



Modelling the population dynamics and host-parasite-interaction of the genus *Striga* ssp. on maize or sorghum with a combination of discrete and continuous models
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Summary

The dynamics of *Striga hermonthica* are modelled by an age-structured Leslie-model. Taking into account how the host dynamics affects the development of the semi-parasite, a simple system of linear differential equations is used to vary the probabilities with respect to host growth. At the same time *Striga* reduces host growth due to parasitism and, in return, changing its probability of development. The interaction within both systems is controlled by certain types of damage function. Based on the data from several field experiments done in 1991 and 1992 the model repeats well the complexity of the observations through time and density in different years and locations. Long time simulations allow the extrapolations of the seed bank dynamics and the analysis of control strategies.

1. Introduction

Striga hermonthica is one of the more severe parasitic problems on different crops in semi-arid areas, well established all over the Sahel in Africa. Like other soil-borne parasites as nematodes the problem exists that crop damage occurs before the parasite will be observable above soil. Numerous research is available about this parasite (MUSELMANN, 1990), however a general overview about the dynamically processes reveals little knowledge about particular influencing factors with respect to the overall population dynamics of *Striga*. Special designed experiments under controlled conditions are missing. This current limited and highly specialised research is not applicable to understand the whole system of *Striga*-host interactions.

Developing mathematical models for different pathogens in agriculture sciences the biology as well the mathematics have to be considered simultaneously. Hence, most of the introduced parameters of a model have to be meaningful in terms of the biology. Consequently a model repeats a certain type of experimental situation, but only a constant set of parameters within a wide range of evaluated situations allows reliable extrapolations to new situation of the parasite dynamics. Simple linear regressions will mostly fail, non-linear system are more likely to fulfil the presumptions. Models can help to overcome missing links between unknown relationships of an agricultural system.

A well defined mathematical structure is individually applied to the situation of *Striga hermonthica* stages and the host dynamics. The parameters are derived from experiments done by the IITA and are considered in an functional and partly heuristically way.

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2. From life cycle to the model

2.1 The *Striga* model

Striga is developing in well defined discrete stages and is concluding one life cycle per season. According to the model of KUNISCH et al. (1991) the following development stages may be identified: From existing seed bank in the soil, a preconditioned part will be stimulated by root exudates (MUSELMAN and DICKISON, 1975), germinate and attach to root system of the host. *Striga* growth continues with emergence above soil. The life cycle is concluded by a maturity period and the newly produced seed (SAUERBORN, 1991).

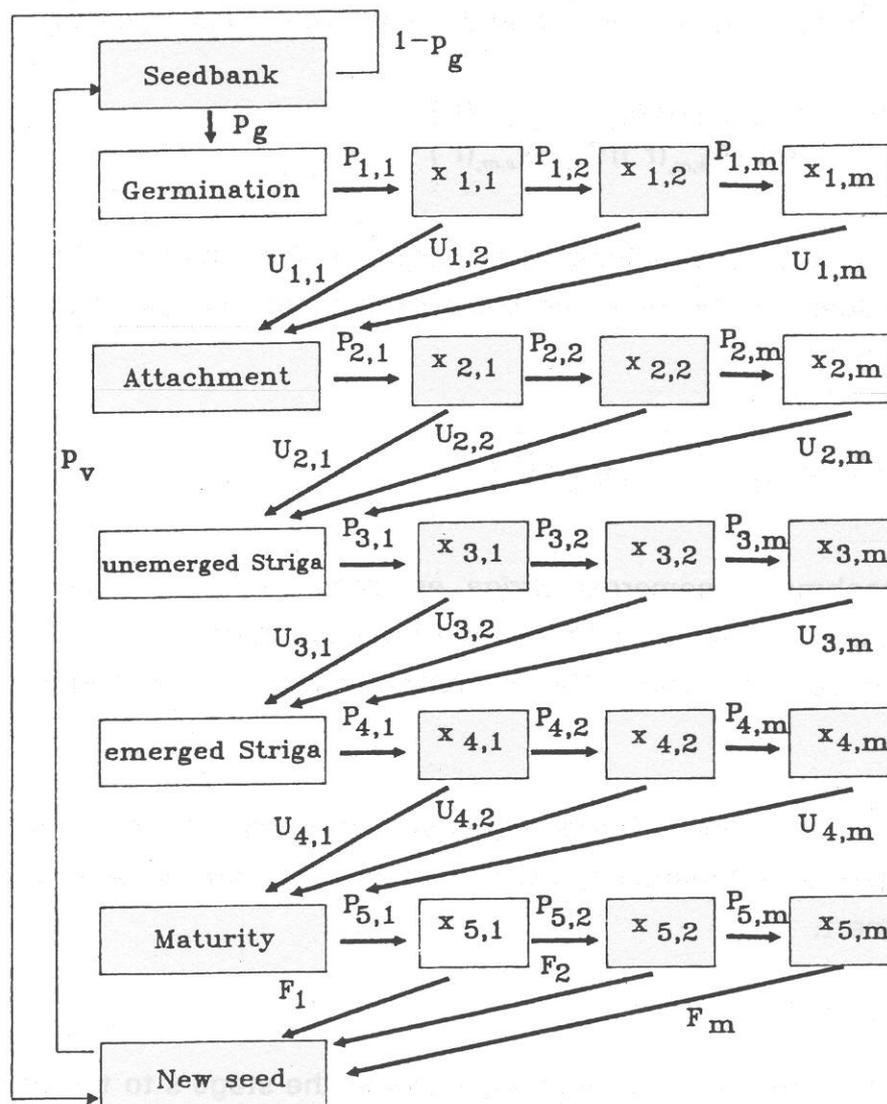


Fig. 1: The compartment model of the *Striga* development stages

The life cycle is transformed to different classes of models. KUNISCH et al. (1991) uses a discrete difference equation with standard formulations of a density



dependent transition probabilities. The model is more conceptual, which gives an overview about the *Striga* system and reflects a general discussion about the overall dynamics. Analysing the intensive research of the IITA of the last years, especially in view of predicting *Striga* influenced crop losses, models with higher resolutions in time and details are required. A generalized Leslie model (RICHTER & SÖNDGERATH, 1990) is an approach to the required resolution. The classes of time dependent parameters are extended by a simple plant growth model in the range of 0,1 probabilities (SCHMIDT, 1992).

Combining to the life cycle of *Striga* and the general concept of age-structured models results in the following compartment model :

The following notations will be used:

- $x_{s,i}(t)$ = expected number of individuals in age class i at time t , $t=1,2,\dots$
 $P_{s,i}$ = probability of surviving from age class i of stage s to age class $(i+1)$ of the same stage
 $U_{s,i}(t)$ = probability of transition from age class i of stage s to age class 1 of stage $(s+1)$ at time t
 F_i = Fecundity of each individual in age class i of the generative stage

The discrete algorithm of the Leslie processes starts with the first age class of the first development stage determining the population size of the next iteration:

$$x_{s,i+1}(t+1) = (1 - U_{s,i}(t)) \cdot P_{s,i} \cdot x_{s,i}(t) \quad \text{Eq. 1}$$

for

s =Germination, Attachment, unemerged *Striga*, emerged *Striga*, maturity and
 m_s = number of age classes of the stage s

The non-hatched individuals are collected in the last age class:

$$x_{s,m_s}(t+1) = (1 - U_{s,m_s-1}(t)) \cdot P_{s,m_s-1} \cdot x_{s,m_s-1}(t) + (1 - U_{s,m_s}(t)) \cdot P_{s,m_s} \cdot x_{s,m_s}(t) \quad \text{Eq. 2}$$

for s = Germination, attachment, unemerged *Striga*, emerged *Striga*, maturity

The individuals in the first age class of the next development stages can be evaluated as:

$$x_{s,1}(t+1) = \sum_{i=1}^{m_{s-1}} U_{s-1,i}(t) \cdot x_{s-1,i}(t) \cdot Z(t) \quad \text{Eq. 3}$$

for s = attachment, unemerged *Striga*, emerged *Striga*, maturity

$Z(t)$ considers the impact of the host on each stage and will be explained in the next chapter.



With respect to the general Leslie structure the population matrix at time $t+1$ becomes:

$$x(t+1) = M_t \cdot x(t) \quad \text{Eq. 4}$$

The transition probability of one age class of the stage s to the first age class of the stage $s+1$ at time $t+1$ is notated as $U_{s,i}$. These time-dependent parameters are estimated by a concept of the normalized development time or the "Biological time" (RICHTER & SÖNDGERATH, 1990). Estimating these parameters, environmental response functions are required.

2.2 The plant growth model (Maize & Sorghum)

The introduced class of time-dependent parameters are extended by a further time dependent classes. It is obvious for a parasite - host system that the influence of the host, which is controlled by climatic conditions, also changes the dynamics of the parasite. The host influence was shortly introduced above as the variable $Z(t)$ (Eq. 3). $Z(t)$ reflects the host dynamics. In theory, the plant model should be based on nutrient flows between plant organs, but this is too detailed for this project. For simplification, it is assumed that *Striga* parasites the nutrients of the host proportional to the existing root biomass. The plant growth model controls by the variable "root growth" and shoot growth the transition probability $U_{s,i}$ of the *Striga* stages. Presupposing a certain type of response on *Striga* attack, the plant model obtain different yield structures variable with climatic conditions.

Crop growth is modelled by a system of differential equations. A differential equation is constructed for a theoretical genetic capacity K (Eq. 5). The capacity term will be approached during growth, but variable with temperature, humidity, plant variety or plant density/m².

$$\frac{dK}{dt} = -s_k \cdot K / \phi \quad \text{Eq. 5}$$

K =genetic capacity

s_k = potential senescence rate

ϕ = environmental response function, normalized to one

It is obviously, that decreasing to zero is not realistic. This problem is avoided, because of the time limit of growth processes. The parameter identification of ϕ will follow later.

Root biomass and stem biomass are modelled by a logistic equation, which reflects the typical change of growth processes in time (GEISLER, 1980)

$$\frac{dR}{dt} = r_r \cdot \xi_{(x)} \cdot \phi \cdot R \cdot \left(1 - \frac{R}{K}\right) - (s_r \cdot C \cdot \frac{R}{K}) \quad \text{Eq. 6}$$



| | |
|------------|---|
| R= | Root biomass |
| ϕ = | environmental response function, normalized to one |
| $\xi(x)$ = | influence of successfully attachments on root biomass |
| r_r = | intrinsic growth rate |
| s_r = | senescence rate |
| C= | cob biomass |
| K= | genetic capacity |

$$\frac{dS}{dt} = r_s \cdot \xi(x) \cdot \phi \cdot S \cdot \left(1 - \frac{S}{K}\right) - (s_s \cdot C \cdot \frac{S}{K}) \quad \text{Eq. 7}$$

| | |
|----------|---|
| S | = Stem biomass |
| Φ | = normalized climatic response function = f(T,H) |
| $\xi(x)$ | = influence of successfully attachments on stem biomass |
| r_s | = intrinsic growth rate |
| s_s | = senescence rate |
| C | = cob biomass |
| K | = genetic capacity |

Although it is not realistic from the biological point of view root and stem biomass are not linked to keep the system as simple as possible.

The decay terms of the biomass equations are coupled with the cob growth establishing a switch from vegetative to the generative growth process.

$$\frac{dC}{dt} = r_c \cdot \phi \cdot C \cdot \frac{R}{K} \cdot \frac{S}{K} \quad \text{Eq. 8}$$

C=Cob biomass

The cob growth is proportional to the existing biomass of root and stem. Cob growth is limited by the senescence of stem and root. Corn yield Y is linearly related to cob biomass (GEISLER, 1980), but is considered in an exponential way. Using a low rate value (Eq. 9) approaches to linearity.

$$\frac{dy}{dt} = r_y \cdot C \quad \text{Eq. 9}$$

Certain yield potentials vary with maize cultivars used. This potential will be approached controlled by the environmental factors prevailing during main growth phase. Sub-optimal temperature regimes or unfavourable humidity conditions will decrease the capacity term, will also reduce stem and root biomass and therefore corn yield.

The following initial values are chosen for maize:

$K_{(0)}=8000$; $R_{(0)}=85$; $S_{(0)}=45.0$; $C_{(0)}=1.1$; $Y_{(0)}=1.1$
 $r_r=0.43$; $r_s=0.43$; $r_c=160$; $sd=0.1$; $\mu=0.001$;



Time t ranges from 0 up to 90 and 130 days taking into account the average growing seasons of different maize varieties in the tropics.

This system of differential equations cannot comply with extended plant growth models (HANKS and RITCHIE, 1991). But it reflects the major phenological pattern of maize (GEISLER, 1980; FISCHER a. PALMER, 1984). It is used as a further class of time-dependent parameters influencing the *Striga* dynamics. Although the crop model is reduced to parsimony, the simultaneous combination of growth and loss results in a certain type of yield structure. It is a model of basic memory. Negative events like any stress influence the result at harvest.

2.3 Linking the systems to Host-Parasite-Interaction

Two independent systems are established, which are derived from common biological discussion. Each of the models is able to simulate a certain type of dynamics, but for a realistic simulation, both have to be linked. The maize-*Striga* system is an interacting system which is roughly summarised to: *Striga* attack is reducing the growth processes of the host, resulting in a reduced probability for *Striga* development, and limiting or decreasing final population density. The range of the feedback varies over time. Low initial seed banks can end up in advanced multiplication rates as the host shows no growth reduction and provides sufficient resources for the parasites. In terms of crop losses observation between nil and all are possible.

2.3.1 Entering the life cycle

The first compartment seed bank (x_{seed}) and the last compartment "New seed" needs further comments (Fig. 1). The measured units of the compartments are seeds/m², but the dynamics of *Striga* is counted in individuals/host. Therefore, a further component of the model has to be established to get the transition probability from the existing seed bank at time t to the first age class of the first stage of *Striga*, starting the iteration and simulate the *Striga* life cycle. This probability is dependent on the host plant density (KUNISCH et al., 1991). The probability of germination varies with plant growth. One possible solution is demonstrated in Fig. 2. The part of the seed bank in soil, which will be able to germinate, may be generalized by following deliberations, despite of all biochemical and physiological processes (KUST, 1963, PARKER, 1983, LINKE et al., 1987). Assuming a random distribution of the seeds within the total plant area (A_{max}), the probability of *Striga* seed germination is developed as follows:

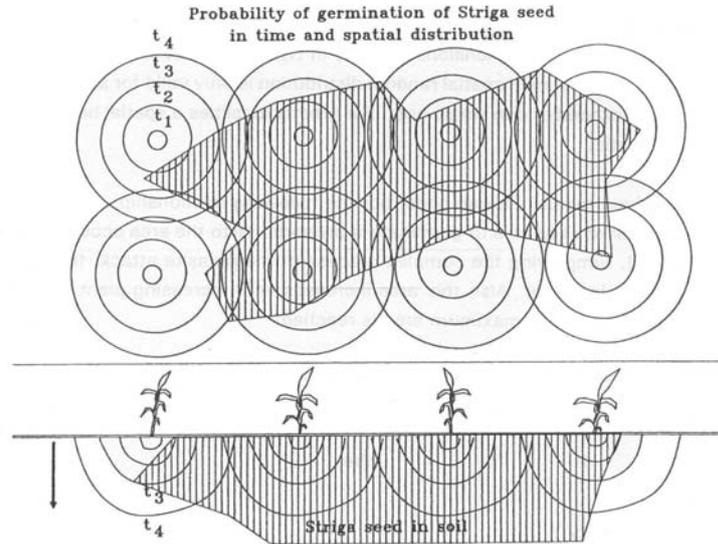


Fig. 2: Time dependent changes of the host parasite association and probabilities $t_1..t_n$.

Regarding the area from the top a plant is growing like a circle. Only those seeds can germinate, which are inside this circles (Fig. 2) from t_n to t_{n+1} . A third dimension, signed in Fig. 2 and used by GILLIGAN (1990) is avoided here to keep the model simple. The radius of the cycle is related to existing root biomass at time t (Eq. 6). The transformation results in a probability in m^2 . The assumed spatial random distribution is valid only for smaller areas, like the neighbourhood of the host. Spatial heterogeneity is more likely in larger areas.

With given radius the following relationships are determined: The number of seeds able to germinate is proportional to the area occupied by each host (A_{pot}). Simplifying the complex process of parasite attack the following assumptions are made: The area increases with increasing plant growth and plant density, until a maximum area A_{max} is reached:

$$A_{pot}(t+1) = \frac{\pi}{4} \cdot \frac{\sum_{i=1}^P (R_i^2(t+1) - R_i^2(t))}{A_{max}} \quad \text{if } R_i(t+1) > R_i(t)$$

Eq.10

where P = plant density per m^2
 $R(t)$ = root biomass at time t
 A_{max} = Maximum area occupied by the host

A_{pot} is defined as a probability from 0 to 1 and A_{max} varies with plant density. The



current probability is time limited to the active growth period of the host, due to root senescence later in the season. The variable A_{max} is necessary as the maximum area/plant will be approached in shorter time with higher plant density and competition effects will affect earlier.

The first age class of the stage germination will be filled by the following relationship:

$$x_{s,1}(t) = x_{seed}(t) \cdot g_{host} \cdot (A_{pot}(t) - A_{pot}(t-1))$$

for stage s = Germination

g_{host} is the host specific maximum rate of germination. EGLEY (1990) provides relevant indices according to root exudates for different host. IITA research allows estimating g_{host} for different hosts as declared in Table 1, while similar results are given from SETTY (1980). EGLEY et al. (1990b) and SAUERBORN (1991) demonstrated that the percentage of germination is also temperature dependent. The model will simulate slower growth processes with sub-optimal temperature regimes, hence the percentage of germination within an m² will be reduced. Given mortality rates within one time step is another factor of varying the percentage of germination. Both processes repeat the observations of SAUERBORN (1991).

Table 1: Maximum germination rate

| Host | g_{host} |
|---------|------------|
| Maize | 0.55 |
| Sorghum | 0.39 |
| Cowpea | 0.31 |

Finally, the current seed bank is reduced by the number of germinated seeds:

$$x_{seed}(t+1) = x_{seed} - x_{s,1} \quad \text{Eq. 12}$$

2.3.2 The fecundity

The newly produced seeds/*Striga* are not able to germinate instantly during the same season (PARKER, 1983). They are stored in a compartment called "new seed" Fig. 1.

The third class of parameters of the Leslie model (RICHTER et al., 1990), the fecundity of each age class, may also influence by the host and is an element to consider density dependency processes.

$$x_{newseed}(t+1) = x_{newseed}(t) + P \cdot \sum_{i=1}^{m_s} U_{s,i}(t) \cdot F_i \cdot x_{s,i}(t) \quad \text{Eq.13}$$

s=stage maturity

F_i=Fecundity of the age class i



P=host plant density

Multiplying the age specific fecundity with the numbers of host/m² transforms *Striga* dynamics/host to a square unit, the scale *Striga* measurements are published. The constant multiplication is a rough assumption, although there could be other relations within one m² and per host.

Two processes are taken into account in modelling the numbers of seeds per developed witchweed (Fecundity = number of capsules/plant or numbers of seeds / capsule):

1. The possibility of producing viable seeds is related to a particular *Striga* age (SAND, 1990).
2. Density dependencies are apparent in the population dynamics of *Striga*. This relationship must be connected with the plant growth model. It is assumed that the maximum seed production is dependent on the growth conditions of the host, although physiological arguments of the host-parasite interaction may be more realistic. Cob growth indicates a basic estimator for crop health at the end of the season and provides a relationship for a maximum *Striga* seed production rate and the way of density dependency.

Combining the age and density factors the fertility rate of the age class *i* is modelled by:

$$F_i = F_{day} \cdot \frac{C(t)}{C_{max}} \cdot \left(1 - \exp\left(-\left(\frac{i}{i_{crit}}\right)^{\alpha_F}\right) \right) \quad \text{Eq. 14}$$

The concept realises the following hypotheses: If the host is damaged by *Striga* attack, a reduced or none cob growth is observable. In the feedback the *Striga* seed production is reduced. On the other side, optimal cob growth conditions will also increases the *Striga* seed production. The age class dependencies of viable seed production may fitted to data of SAND (1990) (Fig. 3). The critical value for cob growth is approached to the parameter set of the differential equation system, while the daily seed production is fitted to LIANG (1984, cited by KUNISCH et al., 1991) observing a maximum reproductive capacity of 30000 seeds/plant. Assuming a time to first flowering 60 to 90 days in Sorghum (PATTERSON, 1990) and a season length of about 160 days the daily seed production rate ranges from 100 to 150 newly produced seeds/*Striga* in low population density (Table 7). The modelled density dependencies of the daily fecundity rate are demonstrated in Fig. 3.

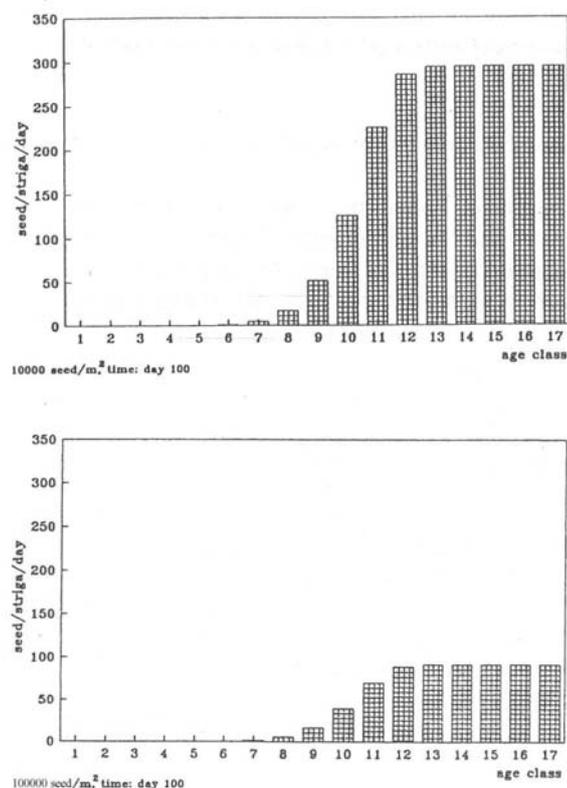


Fig. 3: Simulated daily fertility rates dependent on *Striga* age and initial seed density; top) rates with low initial density; bottom) rates with high density; 100 days after planting

2.3.3 Developing the damage functions

The variables "root growth" and "shoot growth" manipulate on the time-dependent transition probability $U_{s,i}$ of the *Striga* stages. MUMFORD & NORTON (1987) discuss two type of damage functions, how host-parasite-interactions may be formulated. IITA research data (unpublished) suggest a distinction between *Striga* and root and *Striga* and shoot interaction. While the influence of *Striga* on shoot growth seems to be exponential (CARDWELL, unpublished) and is described by a damage function Type I (MUNFORD & NORTON, 1987).

$$\xi_s(x) = \exp\left(-\frac{x}{x_{crit}}\right) \quad \text{Eq. 15}$$

x_{crit} =critical *Striga* density

This simple relationship is not applicable for modelling the *Striga*-root growth interaction. Taken from the sugar beet-nematode system *Heterodera schachtii*-Beta



vulgaris (SCHMIDT, 1992) a certain density scope of *Striga* exists, which support the root growth. In addition, KIM's (IITA, unpublished) observations indicate that *Striga* attack can increase root growth. An 2 to 3 folds higher root/shoot ratio with infestation compared to uninfested crops indicate a more complex *Striga*-root association (PATTERSON et al., 1983).

The observations are a common response to stress by the plant. Increased root growth is also observable in low nutrition levels (MENGEL and KIRKBY, 1982). An adequate model, which describes the potential damage interactions is the following function (SCHMIDT, 1992):

$$\xi_x = \frac{x}{x_{\min}} \cdot e^{-\left(\frac{x}{x_{\min}}\right)} + e^{-\left(\frac{\alpha \cdot x^2}{(1 + \beta \cdot x)^{\frac{\gamma}{\beta}}}\right)} \cdot e^{-\left(\frac{x}{x_{\text{crit}}}\right)^{\delta}} \quad \text{Eq. 16}$$

x =Numbers of *Striga*, weighted to development stage

x_{\min} =density of *Striga* seedlings which increase the root growth

x_{crit} =critical density, which decreases the growth processes

$\alpha, \beta, \gamma, \delta$ = Form parameter of the function

The function controls the relative growth rate of the root (Eq. 7). A trajectory of the function is shown in **Fig. 4**, demonstrating the biological response of the root to different infestation levels. Although the function seems to be over-parameterised from a statistical point of view, the form parameter ($\alpha, \beta, \gamma, \delta$) were directly transferred from the sugar beet - nematode relationships to the current system, indicating a common and stable damage function for different host-parasite systems. Obviously, the parameters x_{\min} and x_{crit} have to be adapted to the current system, and δ may be more sensitive. The type of function holds more advantages. The peak at low densities allows to model compensation effects of host and organ competitions. The equation calculates different crop yield-parasite associations with corn yields variable in high ranges with respect to parasite density.

$\xi(x)$ is the influence of developing *Striga* stages on the root growth rate, while x is the number of *Striga* stages feeding on the host. The variable x needs some more remarks. IITA research (CARDWELL, unpublished) has shown that the absolute numbers of *Striga* attached to the host is decreasing significantly from one to the next development stage. From an average of 50-60 measured "unemerged *Striga*" only 1 or 2 individuals will reach the stage "maturity". However, the negative effect of *Striga* on the host continues until harvest. The current concept is not able to cope with this observation. At end of a season, the number of parasites/host is extremely low, the suppressive effect cannot be simulated anymore, and the organ growth of the host would start again numerically. These new growth processes are not realistic. Weighting x to a linear factor of each development stage in ascending order avoids the discrepancy (table 2).

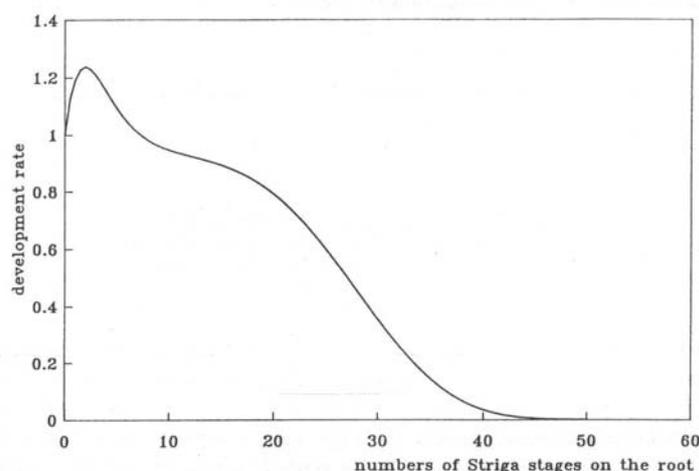


Fig. 4: Damage function of the *Striga*-root association

Table 2: Stage specific weighting factors of the damage functions

| Stage/Organ | Root | Shoot |
|-------------------------|------|-------|
| Attachment | 1 | 1 |
| unemerged <i>Striga</i> | 2 | 2 |
| emerged <i>Striga</i> | 3 | 4 |
| Maturity | 4 | 8 |

From biological point of view, it is not unrealistically to weight the stages with a linear factors. It take into account the time how long each individual parasites on the host. One individual *Striga* plant, which reaches the last stage, feed longest on the host and therefore account most for final crop losses.

The influence of the host on *Striga* development probabilities is calculated by:

$$Z(t) = \min\left(\frac{S(t)}{K(t)} \cdot \frac{R(t)}{K(t)} + \frac{C(t)}{Kap}, 1\right) \quad \text{Eq. 17}$$

and is limited to one. Due to age senescence of root and shoot, cob biomass (C) has to be considered in the probability, combining the transition from vegetative to generative growth periods. Equation 17 finally completes the host-parasite system.

3. Parameter identification

The model combines biological knowledge, hypotheses and the common discussion about the biology and the host-parasite interaction. It is a theoretical system with different classes of parameters. It is obvious, that these numbers of parameters cannot be estimated at all from related designed experiments.

To solve this problem three classes of data are available:

1. directly assessable parameters from experiments under controlled conditions;



2. evaluating parameters from the results of field experiments or controlled conditions;
3. taking parameters from the results of farmer fields and surveys;

The ascending sort symbolizes a decrease of information, but an increase in data variance. The missing information between the classes should be reconciled by the parameterised model. Combining the different levels of data structures, the following procedure of a stepwise calibration is chosen:

All parameters, if possible, should be estimated from designed experiments. These parameters should not be changed again, when calibrating all the remaining parameter of the model to the findings of field experiments. Fragments of data from experiments under controlled conditions will be considered additive, when the data set is too low for parameter estimation. Finally, the calibrated model should reflect the variance found in farmers field surveys and be constant to different situations. These boundaries in parameter identification restrict the extremely large numbers of parameter combinations.

3.1 Environmental response functions

The *Striga* - Maize system is controlled by environmental covariates. The main driving environmental variables are the temperature and soil humidity. While the temperature amplitude is low in tropical areas, the main factor for seasonal variances is searched in soil humidity. RICHTER & SÖNDGERATH (1990) are introducing a method to estimate the stage transition probabilities $U_{s,i}$ of each age class, in formulating these probabilities in terms of the normalized development time and the Biological time (RICHTER & SÖNDGERATH, 1990). The Biological Time is commonly estimated from the temperature response functions.

The selected temperature response functions for the different development stages and the host are based on the O'Neill-Function (SPAIN, 1982).

$$x = (Q_{10} - 1) \cdot (T_{\max} - T_{opt})$$

$$y = x^2 \cdot \frac{\left(1 + \sqrt{1 + \frac{40}{x}}\right)^2}{400}$$

$$z = \frac{(T_{\max} - T)}{(T_{\max} - T_{opt})}$$

$$f(T) = k_{\max} \cdot z^y \cdot \exp\left(y \cdot \frac{(T - T_{opt})}{(T_{\max} - T_{opt})}\right) \quad (\text{Eq. 18})$$

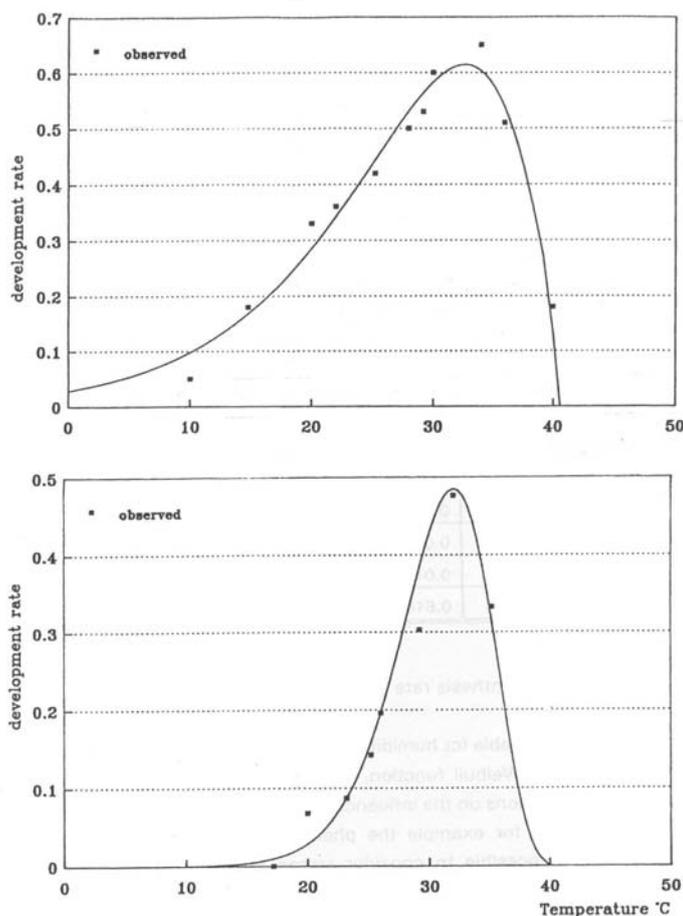


Fig. 5: Fitted temperature response functions (Eq. 18), top, data for maize (KINRI, 1992; bottom: data for *Striga*, PATTERSON, 1987)

Parameter estimation is possible for maize (KINIRY, 1991) and the stage "Germination" (PATTERSON, 1987, 1990). The results of the fits are depicted in Fig. 5. Further data points from PATTERSON (1987, 1990) were too few to fulfil the criteria of parameter estimation. However, the given information limits the range of parameter values of the temperature response functions of the other stages. The combination of estimation procedures and calibration procedures, considering the sparse information from PATTERSON (1990) result in the following list of parameters:

Table 3: List of parameters used for each temperature response function

| Stage/Host | K_{max} | Q_{10} | T_{opt} | T_{max} | Source |
|-----------------------|-----------|----------|-----------|-----------|-------------------|
| Germination | 0.4849 | 2.89 | 32.06 | 42.0 | PATTERSON, 1990 |
| Attachment | 0.303 | 1.6 | 32.0 | 42.0 | |
| Unemerged S. | 0.1657 | 2.2 | 32.56 | 42.8 | PATTERSON, 1990 |
| Emerged <i>Striga</i> | 0.0457 | 3.2 | 32.0 | 42.0 | |
| Maturity | 0.0457 | 1.63 | 31.0 | 42.0 | (PATTERSON, 1987) |



| | | | | | |
|-------|--------|------|-------|-------|-------------|
| Maize | 0.6146 | 1.73 | 32.68 | 41.73 | KINRY, 1991 |
|-------|--------|------|-------|-------|-------------|

Striga's response window to temperature is a narrow one, showing the adoption to tropical and subtropical regions. It cannot cope with cold temperatures. The parameters of the stage „maturity“ are an approach to the temperature dependent net photosynthesis rate of *Striga* (PATTERSON, 1987).

No data are available for soil humidity. The response functions for this factor are based on a double Weibull function. The parameter identifications are calibrated to general discussions on the influence of soil humidity (EGLEY et al. 1990; OSMAN et al., 1991), for example the phenomenon of wet dormancy (PATTERSON, 1990). It is possible to consider strong rainfall events with the calibrated functions.

$$f(H) = H_{rate} \cdot \left(1 - \exp\left(-\frac{H}{H_{min}}\right) \right)^\alpha \cdot \exp\left(-\frac{H}{H_{max}}\right)^\beta \quad (\text{Eq. 19})$$

The parameter used are also shown in Table 4 and Fig. 5 demonstrated the influence of soil humidity to the development rate assumed from the general discussion and the hypothesis of “wet dormancy” of EGLEY et al. 1990, OGBURN, 1972, OSMAN et al., 1991, VALLANCE, 1951. While there are no differences at low humidity levels, *Striga* is susceptible to high humidity levels, while the host is less affected by the upper humidity levels.

Table 4: Parameter of the humidity response function

| Stage/host | H _{rate} | H _{min} | α _H | H _{max} | β _H | Source |
|---------------|-------------------|------------------|----------------|------------------|----------------|----------|
| <i>Striga</i> | 1 | 1.5 | 4.5 | 11.0 | 4.0 | see Text |
| Maize | 1 | 1.5 | 4.5 | 20.0 | 7.0 | see Text |

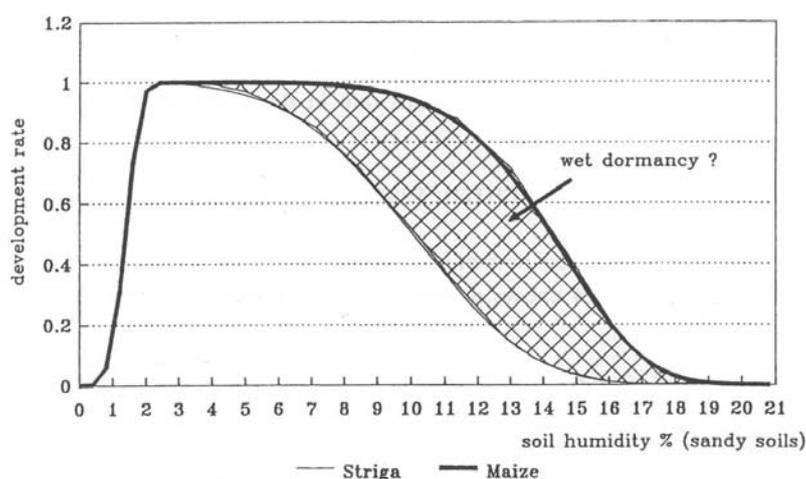


Fig. 6: Calibrated humidity response function of maize and *Striga*



The parameter set of the function is limited to the range of soil humidity in sandy soils (SCHEFFER & SCHACHTSCHABEL, 1982). The link of rainfall to soil humidity may be simulated elsewhere (HANKS & RITCHIE, 1991). Aspects of hysteresis and other problems, as unsaturated water flows in the soil-water-dynamics complex (TIETJE & RICHTER, 1992), are ignored.

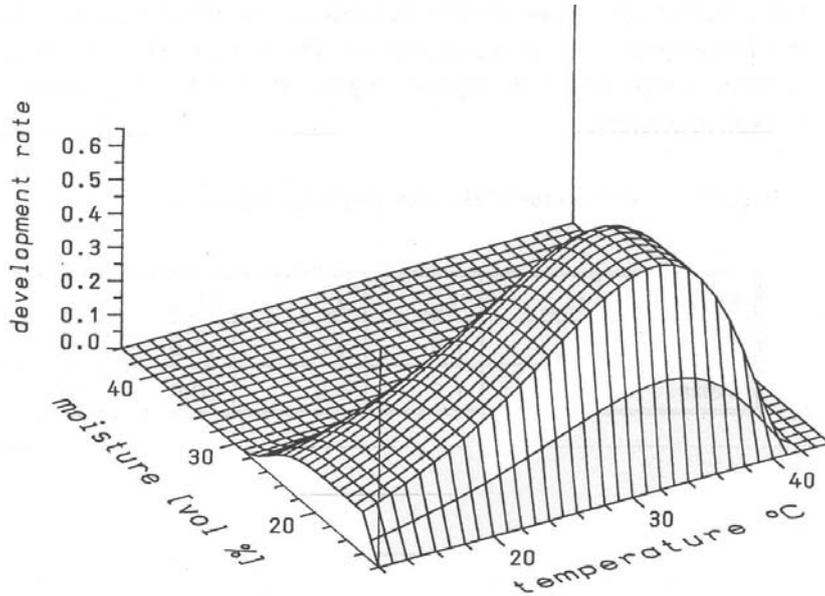


Fig. 7: Host development rate in dependence on temperature and soil humidity

Finally, the Biological time of each stage is the integral of the product of both functions.

$$b_s = d_s(T, H) = f(T) \cdot f(H) \quad \text{Eq. 20}$$

for $s := \text{all stages}$. For the host is $d_s = \varphi$ and the minimum value is limited

The development time is assumed to be Weibull distributed ($G_s(b_s)$), and from the concept of normalized development times the following equation (RICHTER & SÖNDGERATH, 1990) for estimating the $U_{s,i}$ is used:

$$U_{s,i}(t) = \begin{cases} \frac{G_s(b_s(t_{s,i,0}, t)) - G_s(b_s(t_{s,i,0}, t-1))}{1 - G_s(b_s(t_{s,i,0}, t-1))} & \text{falls } G_s(b_s(t_{s,i,0}, t-1)) < 1 \\ 1 & \text{else} \end{cases} \quad (21)$$

While one parameter of the Weibull distribution is determined by the Biological time, the exponent is calibrated to IITA data. The data indicate a smooth transition, consequently the exponent is small. The following table shows the second parameter of the Weibull function β .

table 5: Parameters of β . for each stage

| Stage | β . |
|-------------------------|-----------|
| Germination | 3.1 |
| Attachment | 1.2 |
| unemerged <i>Striga</i> | 1.1 |
| emerged <i>Striga</i> | 1.5 |
| Maturity | 3.1 |

3.2 Other parameters

The survival probabilities from one age class at time t to the next age class at time $t+1$ is assumed to be exponential distributed, so that the m_s parameters are reduced to one secondary one (RICHTER & SÖNDGERATH, 1990). This parameter is most important for a quantitative expression of the dynamics of individual *Striga* plants. The normal range of this parameter by a given time step of one day ranges usually from 0.95 to 1, while 0.95 is a extremely strong mortality over a time period. With respect to the calibration criteria given above the following table of λ . were identified:

Table 6: Parameter λ . of the survival probability

| Stage | λ . |
|-------------------------|-------------|
| Germination | 0.01 |
| Attachment | 0.969 |
| Unemerged <i>Striga</i> | 0.975 |
| Emerged <i>Striga</i> | 0.96 |
| Maturity | 0.989 |

The need for setting such a high mortality rate for the germinated *Striga* seeds is most surprising. It means the existence of just one age class. KUNISCH et al. (1990) suggest similar strong decrease rates in population densities/m² in their conceptual model. Derived from biology those low survival rates are realistic. The very small seeds have stored a low level of nutrients. However, a successful penetration is an energy consuming process. Apparently all germinated seeds die instantly, if the complex physiology of successful attachment to a host fails.

The third class of parameters, the fertility rate of each age class, results in the following list of parameters:

Table 7: Parameter of the daily fecundity

| Parameter | Value | Source |
|------------|-------|-------------|
| F_{day} | 100 | LIANG, 1984 |
| C_{max} | 2000 | |
| i_{crit} | 10.5 | SAND, 1990 |
| α_F | 10.1 | SAND, 1990 |



The parameters of the introduced damage functions are verified as listed in table 8, while x_{crit} is the same in both damage functions. The supporting effect is in very low densities.

Table 8: Parameters of the damage functions

| Parameter | Value |
|------------|-------|
| x_{min} | 2 |
| x_{crit} | 30 |
| α | 1.1 |
| β | 1.22 |
| γ | 3.4 |
| δ | 4.2 |

Table 9: Parameter of the differential equations system

| Initial value | growth rates r. | decay rates sd. |
|---------------|-----------------|-----------------|
| $K_0=8000.0$ | | 0.0015 |
| $R_0=85.0$ | 0.24 | 0.09 |
| $S_0=45.0$ | 0.34 | 0.08 |
| $C_0=1.1$ | 160.0 | 0.03 |
| $Y_0=1.1$ | 0.011 | |

In conjunction with the environmental response function of the host, the following list of parameter reflects the general dynamics of Maize (GEISLER, 1980; FISCHER & PALMIER, 1984). Carefully calibration occurred to IITA data. Although the plant model is constructed just as an additive probability of the stage transitions, with a correct transformation the model simulate plant growth both in probability terms and in absolute weight (g dry matter/plant). The differential equations are just valid with the set of parameters given in table 10. An system analysis of the differential equations with sets of other parameters is not the objective here.

3.3 Host density

The quantitative population dynamics of *Striga* are also dependent by the host plant density. Three stages of plant densities/m² are introduced, representing the following finding:

Table 10: Host plant density

| Host/m ² | Location | Source | A_{max} (Eq. 10) |
|---------------------|--------------|--------|--------------------|
| 3 | Farmer field | IITA | 6000 |
| 5 | Experiment | IITA | 4500 |
| 8 | Europe | | 3300 |

A_{max} defines the variable intra-specific competition effects for different host densities.



The values are inherent and in the range of the model scope. They cannot be estimated by experiments. The modelled feed back to the maize densities was demonstrated in a previous chapter.

3.4 Tolerant cultivars

The breeding sector is searching for resistant host plants against *Striga*. Some tolerant maize varieties are identified. The model has to consider the different behaviour of a tolerant variety. Although the differences between susceptible and tolerant varieties are intensively discussed, the determining factors are not clear. IITA-Research results in a different, variety-specific, humidity response (KIM, per. corn.) or a different root growth behaviour in depth or similar. But exact relationships are difficult to identify and unknown. It is assumed that the use of a tolerant variety is suppressing the *Striga* dynamics, and *Striga* dependent yield losses are reduced. The conceptual model offers some theoretical links, when tolerant varieties are planted. With given objectives to keep the extensions simple within the model hypothetical links are possible:

Reducing the probability of entering the life cycle by a tolerant factor is the simplest way. A_{pot} (eq. 10) is divided by the tolerant factor, reflecting an assumed different root growth behaviour. Furthermore, the influence of attachments and further development stages is lowered. x_{crit} of the damage functions (eq. 15, 16) is multiplied by the same tolerant factor. These simple, linear extension describes well the given biological assumptions when planting a tolerant variety. Only one additional parameter is required.

3.5 Sorghum influence

It is essential expand the system by an additional host, as the *Striga* problem is mostly associated to Sorghum. The generic structure of the current maize model allows an application to the relative differences of sorghum. Physiologically there are enormous differences between the two cops, but reducing the host to a statistical probability, the differences are reduced to some parameters. The following characteristics of sorghum contrary maize may is defined (DOGGET, 1985) within the model system: The season length of sorghum is about 160 days, the biomass production is higher, but the relatively daily growth rate is reduced, the tolerance against *Striga* is higher. While the maximum germination rate is shown in table 1, the changes of the following parameters consider the internal differences:

All other parameters are kept as for maize, and also the environmental response function is assumed to be the same, until a new parameter constellation is available. The differences about this function may not be so significant as both host are populating similar locations.



Table 11: Sorghum parameters

| | | |
|------------|-------|--------|
| | | |
| Y_0 | 12000 | 5 |
| r_r | 0.11 | 6 |
| r_s | 0.19 | 7 |
| r_c | 160.0 | 8 |
| X_{crit} | 100 | 15, 16 |

3.4 Long time modelling

The initial seed bank density of the year $k+1$ is the sum of non-emerged seeds of the year k plus the newly produced seeds in the year k multiplied with the survival probability of the year k (CARDWELL et al., 1991). The survival probability of the seeds from one year to the next can be fitted to an exponential function for a soil depth of 0-30cm (EPLEE, 1990). The natural within season mortality is estimated as 20 % (CARDWELL et al., 1991); hence, a survival probability of 0.8 is used.

4 Results

4.1 Research pattern, data sources and driving variables

Intensive research on the population dynamics of the maize-*Striga* system has been done in 1991 and 1992 over complete seasons (IITA, unpublished). Although the data are not detailed enough to fit the model in a statistical way, the data allow a discussion of the *Striga* dynamics within the whole system and are sufficient for a stepwise calibration.

The data represent the following range of research:

- a) Site Hadagon (1992), Cana (1992), Mokwa (1991)
- b) Uninfested and infested plots
- c) Susceptible and tolerant varieties
- d) Different initial *Striga* densities (only Mokwa, 1991)
- e) intensive regional survey in farmer fields over several years
- f) general yield/loss-relationships

The locations represent typical areas in West Africa at the boundary of the sorghum belt and entering the maize belt. Mixing both crops is usual.



b) and c) include the following information:

- absolute numbers of *Striga* development in unemerged and emerged *Striga* and flowering plants;
- the host biomass has been measured in weekly intervals throughout the season, divided into different units of counts of cm or g dry matter.

For model evaluation the following data are used

- Root dry matter in g
- Shoot dry matter in g, including stem and leaf dry matter
- Cob dry matter in g

representing the host growth over time (maize). For control and comparison, additional data from uninfested soils are available.

Weather records are available from Cotonou, Ibadan, and Kano in different years, representing the range of African temperature and rainfall events.

All information are combined within the model, while already estimated parts of the model remain unchanged. A constant temperature and humidity regime is used for the calibration procedure in a first step to evaluate the common model dynamics.

The reference file of calibration procedure is the data set of the site Hadagon in 1992 in a second step. This data set capitulates the introduced set of model parameter. Fig. 8 shows the result of the observations and demonstrates the high variance found in the field experiments. For model comparison, only mean data are used to reduce the variability.

The main driving variable of the model is temperature. Soil humidity is used additionally for special situation taking into account retarding processes.

4.2 Model simulation with constant temperature and soil humidity

Fig. 9 shows the standard simulations of the *Striga*-maize-system with given season length, initial population density and constant temperatures. Reducing effects of soil humidity are not assumed. Four components are distinguished in the figures:

1. Environment (temperature pattern, actual soil humidity)
2. Seed bank dynamics, also newly produced seed
3. *Striga* stage dynamics
4. Host organ dynamics, infested and control

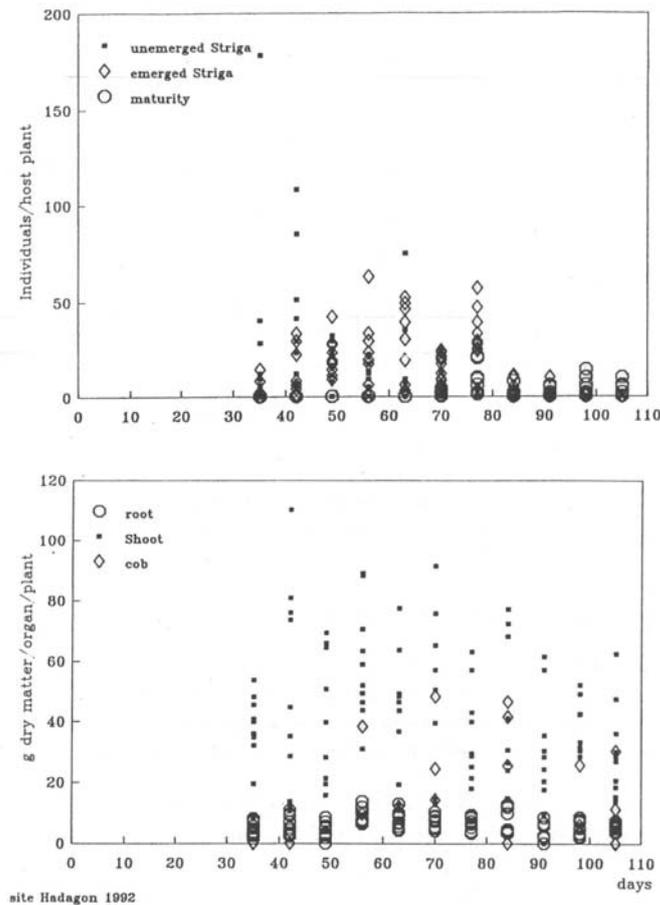


Fig. 8: Observed variances in field data (IITA, 1992, site Hagadon), top: measured *Striga* stages; bottom: measured maize organs

Component 2 is the initial value of the seed bank. It is depicted separately to demonstrate the large differences in absolute quantities between *Striga* seed bank dynamics and the following development stages. Component 3 included the trajectories of the three observed stages, while the host organs has additional six sets of data at each observation (component 4). Taken from the initial model concept the host dynamic is just used as probabilities. Using a linear transformation of the data sets to the model scale yields in correct time dependent quantities and provides a feed back to *Striga* affected yield losses.

The components represent the model run and have to be fitted simultaneously to all data. Exploiting those strong dependencies within the different levels of data and model, the possible combinations of parameters are severely limited.

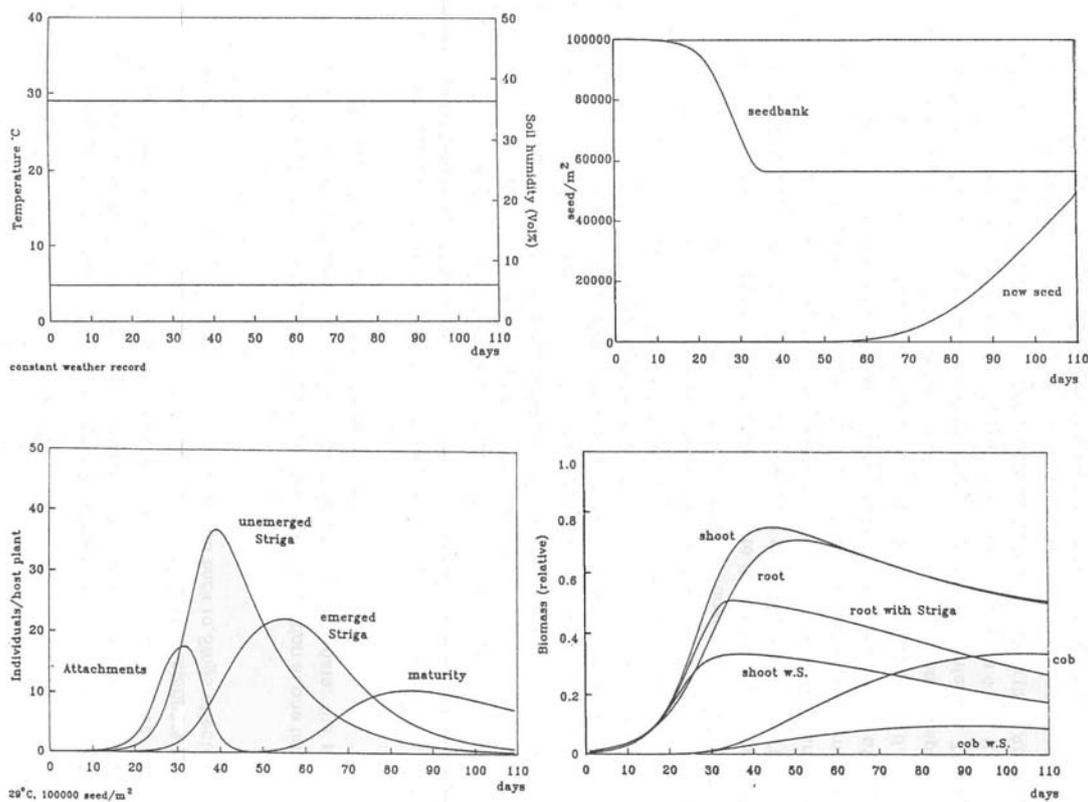


Fig. 9: Standard simulation; top left) climatic conditions; top right) seasonal seed bank dynamics; bottom left) simulated *Striga* stages; bottom right) infested and uninfested maize organ dynamics

The simulations show the following results. The seed bank of the current season is reduced by an environmental variable amount of about 40% from the initial population density. The period of germination stops, when root growth processes of the host reach their maximum. Just a very low percentage of the germinated *Striga* seeds attach successfully to a host. While KUNISCH et al. (1991) demonstrated a relationship of 5000 attachments with an initial population density of 100000 seeds/m² this model concept account for 20 attachments/host only. The significant lower proportion is a result of the overall calibration. Other ratios from stage to stage did not end up in realistically dimensions. The maximum attachments are time limited to the maximum growth of the host. The following stages of unemerged and emerged *Striga* plants continue to occur all the season. After 50 to 60 days the first merged *Striga* plants start flowering, a few days earlier compared to the results of PATTERSON (1987). The optimal temperature conditions yield in a large number of mature *Striga*/maize plant. With a host density of 5 host plants/m², we simulate a similar scope of parasites as KUNISCH et al. (1991) did. The self-limiting of *Striga* is demonstrated in Fig. 9 (bottom right). While uninfested root and shoot biomass will reach their environmental dependent capacity, the parasites organs are severely decreased compared to the control. The differential equation for the variable “capacity” term (eq. 5) is not shown



here. It has to be repeated again the trajectories are mirroring probabilities through time. Absolute shoot biomass is certainly much higher than root biomass. The *Striga* related host suppression starts about three weeks after planting, different growth dynamics are observable about four weeks after planting. Fig. 9 demonstrates how different the organs are affected by the parasite. Finally, the cob biomass is reduced by 80% in the given relationship.

4.2.1 Site Hadagon (Rep. Benin, 1992)

Fig. 10 presents the comparison of simulation and observations separated in *Striga* stage dynamics and each host organ with and without *Striga*. With the given temperature file of Cotonou (Fig. 11, top), the observed data from the site Hadagon in 1992 are simultaneously repeated very well through time as well in quantity. Soil humidity is not considered yet. With given initial seed bank and the underlying weather record the final predicted cob biomass with *Striga* infestation is slightly overestimated, also the numbers of emerged *Striga* vary at the end of season. With a high initial seed bank of about 100000 seeds/m² just a few attachments occur. (No measurements are available for this stage). The maximum of subsoil growth is reached 40 days after planting. Average unemerged *Striga* are in the range of up to about 40 individuals. Only half of this proportion emerges from soil. The maximum of above soil *Striga* plants is reached about 20 days later. Contemporarily the numbers of unemerged *Striga* decreases accordingly. Germination has stopped by now. *Striga* starts flowering about 60 to 70 days after planting. Just a few *Striga* individuals per host are observed. The simulated time and data compares well to the observation of PATTERSON (1987). Maturity does not stop until end of season. Comparing the simulated and observed host growth processes in the infested and uninfested variant the simulated growth processes of root and shoot biomasses start too early in time in comparison to the observations. It would be easily to shift the dynamics with respect to the observations but the changed parameters were not able to give realistic results in the feed back to the measured *Striga* stages.

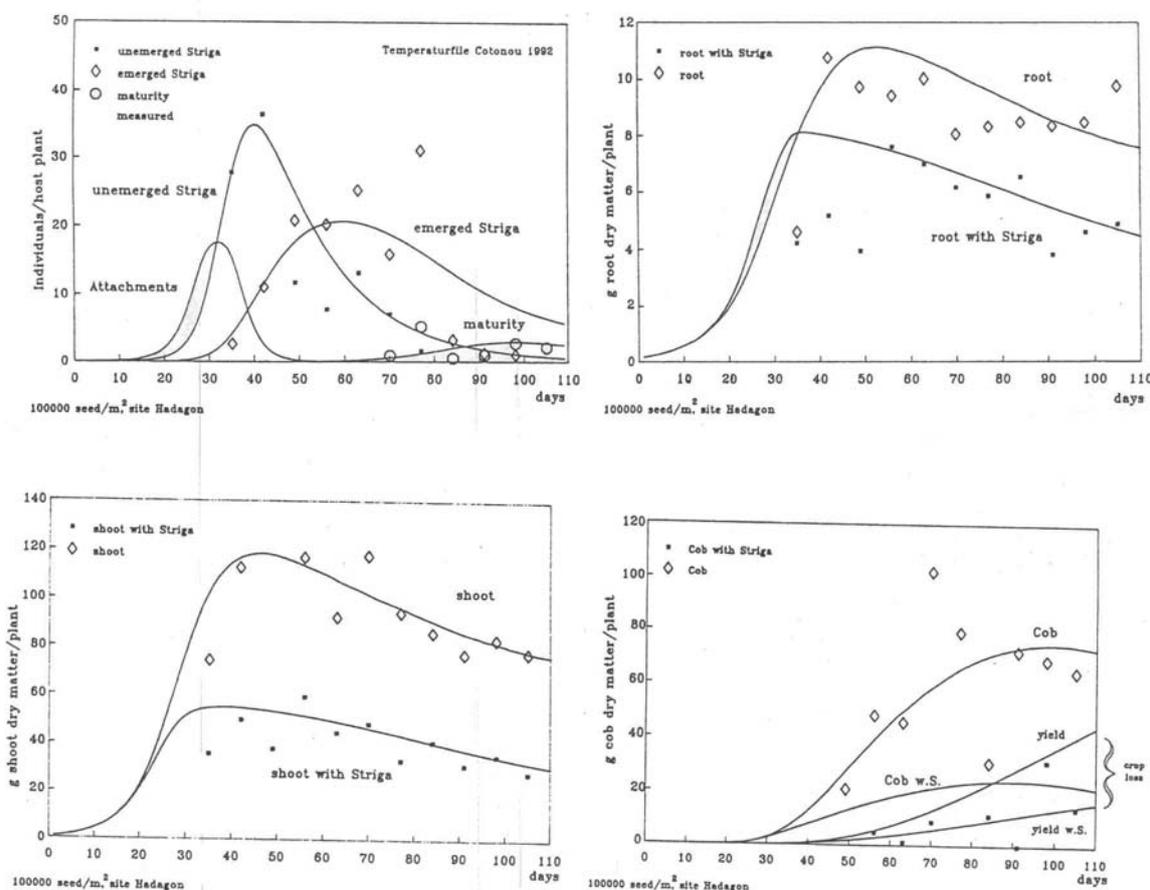


Fig. 10: Comparison of simulation and observation, susceptible variety, site Hagadon, 1992; top left) *Striga* stages; top right) root; bottom left) shoot; bottom right: cob

A transformation factor for each host compartment is required to swap from probabilities to absolute biomass in g. This factor varies with different years. The impact of *Striga* attack on cob growth is demonstrated in Fig. 10 bottom right. The control data show the system of differential equations is a sufficient approach to describe the cob growth processes. Infested root and shoot biomass is simulated well by the model as well, but the final cob biomass seems to be overestimated. No solution can be given by the model. No data were available for corn yield. A linear ratio from cob biomass is used. The demonstrated crop loss ratio reflects real observations and the general discussion about *Striga*-dependent yield loss. This data set was the standard file for calibration; hence, the high correlation for the most organs and stages is not surprisingly. Nevertheless, the model is able to repeat an extremely complex structure. Also some deviation occurs a set of parameter is defined which links the strong theoretical model with the multiple observations, indicating, that the assumed host-parasite-associations are modelled in the correct way. The procedure results in a set of parameters, which should be not changed when applied to different sites. The different climatic conditions of each site should explain the differences in the data.

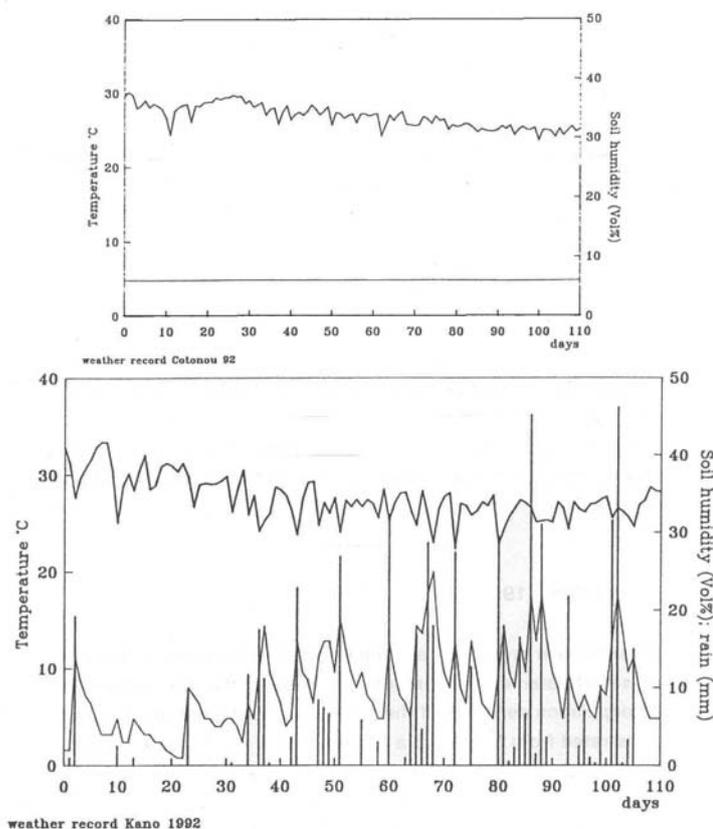


Fig. 11: Used weather records for model simulations; top) Cotonou 1992; bottom) Kano 1992 with rainfall events

4.2.2 Site Cana (Rep. Benin, 1992)

The Kano weather data (**Fig. 11**) of Northern Nigeria is used for the simulations. The file represents similar condition to site Cana. Soil humidity is considered as an additional factor. The initial seed bank value is set to 110000 seeds/m². The time pattern and quantitative approach of unemerged *Striga* and the beginning of the emerged *Striga* compares well, but is over-predicted in the second half of the season Fig. 12. Only a very few flowering plants were found and the model results ends up in very low densities. The plant model agree well with respect to the root dynamics, but no differences between the infested and uninfested variation are found in the data (Fig. 12) The shoot dynamics seems to be over predicted in the uninfested variant, and also in invested data are on a lower level, than the simulations predicted. This overestimation of the shoot growth is continued in the comparison of the predicted and measured cob biomass as the infested as the uninvested version (Fig. 12).

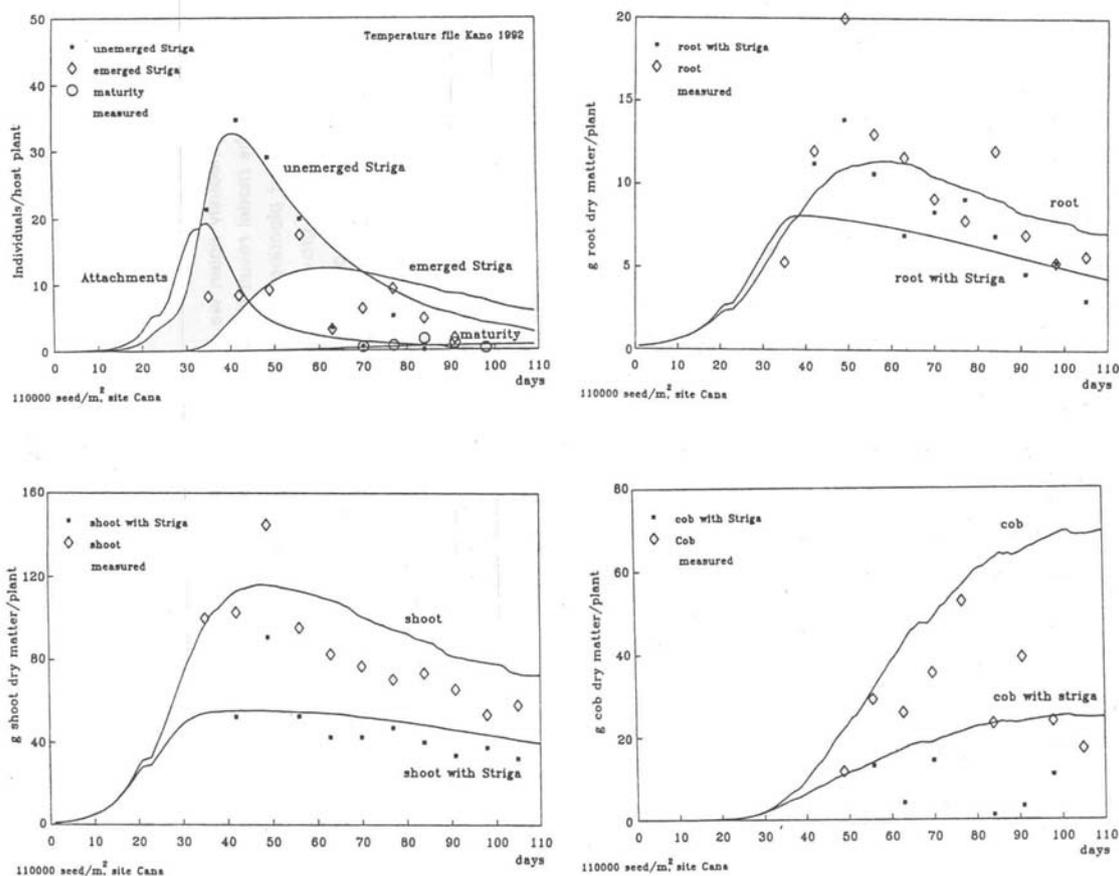


Fig. 12: Comparison of simulation and observations, susceptible variety, site Cana, weather file Kano, 1992; top left) *Striga* stages; top right) root; bottom left) shoot; bottom right: cob

4.2.3 Using tolerant variety on both sites in 1992

The use of tolerant varieties within the model was introduced before. Simple linear links to different model components represent more or less hypothetical assumptions. Absolute *Striga* densities are reduced on a tolerant host compared to a susceptible host for the location Hagadon in 1992 (Fig. 13). (Not significant by the data). The time pattern is similar, the maxima are delayed by about 10 days, but maturity begins about 70 days after planting, equal to the susceptible variant. Derived from the theoretical simplification the process of attachment is prolonged than in a susceptible host system.



Modelling the population dynamics of the witchweed *Striga hermonthica*

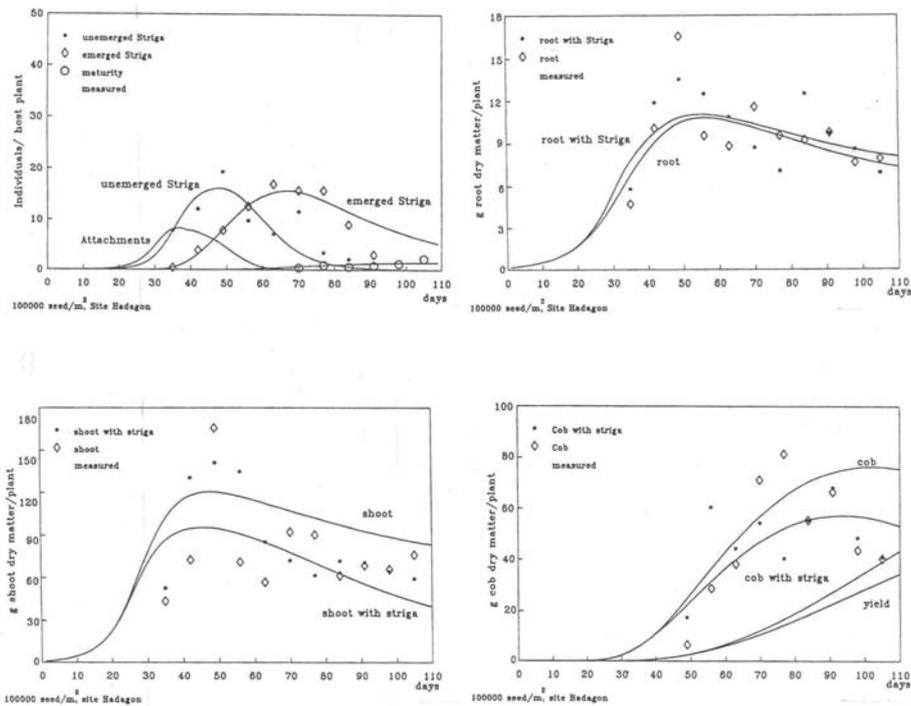


Fig. 13: Comparison of simulation and observations, tolerant variety, site Hagadon 1992; top left) *Striga* stages; top right) root; bottom left) shoot; bottom right: cob

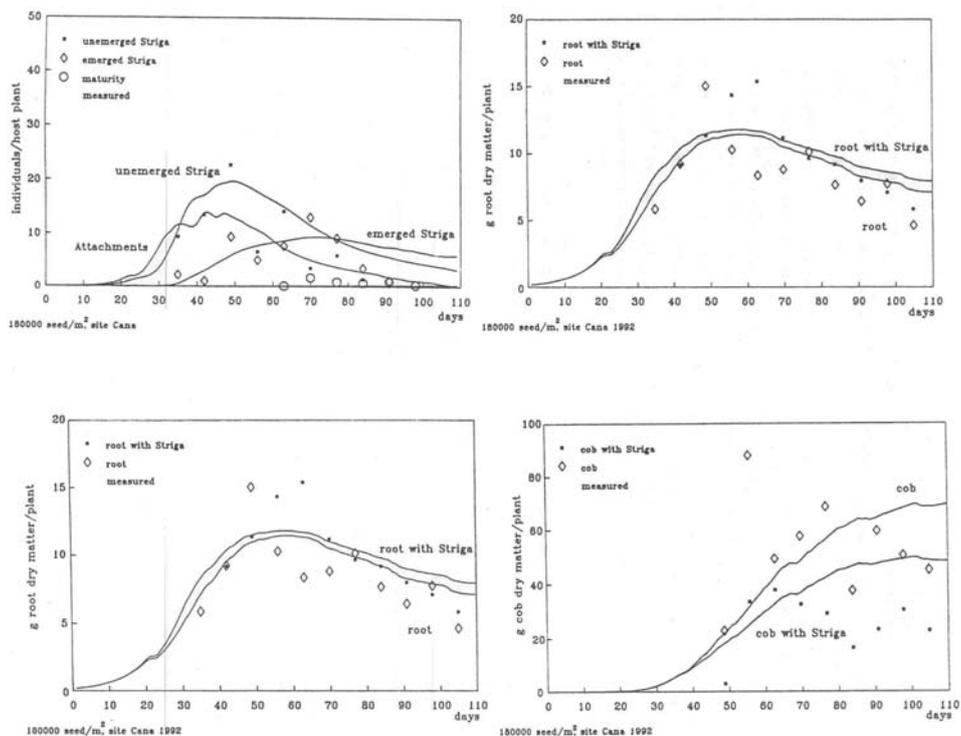


Fig. 14: Comparison of simulation and observations, tolerant variety, site Cana, 1992; top left) *Striga* stages; top right) root; bottom left) shoot; bottom right: cob



The finding cannot be confirmed by observations. The measured results of the tolerant host with the model results (Fig. 13) demonstrate a growth maximum 7 weeks after planting. There are no differences between infested and uninfested root growth processes, and the relative differences between the growth processes of shoot and cob are not as obvious as recorded from the susceptible variant. The model fits the overall data well. Root growth is modelled a little bit higher with *Striga* attack, a result from the damage function. The shoot dynamics without *Striga* seems to be overestimated again. Suppressing effects of *Striga* are noticed, influencing the shoot dynamics as well as cob biomass, yielding in slightly differences in yields (Fig. 13). Simulated yield relationships agree well with the data. Predicted yield losses are in the range of about 10-30 %, which are also observable in the field situations. The model combines all observations with a sufficient accuracy. The fits indicate that the assumption made during equation development yield in an arbitrary model reality, which reflects at least the averaged data, despite the mode of function of tolerant varieties is not clear yet.

Analysing the data of Cana 1992 by using the tolerant variety deviance occur (Fig. 14): Only a higher infestation level agrees well with simulation and measured data. Two reasons are possible and explainable within the model: Firstly the tolerance effects are cracked by *Striga* or secondly the adjusted infestation was higher than expected. The second possibility is more likely when regarding all simulations and data together. The *Striga* dynamics run in low levels only (Fig. 14), and there are no differences between infested and uninfested root growth (Fig. 14). Both factors indicate that a tolerant variety was seeded and the low level resistance is not disturbed. In addition, the very strong shoot reduction is only given with this high population, when a tolerant variety is used. According to the susceptible variant, the shoot dynamics may be overestimated again. The final cob biomasses of the infested and uninfested variant are also overrated in the simulations, especially late in the season. Nevertheless, the relative differences are found as in the model as well in the data. The yield losses are larger than expected as mature *Striga* occurred in very low densities.

Summarizing the application of the model to the data of Cana, as the susceptible as the tolerant variety, it obviously, that the model results and the data differ, and the model evaluation does not fulfil the expectation of the model. The deviations are not large enough to reject the model.

4.2.4 Site Mokwa, Nigeria (1991)

The data set represent unemerged and emerged *Striga* stages only, but the research emphasized on the density dependency problem, hence three different initial seed densities were tested. Monitoring started 4 weeks after planting and stopped 11 weeks after planting, meaning the season was not completed.

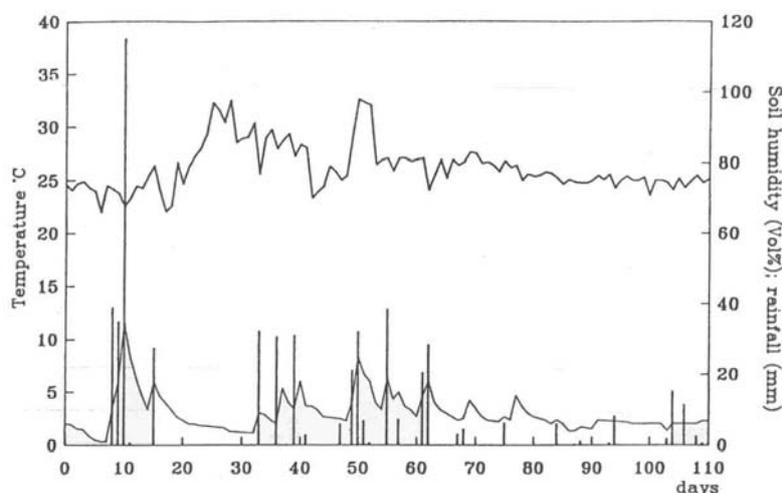


Fig. 15: Used weather record for 1991 with temperature, rainfall and soil humidity information

No climatic data of this year and site are available, so the following set of climatic events, based on the Cotonou file of this year (Fig. 15), is used to run the model with the data. The overall data set of Mokwa is characterised by delays in *Striga* development in the first month of the season, followed by a rapid growth period of the host from day 30 to 50 after planting. To simulate those observations the given weather includes some effects of delay and increases growth. A short period of draught in the first week after planting is assumed, followed by a massive rainfall event, which reduced the development probabilities of *Striga* by an assumed negative influencing soil humidity. These extreme climatic conditions effect the delaying of the development rate of *Striga*. Furthermore, some periods of optimal ranges of temperatures occur 4 and 7 Weeks after planting. That time is also characterised by severe rainfall events, so that short time peaks of high water concentration took place retarding *Striga* development (Fig. 15).

In the following each experimental combination of Mokwa in 1991 are analysed individually with respect to the climatic conditions. A control from uninfested plots is available and compared to all the different *Striga* infestation levels. The result of the experiments at low initial population density is shown in Fig. 16 top left for the *Striga* dynamics, and the others for the maize dynamics. An initial seed bank of 90000 seeds/m² is required to simulate the current trajectories for each stage. The oscillation of the (simulated) attachments is based on the described temperature and soil humidity. Although the first unemerged *Striga* data point is predicted well in time and numbers, just a very few unemerged *Striga* were observed during the continuation of the season, while the simulation runs in high density (Fig. 16).

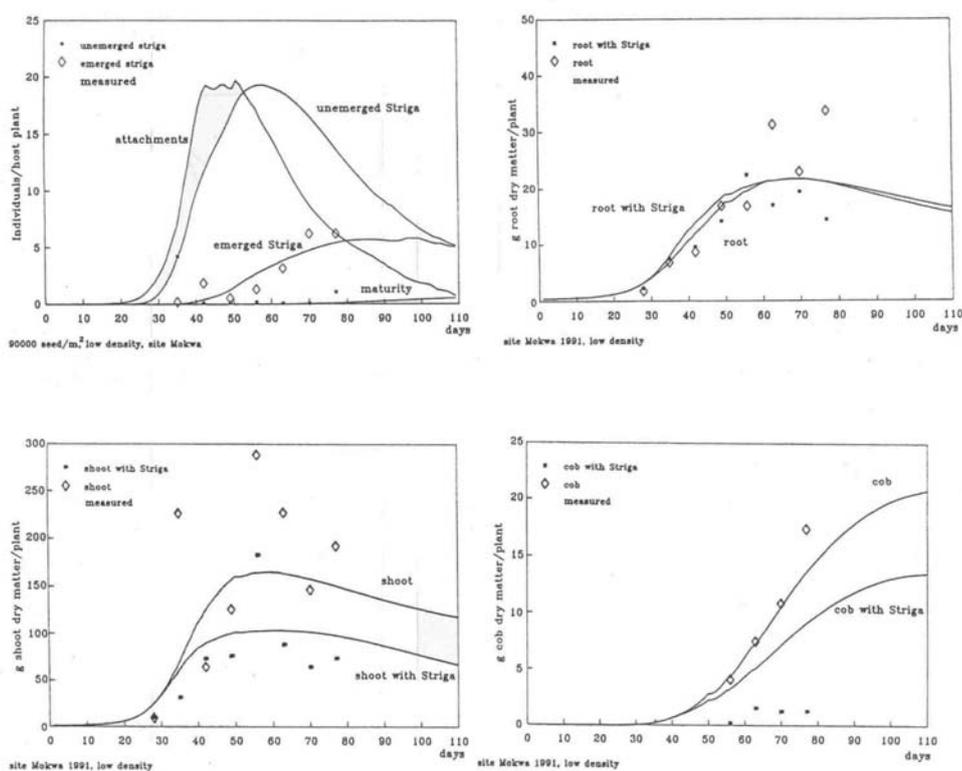


Fig. 16: Comparison of simulation and observations, susceptible variety, site Mokwa 1991; low density; top left) *Striga* stages; top right) root; bottom left) shoot; bottom right: cob

These simulated high densities are required to match the numbers of emerged *Striga*, which are predicted well in time and numbers. Also a very high population density were used, root growth is unaffected by *Striga*. The reason for this phenomenon might be the difference in the response to the climatic conditions. The required coincidence in time for *Striga* to establish successfully is disturbed by the given temperature and soil humidity. However, a strong decrease of shoot biomass is measured; giving reasons for the used initial seed bank value Lower densities would not cause such, reductions in shoot growth. The uninfested cob biomass is predicted very well with the given model constellation, the high cob loss observed in this experiment, cannot be correlated with the existing *Striga* plant in the second half of season. The results of medium density with an input of 150000 seed/m² is demonstrated in Fig. 17 The unemerged *Striga* are overestimated as in the previous example, but also the number of emerged *Striga* is not predicted well. A smaller seed bank would be needed to repeat the time course of the emerged *Striga* infestation, but such densities would not cause such differences in shoot growth as shown in the data. The result of the simulation for root and cob biomass is acceptable compared to the observations. Simulating the high infestation level a seed bank of 200000 seeds/m² are used. Fig. 18 shows the fits.

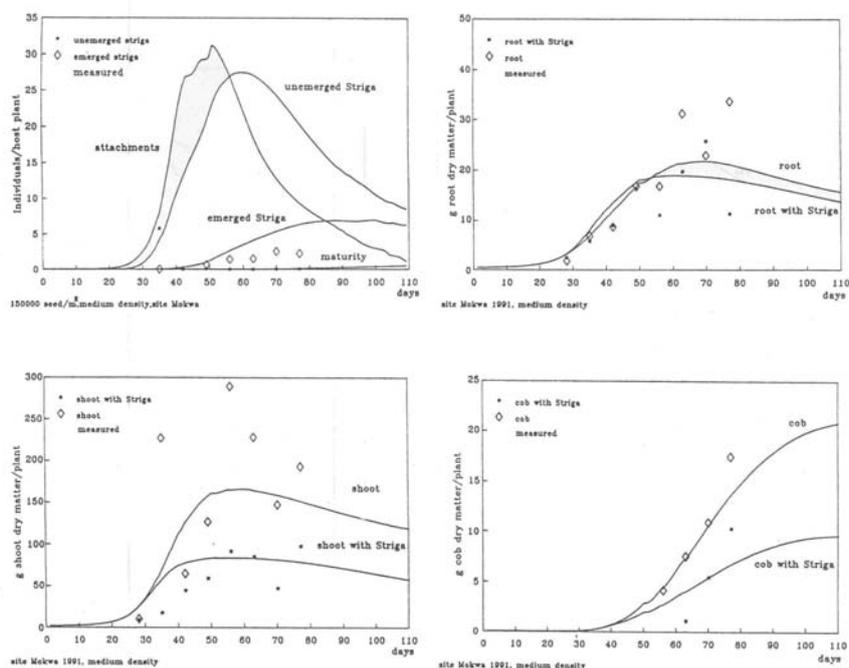


Fig. 17: Comparison of simulation and observations, susceptible variety, site Mokwa 1991; medium density; top left) *Striga* stages; top right) root; bottom left) shoot; bottom right: cob

Under the given climatic regime only such a high *Striga* density reduces the host root biomass. The measurements indicate a decrease at the end of observation time, justified by one data point. It is surprising that such a high population does not affect root growth more severe. Again, a retarding influence of high soil moisture levels might be the reason. The shoot biomass is overrated again, and the nearly total suppression of cob growth is out of the range of the model, even the simulated differences are tall.

4.2.5 Using tolerant varieties in Mokwa (1991)

A further data set is available using tolerant varieties on the same site and year. Again, the linear model generalization is used to compare the simulations with the data. Starting with the medium density example (150000 seed/m²) nearly the same consensus between model and data is observed as illustrated in the previous chapter (Fig. 19). Again only, the emerged *Striga* are predicted well, the deviation from root biomass is negligible. The measured shoot biomass is characterized by a high variance over time; relative treatment differences are both over and underestimated. The cob biomass agrees well in the infested version, but is below the data of the control.

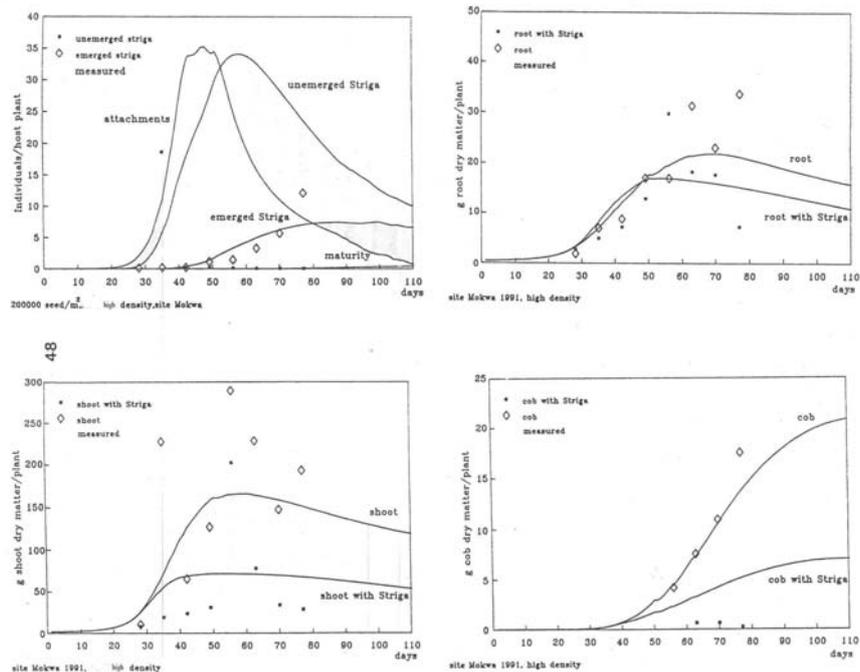


Fig. 18: Comparison of simulation and observations, susceptible variety, site Mokwa 1991; high density; top left) *Striga* stages; top right) root; bottom left) shoot; bottom right: cob

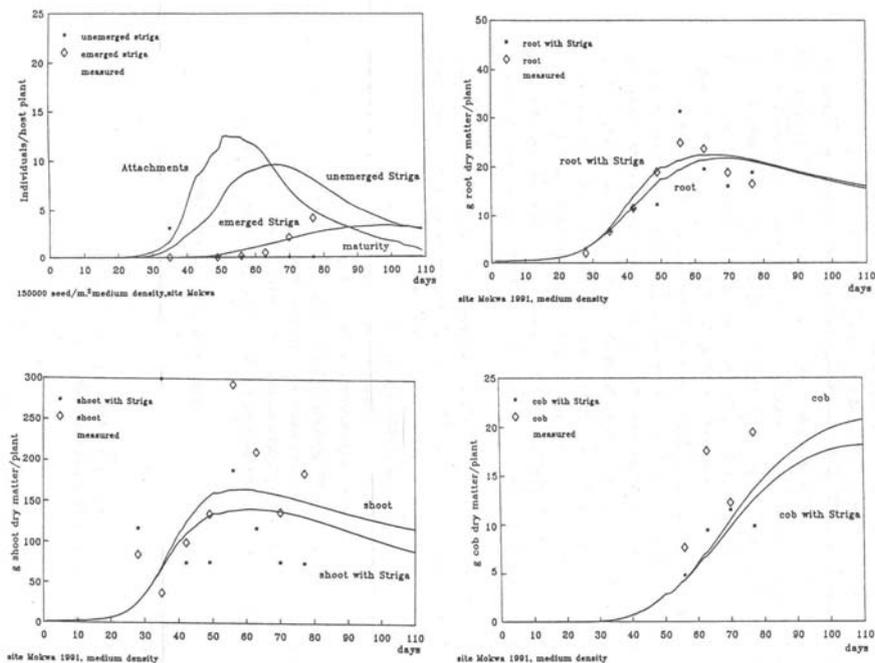


Fig. 19: Comparison of simulation and observations, tolerant variety, site Mokwa 1991; medium density; top left) *Striga* stages; top right) root; bottom left) shoot; bottom right: cob

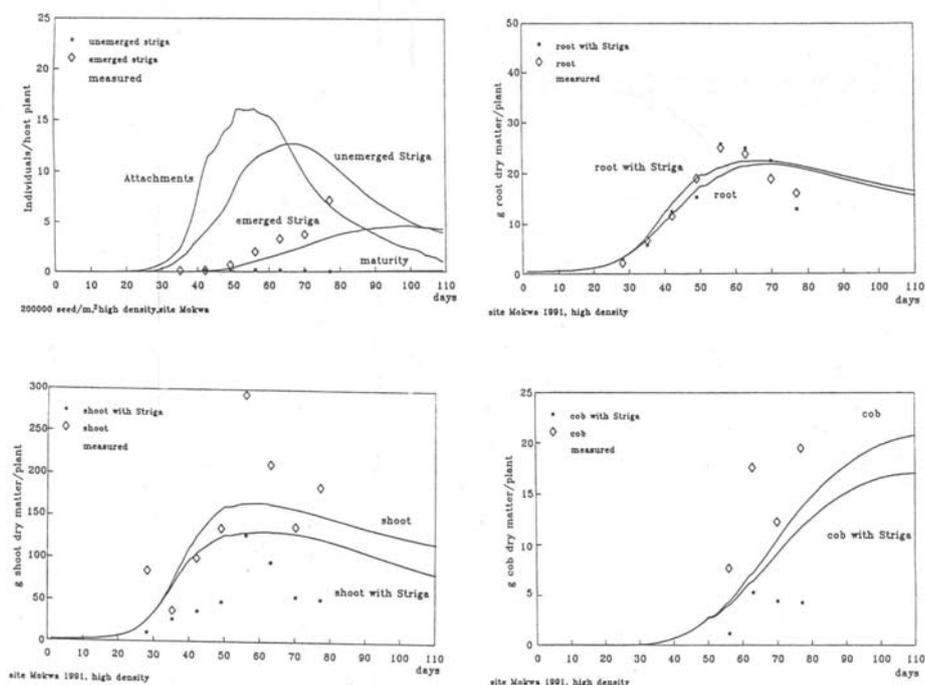


Fig. 20: Comparison of simulation and observations, tolerant variety, site Mokwa 1991; high density; top left) *Striga* stages; top right) root; bottom left) shoot; bottom right: cob

Major discrepancies between data and model show the results of the experiments with low and high *Striga* densities. With the modelled tolerant factor, the emerged *Striga* plants are underestimated (Fig. 20). Simulated root growth and data indicate the use of the tolerant variety. However, the year is characterised by retarding conditions for *Striga*. The simulated shoot dynamics differs low from infested and uninfested version, but the infested shoot weight is over-predicted. The time courses of the observations of both shoot and cob demonstrate a massive *Striga* effect. The relative differences are not repeated by the model (Fig. 20). The low density experiment ended up with the same deviance. To hypothesise the reasons again: model quality, climatic conditions, break down of the tolerance effects. None are plausible. A very simple solution shows up by applying the model with a susceptible variety to the data. The prediction are much more accurate. As the emerged *Striga*, as well the infested shoot and cob biomasses are simulated well (Fig. 21). One possible assumption: A susceptible cultivar instead of a tolerant one was planted in the experiment. The results indicate several solutions for describing the field situations found in the experiments. A clear solution is not found by the model applications, but some hypotheses are identified, while the interactions are identified and confirmed by the model approach.

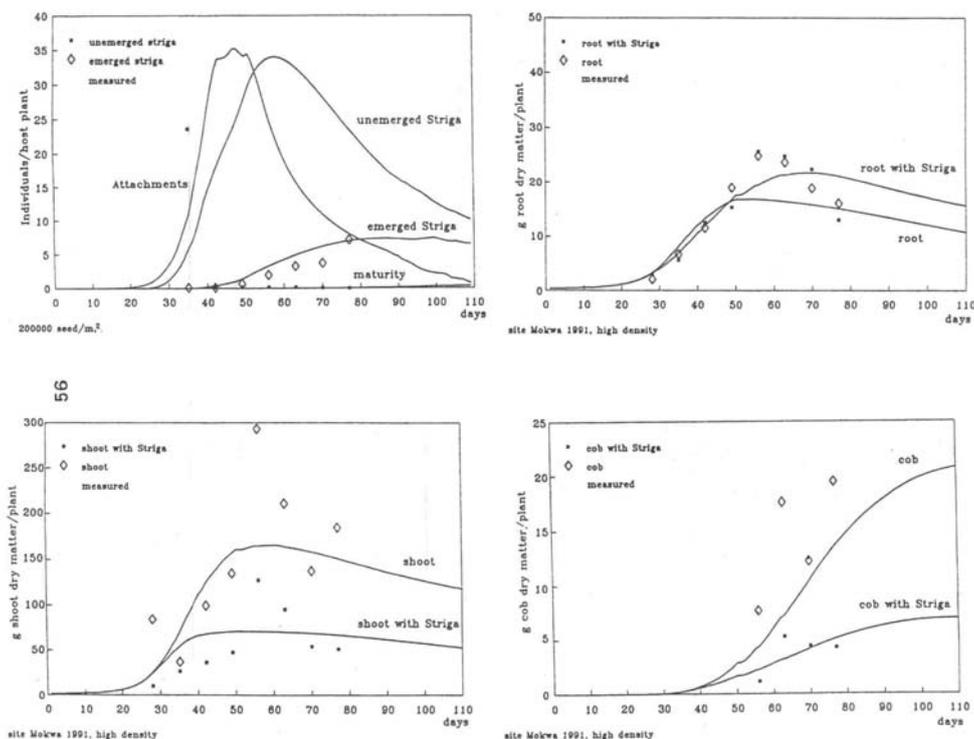


Fig. 21: Comparison of simulation and observations, using a susceptible instead of a tolerant variety, site Mokwa 1991; high density; top left) *Striga* stages; top right) root; bottom left) shoot; bottom right: cob

5 Model extrapolations

The development of control strategies of the *Striga* problem requires knowledge about the long-time behaviour of the seed bank, a) to identify threshold levels and b) to measure the success of any treatments. Repeating the seasonal dynamics with the model and linking the results to the known survival probability and the density dependent seed production, the model extrapolations provide the opportunity to simulate the agro-ecosystem of monocultures with different climatic conditions and basic human influences. All factors have an impact on the multiplication rates of *Striga* within one season. The model allows investigations on the long time dynamics of the seed bank varied by the climatic conditions. KUNISCH et al., (1991) addressed the use of fallow as a control strategy. The time of fallow is easily derived by the average increase rate with given temperature, humidity, and the survival probability between the seasons. The focus is maize monoculture, most commonly in West Africa. KUNISCH et al. (1991) found a maximum equilibrium density of 180000 seeds/m² in permanent cropping system with three host plants/m², when the increase rate is not environmental but density dependent. In farmer fields with low 2-3 Sorghum plants/m² the *Striga* seed density ranges on average from 10000 to 50000 seed/m², while an extremely event ranges up to 150000 seed/m² (WEBER, pers. comment). Those densities are sufficient to cause severe crop losses as IITA-research has shown (KIM, pers. comment). These examples demonstrate the wide



scope of *Striga* dynamics in field situations. The model concept provides several chances to which *Striga* dynamics can be simulated by altering one of the influencing factors and keep all other fixed.

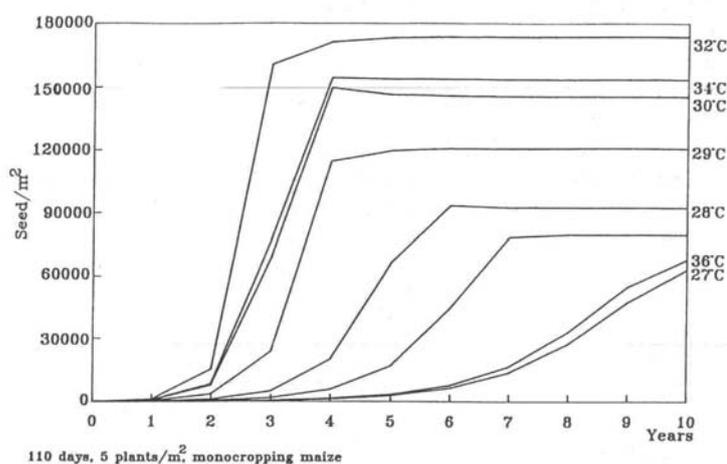


Fig. 22: Seed bank dynamics under different constant temperature regimes

5.1 Simulations with different constant temperature regimes

Although constant daily temperatures are unrealistic, the use illustrates the range of dynamics within variables temperature regimes. Fig. 22 shows the long-time dynamics of the seed bank in a 10 year monoculture with different constant temperatures. The results reflect the estimated temperature response functions. For each temperature level a different equilibrium density is achieved and variable growth rate are observed. The situations are strongly idealized and constant temperature or stable equilibrium densities do not exist. But the model is sufficient flexible to cope with a wide temperature dependency, in which the true dynamics of *Striga* can occur. According to the temperature regime the model is simulating a physiological active temperature window. Inside of the given temperature range from 27°C up to 36°C *Striga* becomes a stable population from very low density within short time. The time needed to establish different equilibrium densities vary with temperature, at optimum from 3 to 4 years, sub-optimum up to 6,7 years. The examples were started with 100 seed/m².

Beyond this active temperature window *Striga* is not successful. The active window ranges only over a few temperature steps, but final equilibrium densities vary between 60000 and 180000 seeds/m². The temperature shape represents the average subtropical temperature regime, and accentuates the importance of temperature on the dynamics of *Striga*. The result is contrary to the stereotype discussion about the low temperature-influence in the tropics and subtropics as temperatures remain fairly constant. Only one environmentally covariate causes sufficient variance within the natural boundaries.

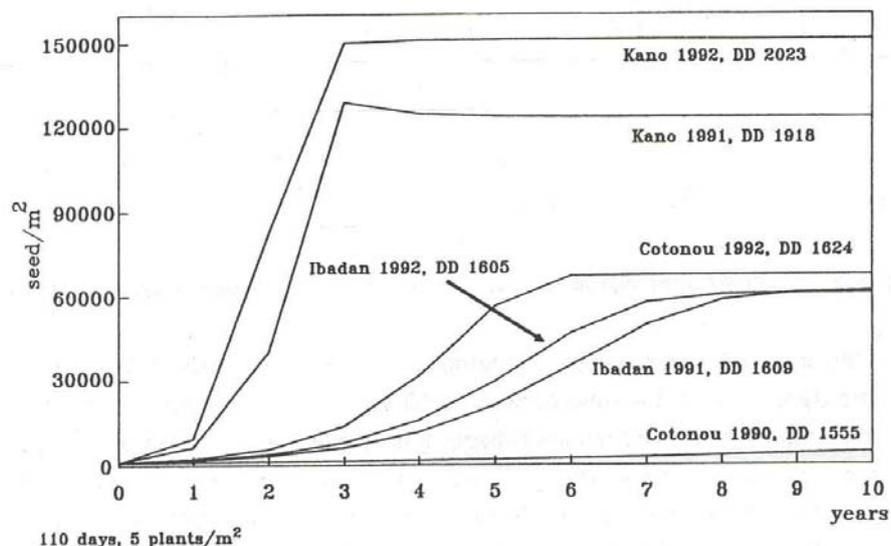


Fig. 23: Seed bank dynamics with different temperature patterns of different years and locations

Between the upper and lower boundary the true dynamics occur as demonstrated in the following examples. Available temperature files from different years and sites were used for a ten years simulation (fig. 5.2). The degree days (accumulated daily mean temperatures above 12°C) are assigned to the single trajectories. The degree days range from 1555 to over 2000 °C. There are differences between the years. Below 1600 °C (for a season length of 110 days) the *Striga* population remains on low levels. A DD of about 1600 °C causes an equilibrium density of 50000 to 60000 seeds/m². The higher temperature pattern of North-Nigeria leads to a higher equilibrium density of 120000 to 150000 seeds/m². For each DD-level exist a related equilibrium density. Linear approaches to temperature response on biological systems are common (HANKS & RITCHIE, 1991). The arbitrary equilibrium density is not problematic but the individual multiplication rates. Both the Ibadan files and the Cotonou file demonstrate the problem. Similar DD's in all three cases lead to a similar equilibrium density, but the growth rates differ. The differences demonstrate the importance of timing of a certain temperature event. This complex model is able transform a temperature pattern to biological response. It demonstrates furthermore that a linear approach to temperature, as the DD's, are the wrong model type and have to be rejected.

Fig. 24 presents a further example. Sorghum is a more favourite host for *Striga hermonthica* than maize (DOGGETT. 1988). Applying the different temperature pattern to a Sorghum system, the simulations show different result. Using the files of Cana, Ibadan and Cotonou in 1992 with Sorghum decreases the population. All three files represent location not suitable for Sorghum. Extreme multiplication rates are detected using temperature files with respect to the corresponding sites of the sorghum belt in West-Africa (Kano files in Fig. 24). Constant temperatures as an idealized situation demonstrate the upper boundary of the population density.



Although no experimental field data are available for *Striga* and Sorghum, the simulations agree with the survey results of the IITA (WEBER, pers. comment). The examples of temperature response explain a large part of the variance found in the field experiments. Expressly the model permit the reciprocate analysis for a given temperature, e.g. the data can by explained by the model application.

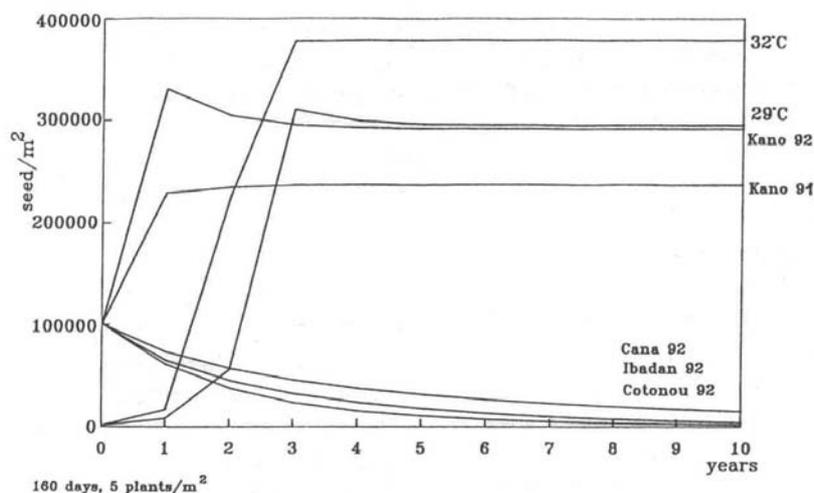


Fig. 24: Seed bank dynamics with different temperature regimes in a Sorghum system

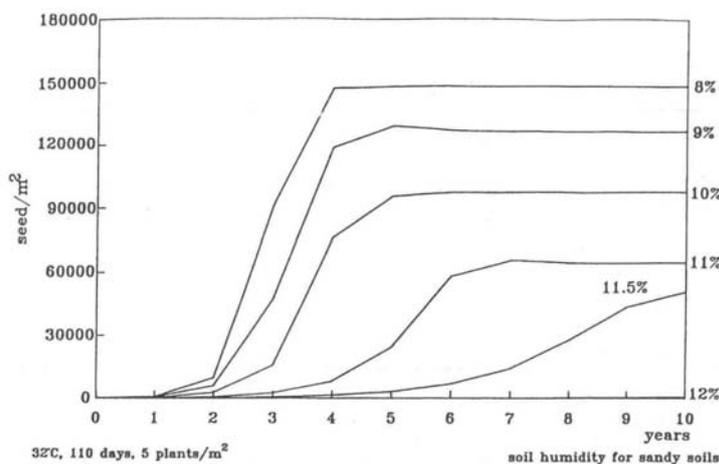


Fig. 25: Seed bank dynamics with different humidity levels

5.2 Simulations with different constant soil humidity regimes

The retarding effects of high soil water contents were shown before. To demonstrate the response of the factor soil humidity, all other factors are fixed to optimal conditions. Different soil water content in sandy soils results in changed equilibrium



densities again. The retarding effects of short-time flooding concentrations were shown in the data of Mokwa 1991 and Cana 1992. Fig. 25 demonstrates the decreasing of the equilibrium density with increasing water content. Irrigate the soil above the field capacity (of sandy soils) would lower or suppress the *Striga* problem. However, the irrigation advice is not practicable, as corn production will reduce either. Fig. 25 gives just some examples, how an additional environmental factor may influence such a system. It is possible to isolate both effects out of the variance of field data.

5.3 Management and system effects

Up to now only factors are introduced, which are hardly to control, especially in low input production systems. The final seed bank is also controlled by the type of husbandry. Several combinations are reviewed and added to the research demands (OBILANA and RAMAIAH, 1992), but known relationships combined with a quantitative approach of *Striga* dynamics are poor. Only some treatments are introduced here: The influence of plant density and the choice of cultivars, exploiting the different variety specific maturity times.

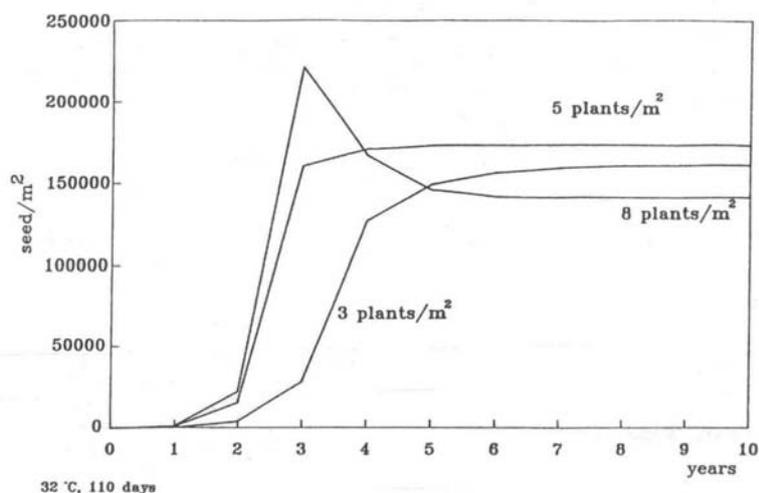


Fig. 26: Seed bank dynamics with different host densities

Different host densities affect *Striga* dynamics. Fig. 26 shows the long-time dynamics, when all other parameter is kept at optimum. While a density of 3 and 5 host plants leads to the specific equilibrium densities, but with different growth rates, the dynamics at 8 plants shows the highest growth rate but end up in a lower density. A system analysis demonstrates the begin of oscillations. The complete system with given parameter set is getting unstable and shows chaotic behaviour. The border from stable to unstable conditions is the upper limit of the parameter combinations. Restricting the system to stable conditions, as done here, is reasonable. The lower equilibrium density is sound. The higher crop density means a smaller root diameter/plant generating a similar density dependency as the modelled seed production. No data are available for this hypothesis. If the dynamics are



mirroring a reality experiments with higher crop densities should be performed.

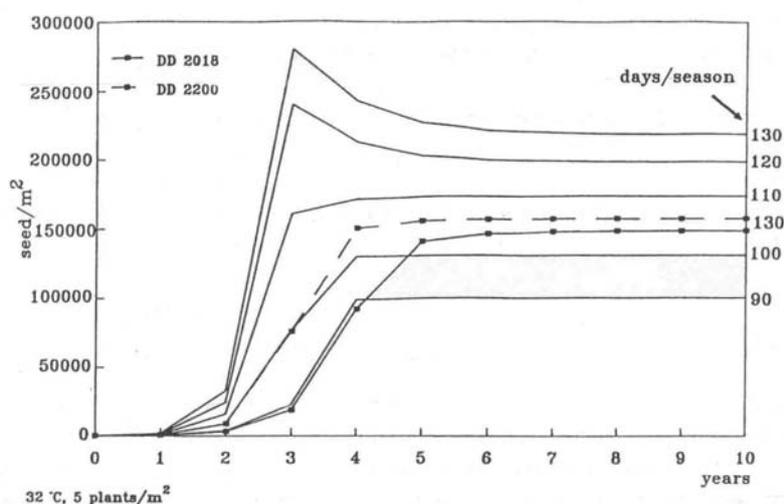


Fig. 27: Seed bank dynamics with season length associated with different maize cultivars

Another strategy is the exploitation of the variable maturity times of maize cultivars. Varieties which require from 90 to about 130 days until harvest with a yield potential of 3-6 tons/ha are available for the tropics. Fig. 27 shows the simulation of different varieties under different climatic conditions. The *Striga* seed bank increases rapidly within one year, as more time for seed production is available, and the equilibrium density changes non-linear with additional time. The relative differences between the methods are large. Basic control decisions within such a monoculture are imaginable. Optimal conditions are used for the simulations. Using a temperature file yield in mutable increase rates and equilibrium densities.

The use of a tolerant variety reduces the number of the *Striga* seeds attached to the host. Long times dynamics with a tolerant variety are not feasible as no information about the seed production are available. The tolerant variety potentially reduces the numbers of *Striga* entering the life cycle ending up in the following situation: The *Striga* associated crop losses are reduced. *Striga* is producing its seeds on a healthier host and has probably a larger daily seed production than a mature plant feeding on a weak host. The extrapolation to a long time dynamics is not definable yet and needs further practical research. The effect of plant nutrition is omitted here and is beyond the scope of the model for the time being.

5.4 Yield losses

A final result of this system is a simulated ratio of *Striga* associated yield losses. An absolute yield prediction is not possible with the simple differential equations. But relative yields assigned to a specific *Striga* seed density are credible. As *Striga* dependent crop losses are predictable by the model, it provides the platform for model extensions to economically decision models taking into account different



decision making processes in different economically scenarios.

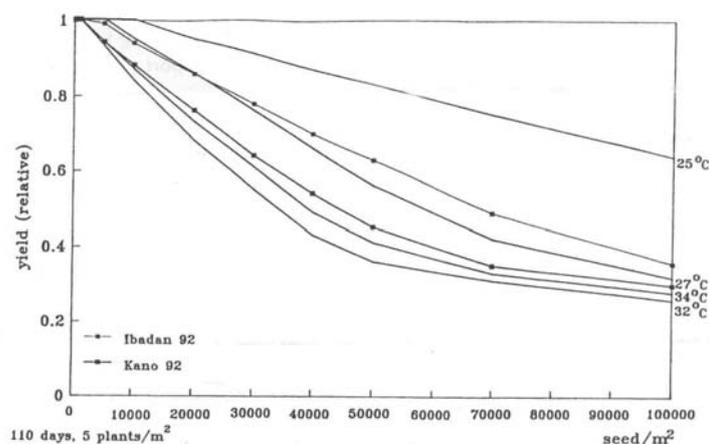


Fig. 28: Density dependent yield losses under different temperature regimes

Fig. 28 shows different crop losses scenarios with a moderate *Striga* seed range. The model is able to reproduce different yield structures as occur in field situations. The maize yield losses begin uniformly with low density levels. With increasing initial density the yield loss structure, diverge with respect to the used temperature pattern. Generally, losses increase rapidly. Above 50000 seeds/m² the relative yield loss flatten with increasing density and the differences between the temperature regimes are getting smaller. Finally, the yield losses will approach a boundary value. The relative yield by differs about 20% when comparing the 27°C and 32°C example at a given density of 50000 seeds/m².

5.5 Simulation of simple control strategies

The model offers a tool of solving an optimisation problem within the Maize-Sorghum-husbandry complex, mirroring the standard farming systems of West Africa. Two contrary management decisions have to be solved: a maximum yield and a minimum *Striga* density. Fig. 29 addresses some practical simulation results. Two standard rotations are introduced as control setting the boundaries with different temperature conditions. In comparison, a designed maize monocropping rotation is introduced with the following toolkit: Host density, short- and long-time varieties, tolerant/susceptible varieties. The climatic files have been introduced before. The population density increases rapidly in the first three years, while the wet conditions of "Mokwa 91" (M91) and the negative temperature response of Ibadan (I92) reduces the seed bank density. Another favourite climate pattern is used in year 7, while an assumed suppressive weather record is applied for the last 3 years. Regardless of *Striga* infestation, a high increase is occurred up to the third year. The sorghum variant result in much higher densities than the maize variant. Simulated crop losses ranges from 4% to 60% in the sorghum variant and from 10% in the

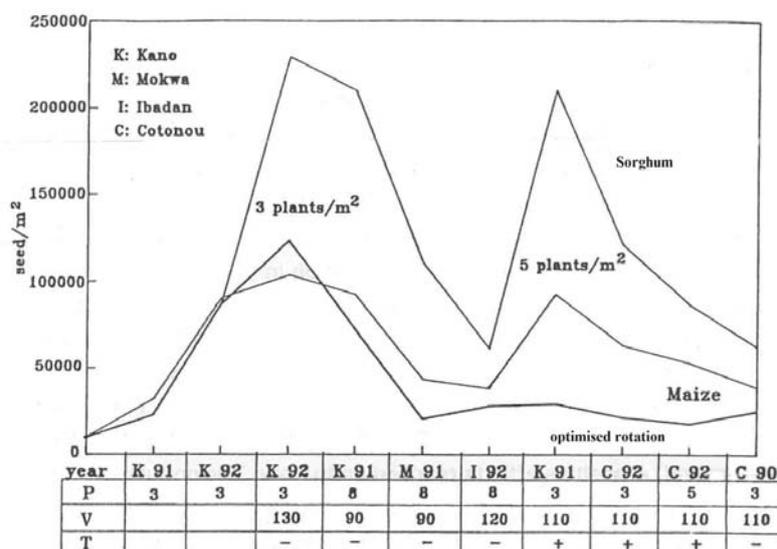


Fig. 29: Influence of different crop husbandry on *Striga* seed bank; P: Plant density; V: Variety, time to maturity; T+: tolerant; T- susceptible

beginning up to 40% and 70% in the standard maize rotation. In comparison to the standard rotations, an optimised rotation is introduced varying the choice of plant density or variety with respect to parasite density. Control techniques begin in year 4. The combination of a short-time variety and 8/plants/m² decreases the populations level. Maize is used like a catch crop with the advanced host density, but corn losses are in the range of 80%. The three host/m² variant resulted in a 13% higher final *Striga* density level. In addition, in the following year a short-time variety is used, as seed bank level is still high. Short-time varieties have only a poor yield structure, so that in the next year a long-time variety is used. The density has been reduced to a moderate range. The given climatic conditions of this year are negative for *Striga* as seen in the control. The chosen combination of a long-time variety and high plant-density the population increases the seed bank slightly. The strong increase in year 7 can be only avoided by the use of a tolerant variety. A susceptible cultivar would annul all positive effects achieved so far. The population would increase up to 67000 seed/m² in a 3 host/m² and up to 104000 in an 8 host/m² variant. Using a tolerant variety in high densities would avoid the threat of large yield losses but preserves the high infestation level. The modelled influence of the use of tolerant varieties has to handle with care, as the effects of tolerant cultivars are not clear yet. As shown in the examples even a monocropping system includes potentials of controlling *Striga*.

The achievement of suppressing *Striga* is negative correlated with the expected yield structure. The different maize rotations are compared by their summarized yield from the third year onwards. The standard rotation has a total yield of 21.8 t/ha after 7 years. The yield of the control with no *Striga* is 40% to 70% higher. The *Striga* controlling rotation has total yield of about 27.4 t/ha under the assumption that tolerant varieties have a similar yield potentials than susceptible varieties. Even a 20% lower yield structure of the tolerant varieties does not change the overall result. Total corn yield would be still 2 t/ha higher. Yields are reduced due to the use of



short-time cultivars. Additionally *Striga* densities are suppressed to acceptable low levels and the temporary use of higher host densities produces higher yields and substitutes former losses. The introduced rotation is just one example. A practical approach must be the objective of further field research.

6 Discussion

This analysis represents one way of modelling the population dynamics of the witchweed *Striga hermonthica* on maize and for a minor part on sorghum. The model offers how *Striga* dynamics could be. Exact relationships are not precisely known; hence, other realisations are assumed and likely. Plenty of the introduced probabilities are based on heuristically assumptions, derived from a general discussion about *Striga*, but also include solid evidences and a combination of mathematical and statistical tools. Finally, the model reduces the complex of individual and independent information of different size and scale to one common model denominator.

A parameter optimisation fails in the view of a statistical demand. All introduced parameter are required by the general discussion and they are derived from biology. The model is kept as simple as necessary and is constructed as complex as the common knowledge and widely discussed ideas demand. A lot of additional information about the *Striga* life cycle may be included to the model. Does the attentions of this additional information improve the predicting and quantitative opinions of the model in comparison about the increasing complexity? Concrete examples are the heavily discussed processes of preconditioning, stimulation, strigol distribution in soil and so on. The complex of spatial distribution and interactive biochemistry is reduced to a two-dimensional rationalized probability. The question, arises, how important are these pre-germination factors for the quantitative dynamics and yield loss relationships, if those factors were easily to ignore. Extensions are possible and required as further data are available. The modules easily allow further extensions to the model.

The given model here compares well with different sets of data and has a high predictive precision within a season. A system analysis is not done. The parameters of the Leslie-model are highly correlated due to the model structure. Hence, the conclusions are limited to the given set of parameter, as these parameters are set constant overall applications and demonstrated examples. The unlimited parameter combinations were reduced by the procedures of the stepwise calibration, fitting the parameter to all data of different resolutions.

The long-time dynamics over a few years are only simulations or extrapolation and are based on critical information, but the model behaviour in its potential / range reflects the field situations of maize and sorghum. With respect to the input parameters, plenty of solutions are generated by the Leslie model to explain the *Striga* dynamics. The introduced relationships are hidden in the variance of



experimental data. The model is a derivation of an unknown reality with numerous interactions. Some situations are left, when this model does not give a satisfying solution. Not everything observed in the data is explainable with these algorithms. Model results and observation are independent events, but agree well in most cases. Although the major part of the model is constructed as a probability, certain information is produced, which can be transferred to practical consultancy.

Striga population growth ranges from very high rates to negative and finally, in association of a certain type of climate, the population density decreases under a threshold level. Similar patterns were observed in northern Nigeria during different surveys of the IITA (KIM, pers. comment). In any long-time investigation, *Striga* died out. One possible solution is given by the model in association with the climatic factors.

The difference in results from field experiments and simulations are that the findings of the model are all explainable and repeatable, contrary to results of field experiments.

Striga is hygienically a long-term problem. Short-time combating strategies seem to be unsuccessful. The model system shows, that the objectives in husbandry have to swap to long-time strategies, with the final target to suppress *Striga* levels as low as possible. The physiological active window of the *Striga* development probability is restricted with respect to temperature and soil humidity and consequently not predictable in extended periods. Soil-borne pathogens include hygienic, long-time aspects, which are only solved by several considerations of the soil-ecosystem (SIKORA, 1992). The model is one part of the numerous aspects of managing the parasite. The necessary climatic conditions for successful establishment do not exist every year. The model results demonstrate how fast *Striga* density can explode, reaching density levels, which reduce the maize production to uneconomically relationships.

The model seems to repeat a particular part of *Striga* reality. Based on the findings it is possible to analyse or develop different control strategies. The assumed very high mortality of the stage transition of germination to attachment could also happen in reality. Combating strategies before the stage "attachment" are questionable. A 99% mortality may not be done better by a soil fumigant or herbicides or any other control measure. On the other hand, the dynamics are strongly density dependent. A reduced probability of attachment has an eminent effect on the long-time behaviour of the *Striga* seed bank density as assumed by the simulations with the use of tolerant varieties.

A possible control method could be the use of a stimulating host as a catch crop. Performing a second, short time intercropping would reduce the seed bank in theory. As seen by the model simulation *Striga* seeds of the soil are released in the current year with a strong dormancy. Hence, only a minimum of the seed bank will be affected by this strategy and is seen not very promising. Although such models are mainly seen negatively from different opinions of science,



modelling is able to isolate single covariates out of a mix of data in a quantitative and not speculative approach. Furthermore, the model contributes one logical solution for several research demands and problems, which are normally formulated verbally only by the *Striga* research science (OBILANA & RAMAIAH, 1992).

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