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A model study on population dynamics of *Striga* that can infect a newly developed resistant *Sorghum* crop, with practical guidelines to safeguard the sustainability of resistant *Sorghum* varieties

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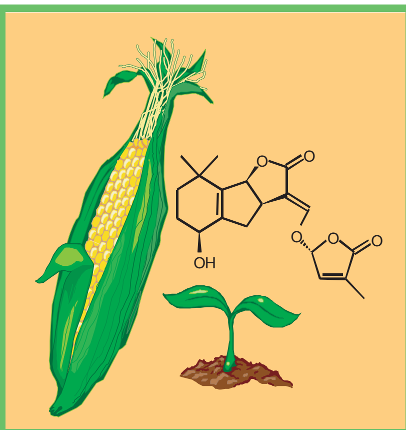
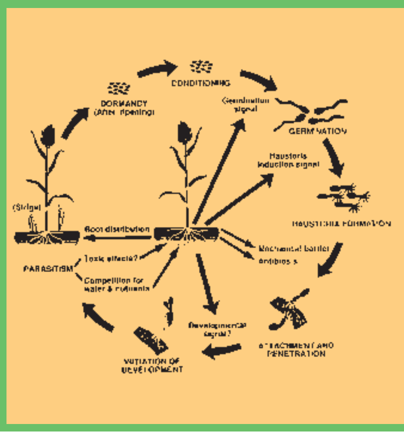
C. Kempenaar, J.A.R. Davies & P.C. Scheepens





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Plant Research International B.V.

Address	:	Droevendaalsesteeg 1, Wageningen, The Netherlands
	:	P.O. Box 16, 6700 AA Wageningen, The Netherlands
Tel.	:	+31 317 47 70 00
Fax	:	+31 317 41 80 94
E-mail	:	postkamer.pri@wur.nl
Internet	:	http://www.plant.wageningen-ur.nl

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Abstract

Within ISCIMAS, a basic model of Den Hollander (1999) has been used to study seed dynamics of *Striga*. In 2002, the basic model was adapted to study population dynamics of a 'mutant type ' of *Striga* that can infect a newly developed, resistant *Sorghum* crop. The 'mutant type' of *Striga* is assumed to be present in mixtures with the 'wild type' of *Striga* that can hardly or not infect the resistant crop. For this purpose, a two equations model was developed. One equation describes the changes in seed density over time for *Striga* (S_1) that can hardly or not infect the resistant crop (the 'wild type') and one equation for *Striga* (S_2) that can infect the resistant crop (the 'mutant type'). The outcome of the two equations model with the parameters for one equation set to zero proved to be the same as that of the one equation model.

The model was used to make a rough estimate how long a *Striga*-resistant *Sorghum* crop will protect farmers from *Striga* damage (the lifespan of the resistant crop) and how the lifespan may be influenced by two management practices: growing *Sorghum* in a rotation with other crops that are non-hosts of *Striga* and removal of *Striga* plants before seed setting.

Based on the model and some assumptions that do not seem to be unrealistic, we can draw the following conclusions:

1. It is not necessary that a *Striga*-resistant *Sorghum* crop prohibits all germination of *Striga*. Some production of new seeds is allowed to exhaust the seed bank of the 'wild type' of *Striga* within a couple of years (Figure 1).
2. The lifespan of a *Striga*-resistant *Sorghum* crop is roughly 15 - 20 years, depending on the initial frequency of the 'mutant type' of *Striga* in the population (Figure 2).
3. Cultivation of a non-host of *Striga* in rotation with a *Striga*-resistant *Sorghum* crop at a high initial relative frequency of the 'mutant type' (10^{-4}) greatly increases the lifespan of the *Striga*-resistant crop (Figure 3A). At a lower initial relative frequency of the 'mutant type' (10^{-8}, Figure 3B) this is even more so. But even at the lower initial frequency, the seed bank of the 'mutant type' in a 1:2 rotation is gradually increasing, and will eventually reach unacceptable levels.
4. Removal of flowering plants also reduces the build up of the 'mutant type' of *Striga*. Killing rates of 0.7 or higher are needed to have a substantial impact if the initial relative frequency of the 'mutant type' is as high as 10^{-4} (Figure 4A). At an initial frequency of 10^{-8} a killing rate between 0.5 and 0.6 is sufficient to get the same effect (Figure 4B).
5. If removal of flowering plants by hand is an option, it is strongly recommended to have the killing rate as high as possible (Figure 5). The total amount of labour over the years is then much less than at lower killing rates. In addition, because the local population of *Striga* becomes extinct by this strategy, the lifespan of the *Striga*-resistant *Sorghum* crop becomes infinite.
6. Because the predicted lifespan of a Striga-resistant variety is short compared to the time required to breed that variety, it is of vital importance to accompany the introduction of a new, *Striga*-resistant crop variety with a management and communication strategy to increase the lifespan of the new variety. Two options to increase the lifespan of a *Striga*-resistant variety are recognised: alternating Sorghum and a non-host in a crop rotation and preventing seed setting of mature *Striga* plants by (hand) picking. Both strategies have the desired impact on the lifespan of the new variety, but local conditions may determine whether or not they are practicable.

1. Introduction

This report is the second report of a study on sustainability of *Striga* resistant sorghum and maize varieties. In the first report, an a priori risk assessment study is presented (Kok & Kempenaar, 2002). The report in front of you is a report in which a model study on population dynamics of *Striga hermonthica* is described. From the model study, practical guidelines were derived and presented to safeguard the sustainability of newly developed resistance against *Striga*.

The studies on sustainability of *Striga* resistant sorghum and maize were part of a large EU INCO project entitled Improved *Striga* control in maize and sorghum (ISCIMAS). Most of the work in this project is focused on development of new varieties and strategies to control *Striga*. Details on this project can be found on the internet-url: http://www.plant.dlo.nl/projects/Striga including a description of the work package (WP 9) of the studies. The project is financed by the EU (INC-DEV ICA4-CT-2000-30012) and several national funds. The contra finances for the studies on sustainability of *Striga* resistant sorghum and maize come from the Dutch Ministry of Agriculture, Nature and Fishery in the frame of research program 330 (North South program).

The aim of the report in front of you is:
1. to present data of a model study on population dynamics of *Striga hermonthica*,
2. to provide practical guidelines to sustain a new resistance.

In chapters 2, 3 and 4 the model is explained and the set up of the study described (materials & methods). In chapter 5, results of the model study are presented and discussed. In chapter 6, practical guidelines are presented. In chapter 7, some questions raised at the ISCIMAS workshop in Wageningen in May 2003 are addressed.

2. Description of the basic model

A demographic approximation of the seed population in the seed bank over a number of years is described by a basic model of Den Hollander (1999). In this model, one mathematical equation describes the seed bank dynamics of plants.

The basic equation is as follows:

$S_{(t+1)}$ =	$(1 - g - m) * S_{(t)}$	+	$(a * (1 - kr) * g * S_{(t)} / (1+a/b\ (1 - kr) * g * S_{(t)}\ )$
	Losses from the seed bank		Production of new seeds

where:

$S_{(t)}$ = the seed density in the seed bank (seeds / m^2) in the initial year t
$S_{(t+1)}$ = the seed density in the seed bank (seeds / m^2) at year t+1
m = fraction of seed which is removed by natural causes
g = fraction of seed which germinates and emerges
kr = fraction of seedlings killed by weed control
a = production of seeds per plant at low plant densities
b = maximum seed production per surface at high plant densities (seeds / m^2)

The equation consists of two parts representing the decrease of seeds in the seed bank and the increase of seeds by a number of seed producing plants, respectively.
Transition factors, related to different development stages, and a density dependent factor for the number of seed producing plants are included in this basic equation. Given the number of seeds in the initial year, the seed density in the seed bank in following years can be calculated.

To predict what will happen if a new *Striga* biotype evolves that can break *Striga* resistance of a *Sorghum* crop, we made a few adaptations of the model of Den Hollander (1999). The adapted version of the model is described below.

3. The adapted model

The adapted version of the model describes the seed bank dynamics for two *Striga* populations that evolve simultaneously when a *Striga*-resistant variety of *Sorghum* is grown: the 'wild type' and a 'mutant' that has broken the resistance of the host.

To describe the seed bank dynamics for the two types of *Striga* seeds, two mathematical equations are needed, one for each type. The part of the equations that describe losses from the seed bank is the same as in the original model. The part that describes seed production is different, because the seed production per plant or per m² depends on de plant density of the two types together.

The equation for the 'wild type' of Striga seeds germination is as follows:

$S1_{(t+1)} =$	$(1 - g1 - m1) * S_{(t)}$	+	$(a1(1\text{-}kr1)g1\ d1\ S1_{(t)}) / (1+a1/b1(1\text{-}kr1)g1\ d1\ S1_{(t)}+a2/b2\ (1\text{-}kr2)g2\ d2\ S2_{(t)})$
'Wild type'	Losses from the seed bank		Production of new seeds

The equation for the 'mutant type' of *Striga* seeds:

$S2_{(t+1)} =$	$(1 – g2 - m2) * S_{(t)}$	+	$(a2(1\text{-}kr2)g2\ d2\ S2_{(t)}) /(1+a2/b2(1\text{-}kr2)g2\ d2\ S2_{(t)}+ a1/b1\ (1\text{-}kr1)g1\ d1\ S1_{(t)})$
'Mutant type'	Losses from the seed bank		Production of new seeds

where:

S1,2 = the seed density in the seed bank (seeds / m²)
m1,2 = fraction of seed which is removed by natural causes
d1,2 = fraction of survived seed producing plants
g1 = fraction of S1-seed ('wild type') which germinates, attaches and emerges despite crop-resistance
g2 = fraction of S2-seed ('mutant type') which germinates, attaches and emerges by breaking crop-resistance
kr1,2 = fraction of seedlings killed by weed control
a1,2 = production of seeds per plant at low plant densities (seeds/plant)
b1,2 = maximum seed production per unit of area at high plant densities (seeds / m²)

4. Parameter-values chosen for the model

Quantitative data on seed dynamics of *Striga* are quite rare. Westerman *et al.* (2002) studied the population dynamics of *Striga hermonthica*. Their study included *Striga* seed dynamics and the linking development stages of germinating *Striga* seeds to seed-producing *Striga* plants. We used the results and data from their study to derive parameters for our model equations for the two *Striga* populations. We assumed that the *Striga*-resistant *Sorghum* will still allow a very small fraction of the 'wild type' *Striga* to germinate and establish a parasitic relationship with the host (g1=0.00001). For the 'mutant type' we assumed the same value for g2 (0.0015) as found by Westerman *et al.* (2002) for a 'wild type' and a susceptible *Striga* host.
The other parameters were given values according to Westerman *et al.* (2002). We assumed that there were no differences between the 'wild type' (equation S1) and 'mutant type' (equation S2). In reality we would expect less fitness of the 'mutant type', probably resulting in a lower value of g2 and probably also a lower value of a2.
Westerman *et al.* (2002) also used a model for population studies in the ISCIMAS project. Their model had a different relation Seed density and seed production. Compared to their model, our model may give an underestimate of seed production when seed densities are low.

Parameter-values in equations

Parameter	Dimension	Equation S1	Equation S2
m	-	0.42	0.42
d	-	0.26	0.26
g1	-	0.00001	
g2	-		0.0015
kr	-	0	0
a	-	5250	5250
b	m^{-2}	100000	100000
$S1_t$	-	100000	
$S2_t$	-		Variable

5. Calculations and analyses with the model

5.1 Sensitivity of the model for changes in parameter g

In this simulation, we regarded only one *Striga* population; the parameter values for the other population were all set to 0 (see table below). The initial *Striga* seed density was set to 100000 seeds per m² (Smith *et al.*, 1993). The value for g ranged from 0.00001 to a maximum of 0.0015 (Westerman *et al.*, 2002).

Parameter-values in equations

Parameter	Dimension	Equation S1	Equation S2
m	-	0.42	0
d	-	0.26	0
g1	-	Varied	
g2	-	0	0
kr	-	0	0
a	-	5250	0
d	m^{-2}	100000	0
$S1_t$	-	100000	

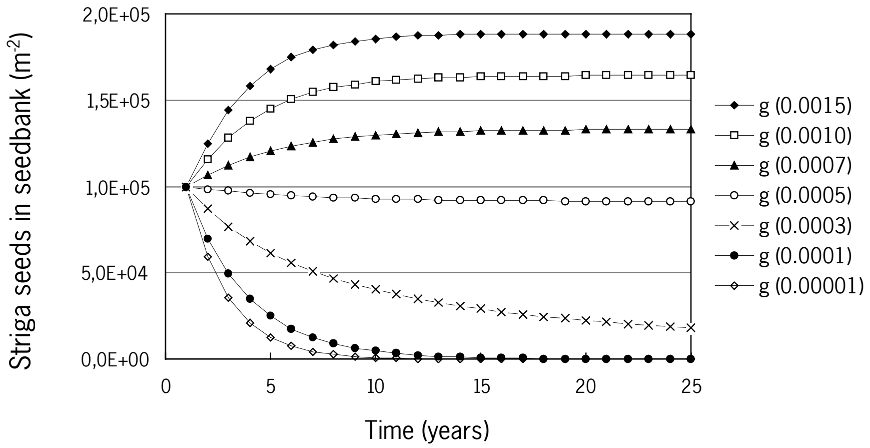

Figure 1. Development of a Striga seed population with time at different fractions of emergence. The Striga seed population starts with 10^5 seeds m^{-2}.

We see that with a g value (the fraction of seeds that germinates, attaches to the host, emerges and produces mature plants) of around 0.0005 there is an equilibrium between seed losses and new seed production over the years. With higher values the seed density stabilises at a higher level after some years, while with lower values at lower levels.

Conclusion: A Striga-resistant variety of Sorghum, where the resistance is based on prevention of Striga germination and attachment should allow an emergence fraction g of less than 0.0005.

5.2 Simultaneous development of a 'wild type' and a 'mutant type' on a *Striga*-resistant *Sorghum* crop

Striga seed dynamics were investigated in a situation with a *Sorghum* crop of which *Striga* susceptibility has been decreased by breeding. The greater part of the total *Striga* seed population consists of the 'wild type' (S1). Only a very small proportion (0.00001) is assumed to germinate and contribute to new seed production. Further we assumed that a very small proportion of the seeds (S2) can break this crop-resistance. A fraction g2 of the seeds germinate and develop to seed-producing *Striga* plants (assumed to be 0.0015). Still another assumption is that these new seeds are also able to break the crop resistance.

Parameter-values in equations

Parameter	Dimension	Equation S1	Equation S2
m	-	0.42	0.42
d	-	0.26	0.26
g1	-	0.00001	
g2	-		0.0015
kr	-	0	0
a	-	5250	5250
b	m^{-2}	100000	100000
$S1_t$	-	100000	
$S2_t$	-		Varied between 10^{-5} and 10

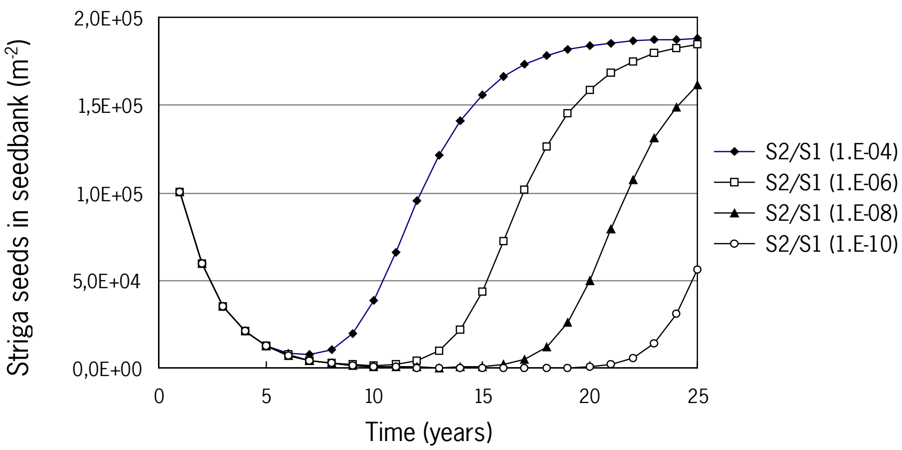

Figure 2. Development of a mixed Striga seed bank with time when a Striga-resistant crop is grown and the initial proportion of 'mutant type' is varied. The Striga seed population starts with 10^5 seeds m^{-2}.

We see initially a decline of the seed bank. From the initial seed bank of 10^5 per m^2 of the 'wild type', approximately 1 seed-producing plant will arise per m^2 during the first year. Because of seed mortality by natural causes, the population of 'wild type' seeds will approximately be halved every subsequent year. For the 'mutant type', we can estimate from figures used for Figure 2 the time it will take to reach a seed population size of 667 m^{-2}, a number that will give rise to 1 seed-producing plant per m^2. For the ratio S2/S1 of 10^{-4}, 10^{-6}, 10^{-8} and 10^{-10}, it will take 6, 11, 15 and 20 years, respectively.
Depending on the initial proportion of the 'mutant type', the total seed population size starts to increase.

Conclusion: The initial size of the 'mutant type' depends on the mutation frequency. Roughly, a gene for Striga-resistance will protect a Sorghum crop for a period of 10-20 years.

5.3 Effect of non-host plants in rotations on *Striga* seed dynamics

Striga seeds will only germinate if they get a chemical signal from a host plant like *Sorghum*. In the absence of a host plant, the decrease of *Striga* seeds by natural causes continues while no new *Striga* seeds are produced.

Parameter-values in equations

Parameter	Dimension	Equation S1	Equation S2
m	-	0.42	0.42
d	-	0.26	0.26
g1	-	0 (odd years) or 0.00001	
g2	-		0 (odd years) or 0.0015
kr	-	0	0
a	-	5250	5250
b	m^{-2}	100000	100000
$S1_t$	-	100000	
$S2_t$	-		10 or 10^{-5}

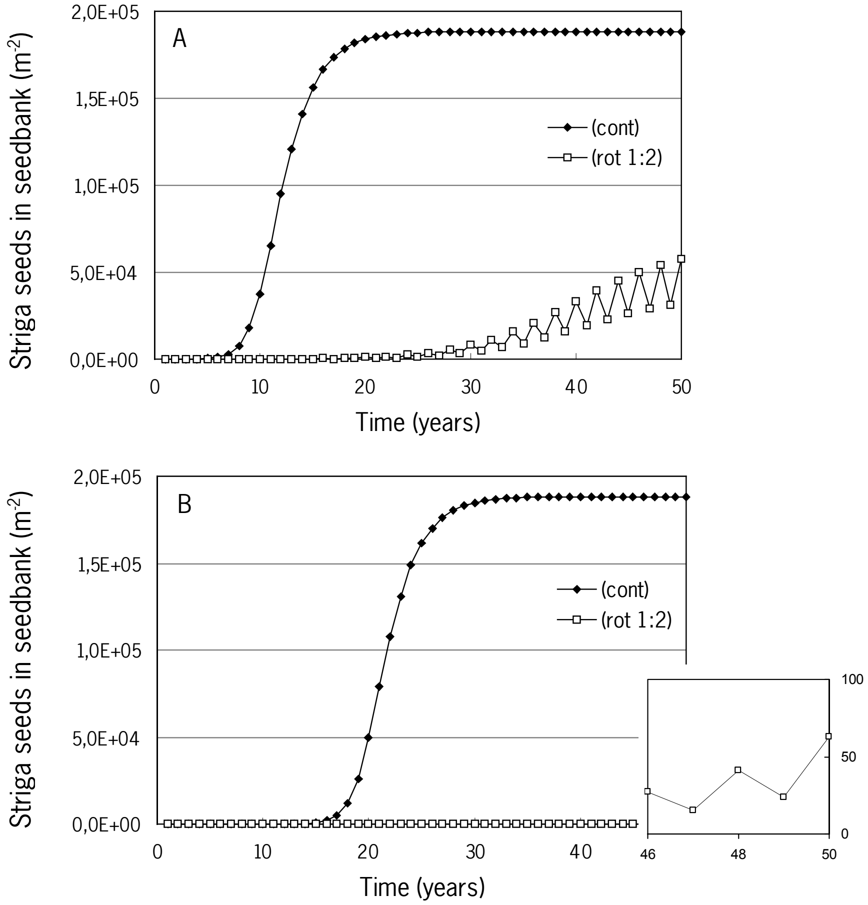

Figure 3. *Development of 'mutant type' seeds of Striga in the seed bank with time at an initial proportion of the 'mutant type' (S2/S1) of 10^{-4} (A) or 10^{-8} (B) in a continuous culture of Striga-resistant Sorghum or a 1:2 rotation between Sorghum and a non-host crop.*

Conclusion: Figure 3A shows that cultivation a non-host of Striga in rotation with a Striga-resistant Sorghum crop at a high initial relative frequency of the 'mutant type' (10^{-4}) greatly increases the lifespan of the Striga-resistant crop. At a lower initial relative frequency of the 'mutant type' (10^{-8}, Figure 3B) this is even more so. The inset in Figure 3B is a magnification for the last 4 years of the considered time. It shows that the seed bank of the 'mutant type' in a 1:2 rotation is gradually increasing, and will eventually reach unacceptable levels.

5.4 Effect of control efficacy on the *Striga* seed population in the seed bank

Removal of *Striga* plants before they deliver new seeds to the seed bank may help to increase the lifespan of a *Striga*-resistant *Sorghum* crop. Different levels of control are simulated in the model by varying the parameter kr in the model.
In Figure 4 the evolution of the number of 'mutant type' seeds of *Striga* in the seed bank is shown for 2 initial ratios of S2 and S1 and several control rates. It is assumed that the control rate for the 'wild type' and the 'mutant type' of *Striga* is the same.

Parameter-values in equations

Parameter	Dimension	Equation S1	Equation S2
m	-	0.42	0.42
d	-	0.26	0.26
g1	-	0.00001	
g2	-		0.0015
kr	-	Varied	Varied
a	-	5250	5250
b	m^{-2}	100000	100000
$S1_t$	-	100000	
$S2_t$	-		10 (in A) or 10^{-3} (in B)

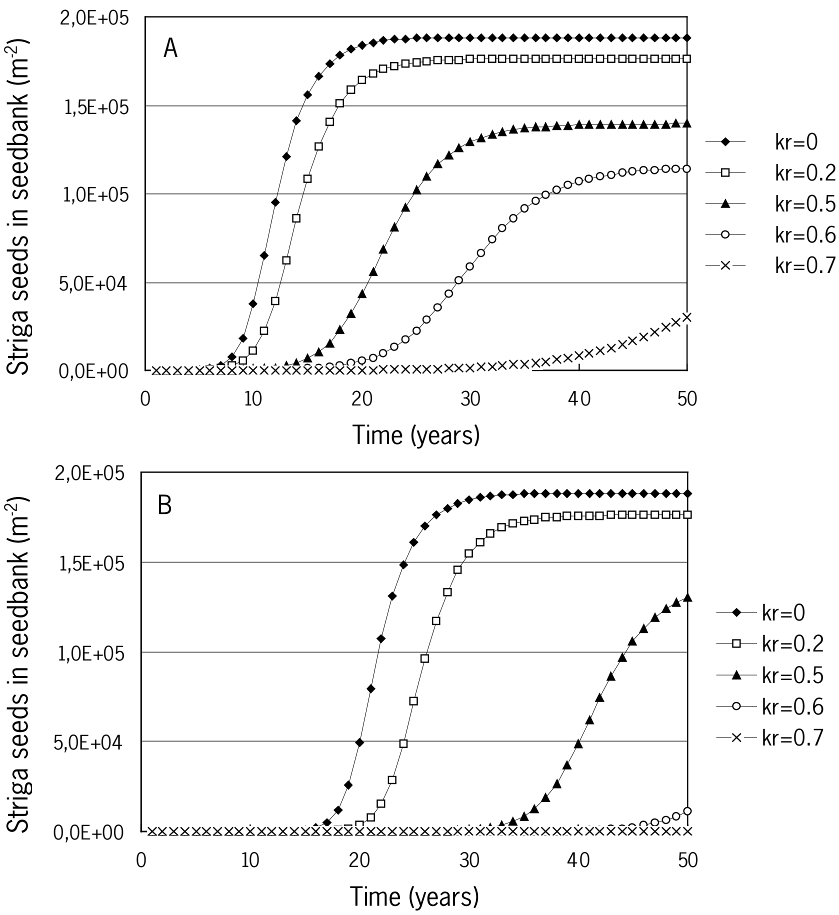

Figure 4. *Development of 'mutant type' seeds of Striga in the seed bank with time at an initial proportion of the 'mutant type' (S2/S1) of 10^{-4} (A) or 10^{-8} (B) and varying levels of control (kr).*

The decrease of 'wild type' seeds of *Striga* with time is not shown in Figure 4; it is comparable with the first several years in Figure 2. The curves for the 'mutant type' move to the right with increasing control efficacy. If we measure the lifespan of a *Striga*-resistant variety of *Sorghum* as the time until a certain unacceptable plant density is reached (for instance 1 per m^2), at a higher rate of mutation ($S2/S1 = 10^{-4}$) a higher control efficacy is needed to reach the same lifespan than at a lower mutation rate ($S2/S1 = 10^{-8}$).

Conclusion 1: A control efficacy of 0.7 considerable extends the lifespan of a resistant variety even at a relatively high mutation rate of Striga.

If it is possible to spend some time on hand weeding every year to remove *Striga* before seed setting, the question arises which strategy should be followed to minimise the total amount of weeding over the years. Figure 5 shows for the *Striga* development as in Figure 4A, on the y-axis, cumulative over the years, the number of plants per m^2 multiplied with the weeding factor kr, which is a measure of labour. The inset is a magnification of the first 10 years.

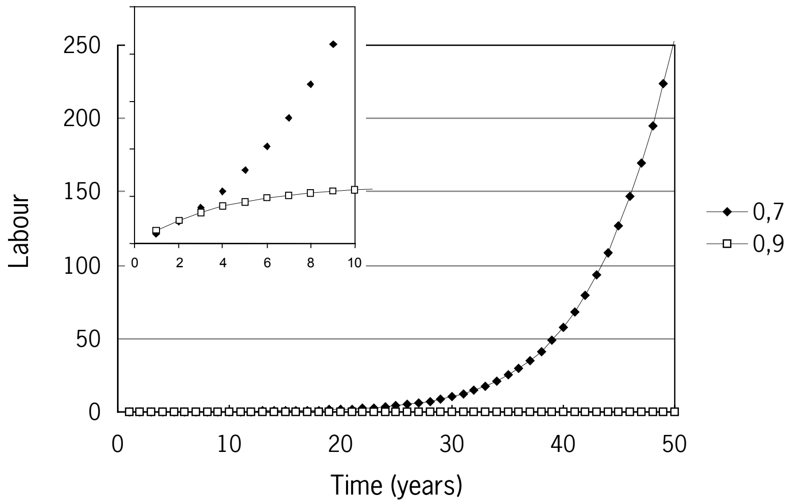

Figure 5. *Relative labour effort for 2 levels of Striga control (cumulative over the years) after development of 'mutant type' seeds of Striga in the seed bank with time at an initial proportion of the 'mutant type' (S2/S1) of 10^{-4} (cf Figure 4A).*

Conclusion 2: It is demonstrated in Figure 5 that it is quite profitable to remove more plants than seems to be necessary from the figures in Figure 4. The inset of Figure 5 shows that already in the 3rd year a weeding intensity of 0.9 requires less weeding than an intensity of 0.7. Another advantage is, that with the high weeding intensity the local Striga population becomes extinct and the Striga-resistant crop now has an infinite lifespan.

6. Practical management guidelines to safeguard the sustainability of varieties with a new resistance

The development of a *Striga*-resistant crop variety is a complex process with many uncertainties. One certainty is that sooner or later after introduction of the new variety mutant types of *Striga* will arise that are able to reproduce on the *Striga*-resistant crop. Depending on the mutation frequency a period of 10 – 20 years has been calculated in this study, which is quite short when compared with the period to breed a new variety. For that reason it is of vital importance to accompany the introduction of a new, *Striga* resistant crop variety with a management and communication strategy to increase the lifespan of the new variety.

Based on calculations with the model, two options to increase the lifespan of a *Striga*-resistant variety are recognised: alternating Sorghum and a non-host in a crop rotation and preventing seed setting of mature *Striga* plants by (hand) picking. Both strategies have the desired impact on the lifespan of the new variety, but local conditions may determine whether or not they are practicable. A 1:1 rotation with another crop means that only half the amount of *Sorghum* can be harvested on the same land area.

The most effective way of increasing the lifespan is by removing most of the *Striga* plants that grow on the resistant variety. If this process is started directly after introduction of the new variety, the number of Striga plants will still be very low and the labour needed is a good investment. It is important to make this clear to local farmers. This conclusion can also be drawn from a study with a bio-economic model of long-run *Striga* control (Mullen *et al.*, 2003).

7. Epilogue

During the ISCIMAS workshop in Wageningen on 21-23 May 2003, the draft of this report was discussed. Three questions were raised:

1. What is the effect of a variety that produces 50%, 75%, 90%, 99% less germination stimulants on the population dynamics of *Striga*?
2. What would happen if a crop was grown on a *Striga* infested fields that causes suicidal germination of *Striga* seeds?
3. How do we translate this report into an extension message?

Question 1. For this question, we need to know the relation between amount of germination stimulant from roots and percentage successful germination and infection (parameter g of the model). This relation is not directly available. Therefore, the question cannot be answered by simply doing another run with the model. However, Figure 1 in this reports can answer the question to some extent. Figure 1 shows a sensitivity analysis on parameter g. Obviously, when g becomes smaller, the final population size will become smaller. It is expected that g will become smaller when the reduction percentage of germination stimulant production gets higher. Probably, we deal with a non linear relation.

Question 2. Growing a suicidal germination crop means that a fraction of the seeds in the seed bank germinates and dies, or dies from natural causes. If this fraction was known, a model run could be made. In the model studies presented in the report, the fraction of seeds that germinate plus the fraction that that dies from natural causes is a little more than 0,42. Figure 2 shows to some extent what may happen if a suicidal germination crop is grown on a *Striga* infested field. During one season, the population size decreased with circa 42%. From Figure 2, it can also be concluded that if such a crop is grown during 5 seasons after one and other, the population size will become very small.

Question 3. A simple answer cannot be given. Every party present at the workshop stressed that it will be very important that the introduction of a newly developed sorghum or maize variety go along with an extension message for farmers to take time for resistance management. The benefits of resistance management should be made clear to the farmers. This reports contains elements for the extension message. In addition, countries should consider additional regulations to prevent that a new resistant crop is grown on a field year after year. Monitoring of Striga development in the new varieties should be stimulated. If observed, *Striga* plants should then be removed at a time that there numbers are still small.

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