A DYNAMIC ANALYSIS OF LONG TERM IMPACTS OF GENETICALLY MODIFIED CROPS

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To study the long-term usefulness of genetically-modified agriculture via herbicide-tolerant crops, a simulation model is built by focusing on the fundamental environmental feedback mechanisms. The most critical mechanism is the evolution of resistance in weeds via natural selection. Agricultural sustainability is investigated under different policies and scenarios, in comparison with conventional crops under two herbicide strategies. In the first strategy, herbicide amount is a function of weed density; in the second it is constant. It is found that superweed emergence increases the rate of resistance evolution in weeds. Under the constant herbicide strategy, GM crop is more effective than the conventional crop. However, this strategy results in a higher rate of resistance development and more herbicide usage than the first strategy. In terms of long term cumulative yield losses, rate of resistance development and herbicide usage, the best policy is discovered to be planting conventional crops under variable herbicide strategy.

Keywords: genetically modified crops, herbicide tolerant crops, agricultural modeling, resistance development, transgenic weeds

1. Introduction

Genetic modification is the use of modern biotechnological techniques to alter the genetic makeup of certain living organisms such as plants in a way that does not occur naturally (EEC, 1990). This technology enabled incorporating genes so as to obtain many desirable traits for crops. Accordingly, genetically modified (GM) crops have been introduced as a solution to world hunger and ecological crisis created by industrial agriculture. However, there is an ongoing risk debate due to unresolved questions about food safety, environmental effects, economic impacts, and ethical issues[1].

The most widely adopted GM products are the ones designed for pest management (James, 2005). A pest species is any species that is considered to be undesirable by humans. Weeds are a type of pest and are usually successful competitors for the food crops. Conventional weed management relies on herbicides which are chemical substances used to destroy weeds possibly damaging the crop as well. With the insertion of a herbicide tolerance[2] gene to the crop species, growers can control weeds without harming the crops. Yet, the introduction of exotic genes into crops can have unpredictable ecological impacts.

1.1. Possible Agricultural Impacts of Herbicide Tolerant Crops

Increased Herbicide Tolerance in Weeds: All natural populations probably contain individuals that show tolerance to one or more herbicides. That is, an individual plant may have a tolerance gene for a specific herbicide naturally. When that herbicide is sprayed, susceptible weeds are destroyed; however, tolerant weeds survive. In this case, the next generation will have a higher number of tolerant individuals and if that population is also exposed to the same herbicide, the proportion of tolerant individuals will further increase. This natural selection mechanism may eventually result in the extinction of susceptible individuals. Such a weed population can no longer be controlled by that specific herbicide and most probably by other herbicides with the same mode of action.

With GM herbicide tolerance technology, continuous use of a single herbicide is encouraged. Such consistent selection pressure has been most responsible for herbicide tolerance evolution. The problems of pest tolerance have resulted in the application of more and other pesticides/herbicides leading to further tolerance and so to more pesticide/herbicide. (Cowan, 1996). This has been called the *pesticide treadmill*, implying that once farmers get on, they find it difficult to get off (Wilson, 2001). Reducing the burden of herbicide usage, GM crops are very likely to cause the same problems probably more quickly and with higher intensity.

Superweeds: Transgenes can spread to weedy relatives, creating 'superweeds' if the transgene increases the fitness of the weed (Hails, 2005; Halfill, 2002 etc.). For example, a weed containing a transgene that provides resistance to draught has an increased fitness in nature and may compete more with beneficial plant species leading to the latter's suppression. On the other hand, herbicide tolerant superweeds will be problematic due to their tolerance to the selected herbicide(s). These superweeds may further speed up the spread of tolerance in the population.

Transgenic Volunteer Crops: A plant that germinates from a seed left behind in the field from a previous crop is called *volunteer*. Volunteers of herbicide tolerant crops are problematic especially if the same herbicide is used throughout the rotation, because these plants are not controllable by the herbicide (Kwon, *et* al., 2001).

All of these issues may further increase herbicide usage in the long run since farmers will need to spray additional herbicides getting on the pesticide treadmill. Significant increase in yields would not be observed unless HT crop is modified to be tolerant to the pack of herbicides applied. Furthermore, increased herbicide usage raise public health concerns due to the accumulation of chemicals in the environment (Carson, 1962).

1.2. Analysis of Genetically Modified Agriculture

Many possible consequences of adopting GM crops will stem from complicated interactions in the environment and will not be evident in the short run. There are some experimental field studies to come up with a farm-scale evaluation of GM crops such as DEFRA (Department of Environment and Rural Affairs) projects in UK (Squire *et al.,* 2003; Firbank *et al.*, 1999) and projects of Danish Environmental Protection Agency (Danish EPA, 1999); however such studies are costly and have to be pursued for sufficiently long time in order to grasp the slow occurring effects.

In this study, the long term effects of herbicide tolerant crops on farming management are analyzed. The aim is to evaluate the sustainability of agriculture with GM herbicide tolerant crops by focusing on the fundamental feedback mechanisms in the environment and the intervention of agricultural practices. Certain causal structures and assumptions of a previous model developed by Dogan and Karanfil (Dogan, et.al, 2002) are taken as a starting point. However, the core of this study is modeling the spread of resistance in the population through natural selection, which has been the biggest source of failure in chemical pest control. The model is intended to provide an experimentation platform to study the impacts of agriculture with GM crops on farming practices under various policies, scenarios and conditions.

2. Model Description

The model is built on farm scale considering an isolated land where GM herbicide tolerant crop is planted. There are primarily 3 sectors, being *Crop*, *Weed* and *Superweeds*. The fundamental interaction between these sectors is the competition among these plants. Weeds (including superweeds) compete with the crop and this competition determines the size of each plant population, or the amount of *yield* from an agro-economic perspective. In order to calibrate the model, canola (Oilseed rape or *Brassica Napus*) and birdseed rape (field mustard or *Brassica rapa*) are chosen as the crop-weed pair. In the literature, high hybridization rates between canola and birdseed rape have been reported and birdseed rape is a common weed in many places where canola is grown which makes the situation problematic (Jorgensen 1994, Halfhill *et al.,* 2002, etc). GM Canola is tolerant to an effective, non-selective herbicide called glyphosate; so in the model the spread of glyphosate tolerance in birdseed rape is traced.

Main assumptions of the model are as follows:

- There is a single weed species in the field
- There are no pests
- The effect of abiotic factors such as rain or wind on plant populations is constant, hence omitted
- Mutations are negligible
- Tolerance is expressed by two alleles[3] of a single gene
- All the tolerant species are 100% tolerant to the herbicide
- Superweeds are morphologically identical to the weeds, except for their reproduction capacity. Hence their seeds can be regarded as weed seeds, treating the second-generation hybrids as weeds.
- A single herbicide is used to treat the weeds.

The *Hardy-Weinberg* model is used to characterize tolerance. The Hardy-Weinberg model is a fundamental model in population genetics due to its notable ability to predict allele frequencies. The model has five basic assumptions: (1) The population is large, (2) There is no gene flow between populations, i.e. no migration, (3) Mutations are negligible, (4) Individuals are mating randomly, (5) Natural selection is not operating on the population. For a population satisfying these assumptions, the expected proportion of alleles and of genotypes remain constant from generation to generation.

In the model, it is assumed that tolerance is conferred by a single allele that is not sex-linked. There are two types of alleles: tolerant (R) and susceptible (S). Each individual plant has two alleles and so can be one of three possible genotypes: RR- a tolerant homozygote, RS- a tolerant heterozygote and SS- a susceptible homozygote[4]. If p is the frequency of tolerance alleles in the weed population in this generation, the Hardy Weinberg model implies that the proportion of each genotype will be p^2, $p\ (1-p)$ and $(1-p)^2$ respectively in the next generation. Note that p is not a constant in this model due to natural selection operating on the system.

Competition is modeled relying on the *carrying capacity* concept. Carrying capacity represents the limit exerted by the environment on the population size of a species on a given area. It is assumed that beyond that limit the species can no longer obtain sufficient nutrition from soil and therefore growth is stopped. Hence, as the total biomass on the specific area approaches the carrying capacity of the species of concern, the net growth rate of the species decreases. In the model, competition affects the net growth rate of the species by changing its regeneration ratio.

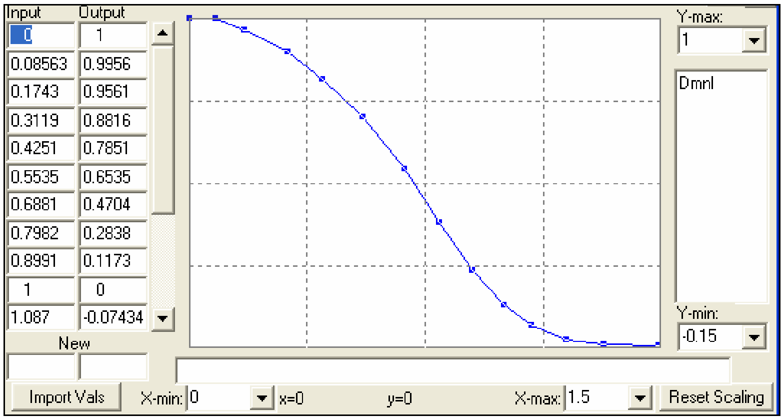
$$\mathit{Net\ Growth\ Rate} = \mathit{Biomass} \times \mathit{Regeneration\ Ratio}$$

$$\mathit{Regeneration\ Ratio} = \mathit{Maximum\ Regeneration\ Ratio} \times \mathit{Effect\ of\ \ Competition}$$

The effect of competition on species *i* is a function of the ratio of total biomass to the carrying capacity of the species.

$$\mathit{Effect\ of\ \ Competition\ on\ Species\ i} = f\left(\frac{\mathit{Biomass}_{i} + \alpha\ \times \sum \mathit{Biomass}_{j}}{\mathit{carrying\ capacity}_{i}}\right)$$

In the equation, α represents the relative impact of the competing species on resource usage. α=1 when the competing species exploits the resource just in exactly the way as the species under concern does. *Effect of Competition on Species i* approaches zero when this scaled total biomass approaches the carrying capacity of the species of concern. If the carrying capacity is overshoot, the function takes negative values implying a negative net growth rate.



Input	Output
0	1
0.08563	0.9956
0.1743	0.9561
0.3119	0.8816
0.4251	0.7851
0.5535	0.6535
0.6881	0.4704
0.7982	0.2838
0.8991	0.1173
1	0
1.087	-0.07434

Y-max: 1
Dmnl
Y-min: -0.15
X-min: 0
x=0
y=0
X-max: 1.5

Figure 2.1. Effect of competition as a function of the ratio of total biomass to the carrying capacity of the species of concern

Life cycle of a crop is composed of three main stages: sowing, growing and harvesting. This is accounted for by the corresponding flows *sowCanola*, *growCanola and harvestCanola* of *GM Canola* stock (Figure 2.2). Canola seeds are sown at a predetermined amount and date, and the crop is harvested completely at a predetermined harvest date as the plants reach maturity.

$$\mathit{sowCanola} = \frac{\mathit{seedweight} \times \mathit{seeds} \times \mathit{TimeToSeed}}{\mathit{seeding\ period}}$$

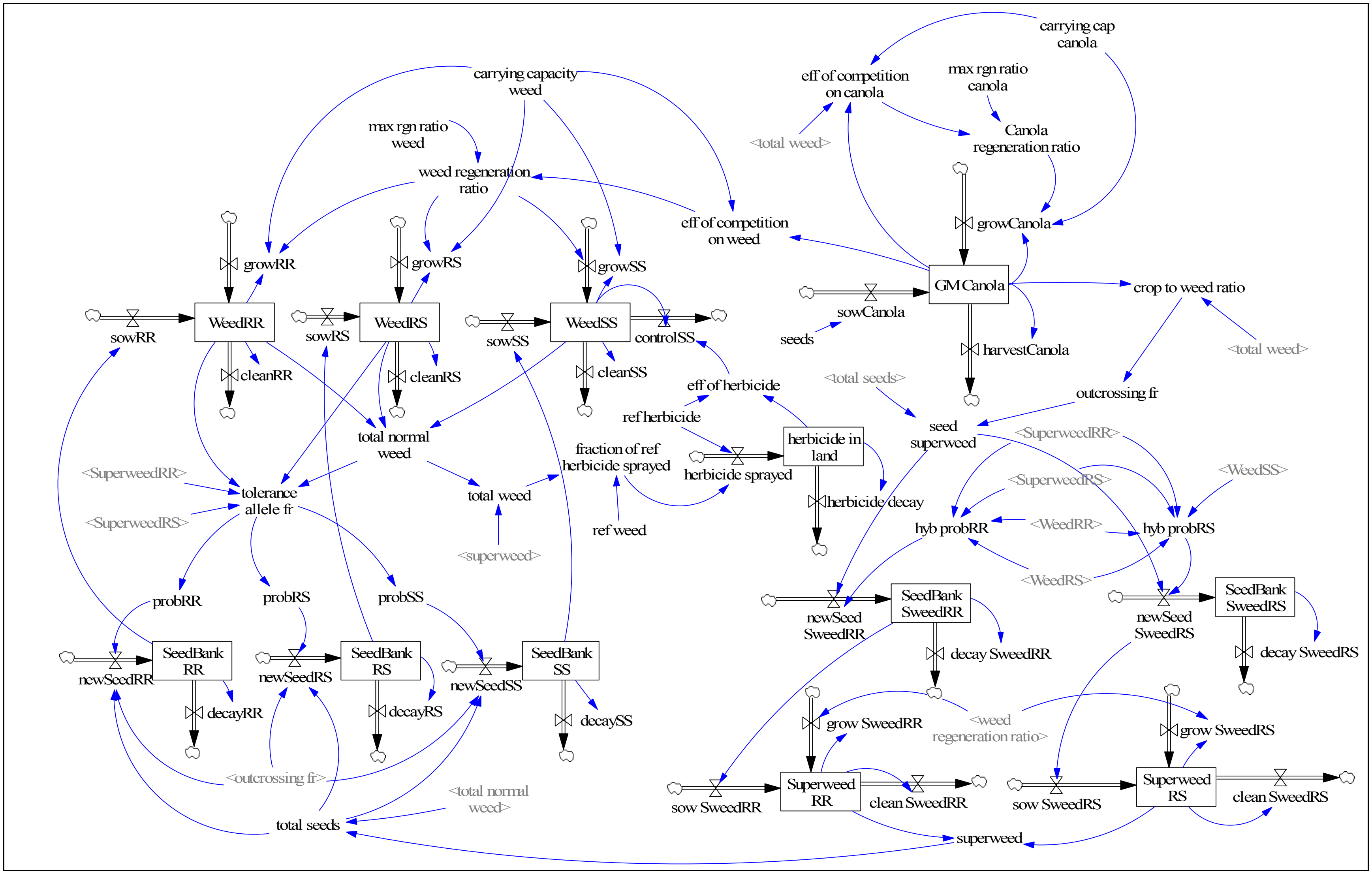


Figure 2.2. Simplified Stock-Flow Diagram

$$harvestCanola = \frac{GM\ \ Canola \times TimeToHarvest}{harvesting\ \ period}$$

The life cycle of weeds is similar to that of crop's except that their seeding is not exogenously set by farmers but determined by their own deposited seeds in soil, which are called seedbanks. Therefore, *Weeds* sector has two subsectors, one to model the current population of weeds and one to model the seedbanks. Seedbank can be thought as a bank into which the species deposit their annual seed production. When seeds are sown, this stock of seeds is reduced. Moreover some of the seeds decay or die due to various reasons throughout the year. *Sow* rate of the *Weeds* is determined by the *SeedBank* size and the fraction of seeds in the *SeedBank* that begins to grow per time, so called the germination frequency.

$$sow = SeedBank \times germination\ fr$$

Since one concern of the model is the evolution of tolerance to herbicides, weed population is disaggregated to three sub population stocks with respect to the three genotypes RR, RS and SS as *WeedRR*, *WeedRS* and *WeedSS* respectively. Each weed stock has its own *SeedBank*, leading to a 6-stock system (Figure 2.2).

In the model, *Superweed*s are modeled similarly to the weed populations: *Superweed* stocks represent the superweed population, whereas *SeedBank Sweed* stocks represent the inventory of hybrid seeds. Since modeling the entire hybridization process is out of the scope of this study, it is assumed that after the first generation of the hybrids between two species, namely the F1 generation, the seeds of superweeds are transferred to the weed seedbanks. This is justified with the fact that after one generation, many of the progeny are similar to the weeds (Halfhill *et al.,* 2002). Therefore, in the model having two stocks for *Superweed*s is sufficient, which are *SuperweedRS* and *SuperweedRR.* These stocks are filled with seeds from their seedbanks *Seedbank SweedRS* and *Seedbank SweedRR* respectively. Seeds produced by superweeds are a part of *total seeds,* which are distributed among weed seedbanks with respect to their genotypes.

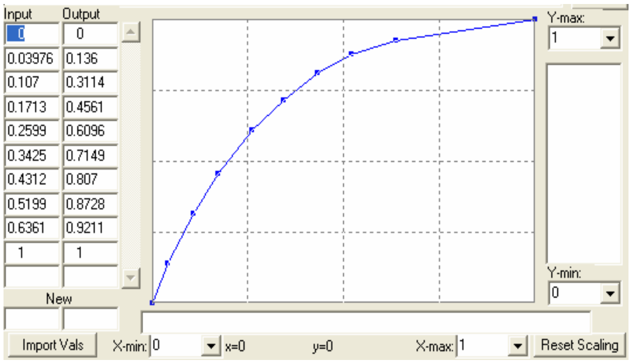
New seeds (of weeds and superweeds) are formed when plants reach maturity and then they are buried in the soil, i.e. deposited in the seedbank. Seed production is determined by the biomass at harvest time, and the *harvest index* (HI), which indicates the ratio of seeds to overall biomass. However a portion of these seeds are lost mostly due to predation, which is accounted for by the variable *seedloss* in the model. Seed production by superweeds also contributes to *total seed*. Hence, the variable *total seeds* is computed as:

$$total\ \ seed = (total\ B\ weed \times HI\ \ Weed + superweed \times HI\ \ Sweed) \times seedloss$$

The hybrid seeds that will enter the seedbank of superweeds are modeled as a fraction of total seeds produced by the weed population. This fraction represents the hybridization rate between the two species and is denoted by *outcrossing fr*.

$$seed\ \ superweed = total\ \ seed \times outcrossing\ fr$$

The more the weed is surrounded by canola plants, the higher the hybridization rate between the two. Different studies point out a quite wide range of hybridization rates, yet all emphasize that as the distance between canola and the weed decreases and as the ratio of crop to wild relative increases, hybridization rate increases (Halfill *et al.*, 2002). Hence in the model, *outcrossing fr* is a function of crop to weed ratio. A reference value which occurs at high crop to weed ratios is provided and the effect of relative abundance of crop is accounted for by *eff of crop to weed ratio on hybridization*, which is a graphical function of *crop to weed ratio*.



Input	Output
0	0
0.03976	0.136
0.107	0.3114
0.1713	0.4561
0.2599	0.6096
0.3425	0.7149
0.4312	0.807
0.5199	0.8728
0.6361	0.9211
1	1

Y-max: 1
Y-min: 0
X-min: 0
x=0
y=0
X-max: 1

Figure 2.3. Effect of crop to weed ratio on hybridization as a function of crop to weed ratio

So, a fraction of total seeds formed through hybridization are deposited into the seedbanks of superweeds and the remaining seeds are directed into weed seedbanks with respect to the associated genotypic frequencies. The proportion of these seeds that belong to seedbanks RR, RS and SS are p^2, 2pq and q^2, respectively, where p is the frequency of the tolerance allele in the population. In the model, these proportions are called *probRR*, *probRS* and *probSS* respectively. Therefore the flow of new seeds to the seedbanks, *newSeed*, can be computed by:

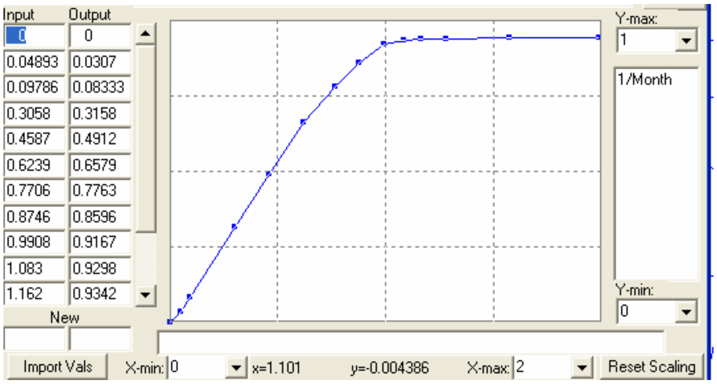
$$newSeedRR = probRR \times total\ seed \times (1 - outcrossing\ fr)$$

The frequency of tolerance allele, which determines the genotypic frequencies, depends on the current population of *WeedRR*, *WeedRS*, *SuperWeedRR* and *SuperWeedRS*. Each RR seed (*Weed* or *Superweed*) contributes two R alleles to the gene pool, whereas RS seeds only one. Each individual has two alleles for tolerance trait. Since seed production is proportional to the related biomass and its harvest index, the formulation for *tolerance allele fr* becomes:

$$\frac{(2 \times WeedRR + WeedRS) \times harvest\ index + (2 \times SuperweedRR + SuperweedRS) \times HI\ Sweed}{2 \times (total\ \ weed \times harvest\ index + superweed \times HI\ Sweed)}$$

Only *WeedSS* is susceptible to the herbicide that is used to control the weeds. *Control* outflow models the impact of herbicide on the *WeedSS* stock.

$$control = WeedSS \times effect\ of\ \ herbicide$$



Input	Output
0	0
0.04893	0.0307
0.09786	0.08333
0.3058	0.3158
0.4587	0.4912
0.6239	0.6579
0.7706	0.7763
0.8746	0.8596
0.9908	0.9167
1.083	0.9298
1.162	0.9342

Y-max: 1

1/Month

Y-min: 0

X-min: 0

x=1.101

y=-0.004386

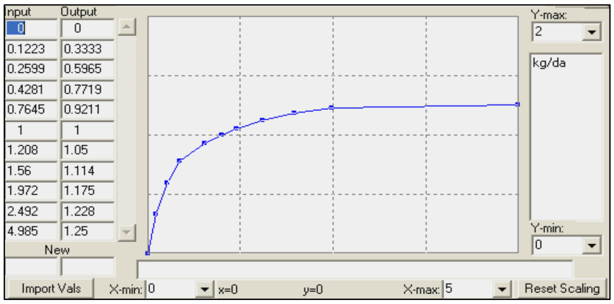
X-max: 2

Figure 2.4. Effect of herbicide on susceptible weeds as a function of herbicide density

Herbicide in land is a stock filled by *herbicide sprayed* and drained by *herbicide decay*. Herbicide sprayed is modeled in two different ways for two different herbicide strategies. In the *constant herbicide strategy*, herbicide is sprayed twice a season at a predetermined amount equivalent to *ref herbicide*. In the *variable herbicide strategy*, weed biomass is observed twice a season and a fraction of *ref herbicide* which is determined by weed density is sprayed as follows:

$$herbicide\ sprayed = fraction\ of\ \ ref\ \ herbicide\ sprayed \times ref\ \ herbicide \times TimeToSpray$$

$$fraction\ of\ \ ref\ \ herbicide\ sprayed = f\,(\frac{total\ weed}{ref\ \ weed})$$



Input	Output
0	0
0.1223	0.3333
0.2599	0.5965
0.4281	0.7719
0.7645	0.9211
1	1
1.208	1.05
1.56	1.114
1.972	1.175
2.492	1.228
4.985	1.25

Y-max: 2

kg/da

Y-min: 0

X-min: 0

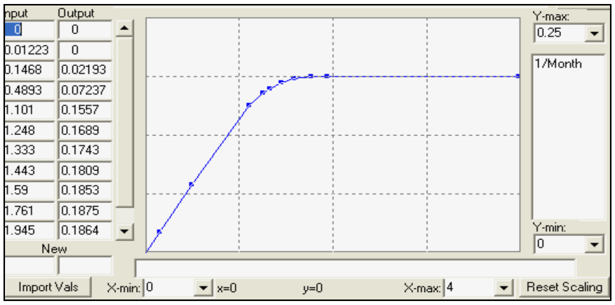
x=0

y=0

X-max: 5

Figure 2.5. Fraction of reference herbicide sprayed as a function of relative weed density

Finally, when conventional canola is planted instead of a GM variety, herbicide application results in a yield loss due to crop response. This loss is modeled via the outflow *yield loss due to herbicide*, which is a function of *eff of herbicide on canola*.



nput	Output
0	0
0.01223	0
0.1468	0.02193
0.4893	0.07237
1.101	0.1557
1.248	0.1689
1.333	0.1743
1.443	0.1809
1.59	0.1853
1.761	0.1875
1.945	0.1864

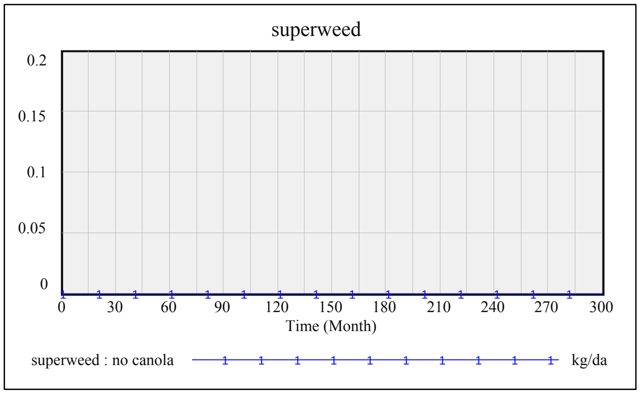
Y-max: 0.25
1/Month
Y-min: 0
X-min: 0
x=0
y=0
X-max: 4

Figure 2.6. Effect of herbicide on canola as a function of herbicide density

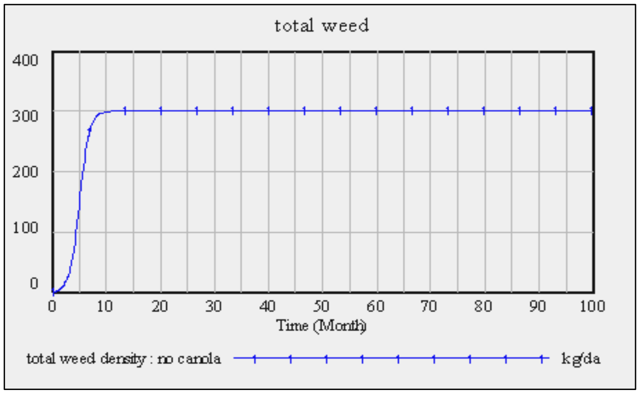
3. Validation and Analysis of the Model

Verification and validation testing of the model are done by carrying out the standard procedures (Barlas, 1996). Direct structure tests are performed by verifying the consistency of the equations with the literature. Due to the lack of data for the dynamics of weed populations that takes into account the spread of tolerance, it is not possible to perform rigorous behavioral validation. Hence, model validation is primarily demonstrated by extreme condition and behavior sensitivity tests. Behavior sensitivity tests will not be discussed as none of the variables were found to be sensitive enough to change the model behavior. Some results from the extreme condition tests are presented below.

3.1.1. No Canola: When GM canola is not planted, *Superweeds* cannot emerge (Figure 3.1.a). In this case, there is no interspecific competition for weed. Hence weed population is expected to behave as if isolated: reach its carrying capacity and saturate there. This holds for the model output, as shown below.

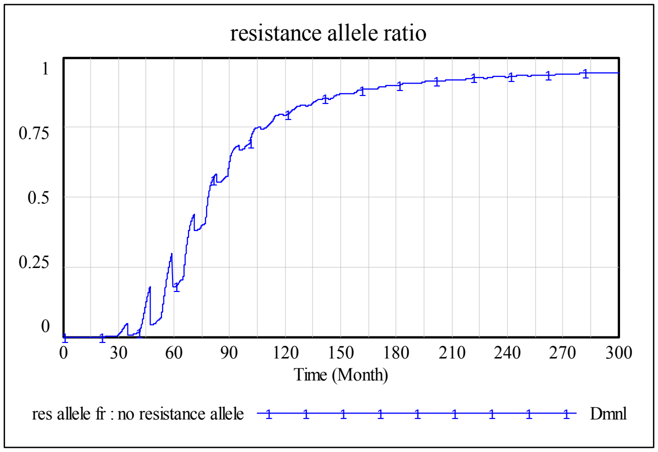


(3.1.a)

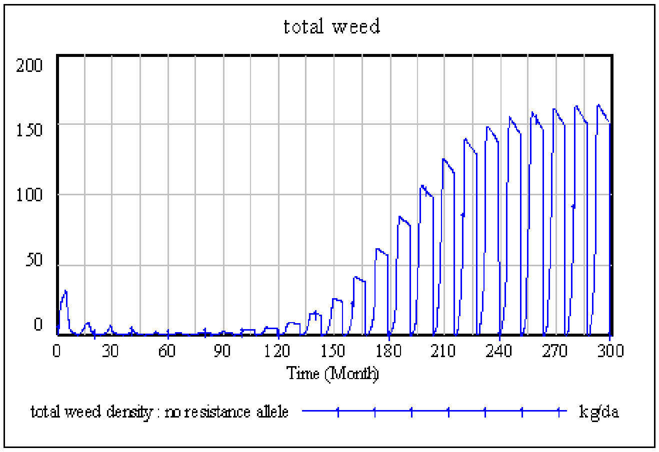


(3.1.b)

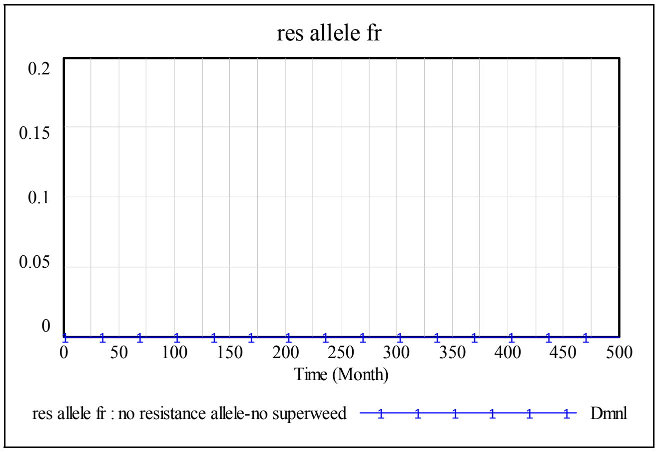
3.1.2 No Resistance Allele: When there is no resistance allele in a weed population and mutation is not allowed, it is expected that resistance cannot evolve. However, when a HT crop is planted, formation of superweeds introduces resistance alleles into the population, allowing resistance evolution (Figure 3.2.a). If there were no hybridization, resistance allele ratio would stay at zero as expected (Figure 3.2.c).



(3.2.a)



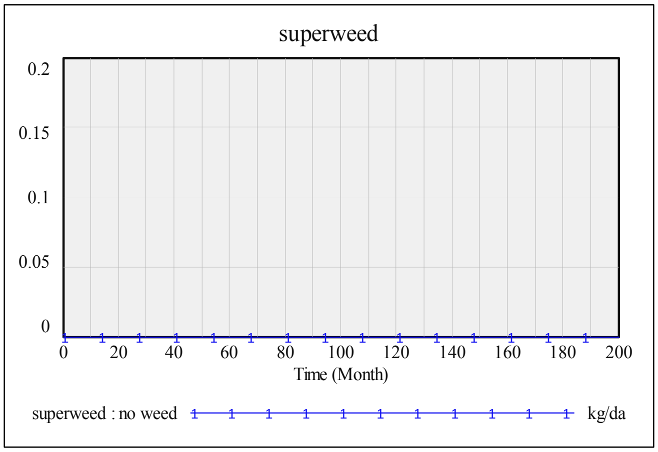
(3.2.b)



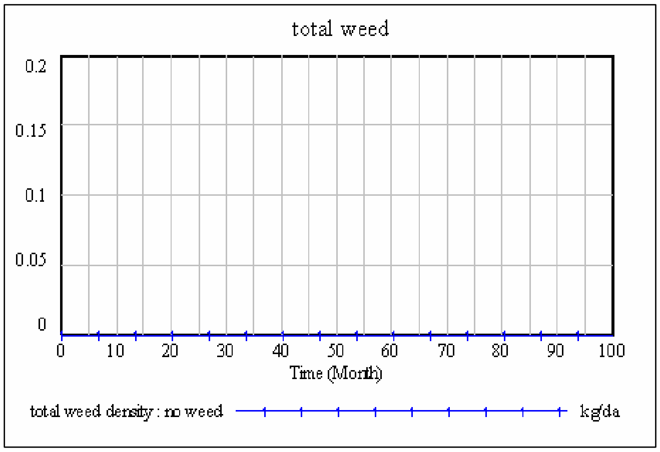
(3.2.c)

3.1.3. Empty Weed Seedbanks

When weed seedbanks are empty, weeds cannot grow, as expected (Figure 3.3.b). In that case, there cannot be hybridization, hence superweeds cannot emerge (Figure 3.3.a).



(3.3.a)



(3.3.b)

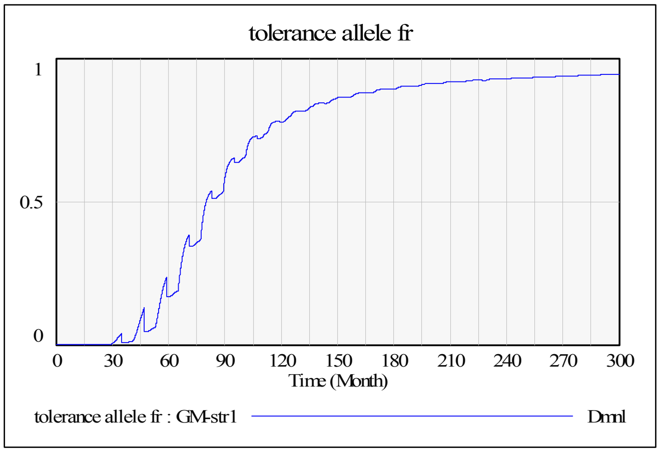
3. 2. Base Behavior of the Model

Base behavior of the model will be analyzed under two herbicide strategies and by simultaneous comparison with conventional canola.

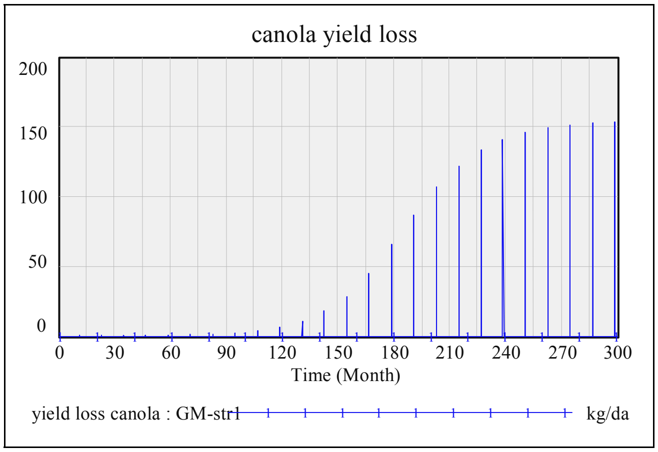
3.2.1. Variable Herbicide Strategy:

The fundamental behavior of the model is the spread of tolerance in the population, which is depicted by the graph of *tolerance allele fr* The fraction of tolerance alleles in the population increases until approximately all alleles are tolerant. This occurs fast in spite of the very low initial tolerance allele frequency (0.0000003). This is due to the high efficacy of glyphosate, dominance of the tolerance allele and formation of superweeds which further contributes tolerance alleles into the seedbanks.

As can be seen in Figure 3.4.a, the weed population can be suppressed by herbicide applications at first. However, with increasing tolerance in the population, the herbicide loses effectiveness and the weed population attains infestation levels. Accordingly, yield losses are very small initially and increase up to one third of the expected yield with (Figure 3.4.b).

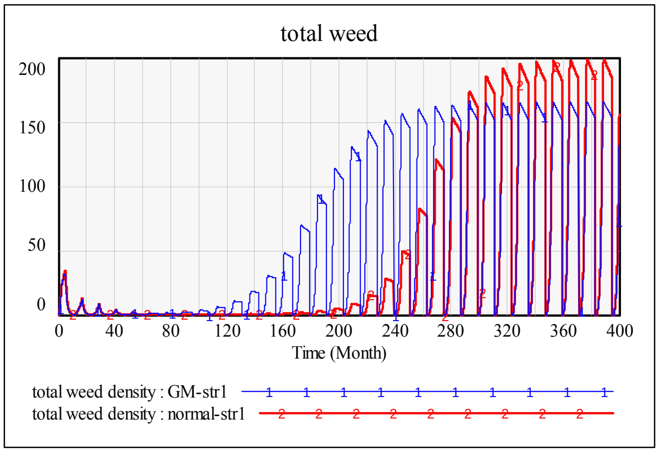


(3. 4. a)

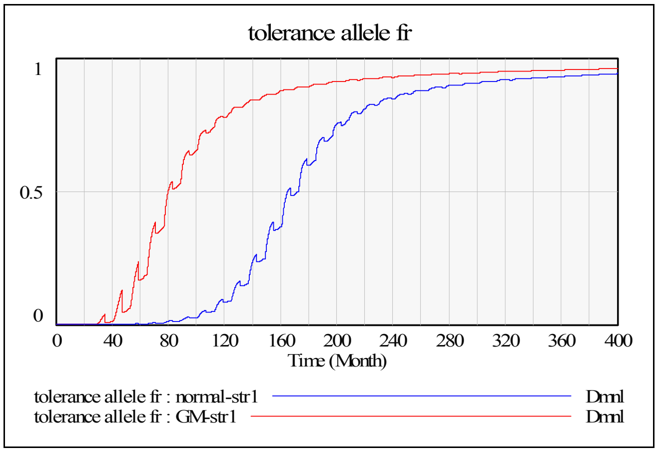


(3.4.b)

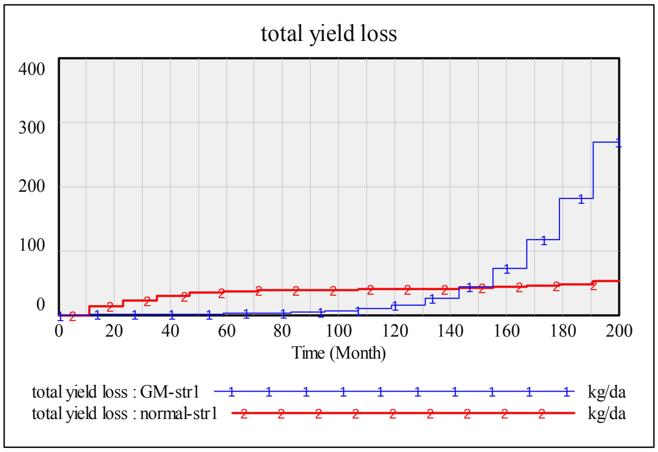
When the dynamics of the weed population under the cases of GM and conventional canola are compared, it is seen that weed population resurges earlier in the GM case (Figure 3.5.a). Since superweeds increase the resistant weed population, more weed survives the herbicide, and more herbicide is sprayed. Increased herbicide usage results in an increased rate of tolerance development as seen in Figure 3.5.b. When cumulative yield losses are compared, in the short run planting GM canola provides higher yield efficiency (Figure 3.5.c). However, this comparative benefit decreases in a relatively short period due to faster evolution of tolerance in the weed population in GM canola case. Furthermore, cumulative herbicide usage is higher when GM canola is planted (Figure 3.5.e), which increases the input costs in agriculture and, perhaps more critical, invokes concerns for food safety.



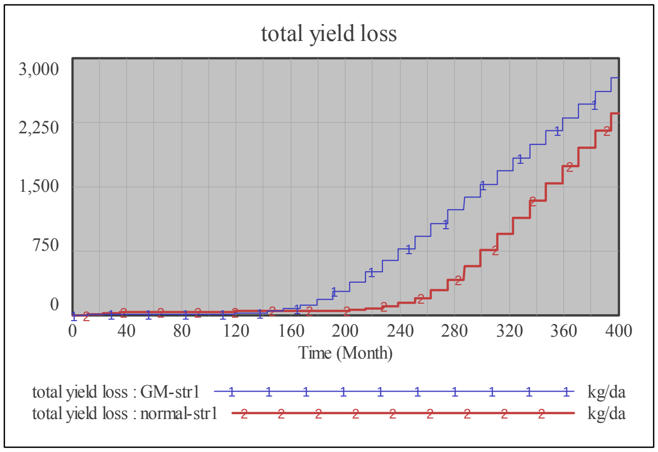
(3.5.a)



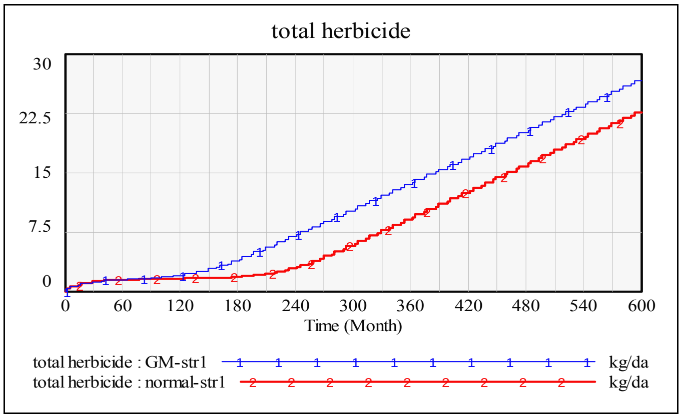
(3.5.b)



(3.5.c)



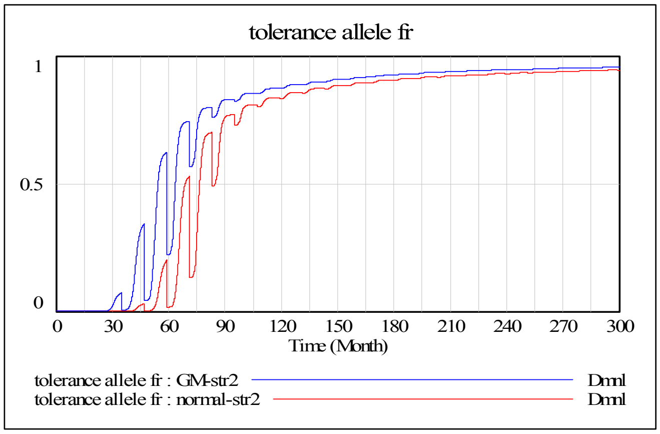
(3.5.d)

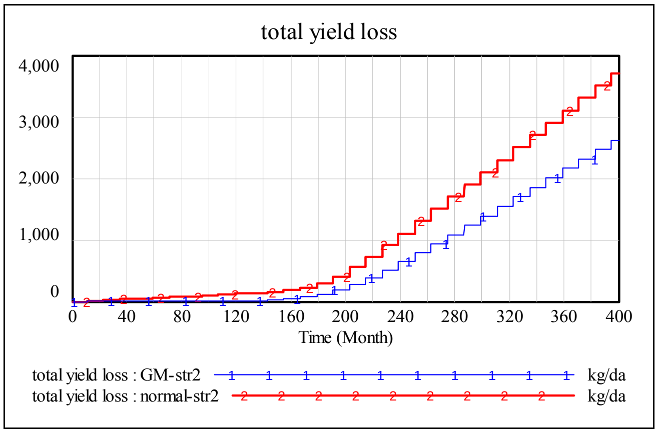


(3.5.e)

3.2.2. Constant Herbicide Strategy

Dynamic behavior of GM canola in this case is almost identical to the behavior obtained under the variable herbicide strategy, however as depicted in the tolerance allele ratio graph in Figure 3.6.a, the gap between the rates of tolerance development in GM and conventional canola is reduced compared to the first case. This is mainly because equivalent amount of herbicide is applied in both fields. The other reason is that since weed population is almost eradicated due to high control efficacy, superweeds cannot come out to considerable levels at first. Hence, they do no grow sufficiently to result in a significant difference in the rate of tolerance development. Under this strategy, GM canola turns out to be a preferable control means (Figure 3.6.b).

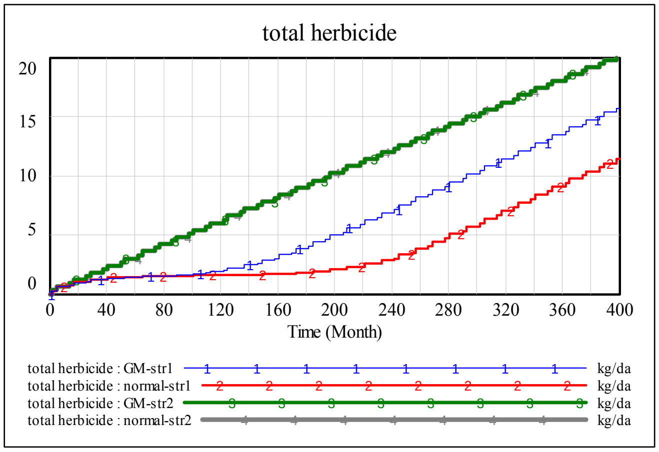


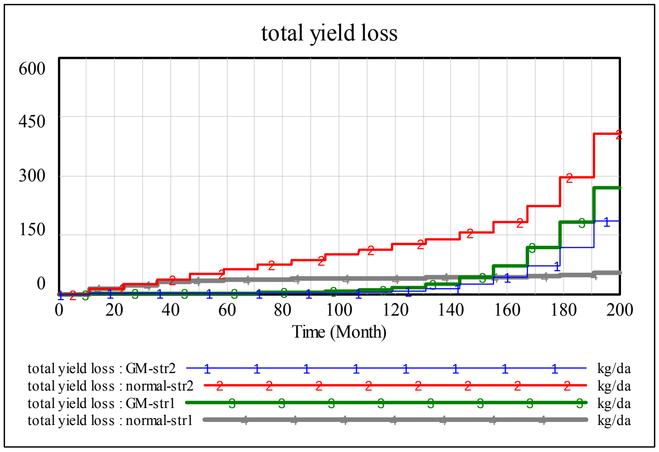


(3.6.a)

(3.6.b)

However note that herbicide usage is promoted which is contrary to the objectives of an environmentally friendly weed management program. In 3.7.a, cumulative herbicide usages under the two strategies and for the two plant varieties are compared. It is seen that the best strategy in reducing herbicide use is planting conventional canola and applying herbicide as a function of weed biomass. On the other hand, when cumulative yield losses are compared, in the short term, GM canola under the second strategy brings higher yields (Figure 3.7.b). However, since tolerance evolution is slow when conventional canola is planted under the first strategy, long run cumulative yield losses are lower than those obtained when GM canola is planted (Figure 3.7.b). Assuming that a herbicide to which weeds gained tolerance will stay in use is unrealistic. However, the point that is tried to be made via this analysis is that comparative benefits of using GM canola decreases and the need for an alternative product rises in relatively short periods.





(3.7.a)

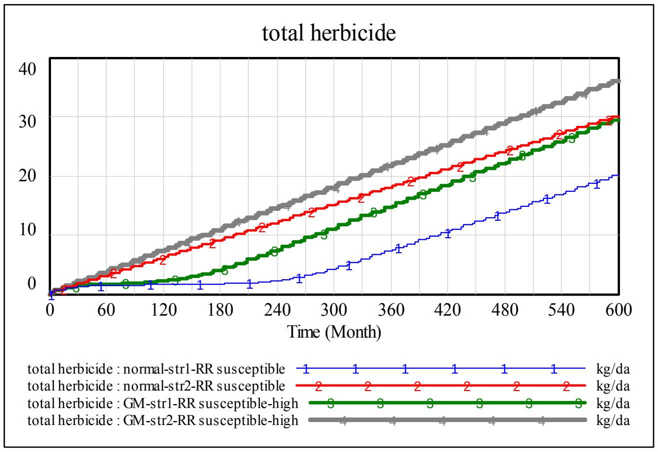
(3.7.b)

3.3. Scenario analysis

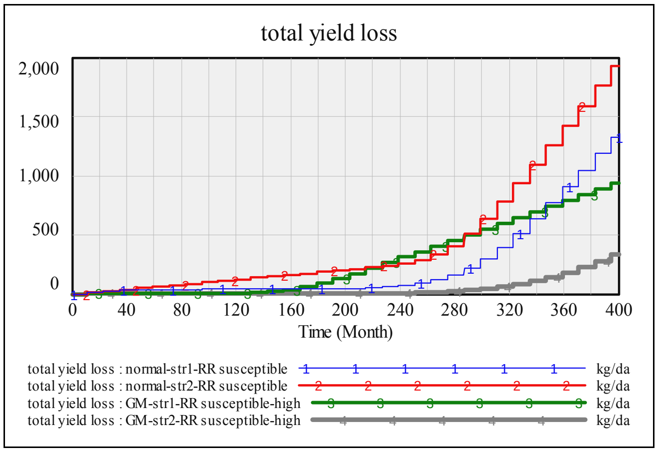
3.3.1. Resistant Weeds Showing Susceptibility at High Doses of Herbicide

In the model it is assumed that resistant weeds of both RR and RS genotype are completely immune to the herbicide. However, in reality tolerance is a matter of degree and especially heterozygote weeds are expected to show some susceptibility at doses higher than the amount sufficient to kill susceptible weeds. In order to see whether treating tolerance in this kind of a continuum changes the general behavior, all weed genotypes are modeled to be controlled by the herbicide at different rates such that *WeedRR* are only modestly affected at very high doses, while *WeedRS* shows some susceptibility even at the current dose. It is seen that the general behavioral pattern is not altered and that the aforementioned relative efficiencies of conventional and GM crops still hold.

However, a different picture is obtained if herbicide spray rate is increased in this new setting. Since HT crops prevent crop damage, it is probable that GM farmers increase their herbicide spray rates in order to fully benefit from the merits of the costly seeds they purchase. Indeed, farmers are reported to spray considerably more herbicides on HT soybean (Benbrook, 2003). Accordingly, in this scenario GM farmer sprays at a higher rate than the rates used for conventional canola planting. When cumulative yield losses of the two plant varieties under the two herbicide strategies are compared, planting GM canola under the constant herbicide strategy and at an increased rate provides the highest yield efficiency throughout the simulation. However, this benefit comes with the cost of increasing herbicide usage dramatically (Figure 3.8.b).



(3.8.a)

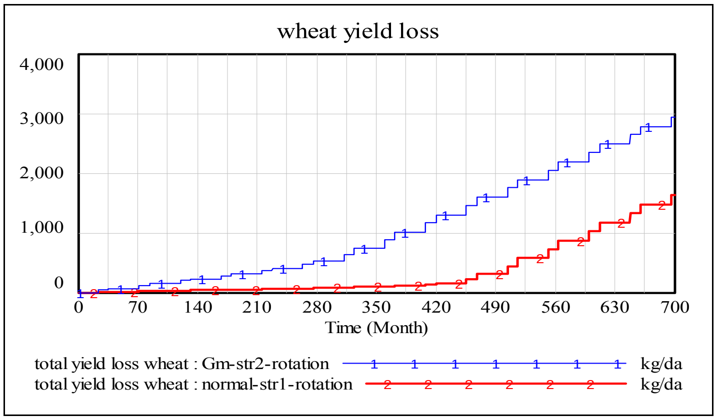


(3.8.b)

3.3.2. Canola Planted in Rotation with Wheat

In the model, agriculture with HT crops is investigated assuming that each year the same crop is planted as a monoculture. In this scenario, a four-year rotation cycle of *Canola-Wheat-Wheat-Canola* is studied and it is assumed that the same herbicide is used throughout the rotation. When crops are planted in rotation, volunteer crops become an issue and it is a concern for genetically modified herbicide tolerant crops especially if the same herbicide is used throughout the rotation, because these plants are not controllable by the herbicide. Volunteer canola has been reported to evolve into a common weed (Shirtliffe, 2003).

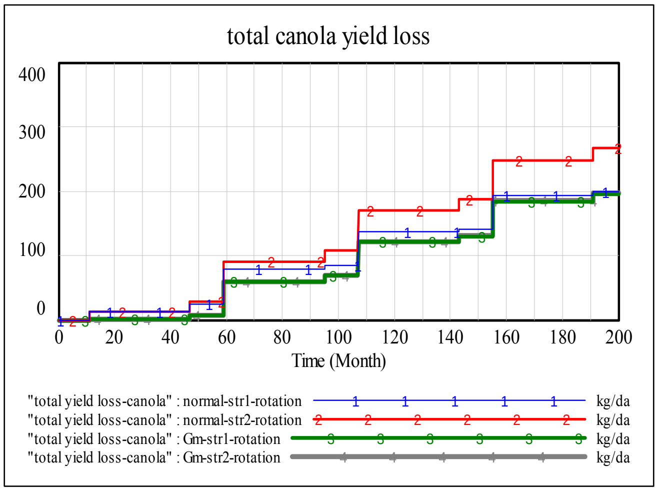
Canola volunteers are modeled similarly to the weed population and they are problematic only when wheat is planted. These weeds result in higher yield losses compared to planting conventional canola where volunteers can be suppressed by the herbicide (Figure 3.9).



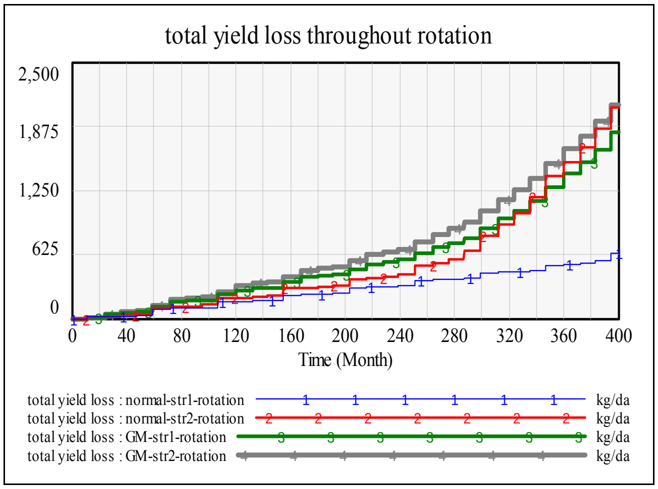
(3.9)

GM canola still provides higher yield efficiency in the short run, though with decreased discrepancy (Figure 3.10.a). However, when the overall yield efficiency of the rotation is considered, this short term advantage is lost due to the fact that canola volunteers cannot be suppressed by glyphosate, which increases weed biomass (Figure 3.10.b).

Of course, a different or an additional herbicide can be used for the rotation crop in order to suppress canola volunteers. Indeed, rotating herbicides is a recommended strategy to delay the evolution of herbicide tolerance. However, it must be kept in mind that when a species gains tolerance to a herbicide, it most probably becomes tolerant to a range of herbicides with a similar mode of action. Finding an appropriate herbicide to suppress volunteers will be especially an issue if crops are modified to be tolerant to a pack of herbicides.



(3.10.a)



(3.10.b)

4. Conclusion and Discussions

The purpose of this research is to study the long-term impacts of GM crops on crop yield and herbicide use under various scenarios and policies, the focus being on the potential environmental and ecological problems discussed in the literature. Agriculture with herbicide tolerant crops is analyzed under two herbicide strategies and by comparing with its conventional counterpart in order to appreciate the relative benefits and disadvantages.

Under the variable herbicide strategy, planting HT crops are shown to be more effective in the short run. But this comparative benefit decreases quickly due to faster evolution of tolerance in the weed population in the GM case because of the formation of superweeds, which increases both the weed burden and the rate of tolerance development. One important phenomenon depicted is that unlike conventional crops in the GM case herbicide tolerance is developed even if there is no tolerance allele in the weed population initially. Superweeds contribute tolerance alleles to the gene pool and speed up the spread of tolerance; hence the herbicide becomes ineffective more rapidly, which outweighs HT crop’s advantage of increased crop safety. Moreover, weed biomass is increased in the presence of superweeds, pushing up the need for spraying herbicide. Hence, in the GM case cumulative herbicide usage is higher, which also increases the rate of tolerance development.

If the amount of herbicide sprayed is fixed and high enough, weed population is so suppressed that hybridization is almost ruled out. In this case superweeds cannot emerge until the tolerant weed population attains a considerable level. Hence, conventional crop loses its advantage of lower weed biomass and decreased herbicide use. Furthermore, it suffers from a higher yield loss due to the adverse effects of the herbicide. Hence, HT crop provides superior yield efficiency compared to conventional crop under this herbicide strategy. When the four possible cases are compared, this is the best option in terms of short-term yields. Yet, this strategy increases the cumulative herbicide usage, which increases input costs to agriculture and more critically, invokes food safety concerns. Furthermore planting conventional crop under the variable herbicide strategy results in a lower cumulative yield loss in the long run, due to slower tolerance evolution.

On the other hand, if HT crop is planted within a rotation where the same herbicide is used consistently, volunteers of the GM crop become a severe weed burden due to their tolerance to the herbicide. In this case, when the overall yield loss throughout the rotation is considered, HT crop is inferior in terms of yields under both herbicide strategies.

In general, when weed biomass is used to determine the amount of herbicide sprayed, cumulative herbicide usage is reduced, which makes it a better practice in terms of environmental impacts. Moreover, since in this case weed biomass does not go down to extremely low levels, the strategy does not threat other organisms that feed on weed seeds. However, one must note that in either case, consistent application of a single herbicide is not a sustainable means of weed management since tolerance development is fast.

To sum up, relative benefits of using GM herbicide tolerant crops decrease and the need for alternative crops rises in relatively short periods. To overcome the tolerance barrier, a sustainable and integrated system needs to be developed regarding the specific conditions on the land of concern. However, one rightful concern is that the short-term success of herbicide tolerant crops will delay the intensive search for novel non-pesticide based pest management technologies and methods.

There are several avenues in which this research can be expanded. One first step is incorporating insect pest problems to the model. Insect resistant GM crops are the second most widely used GM products (James, 2005). As the second stage of this study, another simulation model is built to analyze the long term impacts of agriculture with GM insect-resistant crops (Tan, 2005). However, weed and pest issues generally coexist in practice, resulting in further complicated interactions. So, analyzing the pest management systems with GM crops in a single model may bring to light interesting results.

Since the focus of this study is the sustainability of agriculture with HT crops, economic returns have not been analyzed. The models can be extended to incorporate a long term profitability analysis. However, considering the fact that the market for GM products involves somewhat a higher uncertainty due to unresolved risk issues, the results of such a study should be interpreted with caution.

Finally, as a step in the analysis of effects of GM crops on biodiversity, HT-Model can be further extended to incorporate population dynamics of farm birds and similar animals that feed on weed seeds. Whether birds can survive the effects of intensified weed management is occasionally raised as a concern. A comparison of conventional and HT crop under the aforementioned strategies can reveal interesting results in this biodiversity loss perspective.

ENDNOTES

I. There is an exponentially growing literature on the environmental risks and agricultural impacts of GM crops (e.g. Nelson *et al.*, 2001; Stewart, 2004; Murray, 2003). According to "proponents", GM crops are a natural extension of traditional crop breeding and they offer a solution to feed the growing world population by increasing agricultural efficiency (e.g. Nap *et al.*, 2003; Bennett *et al.*, 2004; Gianessi *et al.*, 2001), while "opponents" claim that GM crops possess unknown ecological risks, promote the further industrialization of agriculture, reduce biodiversity, favor monocultures and direct R&D according to commercial criteria rather than public benefit (e.g. Hansen, 2001; Shiva, 2001; Srivastiva, 1996; etc).

II. Weed scientists distinguish between herbicide resistance and tolerance. The former implies a trait that prevents the plant from experiencing the damaging effects of the herbicide, like a plant enzyme that detoxifies the herbicide (Baucom et al., 2004). The latter is the ability of a plant to compensate for the damaging effects of the herbicide. For the purposes of this study, this distinction is not consequential.

III. The alternative forms of a gene, which are called alleles, lead to alternative forms of a trait. For example, blue eyes or brown eyes are represented by different alleles of the eye color gene. Organisms have two alleles for each trait and this pair of alleles determines the genetic makeup, namely the *genotype* of the individual for that trait. An organism that has different alleles for a given trait is called *heterozygote*, while one having the same alleles is called a *homozygote.*

IV. For the weed-herbicide pair under concern, herbicide tolerance allele is dominant, meaning that heterozygote individuals are tolerant (Hall *et al.*, 2000).

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