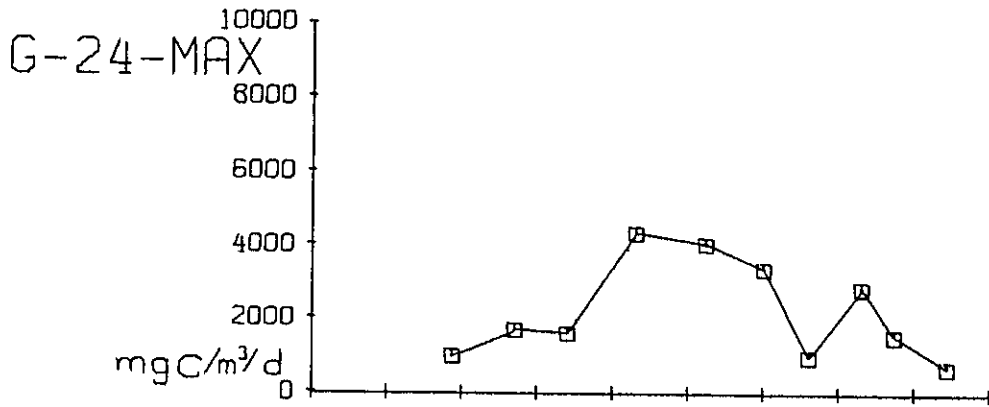
SIL 752



SIL 752

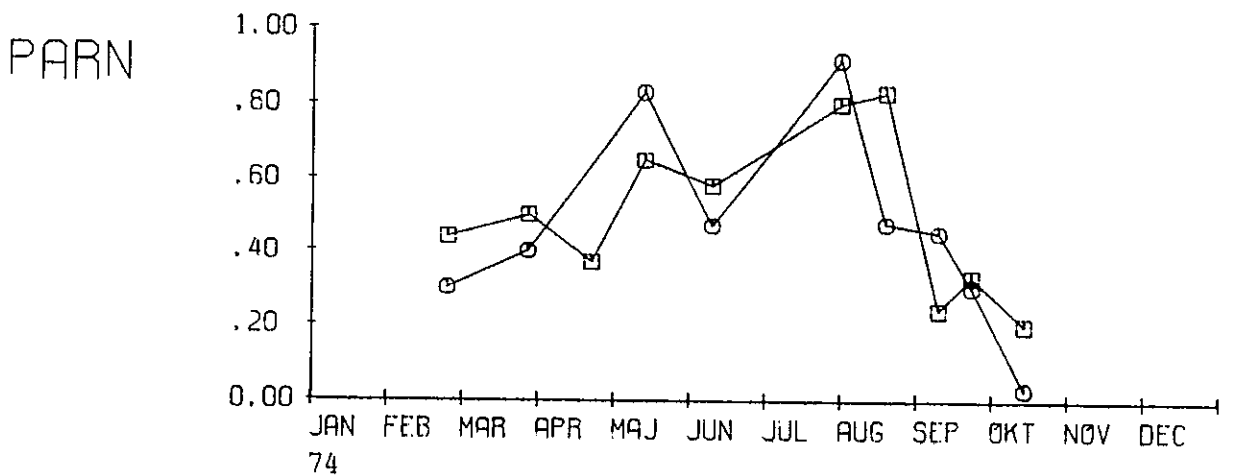
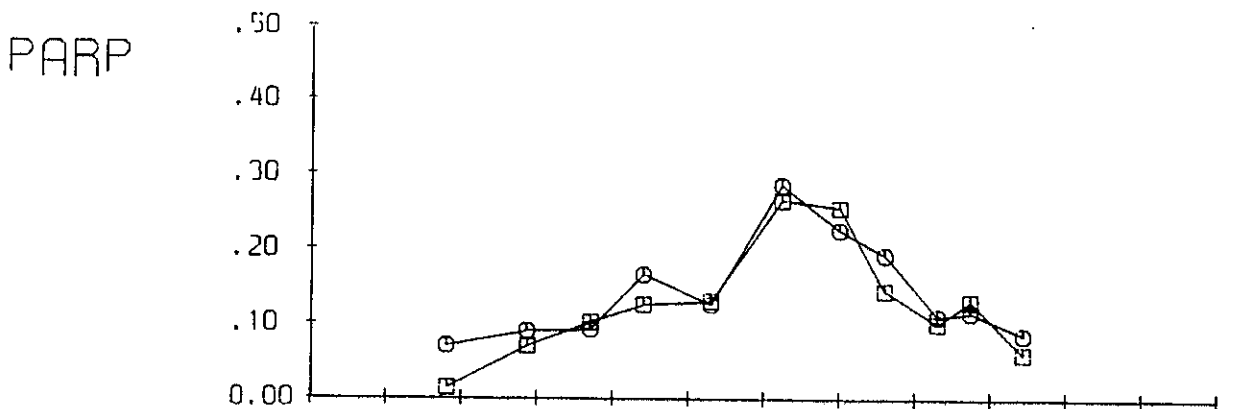
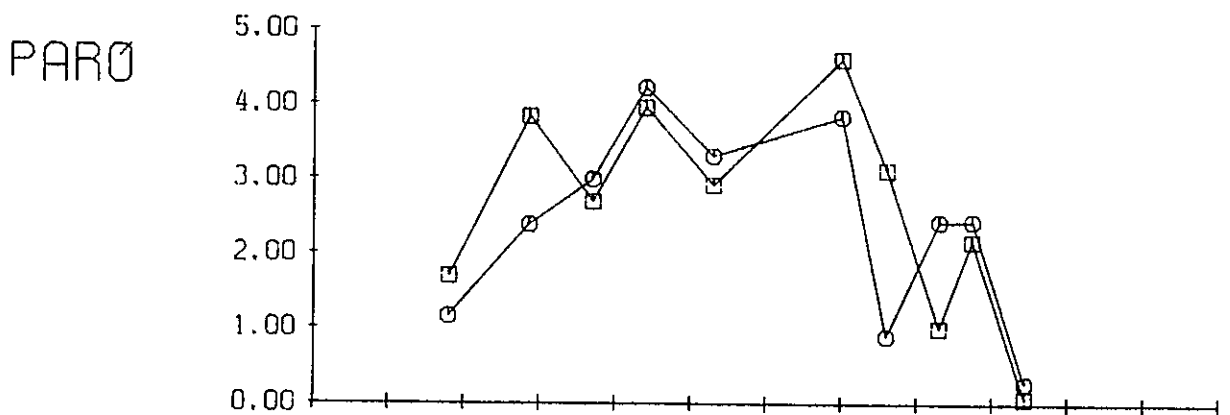
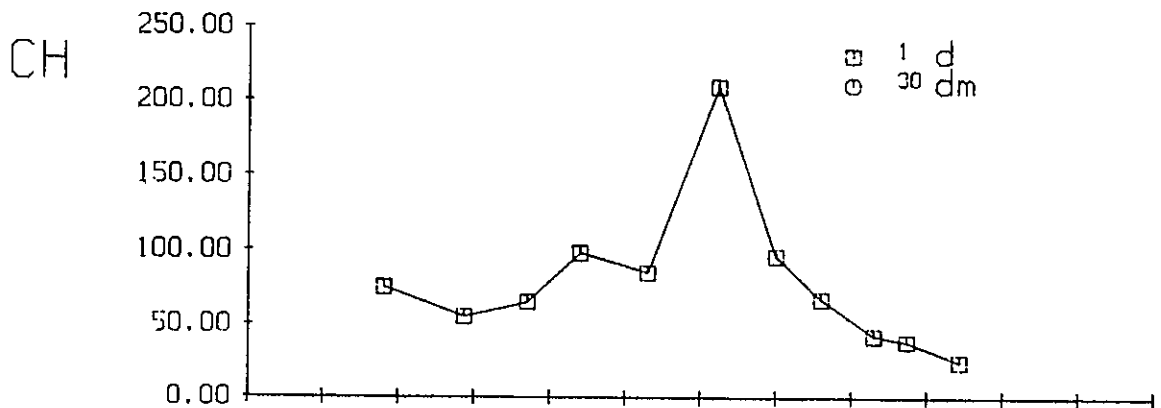


SIL 2

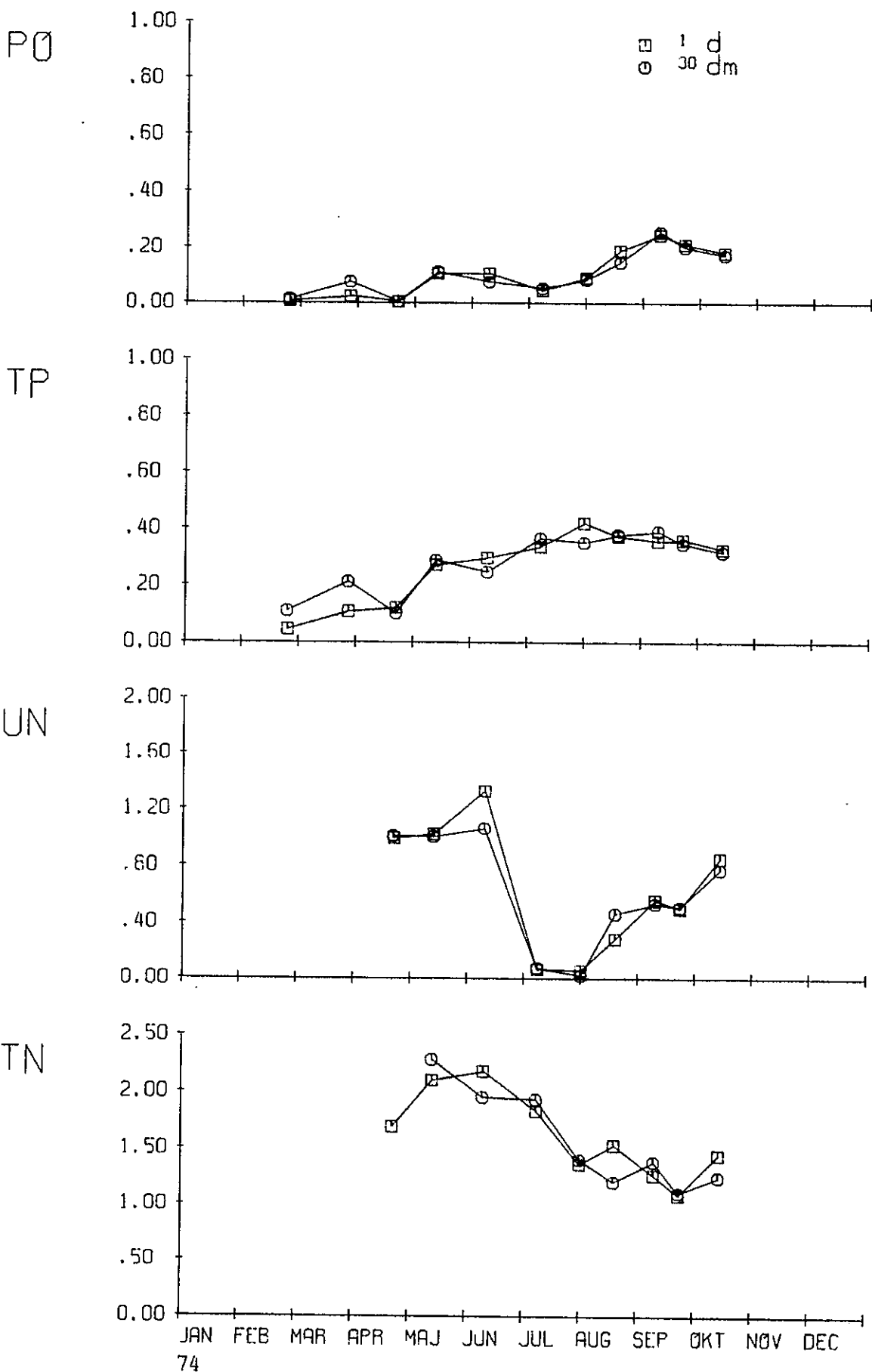


74
ÅRSPROD. 240 gCm⁻²år⁻¹

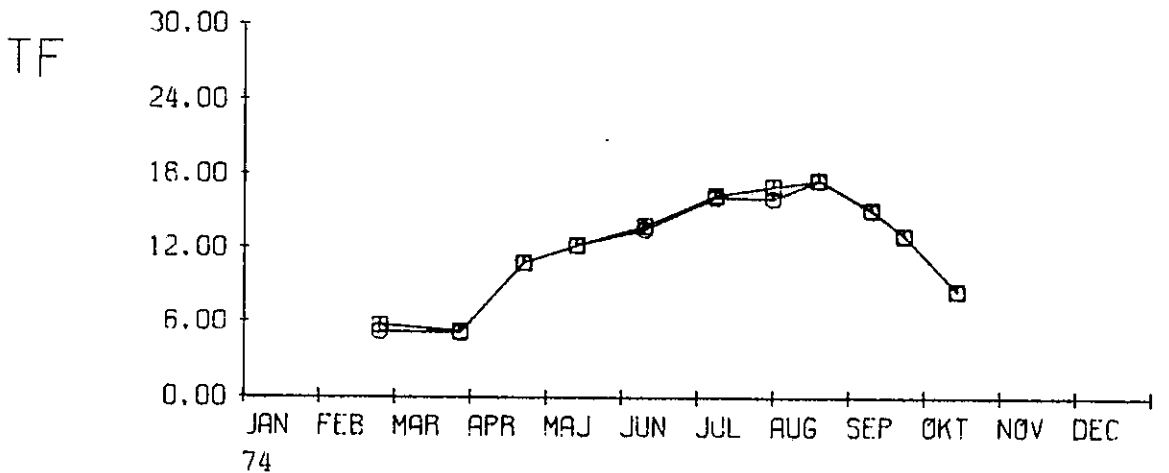
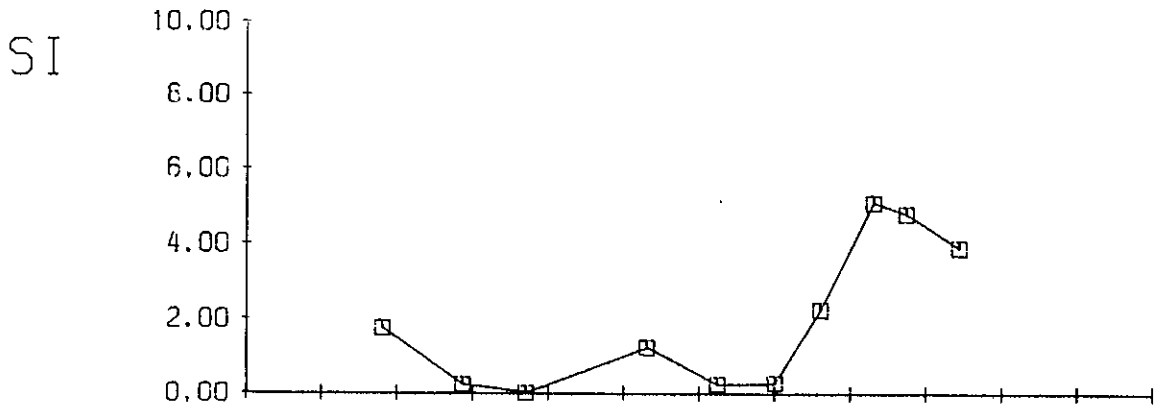
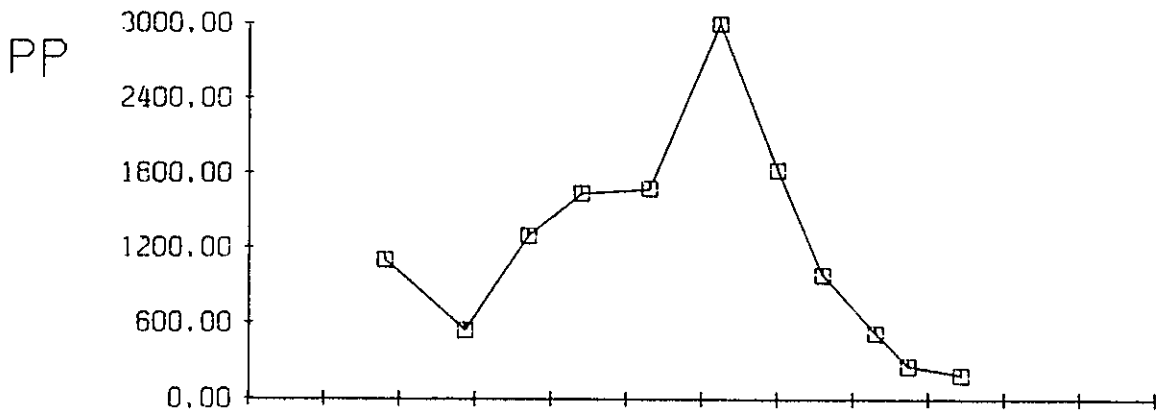
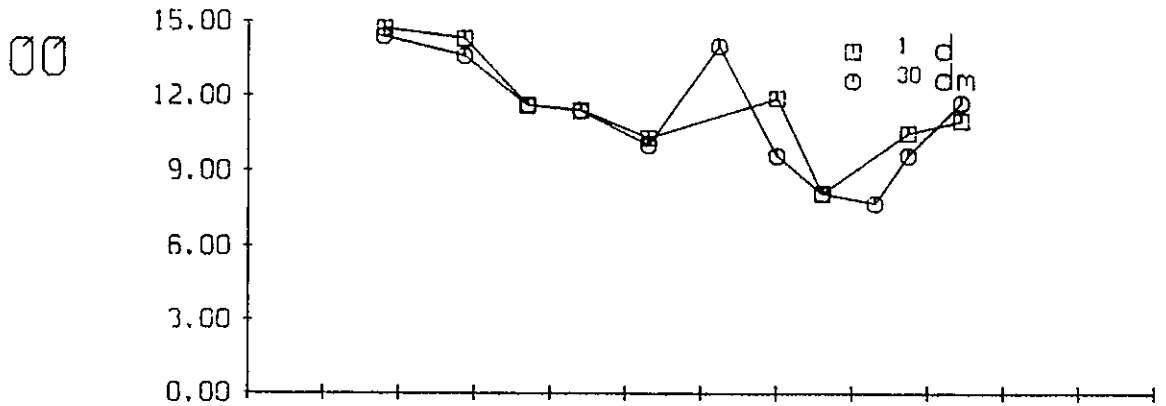
SIL 753



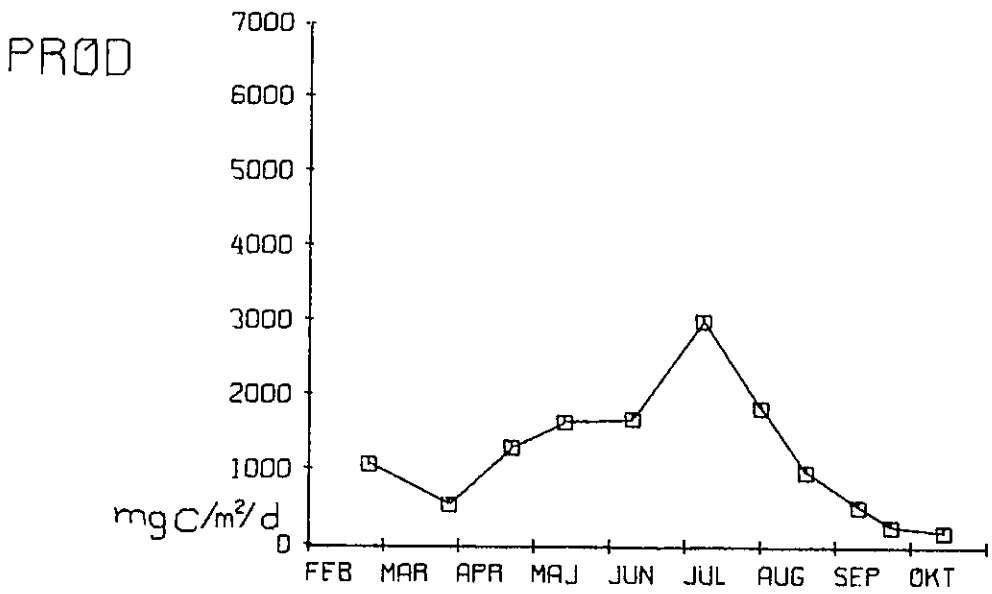
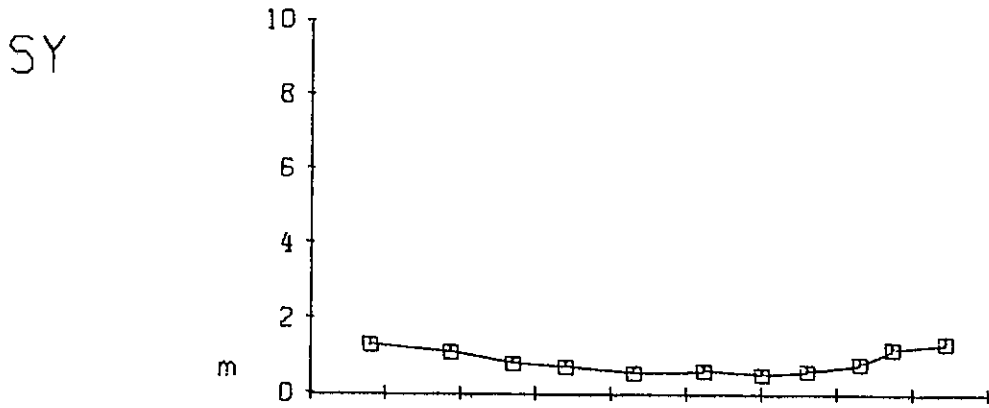
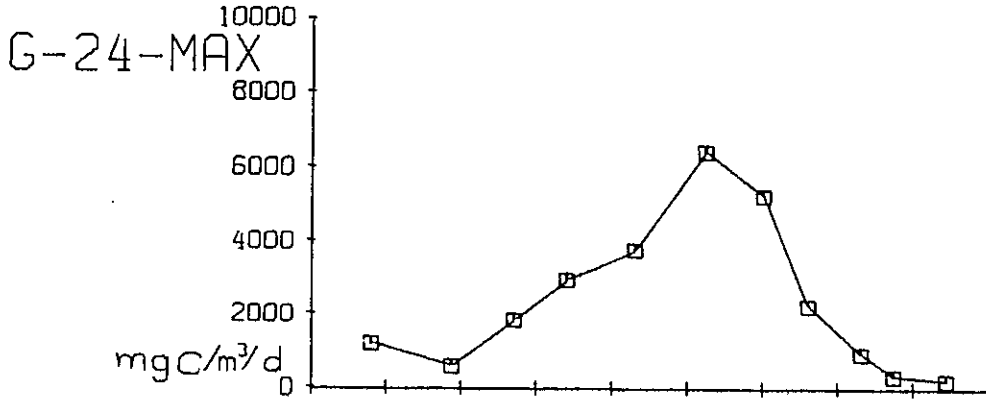
SIL 753



SIL 753



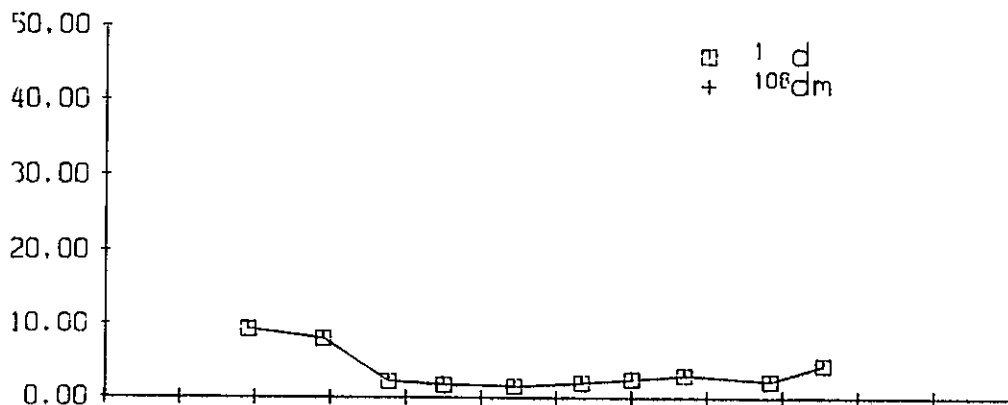
SIL 3



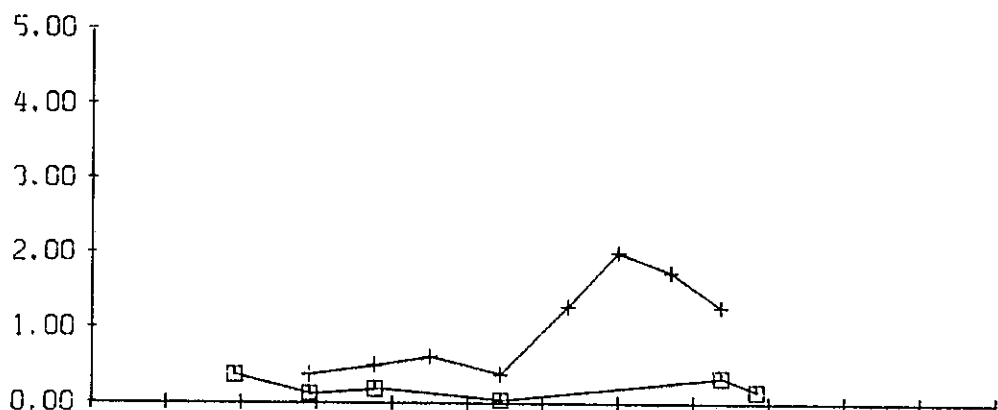
74
ÅRSPROD. 300 gCm²år⁻¹

SLA 751

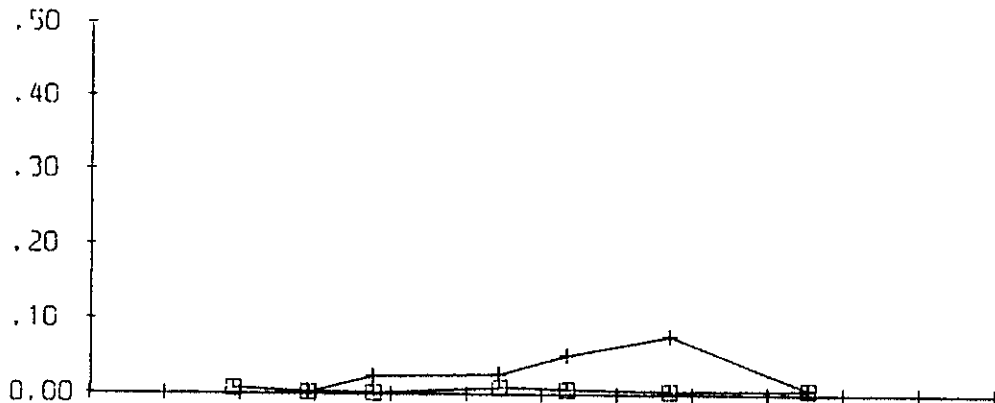
CH



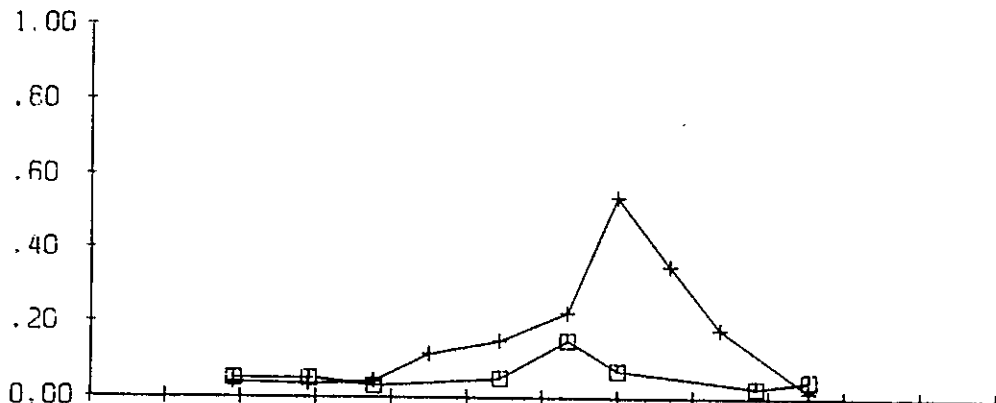
PARO



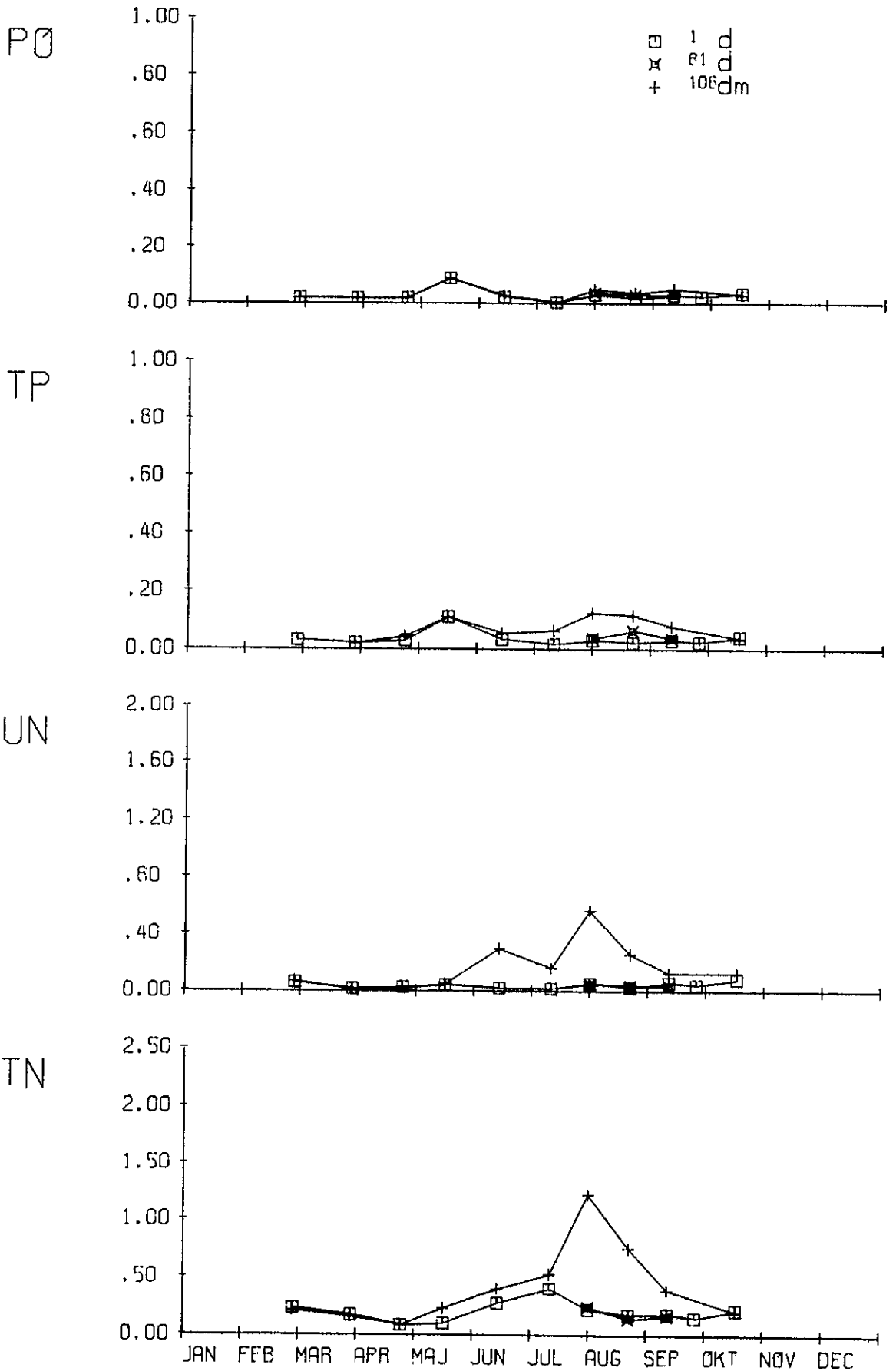
PARP



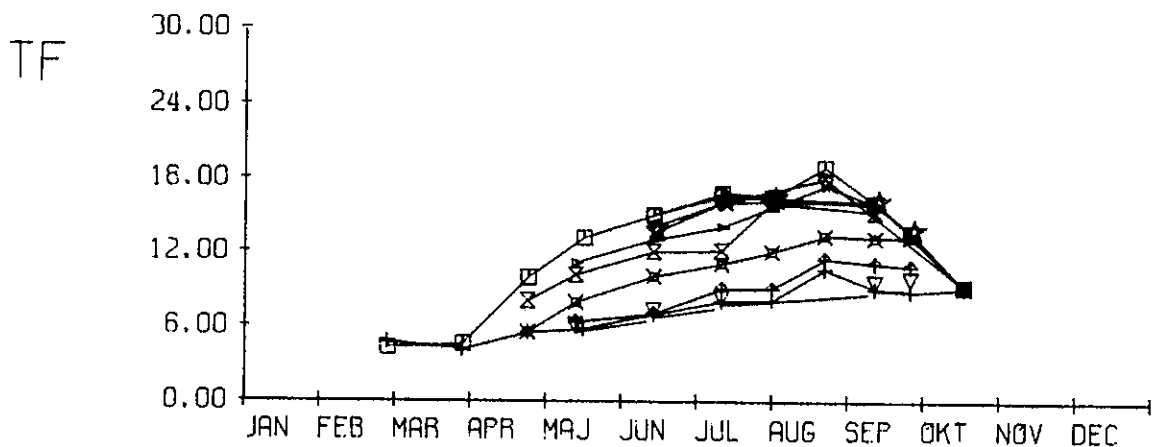
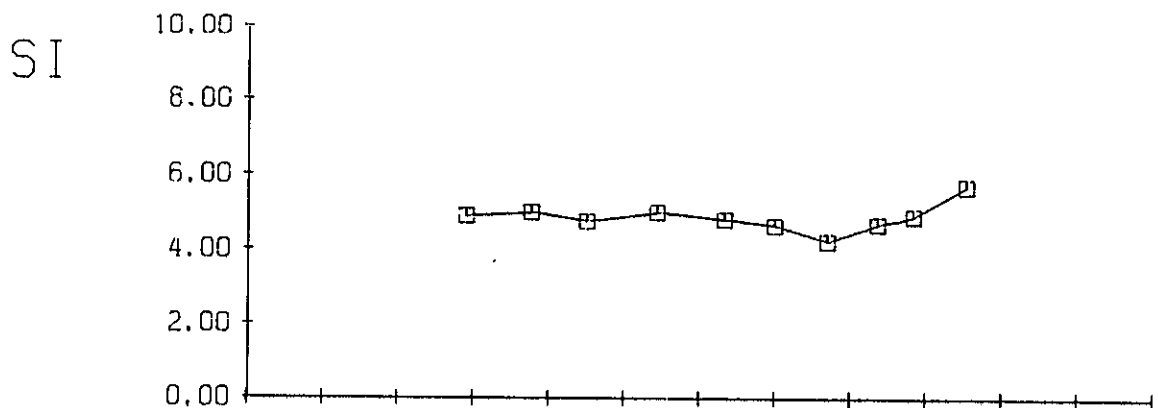
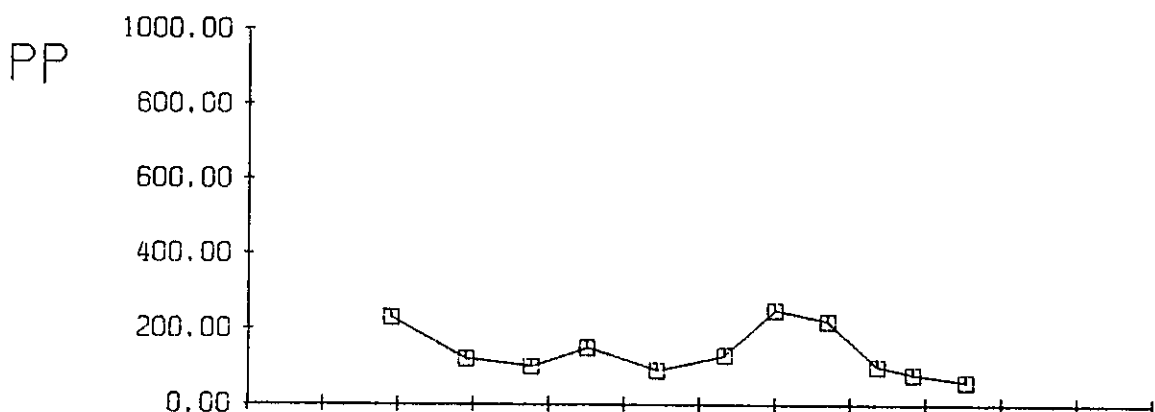
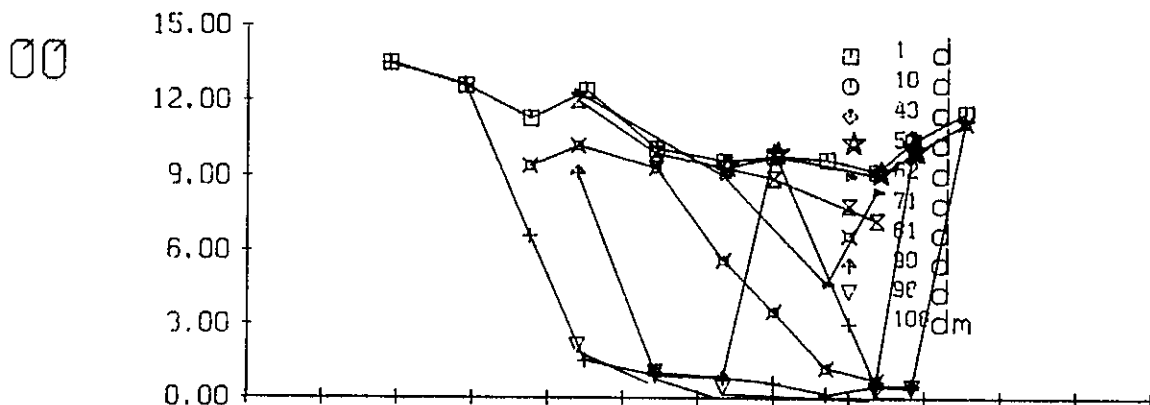
PARN



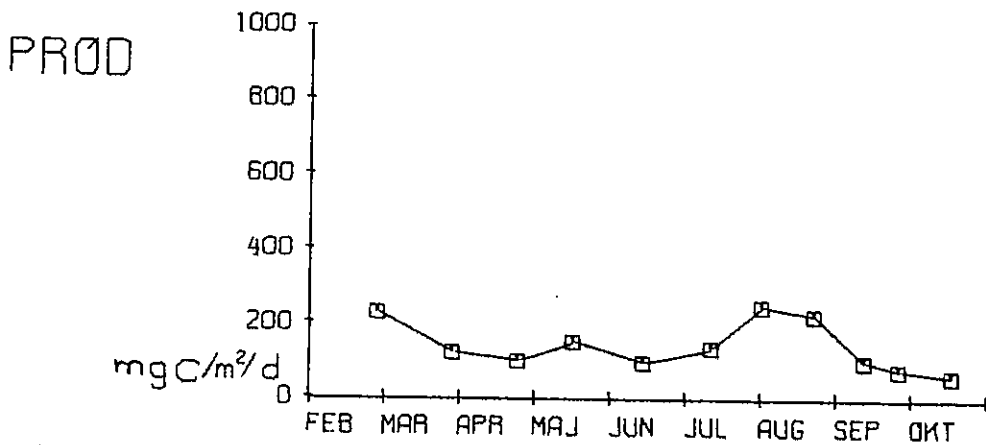
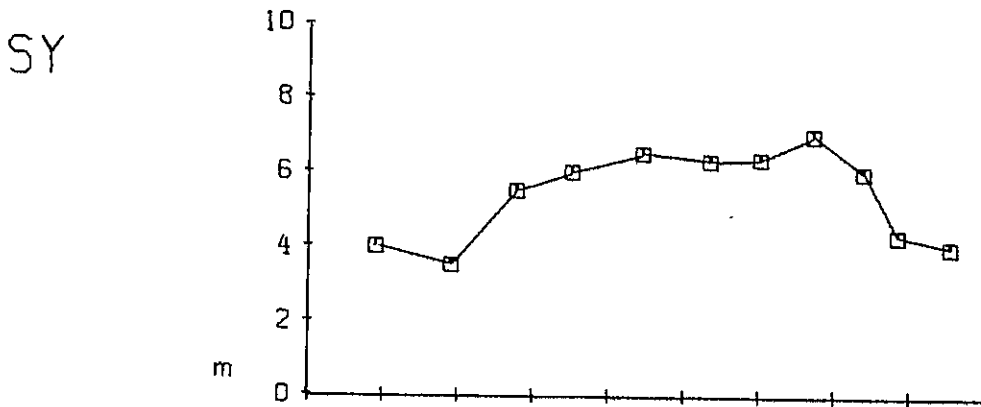
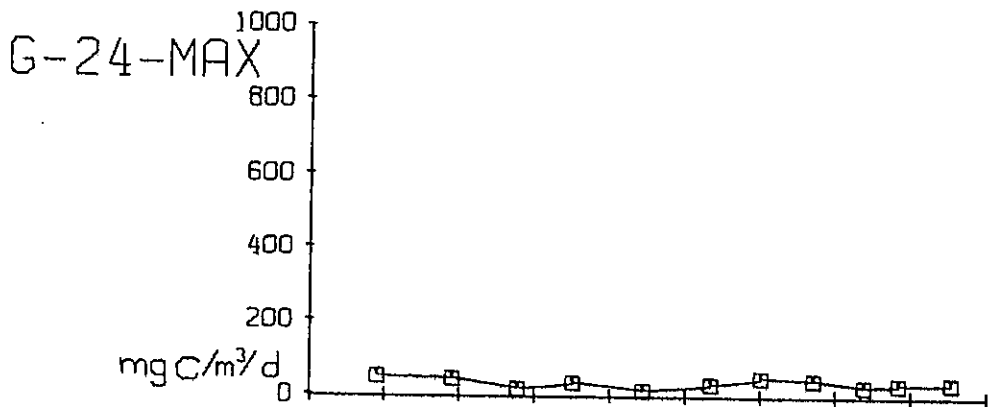
SLA 751



SLA 751

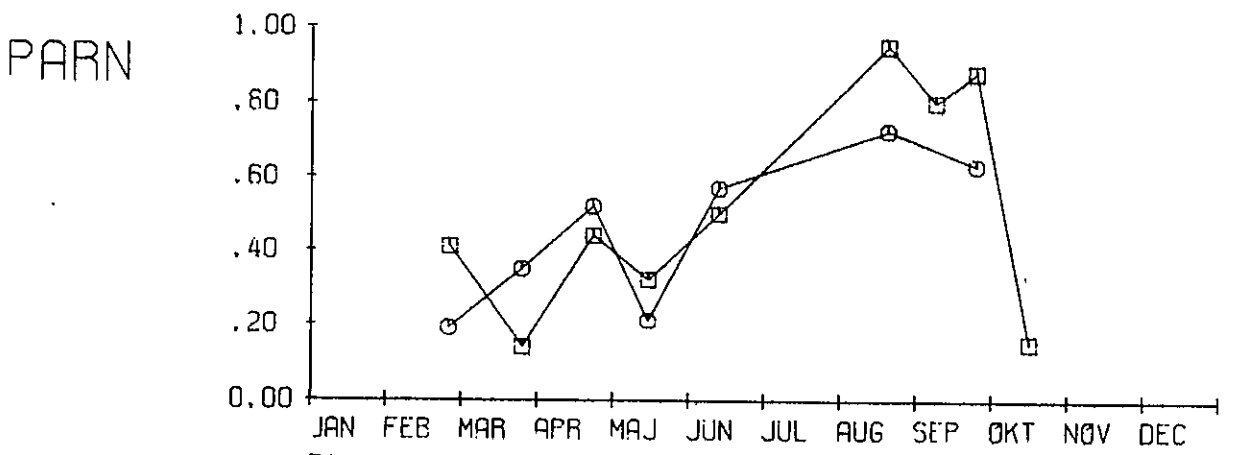
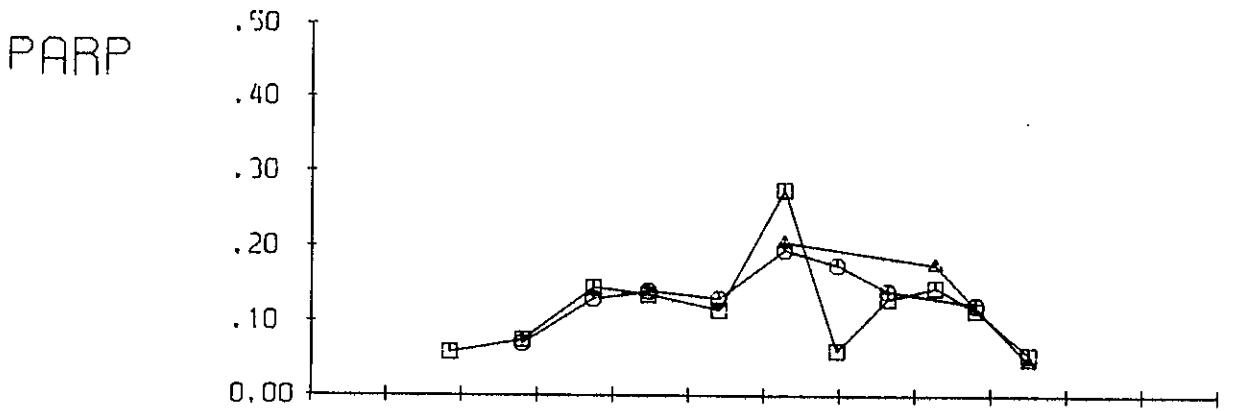
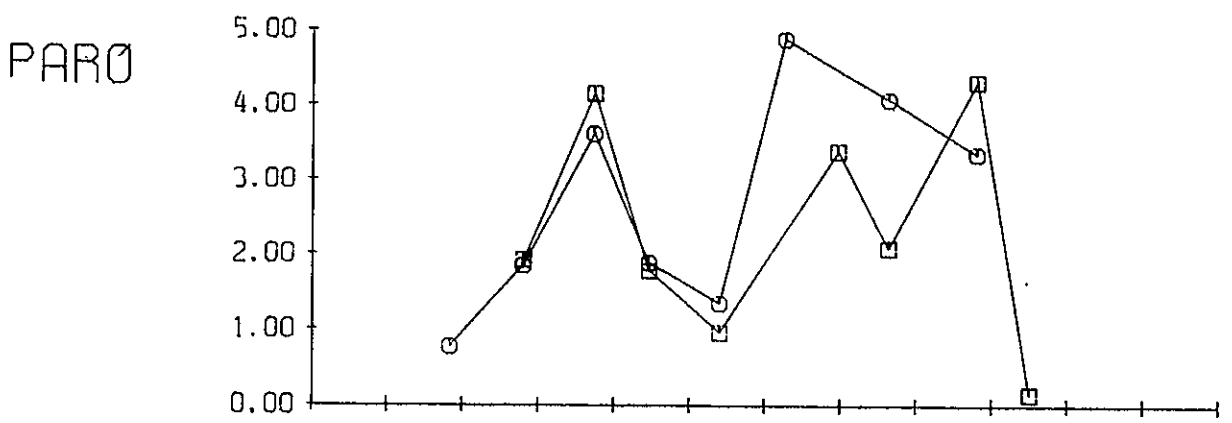
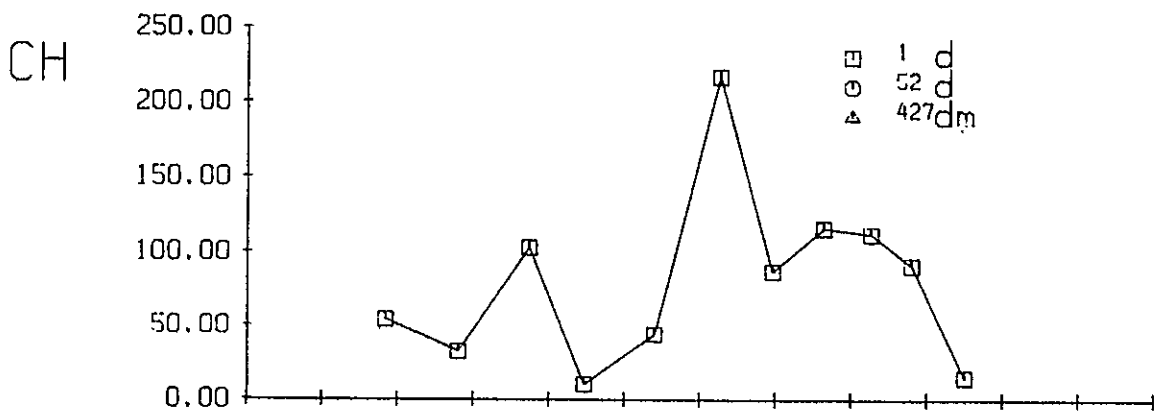


SL\$ 1

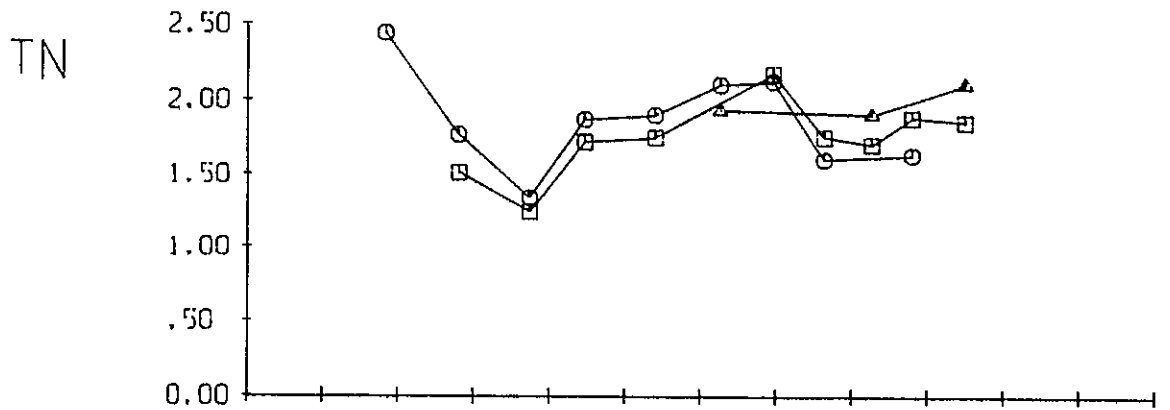
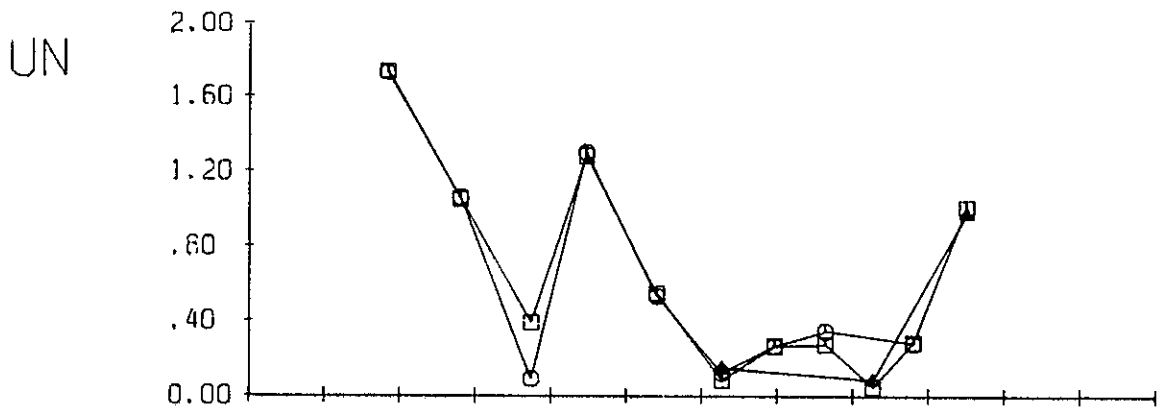
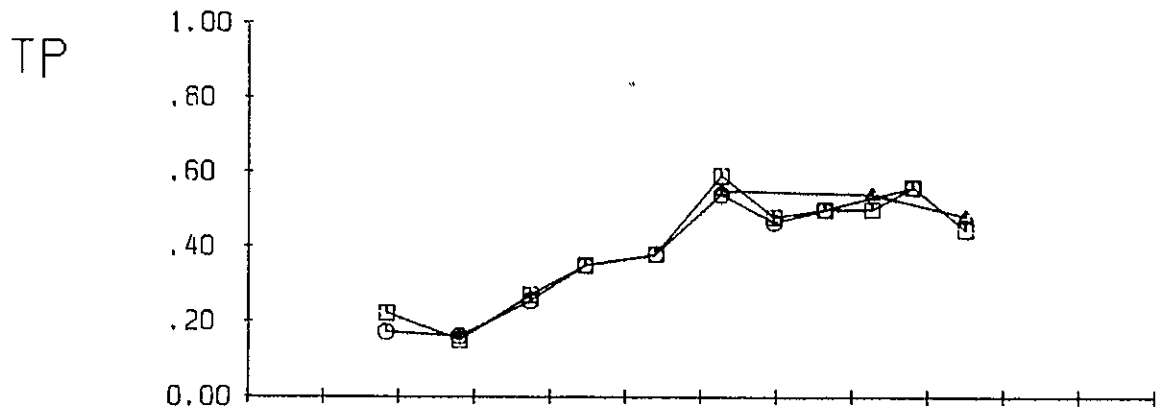
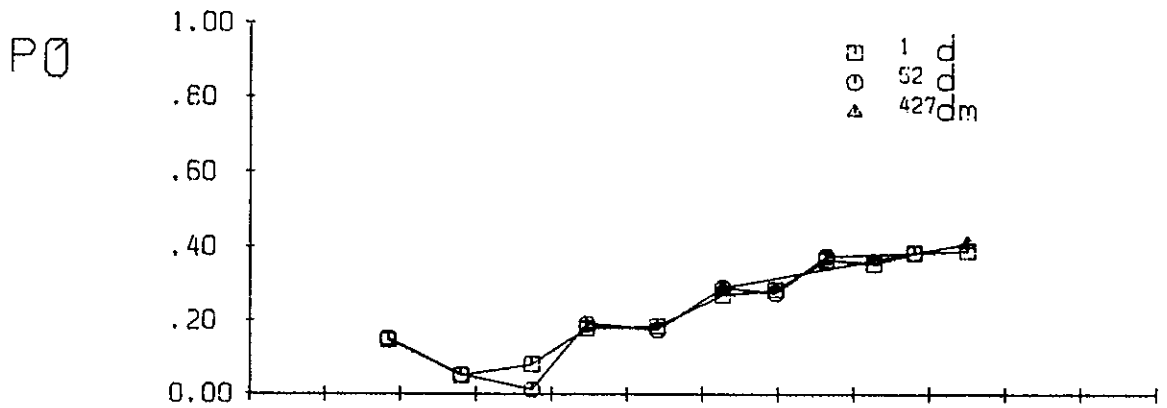


74
ÅRSPROD. 32 gCm⁻²år⁻¹

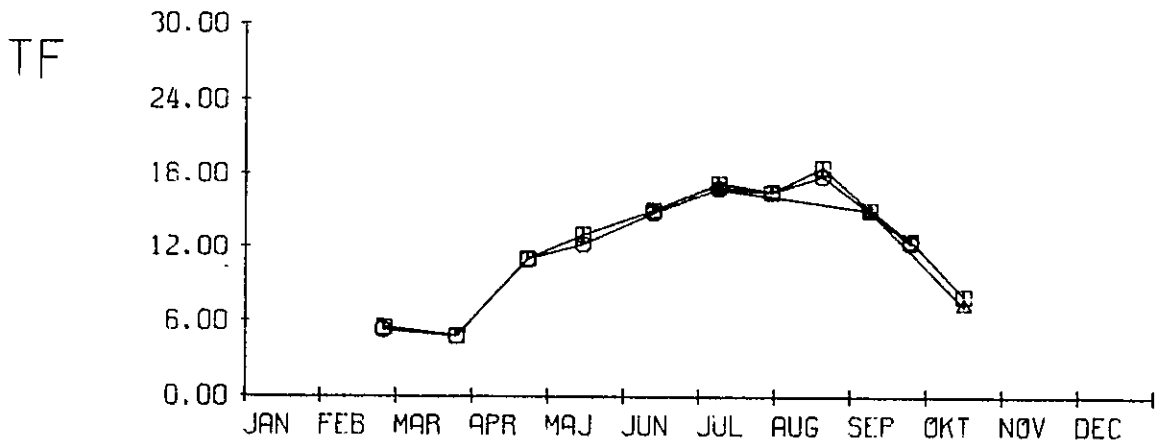
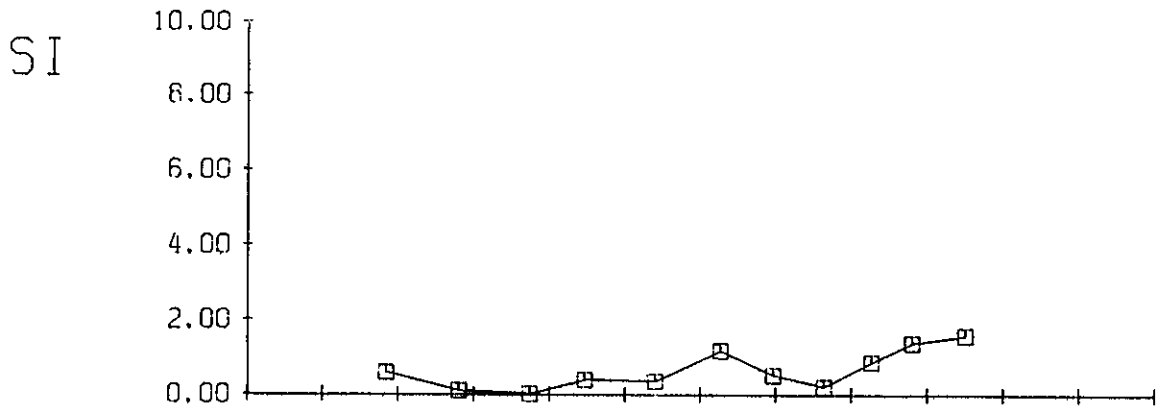
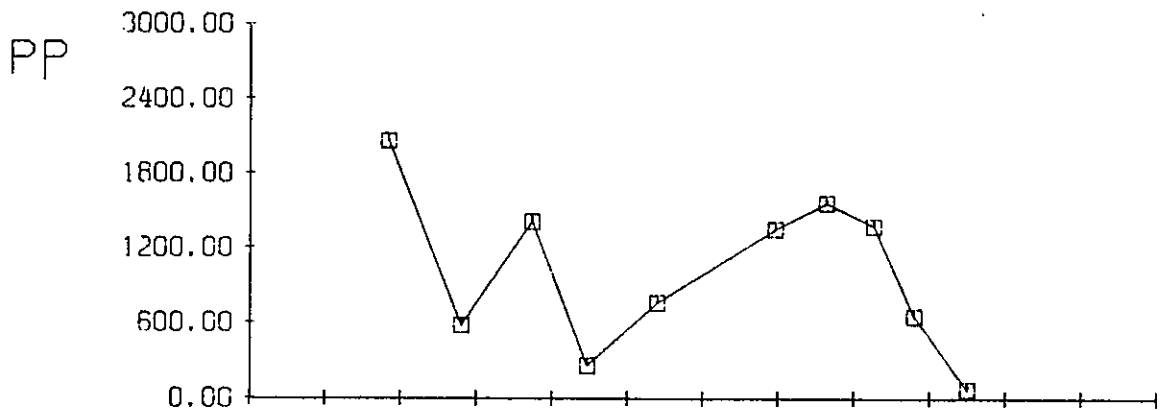
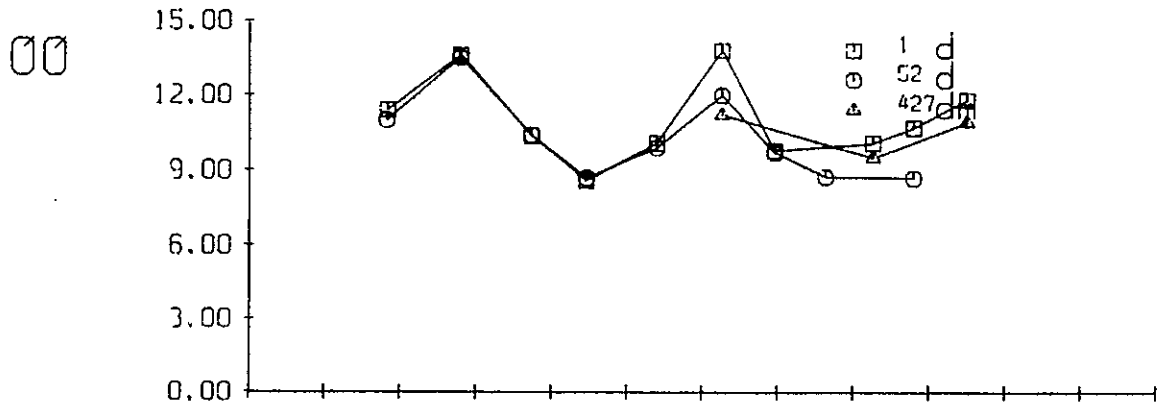
SRS 751



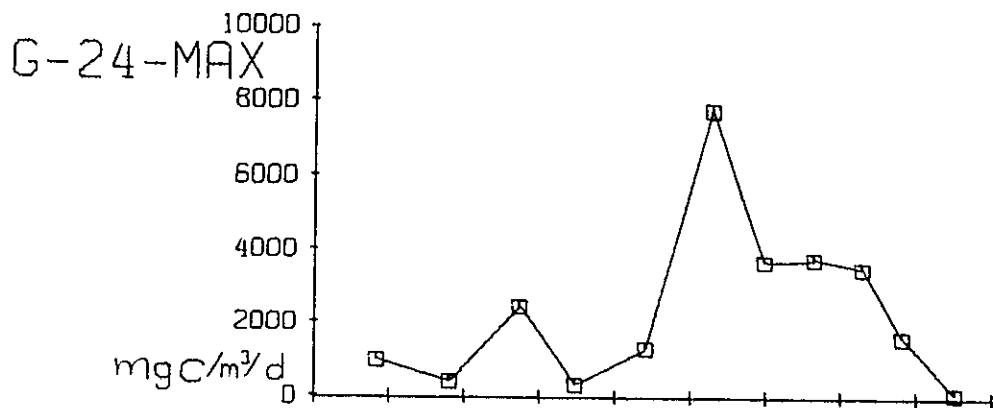
SRS 751



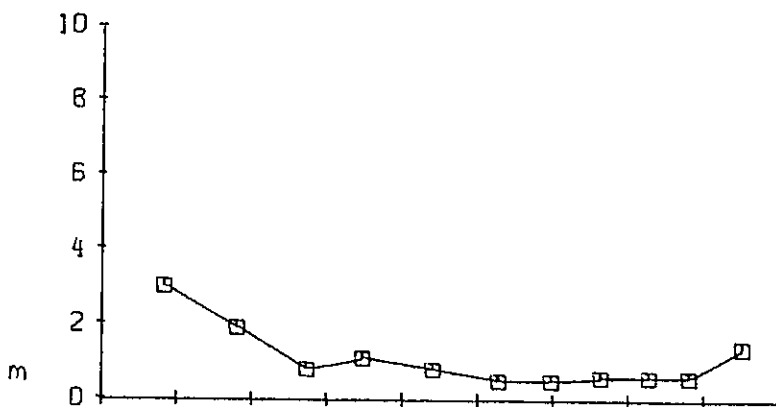
SRS 751



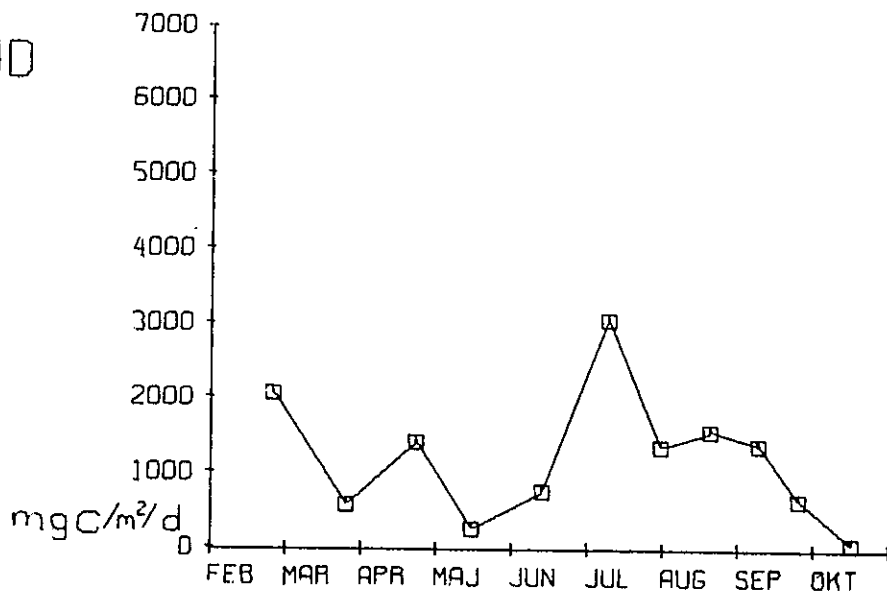
S@N 1



SY



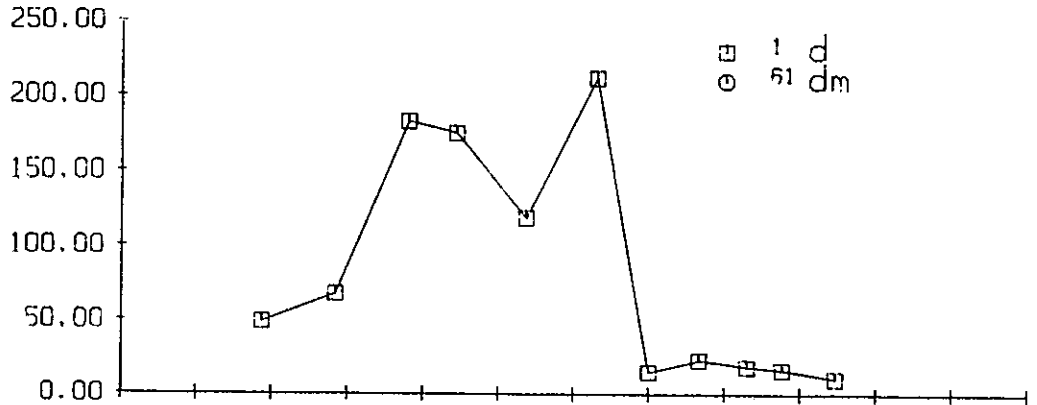
PROD



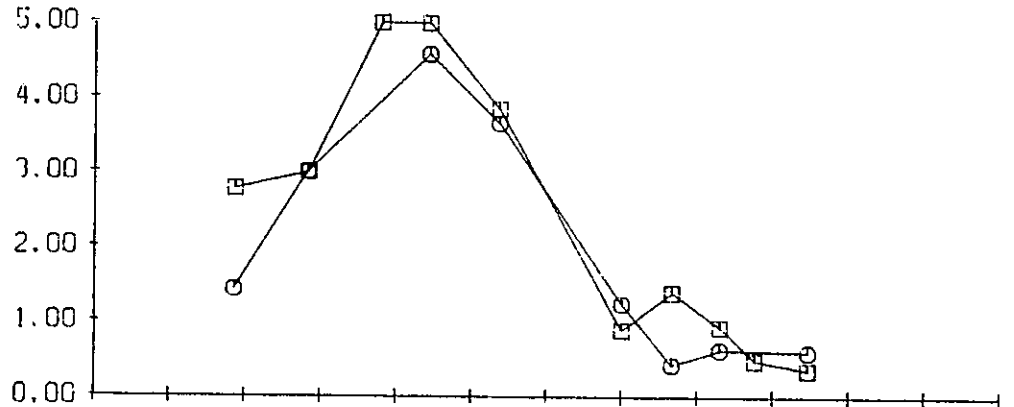
74
ÅRSPROD. 280 gCm⁻²år⁻¹

TAN 751

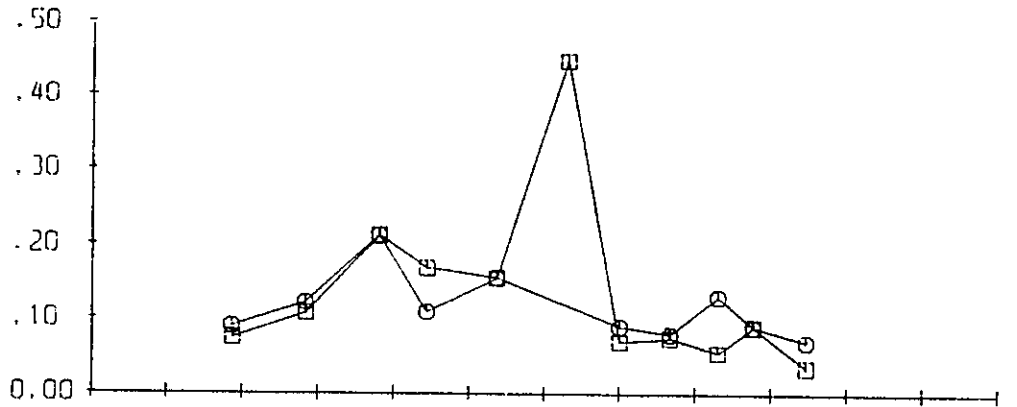
CH



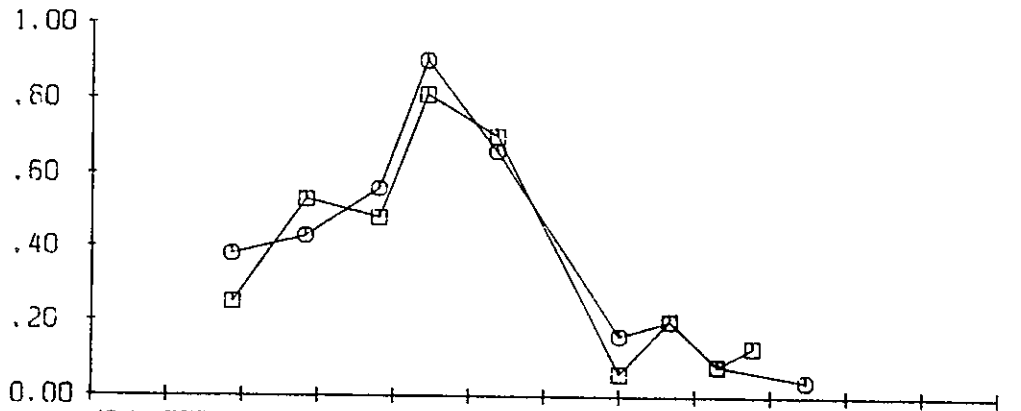
PAR0



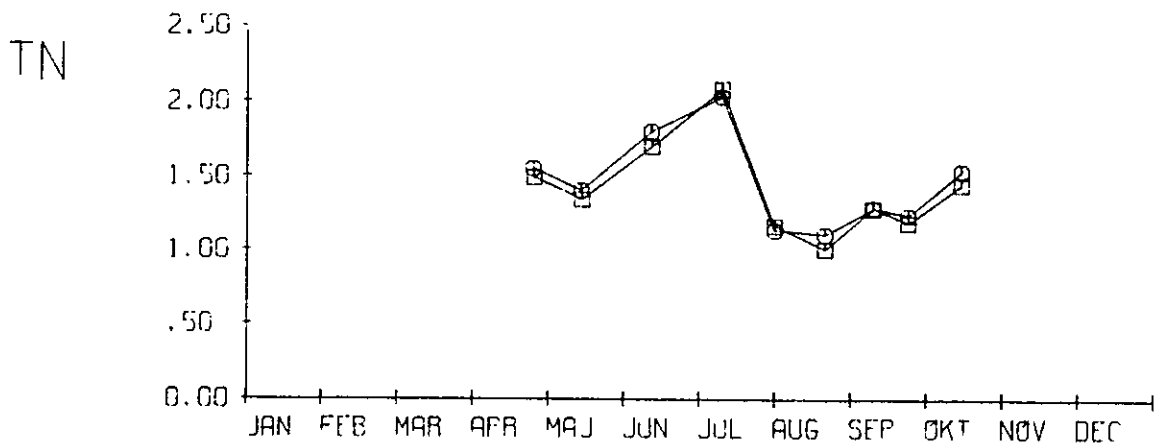
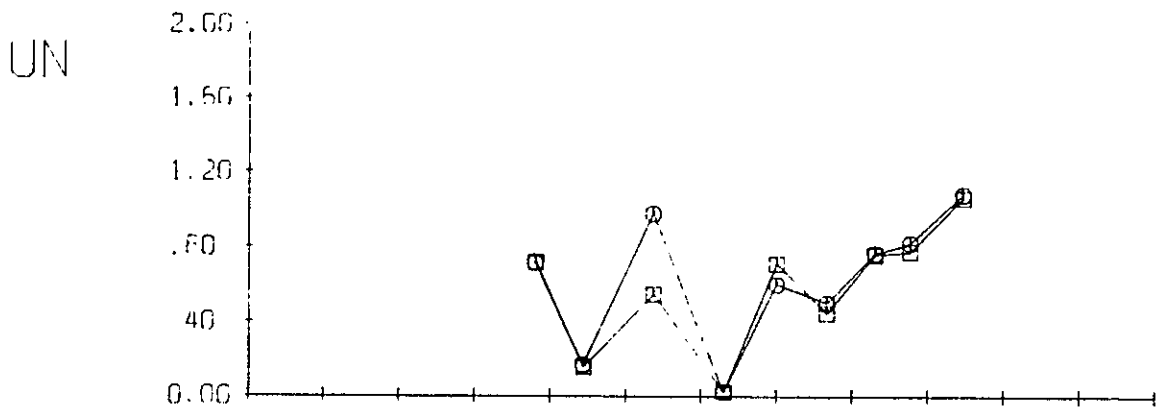
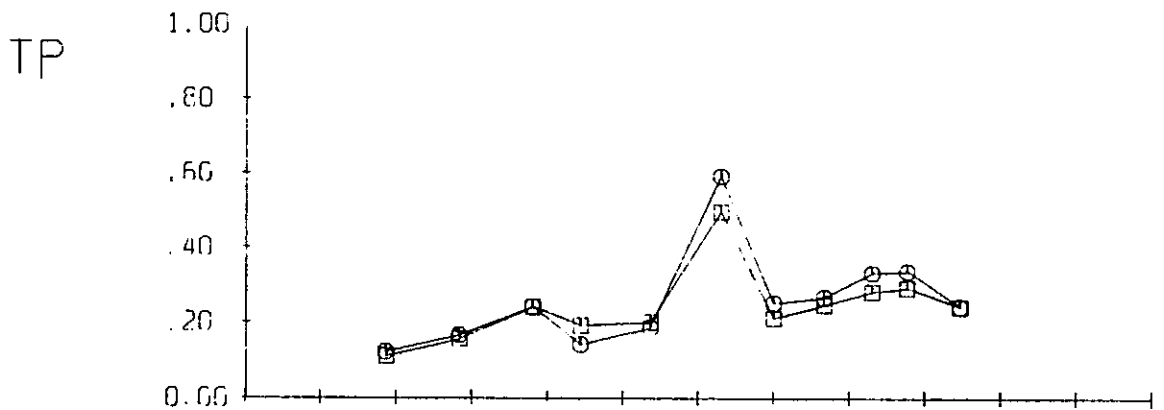
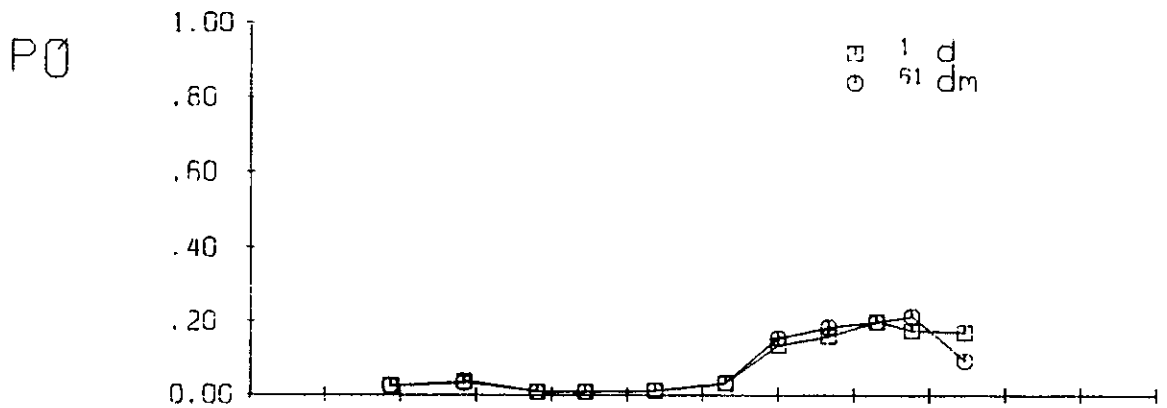
PARP



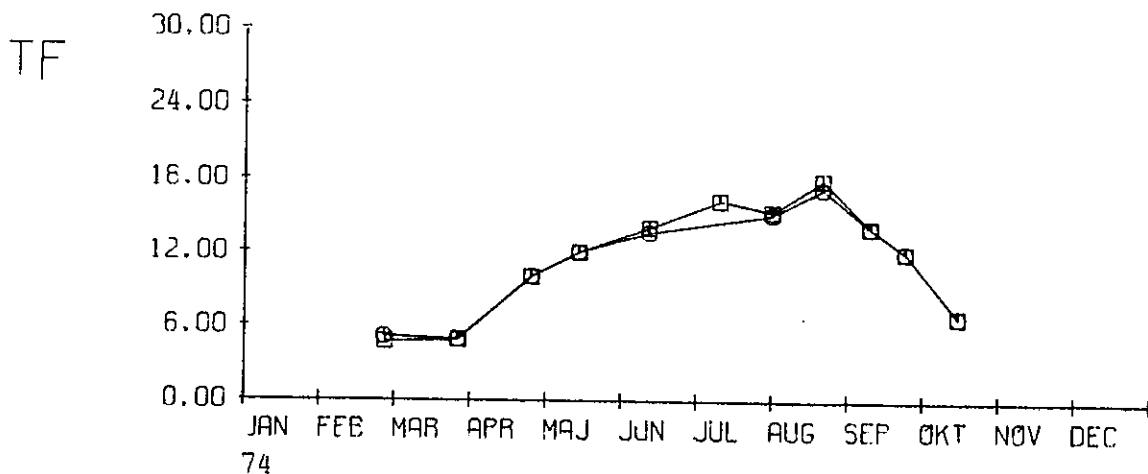
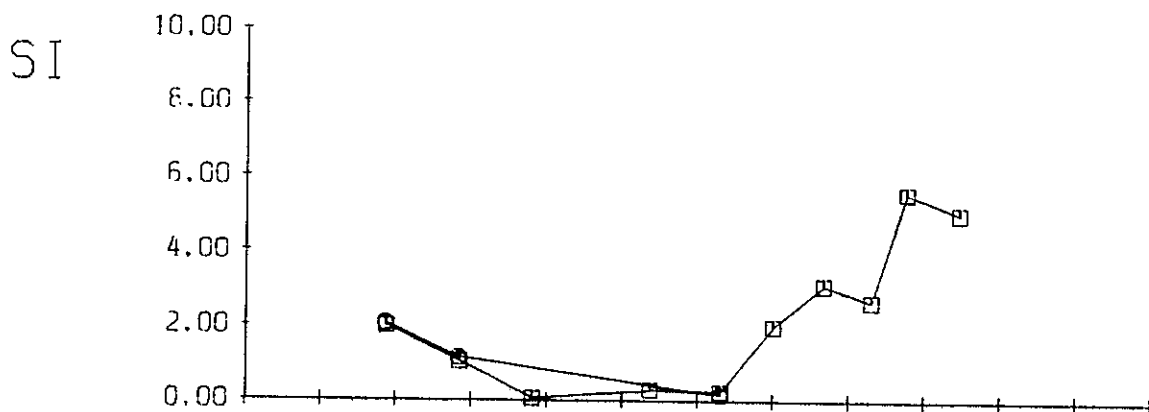
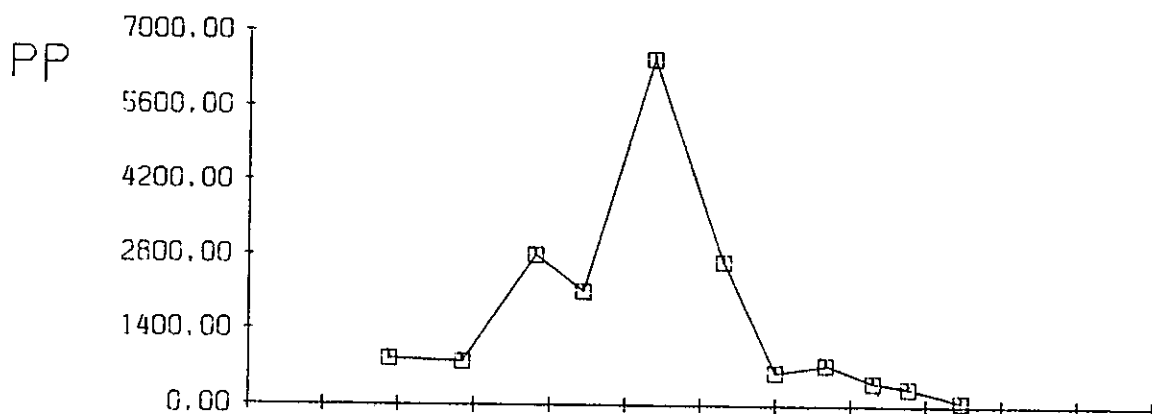
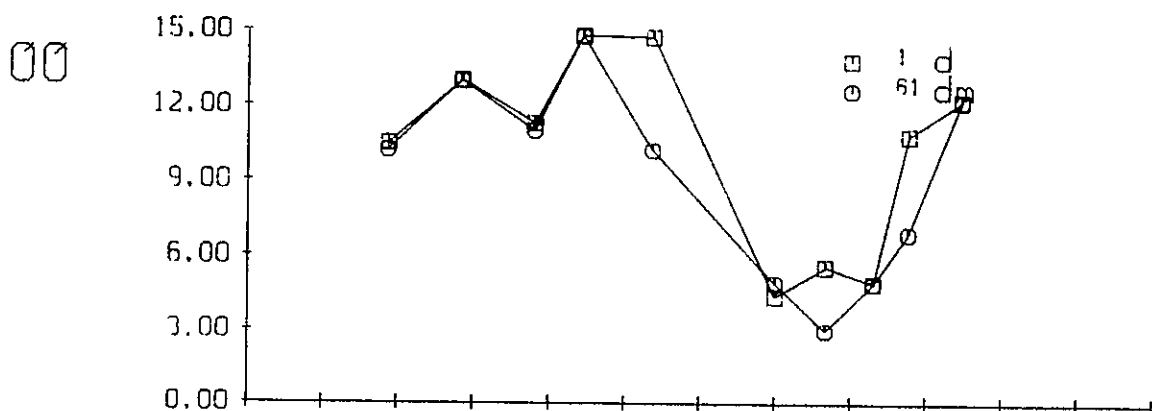
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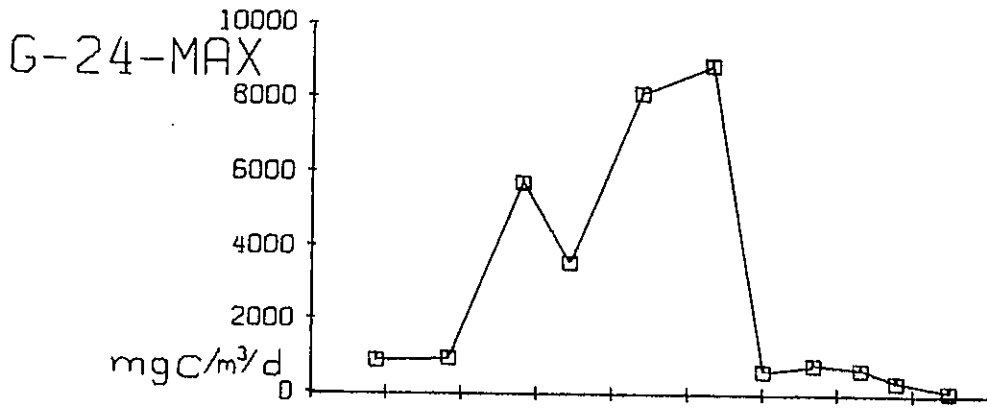
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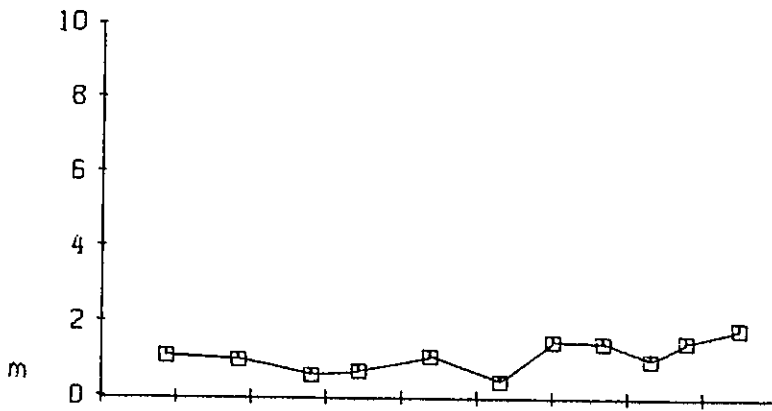
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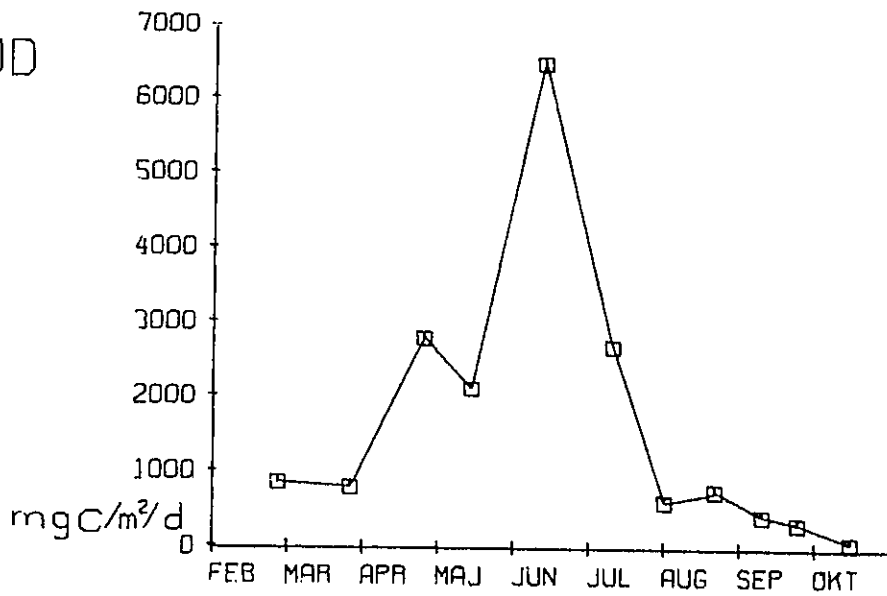
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SY



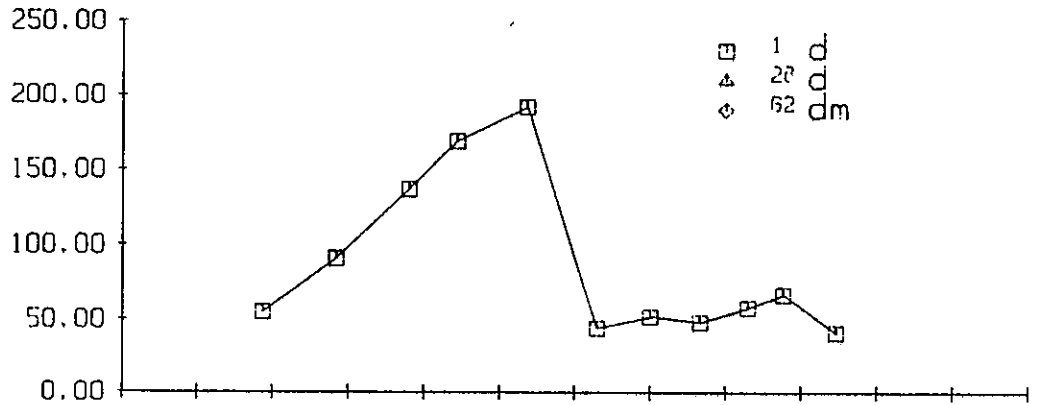
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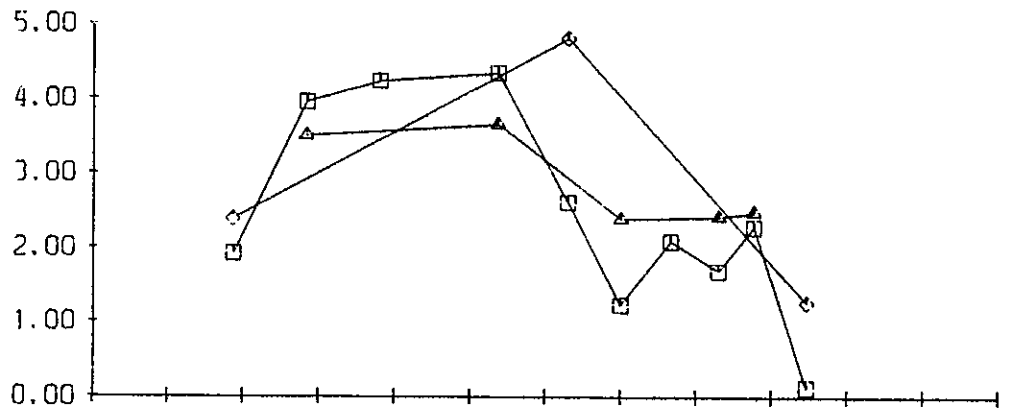
74
ÅRSPROD. 440 gCm⁻²år⁻¹

TAN 752

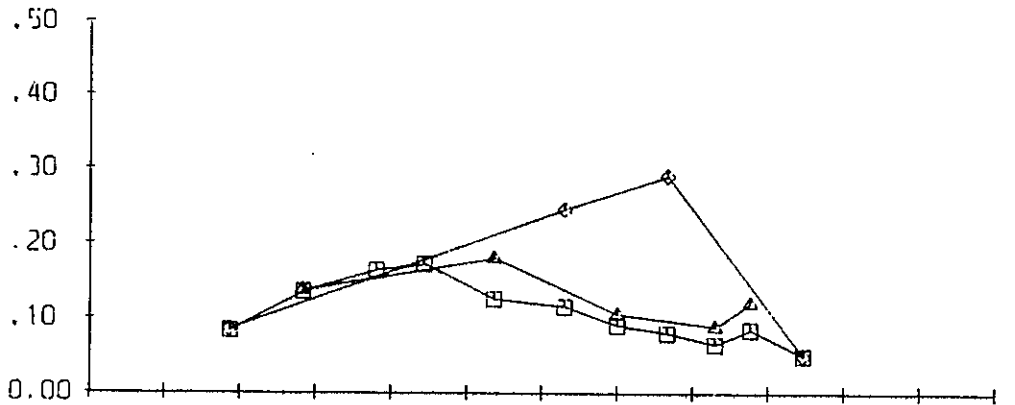
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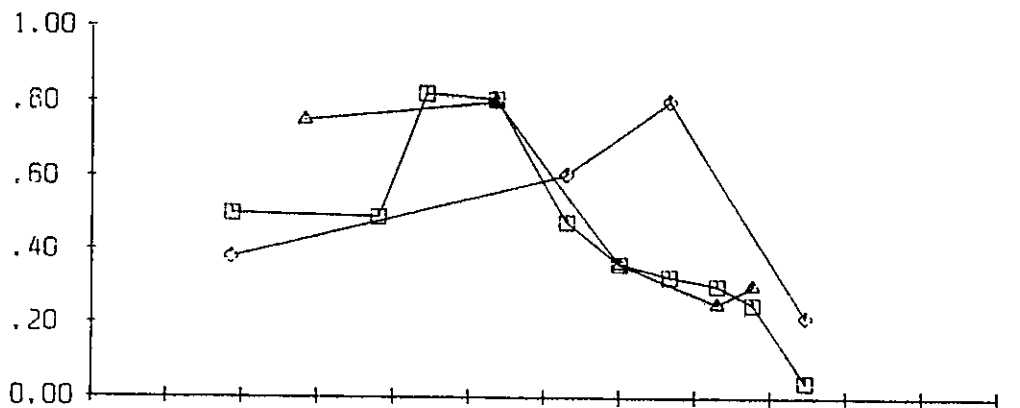
PAR0



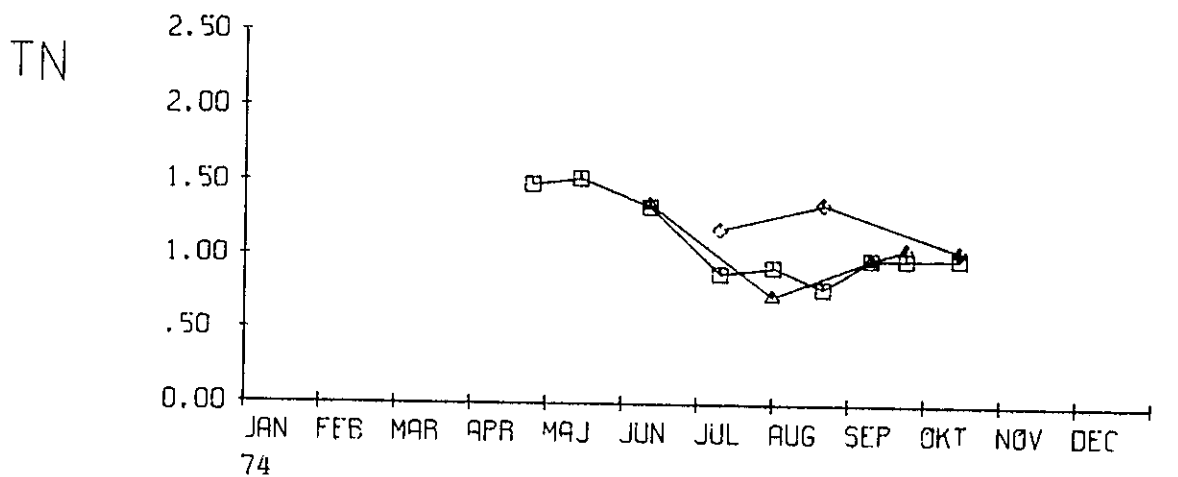
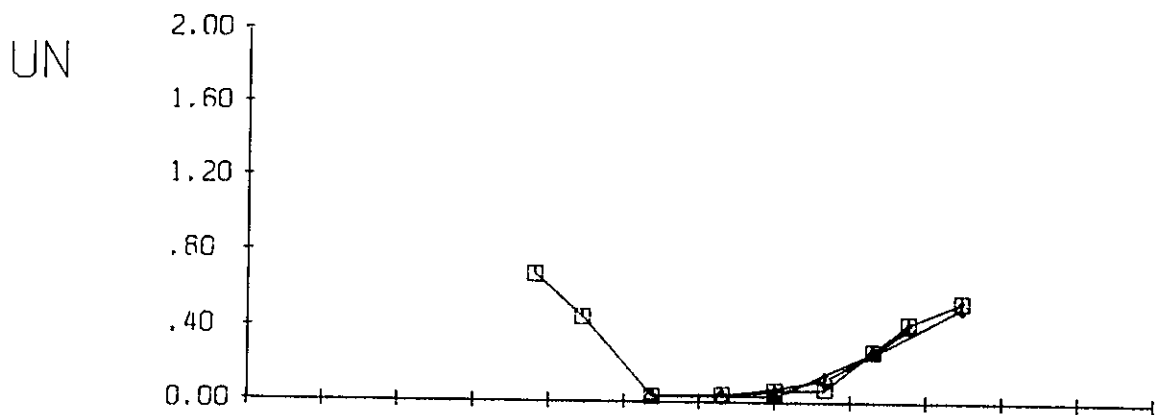
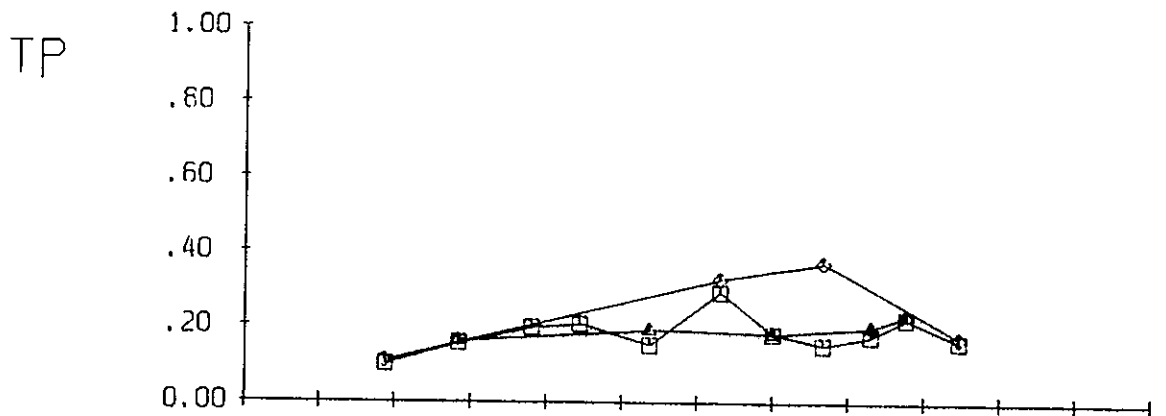
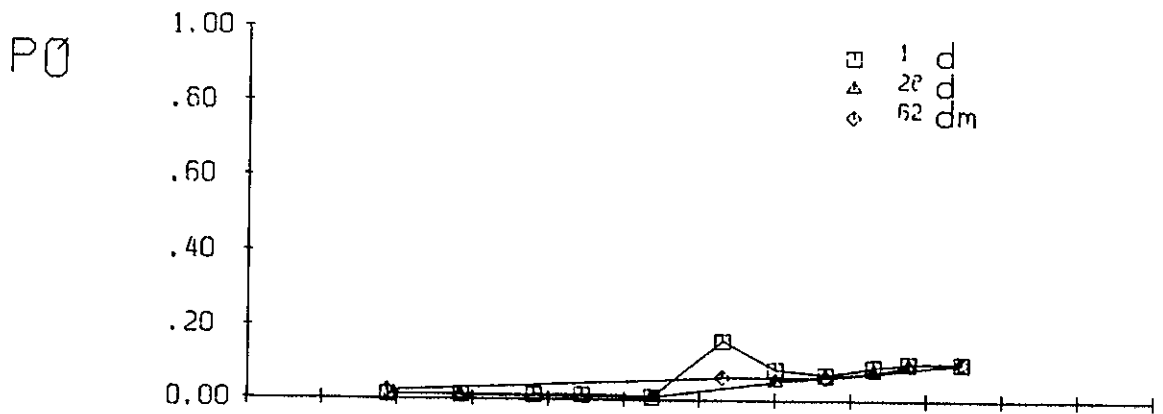
PARP



PARN

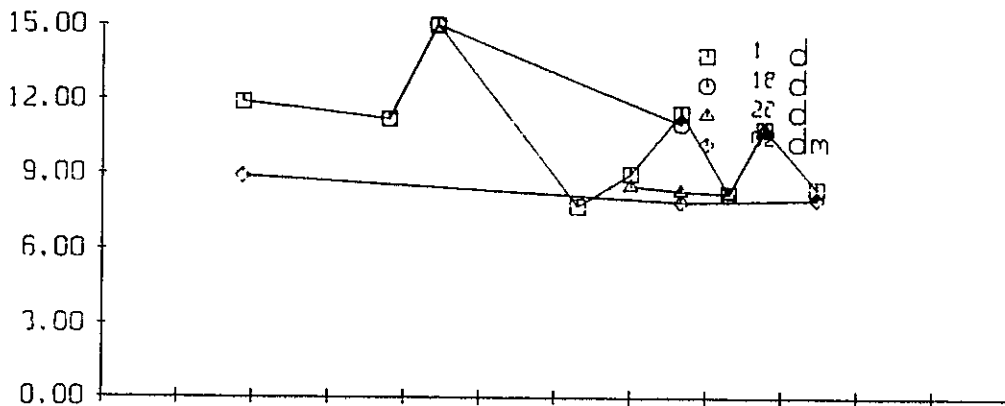


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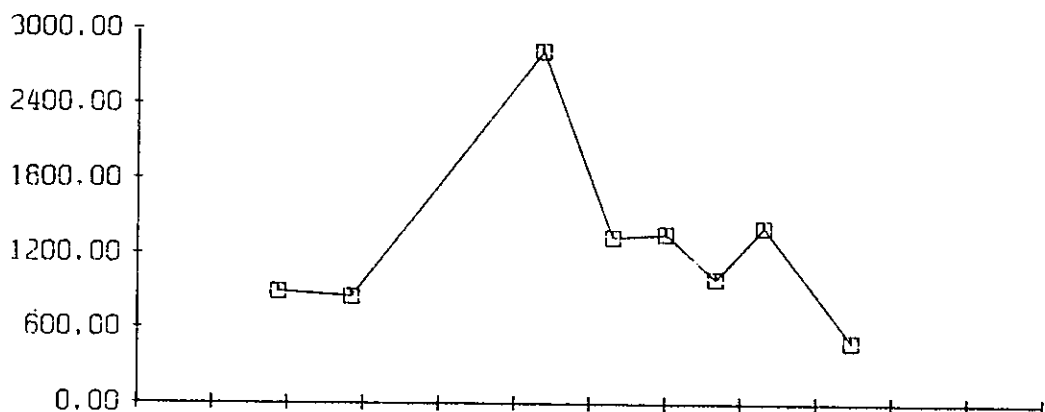


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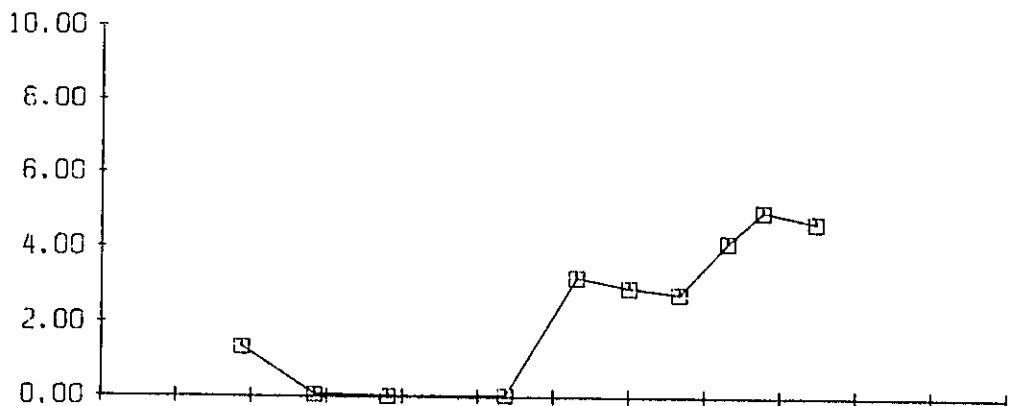
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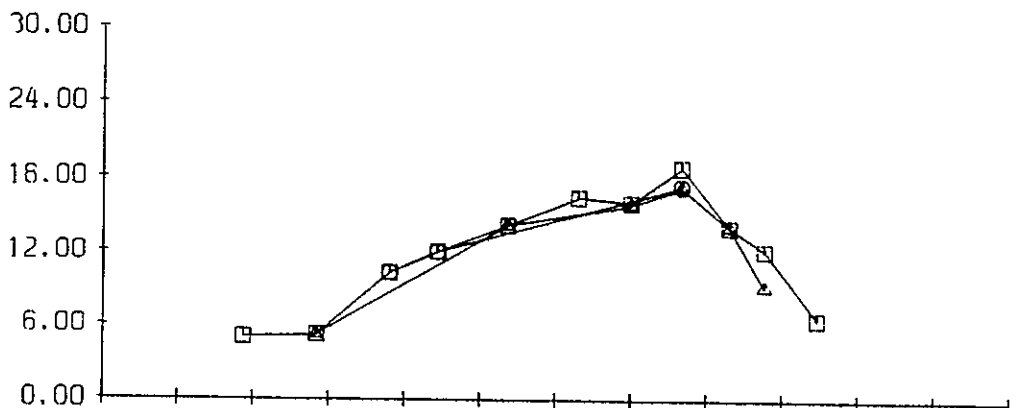
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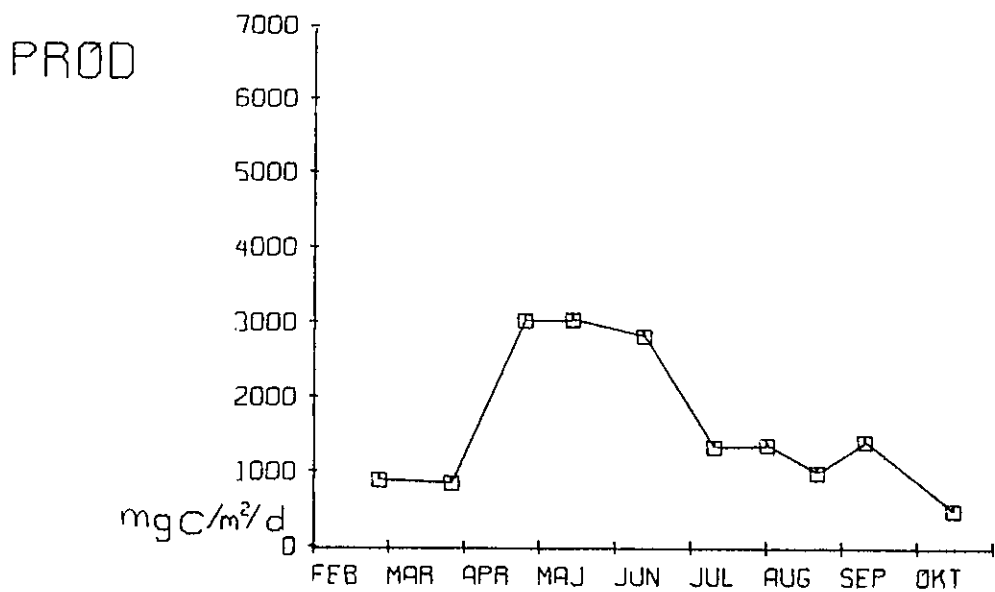
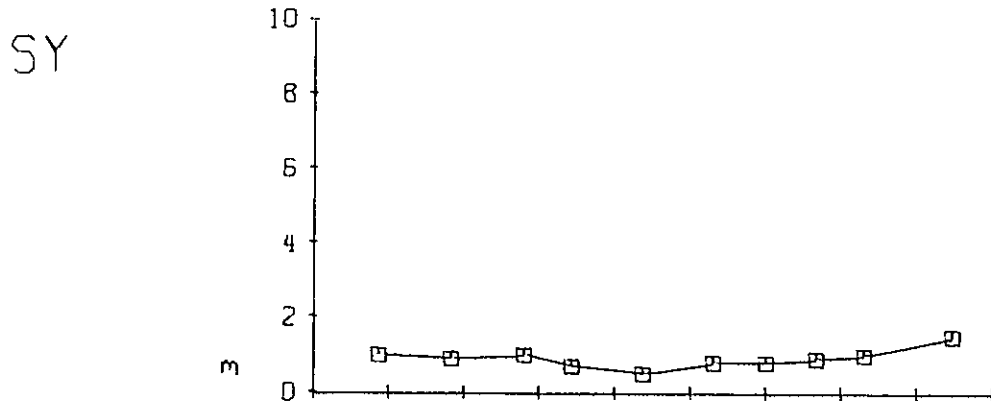
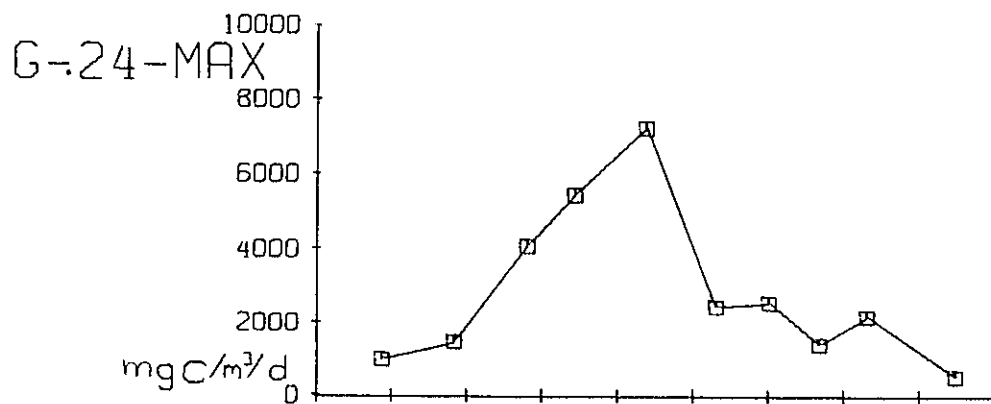
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TF



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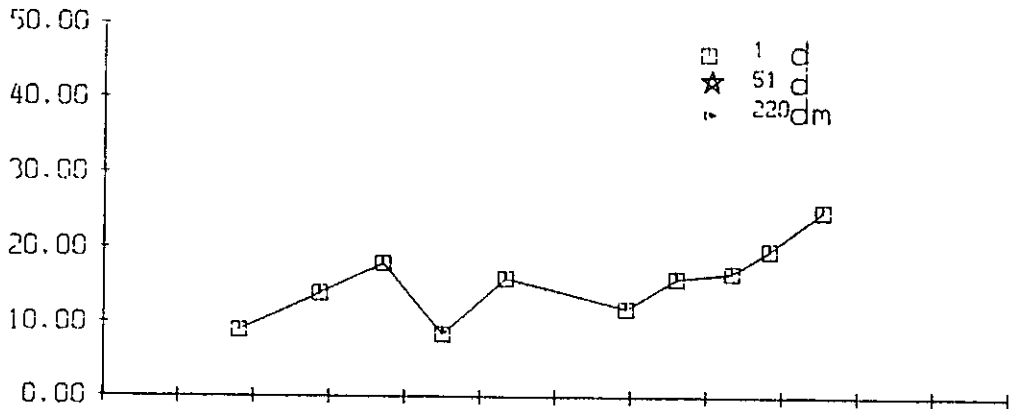


74

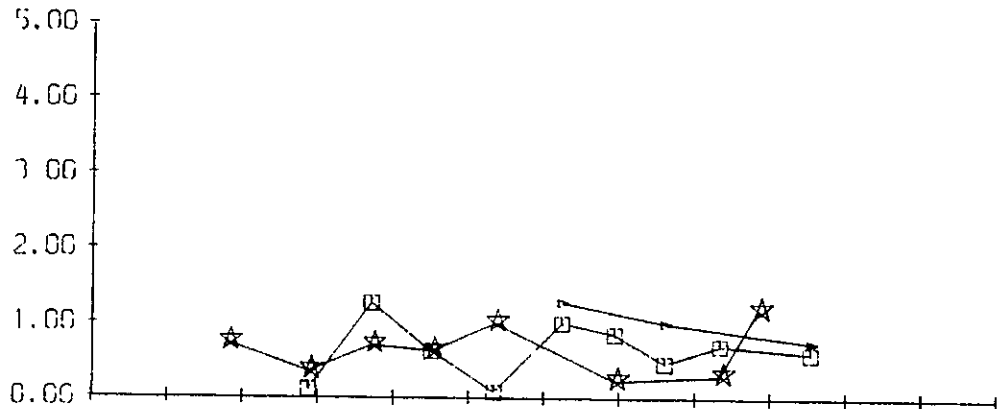
ÅRSPROD. $390 \text{ gC m}^{-2} \text{ år}^{-1}$

THO 751

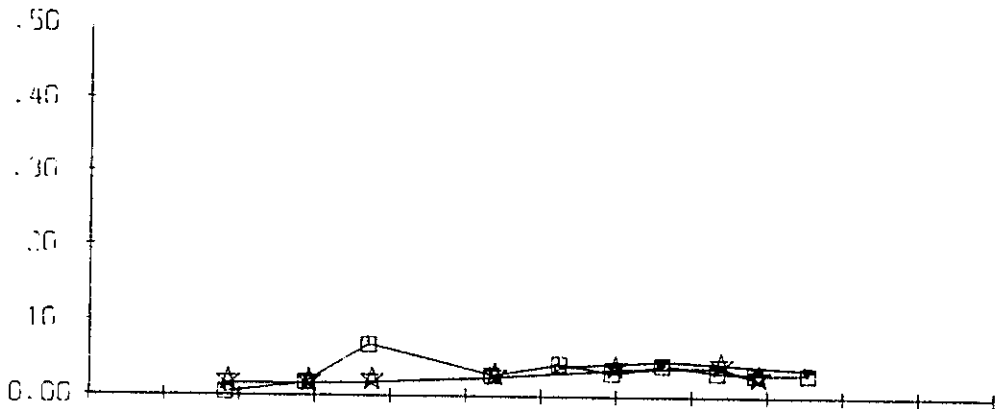
CH



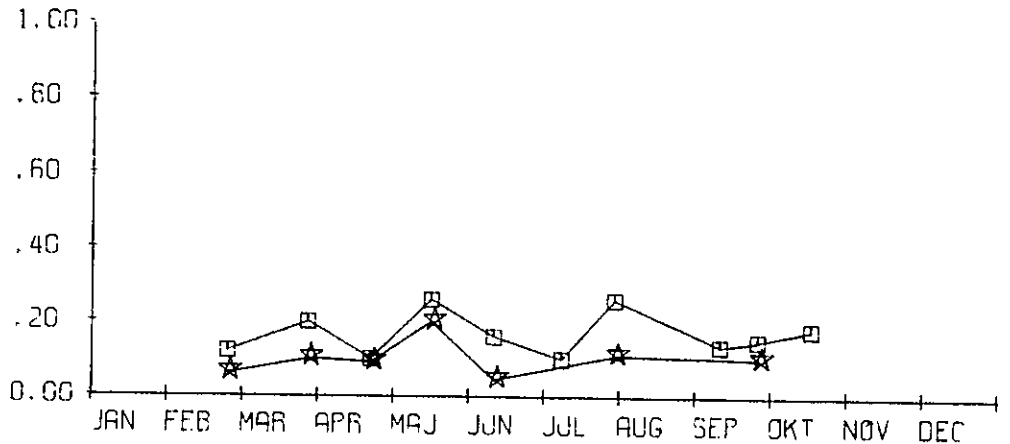
PARO



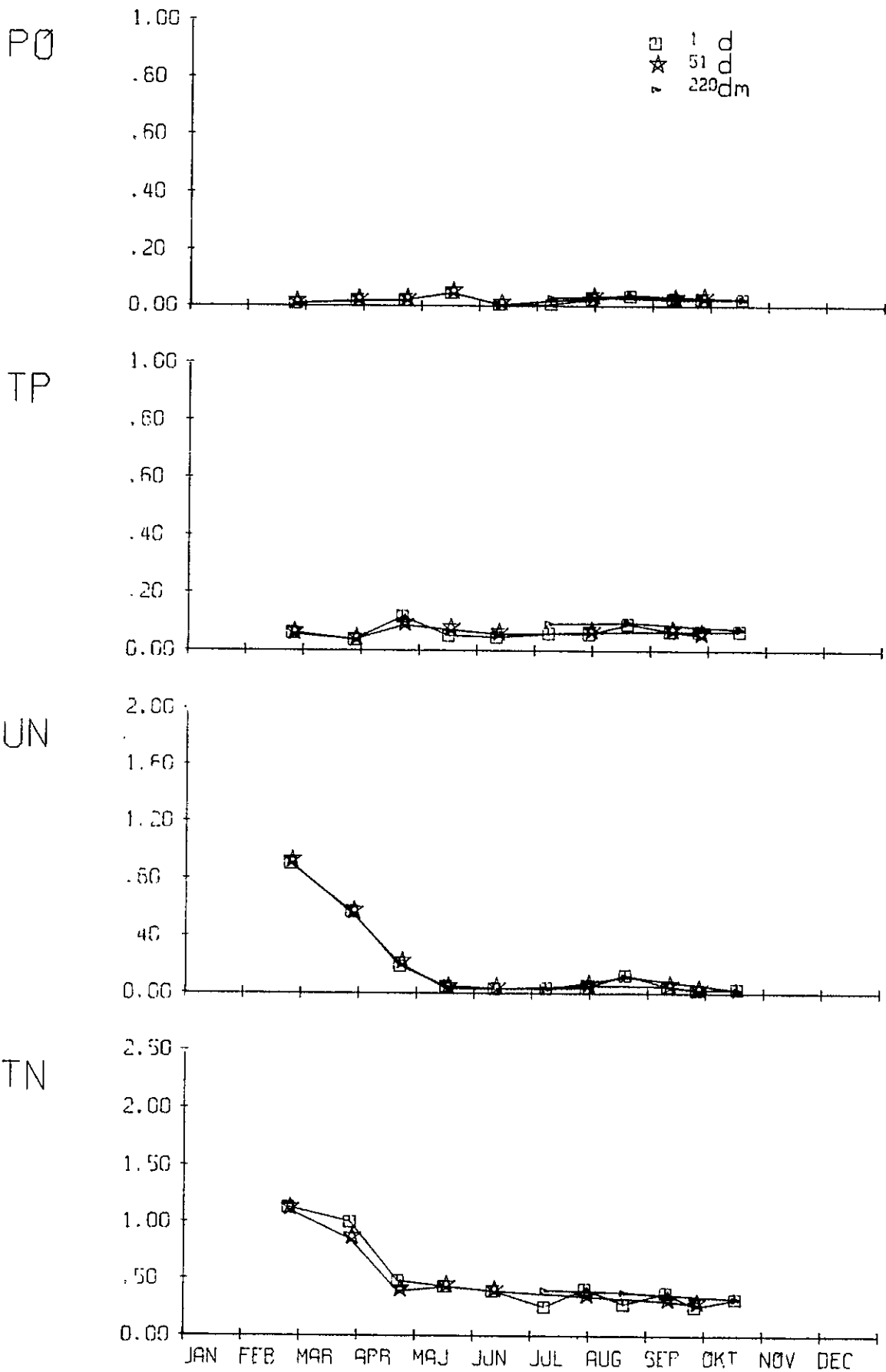
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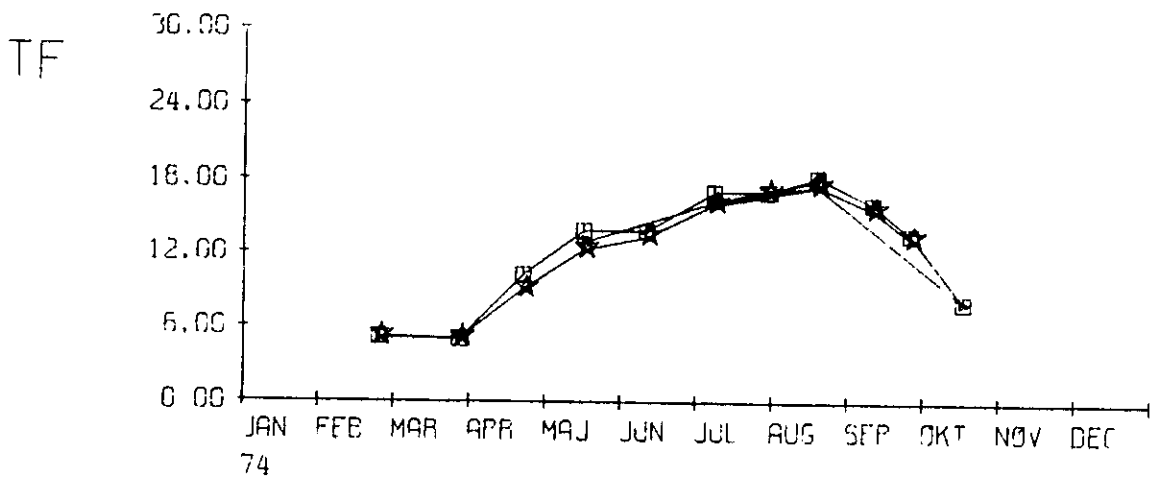
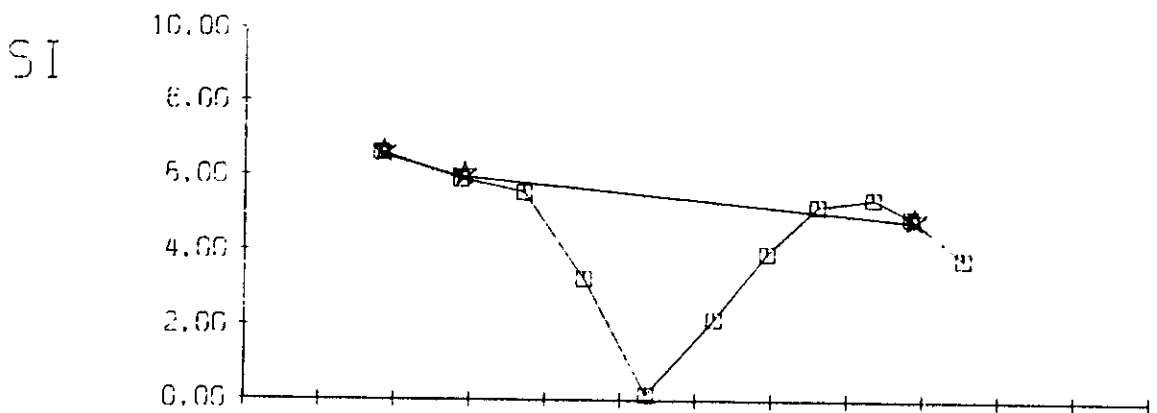
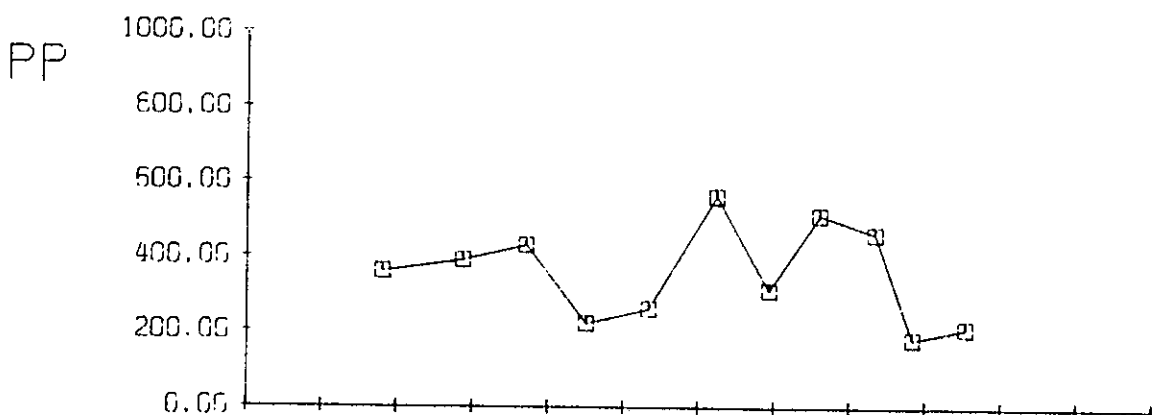
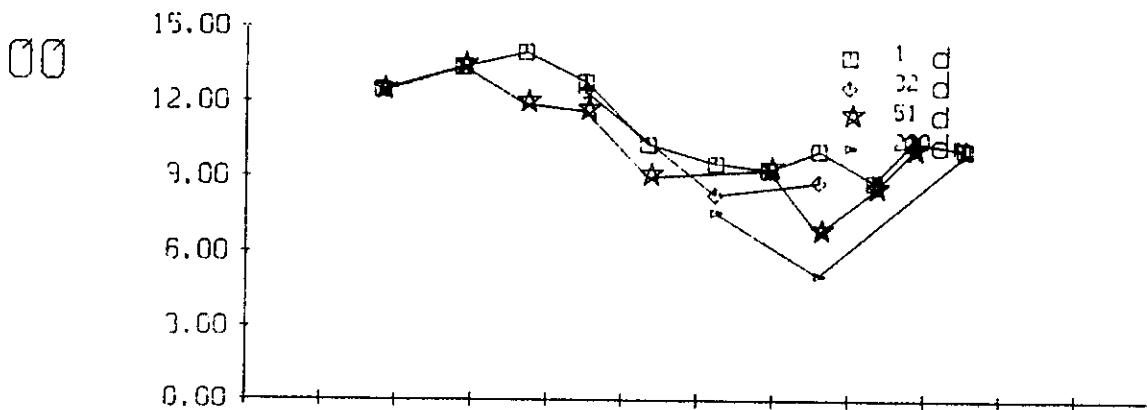
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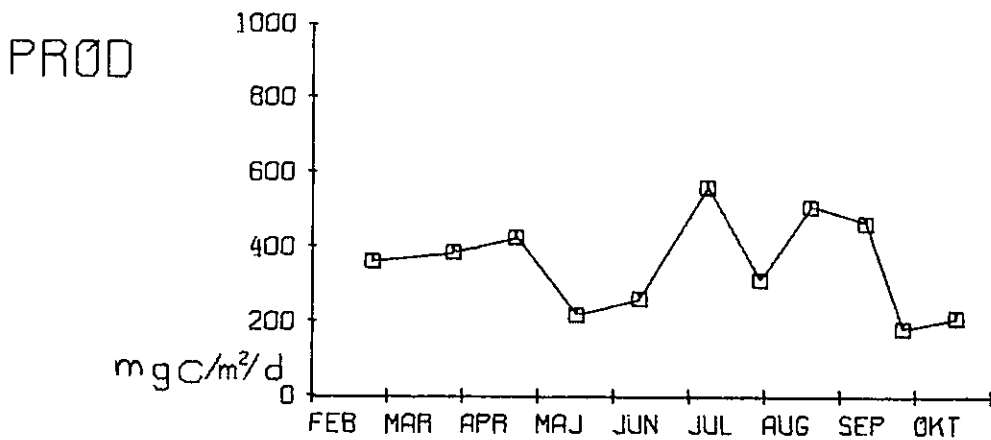
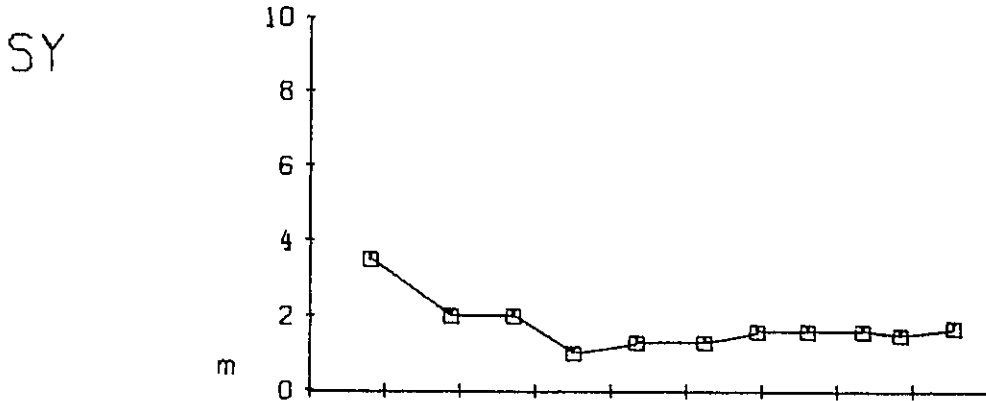
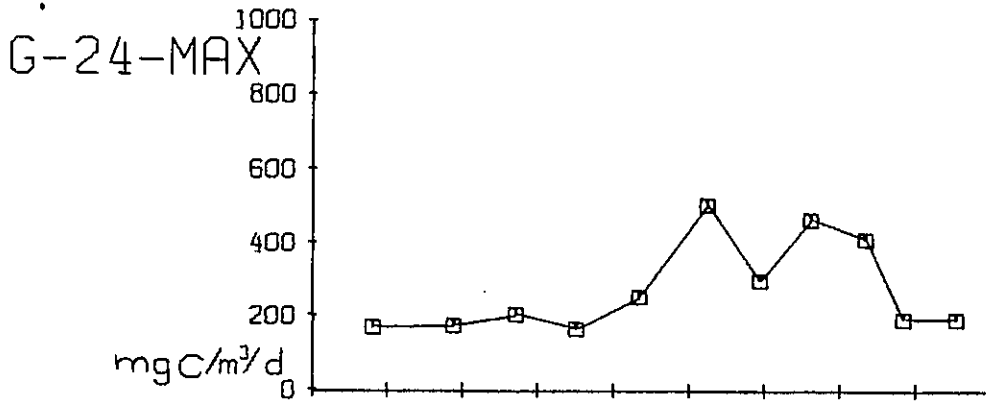
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THO 751



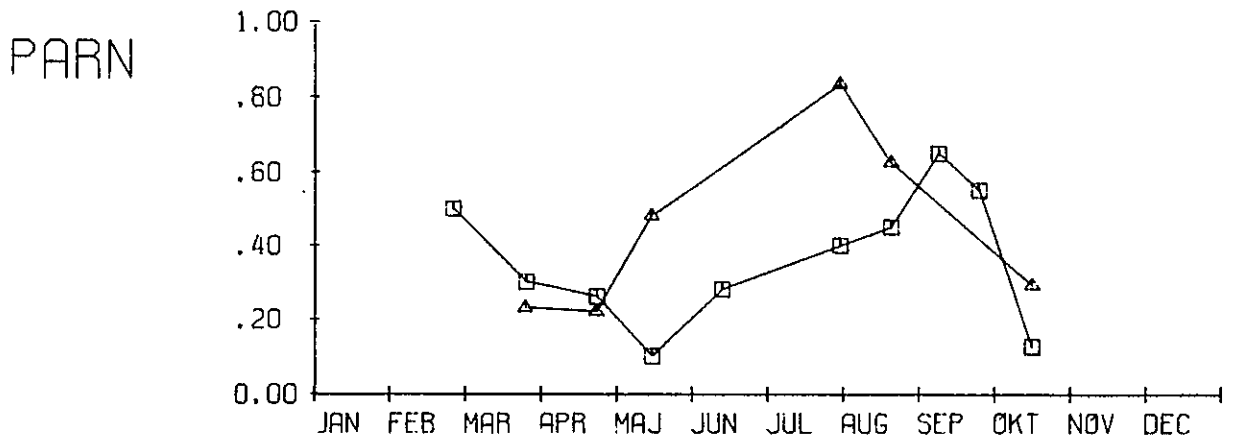
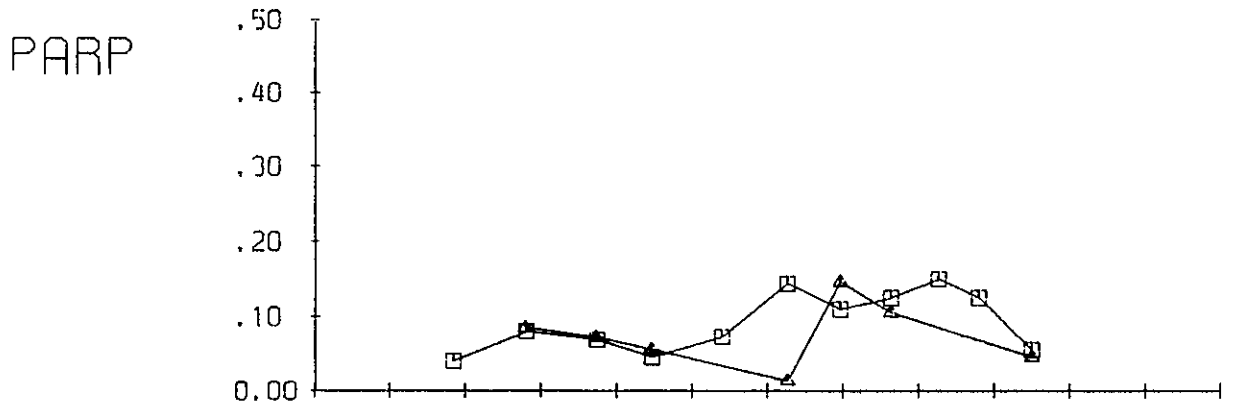
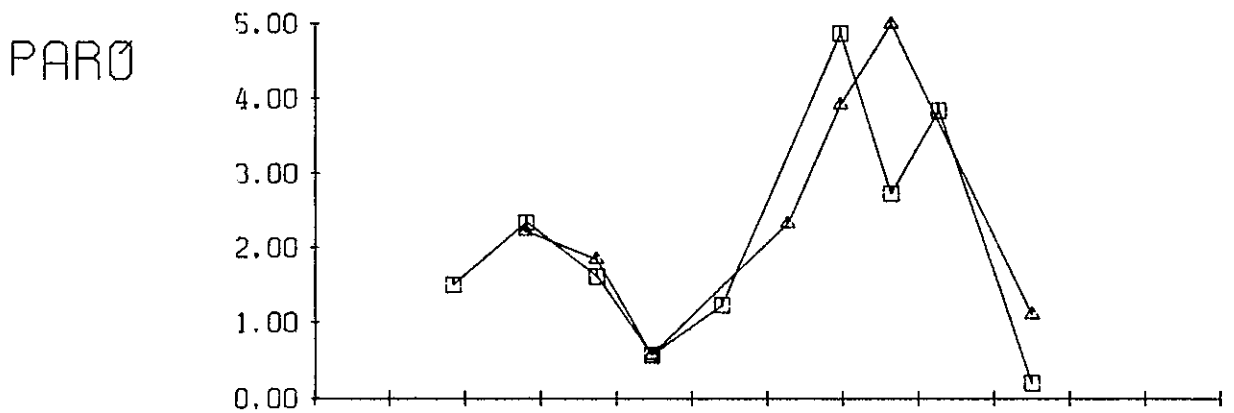
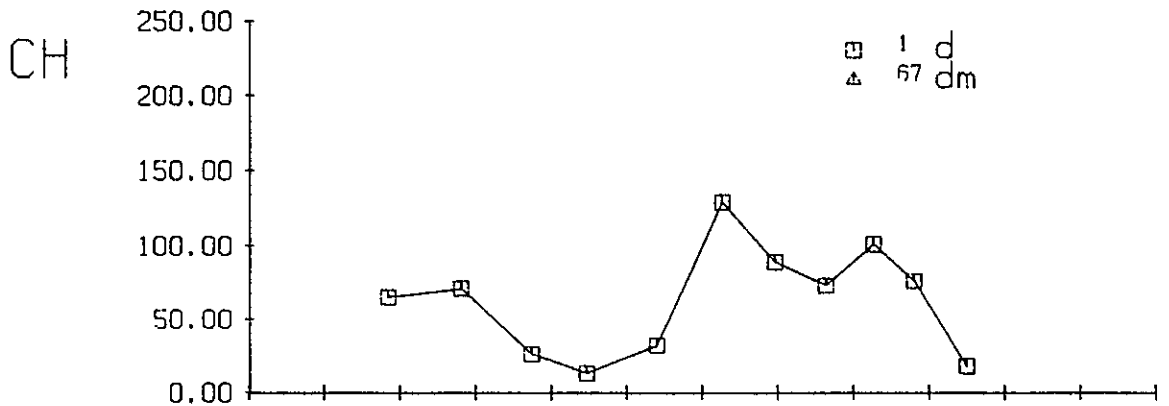
THØ 1



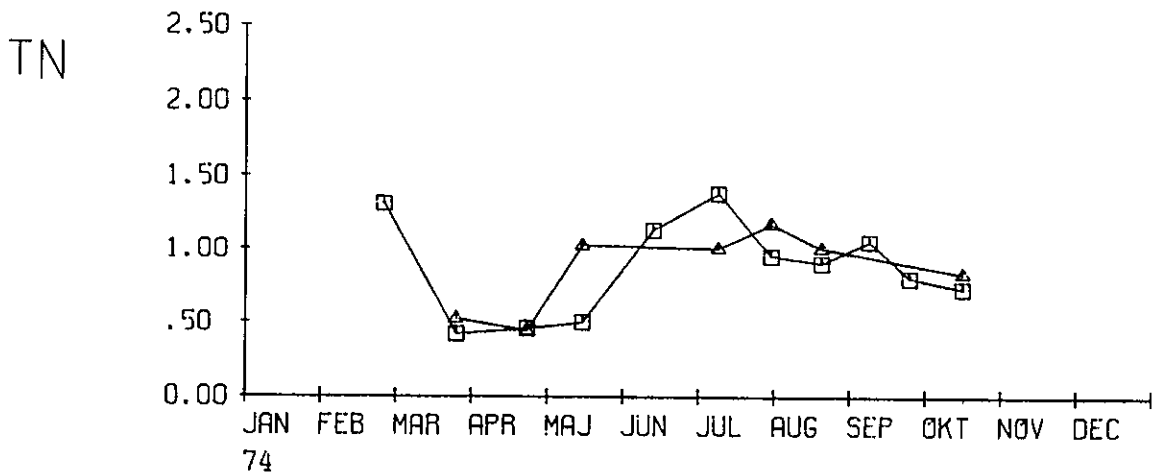
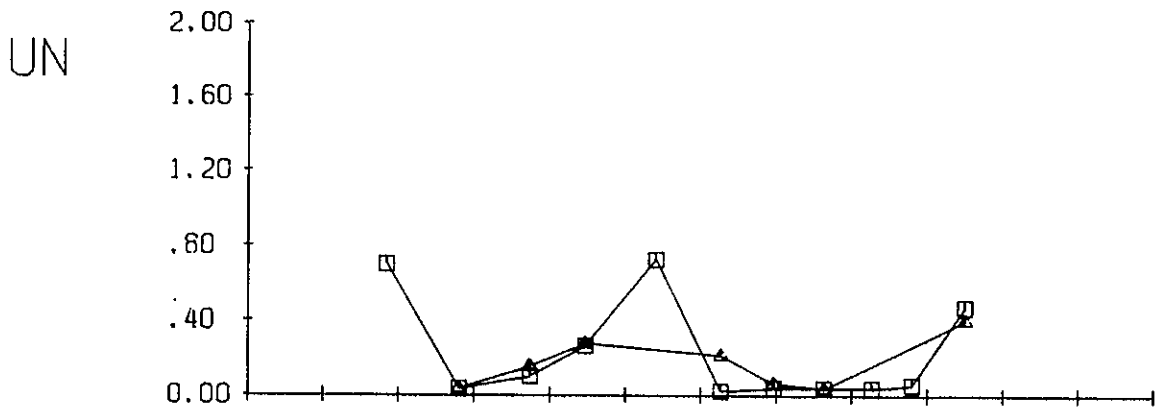
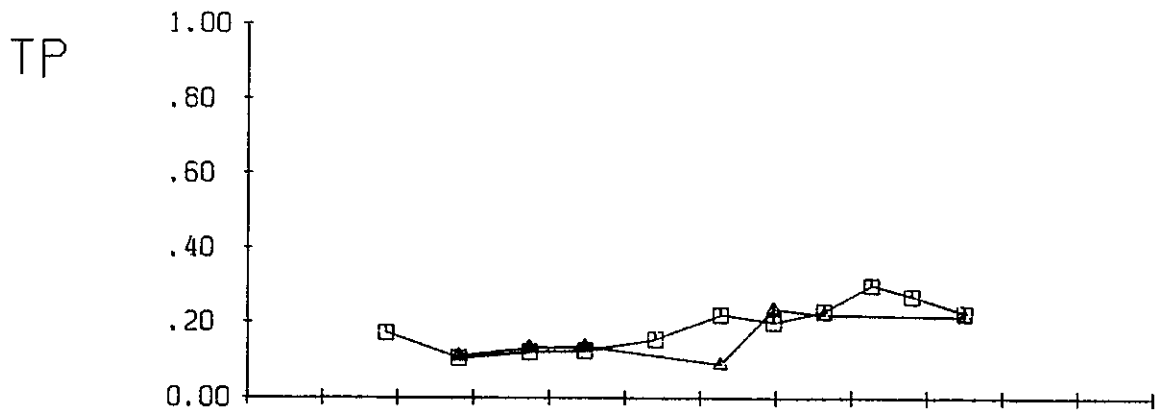
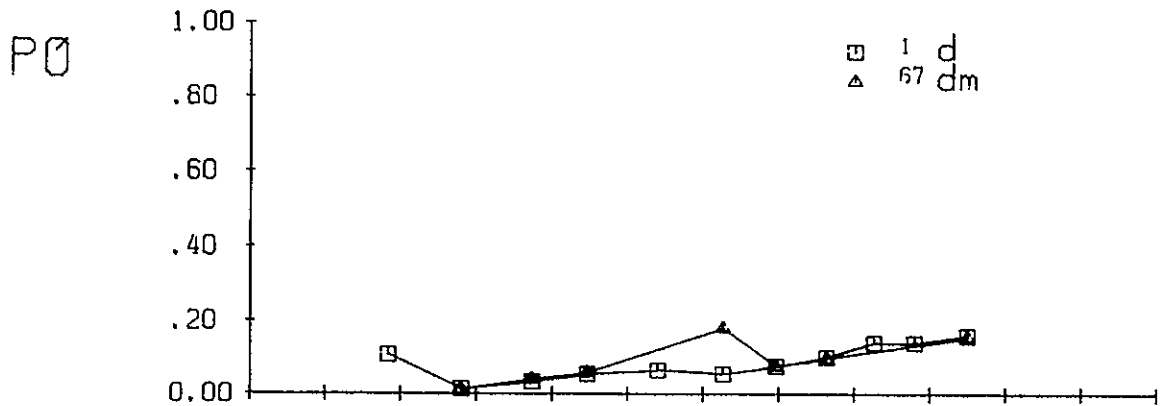
74

ARSPROD. 85 gCm⁻²ar⁻¹

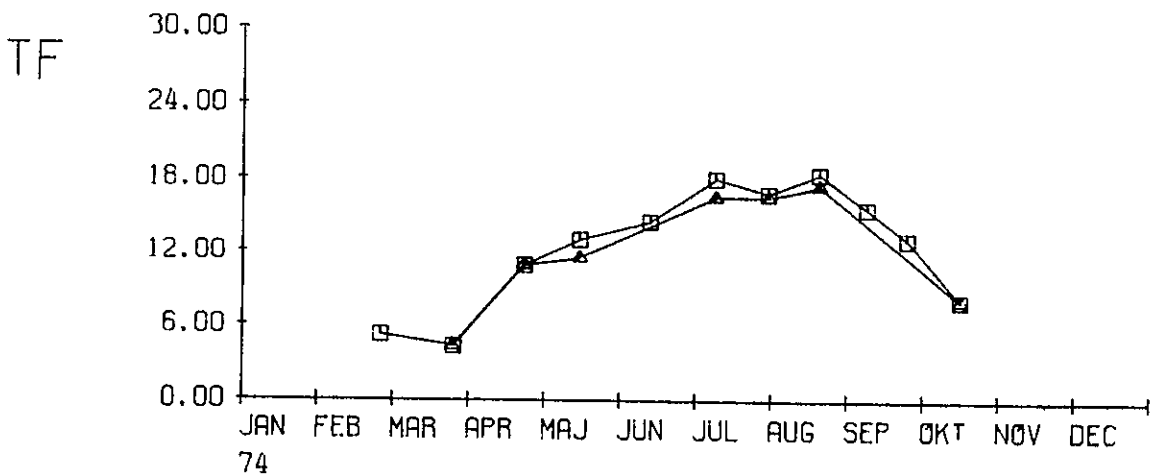
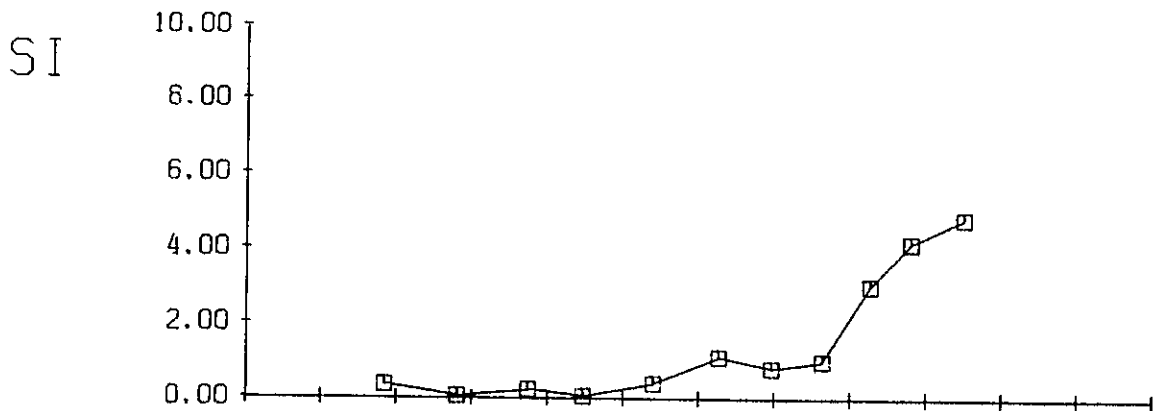
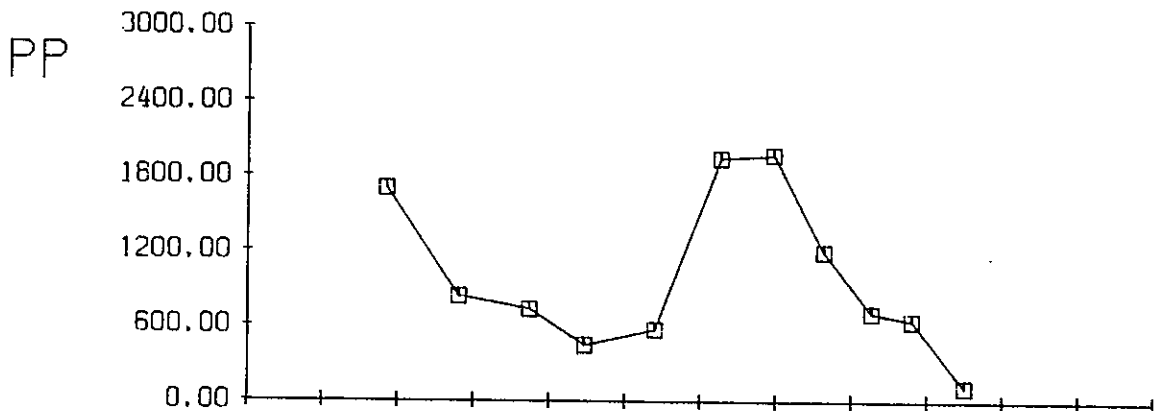
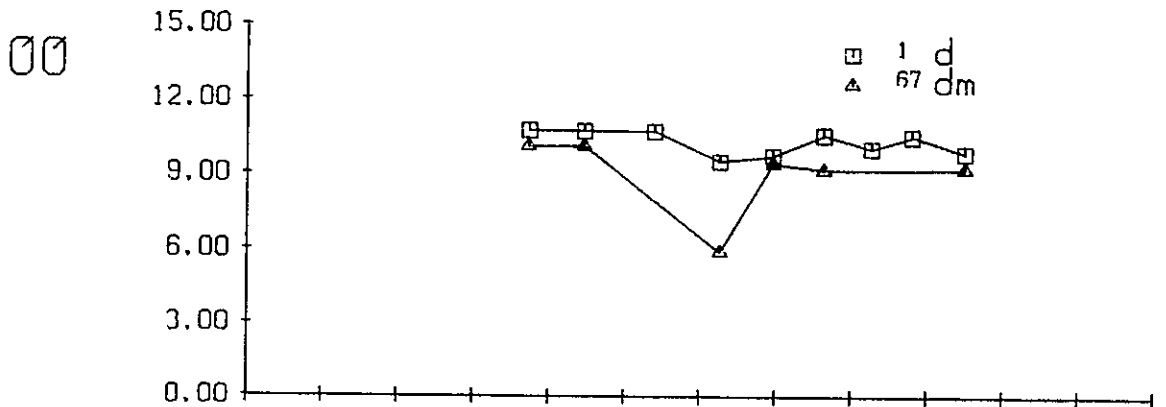
VED 751



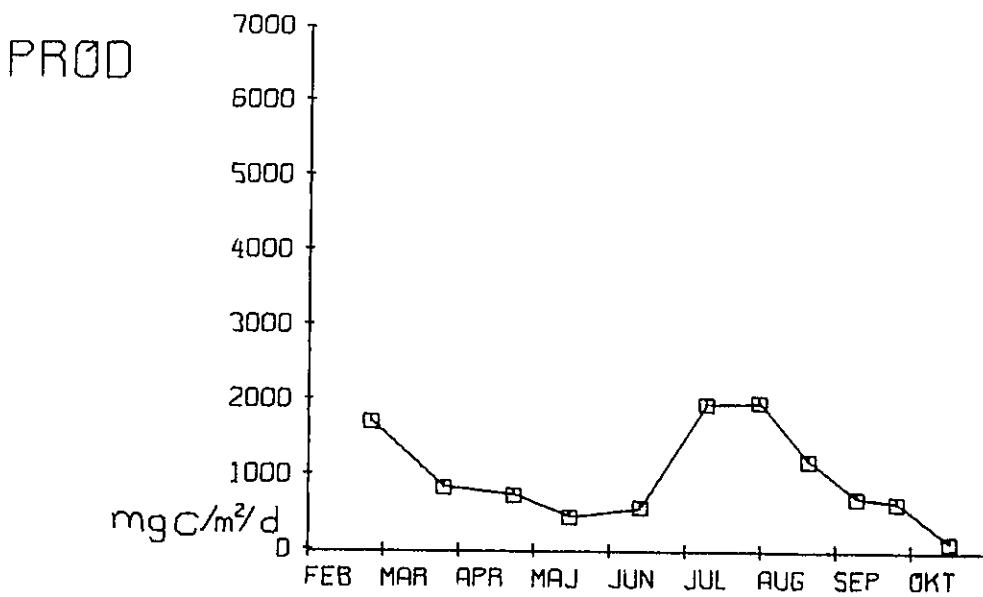
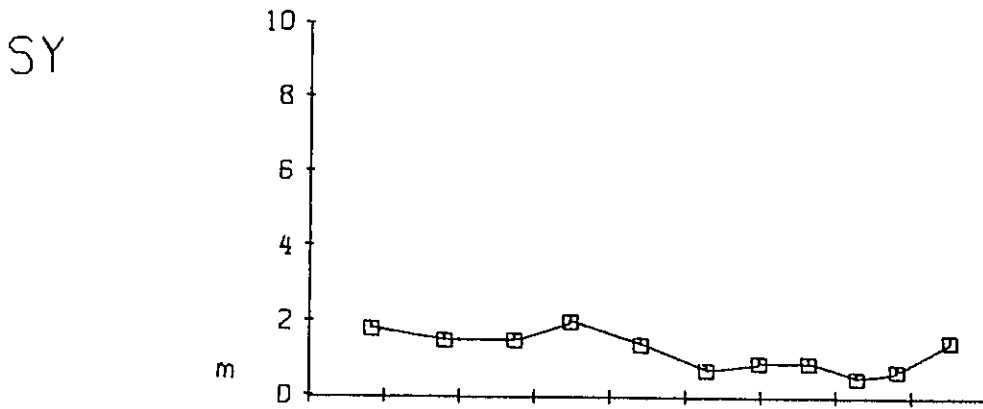
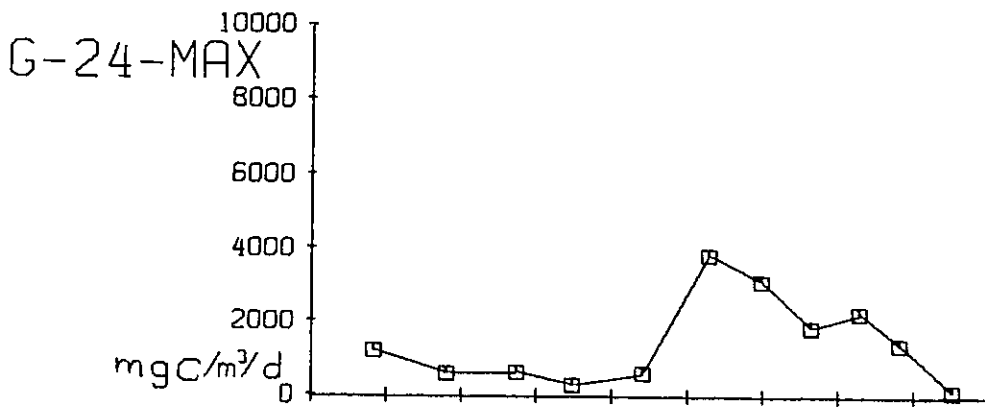
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VED 751



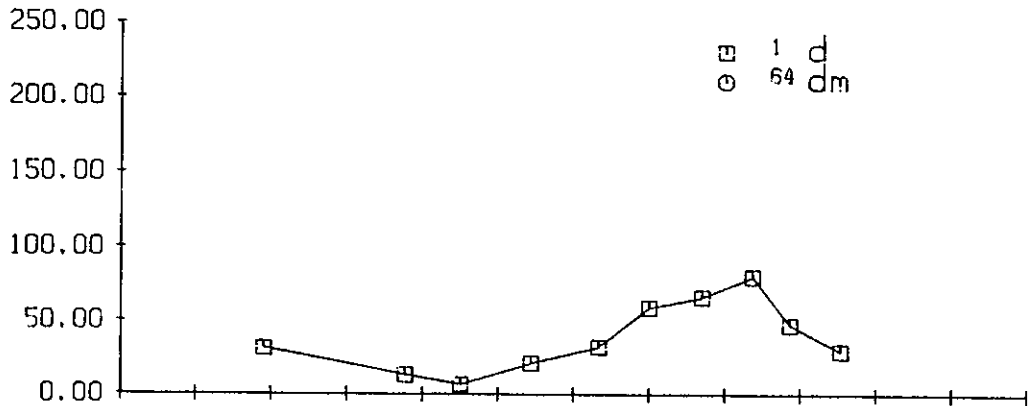
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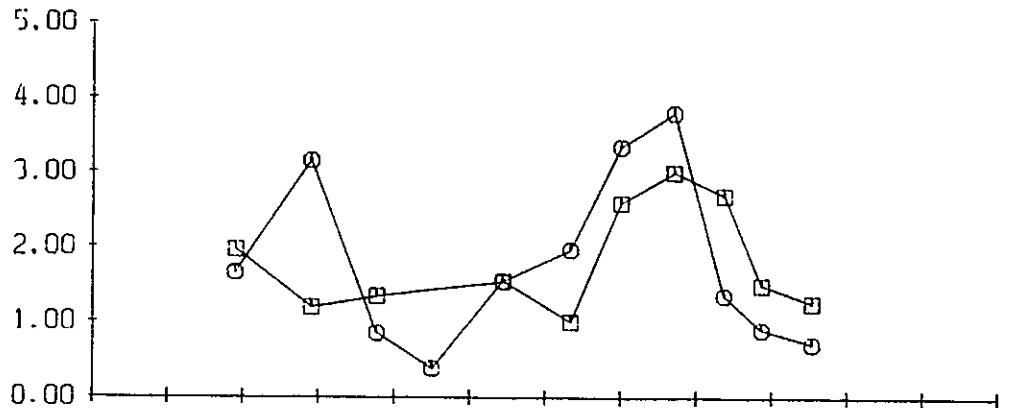
74
ÅRSPROD. 230 gCm⁻²år⁻¹

VES 751

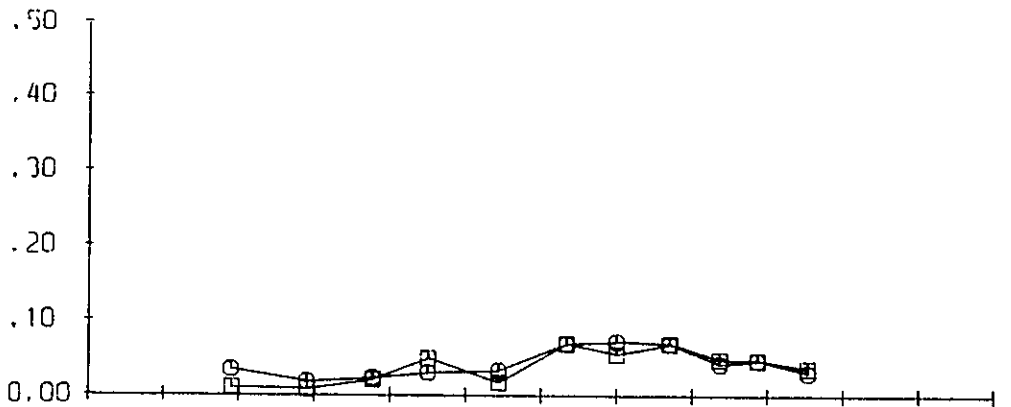
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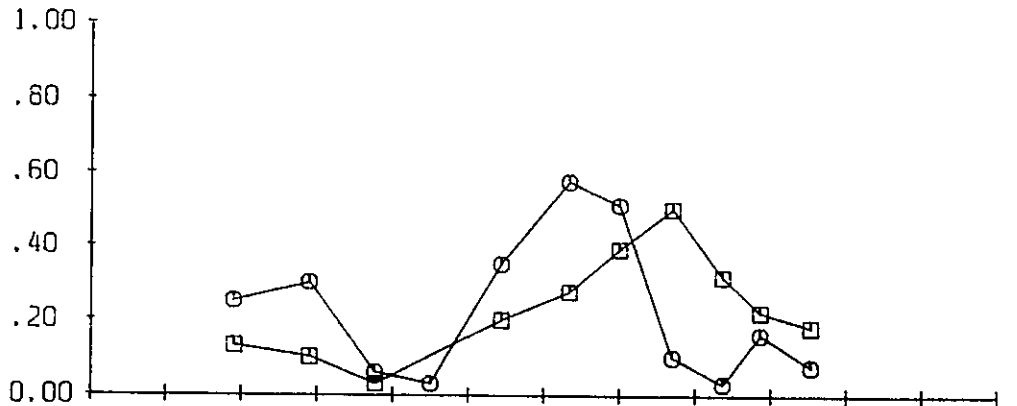
PARO



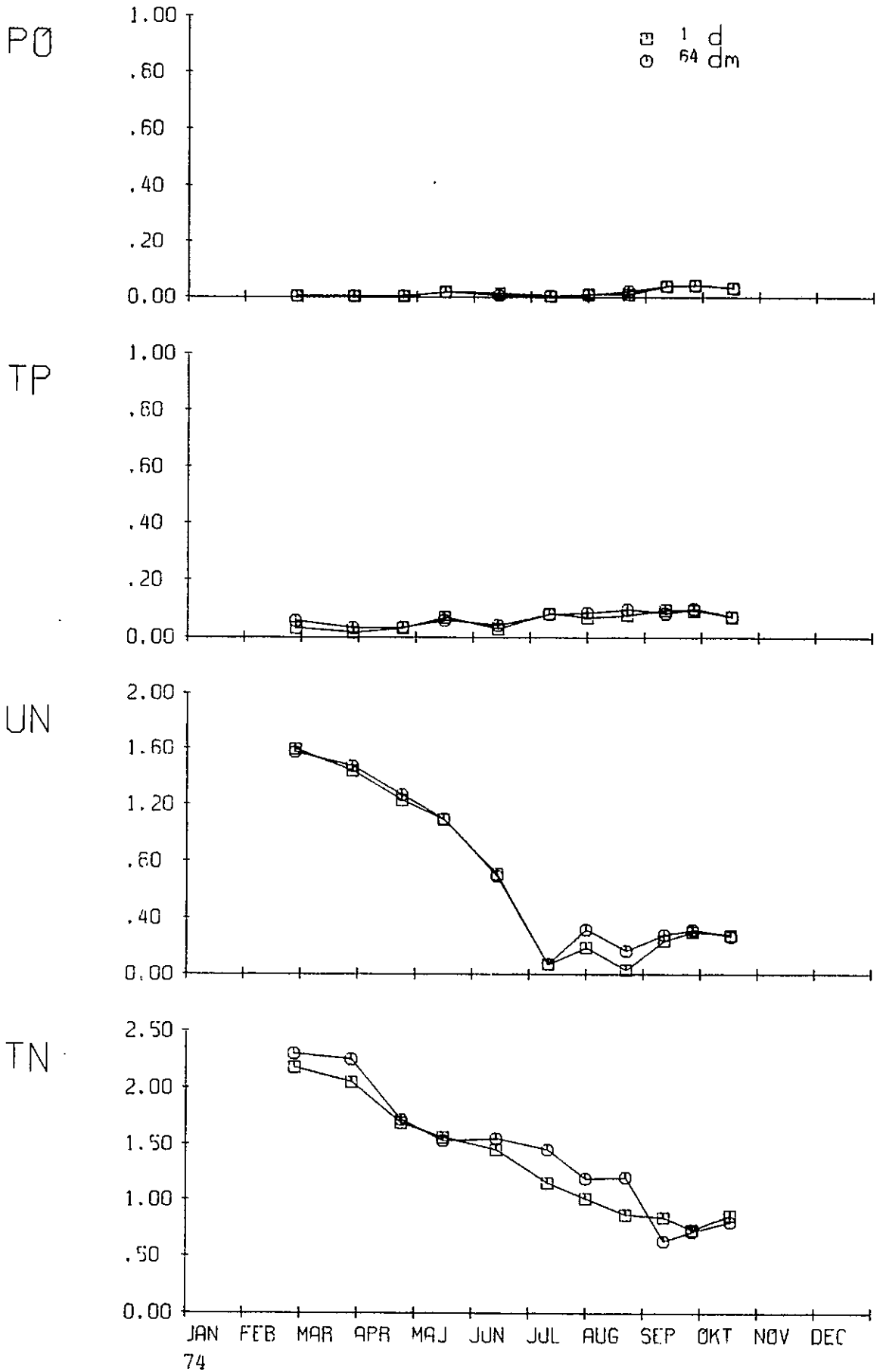
PARP



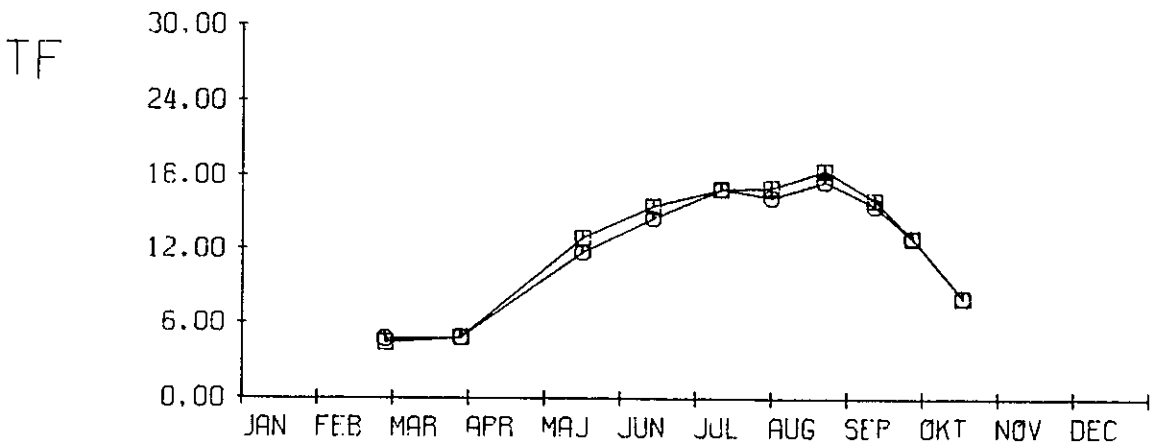
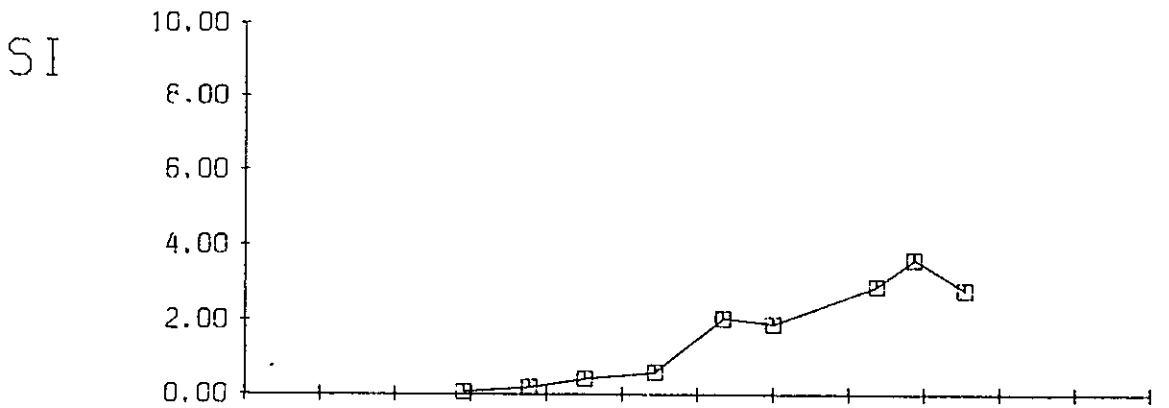
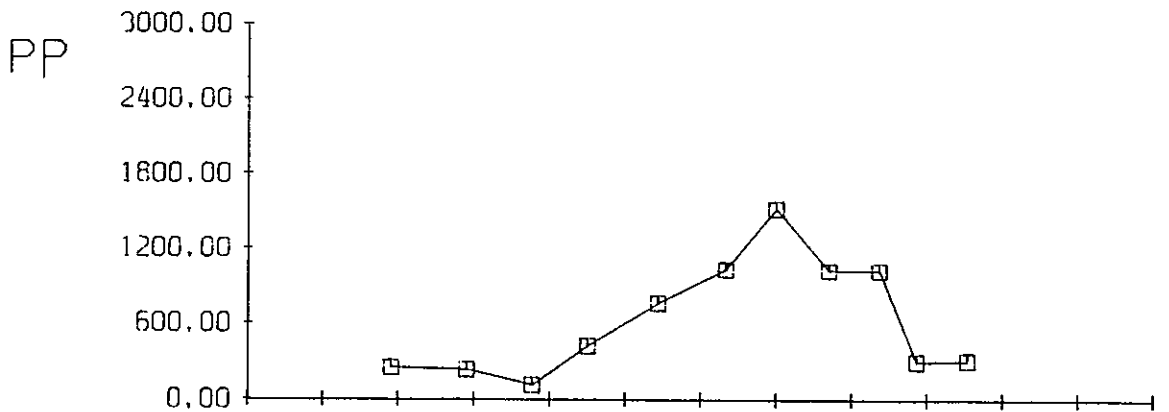
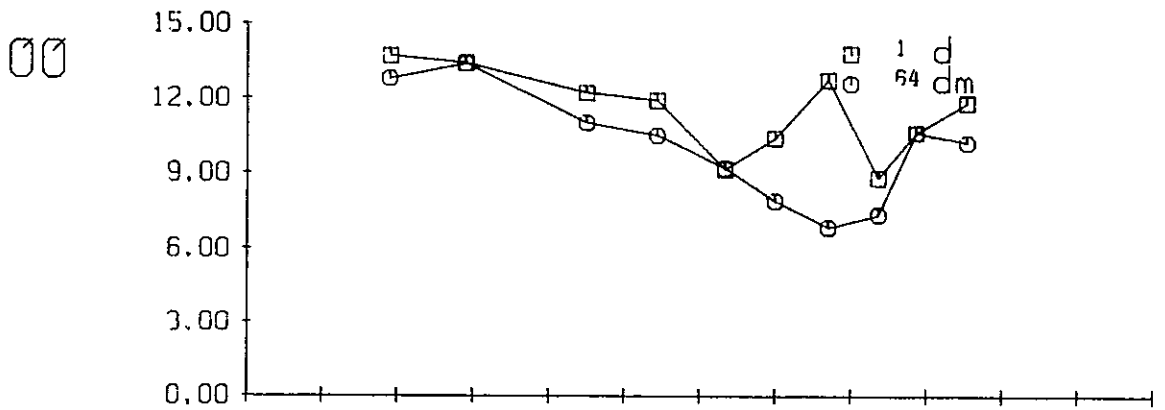
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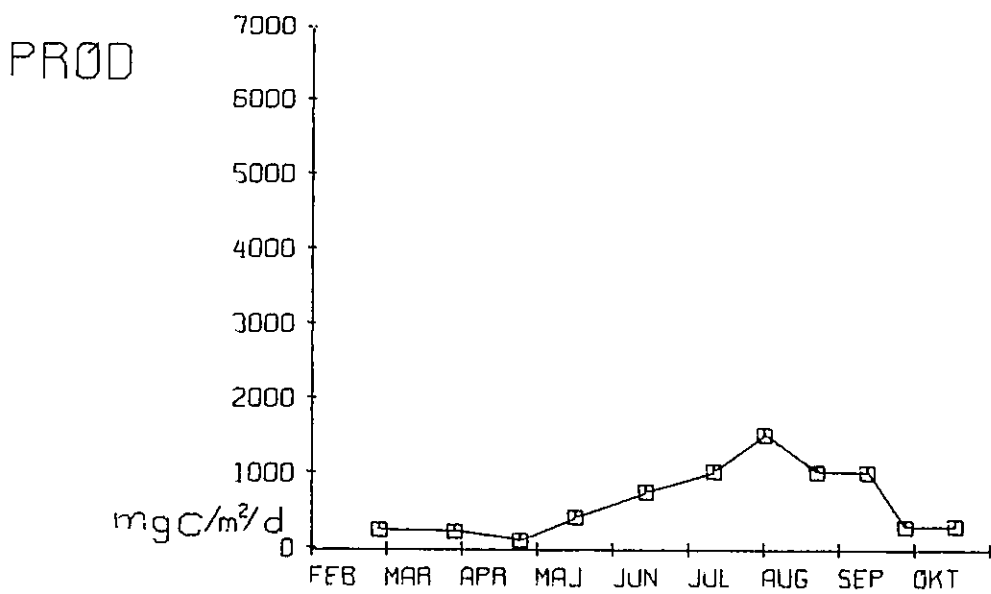
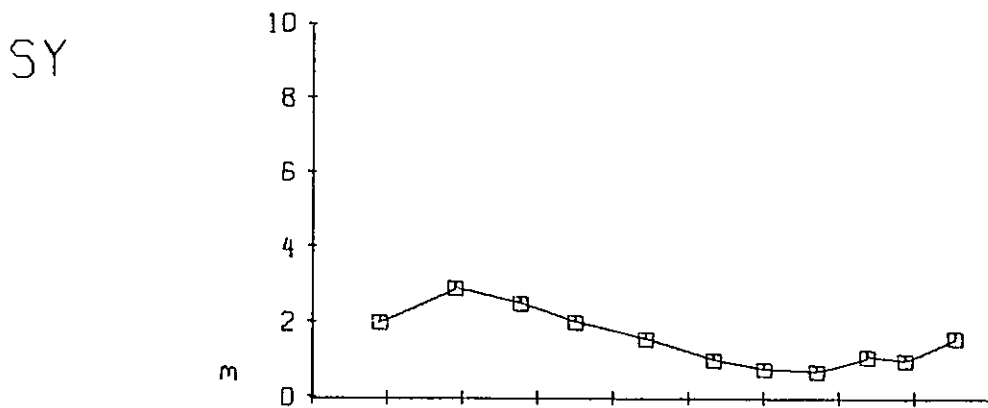
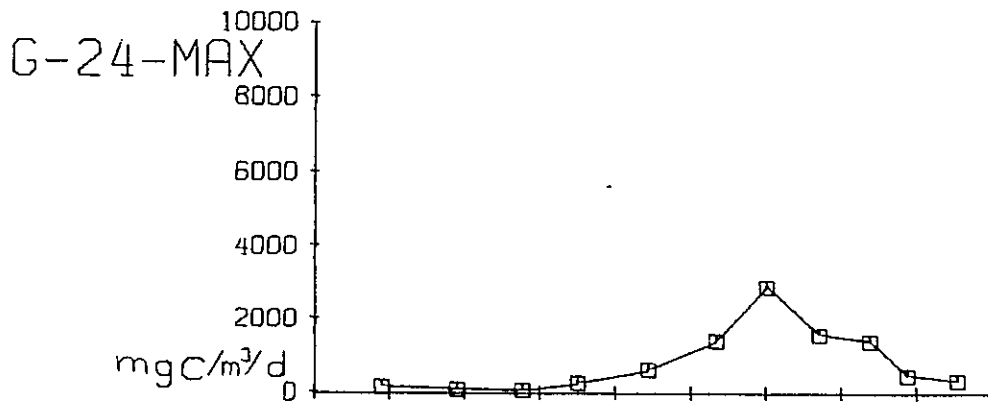
VES 751



VES 751



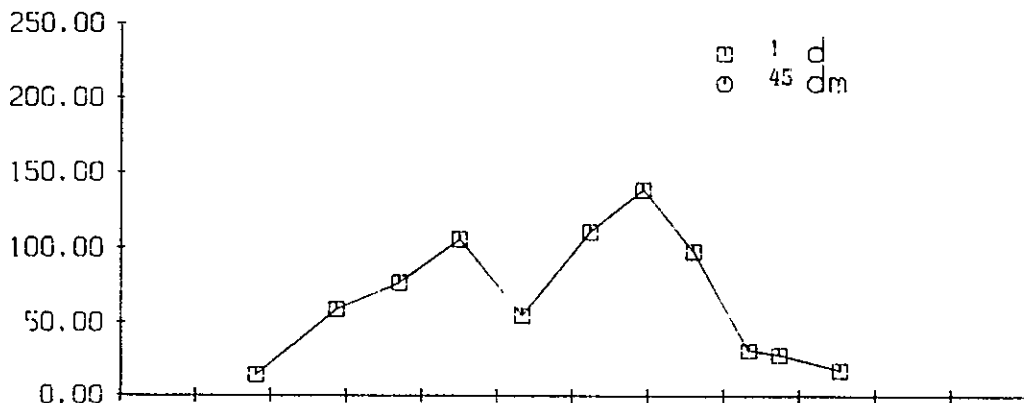
VES 1



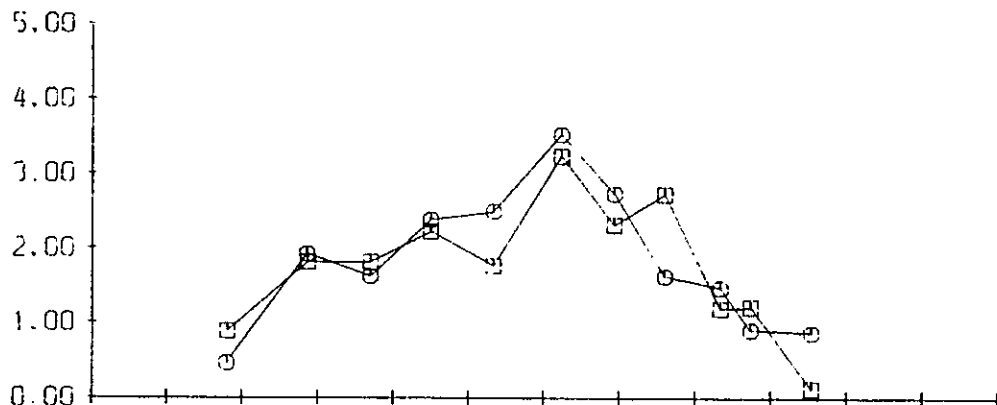
74
ARSPROD. 150 gCm⁻²yr⁻¹

@RS 751

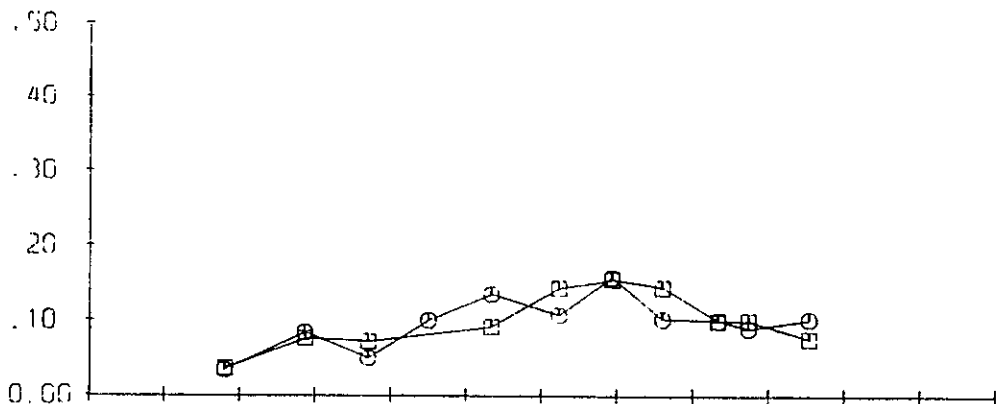
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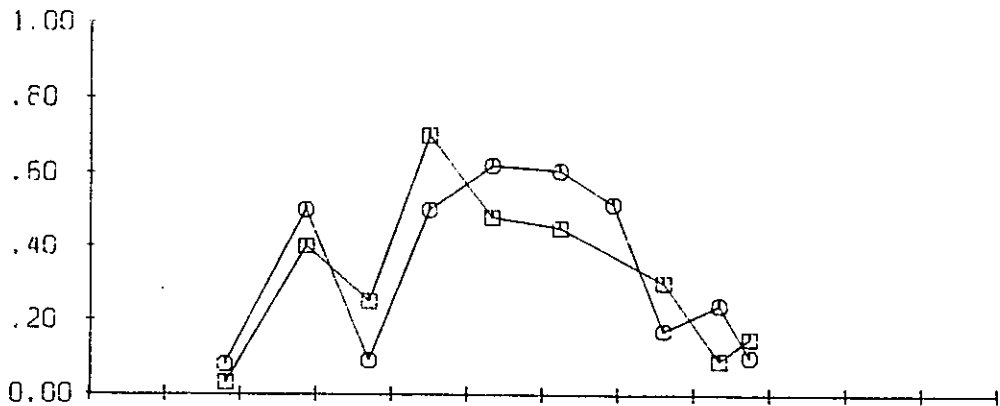
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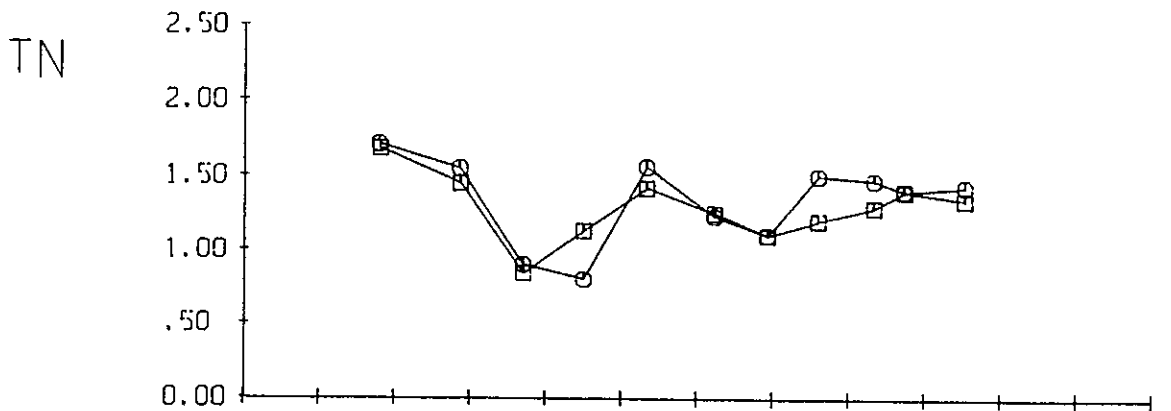
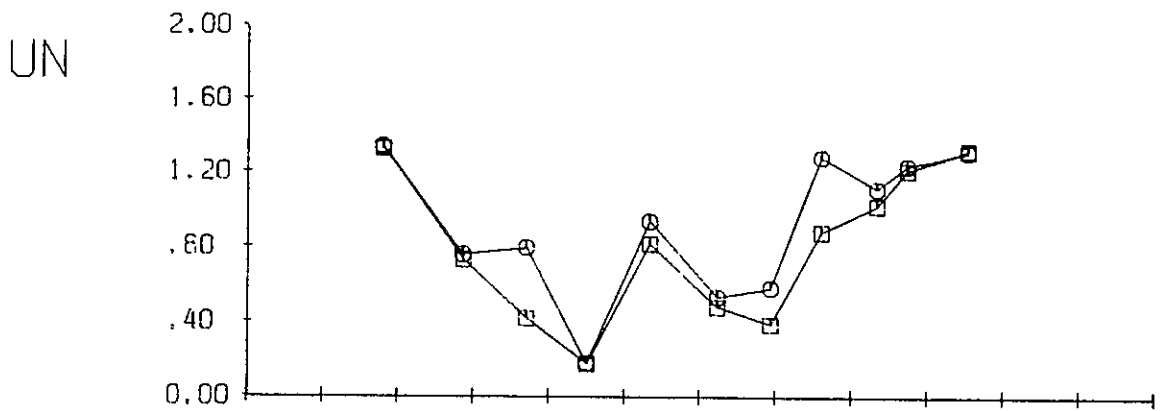
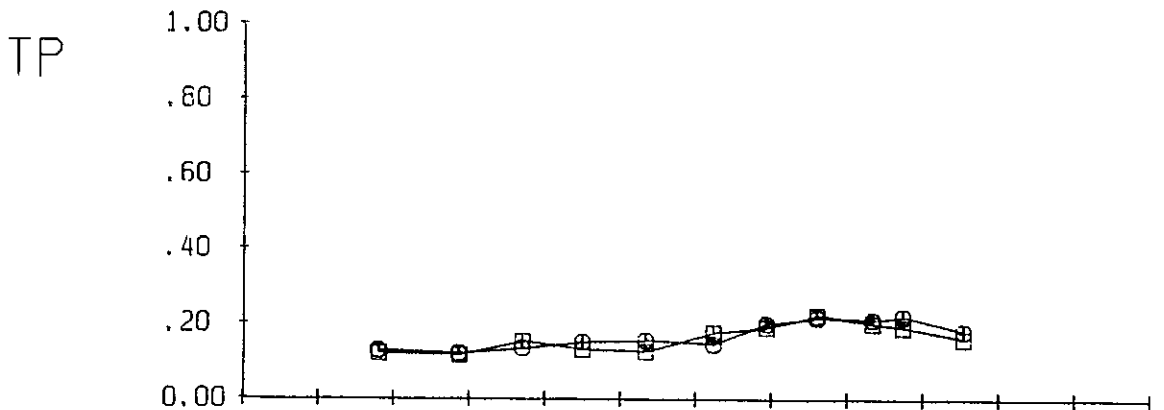
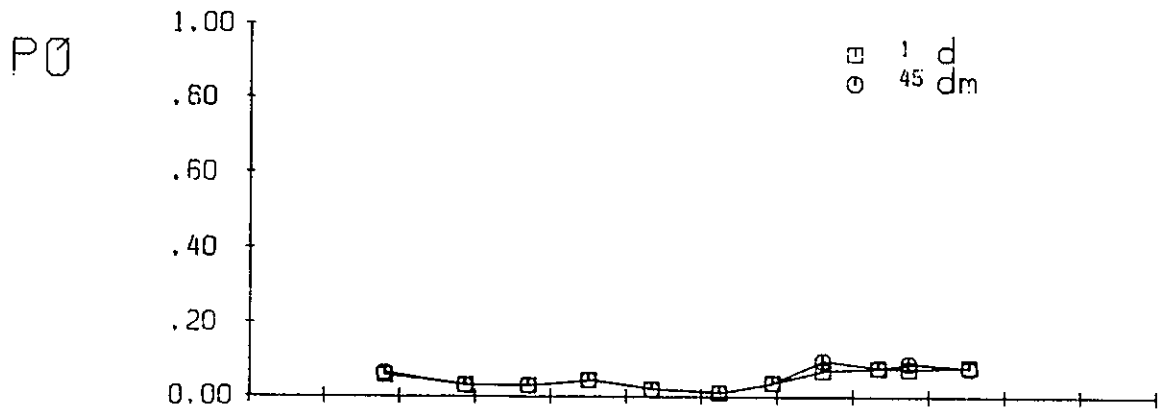
PARP



PARN

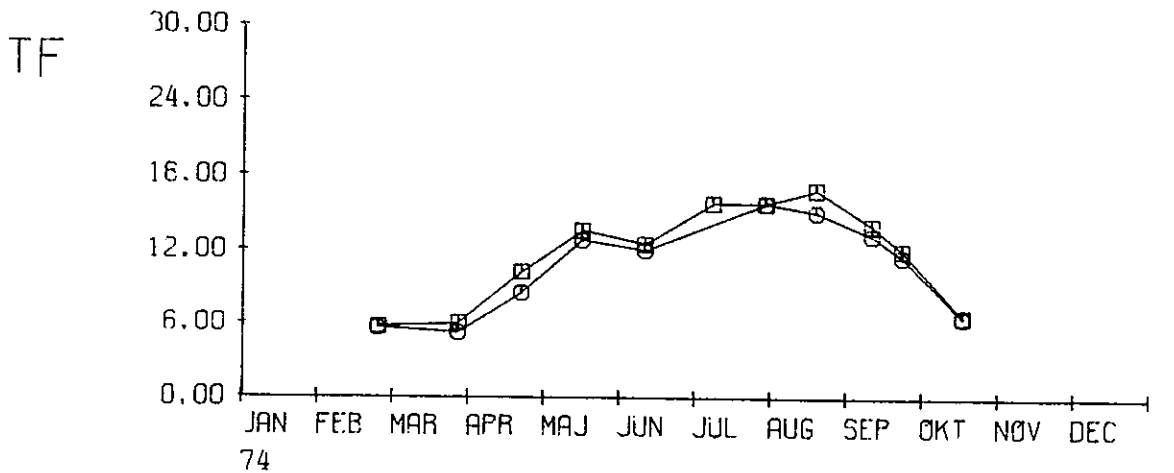
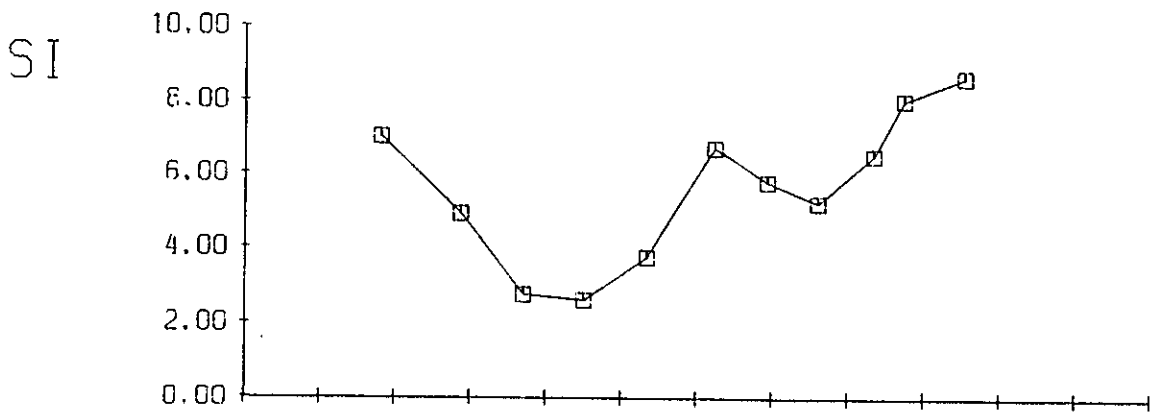
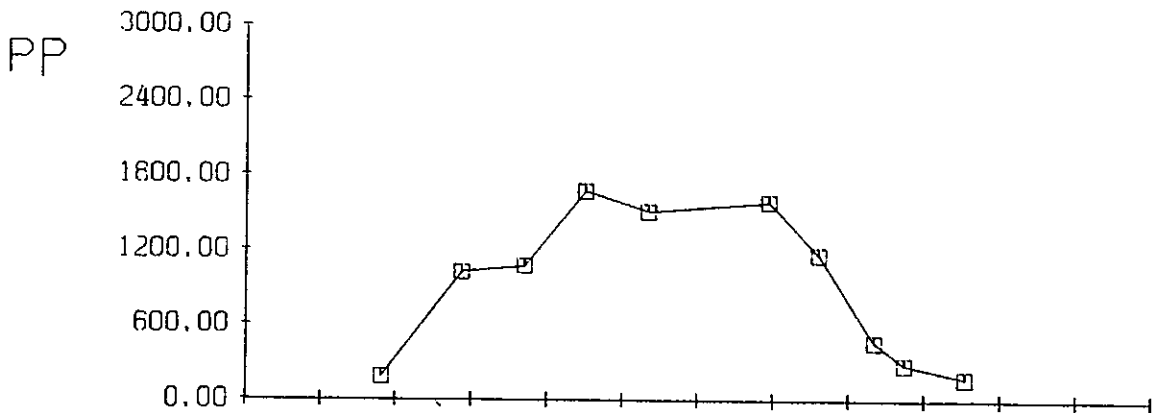
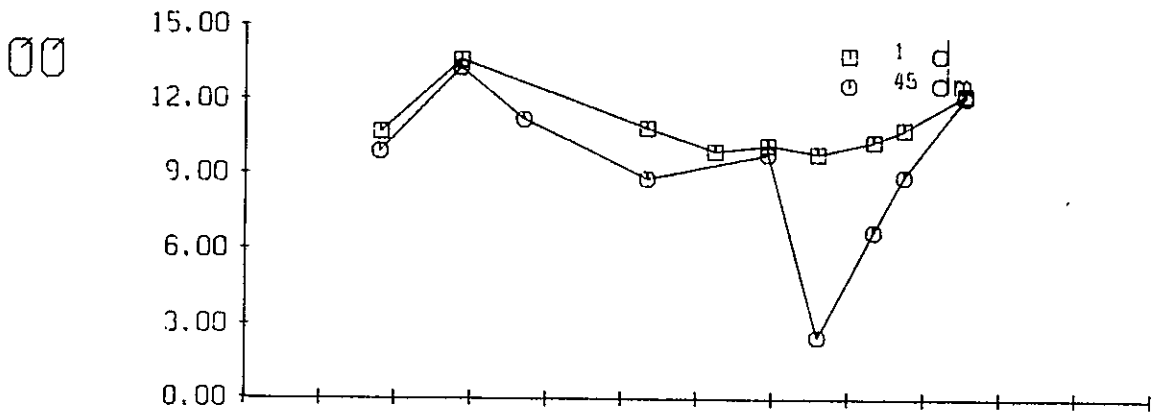


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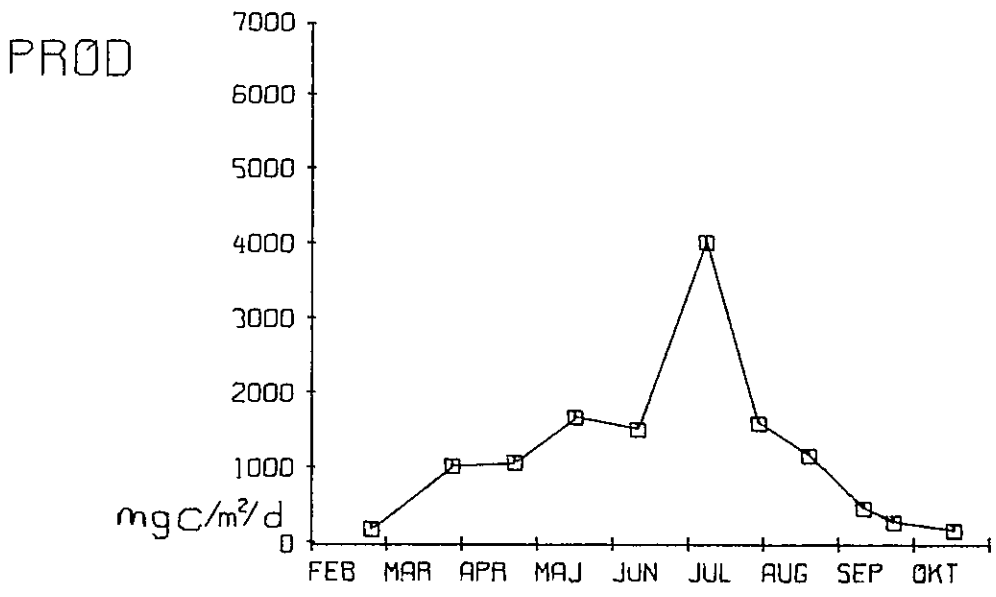
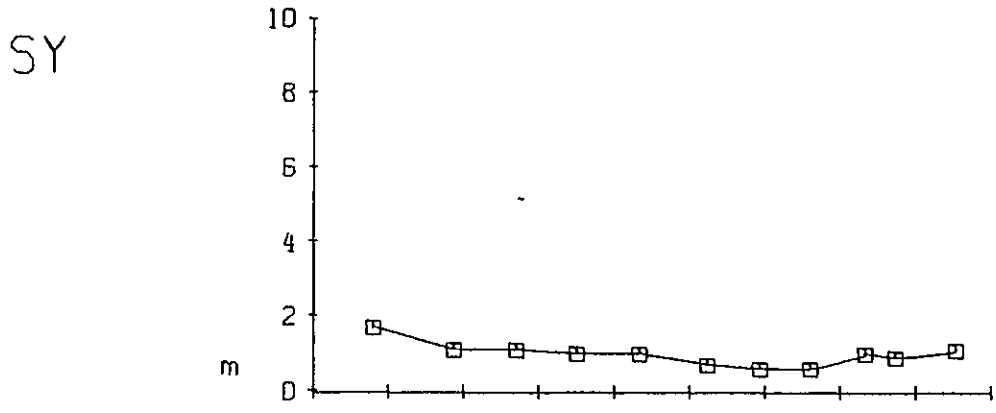
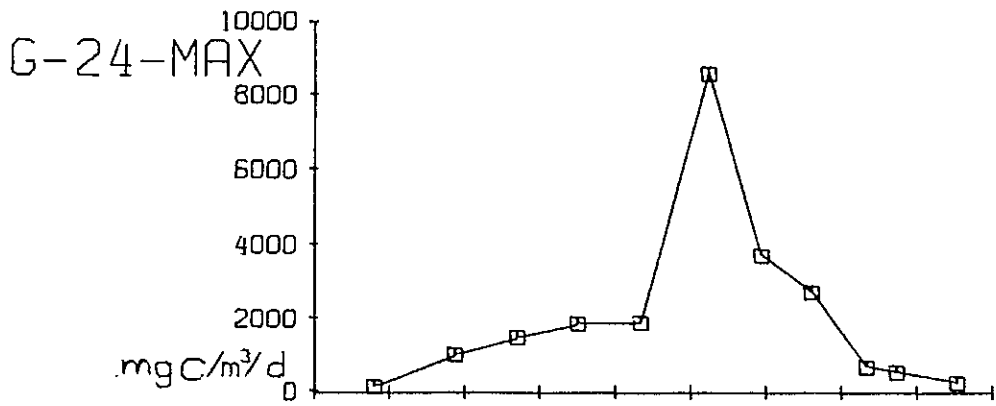


JAN FEB MAR APR MAJ JUN JUL AUG SEP OKT NOV DEC

@RS 751



@RN 1



74
ÅRSPROD. 310 gCm⁻²år⁻¹

B I L A G 2

MALING AF KVÆLSTOFFIXERINGEN.

MÅLING AF KVÆLSTOFFIXERINGEN.

I undersøgelsen indgår måling af blågrønalgenes kvælstoffixering. Målingerne påbegyndes mindre end 1½ time efter prøvernes udtagning. Ved målingen anvendes acetylen-reduktionsmetoden, /2 /. Princippet heri er følgende. Visse blågrønalger kan reducere frit kvælstof (N_2) til en kvælstofforbindelse (NH_3), som algerne kan udnytte.

Alger, der har denne egenskab, kan også reducere acetylen til ethylen. Denne omdannelse kan kvantificeres på en gaschromatograf. Både lys og temperatur er regulerende faktorer for kvælstoffixeringen.

FREMANGSMÅDEN VED MÅLINGERNE VAR FØLGENDE:

Ved inkuberingen blev vandprøverne overført til klare 30 ml McCartney-flasker.

Der blev udført 3 dobbeltbestemmelser samt 1 blindprøve for hver vandprøve.

I hver flaske blev der afpipetteret 15,0 ml prøve.

Flaskerne blev lukket (lufttæt) med et skruelåg, hvori der var indsat en gummimembran.

2,0 ml acetylen blev tilsat hver flaske med en sprøjte påsat en kanyle.

Flaskerne blev inkuberet i 1 time under konstante lys- og temperaturforhold.

Nogle af flaskerne blev (lystæt) indpakket.

Efter inkuberingen blev processerne afbrudt ved tilsætning af 400 µl mættet ammoniumsulfatopløsning.

Dernæst blev flaskernes indhold af ethylen målt på gaschromatograf med flammeionisationsdetektor.

Denne dannede mængde ethylen kan direkte omregnes til fixeret kvælstof.

DETEKTIONSGRÆNSE:

Detektionsgrænsen ved den gaschromatografiske analyse er $0,3 \cdot 10^{-10}$ mol pr. 1000 µl luftfase, svarende til 3,4 mg N m⁻³ døgn⁻¹.

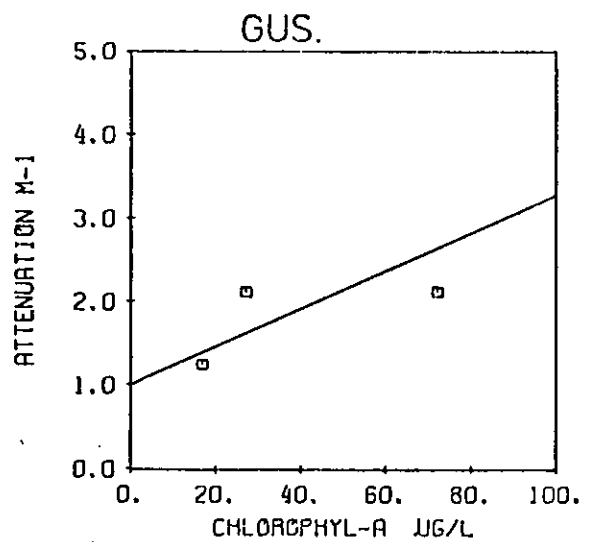
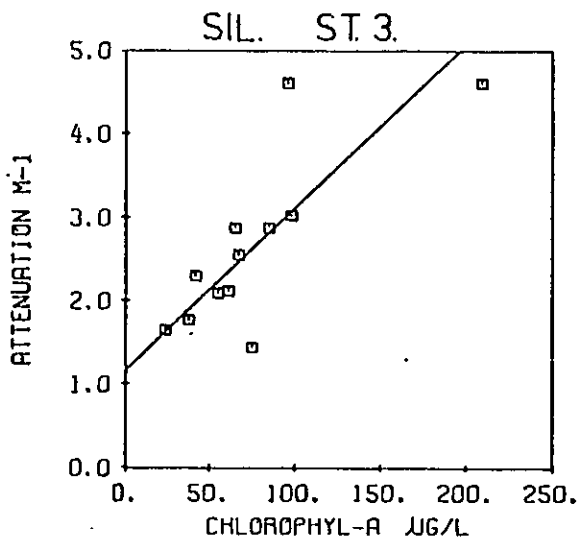
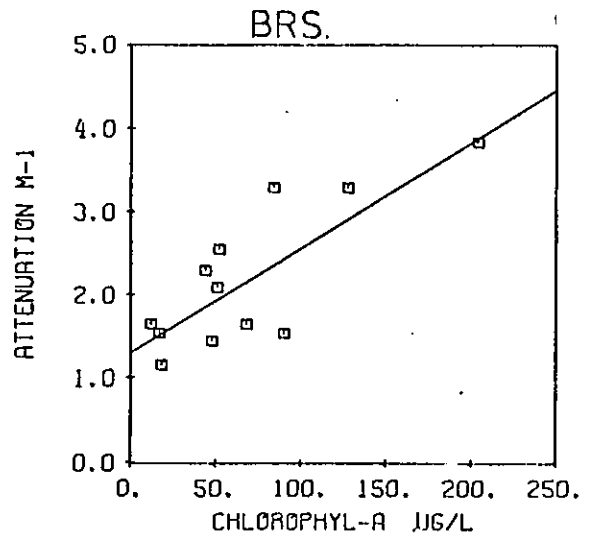
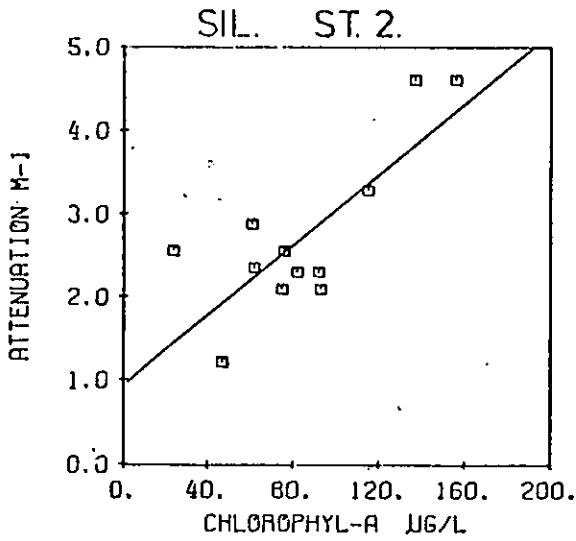
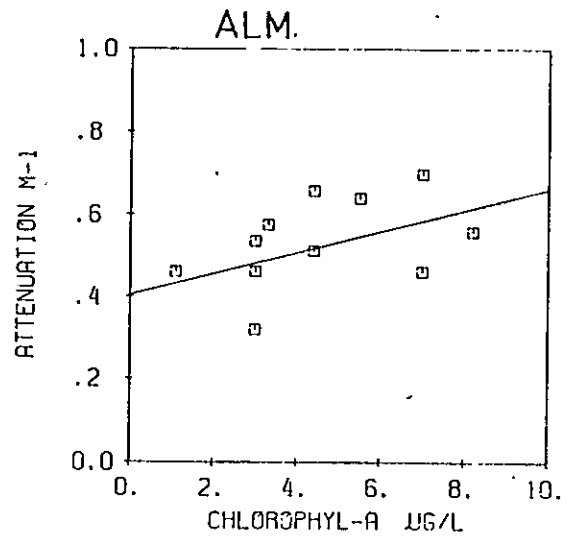
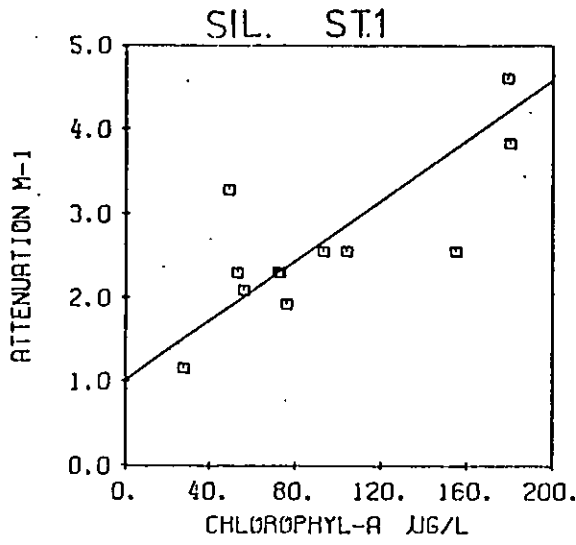
B I L A G 3

SAMMENHÆNG MELLEM LYSFORHOLD
(EXTINKTIONSKØEFFICIENTEN) OG
KLOOROFYLINDHOLDET I DE UNDER-
SØGTE SØER.

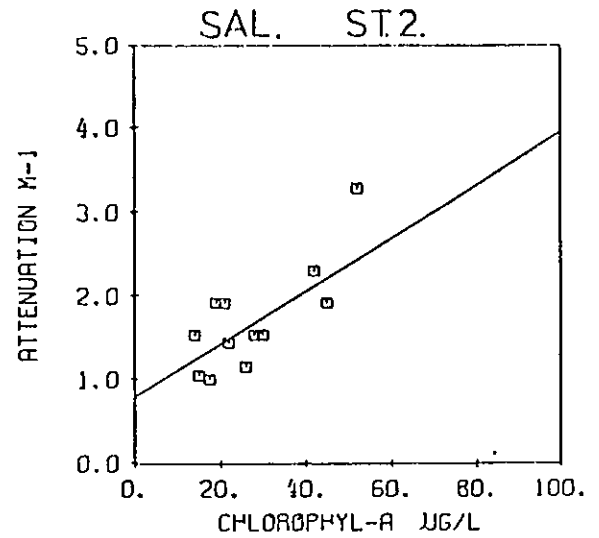
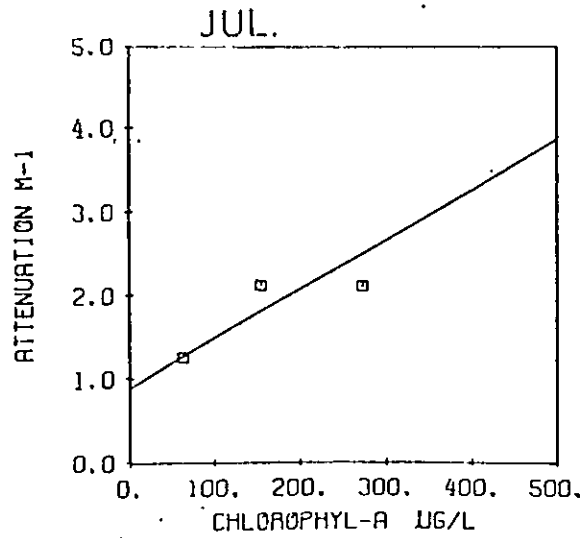
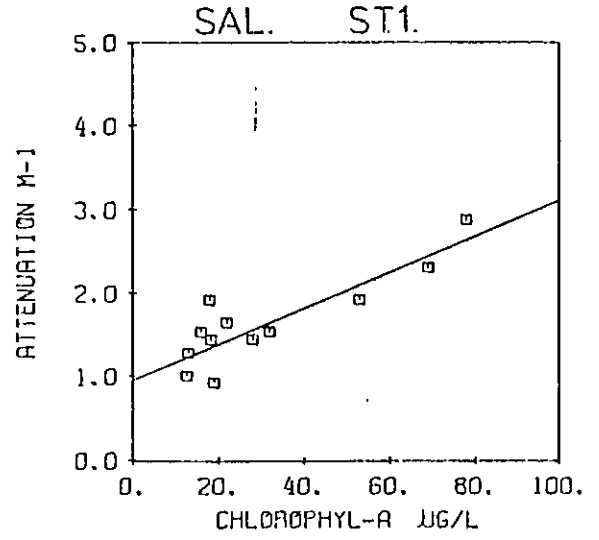
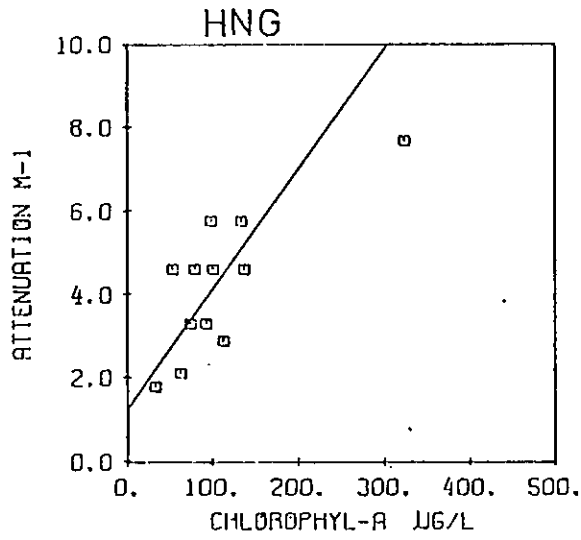
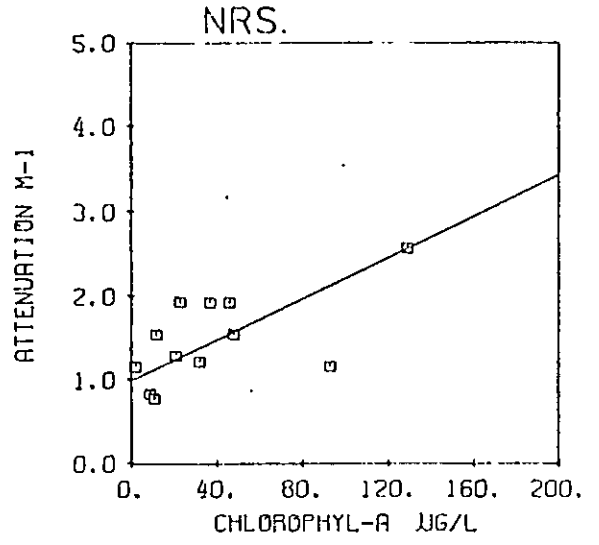
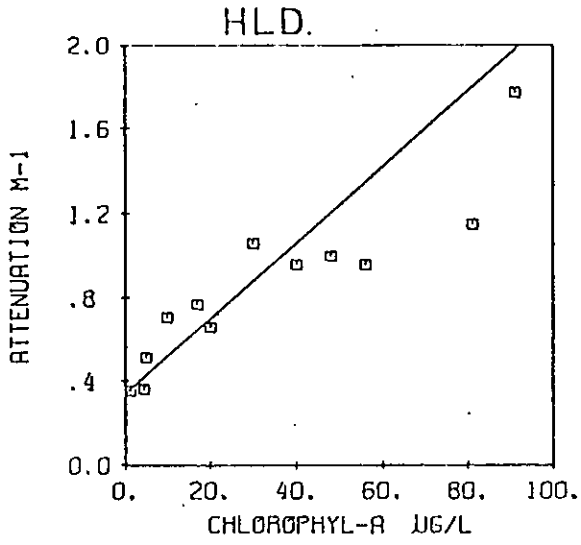
SØNAVN, FORPØRTET	AFSKÆRING a (m^{-1})	HÆLDNING b ($m^{-1} \cdot mg^{-1} \cdot l$)	ANTAL MÅLEPUNKTER
ALM	0,404 ± 0,065	2,6 ± 17	11
BRS	1,30 ± 0,15	12,7 ± 4,9	12
GUS	1,02 ± 0,64	23 ± 26	3
HLD	0,343 ± 0,022	18,0 ± 3,4	12
HNG	1,24 ± 0,65	28,9 ± 8,9	12
JUL	0,89 ± 0,28	6,0 ± 2,8	3
NRS	0,99 ± 0,12	12,2 ± 8,2	12
SIL st. 1	1,02 ± 0,37	17,8 ± 6,0	12
SIL st. 2 *	0,94 ± 0,50	21,1 ± 5,3	12
SIL st. 3	1,17 ± 0,26	19,5 ± 5,0	12
SAL st. 1	0,96 ± 0,19	21,6 ± 9,2	12
SAL st. 2	0,80 ± 0,30	32 ± 13	12
SAL st. 3	1,10 ± 0,57	13 ± 26	4
SLA	0,36 ± 0,47	36 ± 19	12
SRS	1,86 ± 0,25	10 ± 8	12
TAN st. 1	1,14 ± 0,07	11,2 ± 2,9	12
TAN st. 2	1,77 ± 0,58	8,2 ± 9,5	12
THO	0,77 ± 0,16	20 ± 12	12
VED	1,14 ± 0,21	18,7 ± 6,3	12
VES	1,15 ± 0,23	14,2 ± 10,7	10
ØRS	0,92 ± 0,14	18,0 ± 4,4	12

* simpel, uvægtet regression

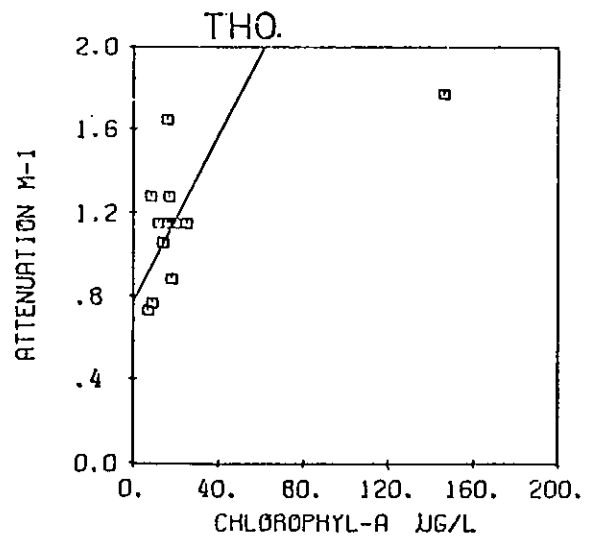
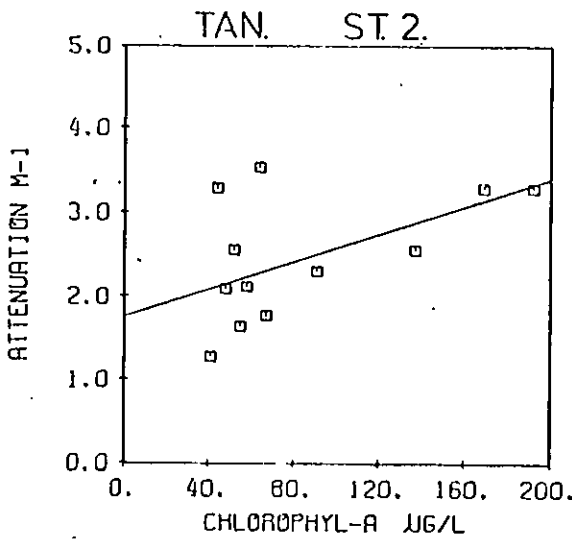
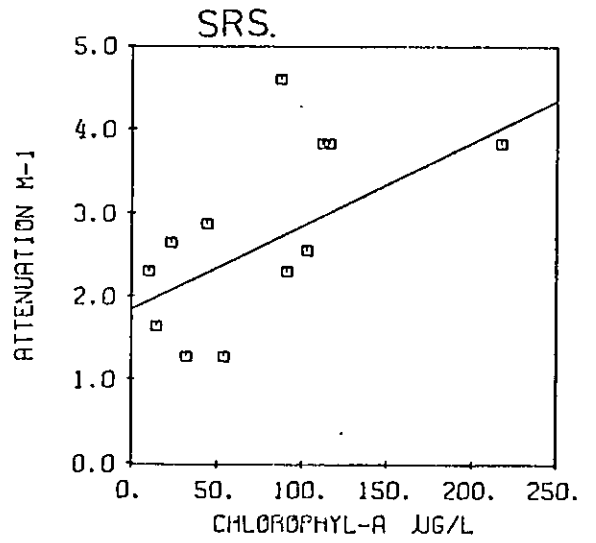
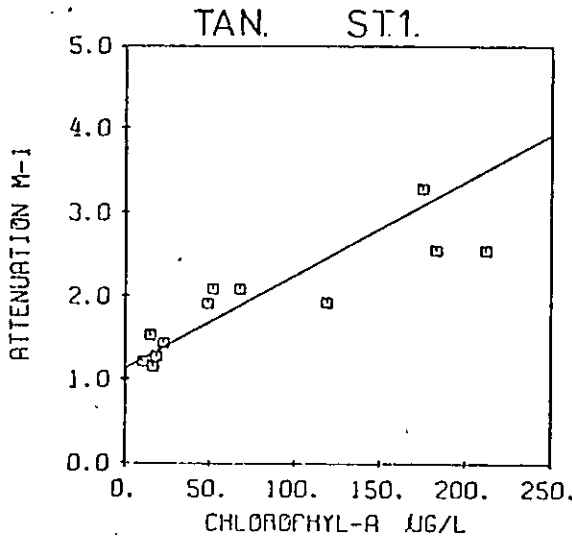
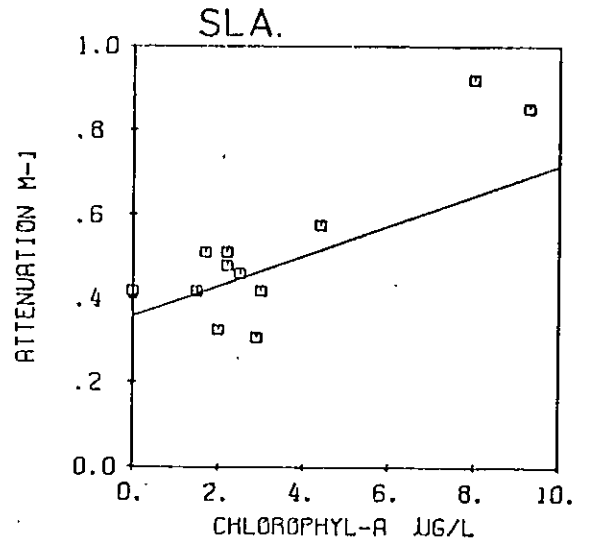
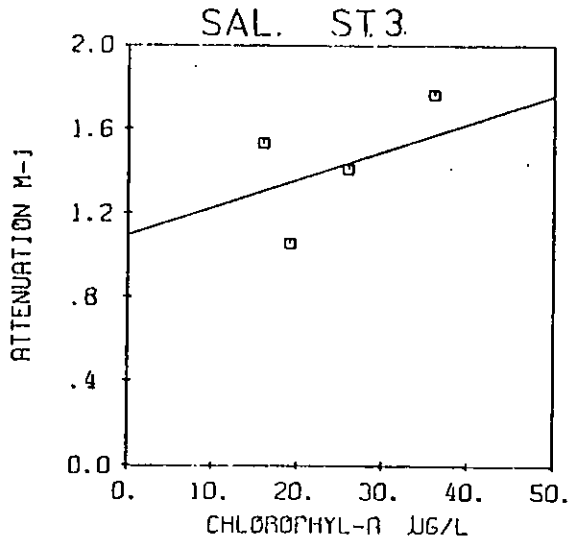
Tabel B 3.1 Vægtet regressionsanalyse af ekstinktionskoefficient mod klorofylkoncentration.



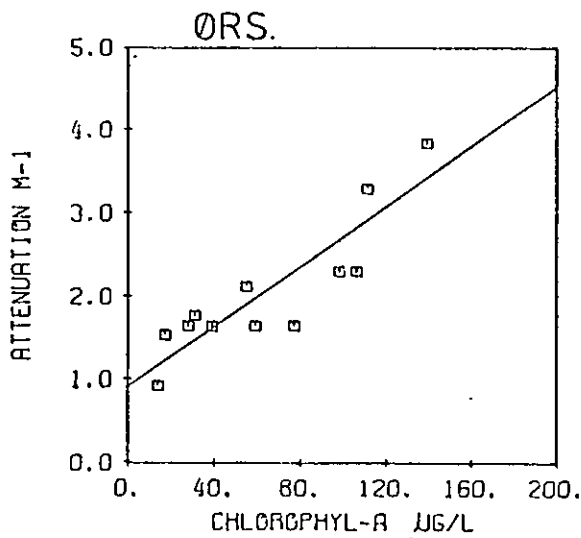
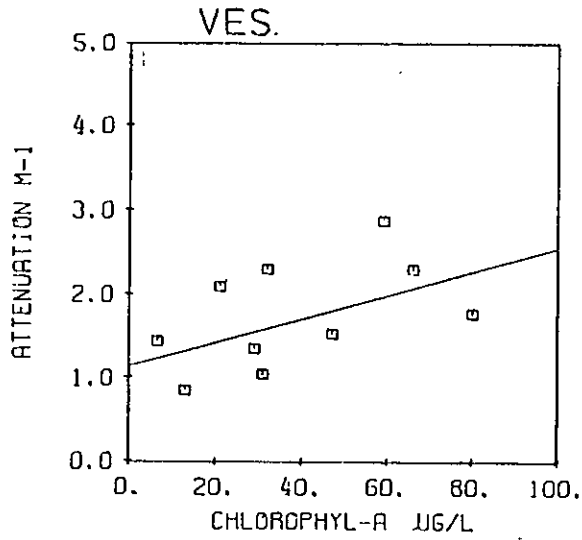
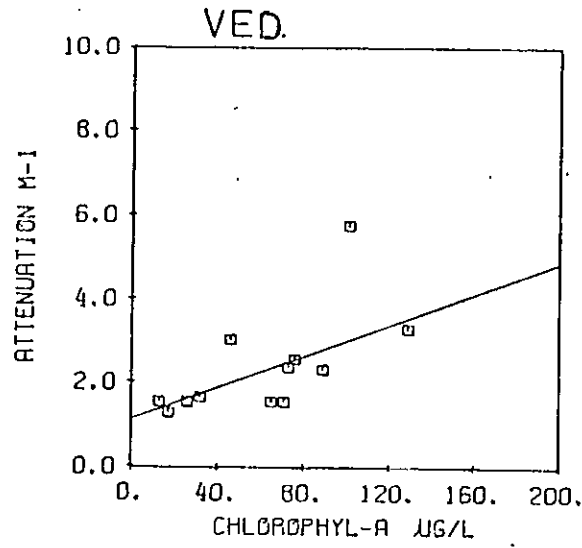
Figur B 3.1 Ekstinktionskoefficient vs. klorofyl-a koncentration.



Figur B 3.1 forts.: Ekstinktionskoefficient vs. klorofyl-a koncentration.



Figur B 3.1 forts.: Ekstinktionskoefficient vs. klorofyl-a koncentration.



Figur B 3.1 forts.: Ekstinktionskoefficient vs. klorofyl-a koncentration.

B I L A G 4

INDLÆG VED S.I.L. KONFERENCE

1977.

THE RELATIONSHIP BETWEEN PHYTOPLANKTON PHOTOSYNTHESIS AND LIGHT, TEMPERATURE AND NUTRIENTS IN SHALLOW LAKES,

EBBE LASTEIN and EIVIND GARGAS

With 8 figures and 5 tables in the text.

ABSTRACT

During the period February to November 1974 estimations of 198 light-saturation curves were carried out on samples from 18 lakes in Jutland comprising lakes of different morphometric types and state of eutrophication. The measurements were carried out in an incubator. Changes in the concentrations of chlorophyll-a, total nitrogen, total phosphorus, temperature and irradiance were measured too. P^B (photosynthesis per unit of chl.a at low light levels, i.e. $3 \cdot 10^{-2} \text{ cal} \cdot \text{cm}^{-2} \cdot \text{min}^{-1}$) showed only slight variations during the sampling period. Average for the 18 lakes P^B ranged from 0.9 to $1.4 \text{ mgC} \cdot (\text{mg chl.a})^{-1} \cdot 2 \text{ hrs}^{-1}$. P_m^B (light saturated photosynthesis per unit of chl.a) showed pronounced variation during the sampling period. Average for the 18 lakes P_m^B ranged from 2.7 to $5.2 \text{ mgC} \cdot (\text{mg chl.a})^{-1} \cdot 2 \text{ hrs}^{-1}$. I_K (irradiance at which the initial and horizontal part of the light-saturation curve intersect) showed pronounced variations during the sampling period. Average for the 18 lakes I_K ranged from 4.0 to $8.2 \cdot 10^{-2} \text{ cal} \cdot \text{cm}^{-2} \cdot \text{min}^{-1}$. Correlation analyses showed that P^B was not significantly correlated to light or temperature. P_m^B and I_K were strongly correlated to temperature but not to light. The highest values of P_m^B and I_K were observed in the most eutrophic lakes, and the lowest values were observed in the most oligotrophic lakes. Analyses of variance indicated that the influence of temperature and light on P_m^B and I_K was stronger than the influence of the trophic state of the lake.

INTRODUCTION

The light-photosynthesis curve plays an important role in all theoretical studies and predictive models for phytoplankton production: RYTHER and YENTSCH (1957), STEELE and BAIRD (1961 and 1962), MARGALEF (1963), STEEMANN NIELSEN and JØRGENSEN (1968 a,b), EPPLEY (1972), FEE (1973), PLATT et al. (1975), PLATT and JASSBY (1976), JASSBY and PLATT (1976), GARGAS et al. (1976), GARGAS and HARE (1976), PLATT et al. (1977) and GARGAS et al. (in press). Most of the theoretical studies and predictive models deal with the 3 parameters: P_m^B (light saturated photosynthesis per unit of chlorophyll-a), α (the slope of the light saturation curve at low light levels, i.e. the linear initial part of the curve estimated as $\text{mgC} \cdot (\text{mg chl.a})^{-1} \cdot \text{h}^{-1} \cdot \text{irradiance}^{-1}$) and $I_K = P_m^B / \alpha$ (irradiance of which the initial and

horizontal part of the light-photosynthesis curve intersect) α and I_K show yearly and diel fluctuations. The state variables, processes, and forcing functions which cause these variations are changes in: irradiance, temperature, nutrients, algal species (i.e. different nutrient requirement, light and temperature dependent growth rate, surface to volume ratio, state of development etc.)

Recently PLATT and JASSBY (1976) have described the variation in P_m^B , R^B (corresponding to dark respiration), and α based on 188 duplicate light-saturation experiments carried out over a period of 2 years in coastal waters. In the present paper we are presenting our examinations on the effect of light, temperature and nutrients on I_K , P_m^B and P^B based on 198 data of each parameter.

Based on an equation given by EPPLY (1972) the specific growth rate of the phytoplankton has been estimated, dependent on temperature and fixed different carbon/chlorophyll-a ratios.

The results used in the present paper make up part of a great investigation of the pollution of the river Guden carried out during 1974-75. This investigation was financed by the counties of Vejle, Viborg, and Arhus, and was carried out by the Water Quality Institute. The counties have kindly made the results available for presentation in this paper.

MATERIAL AND METHODS

Light-saturation measurements were carried out on phytoplankton samples collected from the surface (i.e. 0.2m) of 18 shallow lakes located in Jutland ($9^{\circ} 45'E$, $56^{\circ} 0'N$) during the period February to November 1974. The 18 lakes covered the spectrum from oligotrophic to eutrophic lakes (see Table 1). The photosynthesis measurements were carried out by the ^{14}C -method, STEEMANN NIELSEN (1952) and GARGAS (1975) at various levels of irradiance (fluorescence light 400-700 nm), ranging from 0.9 to $19 \cdot 10^{-2} \text{ cal} \cdot \text{ cm}^{-2} \cdot \text{ min}^{-1}$. The measurements were carried out in an incubator at the same temperatures as those prevailing where the samples were collected. A detailed description of the method is given in GARGAS et al. (1976) and GARGAS and HARE (1976). Analyses of chlorophyll-a have been carried out according to GOLTERMAN (1971). Analyses of phosphorus, nitrogen, pH, alkalinity, and conductivity have been carried out according to STANDARD METHODS (1975). Irradiance has been measured at the climatic station of the Royal Veterinary Agricultural University of Denmark North of Copenhagen ($11^{\circ} 30'E$, $55^{\circ} 45'N$).

RESULTS

The changes in P^B , P_m^B , I_K , I_0 and $\langle I_0 \rangle$ as a mean and standard deviation for all of the 18 lakes during the period February to November 1974 are shown on the figures 1-7.

P^B is the photosynthesis per unit of chlorophyll-a measured at low light levels, i.e. $3 \cdot 10^{-2} \text{ cal} \cdot \text{cm}^{-2} \cdot \text{min}^{-1}$. P_m^B is light-saturated photosynthesis per unit of chlorophyll-a measured at $19 \cdot 10^{-2} \text{ cal} \cdot \text{cm}^{-2} \cdot \text{m}^{-1}$. I_K is the irradiance at which the initial and horizontal part of the light-photosynthesis curve intersect. T is the water temperature at the surface of the lakes, when the samples were collected. I_0 is the irradiance on the days for collection of samples in $\text{cal} \cdot \text{cm}^{-2} \cdot \text{day}^{-1}$, i.e. average over a 4 days period. $\langle I_0 \rangle$ is the irradiance as a mean of 4 days prior or the collection of the samples in $\text{cal} \cdot \text{cm}^{-2} \cdot \text{day}^{-1}$. $\langle I_0 \rangle$ was estimated because of suggestions given by STEEMANN NIELSEN and PARK (1964) that photosynthesis parameters as P_m^B and I_K require some days to respond to changes in I_0 .

Linear regression analyses, based on 11 set of data average for the 18 lakes, give the following equations:

$I_K = 0.008 I_0 + 4.89$	$I_0 = 25.09 I_K + 29.68$
$I_K = 0.006 \langle I_0 \rangle + 5.39$	$\langle I_0 \rangle = 16.96 I_K + 43.58$
$P_m^B = 0.005 I_0 + 3.02$	$I_0 = 40.58 P_m^B + 26.96$
$P_m^B = 0.003 \langle I_0 \rangle + 3.48$	$\langle I_0 \rangle = 21.90 P_m^B + 63.72$
$I_0 = 8.16 T + 89.32$	$T = 0.03 I_0 + 7.25$
$\langle I_0 \rangle = 5.83 T + 80.07$	$T = 0.02 \langle I_0 \rangle + 8.77$
$I_K = 1.39 P_m^B + 0.78$	$P_m^B = 0.58 I_K + 0.33$
$P^B = 8 \cdot 10^{-5} I_0 + 1.117$	$I_0 = -32.3 P^B + 225.50$
$P^B = -3 \cdot 10^{-4} \langle I_0 \rangle + 1.197$	$\langle I_0 \rangle = -91.09 P^B + 255.90$
$P^B = -0.014 T + 1.321$	$T = -16.80 P^B + 31.52$
$P^B = -0.005 I_K + 1.481$	$I = -6.04 P^B + 13.30$

The correlation coefficients of these regression equations are given in Table 2.

DISCUSSION AND CONCLUSION

P^B only shows slight variations during the period of collection of samples. As average for the 18 lakes the highest value obtained was $1.4 \text{ mgC} \cdot (\text{mg chl.a})^{-1} \cdot 2 \text{ hrs}^{-2}$, and the lowest value was $0.9 \text{ mgC} \cdot (\text{mg chl.a})^{-1} \cdot 2 \text{ hrs}^{-2}$. Contrary to P^B P_m^B shows a pronounced variation during the sampling period with the lowest value of $7.7 \text{ mgC} \cdot (\text{mg chl.a})^{-1} \cdot 2 \text{ hrs}^{-1}$ and the highest value of $5.2 \text{ mgC} \cdot (\text{mg chl.a})^{-1} \cdot 2 \text{ hrs}^{-1}$. This is in agreement with other findings, PARSONS and TAKAHASHI (1973), PLATT and RAO (1975), and PLATT and JASSBY (1976).

EPPLEY (1972) states that it is interesting that assimilation numbers greater than about 15 per hour rarely are reported in the literature, and one wonders, whether this is because of a disbelief in the validity of the data or because high μ and high C:chl.a ratios are somehow mutually exclusive in nature. CURLE and SMALL (1965) have advanced the hypothesis that assimilation ratios per hour below 3 are indicative of nutrient deficiency, and values above 5 indicate an adequate nutrient supply.

Fig. 1 shows that there is no seasonal variation of P^B . A seasonal variation exists for both T, I_0 and $\langle I_0 \rangle$. A correlation between P^B and T, and P^B and I_0 therefore is not probable. This is also supported by the correlation coefficients given in Table 2. The independence of I_0 on P^B is in agreement with the theory of basic photochemical reactions, JØRGENSEN and STEEMANN NIELSEN (1965), DUNSTAN (1973) and BANNISTER (1974). PLATT and JASSBY (1976), however, found a marked fluctuation in α (corresponding to our P^B) with I_0 . The lack of correlation between T and P^B is in agreement with the theory of light-processes in the photosynthesis mechanism.

P_m^B shows seasonal variation. However, as shown in Fig. 2, this variation is not in phase with I_0 , and from Table 2 it is seen that the correlation coefficient is not significant. As P_m^B is depending on the activity of the photochemical enzymes in the dark reactions in photosynthesis, one should have expected a positive correlation between these two variables, HALDAL (1970) and ŠESTÁK et al. (1971). It should be mentioned that I_0 , $\langle I_0 \rangle$ have been measured in Copenhagen, whereas the lakes were located in Jutland, i.e. an interval of 300 km. However, also PLATT and JASSBY (1976) found a negative correlation between P_m^B and $\langle I_0 \rangle$.

As it is seen from Fig. 4 the changes in P_m^B follow the changes in temperature. This is in accordance with the theory of fundamental photoenzymatic reactions, JØRGENSEN and STEEMANN NIELSEN (1965), DUNSTAN (1973) and BANNISTER (1974). However, in water bodies, where temperature is believed to be the most limiting factor for algal growth, a much stronger influence of temperature on P_m^B should be expected. EPPLEY (1972) has set up the following equation, which directly relates the assimilation number, the carbon : chlorophyll-a ratio, and the specific growth rate:

$$\mu = \frac{1}{\Delta t} \log_2 \left(\frac{C/\text{chl.a} + \Delta C/\text{chl.a}}{C/\text{chl.a}} \right) \quad (1)$$

In Fig. 9 are shown the changes in estimated μ_{\max} average for the 18 lakes under the assumption of different fixed C:chl.a ratios. μ_{\max} has been estimated by combining equation (1) and the following equation:

$$\mu_{\max}^{(T)} = \mu_{\max}^{(20)} \cdot \theta^{(T-20)} \quad (2)$$

where:

$$\mu_{\max}^{(20)} = 1.5 \text{ day}^{-1}$$

$$\theta = 1.07 \text{ (i.e. } Q_{10} = 2)$$

As it is seen from Fig. 8, μ_{\max} varies between 0.3 (C:chl.a = 120) and 2.7 (C:chl.a = 30). These estimated values of μ_{\max} , however, should only be considered as rough guidelines, as the real values of the C:chl.a ratios of the phytoplankton were not known. In natural water bodies the C:chl.a ratio, P_m^B and I_K change according to changes in species composition and size, temperature, light, and nutrients. A decrease in temperature, light and available nutrients causes a decrease in the C:chl.a ratio, P_m^B and I_K , STEEMANN NIELSEN and HANSEN (1959), ICHIMURA (1960), McALLISTER et al. (1964), STEEMANN NIELSEN and JØRGENSEN (1968 a,b), EPPLEY (1972) and SMETACEK (1975).

I_K shows a seasonal variation ranging from 4.0 to 8.2 $\text{cal} \cdot \text{cm}^{-2} \cdot \text{min}^{-1}$ (400-700 nm). I_K is a derived parameter of the basic photochemical reactions. Therefore, a positive correlation between I_K and irradiance should be expected, STEEMANN NIELSEN and HANSEN (1961) and GARGAS (1971). Fig. 5 and Table 2 show that this is not the case. Also the correlation between I_K and P_B is poor. Fig. 6 and Table 2 show a high correlation between P_m^B and I_K . It therefore can be concluded that I_K has been much more influenced by the changes in the level of P_m^B (and through this the temperature dependent rates of the photoenzymes) than it has been influenced by α (i.e. the light dependent initial parts of the light-photosynthesis curve).

Table 3 and 4 show the frequency with which each lake is represented by a certain sequence number in the range of the lakes with respect to increasing values of I_K and P_m^B , respectively, during each of the 11 sampling periods.

When comparing Table 3 and 4 with Table I it is seen that the highest P_m^B and I_K values are found in the most eutrophic lakes, and the lowest P_m^B and I_K are found in the most oligotrophic lakes. This is in accordance with other observations. MALONE (1971 a,b) also found higher values of P_m^B in eutrophic waters which were in an order of magnitude greater than those found in oligotrophic surface waters of the subtropical and tropical Pacific. A possible explanation for these observations is that phytoplankton in oligotrophic waters often are of a smaller size than the phytoplankton in eutrophic waters, and that the halfsaturation constant (k_S) for uptake of nutrients in large cells is higher than the k_S uptake constant for nanoplankton, EPPLEY et al. (1969), TILMAN, and KILHAM (1976) and NYHOLM (1977).

In order to test the influence of the seasons, i.e. changes in T and I_0 during the 11 weeks on the 3 parameters P^B , P_m^B and I_K average for the 18 lakes, the following null hypothesis was stated: The variance between the 11 weeks of the photosynthetic parameters P^B , P_m^B and I_K is indistinguishable from the error variance. This gave the following value of $F_{18,11}$, $P^B = 1.8$, $P_m^B = 6.0$ and $I_K = 11.0$. This means that concerning P_m^B and I_K the hypothesis was rejected at the 99% confidence level and may be considered to belong to 11 different groups.

In order to test the influence of degree of trophy, i.e. the 18 different lakes on the parameters P^B , P_m^B and I_K the following null hypothesis was stated: The variance between the 18 lakes of the photosynthetic parameters P^B , P_m^B and I_K is indistinguishable from the error variance. This gave the following value of $F_{18,11}$, $P^B = 2.0$, $P_m^B = 5.0$ and $I_K = 2.5$. This means that only for P_m^B the hypothesis was rejected at the 99% confidence level. Concerning variations in P^B and I_K , the 18 lakes therefore may be considered to belong to the same body of water, i.e. the influence of the changes in I_0 and T on P^B and I_K is stronger than the influence of different degree of trophy. (An explanation for this and a reason for using grouped data could be that the data presumably are influenced by different unpredictable sources of errors).

In order to investigate the correlations between the photosynthetic parameters and environmental statevariables and forcing functions on ungrouped data a simple correlation analysis was carried out, i.e. each coefficient has been based on 196 degrees of freedom. The result of this analysis is shown in Table 5. From this table it is seen that P_m^B and I_K are strongly correlated to the temperature, and that P_m^B and I_K are intercorrelated. This is in agreement with the results of the correlation analysis on the grouped data shown in Table 2.

Contrary to the analysis on the grouped data P^B for all data pooled shows a strong correlation to P_m^B . Again it is seen that the influence of light on the photosynthetic parameters apparently is of minor importance compared to the influence of temperature. Also total nitrogen (TN) and total phosphorus (TP) are correlated to the photosynthetic parameters. However the importance of these environmental parameters is somewhat difficult to interpret, because of their apparently random influence on the different photosynthetic parameters.

In order to test the relative influence of the changes in the forcing functions T and $\langle I_0 \rangle$ and the environmental variables TN and TP on the photosynthetic parameters P^B , P_m^B and I_K the following null hypothesis was stated: For a given parameter the variation in time does not exceed the variation in space, i.e. between the different lakes. This hypothesis was only rejected for I_K , $\langle I_0 \rangle$ and T . Concerning P^B and P_m^B the variance in these parameters in time could not significantly be distinguished from the variance in space.

As it is seen from the results presented in the present paper the variation in P^B , P_m^B and I_K is correlated to irradiance, temperature and nutrients in a very complicated way. Therefore, predictions of daily phytoplankton production based alone on measurements of the state variables chlorophyll-a and nutrients and the forcing functions light and temperature will only give a rough estimate of the real values. Improvement in the predictability of light saturation models do require more intensive investigations on the effect of light, temperature, and nutrients on the growth rate of phytoplankton of different size and species.

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- Figure 1 Seasonal variation of P^B and irradiance average for 18 lakes in Jutland.
- Figure 2 Seasonal variation of P_m^B and irradiance average for 18 lakes in Jutland
- Figure 3 Seasonal variation of P^B and temperature average for 18 lakes in Jutland.
- Figure 4 Seasonal variation of P_m^B and temperature average for 18 lakes in Jutland.
- Figure 5 Seasonal variation of I_K and irradiance average for 18 lakes in Jutland.
- Figure 6 Seasonal variation of P_m^B and I_K average for 18 lakes in Jutland.
- Figure 7 Seasonal variation of I_K and irradiance as a mean of 4 days prior to the collection of the samples.
- Figure 8 The variation in maximum specific growth rate with temperature based on different carbon:chl.a ratios. The estimations are based on equations given by EPPLEY, 1972.

- Table 1 Morphometric and environmental data for each of the 18 lakes investigated.
- Table 2 Matrix of sample coefficients for the forcing functions T , I_0 and $\langle I_0 \rangle$, the measured photosynthesis parameters P^B and P_m^B , and the derived parameter I_K . The correlation coefficients are based on 11 set of data, where each set is a mean of 18 data.
- Table 3 Frequency with which each lake is represented by a certain sequence number in the range of lakes with respect to increasing values of P_m^B during each of the sampling periods.
- Table 4 Frequency with which each lake is represented by a certain sequence number in the range of lakes with respect to increasing values of I_K during each of the sampling periods.
- Table 5 Matrix of simple correlation coefficients for the forcing functions T and $\langle I_0 \rangle$, total nitrogen (TN), total phosphorus (TP), the measured photosynthesis parameters P^B and P_m^B , and the derived parameter I_K with all data pooled. Each coefficient is based on 196 degrees of freedom.

Figure 1

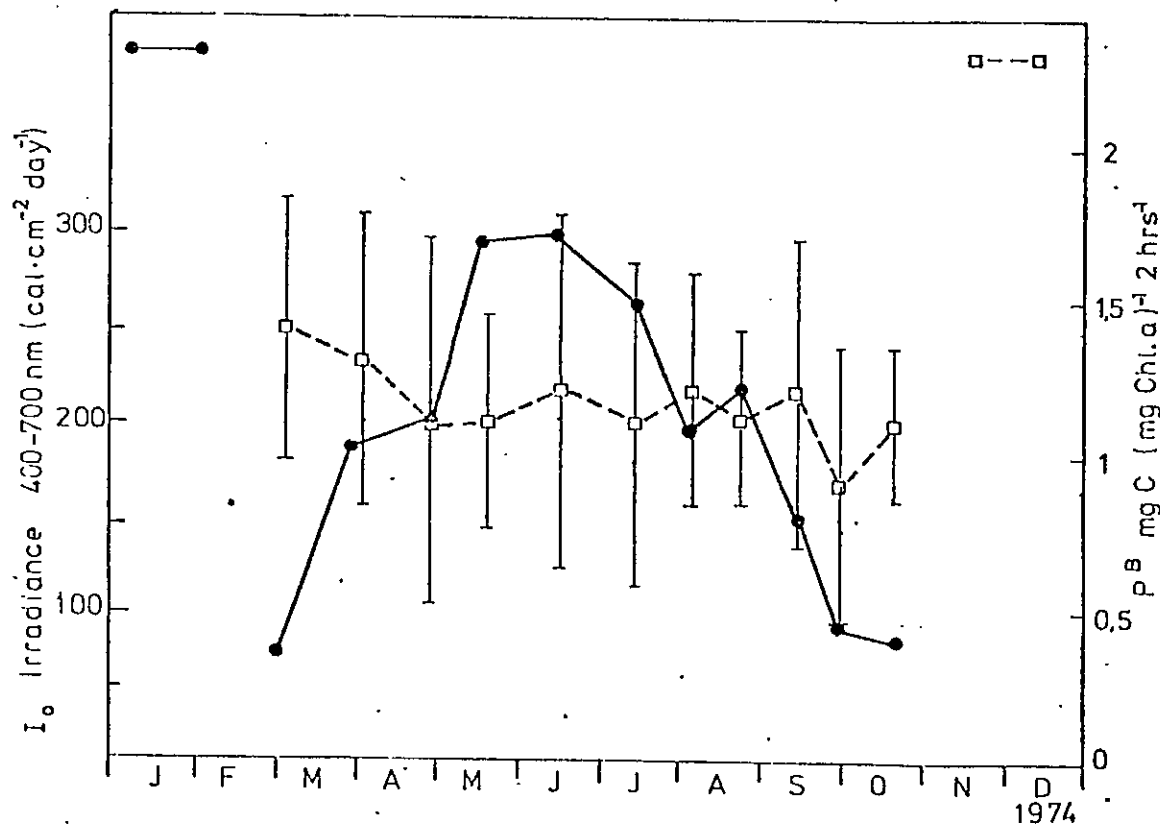


Figure 2

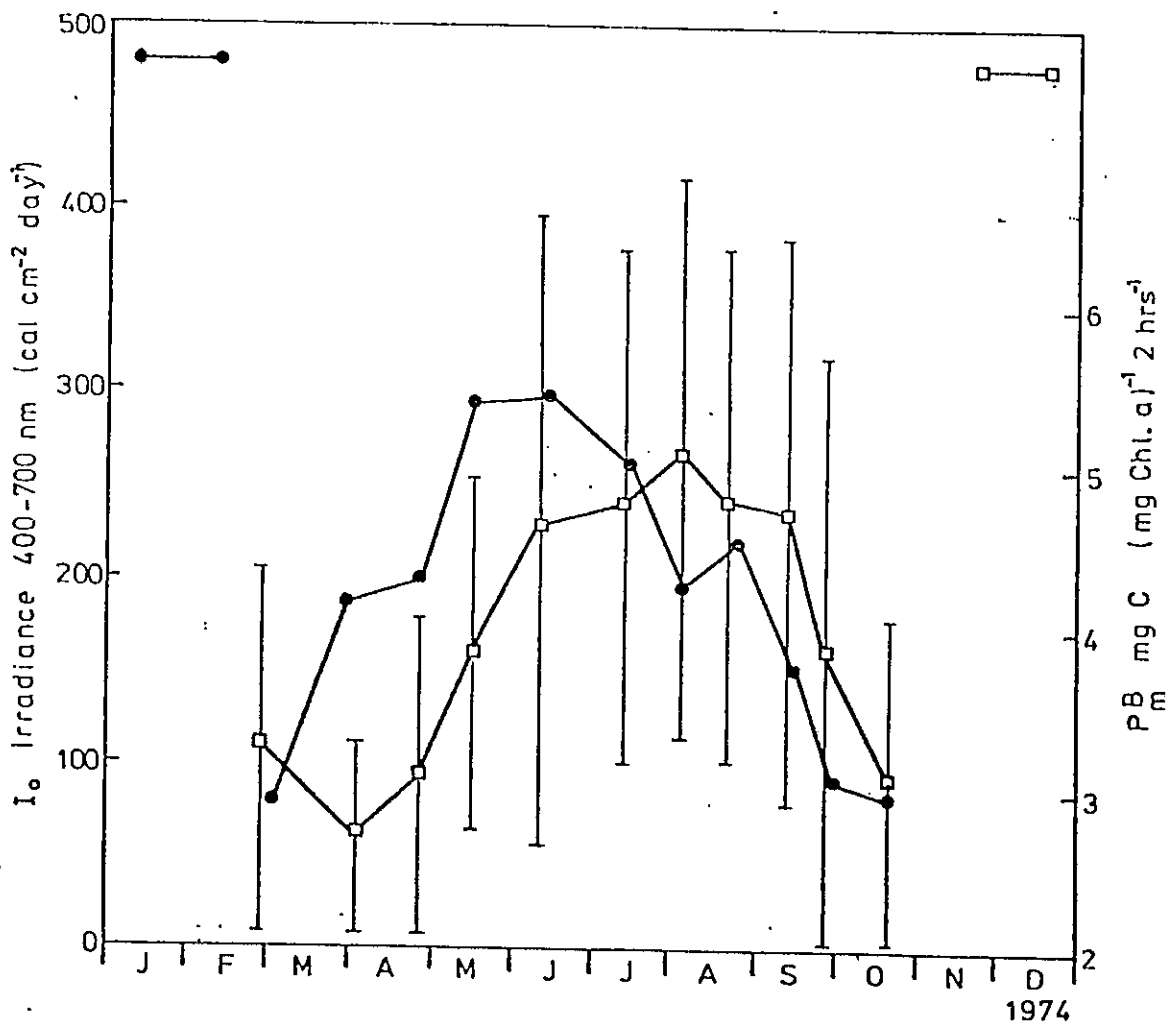


Figure 3

- B 100 -

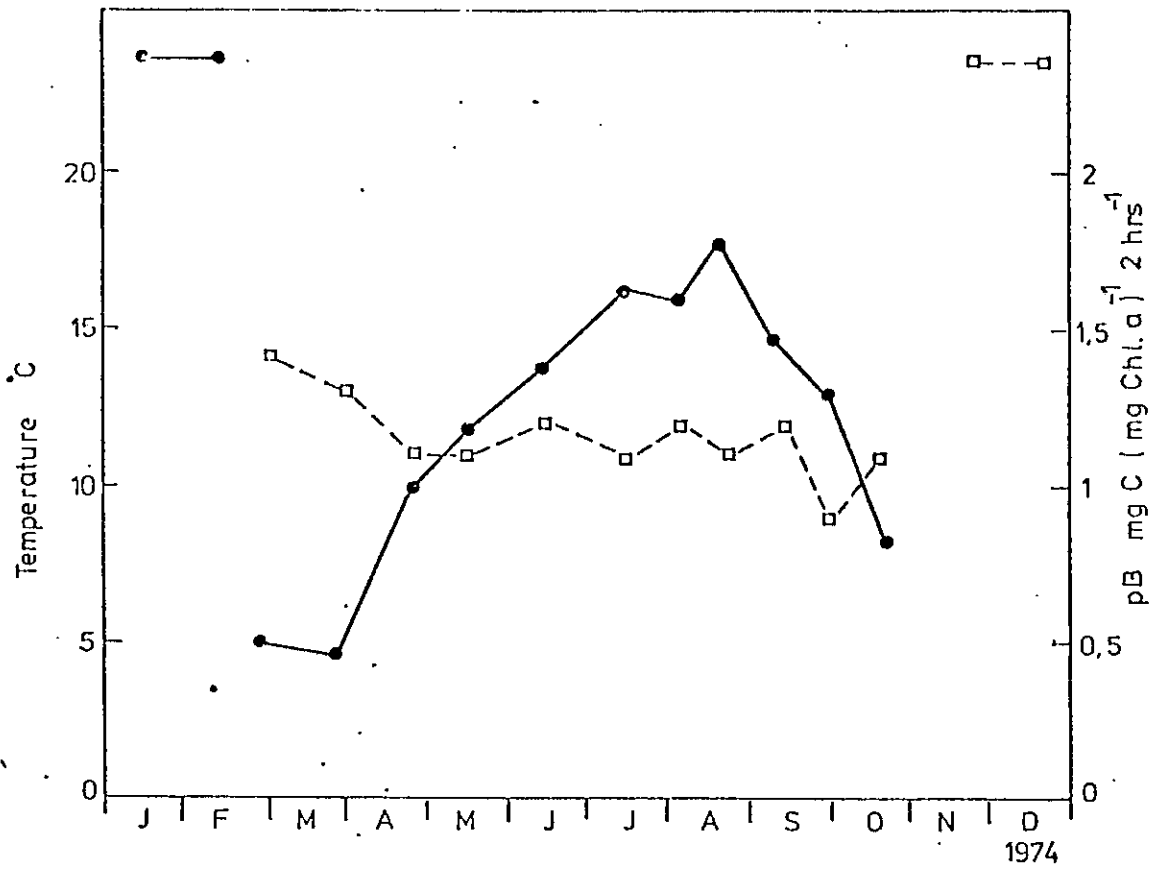


Figure 4

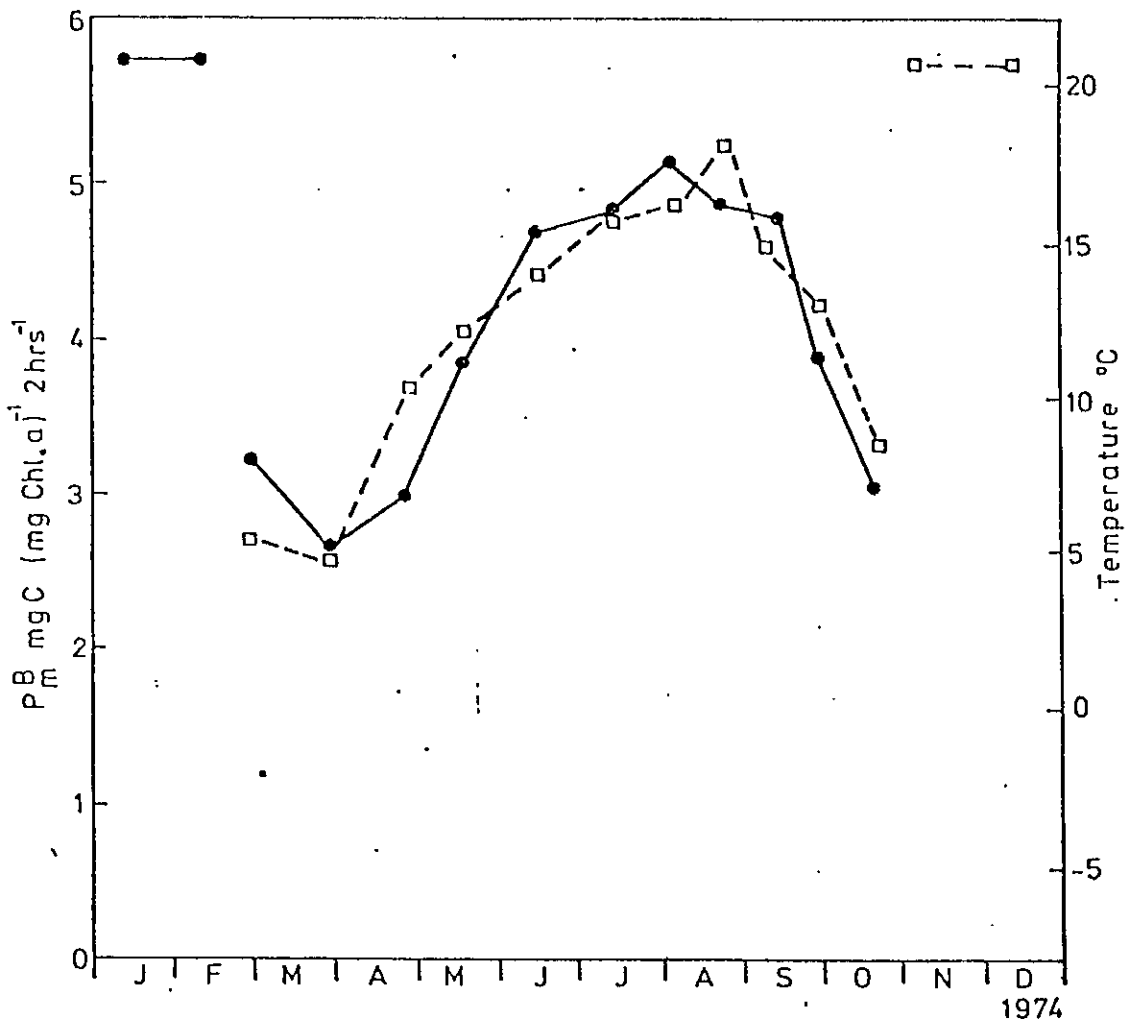


Figure 5

- B 101 -

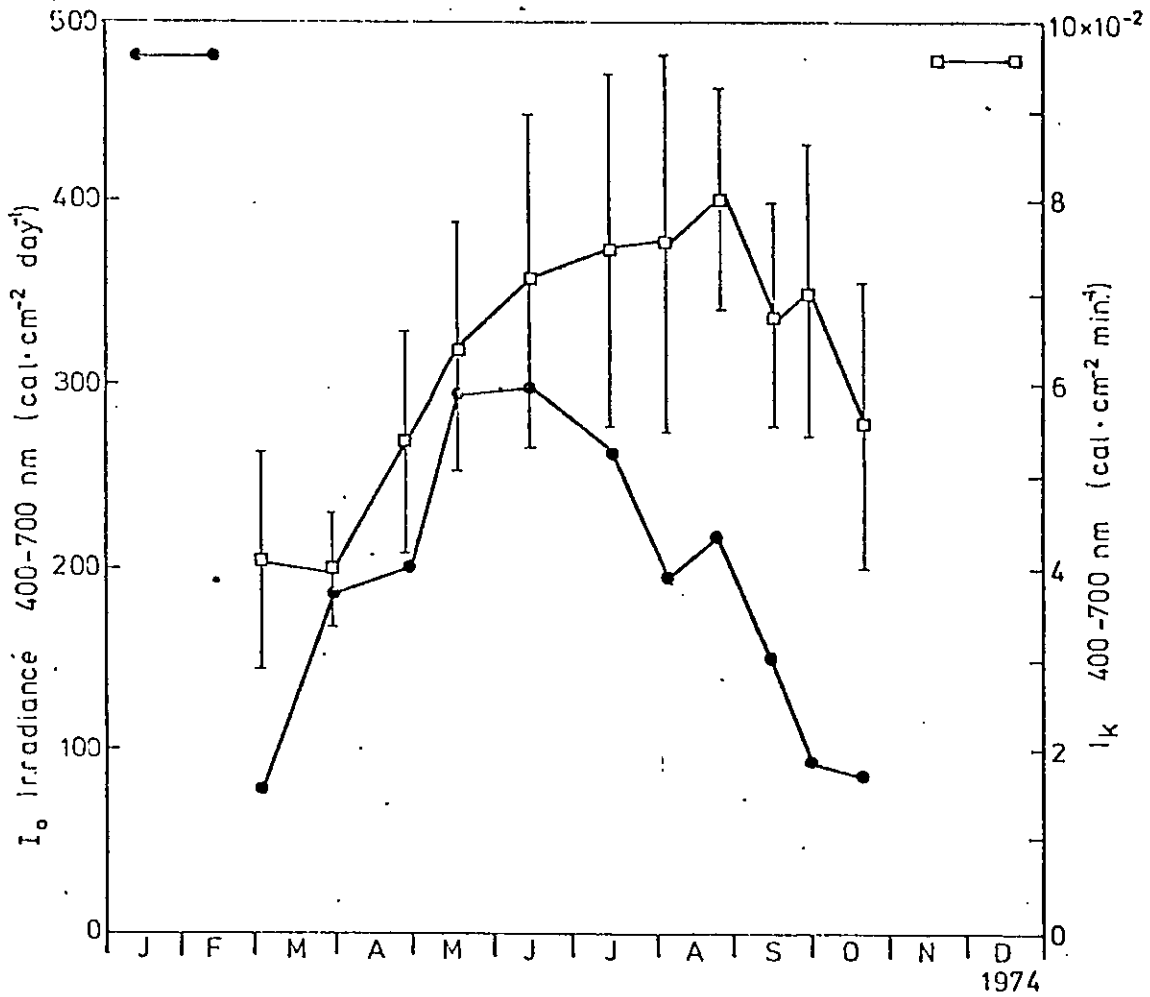


Figure 6

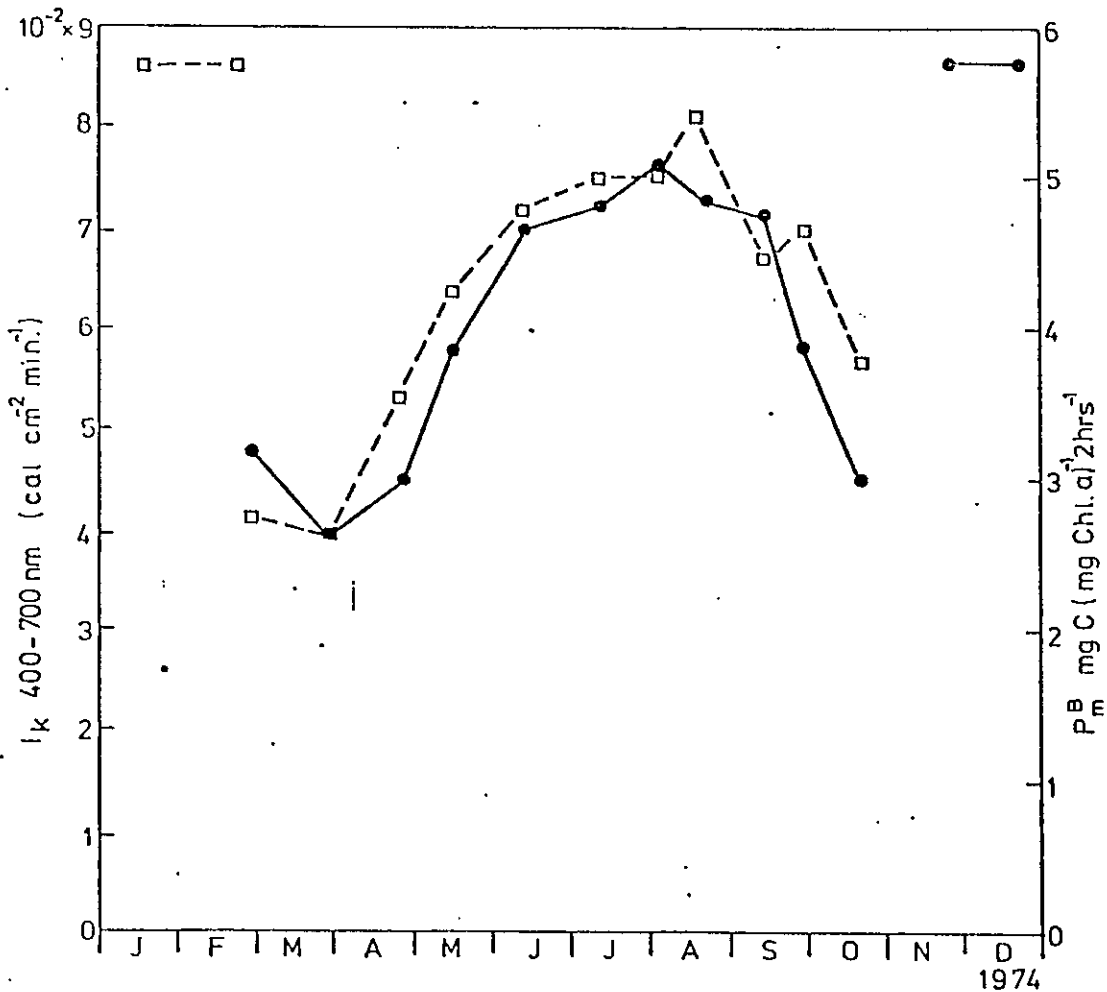


Figure 7

- B 102 -

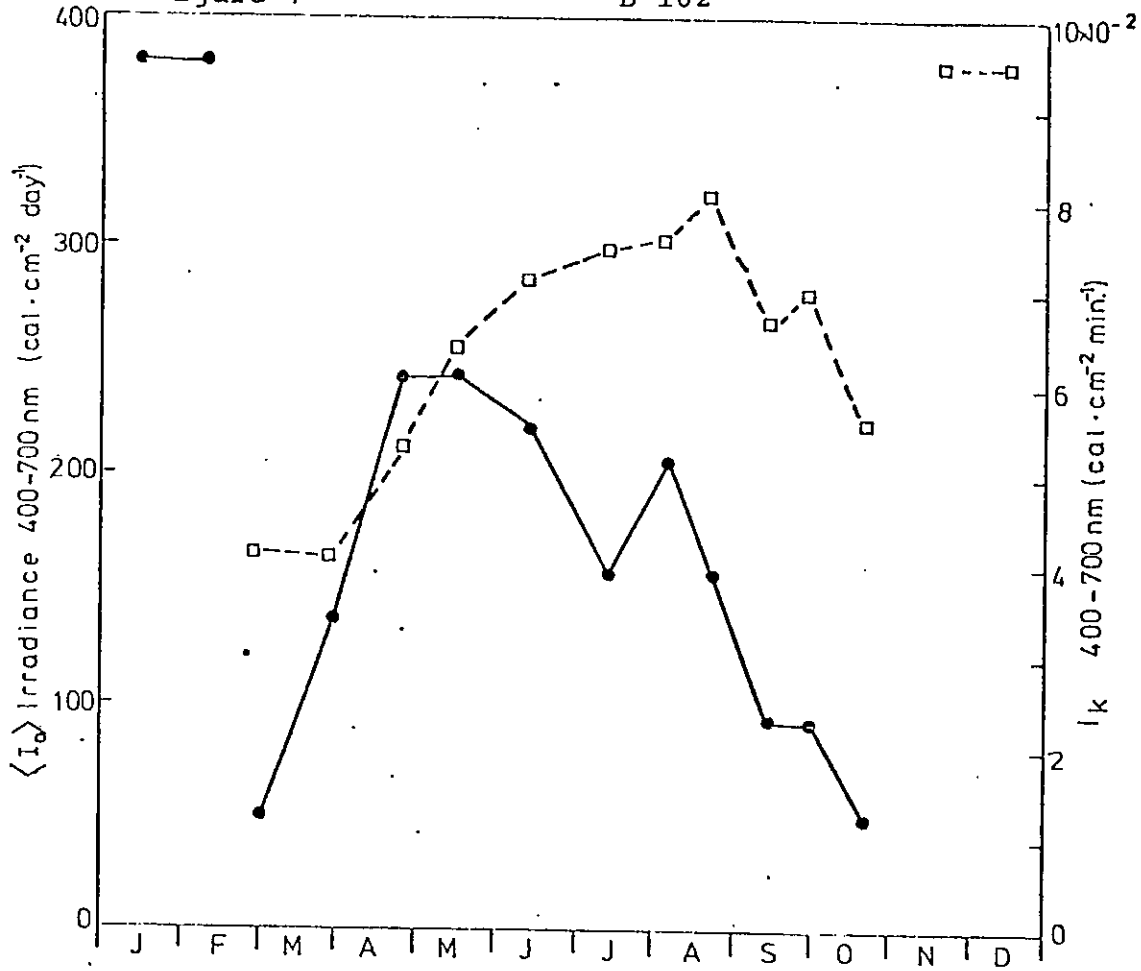


Figure 8

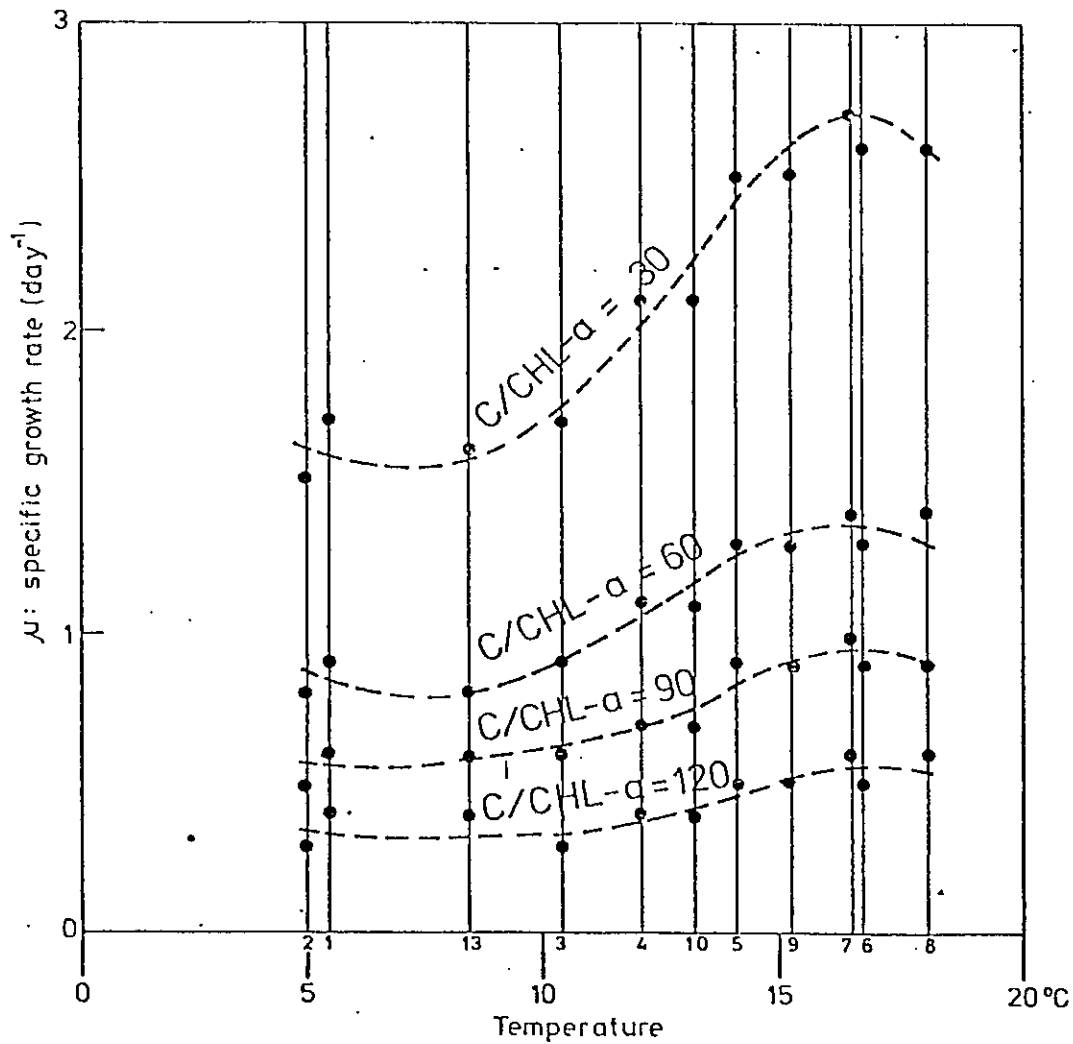


Table 1

NAME OF THE LAKE	AREA 10 ⁶ m ²	MEAN DEPTH m	PRODUCTION mgC·m ⁻² ·year ⁻¹	CHLOROPHYLL-a µg/l			TOTAL NITROGEN mg/l			TOTAL PHOSPHORUS µg/l		
				max	min	mean	max	min	mean	max	min	mean
ALMIND	0.53	10.4	50	8.2	1.1	4.5	0.52	0.18	0.42	0.03	0.01	0.02
BRASSØ	1.14	4.6	260	204	12	70	3.60	0.88	1.79	0.43	0.05	0.19
HALD	3.33	14.6	210	91	1.1	34	1.16	0.43	0.72	0.23	0.08	0.14
HINGE	1.08	2.3	290	323	33	114	6.50	0.94	1.97	0.34	0.07	0.19
NØRPESØ	1.22	7.0	250	129	2.2	33	2.19	1.18	1.55	0.28	0.08	0.19
SALTEN L. I	0.64	6.5	170	78	13	33	1.43	0.42	0.61	0.12	0.05	0.08
SALTEN L. II	1.51	2.2	130	52	14	29	1.45	0.30	0.60	0.12	0.06	0.08
SILFEBORG L. I	0.46	2.6	300	180	28	101	1.75	0.65	1.24	0.23	0.07	0.15
SILFEBORG L. II	0.85	2.8	260	156	24	91	1.73	0.62	1.09	0.28	0.08	0.15
SILFEBORG L. III	0.93	2.0	320	209	24	78	3.46	1.08	1.83	0.42	0.04	0.26
SLÅEN	0.19	7.1	30	9.3	0	3.3	0.23	0.10	0.20	0.11	0.02	0.04
SCANDERSØ	1.44	3.6	300	217	10	80	2.69	1.24	1.94	0.59	0.15	0.44
TANGE I	1.24	1.5	470	212	10	81	3.75	1.00	1.70	0.50	0.11	0.24
TANGE II	4.51	2.5	420	192	41	87	4.38	0.76	1.54	0.29	0.10	0.19
THOR	0.60	3.0	90	146	7	15	1.13	0.25	0.47	0.12	0.04	0.07
VED	1.47	5.4	250	129	13	50	1.31	0.42	0.87	0.30	0.11	0.20
VESSØ	0.60	3.0	160	66	6.6	38	2.18	0.73	1.30	0.10	0.02	0.06
ØRN	0.42	4.1	330	139	14	112	1.68	0.84	1.27	0.22	0.12	0.17

Table 2

	P ^B	P _m ^B	I _K	I _O	⟨I _O ⟩	T
P ^B	1.00	ns 0.17	a 0.56	ns 0.005	ns 0.005	ns 0.48
P _m ^B		1.00	c 0.89	ns 0.46	ns 0.26	c 0.93
I _K			1.00	ns 0.44	ns 0.32	c 0.97
I _O				1.00	c 0.84	ns 0.46
⟨I _O ⟩					1.00	ns 0.36
T						1.00

ns = Not significant

a = Exceeds value expected at the 95% confidence level

b = Exceeds value expected at the 99% confidence level

c = Exceeds value expected at the 99,9% confidence level

Table 3

NAME OF THE LAKE	SEQUENCE OF P _m ^B																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
ALMIND	(2)	2		(5)						1								1	
BRASSØ			1		2	1		1	1		1	1	1			2			
HALD				1	1	1			1			3	1		1			2	
HINGE							1	1		3				2	2		2		
NØRRESØ						1	1			1	1	1	1	1	1	1		2	
SALTEN L. I			1						2		1			3	1	1	1		
SALTEN L. II	2		1							1					1	1	1	1	
SILKEB. I		1	1		1			2	1	2		1			1			1	
SILKEB. II		1		1	1			1		2				1				1	
SILKEB. III				1	2		1	1	1		1		1		1			2	
SLÅEN	1		1	1		1	2			1		2			1	1			
SØNDERSØ					1				1	2		2	1	1		1	2		
TANGE I						1		1	1		1			(1)		2		(3)	
TANGE II			1		1														
THOR	(1)	1	1	2	1	1	1						1				(1)	(2)	(1)
VED						2	2	2			1	1	1			2			
VESSØ					1	1	1	1	1		2		1	2	1				1
ØRN		1				2		2		1	1		1		1	1			1

Table 4

NAME OF THE LAKE	SEQUENCE OF I _K																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
ALMIND	(2)	1	2	2	1	2	1												
BRASSØ	1			2			2		1			1	2		1			1	
HALD		1	3	1	2	1	1	1								1			
HINGE					1				1					1	2	1	1	2	
NØRRESØ							1		1		2	2	1	2			1	1	
SALTEN L. I					1			1	2	2	1		1	1		1			
SALTEN L. II			1	1	1		1		1	1	2	2	1						
SILKEB. I		1	1					1	2			1			1		1	1	
SILKEB. II			1	1		2	1			1	1		1						2
SILKEB. III						1	1	2	1		1		1		2	1			1
SLÅEN	(3)	2		1	1			1	1	1									
SØNDERSØ		1							2		1	1	2	2	1	1			
TANGE I		1				1					(1)	1		2	2	1	1	2	
TANGE II														(2)	3	1	2	2	
THOR		1	1	1		1	1	1		1	1	1							1
VED			1		2	1	1			3		2	1						
VESSØ		1		1	2			2		1		1							1
ØRN		1		1		2		1	1	1			1			3			1

Table 5

	P^B	P_m^B	I_K	$\langle I_o \rangle$	T	TN	TP
P^B	1.00	0.602 ^c	-0.017 ^{ns}	-0.009 ^{ns}	-0.129 ^{ns}	0.336 ^c	0.132 ^{ns}
P_m^B		1.00	0.599 ^c	0.118 ^{ns}	0.422 ^c	0.177 ^a	0.402 ^c
I_K			1.00	0.211 ^b	0.636 ^c	-0.062 ^{ns}	0.381 ^c
$\langle I_o \rangle$				1.00	0.365 ^c	-0.177 ^a	0.028 ^{ns}
T					1.00	-0.331 ^c	0.275 ^b
TN						1.00	0.310 ^a
TP							1.00

ns = Not significant

a = Exceeds value expected at the 95% confidence level

b = Exceeds value expected at the 99% confidence level

c = Exceeds value expected at the 99.9% confidence level