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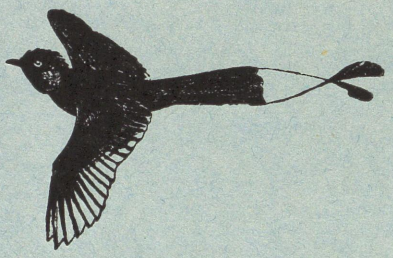

COMPUTER SIMULATION FOR THE WORKSHOP ON CONSERVATION BIOLOGY

N. V. JOSHI

January 1987
Technical Report No. 44

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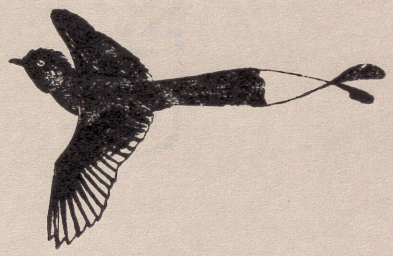

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1. Introduction

An understanding of the dynamics of the evolutionary processes which influence biological and genetic diversity in a habitat is essential for devising effective strategies for conservation. It is, of course, impossible to describe the effects of myriad interactions which take place in any natural community. However, mathematical models developed in the last few decades for describing certain simplified scenarios, provide some valuable insights. It is thus possible to describe how the rate of change of gene frequencies is governed by the population size, population structure, seasonal fluctuations, variability in reproductive success etc. Unfortunately, many biologists - and conservation biologists - do not have adequate familiarity with or knowledge of mathematics to appreciate and exploit these models.

This is exactly the reason why a personal computer can be used as an extremely effective educational aid. Running a computer program, designed for interactive use and with graphics displays for output, enables a person to grasp the concepts underlying the dynamics of evolutionary processes far more effectively than studying an equation. When a biologist sees the gene frequencies in a population at every generation displayed on the computer screen, and when he can see how they change when he changes the various population parameter, he obtains a much better feel for the phenomena.

This technical report describes some of the programs developed for the participants of the first National School on Conservation Biology held at the Centre for Ecological Sciences, Indian Institute of Science, Bangalore between 10 -- 22nd November 1986. Each program was developed to demonstrate the effect of

some specific feature of the population - the sex ratio, seasonal fluctuations - on the evolution of the gene frequences within the population. The programs are to be run in interactive mode, with data to be supplied by the user. The following sections briefly outline the theoretical background for each program, and include suggested input values for the data. The source code is also included. Wherever possible, figures depicting the screen at the time of data input, and also at that time when the simulation is being carried out, are included.

The programs were written in advanced basic (BASICA) of the Microsoft Corporation or in TURBO PASCAL, and are designed to run on IBM PC compatibles. The .BAS files as well as .EXE files (to be run under MS-DOS) may be obtained from the author on supply of a DSDD 5 1/4 inch floppy disc.

2. Effective Population Size

The rate and outcome of the evolutionary process in a given population can be more easily described in terms of an ideal population of size N_e, which is a function of the size as well as the structure of the initial population (Crow & Kimura 1970, Hartl 1982). The value N_e is called the effective population size. The three programs described below demonstrate how the effective population size is influenced by the sex ration, cyclic fluctuations in the population size and by the variability in the reproductive success.

2.1 Influence of the sex ratio

If a population contains N_M males and N_F females, the effective population size is given by

$$Ne = \frac{4 N_M N_F}{N_M + N_F}$$

If one of the alleles (A) at a biallelic locus is selectively advantageous (fitness = 1+s) compared to the other allele (B , fitness = 1) , and if the initial frequency of the advantageous allele A is x, the expected probability of allele A being eventually fixed in the population is given by

$$P = \frac{1 - \mathrm{Exp}(4 N_e s x)}{1 - \mathrm{Exp}(4 N_e s)}$$

The program SEL01 requires input data on the total number of animals (T) in the population , and the total number of males (M). The number of females is (T - F). The value of the selective advantage (s) is also fed in. The advantageous allele (A) is assumed to be present in only one male and in only one female i.e. the frequencies of the allele in males and females are $x_M = 1/M$ and $x_F = 1/F$.

To determine the genetic composition of the males in the next generation, M gametes are chosen from the male gemete pool and M from the female gamete pool. To choose a gamete, a random number Y is generated from the uniform distribution (0-1). If Y is less than $\frac{x.(1 + s)}{1 + s.x}$, then the allele A is assumed to have been chosen ; else, B is chosen. Thus, one can obtain x_M and x_F in the next generation. The procedure is repeated till A is either eliminated ($x_M = x_F = 0$) or fixed ($x_M = x_F = 1$). If out of N trials, allele A reaches fixation in n trials, the <u>realized</u> probability of fixation is n/N.

The user may run the program with T=40 and M=10,20,30,etc., and with S=0.01,0.05 etc., and see how the probability of fixation changes with the asymmetry of the sex ratio. It will be seen that higher the asymmetry in the sex ratio, lower is the effective population size, and lower is the probability of fixation of the

advantageous allele.

Since one random number has to be generated for the choice of one gamete in each generation, the program inevitably takes a long time to run for large population sizes. The second program SEL02 overcomes this problem by adopting an alogrithm described by Kimura (Kimura 1980).

If p is the probability of success , the number of successes in N Bernaulli trials is distributed with mean $N.p$ and variance $N.p.(1-p)$, and the estimated value of p has a mean p and variance $\frac{p.(1-p)}{N}$. Hence, if there are N gametes in the population and the frequency of allele A with selective advantage s is P , its expected frequency in the next generation has a mean $P' = \frac{P(1+s)}{1+P.s}$ and variance equal to $\frac{P'.(1-P')}{N}$. Kimura (1980) has shown that the changes in the gene frequencies could be satisfactorily simulated by choosing the value P' in the next generation from any distribution whose mean and variance are the same as above. In particular , he has shown that P_{next} , the frequency in the next generation can be represented by

$$Pnext = P' + (2.U - 1)\sqrt{\frac{3.P'.(1-P')}{N}}$$

Where U is a random number distributed uniformly between [0-1]. This procedure has been adopted in the program SEL02. Since only one random number has to be generated per generation, the program runs much fastern than SEL01, without apprecially distorting the results of the simulation.

2.2 Fluctuations in the population size

If the population sizes in years 1,2,...,n are N_1 , N_2 ,...,N_n respectively, the effective population size N_e is given by their

harmonic mean, i.e.

$$\frac{1}{N_e} = \frac{1}{n}\sum\frac{1}{N_i}$$

The harmonic mean is strongly influenced by the smaller values of the population (bottleneck effect). The program SEL03 demonstrates this effect. For simplicity, it is assumed that the population can take only two values, N_1 and N_2, in alternate years such that $N_1 = N_3 = \ldots$ and $N_2 = N_4 = \ldots\ldots$ The effective population size is then $\frac{2N_1N_2}{N_1 + N_2}$ For N1=10 and N2=100, Ne is seen to be approximately equal to 18, thus much closer to 10.

The population is assumed to be haploid. If P is the frequency of the (selectivly advantageous) allele A in a generation, the frequency in the next generation is determined by generating N random numbers ($N=N_1$ or N_2, depending on whether it is odd or even generation), with allele A being chosen if a random number (uniformally distributed between (0-1)) is less than $\frac{P(1+s)}{1+P.s}$. The procedure is continued till A is either fixed on eliminated, as described in the earlier section.

The next program SEL04 generalizes the above scenario to include oscillations in the population size with arbitrary cycle length. At present , the maximum cycle length is 20 ; this could easily be changed by the DIM statement at the beginning of the program. This program is designed to run much faster than SEL03 by adopting Kimura's algorithm described earlier.

Another evolutionary process influenced by the effective population size is the retention of genetic variability. A finite population containing equal proportions of selectivoly equivalent alleles A and B eventually loses one of them. The higher the

effective population size, the longer would be the time when this occurs. This concept is illustrated by the program SEL05, written in Turbo Pascal. The program starts with equal frequencies of two alleles, and changes the total population size in each generation as specified by the input. The frequencies from one generation to the next are computed as before i.e., by chosing individual gametes. The process is continued till one of the alleles is eliminated. The program also prints out the average time taken for the loss of one allele. The concept of effective population size is best illustrated by running the program say with population taking a constant value in all years (30 , 30) followed by another run with large changes (55 ,5). The time for loss of heterozygosity is seen to reduce very noticably.

2.3 Variation in the reproductive success.

If the population size is N, and if the variance of the number of offspring produced by these individuals is V, the effective population size is given by (Frenkel and Soule, 1983)

$$Ne = \frac{4N - 2}{V + 2}$$

It is seen that higher the variance, lower the effective population size. Alternatively, by artificially lowering the variance by suitable culling , the effective population size for a captive population could be increased (Frenkel and Soule 1983).

The BASIC program SEL06 demonstrate this phenomenon. For simplicity as well as for keeping the execution time managable, the population size is fixed at 60, and the variances is permitted to take only one of the values (0,2,4,6,8,10). Only a fraction of the individuals are allowed to breed, and those who do, are allotted a large number of offspring, such that the variance in the offspring number is equal to the specified value. The program

starts with an equal proportion of selectively equivalent alleles, and runs till one of them is eliminated. As before, the average time needed for this to occur is computed and displayed ; the higher the effective population size , the longer the time. It is instructive to run this program with V = 0 , V = 2 (poisson distribution) and V = 10 (highly uneven reproduction) and compare the results.

3. Effect of sample size on specie-abundance curve.

The species abundance curves obtained for many natural communities show a long tail --- the log series distribution (Preston 1962). On theoretical grounds , one expects them to follow a lognormal distribution. These two can be reconciled by the fact that the sample sizes used for obtaining the distributions are often not adequate (May 1975).

This is demonstrated by the program SMP01. It simulates samples from a community of 57 species and about 2000 individuals. The specie abundance curve is lognormal. The program initially shows this distribution in the form of a table, and also a histogram. It next requests the sample size as input data (n). The program then generates n random numbers, each number corresponding to one individual being sampled. From the cumulative distribution of individuals vs species, the specie to which each individual belongs is determined. Thus, the observed specie-abundance curve is obtained and displayed on the screen. It is instructive to run the program once with n=30 (low sample size) to see the log series distribution with mode at abundance=1, and once with n = 150 - 200 (adequate sample size) to see an

approximately lognormal distribution , with mode near an abundance = 4. The abundance axis is on a log scale with base 2 ; successive units denote abundance of 1,2,4,8,....etc. The program takes rather long time to run for large sample sizes (> 100).

4. Stochastic Models of species-genera formation.

A study of fossil records seems to indicate certain trends in the pattern of evolution in a given lineage - e.g. towards larger size, towards more complexity etc. Interestingly, similar trends were noticed in the patterns obtained from stochastic models of evolution (Gould 1981 , Raup 1977) . In fact, Raup and his collegues have used stochastic models as a 'giant null hypotheses' to test the significance of various patterns observed in the fossil record. The program EVGS01 described below simulates the evolutionary history in a given lineage using a very simple model (Dewny, 1986). One begins with a single genus, containing a few species. In one unit of time (epoch), each species can either survive or go extinct, with the probability of extinction same from all species, and specified earlier. In addition, each species can give rise, with a small probabilities, to a new species, and with a still smaller probability, to a new genus.

The input values for the program are N, the number of species in the genus at the initial instant, and P1,P2,P3, such that P1 is the probability of extinction, P2-P1 is the probability for survival, P3-P2 is the probability of a new species being formed, and 1-P3, of a new gunus being formed (recommended values are N=8, P1=0.31, P2=0.62 & P3=0.93). At each epoch , for each species, the program generates a random number Y, uniformally distributed between (0-1). If Y < P1 , the species is assumed to go extinct , while P1 < Y < P2 indicates that the speci survives.

For P2 < Y < P3 , a new specie is added to the genus and for Y > P3, a new genus is added. The number of species in each genus is updated at each stage. During this simulation, the screen displays in a graphical form the number of extant species at that epoch. Also shown are the total number of species and genera which came into existance upto that instant of time. The simulation is run for 200 epochs, or till all the species go extinct. For convenience in displaying the lineges, each genus is permitted to sprout at the most six new genera , the maximum number of species in each genus is restricted to 75, and the simulation is terminated when 45 new genera are formed. After the simulation is completed, entering a value '0° displays the lineage on the screen, as shown in the figure. Each vertical progression corresponds to a genus and the width is proportional to the number of species in that genus at that epoch ; the vertical axis denotes time in epochs. Dewny (1985) describes the procedure at length, and Raup (1977) , the paleontological implications of such diagrams.

5.Evolution of Biomorphs

One of the most interesting and spectacular demonstration of evolutionary changes is described by Dawkins (Dawkins 1986), who describes evolution of extraordinary beings (biomorphs) as seen on a computer screen. A simple version of Dawkin's approach is used in the Program BIOMRF. One starts with a simple , bilaterally symmetric pattern of a binay tree ; a stem of length l_1 followed by two branches making an angle t_1 with each other, and each of length l_2. Each of these branches splits into two, with angle t_2 and length l_3. This continues for four more levels. The entire pattern is thus described by six lengths (l_1 ...l_6 and five angles

t_2 ..... t_6). A mutation corresponds to a small change in any one of there parameters ; several simultaneous mutations change several of the parameters.

The program displays the original tree , along with ten mutants. The user may then specify which of these patterns he would chose as a seed for the next frame. Eleven mutants of this seed are next demonstrated on the screen. An important component of the simulation is the interaction with the user ; he can choose patterns which evolve e.g. , towards small size , towards large size, toward having winged appendages etc. The accompanying figure demonstrates the wide variety of patterns obtained in one such simulation. This programs forefully brings home the point that a large number of mutations, if accumulated over time, can lead to a very wide diversity of forms, even if each single mutation causes only a small change. Dawkin (1986) may be consulted for more details.

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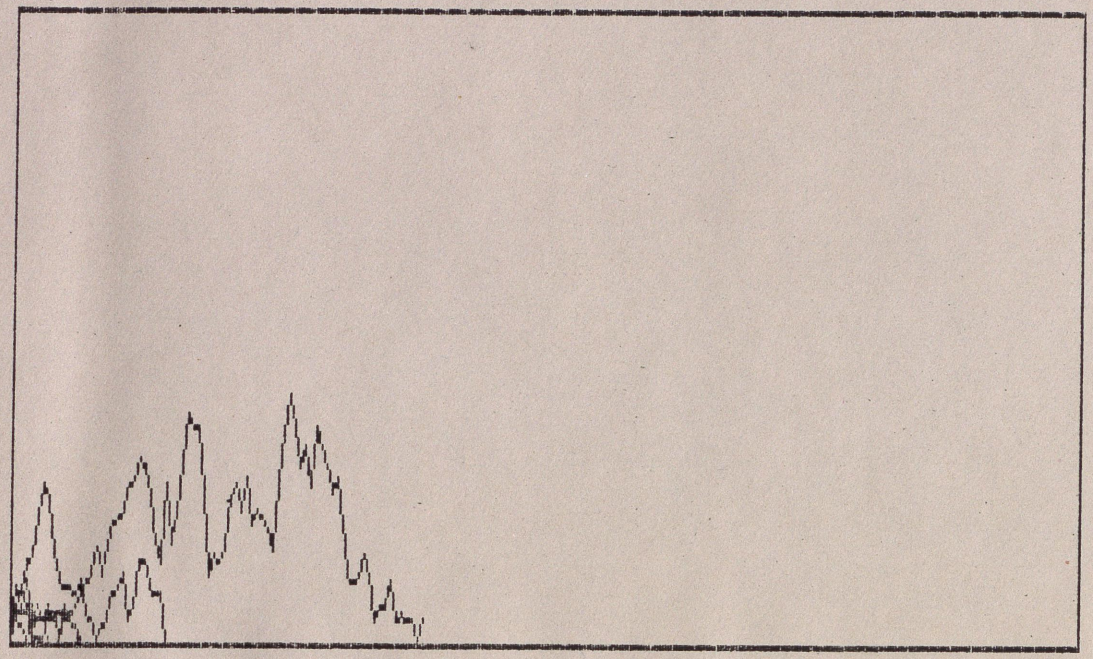
7. Source Codes of the programs

The listings of all the programs described in the text are shown in the following pages.

```
NATURAL SELECTION
EFFECTIVE POPULATION SIZE
NO. OF ANIMALS? 40
NO. OF MALES ? 10
INITIAL FREQUNCY IS
 .025
SELECTION COEFF.  IS ? 0.01
EFFECTIVE POPULATION SIZE IS
 30
EXPECTED PROB. OF FIXATION IS
 4.229285E-02
Random number seed (-32768 to 32767)?
```

```
10 REM SEL01.BAS  5 NOV 1986
20 REM ------------------------------------
30 REM EFFECTIVE POPULATION SIZE
40 REM EFFECT OF SEX-RATIO ASYMMETRY
50 REM ------------------------------------
60 CLS  : SCREEN 1 : PRINT "NATURAL SELECTION " : PRINT
70 PRINT "EFFECTIVE POPULATION SIZE" : PRINT
80 PRINT "NO. OF ANIMALS"; : INPUT T  :  T2=T+T : PRINT
90 PRINT "NO. OF MALES "; : INPUT M : M2=M+M : PRINT
100 F=T-M  :  F2=F+F  :  P1=1!/T
110 PRINT "INITIAL FREQUNCY IS     ",P1," " : PRINT
120 PRINT "SELECTION COEFF.  IS ";  : INPUT S : PRINT
130 S1=1!+S
140 E=4!*M*F/T : PRINT "EFFECTIVE POPULATION SIZE IS ", E ," "
150 X=-4! *S*E
160 PFX=(1!-EXP(X*P1))/(1!-EXP(X)) : PRINT
170 PRINT "EXPECTED PROB. OF FIXATION IS ",PFX," " : PRINT
180 NTR=20!/PFX
190 RANDOMIZE
200 SCREEN 2  :  NGN=400  :  CL=9
210 V=0
220 FOR I=1 TO NTR  : CL=CL+1  :  IF CL=10 THEN GOTO 460
230 PM=1!/M  :  PF=1!/F  :  PP1=100!/T  :  J=0
240 J=J+2  :  IF J>NGN THEN GOTO 440
250 TM=PM*S1/(1!+PM*S) : TF=PF*S1/(1!+PF*S)
260 M1=0  :  F1=0
270 FOR K=1 TO M
280 IF RND<TM THEN M1=M1+1
290 IF RND<TF THEN M1=M1+1
300 NEXT K
310 FOR K=1 TO F
320 IF RND<TM THEN F1=F1+1
330 IF RND<TF THEN F1=F1+1
340 NEXT K
350 PP2=(M1+F1)*100/T2
360 LINE (J-2,200-PP1)-(J,200-PP2)
370 PP1=PP2
380 PM=M1/M2  :  PF=F1/F2
390 IF M1+F1>.95*T2 THEN GOTO 440
400 IF M1+F1<>0 THEN GOTO 240
410 V=V+1
420 LOCATE 2,10 : PRINT "                    "
430 LOCATE 2,10 : PRINT 1!-V/I
440 NEXT I
450 END
460 CL=0  :  CLS
470 LOCATE 1,10  :  PRINT " PROB. OF FIXATION ",PFX
480 LINE (0,200)-(400,200) : LINE -(400,100)  :  LINE -(0,100)
490 LINE -(0,200)  :  GOTO 230
```

PROB. OF FIXATION 4.229285E-02
8.333331E-02

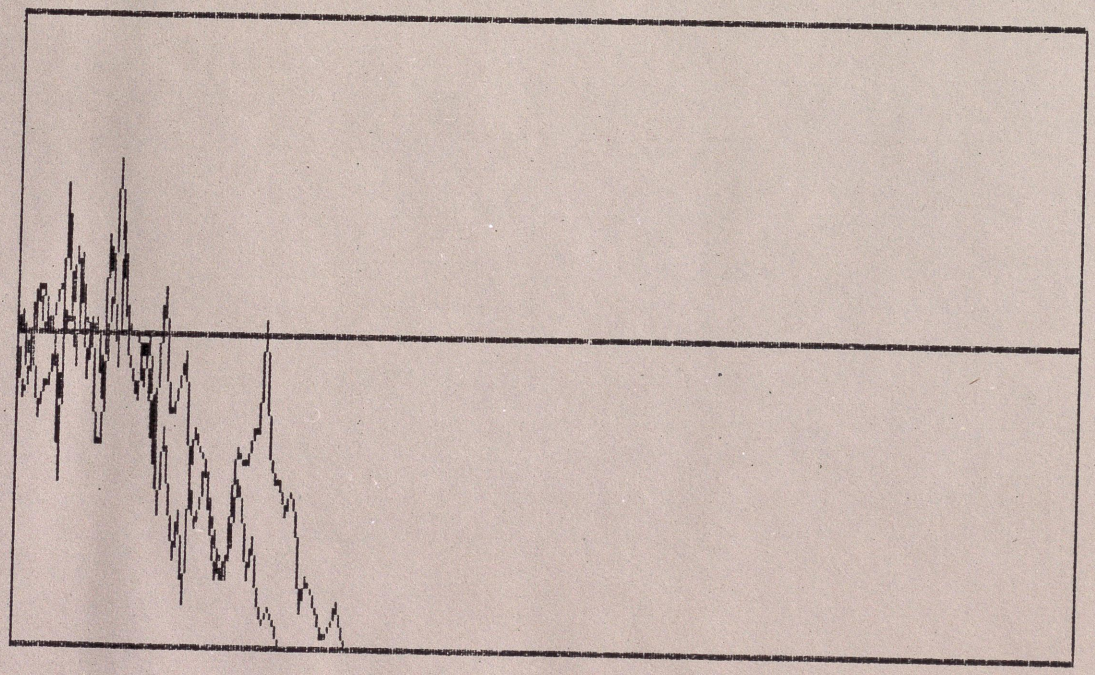


```
10 REM SEL02.BAS  6 NOV 1986
20 REM ------------------------------------
30 REM EFFECTIVE POPULATION SIZE
40 REM EFFECT OF SEX RATIO ASYMMETRY
50 REM KIMURA'S ALGORITHM
60 REM ------------------------------------
70 CLS  : SCREEN 1 : PRINT "NATURAL SELECTION "
80 PRINT :PRINT "EFFECTIVE POPULATION SIZE" : PRINT
90 PRINT "NO. OF ANIMALS"; : INPUT T  :  T2=T+T : PRINT
100 PRINT "NO. OF MALES "; : INPUT M : M2=M+M : PRINT
110 F=T-M  :  F2=F+F  :  P1=1!/T
120 MMIN= 1!/M2  :  FMIN=1!/F2  :  MMAX=1!-MMIN  :  FMAX=1!-FMIN
130 PRINT "INITIAL FREQUNCY IS     ",P1," " : PRINT
140 PRINT "SELECTION COEFF.  IS ";  : INPUT S : PRINT
150 S1=1!+S
160 E=4!*M*F/T : PRINT "EFFECTIVE POPULATION SIZE IS ", E ," "
170 X=-4! *S*E
180 PFX=(1!-EXP(X*P1))/(1!-EXP(X)) : PRINT
190 PRINT "EXPECTED PROB. OF FIXATION IS ",PFX," "
200 PRINT  :  NTR=20!/PFX
210 RANDOMIZE
220 SCREEN 2  :  NGN=400  :  CL=9
230 CM=SQR(3!/M2)  :  CF=SQR(3!/F2)
240 V=0!
250 FOR I=1 TO NTR  :    CL=CL+1  :  IF CL=10 THEN GOTO 530
260 PM=1!/M  :  PF=1!/F  :  PP1=100!/T  :  J=0
270 J=J+2  :  IF J>NGN THEN GOTO 510
280 TM=PM*S1/(1!+PM*S) : TF=PF*S1/(1!+PF*S)
290 ADM=(2!*RND-1)*CM*SQR(TM*(1!-TM))
300 ADF=(2!*RND-1)*CF*SQR(TF*(1!-TF))
310 PM=(TM+TF+ADM+ADF)*.5
320 IF PM<MMIN THEN PM=0!
330 IF PM>MMAX THEN PM=1!
340 M1=PM*M2
350 ADM=(2!*RND-1)*CM*SQR(TM*(1!-TM))
360 ADF=(2!*RND-1)*CF*SQR(TF*(1!-TF))
370 PF=(TM+TF+ADM+ADF)*.5
380 IF PF<FMIN THEN PF=0!
390 IF PF>FMAX THEN PF=1!
400 F1=PF*F2
410 PP2=(M1+F1)*100/T2
420 LINE (J-2,200-PP1)-(J,200-PP2)
430 PP1=PP2
440 PM=M1/M2  :  PF=F1/F2
450 IF M1+F1>.95*T2 THEN GOTO 510
460 IF M1+F1 <=0 THEN GOTO 480
470 GOTO 270
480 V=V+1
490 LOCATE 2,10 : PRINT "                    "
500 LOCATE 2,10 : PRINT 1!-V/I
510 NEXT I
520 END
530 CL=0  :  CLS
540 LOCATE 1,10  :  PRINT " PROB. OF FIXATION ",PFX
550 LINE (0,200)-(400,200) : LINE -(400,100)  :  LINE -(0,100)
560 LINE -(0,200)  :  GOTO 260
```

```
10 REM SEL03.BAS    5 NOV 1986
20 REM ------------------------------------------
30 REM EFFECTIVE POPULATION SIZE
40 REM EFFECT OF FLUCTUATIONS IN SIZE
50 REM ------------------------------------------
60 CLS  : SCREEN 1 : PRINT "NATURAL SELECTION "
70 PRINT  :  PRINT "EFFECTIVE POPULATION SIZE" : PRINT
80 PRINT "NO. OF ANIMALS IN ODD YEARS ";  :INPUT TOD:TOD2=TOD+TOD:PRINT
90 PRINT "NO. OF ANIMALS IN EVEN YEARS ";  : INPUT TEV : TEV2=TEV+TEV
100  PRINT  :  P1=1!/TOD
110 PRINT "INITIAL FREQUNCY IS     ",P1," " : PRINT
120 PRINT "SELECTION COEFF.  IS ";  : INPUT S : PRINT
130 S1=1!+S
140 ER=1!/TOD +1!/TEV
150 E=2!/ER  : PRINT "EFFECTIVE POPULATION SIZE IS ", E ," "
160 X=-4! *S*E
170 PFX=(1!-EXP(X*P1))/(1!-EXP(X)) : PRINT
180 PRINT "EXPECTED PROB. OF FIXATION IS ",PFX," " : PRINT
190 NTR=20!/PFX
200 RANDOMIZE
210 GEN=1
220 SCREEN 2  :  NGN=400  :  CL=9
230 V=0!
240 FOR I=1 TO NTR  :  CL=CL+1  :  IF CL=10 THEN GOTO 520
250 GEN=1
260 PM=1!/TOD : PF=1!/TOD : PP1=100!/TOD : J=0
270 J=J+2  :  IF J>NGN THEN GOTO 500
280 GEN =1-GEN : POP=TEV : IF GEN=0 THEN POP=TOD
290 TM=PM*S1/(1!+PM*S) : TF=PF*S1/(1!+PF*S)
300 M=POP/2  :  F=M
310 T2=POP+POP : M2=POP  :  F2=POP
320 M1=0  :  F1=0
330 FOR K=1 TO M
340 IF RND<TM THEN M1=M1+1
350 IF RND<TF THEN M1=M1+1
360 NEXT K
370 FOR K=1 TO F
380 IF RND<TM THEN F1=F1+1
390 IF RND<TF THEN F1=F1+1
400 NEXT K
410 PP2=(M1+F1)*100/T2
420 LINE (J-2,200-PP1)-(J,200-PP2)
430 PP1=PP2
440 PM=M1/M2 : PF=F1/F2
450 IF M1+F1>.95*T2 THEN GOTO 500
460 IF M1+F1<>0 THEN GOTO 270
470 V=V+1
480 LOCATE 2,10 : PRINT "                    "
490 LOCATE 2,10 : PRINT 1!-V/I , I
500 NEXT I
510 END
520 CL=0  :  CLS
530 LOCATE 1,10  :  PRINT " PROB. OF FIXATION ",PFX
540 LINE (0,200)-(400,200) : LINE -(400,100)  : • LINE -(0,100)
550 LINE -(0,200)  :  GOTO 260
```

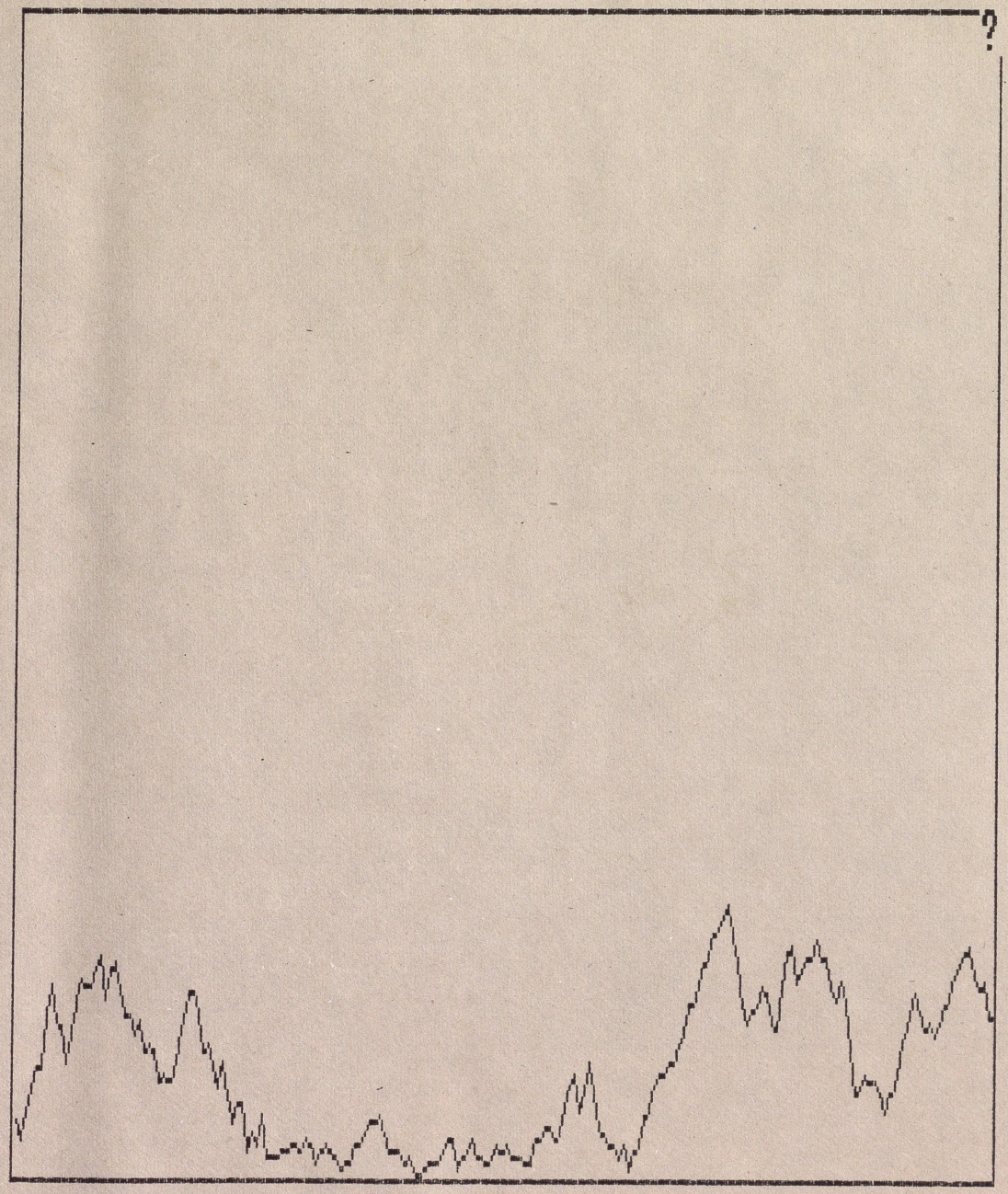
```
10 REM SEL04.BAS  6 NOV 1986
20 REM ------------------------------
30 REM EFFECTIVE POPULATION SIZE
40 REM EFFECT OF FLUCTUATIONS - ARBITRARY CYCLE LENGTH
50 REM KIMURA'S ALGORITHM
60 REM ------------------------------
70 DIM NPOP(20)
80 CLS : SCREEN 1 : PRINT "NATURAL SELECTION " : PRINT
90 PRINT "EFFECTIVE POPULATION SIZE" : PRINT
100 X=0!
110 PRINT " WHEN POPULATION OSCILLATES " : PRINT
120 PRINT "CYCLE SIZE ( < 10 PLEASE ) "; : INPUT NCY
130 FOR I=1 TO NCY : PRINT "POP. IN YEAR",I ;: INPUT NPOP(I)
140 X=X+1!/NPOP(I) : NEXT I
150 X=X/NCY : PRINT
160 P1=1!/NPOP(1)
170 PRINT "INITIAL FREQUNCY IS     ",P1," " : PRINT
180 PRINT "SELECTION COEFF.  IS "; : INPUT S : PRINT
190 S1=1!+S
200 E=1!/X: PRINT "EFFECTIVE POPULATION SIZE IS ", E ," "
210 X=-4! *S*E
220 PFX=(1!-EXP(X*P1))/(1!-EXP(X)) : PRINT
230 PRINT "EXPECTED PROB. OF FIXATION IS ",PFX," " : PRINT
240 NTR=20!/PFX
250 RANDOMIZE
260 SCREEN 2 : NGN=400 : CL=9
270 V=0!
280 FOR I=1 TO NTR : CL=CL+1 : IF CL=10 THEN GOTO 510
290 G=-1 : PM=1!/NPOP(1) : PP1=PF*100 : J=0
300 J=J+2 : IF J>NGN THEN GOTO 490
310 G=G+1 : K= G MOD NCY+1 : POP=NPOP(K) : T2=POP+POP
320 M2=POP : F2=POP
330  CM=SQR(3!/T2)
340 MMIN=1!/T2 : MMAX=1!-MMIN
350 TM=PM*S1/(1!+PM*S)
360 ADM=(2!*RND-1)*CM*SQR(TM*(1!-TM))
370 PM=TM+ADM
380 IF PM<MMIN THEN PM=0!
390 IF PM>MMAX THEN PM=1!
400 PP2=PM*100
410 LINE (J-2,200-PP1)-(J,200-PP2)
420 PP1=PP2
430 IF PM>.95 THEN GOTO 490
440 IF PM=0 THEN GOTO 460
450 GOTO 300
460 V=V+1
470 LOCATE 2,10 : PRINT "                    "
480 LOCATE 2,10 : PRINT 1!-V/I , I
490 NEXT I
500 END
510 CL=0 : CLS
520 LOCATE 1,10 : PRINT " PROB. OF FIXATION ",PFX
530 LINE (0,200)-(400,200) : LINE -(400,100) : LINE -(0,100)
540 LINE -(0,200) : GOTO 290
```

```
-------THIS PROGRAM IS SEL05.PAS , WRITTEN IN TURBO-PASCAL. --
------- EFFECTIVE POPULATION SIZE    ----
------- EFFECT OF SIZE FLUCTIONS ON THE RETENTION OF
------- GENETIC VARIABILITY IN THE POPULATION
VAR
   Z,M  :  ARRAY[1..3] OF REAL;
   TIM,CL,SSZ,X1,X2,P1,P2,HP,CA,Y,CB : REAL;
   TA,TB,PMC,PC,MC,H,AV : REAL;
   I,JJ,J,NGN,K,L,N,IBS,NCY,NTR : INTEGER;
   NPOP : ARRAY[1..20] OF INTEGER;
BEGIN
   TEXTMODE; AV:=0.0; X1:=0.0;
   WRITE('WHAT IS THE CYCLE LENGTH ?    ') ; READ(NCY); WRITELN(' ');
   X2:=NCY;
   FOR I:=1 TO NCY DO
   BEGIN
    WRITE('POPULATION IN YEAR ',I:5,' ? ');READ(NPOP[I]);WRITELN(' ');
    X1:=X1+TRUNC(NPOP[I]);
   END;
 Z[1]:=-1.0 ; Z[2]:=0.50  ; Z[3]:=2.0;
NTR:=1  ; NGN:=400 ; TIM:=0.0 ; CL:=0.0 ; SSZ:=0.0;
HIRES;
WHILE NTR=1 DO
BEGIN
CL:=CL+1.0 ; IF CL=1.0 THEN
BEGIN
HIRES;DRAW(0,199,400,199,1) ; DRAW(400,199,400,100,1);
DRAW(400,100,0,100,1) ; DRAW (0,100,0,199,1);
DRAW (0,150,400,150,1); CL:=0.0; WRITELN(SSZ:8:1,AV:8:1);
END;
P1:=0.0 ; P2:=1.0 ; J:=0  ;  HP:=100.0; JJ:=0;
REPEAT
   J:=J+2 ; M[1]:=0.0 ; M[2]:=0.0 ; M[3]:=0.0;
   JJ:=JJ+1 ; IF JJ>NCY THEN JJ:=1 ; N:=NPOP[JJ];
   FOR K:=1 TO N  DO
   BEGIN
      CA:=2.0 ; Y:=RANDOM ; IF Y<P1 THEN CA:=1.0;
      IF Y>P2 THEN CA:=3.0 ; CB:=2.0 ; Y:=RANDOM  ;
      IF Y<P1 THEN CB:=1.0 ; IF Y>P2 THEN CB:=3.0;
      TA:=Z[ROUND(CA)] ; TB:=Z[ROUND(CB)];
      PC:=0.0  ;  IF RANDOM < TA  THEN PC:=1.0;
      MC:=0.0  ;  IF RANDOM < TB  THEN MC:=1.0 ;
      PMC:=PC+MC+1.0 ; M[ROUND(PMC)]:=M[ROUND(PMC)]+1.0;
   END;
   P1:=M[1]/N  ;  P2:=P1+M[2]/N ; H:=M[2]*100.0/N ;
   DRAW (J-2,ROUND(200.0-HP),J,ROUND(200-H),1) ; HP:=H;
   IF (H<0.50)  OR (J=NGN) THEN
     BEGIN
      TIM:=TIM+INT(J DIV 2); SSZ:=SSZ+1.0  ;  AV:=TIM/SSZ; J:=NGN;
      END;
 UNTIL J=NGN;
WRITELN('PRESS 1 TO REPEAT , 0 TO QUIT '); READ(NTR);
END;
WRITELN(SSZ:8:1,AV:8:1);
WRITELN('PRESS 0 TO QUIT'); READ(N);
TEXTMODE;
END.
```



```
10 REM SEL06.BAS  7 NOV 1986
11 REM ------------------------------------
12 REM EFFECTIVE POPULATION SIZE
13 REM EFFECT OF VARIATION IN REPRODUCTIVE SUCCESS
14 REM ------------------------------------
20 DIM Z(3),M(3)
30 Z(1)=-1!  :  Z(2)=.5  :  Z(3)=2!
40 CLS  :  SCREEN 1  :  PRINT "VARIANCE ? (0,2,4,6,8,10 ) ";  : INPUT V
50 N=120  :  BS=2+V*.5  :  BI=N/BS
55 N=60  :  BI=N/BS
60 NTR=100 : NGN=400  :  TIM=0 : CL=9  :  SSZ=0
70 RANDOMIZE
75 SCREEN 2
80 FOR I=1 TO NTR  :  CL=CL+1  :  IF CL=10 THEN GOTO 500
90 P1=.25  :  P2=.75  :  J=0  :  HP=50!
100 J=J+2  :  IF J>NGN THEN GOTO 300
110 M(1)=0  :  M(2)=0  :  M(3)=0
120 FOR K=1 TO BI
130 CA=2  :  Y=RND  :  IF Y<P1 THEN CA=1
140 IF Y>P2 THEN CA=3
150 CB=2  :  Y=RND  :  IF Y<P1 THEN CB=1
160 IF Y>P2 THEN CB=3
170 TA=Z(CA)  :  TB=Z(CB)
180 FOR L=1 TO BS
190 PC=0  :  IF RND<TA THEN PC=1
200 MC=0  :  IF RND<TB THEN MC=1
210 PMC=PC+MC+1  :  M(PMC)=M(PMC)+1
220 NEXT L  :  NEXT K
230 P1=M(1)/N  :  P2=P1+M(2)/N
240 H=M(2)*100/N
250 LINE (J-2,200-HP)-(J,200-H)
255 HP=H
260 IF H>.5 THEN GOTO 100
270 TIM=TIM+J/2  :  SSZ=SSZ+1  :  AV=TIM/SSZ
280 LOCATE 2,10 : PRINT "                                                    "
290 LOCATE 2,10 : PRINT SSZ,AV
300 NEXT I
310 END
500 CLS  :  LINE (0,200)-(400,200) : LINE -(400,100) : LINE -(0,100)
510 LINE -(0,200)  :  LINE (0,150)-(400,150)  :  GOTO 90
```

```
10 REM SMP01.BAS : 19.11.86
20 REM ----------------------------
30 REM EFFECT OF SAMPLE SIZE ON SPECIES-ABUNDANCE CURVE
40 REM ----------------------------
50 DIM A(100),B(100),BL(100),BU(100),BF(100),AF(100)
60 BL(1)=1 : BL(2)=2 : BL(3)=3 : BL(4)=5 : BL(5)=9
70 BL(6)=17 : BL(7)=33 : BL(8)=65 : BL(9)=129
80 BU(1)=1 : BU(2)=2 : BU(3)=4 : BU(4)=8 : BU(5)=16
90 BU(6)=32 : BU(7)=64 : BU(8)=128 : BU(9)=256
100 BF(1)=1 : BF(2)=4 : BF(3)=7 : BF(4)=10 : BF(5)=13
110 BF(6)=10 : BF(7)=7 : BF(8)=4 : BF(9)=1
120 CL=9 : CLS : SCREEN 1 : TT=0 : TS=0
130 FOR I=1 TO 9 : TT=TT+BF(I)*BU(I) : TS=TS+BF(I)
140 PRINT USING "#####";I,BL(I),BU(I),BF(I) : NEXT I
150 LOCATE 24,30 : INPUT X
160 CLS : LINE (0,0)-(0,199) : LINE -(599,199)
170 FOR I=1 TO 13 : J=I*6 : LINE (0,199-J)-(599,199-J) : NEXT I
180 FOR I=1 TO CL : J=I*10 : K=199-BF(I)*6
190 FOR L=J TO J+5 : FOR M=K TO 199
200 PSET (L,M) : NEXT M : NEXT L : NEXT I
210 LOCATE 2,30 : INPUT X : CLS : RANDOMIZE
220 K=0 : X=0! : FOR I=1 TO CL
230 J=BF(I) : M=BU(I) : FOR L=1 TO J : K=K+1
240 X=X+M/TT : B(K)=X : NEXT L : NEXT I
250 CLS : PRINT "SAMPLE SIZE " : INPUT N : IF N=0 THEN GOTO 430
260 FOR I=1 TO TS : A(I)=0 : AF(I)=0 : NEXT I
270 FOR I=1 TO N : Y=RND : J=0
280 J=J+1 : IF Y>B(J) THEN GOTO 280
290 A(J)=A(J)+1 : NEXT I
300 FOR I=1 TO TS : J=0 : K=A(I)
310 IF K=1 THEN J=1
320 IF K=2 THEN J=2
330 IF K<=2 THEN GOTO 360
340 J=J+1 : IF K>BU(J) THEN GOTO 340
350 J=J-1
360 AF(J)=AF(J)+1 : NEXT I
370 CLS : LINE (0,0)-(0,199) : LINE -(599,199)
380 FOR I=1 TO 13 : J=I*6 : LINE (0,199-J)-(599,199-J) : NEXT I
390 FOR I=1 TO CL : J=I*10 : K=199-AF(I)*6
400 FOR L=J TO J+5 : FOR M=K TO 199
410 PSET (L,M) : NEXT M : NEXT L : NEXT I
420 LOCATE 2,35 : INPUT X : GOTO 250
430 END
```



EPOCH 200
SPECIES 30
GENERA 24

```
10 REM EVGS01.BAS : 2-NOV-1986
20 REM ------------------------------
30 REM EVOLUTION OF SPECIES AND GENERA
40 REM STOCHASTIC SIMULATION
50 REM ------------------------------
60 DIM G(200,50),B(50),D(50),L(50),M(50),V(50),W(50),S(50),P(50),C(50)
70 FOR I=1 TO 50 : B(I)=0 : D(I)=0 : L(I)=0 : V(I)=0 : W(I)=0
80 S(I)=0 : P(I)=0
90 FOR J=1 TO 20 : G(J,I)=0 : NEXT J : NEXT I
100 B(1)=1 : L(1)=0 : V(1)=1 : M(1)=1000000! : M(2)=100000!
110 M(3)=10000 : M(4)=1000
120 M(5)=100 : M(6)=10 : M(7)=1 : CLS
130 TG=1 : SG=1 : PRINT "NSP,P1,P2,P3" : INPUT NSP,P1,P2,P3
140 RANDOMIZE : CLS : SCREEN 2 : LINE (0,199)-(400,199) :LINE -(400,0)
150 LINE -(0,0) : LINE -(0,199) : G(1,1)=NSP : W(1)=NSP: I=1: SSP=NSP
160 I=I+1 : IF I>200 THEN GOTO 440
170 IF T>45 THEN GOTO 440
180 IF SSP=0 THEN GOTO 440
190 SS=0 :J=I-1:T=TG : FOR K=1 TO TG : L=G(J,K):IF L=0 THEN GOTO 340
200 LL=L : FOR N=1 TO L : Y=RND
210 Q=-1 : IF Y>P1 THEN Q=0
220 IF Y>P2 THEN Q=1
230 IF Y<P3 THEN GOTO 290
240 Q=0 : IF S(K)=7 THEN GOTO 290
250 T=T+1 : B(T)=I : L(T)=L(K)+1 : W(T)=1
260 G(I,T)=1
270 S(K)=S(K)+1 : P(T)=K
280 V(T)=V(K)+M(L(T))*(9-S(K))
290 LL=LL+Q : NEXT N
300 IF LL>75 THEN LL=75
310 IF W(K)<LL THEN W(K)=LL
320 SS=SS+LL
330 G(I,K)=LL : IF LL=0 THEN D(K)=I
340 NEXT K
350 TG=T
360 LINE (J*2,200-SSP)-(I*2,200-SS) : SSP=SS
370 LOCATE 2,65:PRINT "                ":LOCATE 2,65:PRINT "EPOCH ";:
380 PRINT USING "####";I : LOCATE 3,55 : PRINT "                "
390 LOCATE 3,55 : PRINT "SPECIES ";
400 PRINT USING "####";SS : LOCATE 4,65 : PRINT "                "
410 LOCATE 4,55 : PRINT "GENERA ";
420 PRINT USING "####";T
430 GOTO 160
440 LOCATE 1,50 : INPUT X : CLS : X=0 : I=0
450 I=I+1 : VV=1E+15 : IF I>TG THEN GOTO 560
460 FOR J=1 TO TG : IF V(J)<0 THEN GOTO 490
470 IF VV < V(J) THEN GOTO 490
480 VV=V(J) : K=J
490 NEXT J : V(K)=-V(K)
500  X=X+W(K)*3+6 : C(K)=X : IF X>599 THEN GOTO 560
510 FOR J=B(K) TO D(K) : GG=G(J,K)*1.5
520 IF GG<1 THEN GG=1
530 LINE (X-GG,J)-(X+GG,J) : NEXT J
540 IF K>1 THEN LINE(C(K),B(K))-(C(P(K)),B(K))
550 GOTO 450
560 LOCATE 24,78 : INPUT Y
570 END
```

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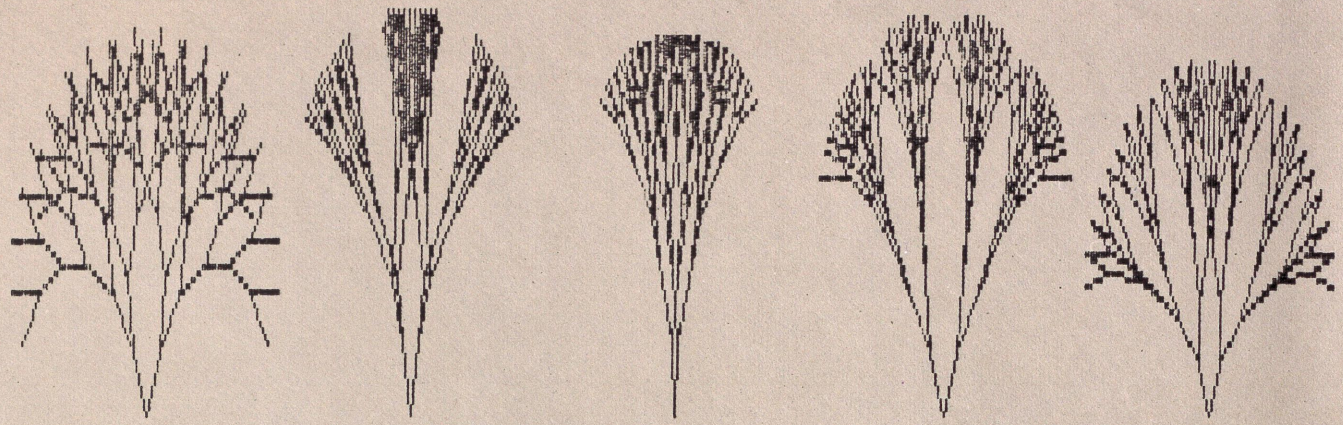

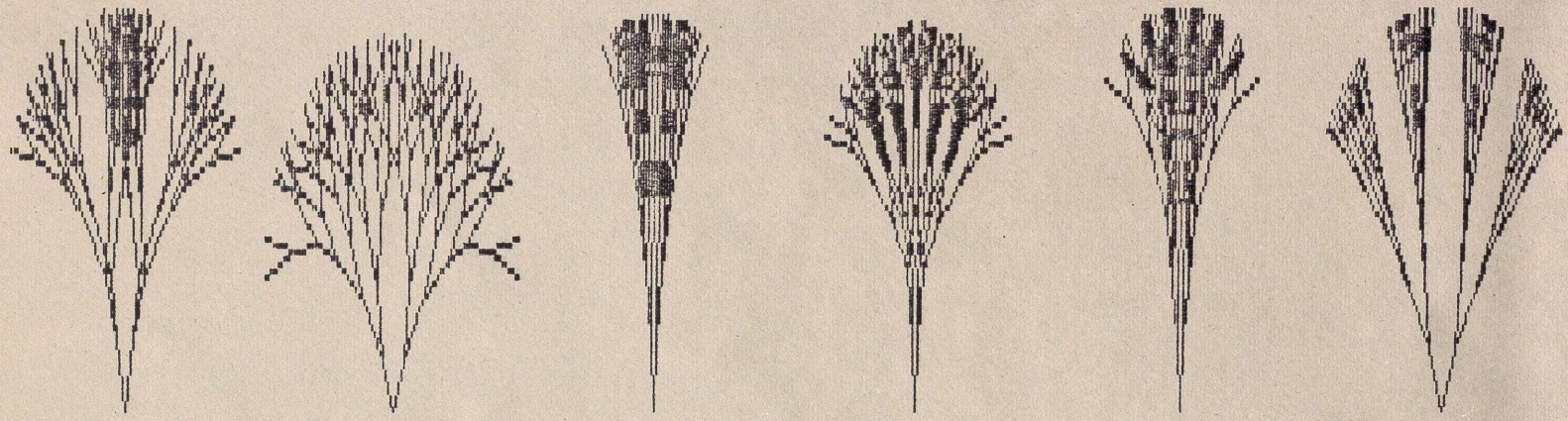

```
10 REM BIOMRF.BAS :  18-OCT-1986
20 DIM BL(6),BA(6),BLI(6),BAI(6)
30 DIM LT(11,6),AT(11,6),X1(11),Y1(11)
40 DIM XX(100),YY(100),TT(100),XXX(100),YYY(100),TTT(100)
50 FOR I=1 TO 11 : READ X1(I),Y1(I) : NEXT I
60 DATA 50,1,150,1,250,1,350,1,450,1,550,1
70 DATA 50,101,150,101,250,101,350,101,450,101
80 CV=3.1416/180!
90 FOR I=1 TO 6 : READ BL(I),BA(I),BLI(I),BAI(I) : BA(I)=BA(I)*CV
100 BAI(I)=BAI(I)*CV  :  NEXT I : CLS
110 DATA 10,15,1,10,10,15,1,10,10,15,1,10,10,15,1,10,10,15,1,10
115 DATA 10,15,1,10
120 RANDOMIZE  :  SCREEN 2 : K=1
130 FOR G=1 TO 100 : IF K=0 THEN GOTO 410
140 CLS  :  FOR I=1 TO 11 : FOR J=1 TO 6
150 LT(I,J)=BL(J) : AT(I,J)=BA(J) : NEXT J : NEXT I
160 FOR I=1 TO 11 : FOR J=1 TO 6 : AT(I,J)=BA(J) : LT(I,J)=BL(J)
170 X=1! : Y=RND : IF Y<.33 THEN X=-1! : IF Y>.66 THEN X=0!
180 LT(I,J)=LT(I,J)+X*BLI(J) : X=1! : Y=RND : IF Y>.66 THEN X=-1!
190 IF Y<.33 THEN X=0!
200 AT(I,J)=AT(I,J)+X*BAI(J)
210 NEXT J : NEXT I
220 FOR F=1 TO 11 :X1F=X1(F) : Y1F=Y1(F) : XX(1)=LT(F,1)*SIN(AT(F,1))
230 YY(1)=LT(F,1)*COS(AT(F,1)) : TT(1)=AT(F,1) : TT(2)=-TT(1)
240 XX(2)=XX(1) : XX(1)=XX(1)+X1F : XX(2)=X1F-XX(2) : YY(1)=Y1F+YY(1)
250 YY(2)=YY(1):LINE(X1F,Y1F)-(XX(1),YY(1)):LINE(X1F,Y1F)-(XX(2),YY(2))
260 N=2  :  FOR S=2 TO 6  :  L=0 : BLX=LT(F,S) : BAX=AT(F,S)
270 FOR J=1 TO N : T1=BAX+TT(J) : T2=TT(J)-BAX
280 XXX(L+1)=XX(J)+BLX*SIN(T1):YYY(L+1)=YY(J)+BLX*COS(T1):TTT(L+1)=T1
290 XXX(L+2)=XX(J)+BLX*SIN(T2):YYY(L+2)=YY(J)+BLX*COS(T2):TTT(L+2)=T2
300 LINE (XX(J),YY(J))-(XXX(L+1),YYY(L+1))
310 LINE(XX(J),YY(J))-(XXX(L+2),YYY(L+2))
320 L=L+2  :  NEXT J
330 N=N*2  :  FOR J=1 TO N  :  XX(J)=XXX(J)  :  YY(J)=YYY(J)
340 TT(J)=TTT(J)  :  NEXT J
350 NEXT S  :  NEXT F
360 LOCATE 23,75 : PRINT "  "
370 LOCATE 23,75 : INPUT K
380 IF K=0 THEN GOTO 410
390 FOR I=1 TO 6 : BL(I)=LT(K,I)
400 BA(I)=AT(K,I) : NEXT I
410 NEXT G : LOCATE 24,79 : INPUT K
420 END
```

30

A SIMULATION MODEL OF HUMAN RESOURCE USE

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INTRODUCTION

A comprehensive model of human resource use incorporating the following features has been developed: (i) a number of harvesters, (ii) a number of resources, (iii) a number of sites with a variety of geometrical configurations, (iv) allocation of available effort between territorial defence and resource harvesting, (v) Usurpation of resources, (vi) exchange of resources, (vii) migration of the harvesters, (viii) a variety of social interactions amongst the harvesters including kinship and reciprocation, (ix) birth and death rates dependent on success in acquisition of resources. This simulation model involving about 1000 Fortran IV statements has been made operational. Obviously, a series of submodels have to be investigated one by one. The first problem taken up for investigation is whether a harvester can arrive at the optimal harvesting strategy based on information relating to yield and effort levels alone. It has been shown that any simple algorithm tends to result in over-exploitation and resource exhaustion. Only a very long range averaging process can permit the harvester to arrive at the optimal effort. This is unlikely to obtain in practice

MAIN FEATURES OF THE MODEL

The central features in the model are different habitats, renewable resources and the harvester population.

There are NYS habitats or sites. These sites are distributed in the space on x,y plane which are separated from

each other as given by the distance matrix DST.

The renewable resources characterized by growth rate GR are distributed on different sites. Each site has a carrying capacity CKR for the resource and a threshold value DR below which a resource cannot be harvested. The initial level VR of the resource on each site and the transport cost of the resource over unit distance are specified at the initial time.

Harvester population may be thought of as individuals, households and communities. They are located in different sites and are characterized by genotype IGN. Thus there are NGEN different number of genotypes on each site I. At a given site, each genotype has a different number of harvesters IGEN. Thus the total number of harvesters on a given site is the sum of all harvesters belonging to different gentypes existing on that site NXH(I).

At a given time, each harvester has a location as its head quarters IHQ. This is essentially a site or habitat located on the space. Each harvester has a certain wealth WLTH either earned by own labour or through social exchange and a minimal need for the resource. Each harvester is related to other harveters by bonds of alliance given by the alliance matrix ALPH or $[\alpha_{ij}]$. Harvester i is cooperative with the harvester j if α_{ij} is positive and antagonistic if α_{ij} is negative.

Each harvester on each site puts efforts to exploit the resource to its benefit. This is specified in the model as the harvesting effort HR , war effort WR and the resource defence effort DF. Harvesting effort is the proportion of the effort devoted by the harvester to harvest the resource. War effort is the proportion of the effort devoted to usurp the wealth from other harvesters. Rest of the effort is devoted to counter the war efforts exerted by other harvesters.

RESOURCE DYNAMICS OF THE MODEL

Resources are utilized by the harvesters to their benefits. The proportion of the resource j at site i, exploited by the harvester k (effective harvesting effort EH in the model) is determined as the function of the harvester's actual harvesting effort AH and its and other harvesters' defence harvesting effort BH.

$$AH_{i,j,k} = WLTH_{i,k} * PR1_{i,j,k,it} * HR_{i,k,it}$$

$$BH_{i,j,k} = WLTH_{i,k} * PR2_{i,j,k,it} * DF_{i,k,it} \qquad (1)$$

where

PR1 = Proportion of the wealth used for actual harvest

PR2 = Proportion of the wealth used to defend the resorce

The effective harvesting effort of the harvester is now given by

$$EH_{i,j,k} = AH_{i,j,k} * (1 - \exp(-X))$$

where

$$X = \frac{\sum_{k1}^{NXH(i)} \alpha_{i,i,k,k1} * BH_{i,j,k}}{\sum_{k1}^{NXH(i1)} | \alpha_{i,i1,k,k1} | * BH_{i,j,k}} \qquad (2)$$

α = alliance of the harvester with other harvesters.

Total harvesting effort of all the harvesters for each resource on each site is determined as the sum of the effective harvesting efforts of all the harvesters.

$$TOTH_{i,j} = \sum_{k=1}^{NXH(i)} EH_{i,j,k} \qquad (3)$$

The total yield from a given resource on a given site is given by

$$YIELD_{i,j} = (VR_{i,j} - DR_{i,j}) * (1 - \exp(-TOTH_{i,j}/(VR_{i,j}+DR_{i,j}))) \qquad (4)$$

$YIELD_{i,j} = 0$ if the resource level $VR_{i,j}$ goes below the threshold $DR_{i,j}$ below which a resource cannot be harvested. This yield is shared among all the harvesters in proportion to their effort. The individual yield of each harvester is now given by

$$YK_{i,j,k} = YIELD_{i,j} * EH_{i,j,k} / TOTH_{i,j} \qquad (5)$$

As a result of the harvest, the level of the resource at each site becomes

$$VR_{i,j} = VR_{i,j} - YIELD_{i,j} \qquad (6)$$

Resources migrate from one site to another in some proportion. After migration the resource at each site grows according to the equation

$$VR_{i,j} = VR_{i,j} + VR_{i,j} * GR_j * (1 - VR_{i,j} / CKR_{i,j}) \qquad (7)$$

This resource is used by the harveter in the next time step.

The yield acquired by the harvester is transported to its head quarters. The total yield received by each harvester from a resource pooled from all sites is given by

$$BTOT_{i,j,k} = \sum_{i1}^{NYS} (YK_{i,j,k} - TR_j * DST(i1, IHQ(i,k))) \qquad (8)$$

Wealth of each harvester depends on the minimal need for the resource. It is given by

$$WLTH_{i,k} = \sum_{j}^{NZR} BTOT_{i,j,k} / NEED_{i,j,k} \qquad (9)$$

Harvesters who belong to the same alliance group usurp the wealth from the harvesters who are the members of a less powerful alliance. The collective power of each alliance of the harvesters is given by

$$PW_{i,k} = \sum_{j}^{NZR} WLTH_{i,j} * WR_{i,j} \qquad (\text{if } \alpha_{i,j} > 0) \qquad (10)$$

After usurpation, we have the final wealth position of each harvester. If a harvester has gained wealth over previous time step, it stays put, otherwise it settles randomely in any of the available habitat.

A harvester risks death depending on its wealth relative to the maximum wealth.The dead harvester being removed, the survivors are renumbered appropriately and are characterized by head quarters,genotype,war effort,harvesting effort and wealth. Surviving harvesters do or do not reproduce depending on their wealth and luck. Reproduction is simple binary fission. Both daughter harvesters inherit half the wealth and all other properties of the parent. The harvesters ,then decide on the harvesting effort and the resource defence strategies for the next time step so that it can exploit the resource at the optimal level. The functional flowchart of the model is included in the appendix A.

MAIN OBJECTIVES OF THE MODEL

The model aims to explore questions of the type :

(1) How an individual can learn to exploit a resource at an optimal level ? It can be trial & error , social learning or insightful learning etc.

(2) What is an optimal level if there are many sites and many resources ?

(3) Can a group exploit the resource at an optimal level ? How are co-operative and non- cooperative solutions arrived at ?

OPTIMUM HARVESTING EFFORT

To explore the first question, we considered a simple case wherein only one resource at a single site is harvested by a single harvester. Naturally, there is neither harvester migration nor resource migration. Further, the harvester is restricted from reproduction and is assumed to be immortal. We are interested in how a harvester decides on the optimum harvesting effort strategy. By optimum harvesting effort, we mean the harvesting effort corresponding to maximum yield on a sustainable basis.To get the optimum harvesting effort, we solved the equations (1) through (10) numerically for steady state for a given carrying capacity of the site for the resource, the threshold below which the resource cannot be harvested, need of the harvester for the resource and intrinsic growth rate of the resource.

Steady state curves for yield and resource levels are contained in the figures 1.0 to 1.9. The figures 1.0,1.1,1.2,1.3 & 1.9 show that as the need of the harvester for the resource increases, the optimum harvesting effort also increases irrespective of the intrinsic growth rate of the resource. The figures 1.0,1.1,1.2,1.3,1.4,1.5 show the influence of the growth rate of the resource on the maximum yield one can obtain. As the

growth rate of the resource increases, the maximum yield obtained also increases irrespective of the need of the harvester for the resource. As we increase the value of the threshold below which a resource cannot be harvested, the optimum harvesting effort also increases though there is no change in the corresponding or the maximum yield obtained. This is shown clearly in the figures 1.6,1.7,1.8,1.9 . Thus the optimum harvesting effort depends on the need of the harvester for the resource and the quantity of the resource that is available for harvesting while the maximum yield obtained varies directly as the intrinsic growth rate of the resource.

Table 1 summarizes the optimum harvesting effort and the corresponding yield for different values of intrinsic growth rate of the resource, the need of the harvester for the resource and the thrshold below which a resource cannot be harvested.

OPTIMUM HARVESTING EFFORT STRATEGY

Harvester uses various methods to exploit the resource at the optimal level for its benefit. One of these methods is the trial & error method. In this method , the harvester learns to exploit the resource based on its past experience. This essentially requires the information on the harvesting effort and the corresponding yield or wealth obtained at the previous two consecutive time steps. Now, the harvester decides on the new harvesting effort strategy as follows:

(a) It increases the harvesting effort if the increase in the harvesting effort has increased the wealth OR the decrease in the harvesting effort has decreased the wealth .

(b) It decreases the harvesting effort if the increase in the harvesting effort has decreased the wealth OR the decrease in the harvesting effort has increased the wealth.

Let HR_t & HR_{t-1} be the harvesting efforts at time t & t-1 time steps.

Let W_t & W_{t-1} be the corresponding Wealth or yield. Then the new harvesting effort at time t+1 is given by

$$HR_{t-1} = HR_t + \Delta H_{new}$$

ΔH_{new} is +ve if $\Delta H_{old} >= 0$ & $\Delta W >= 0$

or

if $\Delta H_{old} < 0$ & $\Delta W < 0$

ΔH_{new} is -ve if $\Delta H_{old} >= 0$ & $\Delta W < 0$

or

if $\Delta H_{old} < 0$ & $\Delta W >= 0$

where $\Delta H_{old} = HR_t - HR_{t-1}$

$\Delta W = W_t - W_{t-1}$

Resource information in determining the new harvesting effort is of no use because it gives the same result as the wealth or yield information does.

Several methods are proposed to calculate the value of ΔH_{new} .

Method 1:-

In this method, we calculate ΔH_{new} as

$$\Delta H_{new} = C * \Delta W$$

where C is a constant and the harvesting effort is altered every time step based on the above criteria. For different initial conditions of resource level, wealth and harvesting effort and different values of C , this method did not yield the optimum harvesting effort.

Method 2:-

$$HR_{t+1} = HR_t + C * \Delta W / \Delta H_{old}$$

To start with, we assumed one harvesting effort held constant at HE1 for T time steps. Then we assumed another harvesting effort held constant at HE2 for the same T time steps. The wealth W1 & W2 corresponding to the harvesting efforts HE1 and HE2 are noted at the end of T time steps. Then, the new harvesting effort HE3 is derived as

$$HE3 = HE2 + C * \Delta W / \Delta H_{old}$$

where $\Delta H_{old} = HE_2 - HE_1$

$\Delta W = W_2 - W_1$

Now set $HE_1 = HE_2$ and $HE_2 = HE_3$

The above steps are repeated till the wealth or the Yield stabilizes. The value of C is held constant through out the experiment.

This method failed as the harvesting effort did not reach the optimum value for different initial conditions of harvesting effort, resource level and wealth and for different values of C.

Method 3:-

$$HR_{t+1} = HR_t + SLF$$

where, $SLF = C * \Delta W / \Delta H_{old}$ and $-0.1 < SLF < 0.1$

In this method, we fixed the lower & upper bounds on the sloping function SLF to be -0.1 & +0.1 , in addition to all the steps of method 2. This method also failed in reaching the optimum harvesting effort.

Method 4:-

$$HR_{t+1} = HR_t + C * \Delta W / \Delta H_{old}$$

In this method, the value of C is altered in some proportion whenever $\Delta W / \Delta H_{old}$ changes the sign and all the other steps of method 2 are retained. Harvesting effort reached the optimum value after a large number of time steps and for a long time interval T(= 20 time steps).

Method 5 ;-

$$HR_{t+1} = HR_t + C * Sign\ (\Delta W / \Delta H_{old})$$

This method includes all the steps of method 4 except that here we consider the sign of $\Delta W / \Delta H_{old}$ which essentially gives the direction in which harvesting effort should be altered and C gives the magnitude by which it should be altered.

The results for the time interval T=15 or 20 show that the harvesting effort stabilizes at the optimal value considerably at a faster rate where as for time interval T=10, the harvesting effort did not reach the optimal value though it stabilizes.This is shown clearly in the figures 2.1 to 2.10 which contain the time trajectories for different initial conditions of wealth , resource level , harvesting effort and varying C in different proportions for a given carrying capacity of the site,the need of the harvester for the resource and the threshold below which a resource can not be harvested

REFUGIUM PROBLEM

This includes the investigation of the role played by a portion of the resource which is not harvested, in determining the optimal harvesting effort.Here, we assume the resource at one site is exploited out of two sites and a fraction of the resource is allowed to migrate from one site to another site every time step.

As earlier the equations (1) through (10) are solved numerically for the steady state to get the optimal harvesting effort for different carrying capacities of the two sites for the resource and for different proportions of migration of the resource for a given growth rate of the resource and given need of the harvester for the resource. The resource at site 1 is allowed for maximum exploitation by keeping the threshold below which a resource can not be harvested at zero. The steady state curves for the carrying capacities 2.25&2.25 ,3.0&1.5 and 1.5&3.0

of the two sites and for migration levels 75%,50% & 25% are contained in the figures 3.1 to 3.9 .

The steady state curves for yield in figures 3.1 to 3.3 show that when the resource migration is at lower rate(25%),the yield obtained is maximum if the resource at the smaller site is harvested, the optimum harvesting effort being comparitively high. These figures also contain the steady state curves for resource levels at two sites which indicate that if the resource migration is at lower rate, then the resource at two sites are not completely wiped off even if the harvester puts more and more effort in harvesting the resource. On the other hand, the steady state curves for resource in the figures 3.4 to 3.9 show that if the resource migration from two sites is comparitively at higher rate, then the resource at two sites get completely wiped off as the harvester puts more and more harvesting effort.

Table 2 summarizes the optimal harvesting effort and the corresponding yield obtained for three different carrying capacities of the sites for the resource and three different proportions of resource migration. It is clear from the table that if the carrying capacities of the two sites ,exploited and unexploited are equal, then the yield obtained at the exploited site is maximum when the rate of resource migration from the two sites is 50% .

If the carrying capacity of the exploited site is less than the carrying capacity of the unexploited site then the yield obtained is maximum when the resource migration is at lower

rate. The optimum harvesting effort in this case, is on the higher side. As the migration rate of the resource increases, the yield obtained at the exploited site decreases along with the optimum harvesting effort. This is clearely brought up in the figure 4.3 where in the carrying capacity of the exploited site is 1.5 which is less than the carrying capacity of the unexploited site (=3.0).

It is just opposite if we consider the larger carrying capacity site is harvested while the smaller carrying capacity site is untouched by the harvester .This is shown in the figure 4.2 where in the carrying capacity of the exploited site is 3.0 and that of the unexploited site is 1.5 . The yield obtained at the exploited site is maximum when the rate of migraion of the resource is very high (i.e., at 75%) from both the sites.

TABLE - 1

Sl. No.	GIR	NEED	THRESHOLD	OPTIMUM HR EFFORT	RESOURCE	YIELD
1.	1	0.1	0.4	0.295	1.1278	0.3750
2.	1	0.2	0.4	0.59	1.1278	0.3750
3.	2	0.1	0.4	0.29	1.5	0.75
4.	2	0.2	0.4	0.58	1.5	0.75
5.	3	0.1	0.4	0.29	1.8779	1.1250
6.	4	0.1	0.4	0.295	2.2471	1.5
7.	1	0.1	0.0	0.12	1.186	0.37
8.	1	0.1	0.5	0.395	1.1276	0.3750
9.	1	0.1	0.6	0.575	1.1256	0.3750
10.	1	0.2	0.5	0.795	1.1244	0.3750

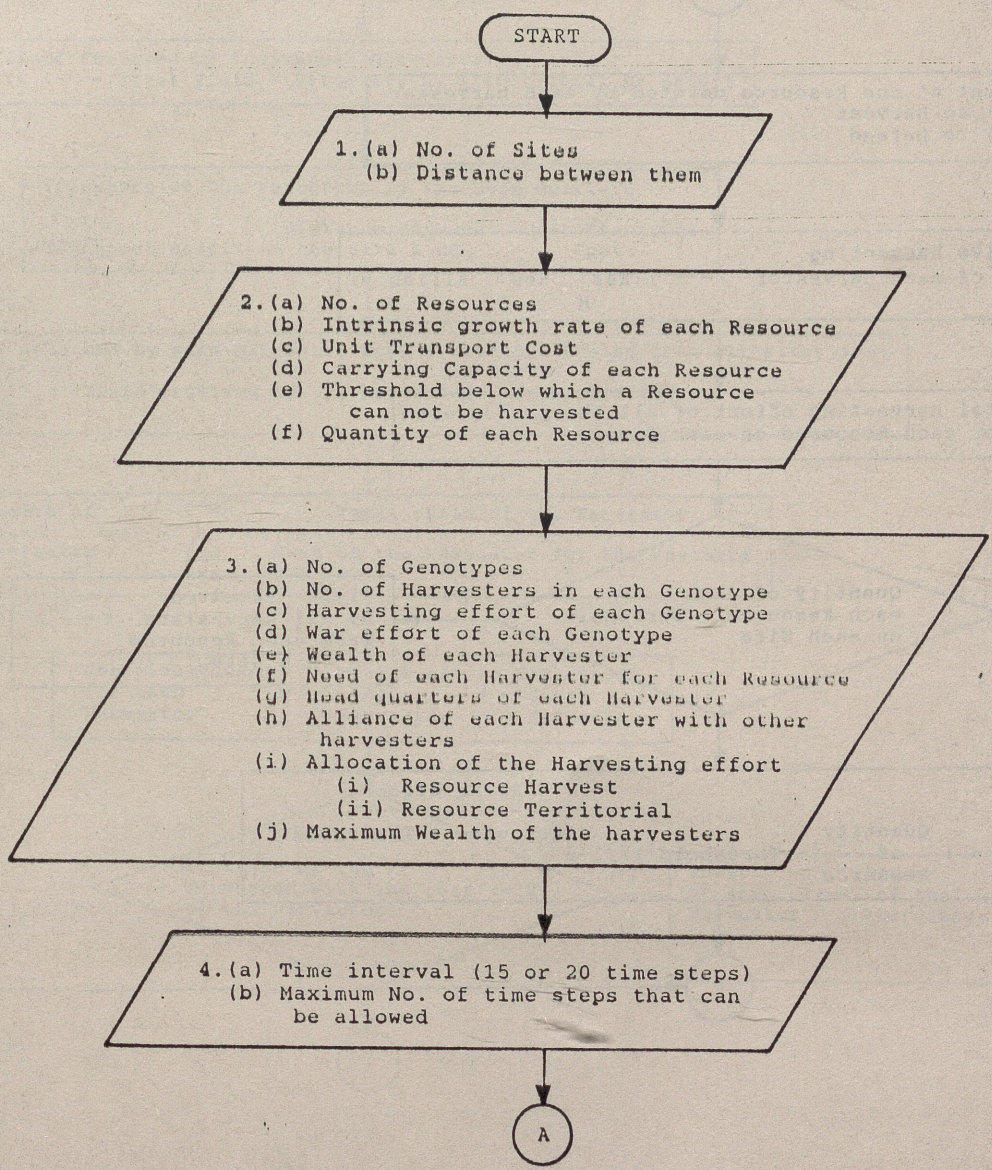
TABLE - 2

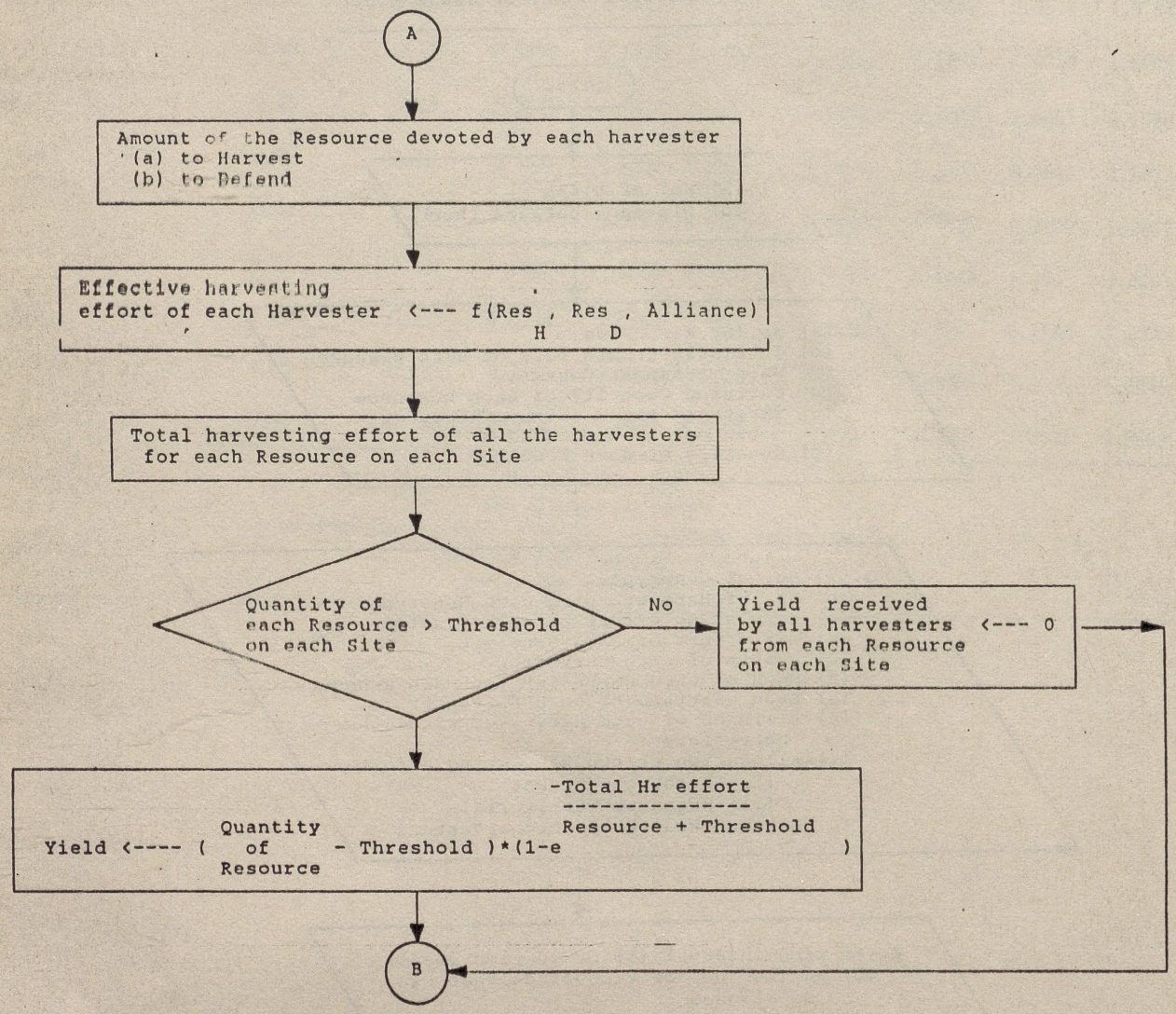
Sl. No.	Carrying capacities		Proportion of Migration Everytime step	Optimum Harvesting effort at Site 1	Resource level at site 1			Yield at Site 1	Resource level at site 2		
	Site 1	Site 2			After harvest	After migration	After growth		After harvest	After migration	After growth
1.	2.25	2.25	0.75	0.155	0.7833	1.3348	1.8777	1.09437	1.5186	0.9672	1.5186
			0.50	0.165	0.5599	1.1224	1.6849	1.1249	1.6849	1.1224	1.6849
			0.25	0.17	0.4241	0.8455	1.3733	0.9492	2.1098	1.6883	2.1098
2.	3.0	1.5	0.75	0.15	0.7633	1.1263	1.8297	1.0664	1.2473	0.8843	1.2473
			0.50	0.16	0.5532	0.9109	1.5453	0.9920	1.2686	0.9109	1.2687
			0.25	0.135	0.9345	1.0720	1.7609	0.8264	1.4843	1.3469	1.48437
3.	1.5	3.0	0.75	0.155	0.5334	1.0780	1.3813	0.8478	1.2595	0.7149	1.2595
			0.50	0.185	0.3323	0.9985	1.3323	0.9999	1.6646	0.9985	1.6646
			0.25	0.765	0.0004	0.6670	1.0374	1.0370	2.6668	2.0002	2.6668

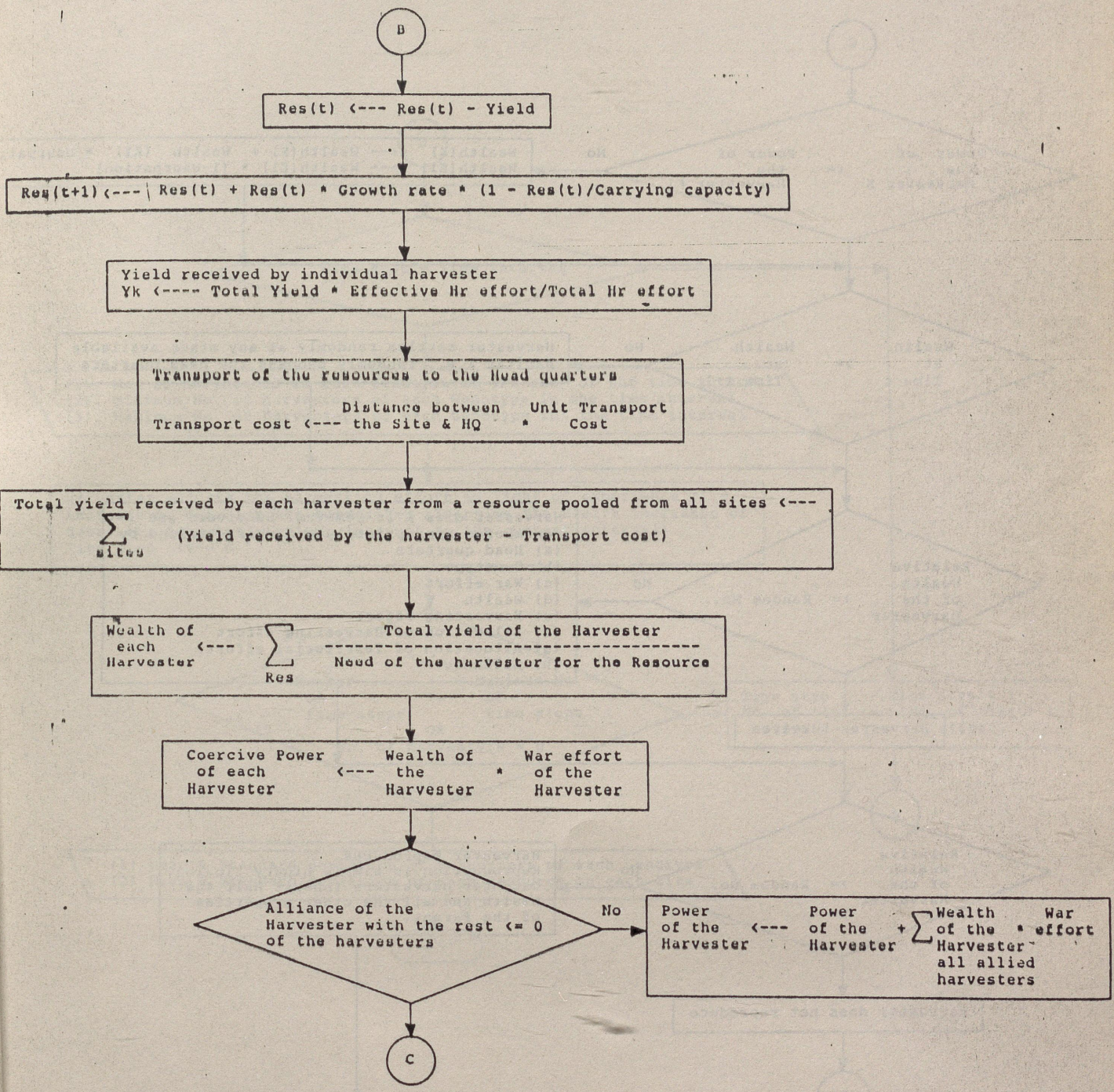
No. of Sites = 2
No. of resources = 1
Threshold below which a resource cannot be harvested = 0.0
Need for the resource = 0.1
Harvesting is at Site 1.

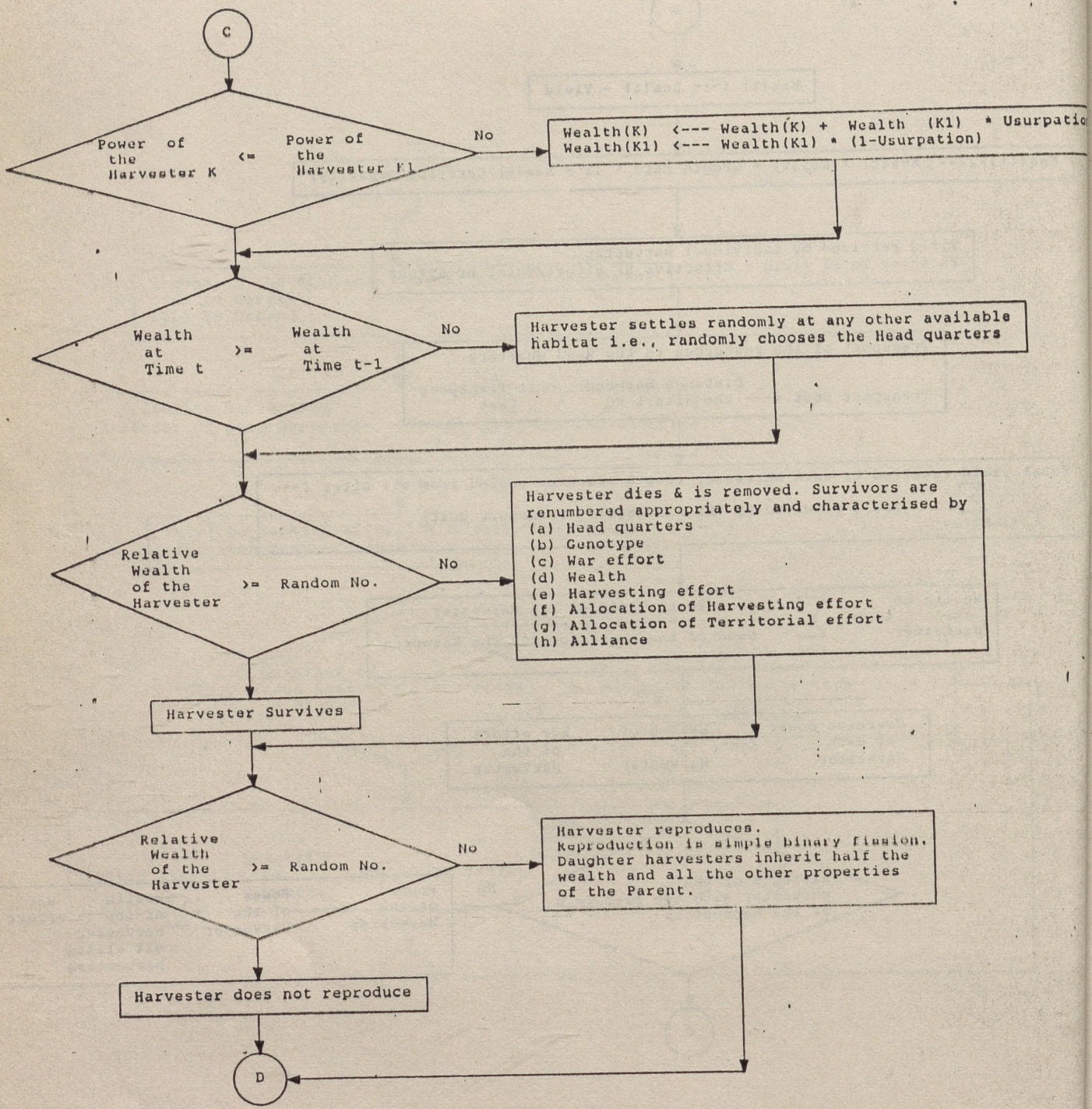
APPENDIX-A

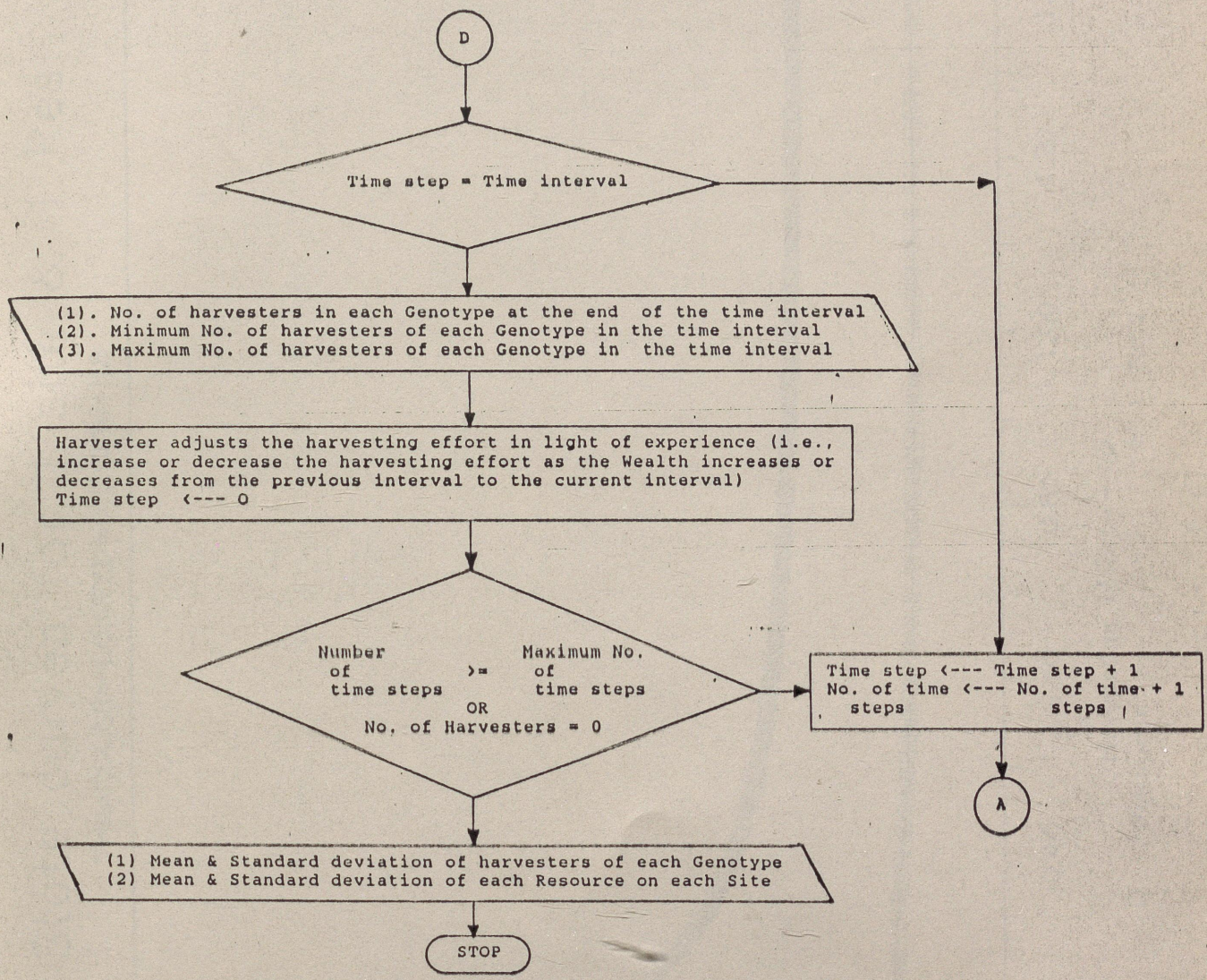
FUNCTIONAL FLOW CHART OF GRUSE MODEL




A
Amount of the Resource devoted by each harvester
(a) to Harvest
(b) to Defend
Effective harvesting
effort of each Harvester <--- f(Res , Res , Alliance)
H D
Total harvesting effort of all the harvesters
for each Resource on each Site
Quantity of
each Resource > Threshold
on each Site
No
Yield received
by all harvesters <--- 0
from each Resource
on each Site
-Total Hr effort
Yield <---- (Quantity of Resource - Threshold)*(1-e)
Resource + Threshold
B


B
Res(t) <--- Res(t) - Yield
Res(t+1) <--- Res(t) + Res(t) * Growth rate * (1 - Res(t)/Carrying capacity)
Yield received by individual harvester
Yk <---- Total Yield * Effective Hr effort/Total Hr effort
Transport of the resources to the Head quarters
Transport cost <--- Distance between the Site & HQ * Unit Transport Cost
Total yield received by each harvester from a resource pooled from all sites <---
∑ sites (Yield received by the harvester - Transport cost)
Wealth of each Harvester <--- ∑ Res Total Yield of the Harvester / Need of the harvester for the Resource
Coercive Power of each Harvester <--- Wealth of the Harvester * War effort of the Harvester
Alliance of the Harvester with the rest of the harvesters <= 0
No
Power of the Harvester <--- Power of the Harvester + ∑ all allied harvesters Wealth of the Harvester * War effort
C


C
Power of the Harvester K
<=
Power of the Harvester K1
No
Wealth(K) <--- Wealth(K) + Wealth (K1) * Usurpatio
Wealth(K1) <--- Wealth(K1) * (1-Usurpation)
Wealth at Time t
>=
Wealth at Time t-1
No
Harvester settles randomly at any other available habitat i.e., randomly chooses the Head quarters
Relative Wealth of the Harvester
>=
Random No.
No
Harvester dies & is removed. Survivors are renumbered appropriately and characterised by
(a) Head quarters
(b) Genotype
(c) War effort
(d) Wealth
(e) Harvesting effort
(f) Allocation of Harvesting effort
(g) Allocation of Territorial effort
(h) Alliance
Harvester Survives
Relative Wealth of the Harvester
>=
Random No.
No
Harvester reproduces. Reproduction is simple binary fission. Daughter harvesters inherit half the wealth and all the other properties of the Parent.
Harvester does not reproduce
D


D
Time step = Time interval
(1). No. of harvesters in each Genotype at the end of the time interval
(2). Minimum No. of harvesters of each Genotype in the time interval
(3). Maximum No. of harvesters of each Genotype in the time interval
Harvester adjusts the harvesting effort in light of experience (i.e., increase or decrease the harvesting effort as the Wealth increases or decreases from the previous interval to the current interval)
Time step <--- 0
Number of time steps >= Maximum No. of time steps
OR
No. of Harvesters = 0
Time step <--- Time step + 1
No. of time steps <--- No. of time steps + 1
A
(1) Mean & Standard deviation of harvesters of each Genotype
(2) Mean & Standard deviation of each Resource on each Site
STOP

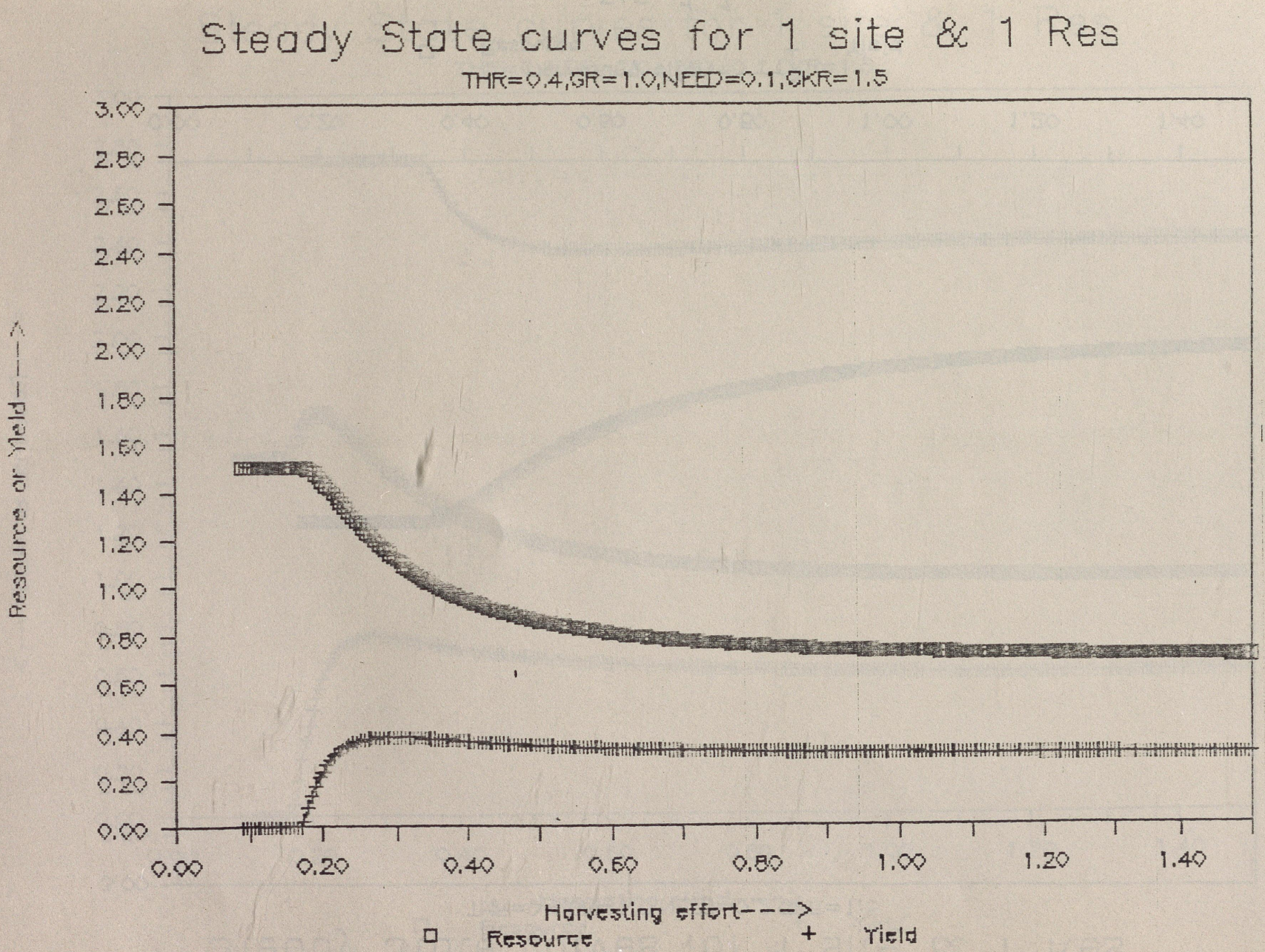

Steady State curves for 1 site & 1 Res
THR=0.4,GR=1.0,NEED=0.1,CKR=1.5
Resource or Yield--->
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
Harvesting effort--->
Resource
Yield

FIG 1.0

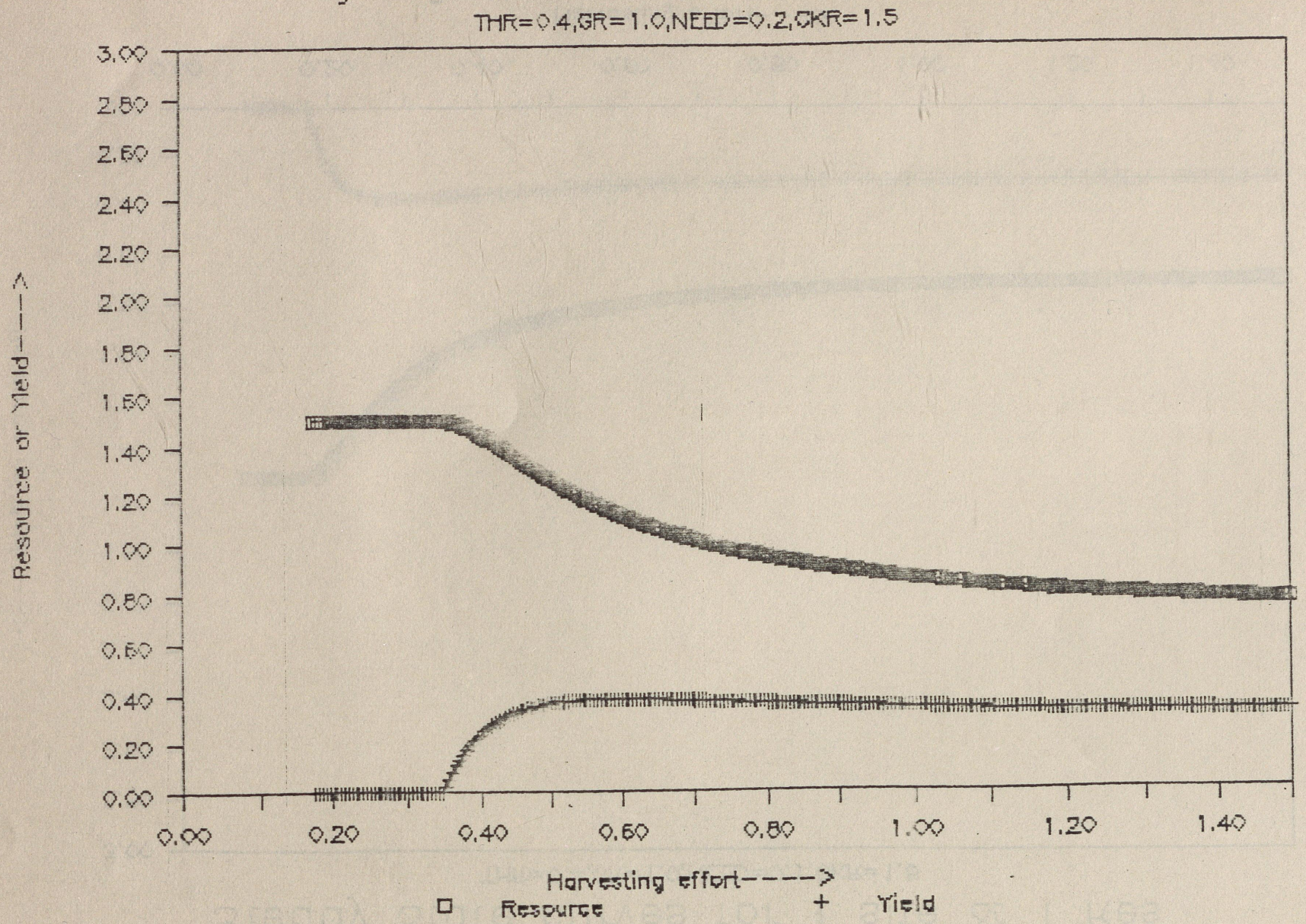


FIG. 1.1.

Steady State curves for 1 site & 1 Res

□ Resource

FIG. 1.1.

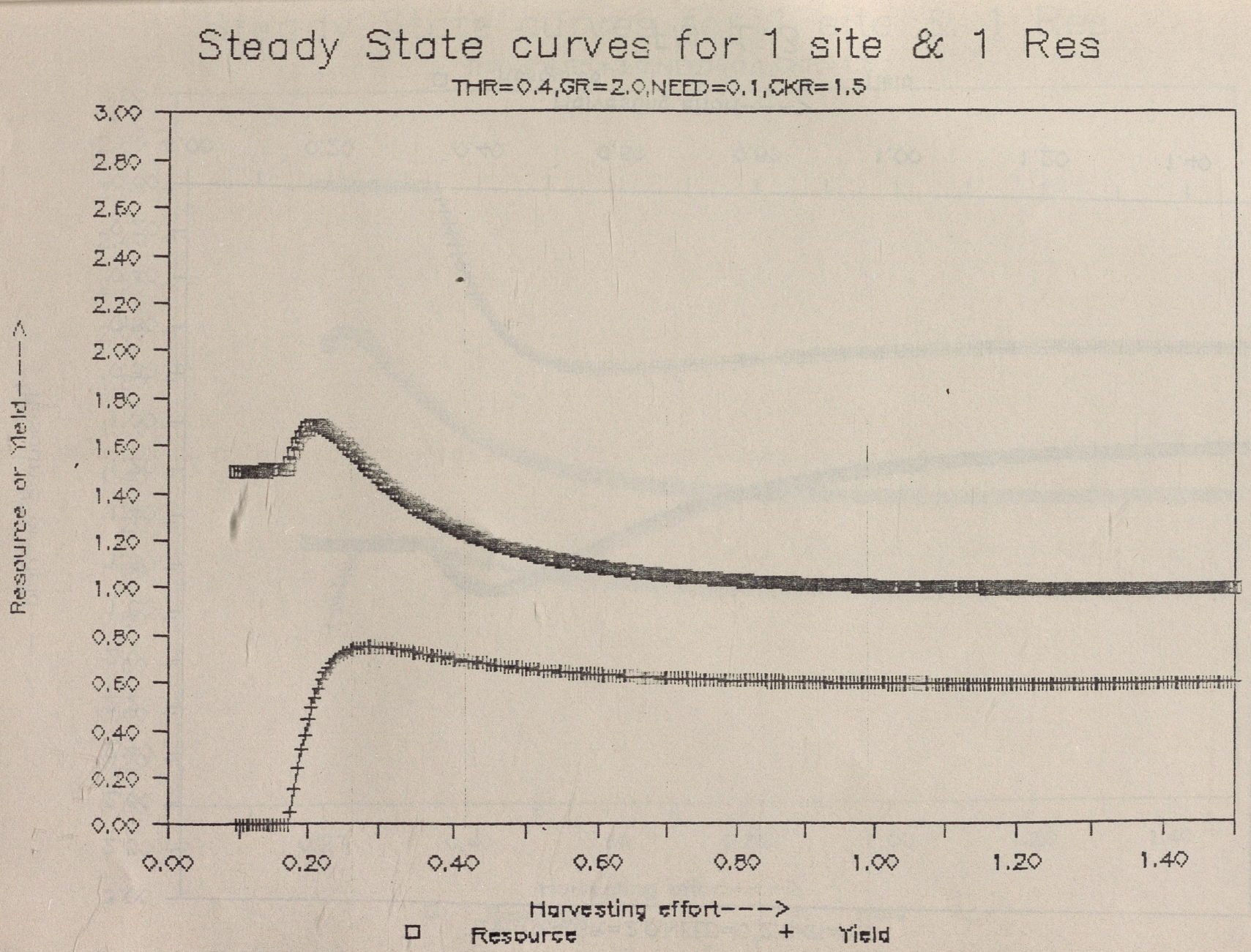


FIG. 1.2

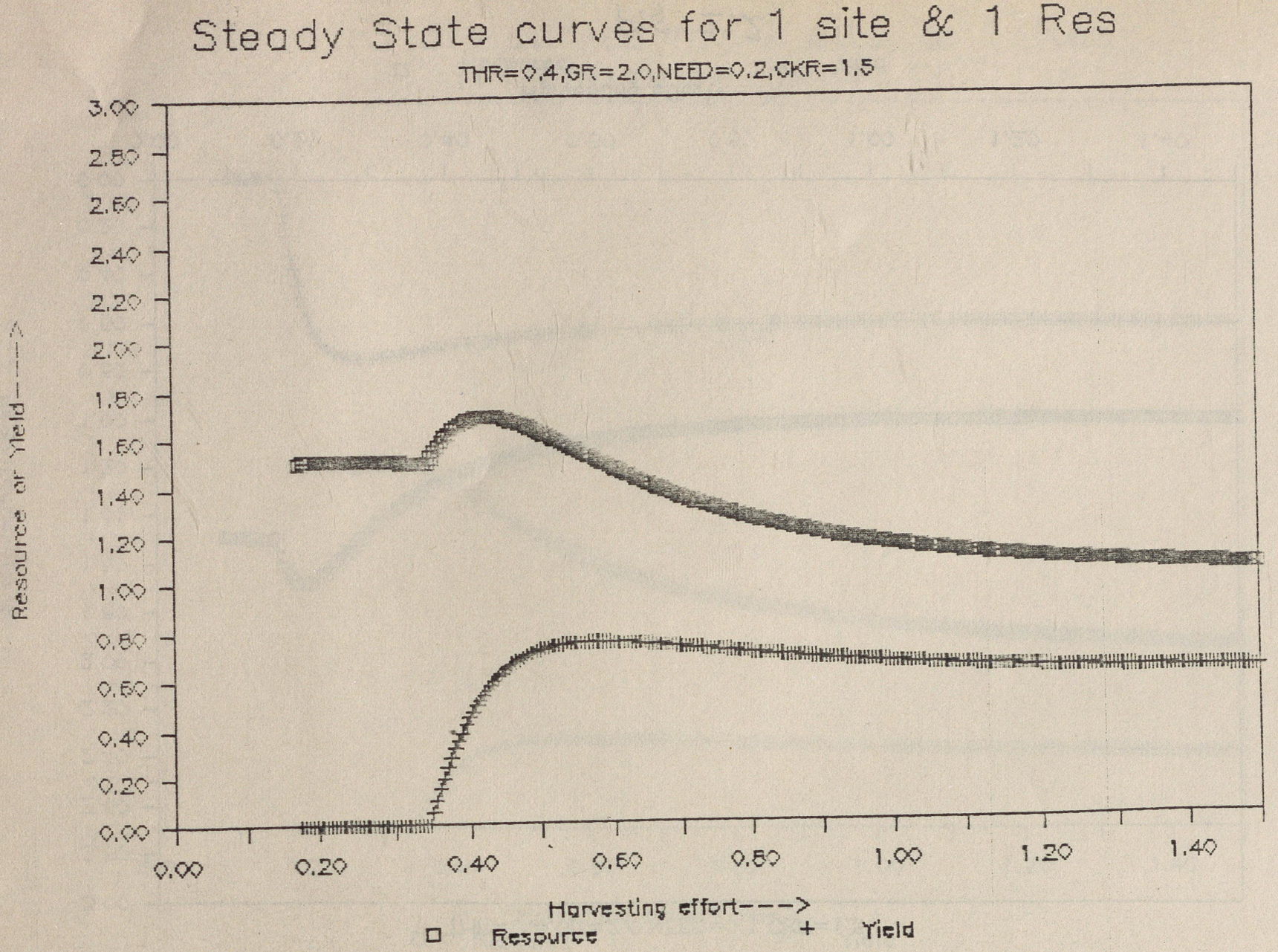


FIG. 1.3

Steady State curves for 1 site & 1 Res

FIG. 1.3

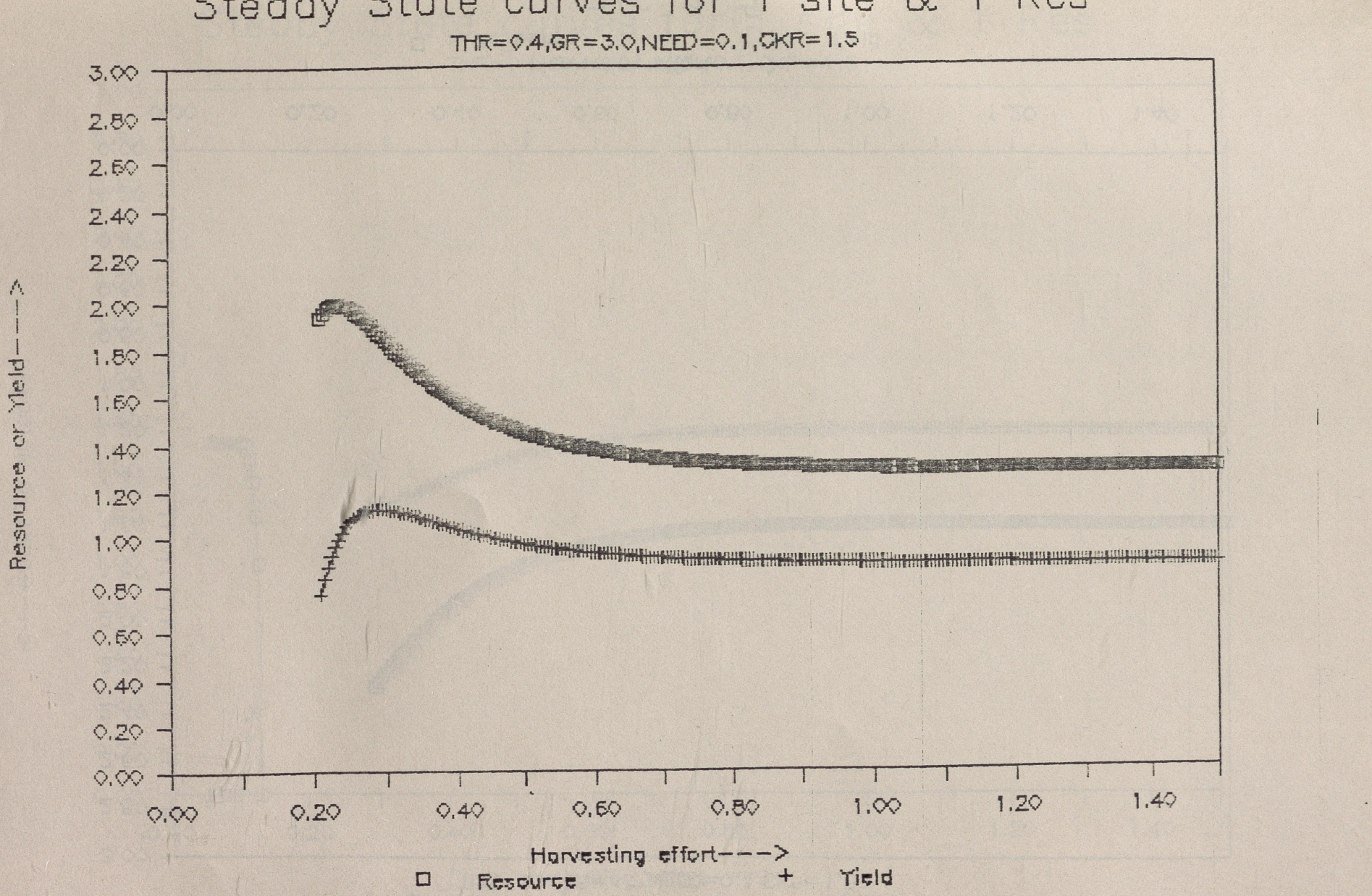

Steady State curves for 1 site & 1 Res
THR=0.4,GR=3.0,NEED=0.1,CKR=1.5
Resource or Yield--->
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
Harvesting effort--->
Resource
Yield

FIG. 1.4

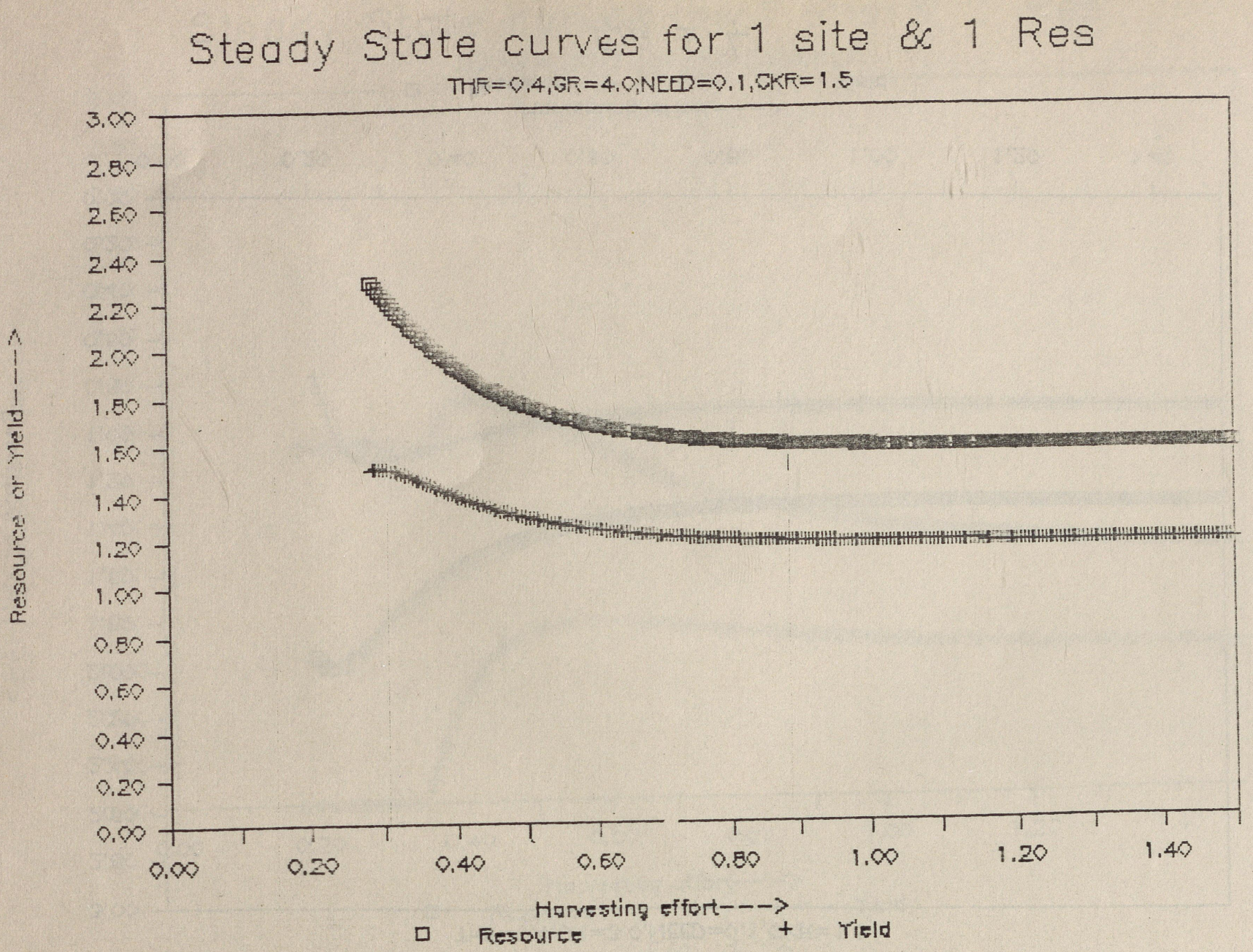

Steady State curves for 1 site & 1 Res
THR=0.4,GR=4.0,NEED=0.1,CKR=1.5
Resource or Yield--->
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
Harvesting effort--->
Resource
Yield

FIG. 1.5

□ Resource + Yield

FIG. 1.5

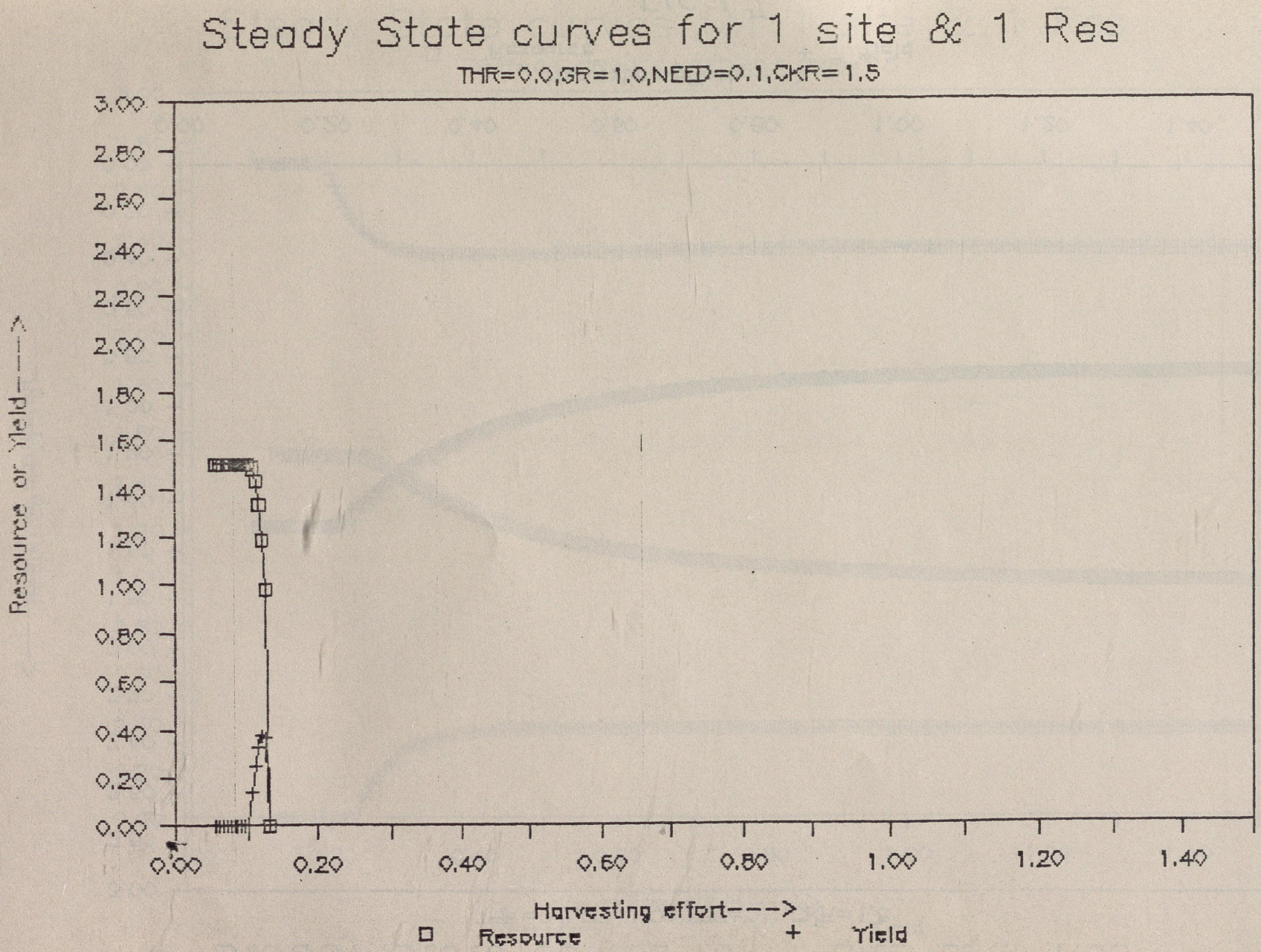


FIG. 1.6

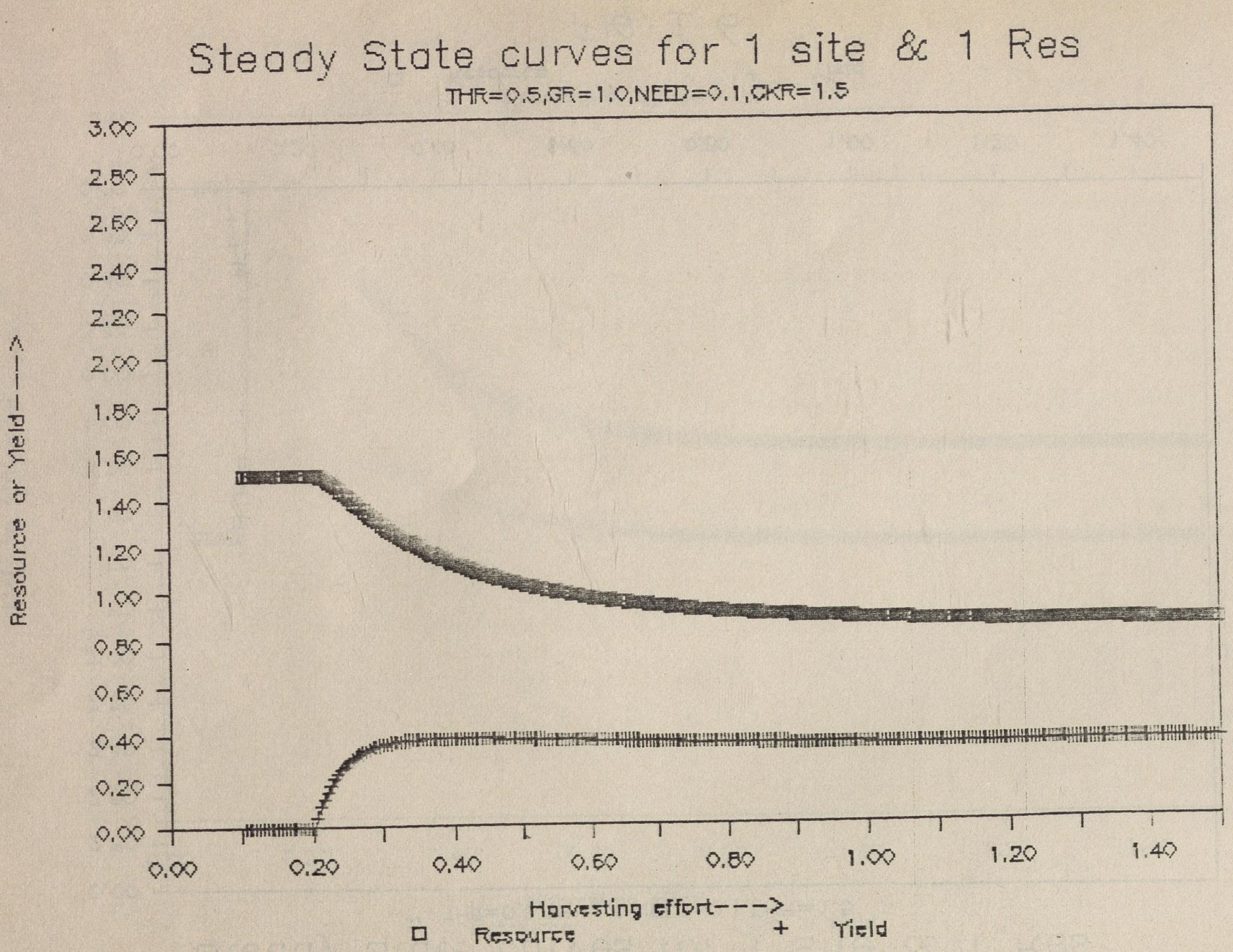


FIG. 1.7

Steady State curves for 1

□ Resource

FIG. 1.7

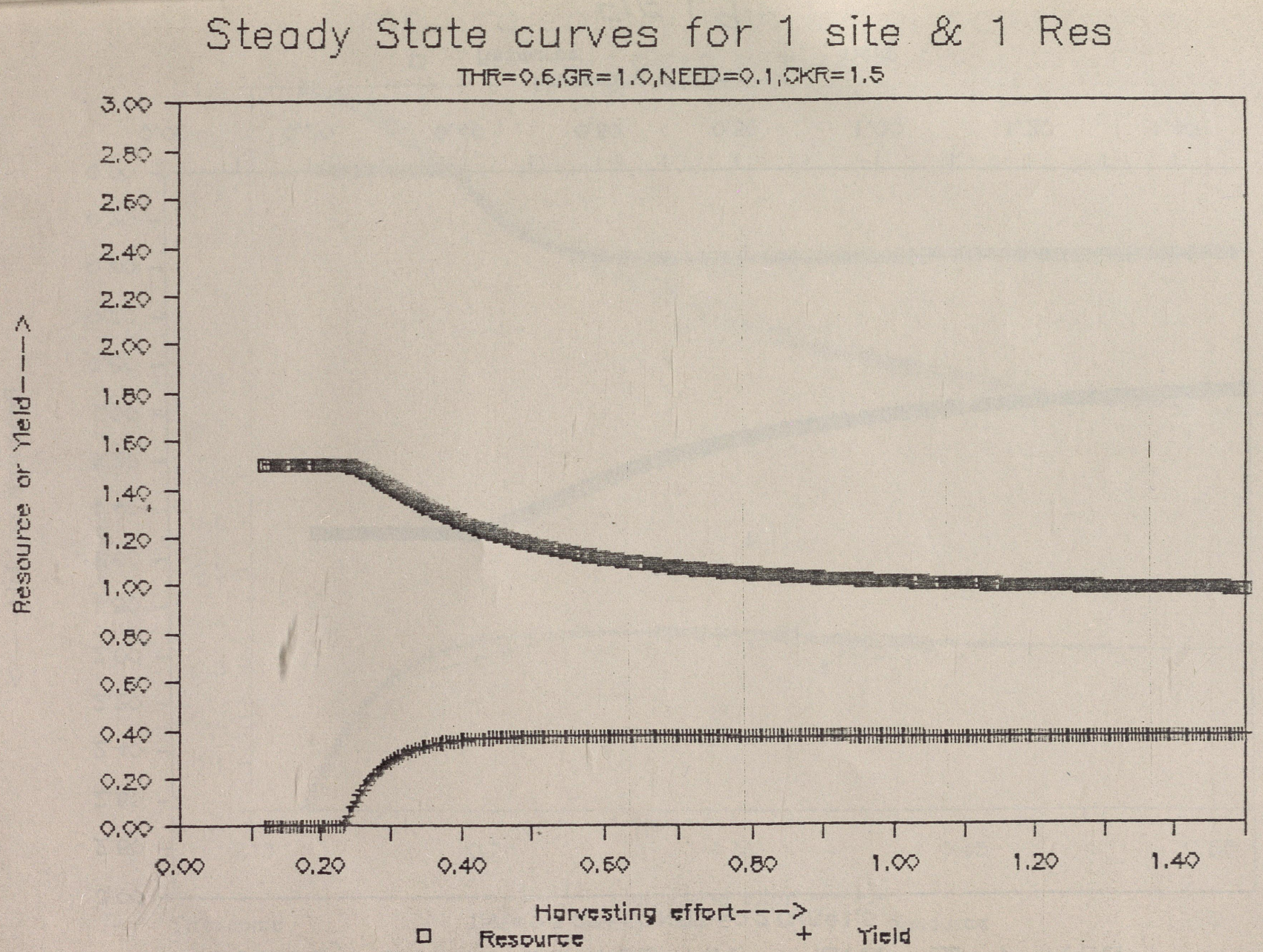


FIG. 1.8

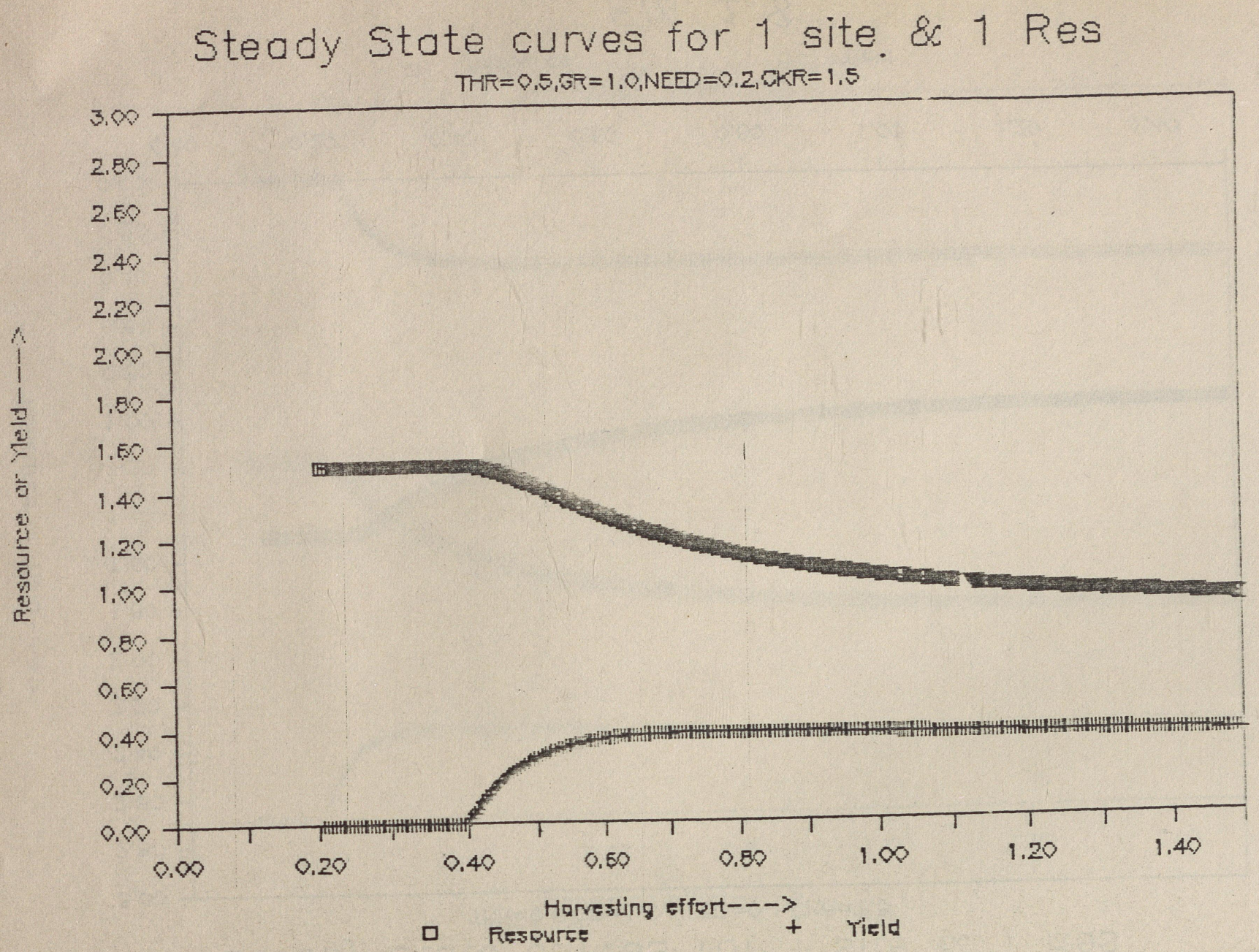


FIG. 1.9

Time Trajectory with initial

□ Resource

FIG. 1.9

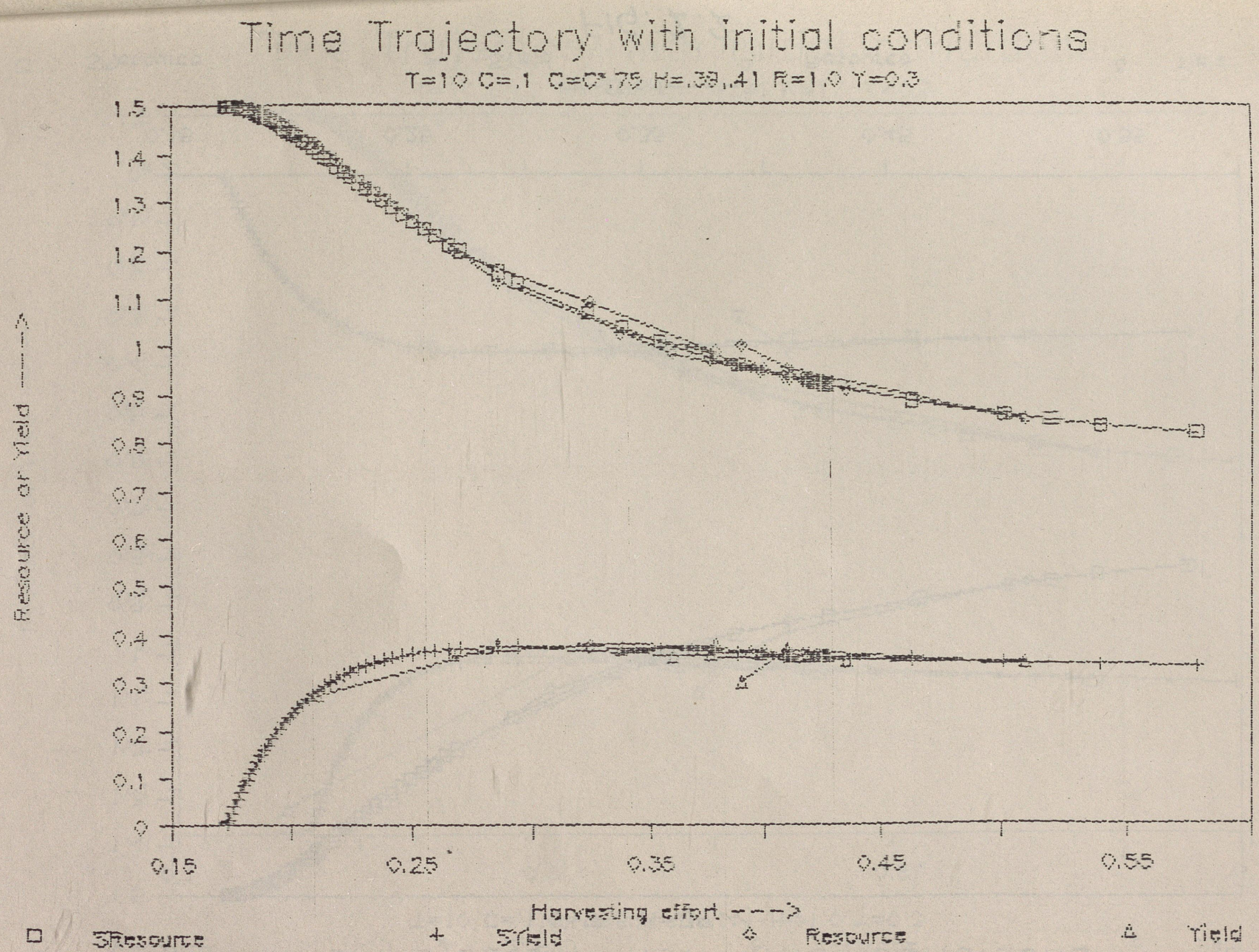


FIG. 2.1.

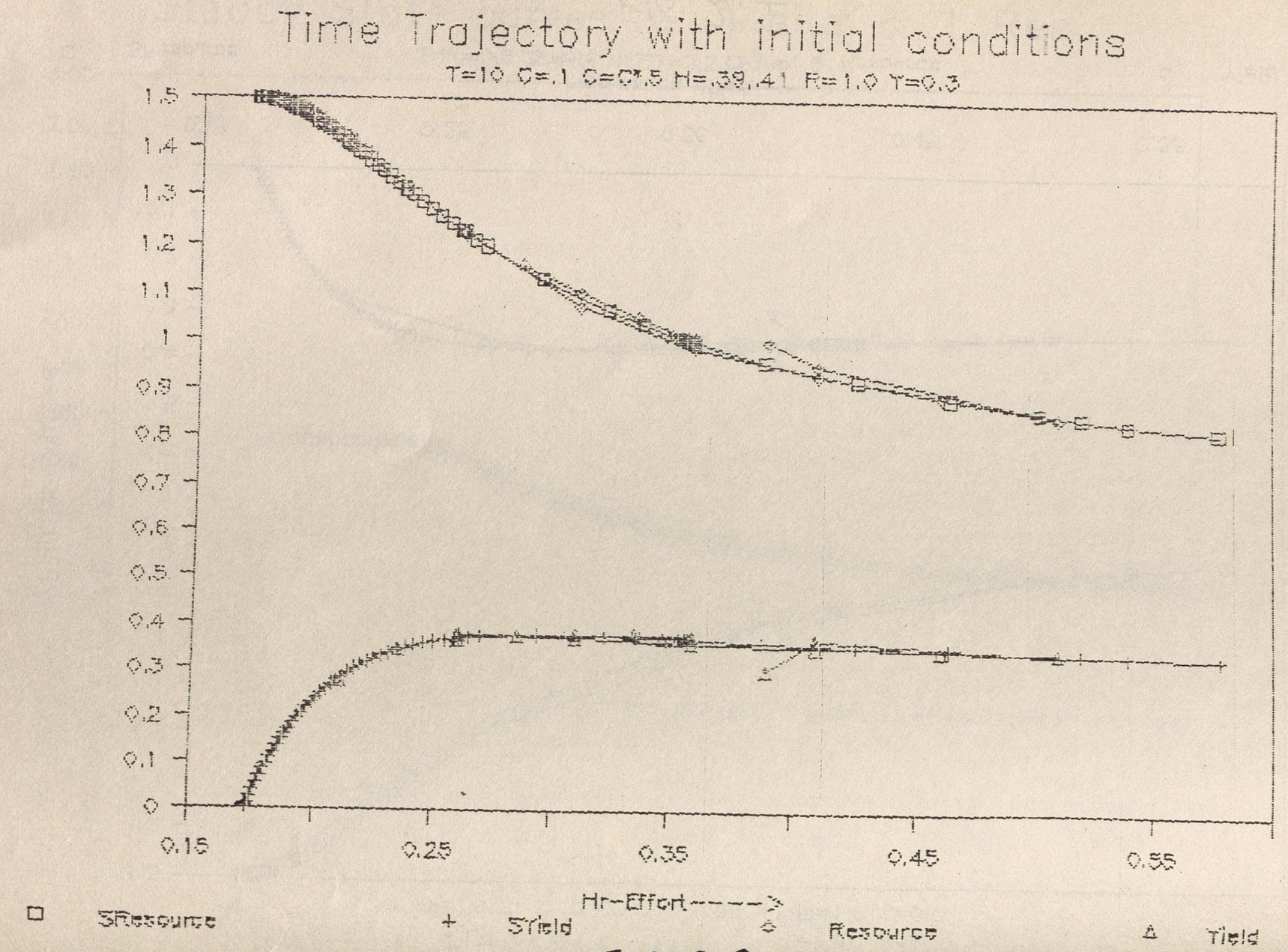

Time Trajectory with initial conditions
T=10 C=.1 C=C*.5 H=.39,.41 R=1.0 Y=0.3
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.15
0.25
0.35
0.45
0.55
Hr-Effort---->
SResource
Yield
Resource
Yield

FIG. 2.2

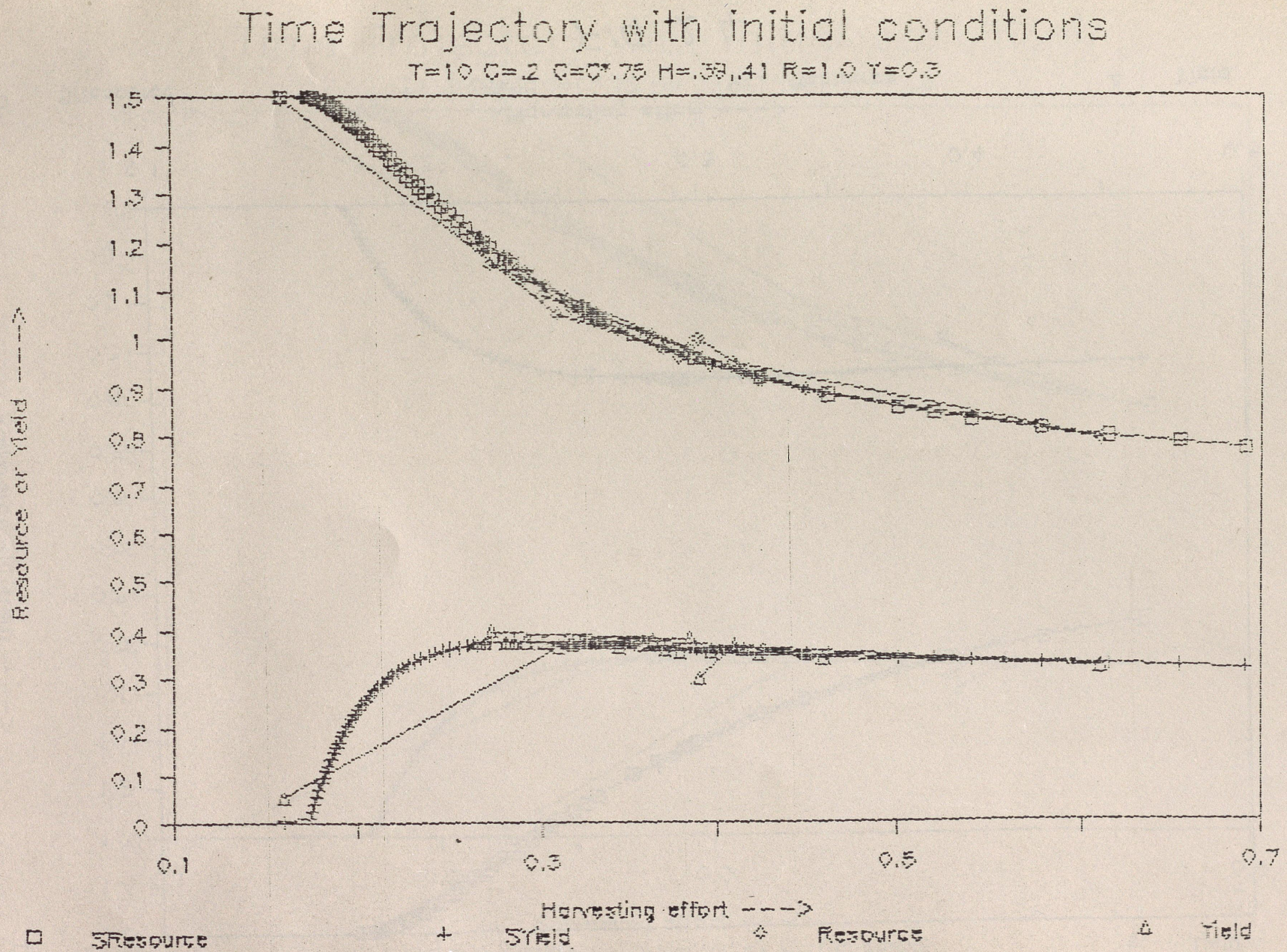

Time Trajectory with initial conditions
T=10 C=.2 C=0*.75 H=.38,.41 R=1.0 Y=0.3
Resource or Yield ---->
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.1
0.3
0.5
0.7
Harvesting effort ---->
Resource
Yield
Resource
Yield

FIG 2.3

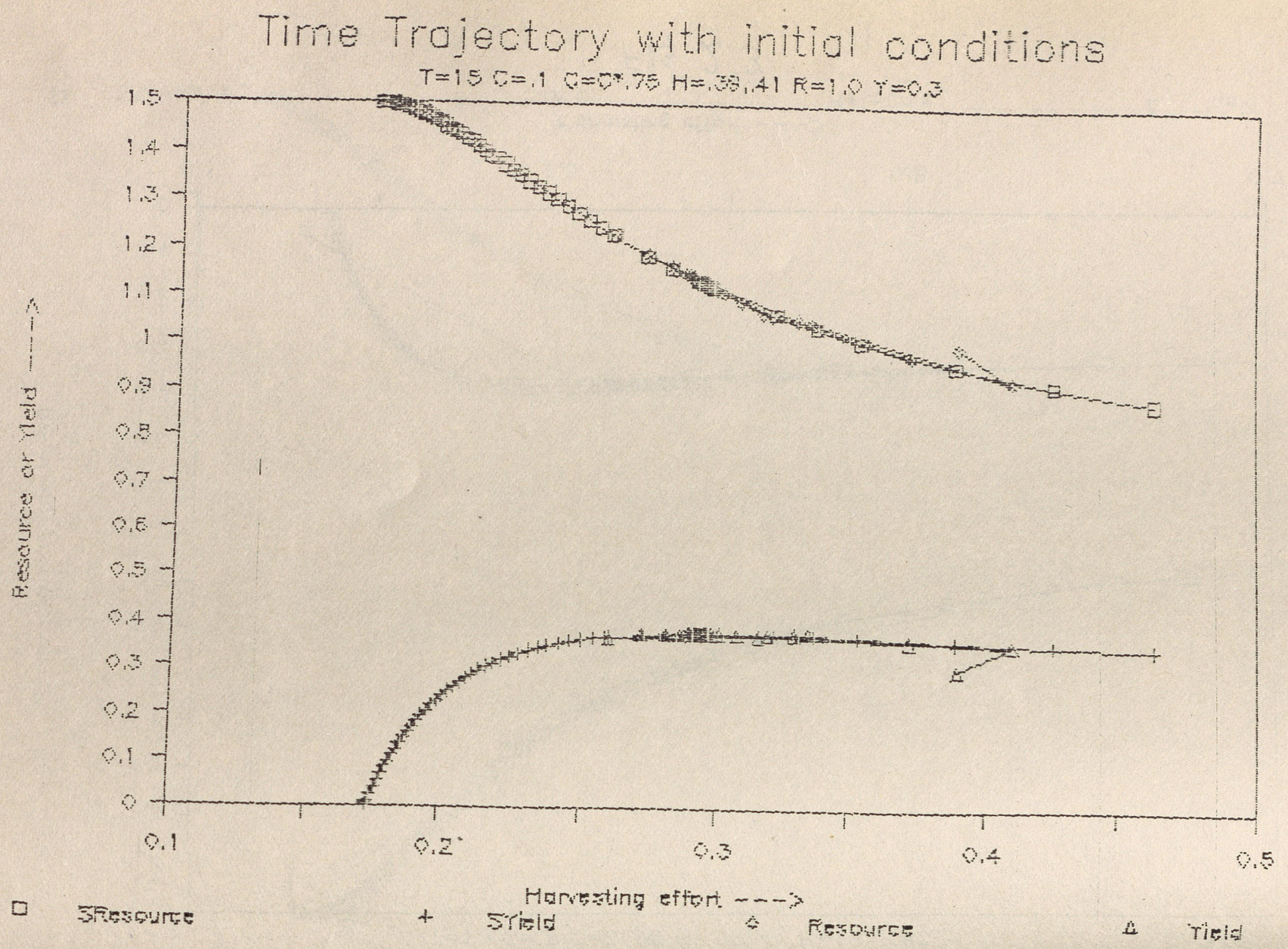

Time Trajectory with initial conditions
T=15 C=.1 Q=0*.75 H=.38,.41 R=1.0 Y=0.3
Resource or Yield ---->
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.1
0.2
0.3
0.4
0.5
Harvesting effort ---->
SResource
SYield
Resource
Yield

FIG. 2.4

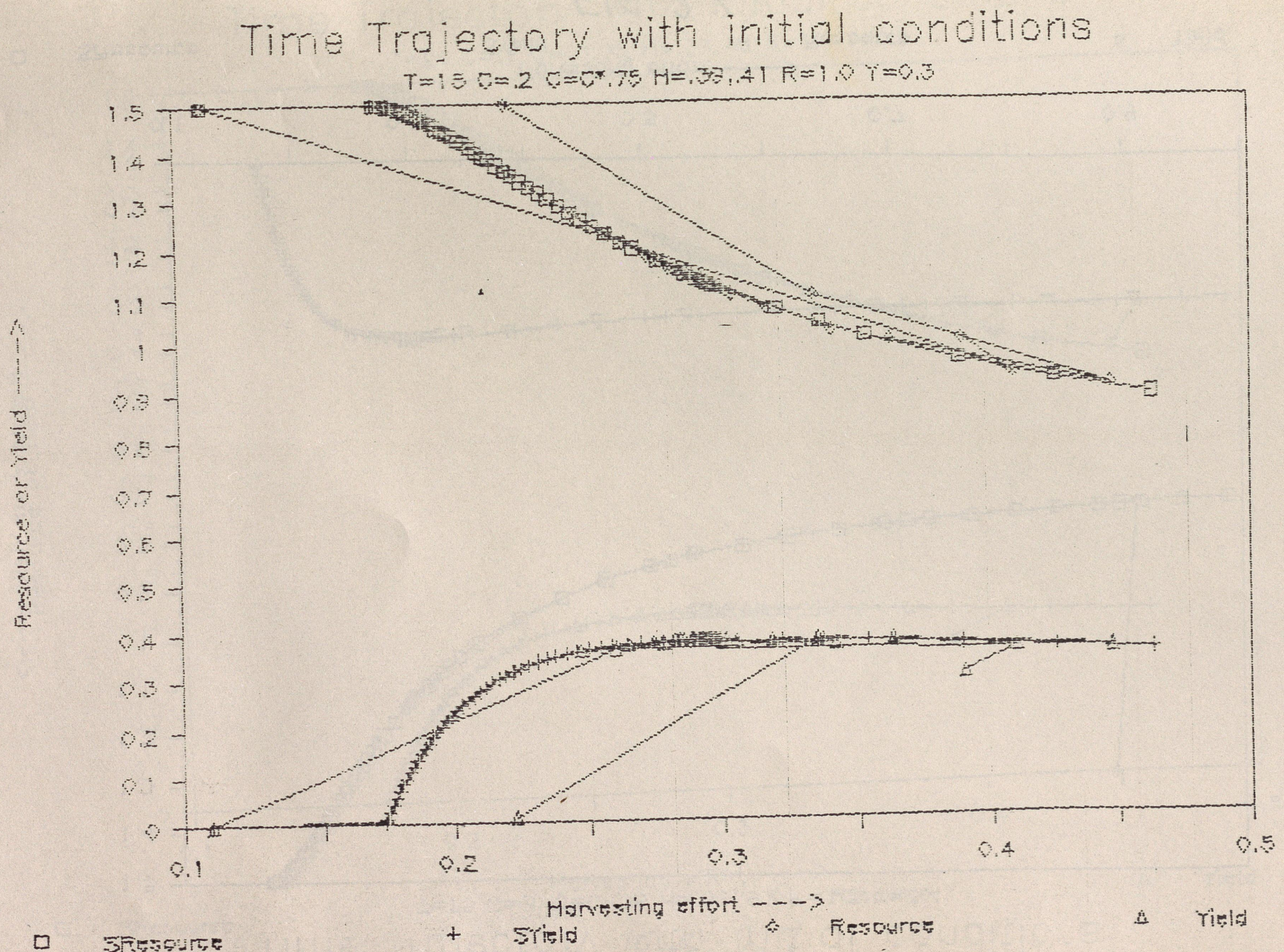

Time Trajectory with initial conditions
T=15 C=.2 C=C*.75 H=.33,.41 R=1.0 Y=0.3
Resource or Yield ---->
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.1
0.2
0.3
0.4
0.5
Harvesting effort ---->
□ 3Resource
+ 3Yield
◇ Resource
△ Yield

FIG. 2.5

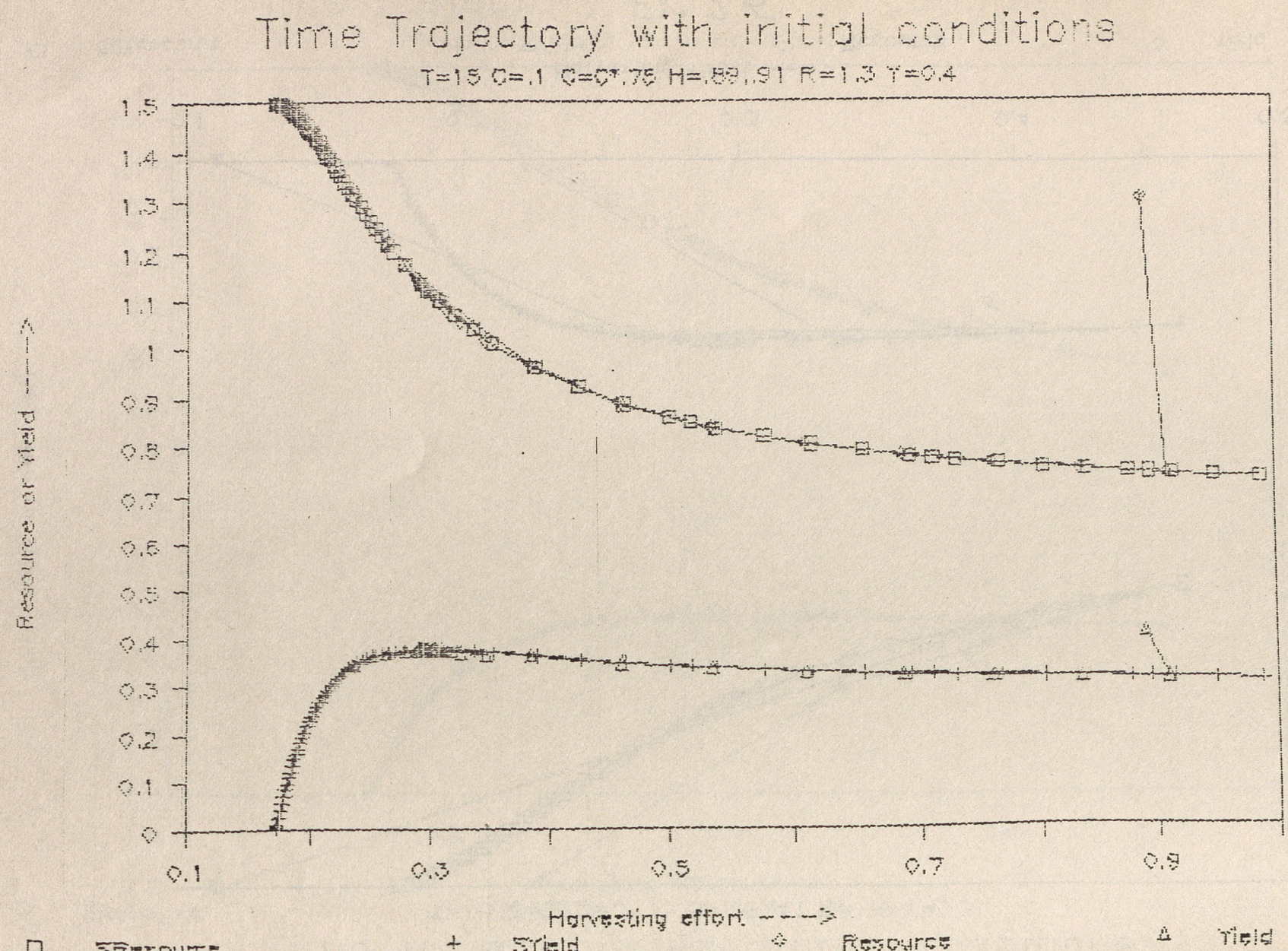

Time Trajectory with initial conditions
T=15 C=.1 Q=0*.75 H=.88,.91 R=1.3 Y=0.4
Resource or Yield ---->
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.1
0.3
0.5
0.7
0.9
Harvesting effort ---->
SResource
SYield
Resource
Yield

FIG. 2.6

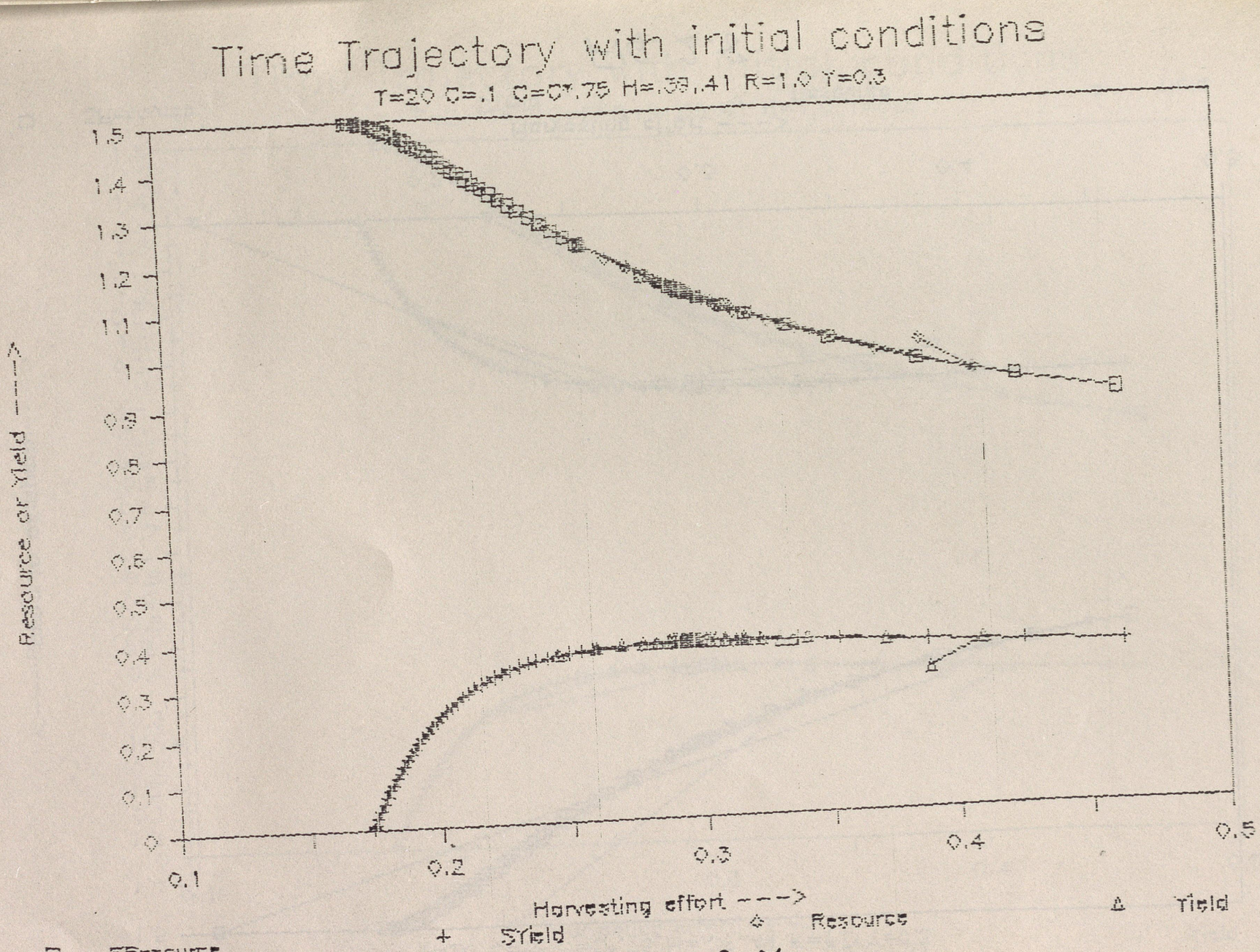

Time Trajectory with initial conditions
T=20 C=.1 C=.75 H=.38,.41 R=1.0 Y=0.3
Resource or Yield ---->
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.1
0.2
0.3
0.4
0.5
Harvesting effort ---->
□ SResource
+ SYield
◇ Resource
△ Yield

FIG. 2.7

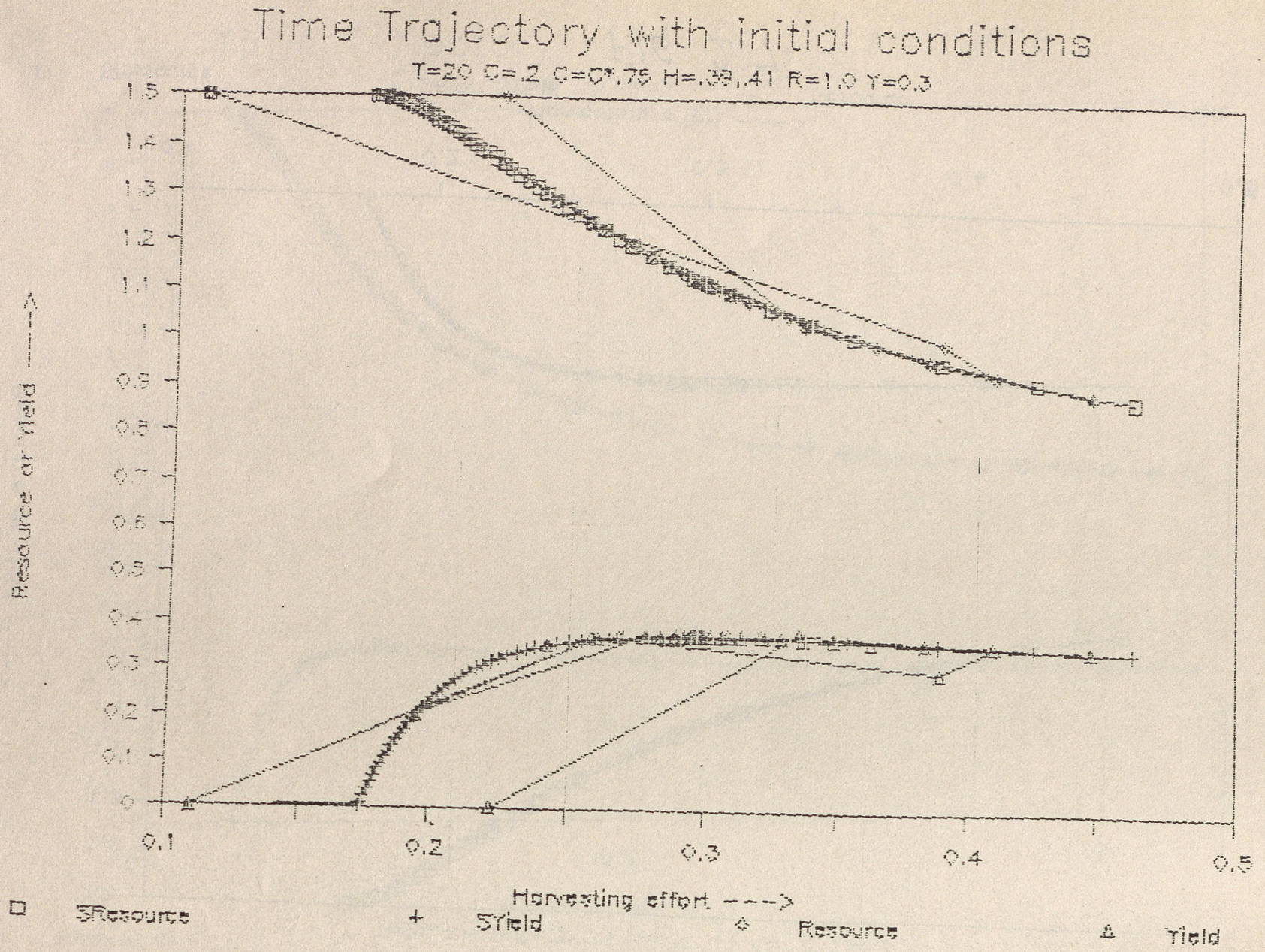

Time Trajectory with initial conditions
T=20 C=.2 C=0*.75 H=.38,.41 R=1.0 Y=0.3
Resource or Yield ---->
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.1
0.2
0.3
0.4
0.5
Harvesting effort ---->
SResource
Yield
Resource
Yield

FIG. 2.8

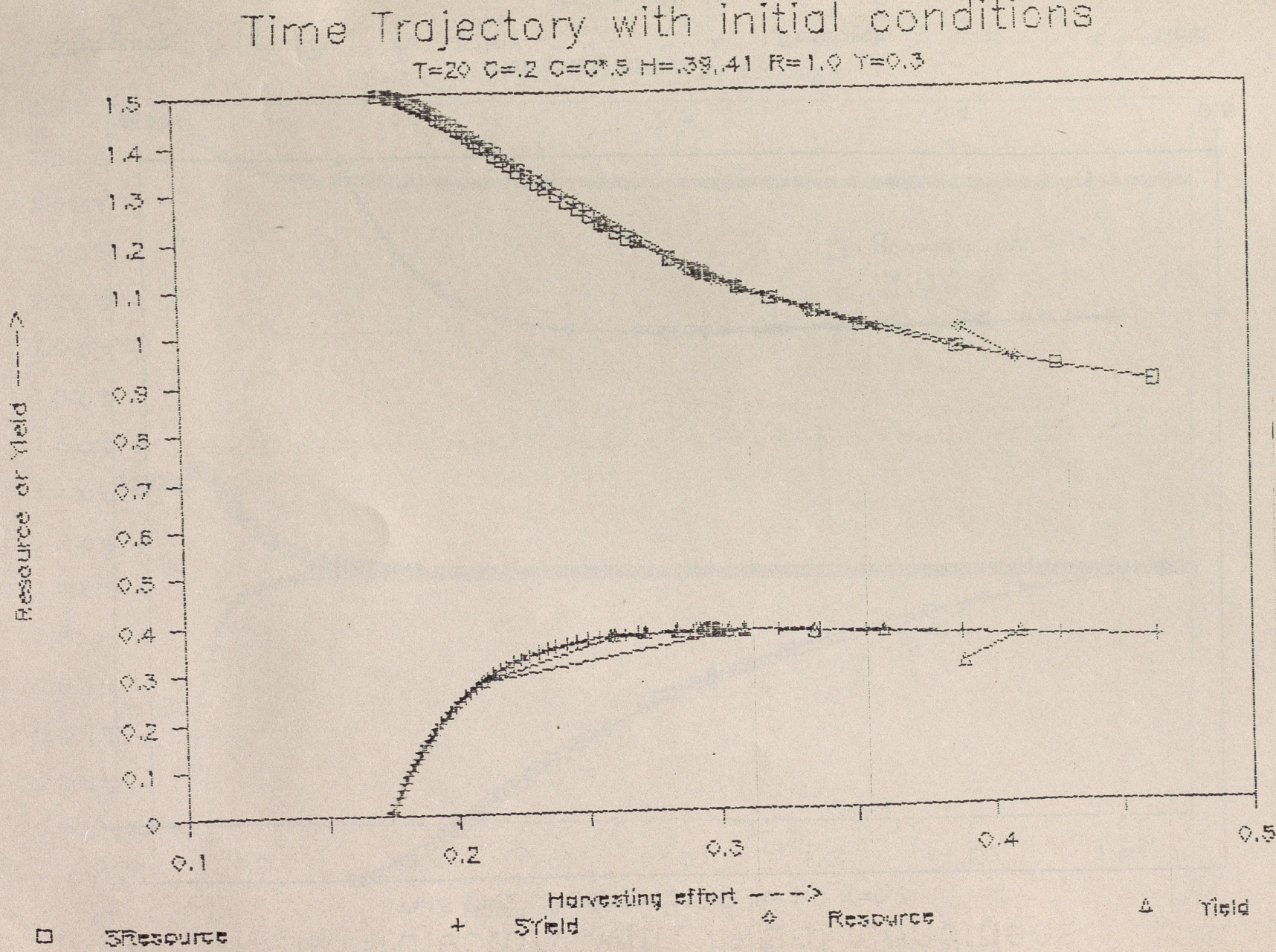

Time Trajectory with initial conditions
T=20 C=.2 C=C*.5 H=.39,.41 R=1.0 Y=0.3
Resource or Yield ---->
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.1
0.2
0.3
0.4
0.5
Harvesting effort ---->
□ 3Resource
+ 3Yield
◇ Resource
△ Yield

FIG. 2.9

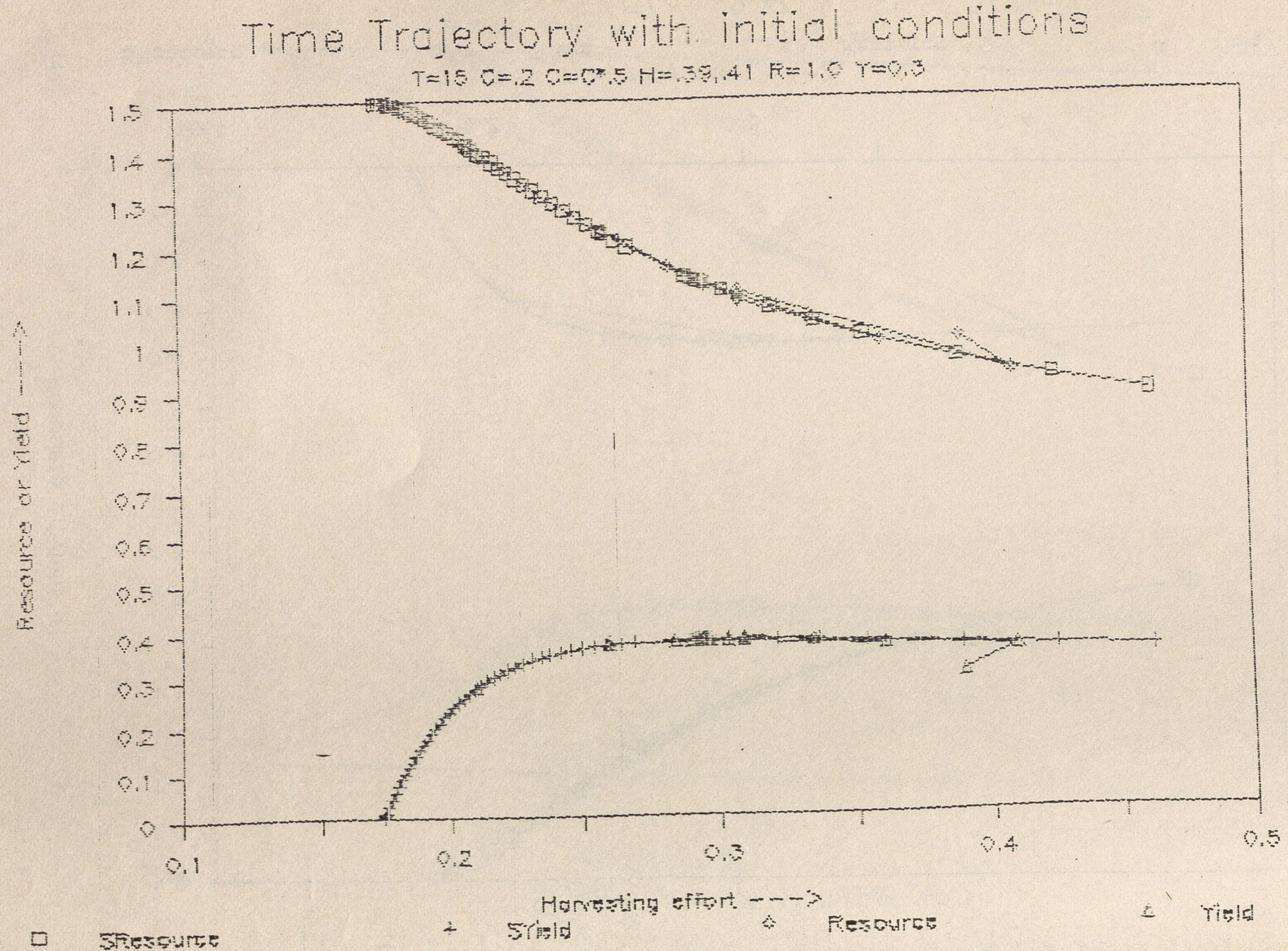

Time Trajectory with initial conditions
T=15 C=.2 C=C*.5 H=.38,.41 R=1.0 Y=0.3
Resource or Yield ---->
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.1
0.2
0.3
0.4
0.5
Harvesting effort ---->
□ SResource
+ SYield
◇ Resource
△ Yield

FIG. 2.10

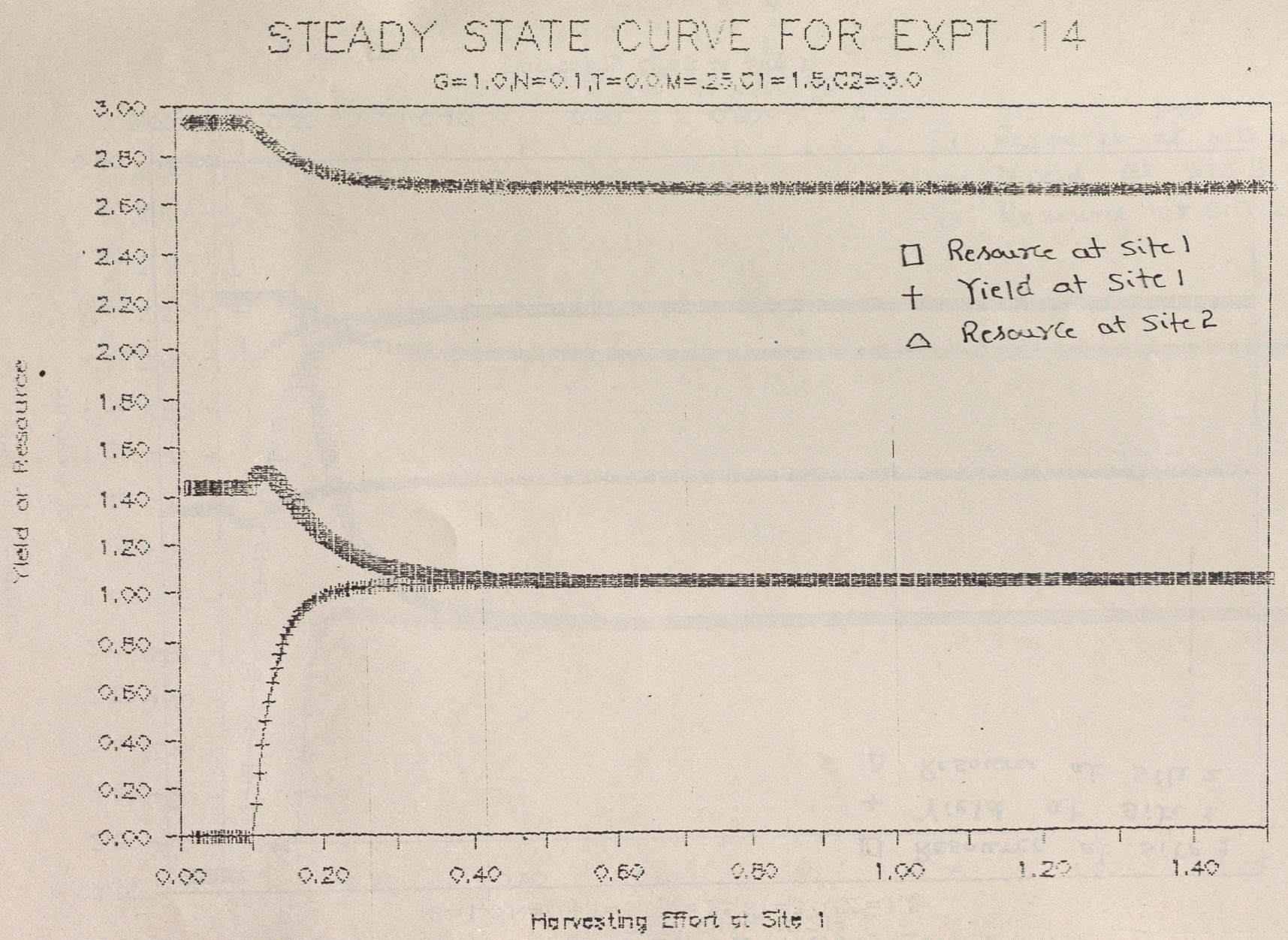

STEADY STATE CURVE FOR EXPT 14
G=1.0,N=0.1,T=0.0,M=.25,C1=1.5,C2=3.0
Yield or Resource
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
Harvesting Effort at Site 1
Resource at site 1
Yield at Site 1
Resource at Site 2

Fig. 3.1

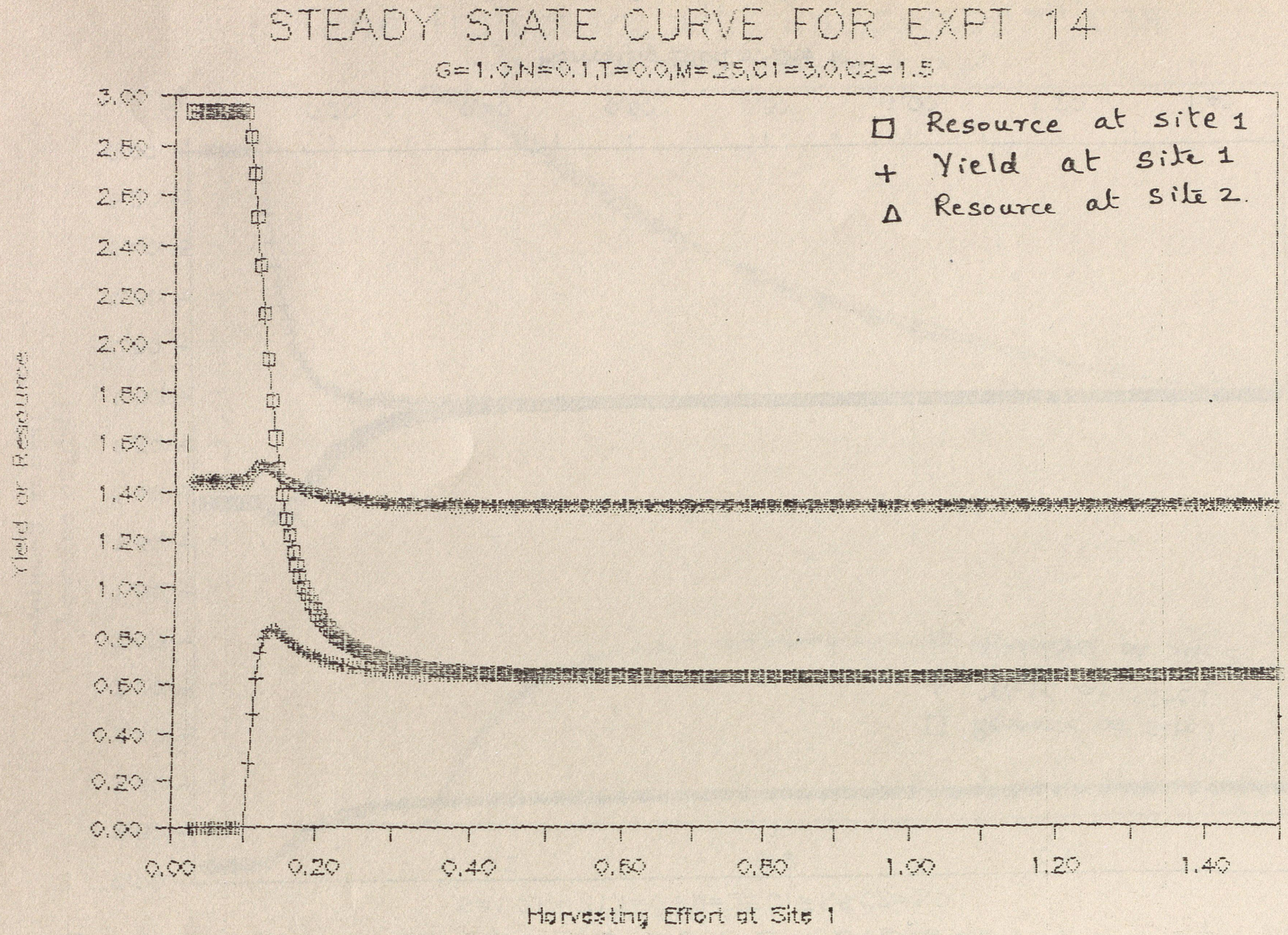

STEADY STATE CURVE FOR EXPT 14
G=1.0,N=0.1,T=0.0,M=.25,C1=3.0,C2=1.5
Resource at site 1
Yield at site 1
Resource at site 2.
Yield or Resource
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
Harvesting Effort at Site 1

FIG. 3.2

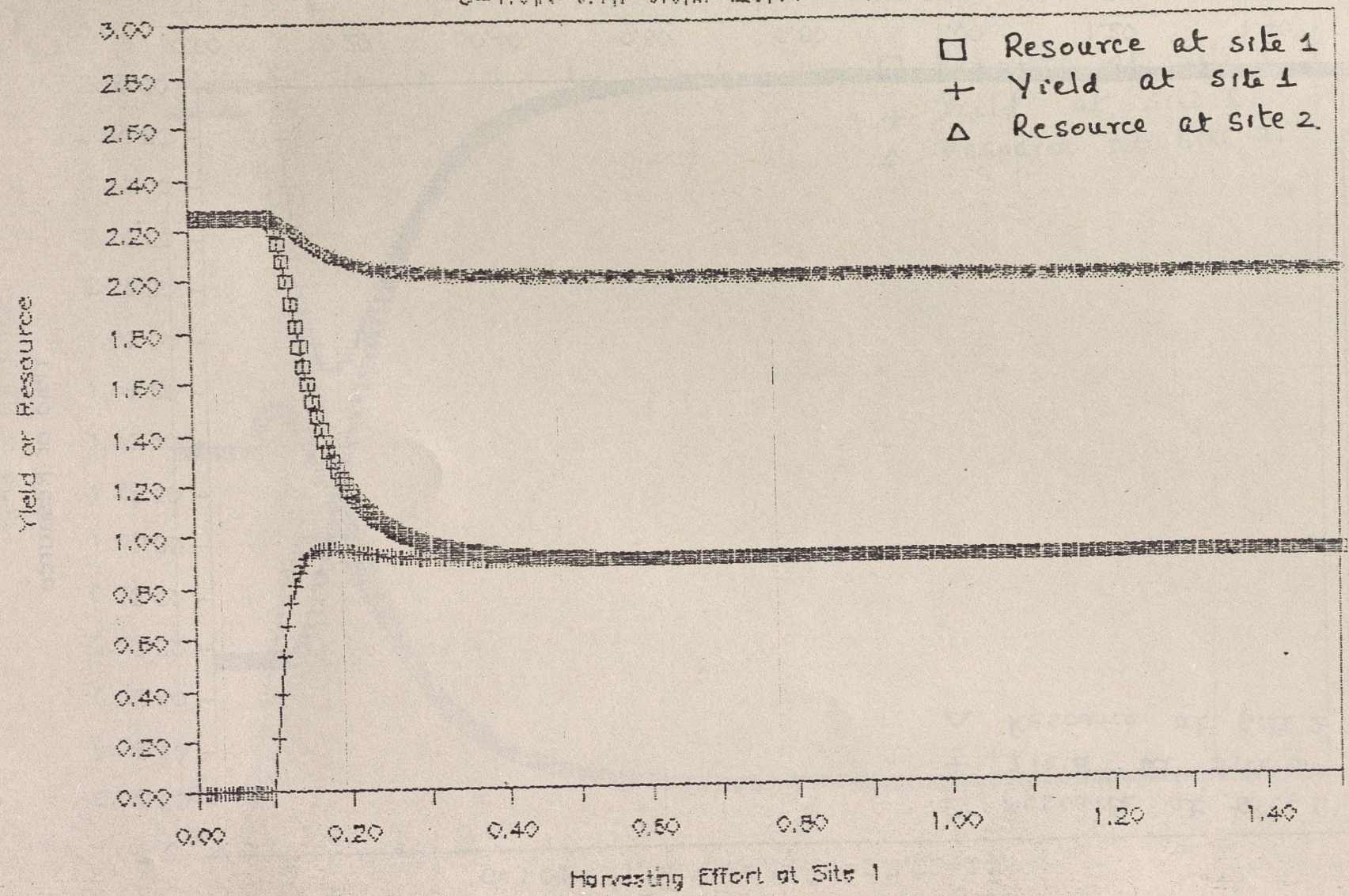

STEADY STATE CURVE FOR EXPT 14
G=1.0,N=0.1,T=0.0,M=.25,C1=2.3,C2=2.3
Resource at site 1
Yield at site 1
Resource at site 2.
Yield or Resource
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
Harvesting Effort at Site 1

FIG. 3.3

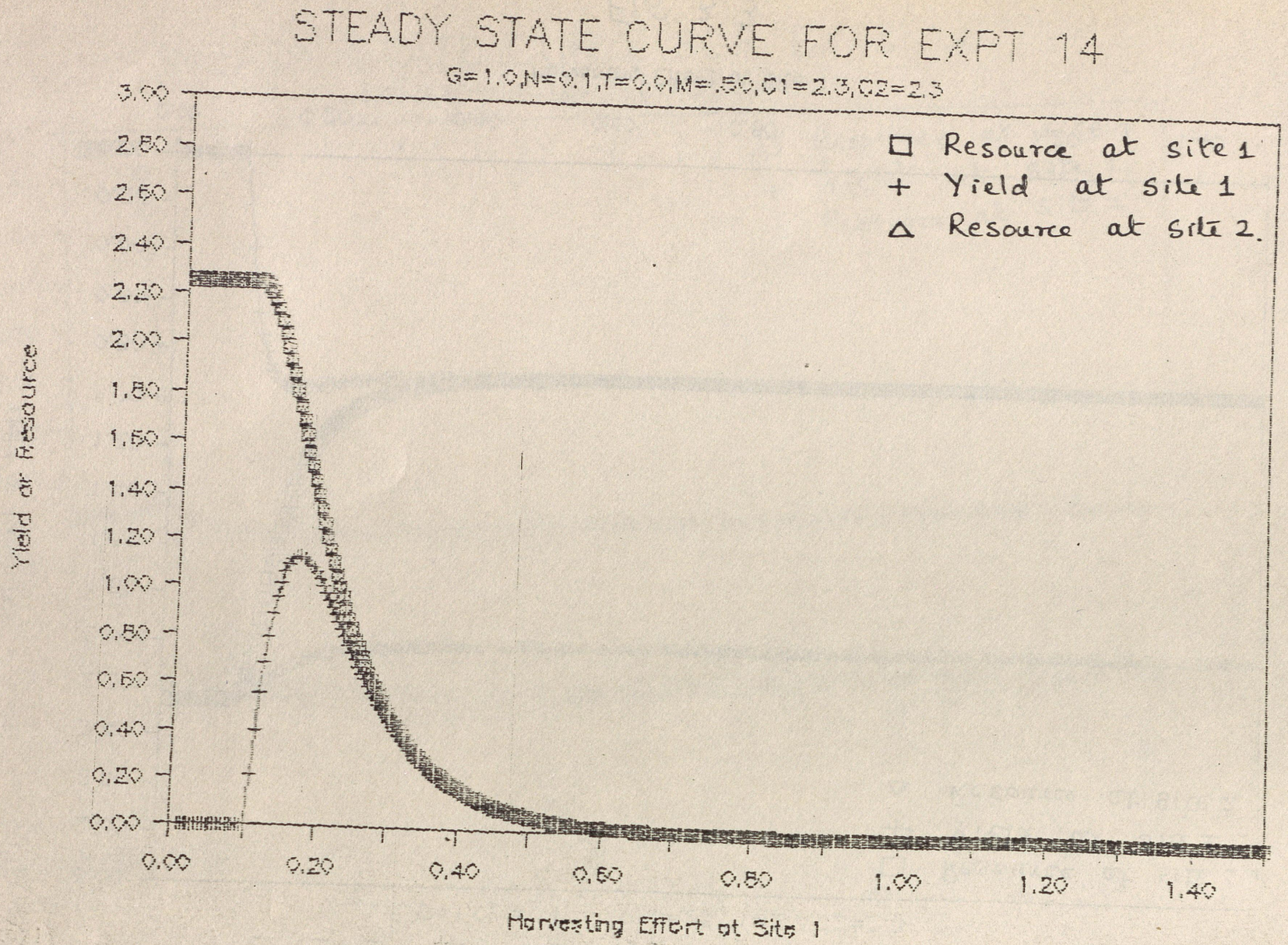

STEADY STATE CURVE FOR EXPT 14
G=1.0,N=0.1,T=0.0,M=.50,C1=2.3,C2=2.3
□ Resource at site 1
+ Yield at site 1
△ Resource at site 2.
Yield or Resource
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
Harvesting Effort at Site 1

FIG 3.4

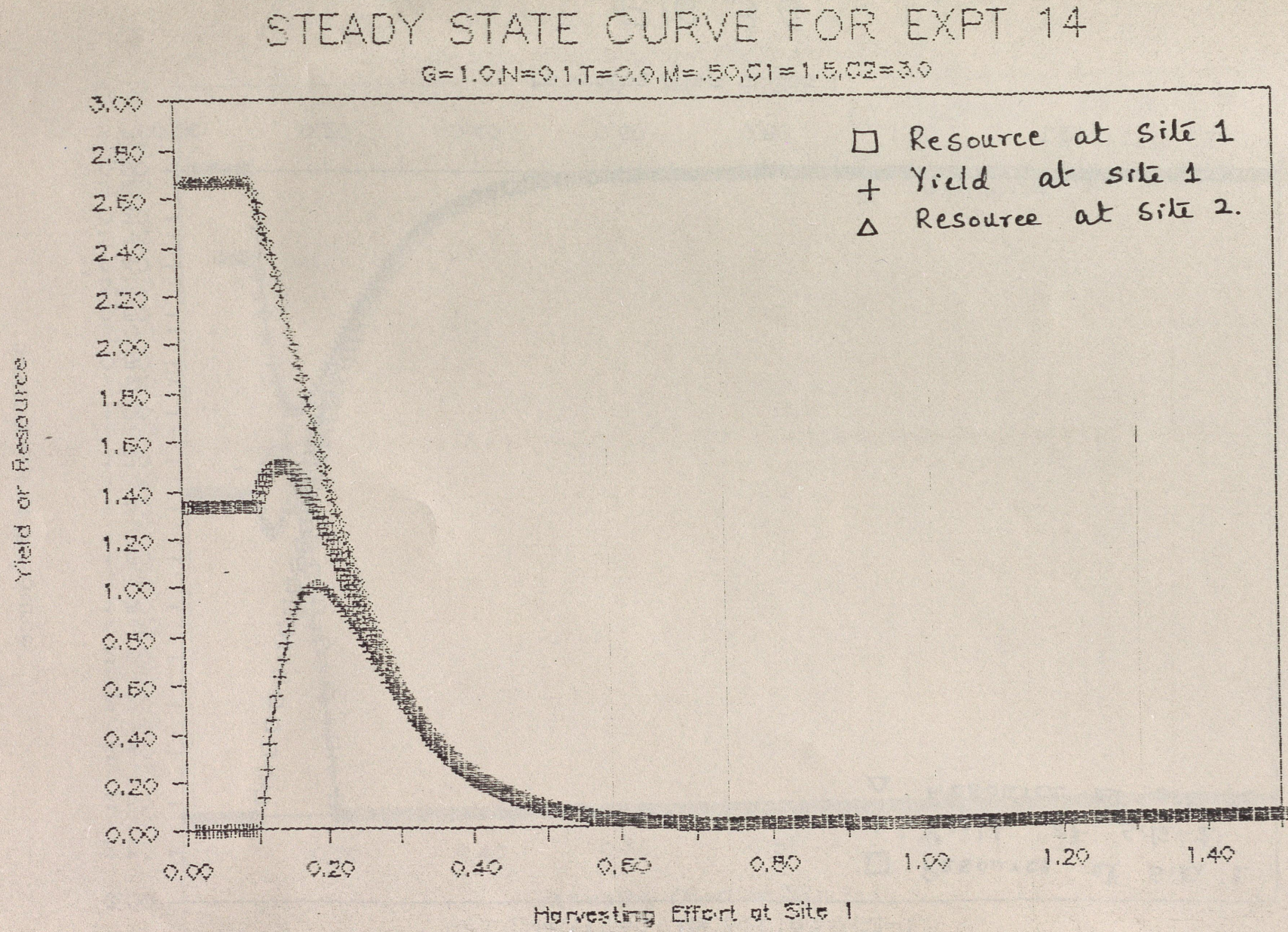

STEADY STATE CURVE FOR EXPT 14
G=1.0,N=0.1,T=0.0,M=.50,C1=1.5,C2=3.0
Resource at Site 1
Yield at site 1
Resource at Site 2.
Yield or Resource
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
Harvesting Effort at Site 1

FIG 3.5

STEADY STATE CURVE FOR EXPT 14

G=1.0,N=0.1,T=0.0,M=.50,C1=3.0,C2=1.5

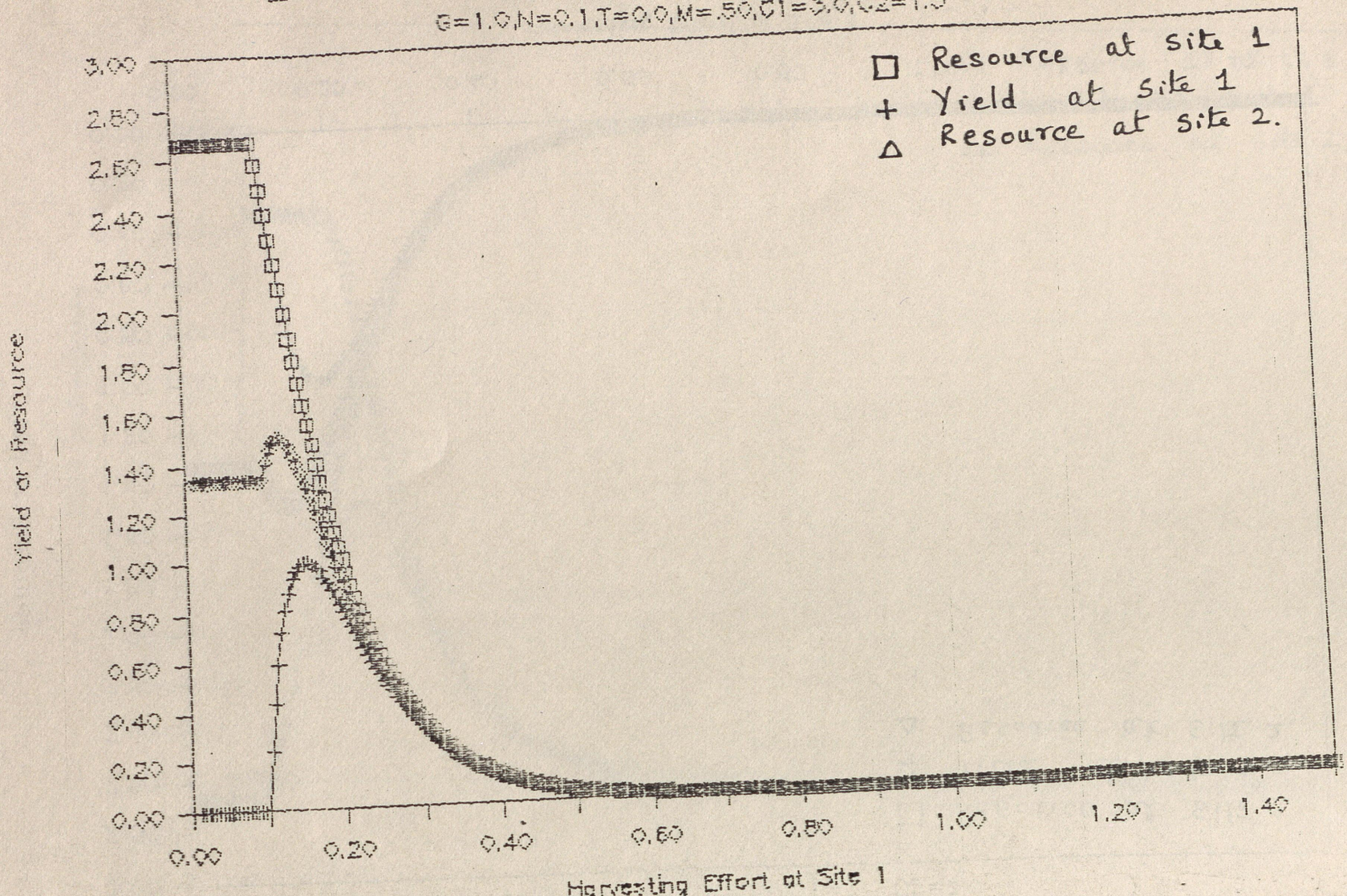


FIG 3.6

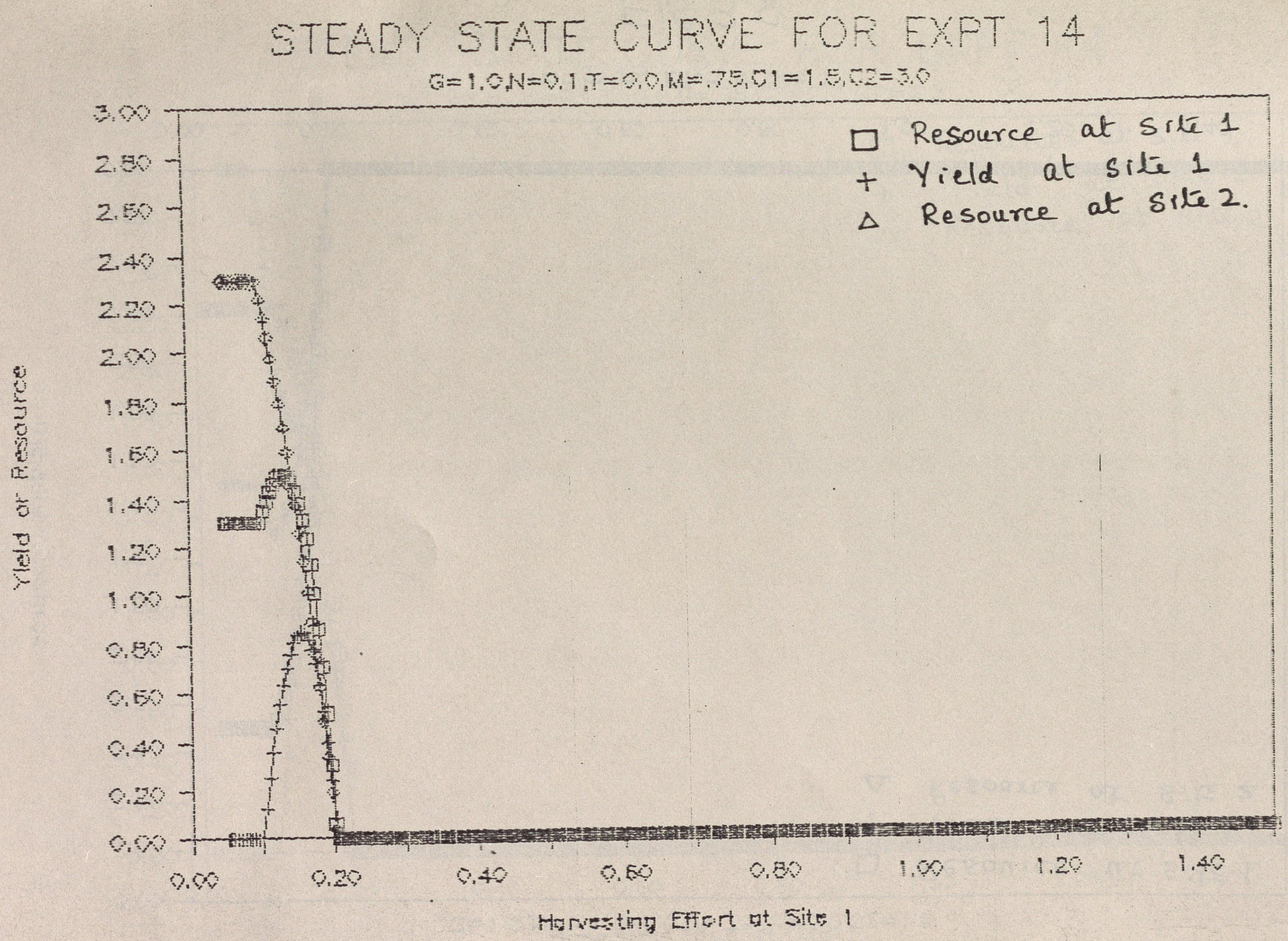

STEADY STATE CURVE FOR EXPT 14
G=1.0,N=0.1,T=0.0,M=.75,C1=1.5,C2=3.0
Resource at site 1
Yield at site 1
Resource at site 2.
Yield or Resource
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
Harvesting Effort at Site 1

FIG 3.7

STEADY STATE CURVE FOR EXPT 14

G=1.0,N=0.1,T=0.0,M=.75,C1=3.0,C2=1.5

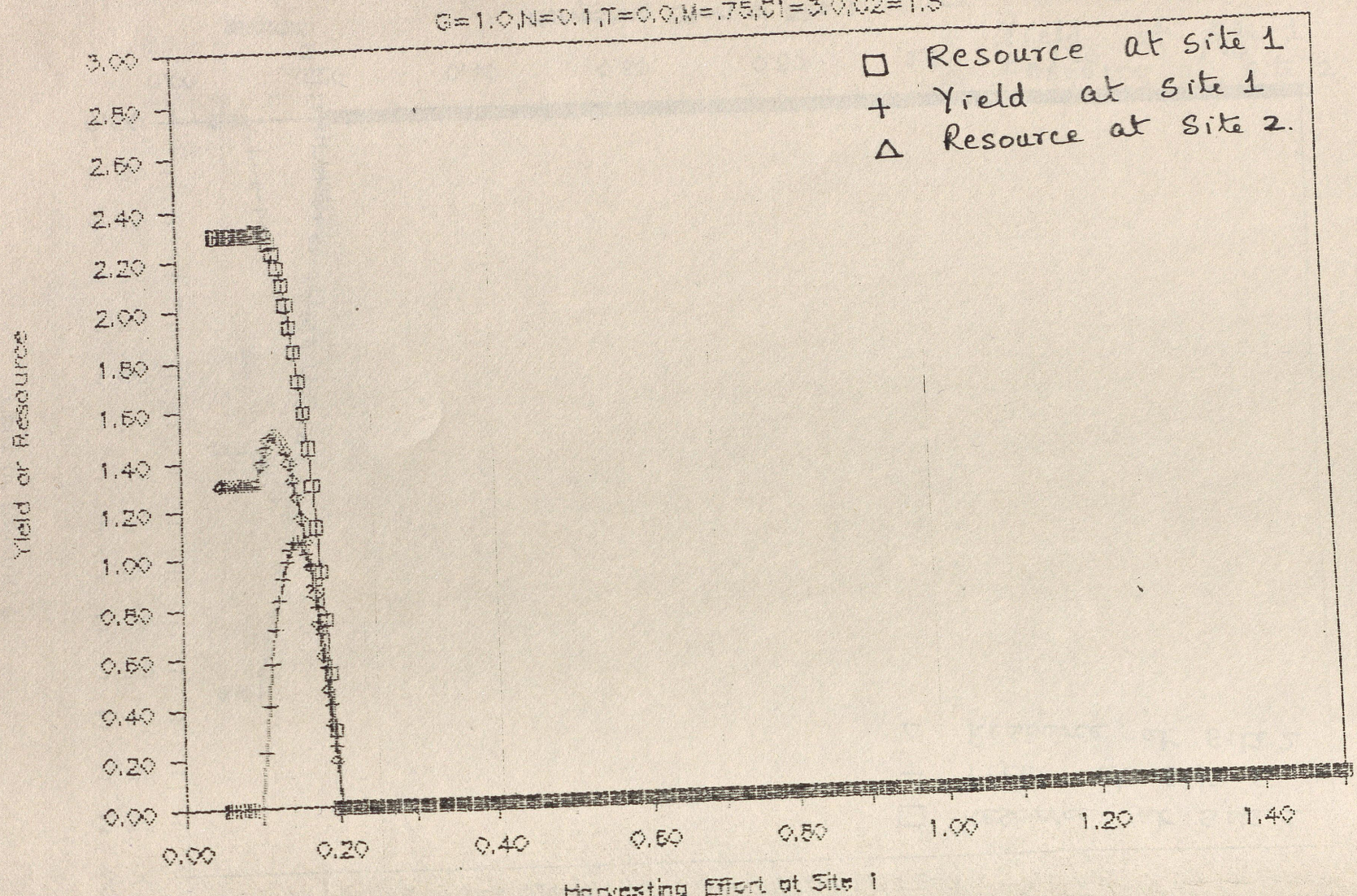


FIG 3.8

STEADY STATE CURVE FOR EXPT 14

G=1.0,N=0.1,T=0.0,M=.75,C1=2.3,C2=2.3

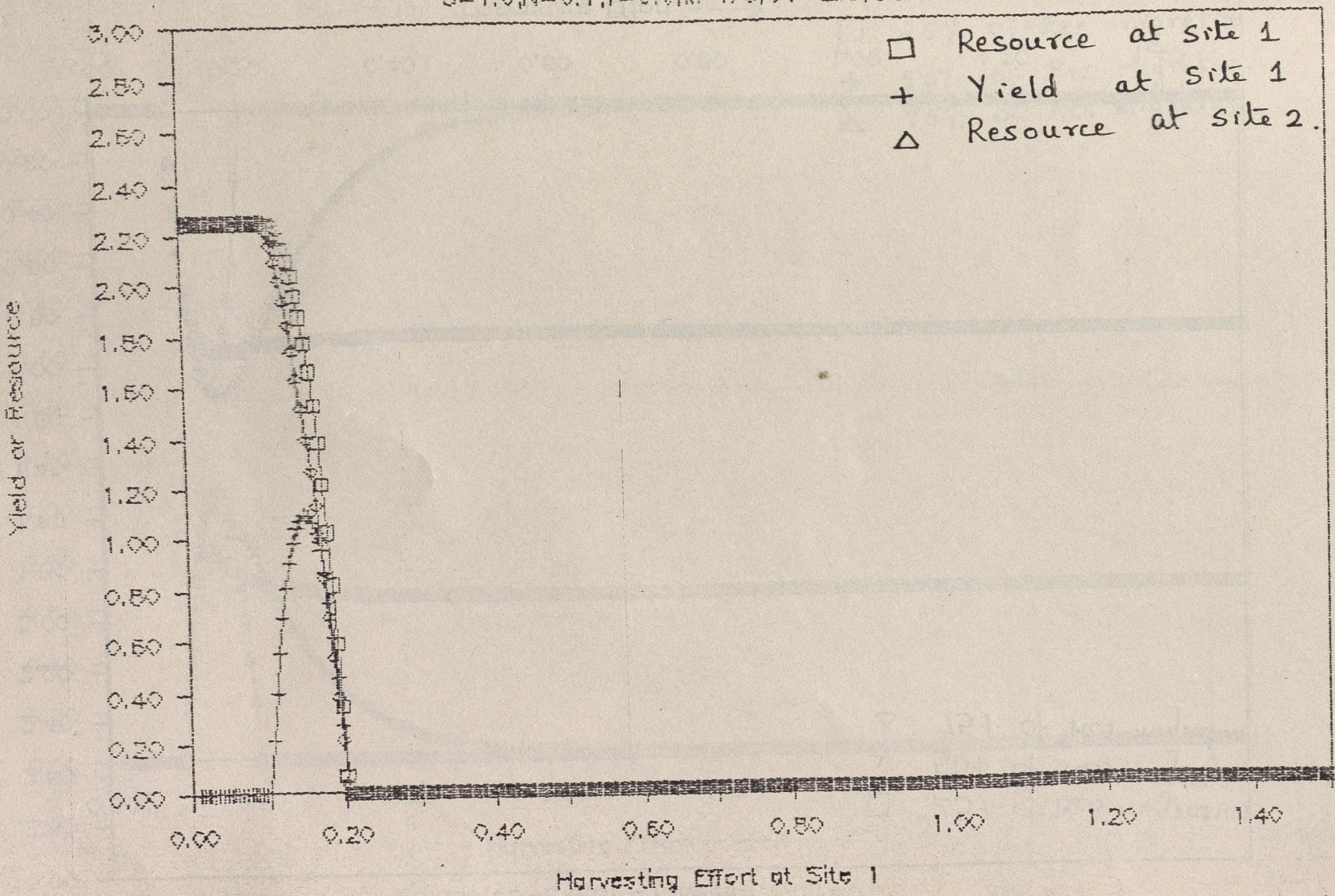


FIG 3.9

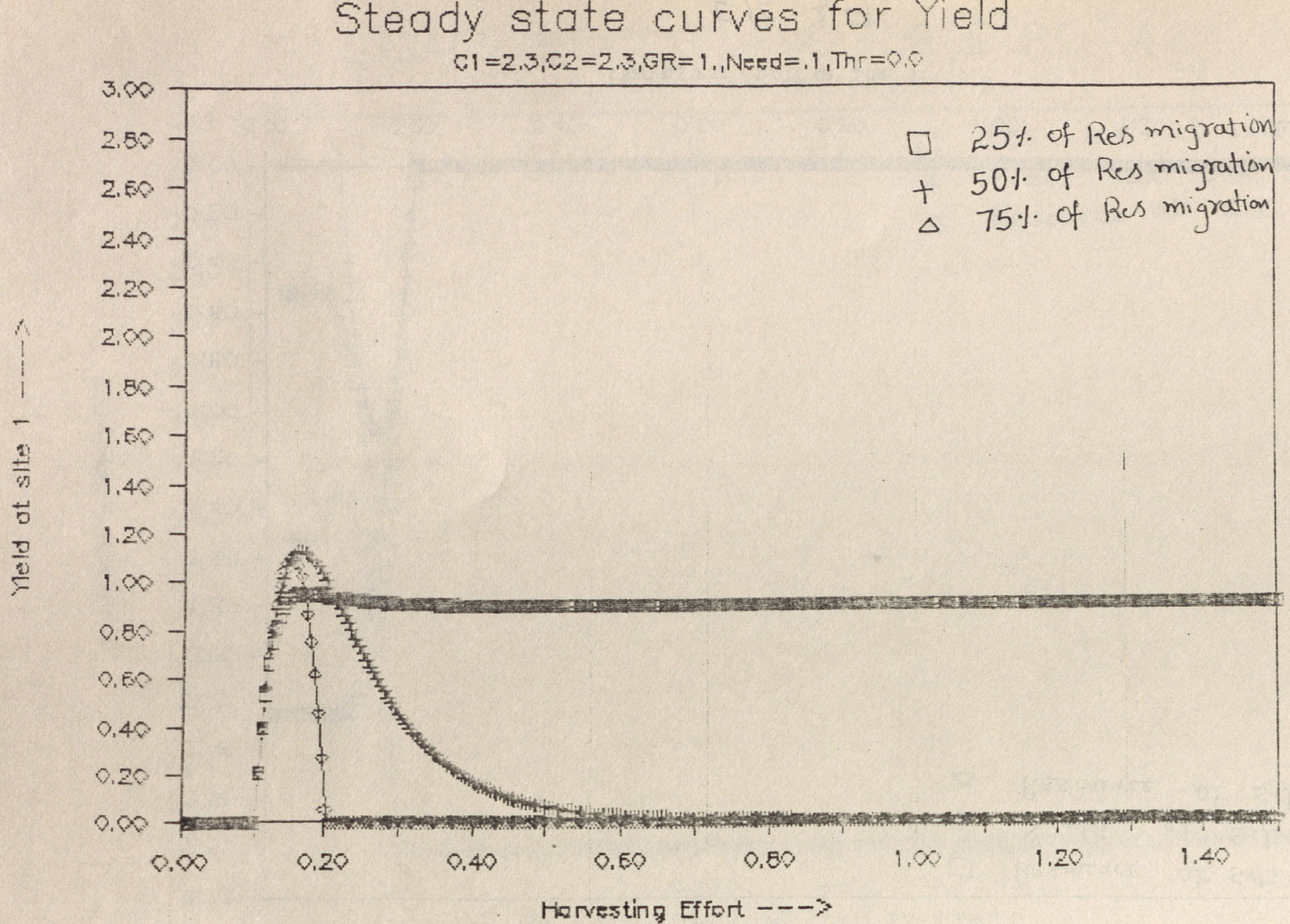
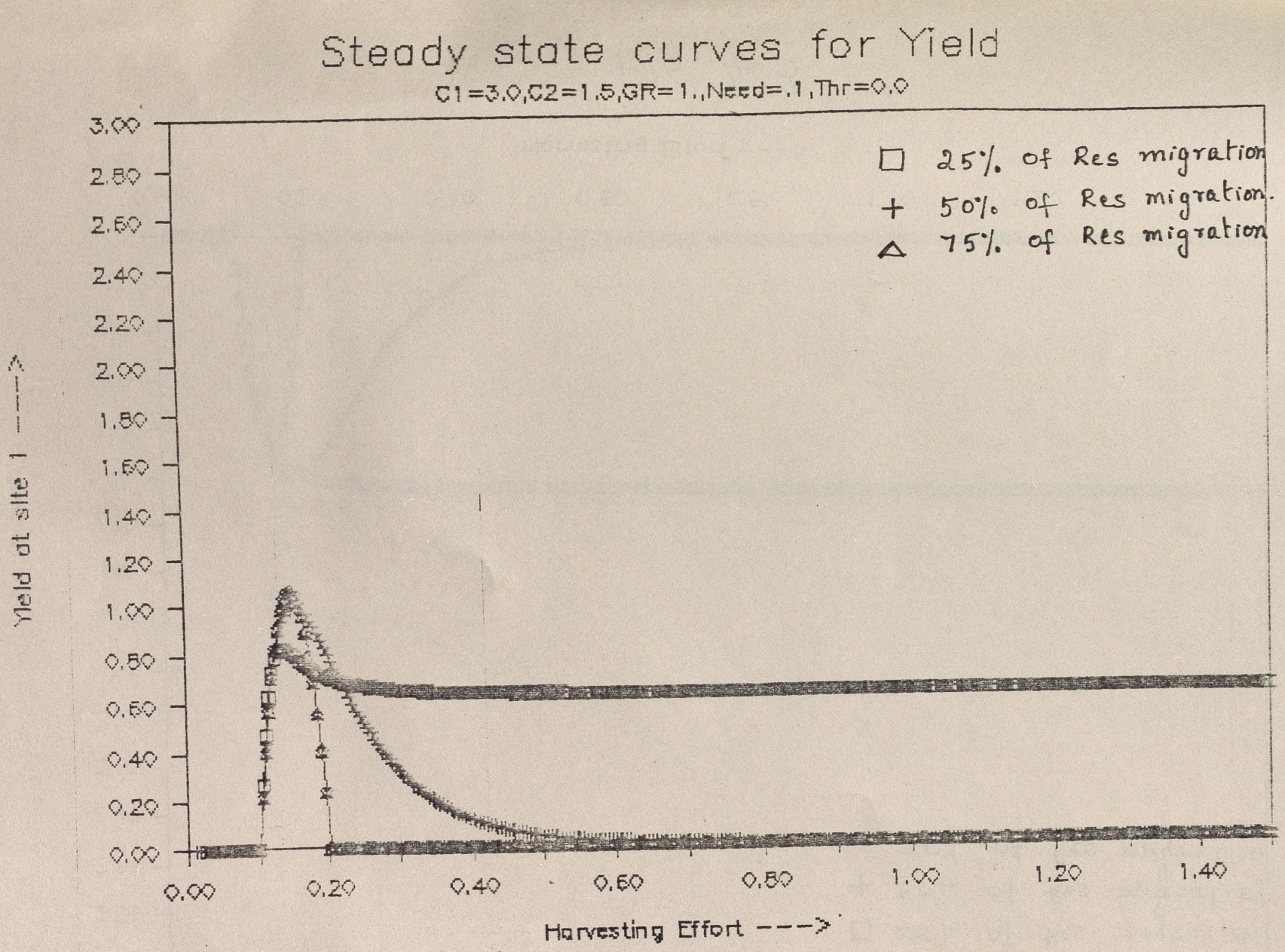

Steady state curves for Yield
C1=2.3,C2=2.3,GR=1.,Need=.1,Thr=0.0
□ 25% of Res migration
+ 50% of Res migration
△ 75% of Res migration
Yield at site 1 ---->
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
Harvesting Effort --->

FIG. 4.1


Steady state curves for Yield
C1=3.0,C2=1.5,GR=1.,Need=.1,Thr=0.0
□ 25% of Res migration
+ 50% of Res migration
△ 75% of Res migration
Yield at site 1 --->
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
Harvesting Effort --->
FIG 4.2

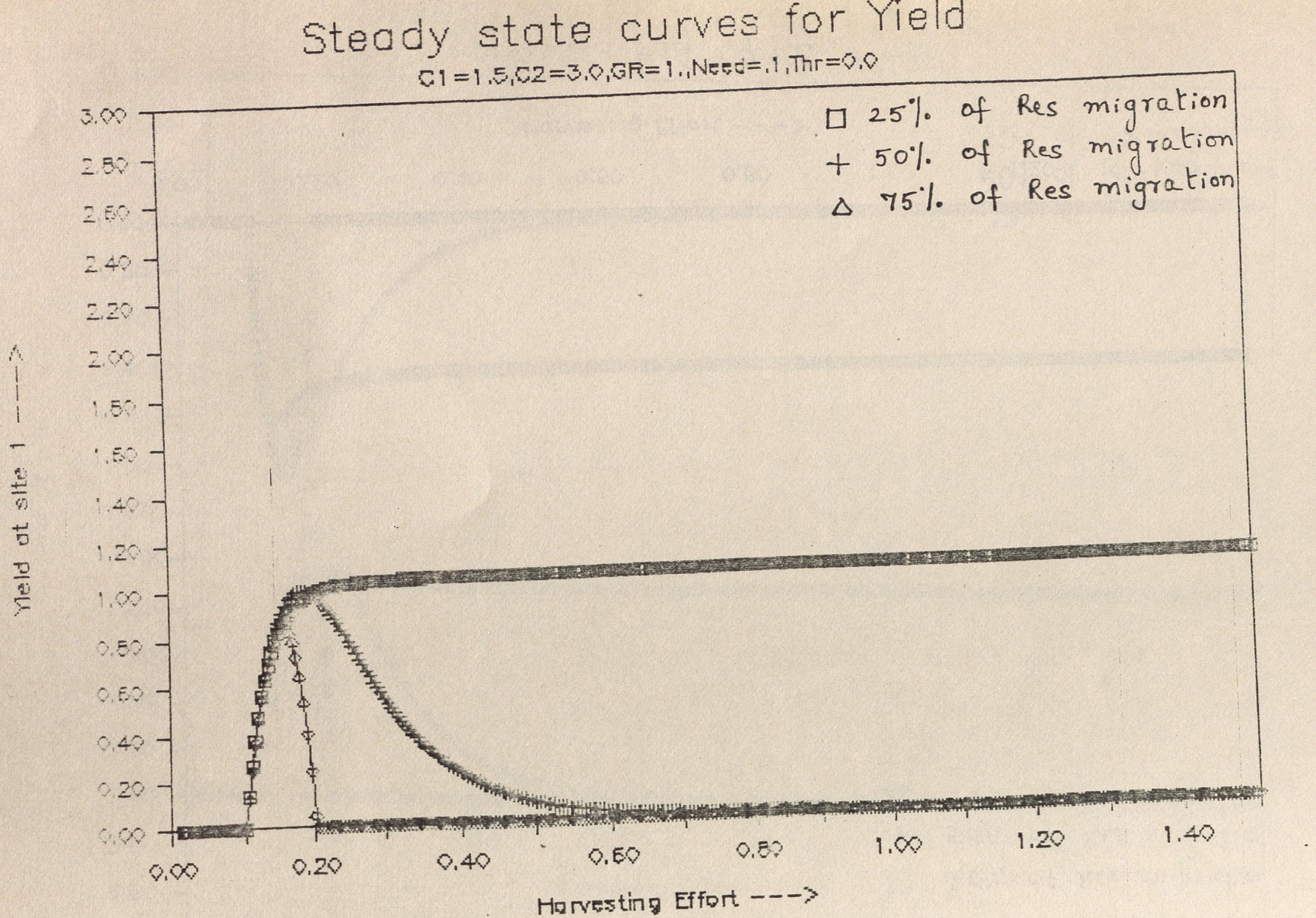

Steady state curves for Yield
C1=1.5,C2=3.0,GR=1.,Need=.1,Thr=0.0
□ 25% of Res migration
+ 50% of Res migration
△ 75% of Res migration
Yield at site 1 ---->
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
0.00
0.20
0.40
0.60
0.80
1.00
1.20
1.40
Harvesting Effort --->

FIG. 4.3