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Contributed Paper prepared for presentation at the 89th Annual Conference of the Agricultural Economics Society, University of Warwick, England
13 - 15 April 2015

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Abstract

Transgenic crops that contain Cry genes from *Bacillus thuringiensis* (*Bt*) have been adopted by farmers over the last 17 years. *Bt*'s toxicity spectrum, unlike traditional broad spectrum chemical insecticide, is relatively narrow and selective, which may indirectly benefit secondary insects that may become important pests. The economic damage caused by the rise of secondary pests could offset some or all of the benefits associated with the use of *Bt* varieties. We develop a bioeconomic model to analyse the interactions between primary and secondary insect populations and the impact of different management options on insecticide use and economic impact over time. Results indicate that some of the benefits associated with the adoption of genetically engineered insect resistant crops may be eroded when taking into account ecological dynamics. It is suggested that secondary pests could easily become key insect pests requiring additional measures - such as insecticide applications, or stacked traits– to keep their populations under the economic threshold.

Keywords: Bacillus thuringiensis; *Bt* maize; population dynamics; Mediterranean corn borer; Sesamia nonagrioides; Mythimna Unipuncta; insecticide; optimization; secondary pests

Introduction

In 1996, the first generation of genetically engineered insect resistant (GEIR) crops expressing toxins (crystalline (Cry) proteins) from the soil bacterium *Bacillus thuringiensis* (*Bt*) were made commercially available. Since then they have been used worldwide for controlling insect pests of major crops such as maize and cotton (James 2013). So far the benefits of commercialized GEIR crops have exceeded expectations (Carrière *et al.* 2010). It is now broadly accepted that any eventual detrimental impact on non-target organisms (NTO) is lower for *Bt* crops than for conventional crops requiring broad-spectrum insecticides (Cattaneo *et al.* 2006). There is evidence from the use of a number of environmental impact indicators that GEIR crops have reduced (or at least have not increased) the impacts of agriculture on biodiversity through selective targeting and associated reductions in the use of broad-spectrum insecticides (Carpenter 2010; Areal & Riesgo 2015). Furthermore, the economic benefit of *Bt* crops associated with the regional suppression of specific pest populations appear to be significant (Gomez-Barbero *et al.* 2008; Carpenter 2010; Hutchison *et al.* 2010; Areal *et al.* 2013). The damage caused by stalk-boring feeding insects, such as the European corn borer (ECB) [*Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae)], is enough to cause a significant reduction in maize yields (Malvar *et al.* 1993; Bohn *et al.* 1999). Hutchison *et al.* (2010) estimated the cumulative benefits of controlling ECB with *Bt* maize over the last 14 years at $6.8 billion for maize growers in the US Midwest, with more than 60% of this total accruing to non-*Bt* maize growers. On the other hand, in Europe, in countries where *Bt* maize has still not been employed, yield losses without control may reach up to 30% in areas highly infested with stalk-borer feeding insects (Meissle *et al.* 2010). According to Park *et al.* (2011) this represents a loss to farmers of between 157 million and 334 million Euros each year.

Regardless of its wide adoption, the sustainability of *Bt* crops is still a controversial topic among the scientific community. Two concerns are usually raised: i) ecological shifts may take several years to manifest (Ho *et al.* 2009), hence, the long term ecological interactions around GEIR crops are important to understand(Snow *et al.* 2005) and ii) the impacts of *Bt* crops on NTOs in field conditions may not reflect the results obtained in laboratory studies (Andow *et al.* 2006; Lövei *et al.* 2009). In particular, researchers have predicted that NTOs could appear in such numbers that they may become key secondary insect pests[1] in *Bt* crop fields (Andow & Zwahlen 2006). Citing Harper (1991, p.22), “ignoring secondary pests can lead to devastating crop damage that may continue over a considerable period of time”. Such occurrence of secondary pests would require additional spraying with conventional broad-spectrum insecticides, which may erode (at least) some of the benefits of GEIR crop technology (Pemsl *et al.* 2011). (Harper 1991)

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[1] A secondary pest is a "non-targeted" pest that has historically posed a small or no economic threat, but which could be directly or indirectly affected by changes in insecticide use patterns, such as those caused by *Bt* cropping, associated with the management of a primary pest (FIFRA Scientific Advisory Panel 1998).

We develop a bioeconomic model to evaluate the impact of a number of pest management options on primary and secondary pest populations, as well as on insecticide use and related economic outcomes. We use a production function based on a system of two first order differential equations that represent the ecological interactions of the primary and secondary pests with the pest management practices. As far as we are aware such an approach has not yet been considered in the literature. The model takes into consideration the dynamics of two surrogate pest species, the Mediterranean corn borer (MCB) [*Sesamia nonagrioides* (Lefebvre) (Lepidoptera: Noctuidae)], a target pest, and the true armyworm (TAW), [*Mythimna (Pseudaletia) unipuncta* (Haworth) (Lepidoptera: Noctuidae)], a secondary pest. Their effects on the production function are used to predict pest control decisions. Optimal insecticide applications under deterministic conditions are calculated through a Differential Evolution dynamic nonlinear optimization technique[2] (Storn & Price 1997; Mullen *et al.* 2011). Furthermore, numerical simulations of various scenarios arising from different hypotheses are developed and analysed. In particular this focuses on farmers' net returns due to the changes in insecticide use and the development of secondary pests on *Bt* maize. We conclude by considering the management implications of the results as well as suggesting future research directions.

Secondary pest outbreaks in the context of GEIR crops

Bt toxins have a narrow efficacy spectrum aimed at controlling only the target pest. This offers a safe environment for the development of non-target pests (Sharma & Ortiz 2000; Lu *et al.* 2010), which may lead to crop damage (Sharma & Ortiz 2000; Wu & Guo 2005). Depending on the magnitude of the impact, the adoption of *Bt* crops might convey unexpected negative effects on agricultural ecosystem interactions and consequently on farm profits (Sharma & Ortiz 2000; Wolfenbarger & Phifer 2000).

In the context of GEIR crops, three main causes may trigger an outbreak of secondary pest species: i) a reduction in broad-spectrum insecticide applications (Wang *et al.* 2008; Lu *et al.* 2010; Naranjo 2011; Pemsl *et al.* 2011; Stone 2011); ii) a sufficient reduction in pests' natural enemies (Naranjo 2005b, a; Marvier *et al.* 2007); or iii) a decrease in inter-specific competition with the lowering of target pest numbers (Catangui & Berg 2006; Dorhout & Rice 2010; Virla *et al.* 2010). These causes are not necessarily independent.

It is postulated that whatever the cause of the rise in secondary pest numbers, insecticide spraying would be the only immediate solution at a farmers' disposal. The most notorious case concerns sap-feeding bugs on *Bt* cotton plants in China. Presently, in order to control these secondary pests, Chinese

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[2] Differential Evolution (DE) is a simple yet powerful global optimization method which belongs to the class of Evolutionary Algorithms (EA) (Storn & Price 1997; Price 1999) . This metaheuristic method attempts to find the optimum of the problem by iteratively refining the candidate solution with respect to the objective function (function to be optimized) value (Storn & Price 1997; Price *et al.* 2005) (Price et al., 2005; Storn and Price, 1997). Due to its convergence speed, accuracy, and robustness it is often preferred to other optimization methods (e.g. genetic algorithm and evolutionary programming) in order to solve real-world problems over continuous domains (Vesterstrom & Thomsen 2004).

Bt cotton farmers are applying about 20 sprayings per season (for more details see Lu *et al.* 2010; Pemsl *et al.* 2011). Such application rates are similar to those before *Bt* cotton adoption when insecticides were used mainly to control cotton bollworm (Wu & Guo 2005). Insecticide spraying on *Bt* crops may convey ecological disturbances with knock-on consequences, such as the destruction of the primary and/or secondary pest's natural enemies' complex. Hence, if non-susceptible secondary pest populations exceed economic thresholds, the sustainability of *Bt* technology may be put in jeopardy. The model developed in the following section, demonstrates the interaction and economic impact of such an event.

Methods

Study context

Although several other events are under evaluation by the European Food Safety Authority (EFSA) , the only *Bt* maize currently allowed for cultivation in Europe contains the transformation event MON810 (Monsanto Company), expressing Cry1Ab *Bt* toxin (EFSA 2010). This transgenic maize presents a high level of resistance to its primary pests – the two main maize borers present in the EU, the MCB and the ECB (González-Núñez *et al.* 2000). From the total of 441,000 hectares of maize cropped in Spain in 2013 (MAGRAMA 2013), about 1/3 was devoted to *Bt* maize. This makes Spain the largest European adopter, growing 94% of the total *Bt* maize hectarage in the EU (James 2013). *Ex post* economic analysis on the performance of *Bt* maize shows that Spanish adopters have obtained higher yields, higher gross margins and better quality of harvested product, along with a significant decrease in insecticide applications compared with conventional farmers (Gomez-Barbero *et al.* 2008; Riesgo *et al.* 2012). In this region two other Lepidoptera, the TAW, and the corn earworm, *Helicoverpa armigera* (Hübner), are considered to be important secondary pests causing occasional but severe damage to maize (Eizaguirre *et al.* 2010; Pérez-Hedo *et al.* 2012). While under normal conditions the MCB tends to outcompete the TAW (Eizaguirre *et al.* (2009), it has been suggested that the increase of transgenic maize could affect the population dynamics of these secondary Lepidopteran pests due to the high efficiency of *Bt* maize against its target pests (López *et al.* 2000; López *et al.* 2008; Eizaguirre *et al.* 2010). This would arise if TAW takes advantage of the absence of the major corn borers (Eizaguirre *et al.* 2010). These species are representative of the problem of secondary pests explored in this paper, as both species compete for the same food resource – maize – and the MCB, although biologically stronger than the TAW, is efficiently controlled by *Bt* maize.

Mediterranean corn borer

The MCB, is here used as an example of a primary pest due to its historical importance and present susceptibility – 99% – to the Cry1Ab toxin (González-Núñez *et al.* 2000; Farinós *et al.* 2011). The MCB, is a cosmopolitan multivoltine species with a wide range of host plants, including maize (Kfir *et* *al.* 2002; Eizaguirre & Fantinou 2012). It is considered to be the most important maize production pest in Spain and in other countries around the Mediterranean basin (Cordero *et al.* 1998; Malvar *et al.* 2002). Since maize production areas have increased in these areas during the past the pest has consequently expanded (Eizaguirre & Fantinou 2012). Larvae cause damage by tunnelling into stems or the ear until pupation, weakening the plants and consequently reducing yield (Malvar *et al.* 1993). Economic losses accrued to MCB in Spain have not been fully quantified, since the injury is undistinguishable from that caused by ECB (Eizaguirre & Fantinou 2012). It has been reported that the damage caused by MCB can reach up to 30% of the maize yield depending on the date of sowing and on the plant development stage when attacked (Butrón *et al.* 1999; Malvar *et al.* 2004; Velasco *et al.* 2004; Butrón *et al.* 2009).

The effect of photoperiod and temperature on MCB diapause induction and development has been extensively studied (e.g. Eizaguirre *et al.* 1994; Fantinou *et al.* 1995). In Spain usually this species achieves two complete generations and one incomplete generation per year (Eizaguirre *et al.* 2002; Eizaguirre *et al.* 2008). According to Gillyboeuf *et al.* (1994) only about 5 to 25% of the overwintering larvae survive to pupate in spring, with the minimum threshold temperature for the pest being around 10ºC (Eizaguirre *et al.* 2008), thus limiting its dispersal capacity.

In conventional maize cropping MCB control through the use of insecticides is only moderately effective since larval development occurs mainly inside the stalk (Albajes *et al.* 2002). Depending on application timing, Clark *et al.* (2000) report an efficacy of between 67 and 80%. Natural enemies – generalist ground dwelling predators such as ground beetles, spiders, *T. busseolae* (Hymenoptera: Scelionidae), and parasitoides of *S. nonagriodes* – play an important role in the control of this pest (Alexandri & Tsitsipis 1990; Eizaguirre & Pons 2003; Farinós *et al.* 2008). Due to the cryptic nature of the larvae (i.e. they live in the stalks), the window of opportunity for any sort of predation is quite narrow (Monetti *et al.* 2003). Predation pressure comes from egg parasitoides which may be responsible for up to 65% egg mortality depending on natural environmental conditions (Alexandri & Tsitsipis 1990; Figueiredo & Araujo 1996; Monetti *et al.* 2003).

True Armyworm

The TAW is an important cosmopolitan secondary pest of the Noctuidae family in Europe and North America (Bues *et al.* 1986; McNeil 1987). It is an invasive species that was first noticed in Europe in the 19th century (Bues *et al.* 1986). The TAW feeds on the leaves of several non-agricultural and cultivated gramineous plants, including maize (Guppy 1961). Sporadic outbreaks, with large numbers of larvae marching across the landscape, can have devastating economic impacts (McNeil 1987). In Europe, it is more prevalent in the Mediterranean basin due to the larvae's low ability to survive prolonged temperatures below freezing (Bues *et al.* 1987). In Spanish climatic conditions this species typically completes 4 generations (López *et al.* 2000). Despite conducive climatic conditions and their high capacity for mobility, the inconsistency of TAW prevalence is related to a combination of two other factors. Firstly, the existence of natural enemies, and secondly, the implementation of tillage practices and regular weed control (Willson & Eisley 1992; Clark *et al.* 1994). Contrary to MCB, this species is highly susceptible to natural enemies, Menalled *et al.* (1999) note an 80% mortality on field experiments. It is not uncommon to observe parasitism and other sorts of predation at rates capable of maintaining the population at endemic levels (Guppy 1967; Kaya 1985; Laub & Luna 1992).

Although the devastating effects of armyworm larvae have been commonly documented, the impact on maize yields specifically is not clear due to the erratic nature of outbreaks (Douglas *et al.* 1981; Hill & Atkins 1982; Buntin 1986). Musick (1973) reported that six larvae were enough to destroy one plant, while Harrison *et al.* (1980) noted that an infestation level of one larva per plant was sufficient to cause a significant yield impact.

Several studies have evaluated the efficacy of different *Bt* maize transgenic lines against the TAW, reporting substantial plant damage on the varieties assessed (e.g. Pilcher *et al.* 1997; Schaafsma *et al.* 2007; Eizaguirre *et al.* 2010; González-Cabrera *et al.* 2013; Pérez-Hedo *et al.* 2013). Eizaguirre *et al.* (2010) found no difference in the number of TAW larvae per plant between *Bt* and isogenic varieties in the majority of field trials. Pérez-Hedo *et al.* (2013) noted that larvae complete their development, presenting similar growth rates, regardless of whether they are fed on a *Bt* or non-*Bt* diet. In laboratory experiments González-Cabrera *et al.* (2013) found TAW survival rates of approximately 80% when fed on a diet of *Bt* maize Cry1Ab. It is therefore possible that the increasing use of transgenic maize expressing Cry1Ab toxin might amplify TAW's economic importance (Eizaguirre *et al.* 2010). In the following section we explore the population dynamics of TAW and MCB and their impact on a profit maximizing farmer's Net Present Value (NPV).

Bioeconomic model

Following Lichtenberg and Zilberman (1986)[3], we designed a bioeconomic model where pest interactions are incorporated into a production function. The damage-abating role of insecticides is taken into account explicitly in the production function through an asymmetric treatment of "productive" inputs (x) and "damage-abating" pesticides (z): $y = F(x, D(z))$. $D(z)$ is the so called damage-abatement function, representing the role of insecticides in the model, which do not have the potential to increase the output but indirectly mitigate yield loss through pest elimination. The effect of pest impact on the output is based on the Lotka-Volterra model which defines the population dynamics of two species competing for the same resource. Although the Lichtenberg and Zilberman (1986) damage control approach is not free from criticism (Lansink & Carpentier 2001; Zhengfei *et al.* 2006), it has been successfully used in other bioeconomic models of GMOs(Huang *et al.* 2002; Pemsl *et al.* 2008; Qaim 2009) and to model the management of invasive alien species (Ceddia *et al.* 2009).

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[3] For a detailed review on the Lichtenberg and Zilberman (1986) damage control approach see Sexton *et al.* (2007).

The initial model assumptions are as follows. The agricultural product is attacked by two rather different pests: the MCB – primary pest (N_1) – is a highly competitive pest that is also highly susceptible to *Bt* toxin; and the TAW – secondary pest (N_2) – is negatively affected by the first species, but has a higher tolerance to the *Bt* toxin. Both have the same negative impact upon the yield. The dynamic behaviour of both species, with and without pest control, is analysed below. It is assumed that the farmer has only two means to suppress pests, by adopting *Bt* varieties and spraying insecticides when pests densities exceed an economic threshold (ET[4]).

i. Actual output

Let *G(Z)* denote the aggregate potential maize output over a landscape, which includes both conventional maize (G_c) and GEIR maize (G_{Bt}), where *Z* represents a vector of non-insecticide inputs (i.e., labour, seeds, fertilizers etc.). The damage control framework models the actual output, *Y*, as a function of potential output, *G(Z)*, damage, $D(N_1,N_2)$, and proportion of the total landscape planted with *Bt* maize (*Ω*). The actual output is given by:

$$Y = G(Z)[1 - D\,(N_1, N_2)] \tag{1}$$

With:

$$G(Z) = (1 - \Omega)G_c(Z) + \Omega G_{bt}(Z)$$

$$G' > 0, G'' < 0$$

Damage is a function of the density of both pest populations – N_1 and N_2 – and expresses the fraction of yield lost (I) due to the sum of damage caused. It is assumed that both pests can act simultaneously and the nature of the damage is species independent:

$$D = D_{N_1} + D_{N_2} \tag{2}$$

With:

$$D_{N_1} = \frac{IN_1}{Plant\ density} \tag{2a}$$

$$D_{N_2} = \frac{IN_2}{Plant\ density} \tag{2b}$$

ii. Economic Threshold

The ET is a practical operational rule difficult to access theoretically, hence we have set the ET at a fixed level – 25% – below the Economic Injury Level (EIL), as suggested by Pedigo *et al.* (1986).

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[4] Economic threshold is defined as the "density at which control measures should be determined to prevent an increasing pest population from reaching the economic injury level". The economic injury level was defined by these authors as the "lowest population that will cause economic damage" " (Stern *et al.* 1959).

Following the same author, the EIL is composed of five primary variables: w, the cost of management per unit (€/ha); p, the product market value per ton (€/ton); I, damage caused per insect (%); D_y, yield lost per larvae (tons/ha); and s, the proportion of larvae killed (%).

$$ET = \frac{EIL}{4} \tag{3}$$

With:

$$EIL = \frac{w}{pID_y s} \tag{3a}$$

iii. Population dynamics

The pest populations grow according to a classical logistic growth equation where population dynamics without control are influenced by: the growth rate, r_i, the species' intrinsic carrying capacity, k_i; intra-competition, b_{ii}; inter-competition, b_{ij}; and by mortality attributed to natural enemies, m_i ($i=1,2;\ i\neq j$).

$$\begin{cases} \dfrac{dN_1}{dt} = r_1 N_1 \left(1 - b_{11}\dfrac{N_1}{k_1} - b_{12}\dfrac{N_2}{k_1} - m_1\right) \\ \dfrac{dN_2}{dt} = r_2 N_2 \left(1 - b_{22}\dfrac{N_2}{k_2} - b_{21}\dfrac{N_1}{k_2} - m_2\right) \end{cases} \tag{4}$$

Within this basic framework, two forms of pest control are introduced: the adoption of *Bt* seeds (Ω) and the application of broad-spectrum insecticides (x). The parameter q_i ($i=1,2$) indicates the effectiveness of *Bt* in controlling each pest population. The pest dynamics become:

$$\begin{cases} \dfrac{dN_1}{dt} = r_1 N_1 (1 - b_{11}\dfrac{N_1}{k_1} - b_{12}\dfrac{N_2}{k_1} - \phi u(x) m_1 - q_1 \Omega - \phi h(x)) \\ \dfrac{dN_2}{dt} = r_2 N_2 (1 - b_{22}\dfrac{N_2}{k_2} - b_{21}\dfrac{N_1}{k_2} - \phi u(x) m_2 - q_2 \Omega - \phi h(x)) \end{cases} \tag{5}$$

Farmers' adoption of *Bt* technology is assumed to be exogenous and develops according to the following logistic function:

$$\Omega = \frac{\lambda_f \lambda_i e^{r_\Omega t}}{\lambda_f + \lambda_i (e^{r_\Omega t} - 1)} \tag{6}$$

The insecticide's effectiveness is specified by $h(x)$ which is a function of the number of insecticide applications (x), and by ϕ, a dummy variable, assuming the value of one if $N_1 \geq ET_{N_1}$ or $N_2 \geq \mathrm{ET}_{N_2}$, and zero otherwise. Both pests are equally affected by the insecticide. It is important to note the insertion of the new component into the natural enemies' variability parameters $\phi u(x)$ which reflects the negative impact of insecticide applications on natural enemies (eq. 8).

Following Shoemaker (1973) and Bor (1995), mortality rate is an exponential function of insecticide dosage because high insect mortality requires a large dosage of insecticide. Consequently, the following kill efficiency function is written as:

$$h(x) = (1 - e^{-x(t)s_p}) \tag{7}$$

$$x(t) = \ a + bt + ct^2 + dt^3 \tag{7a}$$

$$u(x) = (1 - e^{-x(t)s_{ne}}) \tag{8}$$

h(x) is assumed to be monotonically increasing in *x(t)s*, which represents the application of insecticide at time t, and satisfies $h\,(0) = \ 0, \ \ \lim\limits_{X \to \infty} h(x) \leq 0$. We assume the farmer applies insecticides as a preventative measure (Sexton *et al.* 2007). Under this approach the farmer makes a long-term educated guess about the possibility of pests occurring according to their known biological dynamics. The parameters a, b, c and d in this expression are estimated though the maximisation of the farmer's net present value as specified below. Insecticide applications assume a cubic form in order to provide a higher degree of freedom when carrying out the optimization process.

iv. Net present value

An agricultural landscape (whose area is normalized to 1 ha) populated by a profit maximizing farmer is used to explore the economic implications of different pest management decisions. The problem is formulated in terms of the maximization of NPV after 25 years of aggregate landscape profits, subject to the pest management problem over a time interval *[0, T]*. This is accomplished by choosing the appropriate amount of insecticide to apply throughout the cropping season according to the economic threshold given the above pest dynamic scenario. The farmer determines his optimal insecticide application at the beginning of the planning horizon by choosing the values of parameters *a*, *b*, *c* and *d* in expression (*7a*) so as to maximize his NPV over the given time horizon. To make the problem more treatable, it is also assumed that all other inputs (*Z*) in the equation below are applied in fixed proportions.

Letting *p* denote output price, u_c and u_{Bt} the prices of conventional and GEIR maize inputs unrelated to damage control, *w* the price of a unit of insecticide *(x)*, then the problem is:

$$\max_{\{a,b,c,d\}} \int_0^T e^{-\delta t} \ \{pg(Z)[1 \ - \ D(h(N_1, N_2, q, X))] \ - Z[(1 - \Omega)u_c + \Omega u_{bt}] \\ - \phi w x\} \, dt \tag{9}$$

s.t.

$$\frac{dN_1}{dt} = r_1 N_1 (1 - b_{11}\frac{N_1}{K_1} - b_{12}\frac{N_2}{K_1} - (1 - \phi) m_1 - \Omega q_1 - \phi h(x)))$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - b_{22}\frac{N_2}{K_2} - b_{21}\frac{N_1}{K_2} - (1 - \phi) m_2 - \Omega q_2 - \phi h(x)))$$

With

$$\phi = \begin{cases} 1, \ N_1 \geq \ ET_{N_1} \\ 1, \ N_2 \geq \ ET_{N_2} \\ 0, \ otherwise \end{cases}$$

The model therefore computes aggregate maize output as the potential yield minus the fraction of the crop that is lost due to the damage caused by both pest species. The model excludes external social and environmental costs of insecticide use for both society and the farmer. Two different scenarios are analysed – before and after Bt maize adoption. Each scenario includes the two cases: a) the use of insecticides and b) the non-use of insecticides..

Model parameterization

Population growth rates for the pests were derived from laboratory data given in peer-reviewed scientific publications (see appendix 1 and 2). The laboratory conditions in these experiments represent the typical temperature and photoperiod conditions of the Mediterranean basin area.

In Spanish conditions, researchers have found not more than five larvae of MCB and TAW larvae per plant (Velasco *et al.* 2004; Velasco *et al.* 2007; López *et al.* 2008; Eizaguirre *et al.* 2010). Hence it was assumed this value as the maximum larvae number, for each species, per maize plant. Consequently the carrying capacity (k1 and k2) is equal to the maximum possible density of larvae within the cropped field, assuming a plant density of 90,000 per ha (AGPME 2012). Due to the large available habitat we incorporate the intraspecific competition parameter within the carrying capacity, b_{ii}=1. Considering a maximum carrying capacity of five larvae per plant and a maximum damage of 30 % (as indicated above), we assume that each MCB and TAW larvae is able to reduce yields by 6% per plant. It has been suggested that the due behavioural characteristics, MCB may influence negatively the TAW, however until now this effect has not been quantified (López et al. 2003; Eizaguirre et al. 2009). We study the case in which MCB has a strong negative effect on TAW (b_{21}=0.9), while the reciprocal effect is relatively small (b_{12}=0.1).

The parameters m_1 and m_2 take into account the impact of natural enemies on MCB and TAW populations respectively and the random effect of variable external factors that can affect predatory activity, such as temperature, humidity or agricultural practises (Kaya & Tanada 1969). Since we have little information about these we assume that m_1 and m_2 follow random uniform distributions with m_1 varying between 0.1 and 0.65 and m_2 between 0.1 and 0.9. The difference between the ranges of m_1 and

m_2 is explained by the cryptic nature of the MCB larvae which reduces its vulnerability to predation (see section 0 and 0 for further details). Small values of m_i, reflect a bad year for the occurrence, abundance and subsequent predatory activity of natural enemies; high values of m_i reflect high levels of pressure by natural enemies and efficiency in capturing the pest. The parameter q_i ($i=1,2$) which indicates the effectiveness of *Bt* in controlling each pest population takes values q_1=0.99 and q_2=0.2. These values indicate the different pest susceptibility to the *Bt* toxin. It is assumed that N_1 is highly susceptible and that N_2 is weakly susceptible to *Bt* technology, q_1>>q_2. It is hypothesized that full adoption of the *Bt* varietiy happens within 10 years ($r_\Omega = 0.8$). Initial adoption for our model is 10% ($\lambda_i = 0.1$) and the maximum adoption is 80% ($\lambda_f = 0.8$) reflecting the minimum 20% refuge commonly advised. When adoption reaches a plateau it means that 100% of the agricultural land is under a GM crop scheme.

In this study, although potentially very important, we did not take into consideration any eventual impact of *Bt* toxin on the natural enemies of our case study pests. Nonetheless, it should be noted that at least for Cry1Ab, no significant impacts have been reported especially when compared with insecticides (Naranjo 2005a; Cornell 2010). It is assumed that the farmer applies insecticides with optimal timing, obtaining an 80% (s_{ne}) control efficiency per application (Hyde *et al.* 1999; Folcher *et al.* 2009). We assume that insecticides have a 100% efficiency on the natural enemies' complex$\left(s_p = 1\right)$ since it has been reported that the effect of insecticides on natural enemies is greater than the effect on pests. (because of the former's carnivorous feeding habits versus herbivory by crop pests) (Longley & Jepson 1996; Van Emden 2014). It is also assumed that insecticide applications change over time according to expression (*7a*).

The parameters for the economic and ecological components of the model are presented in table 1 and table 2 respectively. The time horizon considered in the analysis extends over 25 years after the initial (hypothetical) adoption of *Bt* varieties (so T=25). The model is numerically solved with R software (R-Core-Team 2012) with support from the packages "deSolve" and "RcppDE" (Soetaert *et al.* 2010; Eddelbuettel 2015; Soetaert *et al.* 2015). After calibration, the numerical results appear consistent with data reported in recent studies (e.g. Gomez-Barbero *et al.* 2008; Meissle *et al.* 2010; Areal *et al.* 2013). The model sensitivity analysis is presented in the following section.

Sensitivity analysis

To assess the influence and importance of the biological parameters {r_1, r_2, m_1, m_2, b_{12}, b_{21} , b_{11}, b_{22}} on the model results, we conducted a global sensitivity analysis (GSA) using the Morris (1991) method[5] (Saltelli *et al.* 2000b). The Morris method has been used in several dynamic agroecosystem modelling projects (e.g. Confalonieri *et al.* 2010; DeJonge *et al.* 2012; Ben Touhami *et al.* 2013). The use of this method of sensitivity analysis aids the selection of which parameters have greater influence

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[5] The GSA was conducted in R software using the 'sensitivity package' (Pujol *et al.* 2015).

on the model final output variability. The parameter's uncertainty distribution values are shown in table 3.

The Morris analysis has been used in several dynamic agroecosystem modelling projects (e.g. Confalonieri *et al.* 2010; DeJonge *et al.* 2012; Ben Touhami *et al.* 2013). The generated results give two measures of sensitivity, firstly the final output mean variation (μ^*) in relation to the computed values (horizontal axis), and secondly the correspondent effect standard deviation (σ) (vertical axis). Parameters with higher μ^* will have a stronger influence on the final output, while parameters with a high σ implies dependency through nonlinear responses and/or interactions with other parameters (Saltelli *et al.* 2000a; Saltelli *et al.* 2004). The sensitivity analysis using the Morris method showed that interspecific competition between primary and secondary pest (b_{12}) is the most influential parameter (Figure 1). Other four other parameters: natural enemies on secondary pest {m_2}, primary and secondary pest intraspecific competition {b_{11} , b_{22}}, and the effect of the primary pest on secondary pest {b_{21}} are as well noticeably influential, while the remaining parameters have a sensitivity which is about threefold lower (Figure 1).

Results and Discussion

The NPV maximization over 25 years (eq. 9) was solved numerically using the follow postulated pest management options scenarios. In our first assessed scenario (section 0) we modelled the pest dynamics and NPV after 25 years, with and without insecticide control, assuming that the farmer did not have access to *Bt* maize seeds. In the second scenario (section 0), a new control technology – *Bt* maize expressing Cry1Ab toxin – becomes available. The adoption rate is not linear (eq.6). It is assumed that at time T=0, 10% of the area is covered with *Bt* maize, reaching an 80% plateau after approximately 11 years. We assume that the farmer may lack a full understanding of the capacity and limitations of *Bt* technology. Hence we tested two different cases: the first assumes that the farmer will rely on GM technology completely and all insecticide applications are stopped; the second assumes the farmer utilizes both of the pest control means at his/her disposal, with the *Bt* seeds adopted at the projected rate and insecticide applications used whenever pest numbers exceed the ET. We also compared the results obtained with a conjectural case where both pests are highly susceptible to *Bt* toxin. In section 4.3, we explore two additional scenarios: a) a +/- 25% variation of seven parameters shown to influence pest dynamics {$r_1, r_2, b_{12}, b_{21}, q_1, q_2, \lambda_i$}; and b) due to the importance of natural enemies, we assesed five additional cases of different natural enemies' densities (representing different levels of ecosystem disruption) with the assumption that the farmer uses a selective insecticide harmless to these enemies. In both additional scenarios, we compared the resulting NPV after 25 years and the number of insecticide applications with the results obtained in the optimal pest management control strategy (when insecticides are used along with *Bt* maize).

Scenario 1: Prior to *Bt* maize adoption

Figures 2a and 2b show the dynamics of a conventional system with and without pest control. In both cases the MCB is the major pest causing damage. Without pest control (figure 2a) the TAW density passes unnoticed for most of the period due to strong competition from the MCB and pressure from natural enemies. This leads to high crop damage and a low NPV after 25 years, and is therefore not desirable to the farmer (table 4). Figure 2a Pest dynamics prior to *Bt* adoption with no control b shows the results under a conventional maize cropping system with the farmer applying insecticides. In this case, over 25 years, an average of 2.55 insecticide application per ha are made (s.d.= 0.28), obtaining a total NPV of 8296 €/ha (table 4).

The small variability in the amount of insecticide used occurs because the farmer is not able (and not economically willing) to completely eradicate the pest, but seeks to keep it under the ET. Having the latter goal in mind, the farmer only reacts when a pest reaches the ET. Because the MCB's proliferation capacity is high its density will always rebound above the ET obliging the farmer to keep constant attention on the fields. Assuming that resistance factors are constant, pest populations will then oscillate in line with population numbers in previous years. Accordingly, it is expected that this insecticide application pattern continues. In this scenario the farmer may have no "knowledge" of the economic impact of TAW since it is always kept under the ET by either the effect of insecticide or MCB competition pressure.

Scenario 2: *Bt* maize adoption

This scenario is illustrated in figure 3. In the first case, farmer relies solely in the efficiency of Bt maize putting aside insecticides. After an initial rise in both pest densities, the TAW population is slightly supressed by the MCB. However due to the increasing presence of *Bt* toxin, after the MCB population peaks, its density steadily declines. The ET is reached around the 5th year of adoption and with 73% of the maize area planted with *Bt* varieties. This translates into a decrease in the MCB's competition capacity and with a corresponding ascension in TAW numbers. In this case the TAW population has stablish as the main pest being always be above the ET, causing serious damage to the crop. The oscillation in TAW numbers is due to the variable pressure of environmental factors and natural enemies affecting it. After 25 years, MCB population is marginal and its complete eradication is never achieved. However, a quick recovery of the population will occur in the case that Bt seeds stop being used. In this case, where *Bt* maize is used but without insecticides, the farmer obtains an NPV of just 7051 €/ha after 25 years, which is about 85% of what was achieved when relying solely on insecticides (table 4). This scenario is slightly unrealistic as it fails to take into consideration the insecticide applications of non-adopting farmers. Nonetheless it clearly demonstrates the problem of relying on a single pest control technique and illustrates what happens when a farmer is not aware of the secondary pest problem.

More realistically, farmers can be expected to utilise both of the pest control means at their disposal (figure 3b), with the *Bt* seeds adopted at the projected rate (as in equation 6) and insecticide applications used whenever pest numbers exceed the ET. In this case, due to the rapid insecticide action, both pests decrease rapidly in the first year. Competition pressure is evident during the second year. MCB temporarily plateaus until 33% of maize area planted with *Bt* variety (2nd year). At this point due to both control measures pressure, the MCB density steadily falls below the ET until it is entirely eradicate after approximately 14 years. Due to the pressure upon TAW from insecticides and MCB competition, its populations declines until MCB plateaus. After which steadily increase its density up to the ET, where it stabilizes. It is the MCB decline, hence the lack of competition that causes a plateauing of TAW at the ET. Here, the farmer continues to apply insecticides but now in order to control TAW.

The insecticide application frequency falls to an average of 1.22 applications per ha (s.d.= 0.53) ( ). This amount represents a reduction of about 50% in the number of insecticide applications compared to conventional maize use. This noteworthy decline is accrued to the use of *Bt* and its efficiency in controlling MCB, and additionally its provision of a safer environment for the natural enemies of TAW. In the section 4.3 the impact magnitude of natural enemies is discussed. The reduction in insecticide applications found here is sufficient to compensate the farmer for the extra cost of *Bt* seeds (roughly 10% more expensive than conventional seeds). After 25 years the farmer would realize an NPV of 9508 €/ha (table 4), which is higher than what is realized with both conventional seeds and using only *Bt* maize (table 5).

For comparison, in a case of Bt maize with stacked genes conferring a perfect control to both pests, insecticide applications steadily decrease until the farmer stops applying insecticides altogether after the 3rd year of adoption (at which point 45% of the total maize cropping area is planted with stacked *Bt* maize). The farmer achieves the goal of entirely eradicating both pests and, logically, realises a higher NPV of 10693 €/ha after 25 years (figure 4). Realistically however, this situation is unlikely for two reasons: firstly agriculture is not a closed system, migration into crop fields by either known or unknown pests must be taken into consideration; secondly, as happened in our assessment, a species whose population is significantly subdued so as to in effect be 'concealed' by the present insecticide or by the effect of a strong competitor, could unexpectedly appear.

Further scenarios

In this section we explore two further scenarios in which the five key parameters implicated in pest dynamics are varied – growth rate (*ri*), interspecific competition (*bij*), susceptibility to *Bt* toxin (*qi*), initial *Bt* adoption (λ_i) and natural enemy mortality (m_i). The full results are presented in table 4 and 5. When decreasing the parameters {*bij*; *qi*; λ_i} by 25%, we expect the NPV to decrease and insecticide applications to increase. Similarly, when increasing these parameters by 25%, we expect the NPV to increase and insecticide applications to decrease. It was also expected that *ri* would respond in the opposite direction to its counterparts. From the 16 results obtained, 14 had expected outcomes. The two unexpected outcomes have relatively small deviation values (see values marked with * in table 6); although the mean insecticide applications varied as expected, the NPV varied in the opposite direction. This unexpected outcomes are believed to represent an active response from the farmer to lower/higher pest density in the initial cropping period, initiating insecticides applications accordingly.

Due to the high importance of natural enemies, we have assessed the individual impact of this parameter in model uncertainty. We explore five scenarios representing various levels of disturbance in the ecosystem, assuming that the farmer uses a selective insecticide which does not causes harm to natural enemies (Table 7). In the first, the impact of natural enemies' on pest dynamics varies randomly as in the baseline cases in sections 0 and 0; in the second, there are no natural enemies present; and in the third, fourth and fifth, the impact of natural enemies is low, medium and high respectively. All results are as expected, the higher the natural enemies' impact the lower the need for insecticide applications, yielding a higher NPV. It is interesting to note that the previous optimal outcome in terms of NPV (deriving from the use of *Bt* maize with a broad-spectrum insecticide) lies between a scenario in which natural enemies are absent, and one where the impact of natural enemies on pest populations is low. This results suggests that boosting the population of natural enemies through selective use of insecticides, rather than broad-spectrum insecticides, has a knock on positive impact on NPV. Assuming the utopia around the last scenario, we would like to point out the scenario where m_i=0.8, reflecting a substantial constant presence of natural enemies. Here, the farmer would ultimately cease the insecticide applications, while increasing the NPV after 25 years by 11%.

These results indicate that pest populations are highly sensitive to natural means of control, and that pest populations could be managed with a relatively small increase in natural enemy numbers. In addition, as we have demonstrated with the case where both pests are equally and highly susceptible to the *Bt* toxin, increasing secondary pest susceptibility to the toxin would be a major factor in increasing the NPV and decreasing insecticide applications.

Conclusion

We use a bioeconomic model to analyse different pest control approaches – *Bt* technology and insecticides – on secondary pest outbreaks, a problem that has been largely ignored until now, and subsequent effects on farm profits. Optimized insecticide applications under deterministic conditions were achieved through a dynamic nonlinear optimization technique. The model developed in this study is capable of effectively evaluating the impact of GEIR crops on two pest species that compete for the same resource. As shown in section 0, the model enables the incorporation of different scenarios, such as insecticide restrictions, new transgenic traits and other means of pest control.

Results from the sensitivity analysis showed that when holding prices, costs and other input parameters constant, the results suggest that, the parameters related with the secondary pest are more influential on the final output than those related with primary pest. The uncertainty in the results arises from two main areas: a) it is unlikely that available data and model parameters are error-free; and b) no simulation model is an entirely true reflection of the physical process being modelled. Results show the need to be conscious of the possibility of an outbreak from a secondary pest and the consequences of such an event upon yields and farm profits. We found that it may take several years for secondary pests to proliferate to relevant levels of importance, thus the need to understand pest dynamics (Ho *et al.* 2009). We defined a model where the outbreak of a secondary pest in *Bt* fields is not a random event. It can arise as a natural result of the use of *Bt* technology, and may be predicted with access to accurate data. The model shows that insecticide applications and the presence of natural enemies, contribute most to achieving a higher NPV. The presence of natural enemies is intrinsically related to environmental conditions, and agricultural procedures, which in turn will certainly influence the number of insecticide applications needed each year. This is an important insight to take into consideration, given future climate shifts that are expected. Hence, alongside the deployment of GEIR crops, it is therefore highly advisable to also promote agricultural practices that could enhance the presence of natural enemies. When farmers effectively comply with certain procedures, such as having a refuge strategy and using extra selective insecticide applications (Meissle *et al.* 2011), the economic, environmental and social benefits can be substantial (Wesseler *et al.* 2007; Skevas *et al.* 2010).

Our work corroborates the hypothesis that secondary pests might emerge due to a significant reduction in insecticides applications (Lu *et al.* 2010; Pemsl *et al.* 2011; Catarino *et al.* 2015). We have shown that a) a secondary pest can become the key insect pest in unsprayed *Bt* maize compared with sprayed *Bt* fields, due to the high specificity of Cry1Ab toxin; and b) the damage to crops from secondary pests can increase with the expansion of *Bt* technology if no additional measures – such as insecticide applications – are taken. One of the claimed benefits of *Bt* crops is that they decrease the use of insecticides, in turn diminishing contamination of food and the environment, as well as increasing farm profits. Indeed the use of Bt maize has a has a knock on positive impact on NPV, as well as in the environment by decreasing the need for insecticides. Furthermore, the farmer would accomplished the goal of entirely eradicate the MCB after 14 years. Nonetheless, insecticides applications would not cease due to the outbreak of TAW, the secondary pest.

Models of pest dynamics are a valuable tool, especially within a world affected by strong environmental and agricultural shifts. For example, forecasted global warming and increases in GEIR cropping could enable insect pests to spread into new habitats (Maiorano *et al.* 2014). We have shown that a profounder knowledge of how agro-ecological systems work is needed to evaluate the full benefits of *Bt* crops. If new agricultural technologies aim to be used as a viable IPM solution, understanding insect dynamics is vital, requiring an integration of ecosystem services into management decisions.For that, further research should be accurately estimated, either in field trials or in the laboratory, the nature of intra and interspecific pest competition.

Acknowledgements

This modelling forms part of the ‘Assessing and Monitoring the Impacts of Genetically Modified Plants on Agro-ecosystems’ (AMIGA) project. The AMIGA project was funded by the European Commission under Framework Programme 7.

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Figures

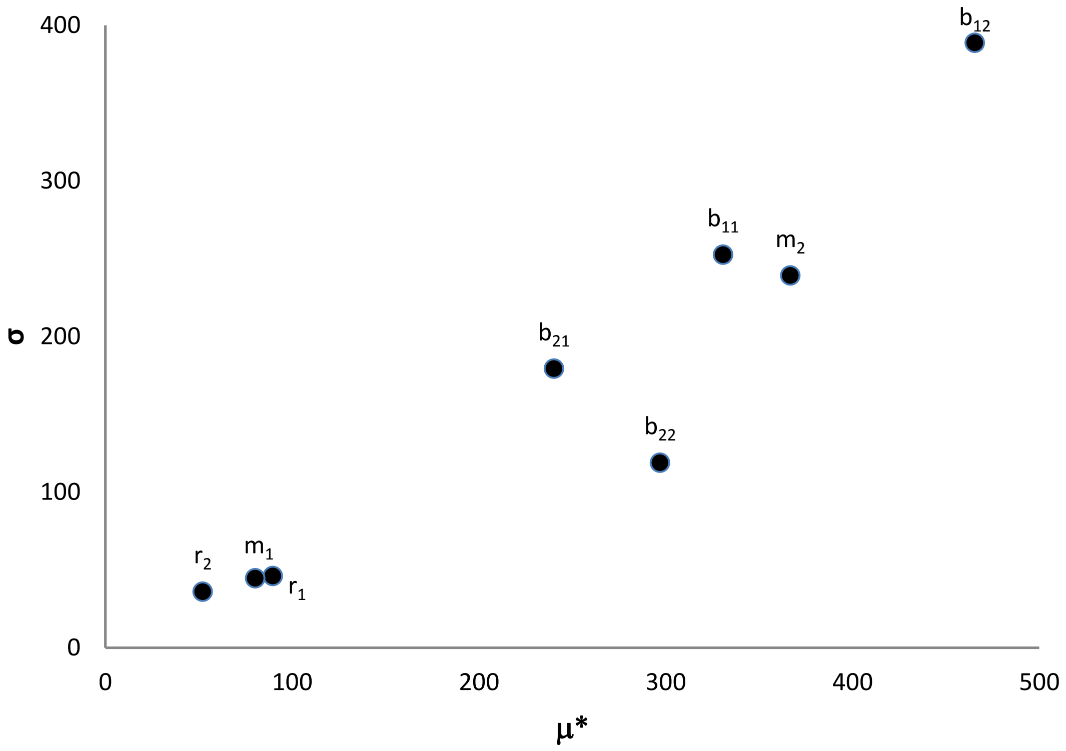


Figure 1 - Results of the Morris method (across 30 trajectories, 16 levels and 8 grid jumps) on mean (μ*) and standard deviation (σ) associated with the NPV after 25 years. Parameters were automatically scaled before computing the elementary effects so that all factors would vary within the range [0,1]. It was implicitly assumed here that the uncertain model parameters were uniformly distributed. For each parameter, the tested range before scaling is shown in table 3.

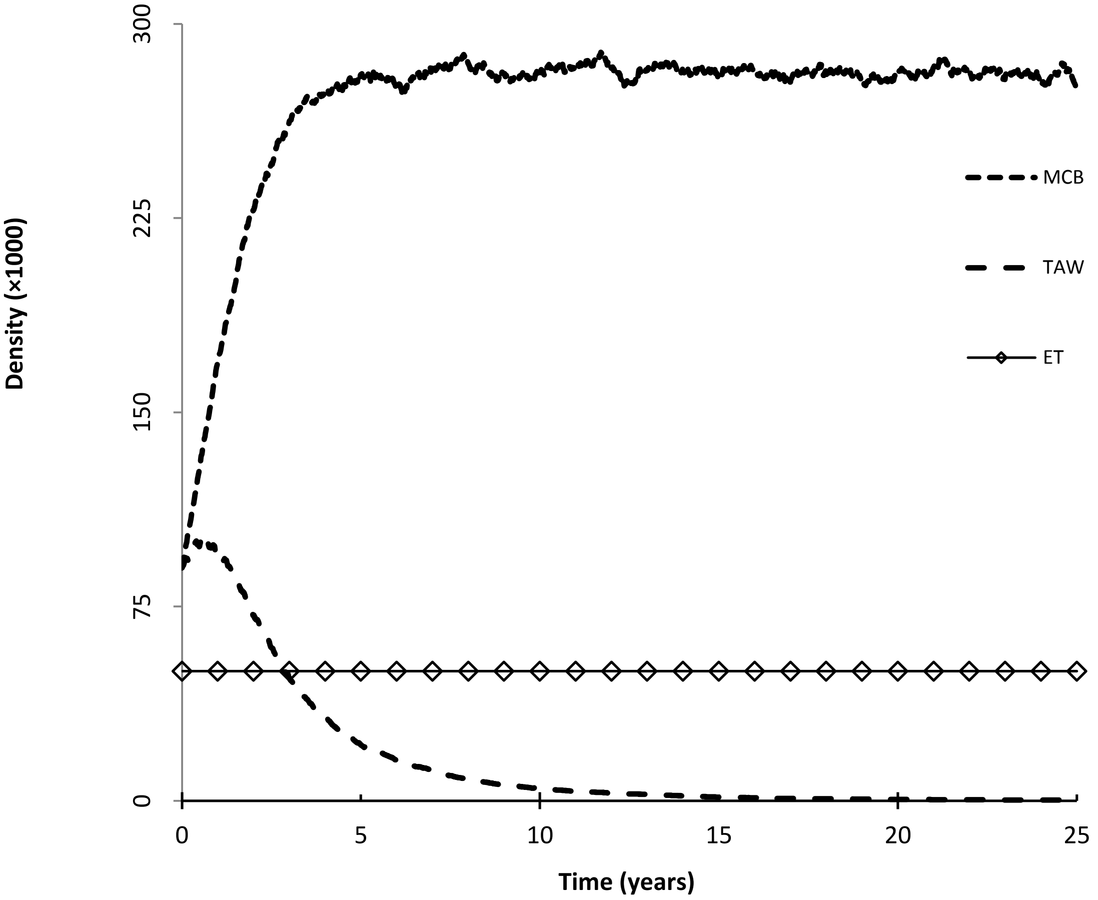


Figure 2a Pest dynamics prior to *Bt* adoption with no control

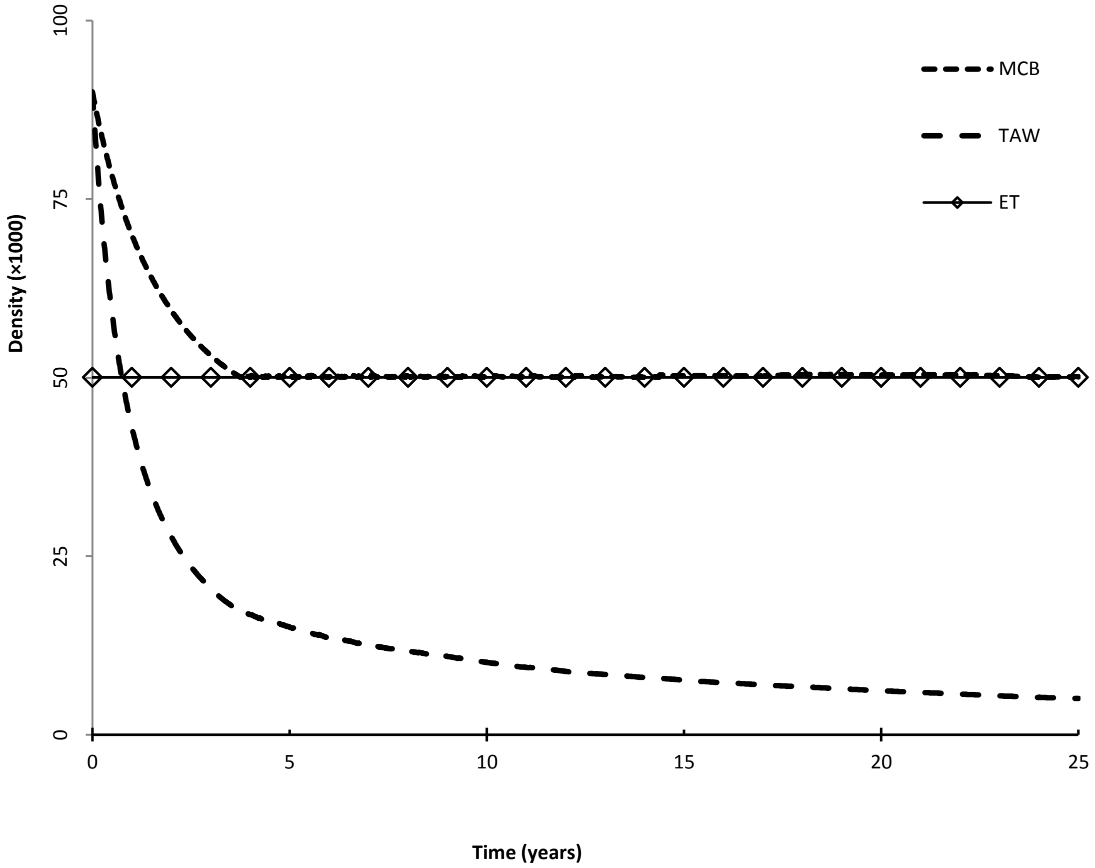


Figure 2b Pest dynamics prior to *Bt* adoption with insecticide control

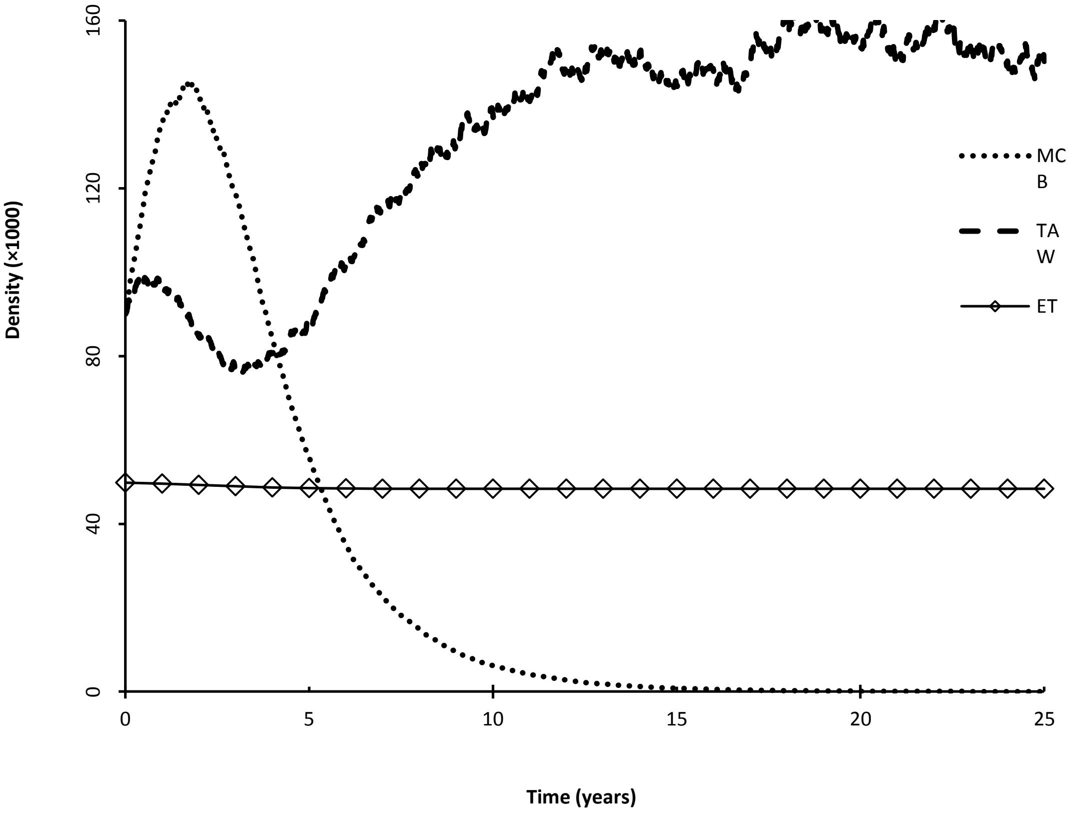


Figure 3a Pest dynamics after *Bt* adoption, with *Bt* control only

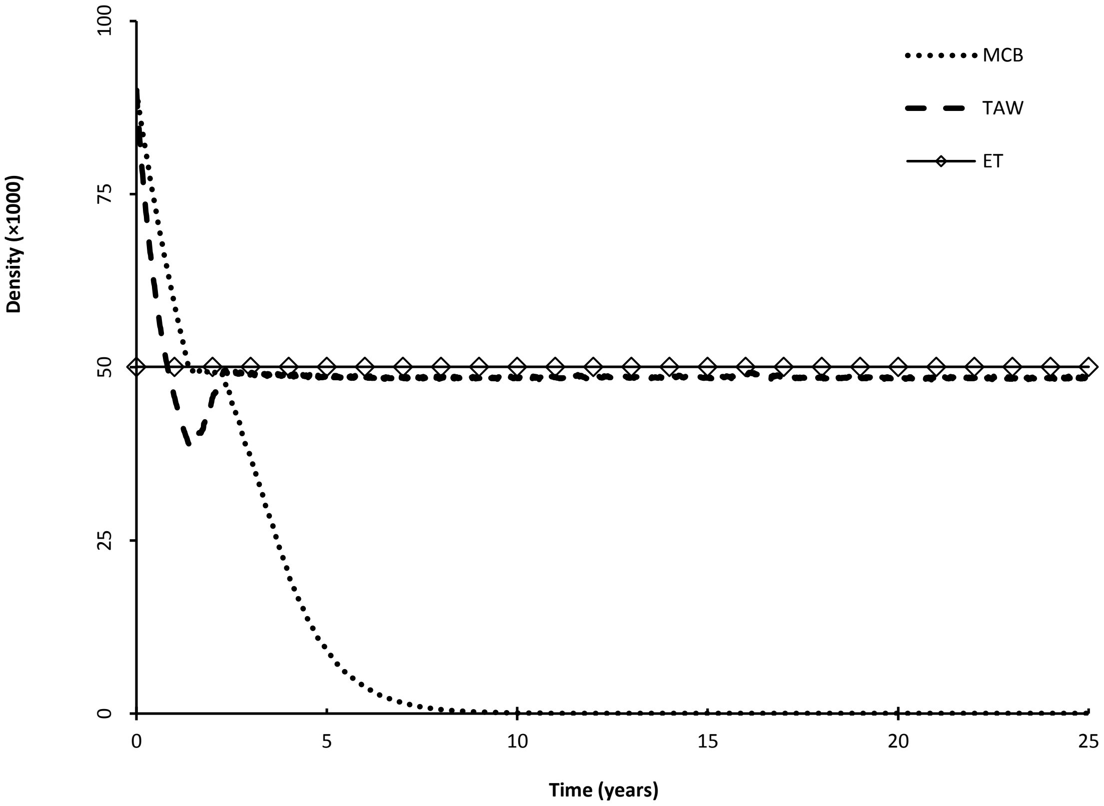


Figure 3b Pest dynamics after *Bt* adoption, with *Bt* and insecticide control

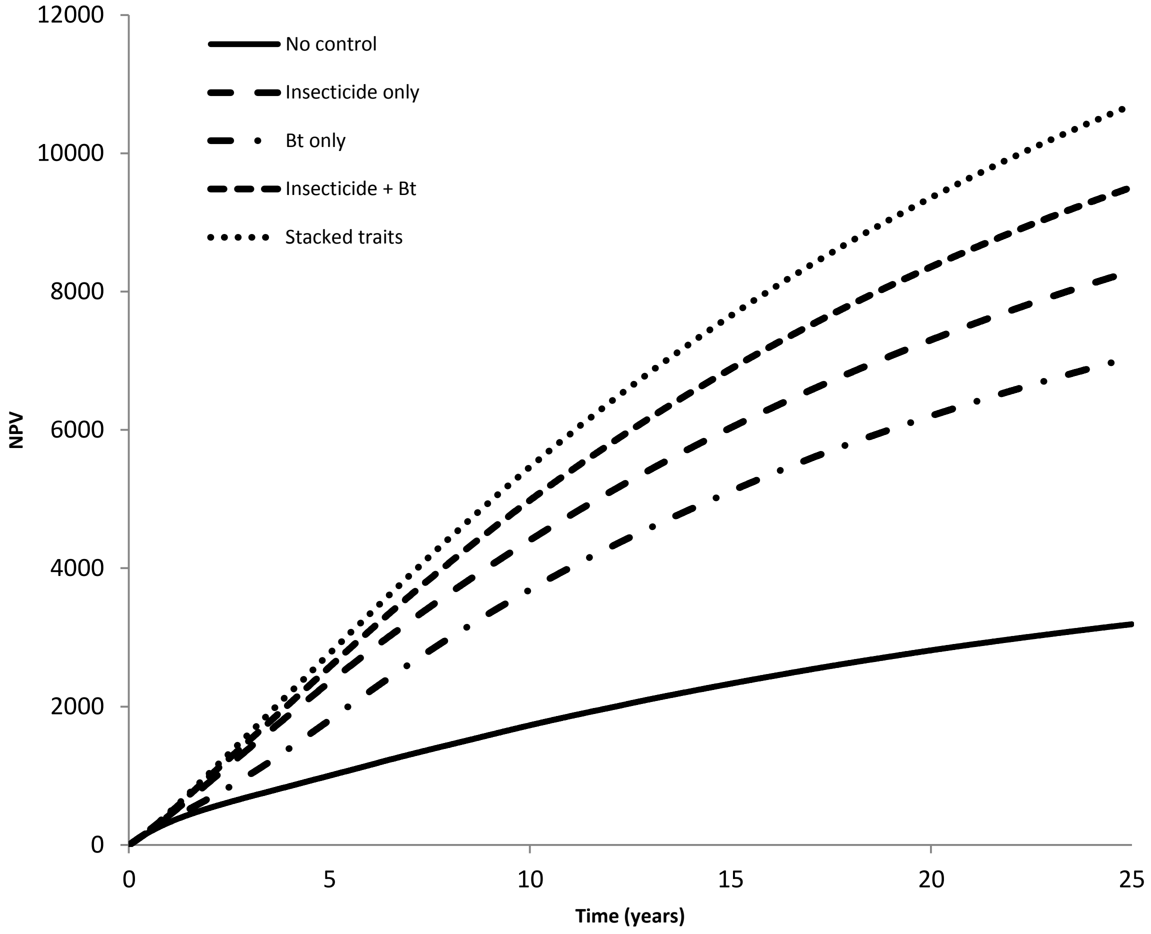


Figure 4 Optimized NPV after 25 years for the different scenarios

Tables

Table 1 - Economic parameters

Parameters	Value
Plant density per hectare	90000[a]
Potential conventional maize yield (Y_c)	11.30 T/ha [b]
Potential *Bt* maize yield (Y_{Bt})	11.80 T/ha [b]
Price maize (p)	248.70 €/T [a]
Conventional seed price (S_c)	253.80 €/ha
Bt seed price (S_{Bt})	284.40 €/ha [a]
Fixed costs (u_c)	1797.88 €/ha [a]
Fixed costs (u_{Bt})	1815.88 €/ha [a]
Insecticide cost per application (w)	18 €/ha/app[a]
Discount rate (δ)	0.05 [d]
Initial adoption (λ_i)	0.10[d]
Full adoption (λ_f)	0.80 [d]

[a] (AGPME 2012)

[b](Gomez-Barbero *et al.* 2008)

[c] (MAGRAMA 2014)

[d] assumption

[e] (Maund 2002)

Table 2 - Biological parameters for MCB and TAW

Parameters	N_1 (MCB)	N_2 (TAW)
Growth rate (r_i)	2.02 [a]	3.13 [a]
Intraspecific competition (b_{ii})	1[b]	1 [b]
Interspecific competition (b_{ij})	0.10[b]	0.90[b]
Environmental impact (m_i)	0.50[b]	0.50[b]
Susceptibility to *Bt* toxin (q_i)	0.99[c]	0.20[d]
Susceptibility to insecticide (s)	0.80[e]	0.80[e]
Minimum natural enemies impact	0.1[b]	0.1[b]
Maximum natural enemies impact	0.65[b,f]	0.90[b,g]
Maximum larvae per plant	5[h]	5[h]
Initial population	9×10^4 [b]	9×10^4 [b]
Damage per larvae (I)	0.06[b]	0.06[b]

[a] appendix 1

[b] assumption

[c] (Hellmich *et al.* 2008)

[d] (González-Cabrera *et al.* 2013)

[e] (Hyde *et al.* 1999; Folcher *et al.* 2009)

[f] (Alexandri & Tsitsipis 1990; Figueiredo & Araujo 1996; Monetti *et al.* 2003)

[g] (Guppy 1967; Kaya 1985; Laub & Luna 1992; Menalled *et al.* 1999; Costamagna *et al.* 2004)

[h] (Butrón *et al.* 1999; Malvar *et al.* 2004; Velasco *et al.* 2004; Butrón *et al.* 2009)

Table 3 – Uncertainty distribution of parameter values used in the global sensitivity analysis

Parameter	Nominal Value	Uncertainty interval
r_1	2.02	1.01-3.03
r_2	3.13	1.57-4.70
b_{11}	1	0.5-1
b_{22}	1	0.5-1
b_{12}	0.1	0.05-0.15
b_{21}	0.9	0.45-1
m_1	0.1-0.65	0.05-0.75
m_2	0.1-0.9	0.1-0.99

Table 4 - NPV, insecticides applications and damage results accrued from the 4 different scenarios

Scenario	NPV (€/ha)	Insecticide applications				Damage	
		Min	Max	Mean	s.d.	Mean	s.d
No pest control	3191					19.1%	1.04%
Only insecticide[1]	8296	0.00	3.21	2.55	0.28	4.34%	1.23%
Only *Bt*	7051					10.59%	1.63%
Bt + insecticides[2]	9508	0.00	2.54	1.22	0.53	3.85%	1.41%

[1] with: a=3.205892e+00;b= -1.144386e-01;c= 5.064257e-03;d= -6.839178e-05

[2] with: a= 2.543207e+00;b= -2.220972e-01;c= 9.175168e-03;d= -7.497778e-05

Table 5 - NPV difference between different control strategies

	Only *Bt*	Only insecticide
Bt + insecticides	2458 € (+34.9%)	1212€ (+14.6%)

Table 6: Results accrued from the ±25 % variation in four parameters implicated in pest dynamics {ri; bij; qi; λ_i}

Parameters	NPV (€)	Insecticide applications (mean)
	Deviation (-25%)	
Growth rate (ri)[1]	-64.60*	-0.04
Interspecific competition (bij)[2]	-4.88	0.02
Bt susceptibility (qi)[3]	-118.45	0.17
Initial *Bt* adoption (λ_i)[4]	-54.25	0.03
	Deviation (+25%)	
Growth rate (ri)[5]	40.56*	0.05
Interspecific competition (bij)[6]	3.21	-0.04
Bt susceptibility (qi)[7]	26.40	-0.26
Initial *Bt* adoption (λ_i)[8]	40.36	-0.04

[1] with: a= 2.273808e+00; b= -1.944295e-01;c= 8.639238e-03;d= -8.730315e-05

[2] with: a=2.402405e+00;b= -2.033086e-01;c= 8.747742e-03;d= -8.912616e-05

[3] with: a= 2.422293e+00;b= -1.509471e-01;c= 5.066767e-03;d= -2.297077e-05

[4] with: a= 2.441820e+00;b= -2.013704e-01;c= 7.462853e-03;d= -3.902218e-05

[5] with: a=2.281515e+00;b= -1.902639e-01;c= 8.164678e-03;d= -8.016763e-05

[6] with: a= 2.3480676261;b= -0.2179550048;c= 0.0097919141;d= -0.0000858817

[7] with: a= 2.546021e+00;b= -2.645330e-01;c= 1.103379e-02;d= -9.624222e-05

[8] with: a=2.228979e+00;b= -1.739191e-01;c= 6.393760e-03;d= -1.513402e-05

*not expected

Table 7 - Results accrued from the natural enemies impact when selective insecticide is used

Scenario	Parameters values			Deviation	
	NPV(€)	Insecticide applications		NPV(€)	Insecticide applications
		Mean	sd		Mean
NE base variation[2]	9477	0.37	0.23	254	-0.85
No NEs (m_i=0)[2]	9360	1.84	0.23	-148	0.62
Low NEs density (m_i=0.2)[3]	9591	1.17	0.27	289	-0.83
Medium NEs density (m_i=0.5)[4]	9797	0.39	0.31	289	-0.83
High NEs density (m_i=0.8)[5]	10556	0.03	0.26	1047	-1.19

[1] with: a= 1.986923e+00;b= -2.666653e-01;c= 1.192148e-02;d= -7.217041e-05

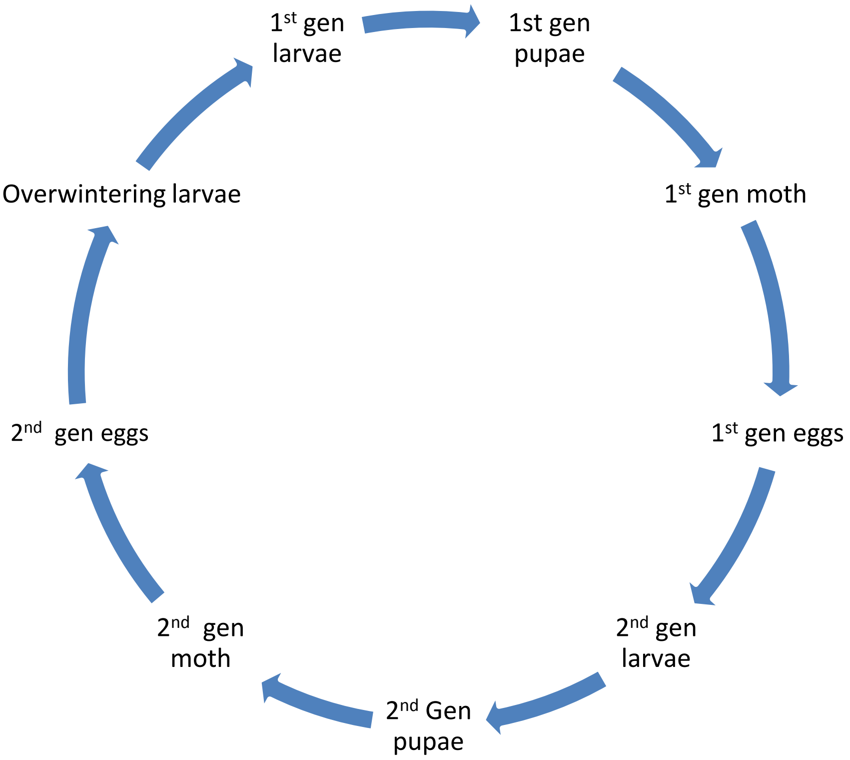
[2] with: a=2.575190e+00;b= -1.508283e-01;c= 7.395081e-03;d= -9.961102e-05

[3] with: a= 1.994130e+00;b= -1.641846e-01;c= 7.787084e-03;d= -9.856487e-05

[4] with: a=1.768619e+00;b= -2.138725e-01;c= 9.347525e-03;d= -9.887529e-05

[5] with: a=2.398247e+00;b= -6.528079e-01;c= 3.350325e-02;d= 8.987545e-05

Appendix 1- MCB Growth rate scheme



Coefficients	Values	References
Larvae winter mortality	0.9	(Gillyboeuf *et al.* 1994)
1st generation		
Larvae survival (L1)	0.74	(Fantinou *et al.* 1996)
Pupae survival (P1)	0.8135	(Fantinou *et al.* 2003)
Oviposition per moth (O1)	550	(Fantinou *et al.* 2004)
Eggs hatch (E1)	0.6	(Gillyboeuf *et al.* 1994)
2nd generation		
Larvae survival (L2)	0.74	(Fantinou *et al.* 1996)
Pupae survival (P2)	0.88	(Fantinou *et al.* 2003)
Oviposition per moth (O2)	375	(Fantinou *et al.* 2004)
Eggs hatch (E2)	0.4	(Gillyboeuf *et al.* 1994)

$$Annual\ growth\ rate = Log\left(\frac{TAW_{2,4}}{TAW_{1,4}}\right) = 2.024284$$

MCB Annual growth rate:

Initial population (IL_0): 9×10^4 larvae

Year 1:

$$MCB_{1,1} = IL_0 \times L_1 \times P_1 \times O_1 \times E_1$$

$$MCB_{1,2} = MCB_{1,1} \times L_2 \times P_2 \times O_2 \times E_2$$

$$MCB_{1,3} = MCB_{1,2} \times L_3 \times P_3 \times O_3 \times E_3$$

$$MCB_{1,4} = MCB_{1,3} \times L_4 \times P_4 \times O_4 \times E_4 \times W$$

Year 2:

$$MCB_{2,1} = MCB_{1,4} \times L_1 \times P_1 \times O_1 \times E_1$$

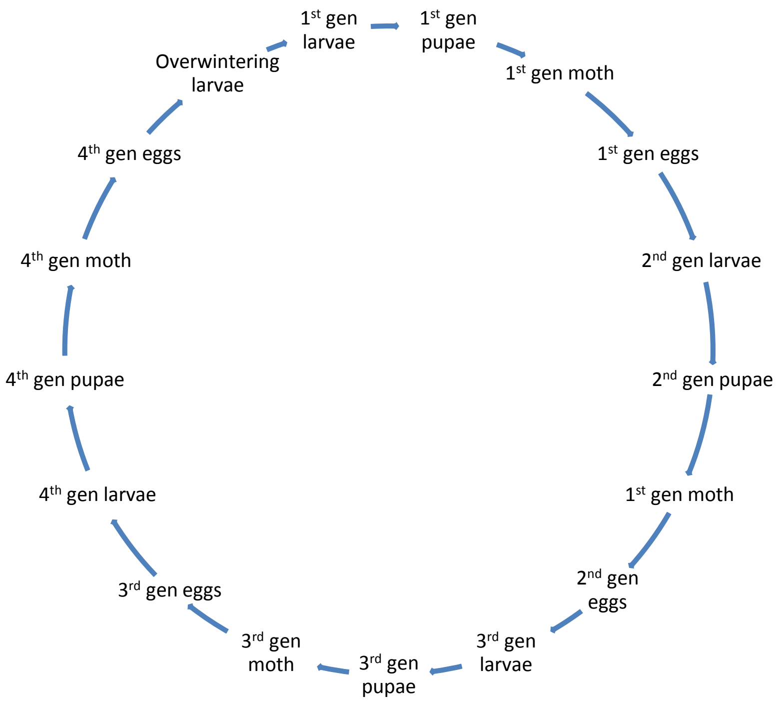
$$MCB_{2,2} = MCB_{2,1} \times L_2 \times P_2 \times O_2 \times E_2$$

$$MCB_{2,3} = MCB_{2,2} \times L_3 \times P_3 \times O_3 \times E_3$$

$$MCB_{2,4} = MCB_{2,3} \times L_4 \times P_4 \times O_4 \times E_4 \times W$$

$$Annual\ growth\ rate = Log\left(\frac{MCB_{2,4}}{MCB_{1,4}}\right) = 3.163268$$

Appendix 2 – TAW Growth rate scheme



Coefficients	Values	References
Larvae winter mortality (W)	0.9	(Naibo 1984)
1st generation		
Larvae survival (L1)	0.66	(McDonald 1990)
Pupae survival (P1)	0.93	(McDonald 1990)
Oviposition per moth (O1)	1302	(Smith 1986)
Eggs hatch (E1)	0.563	(Smith 1986)
2nd generation		
Larvae survival (L2)	0.31	(McDonald 1990)
Pupae survival (P2)	0.7	(McDonald 1990)
Oviposition per moth (O2)	1393	(Smith 1986)
Eggs hatch (E2)	0.953	(Smith 1986)
3rd generation		
Larvae survival (L3)	0.93	(McDonald 1990)
Pupae survival (P3)	0.78	(McDonald 1990)

Oviposition per moth (O3)	1470	(Smith 1986)
Eggs hatch (E3)	0.967	(Smith 1986)
4th generation		
Larvae survival (L4)	0.53	(McDonald 1990)
Pupae survival (P4)	0.89	(McDonald 1990)
Oviposition per moth (O4)	1656	(Smith 1986)
Eggs hatch (E4)	0.892	(Smith 1986)

TAW Annual growth rate:

Initial population (IL_0): 9×10^4 larvae

Year 1:

$$\begin{aligned} TAW_{1,1} &= IL_0 \times L_1 \times P_1 \times O_1 \times E_1 \\ TAW_{1,2} &= TAW_{1,1} \times L_2 \times P_2 \times O_2 \times E_2 \\ TAW_{1,3} &= TAW_{1,2} \times L_3 \times P_3 \times O_3 \times E_3 \\ TAW_{1,4} &= TAW_{1,3} \times L_4 \times P_4 \times O_4 \times E_4 \times W \end{aligned}$$

Year 2:

$$\begin{aligned} TAW_{2,1} &= TAW_{1,4} \times L_1 \times P_1 \times O_1 \times E_1 \\ TAW_{2,2} &= TAW_{2,1} \times L_2 \times P_2 \times O_2 \times E_2 \\ TAW_{2,3} &= TAW_{2,2} \times L_3 \times P_3 \times O_3 \times E_3 \\ TAW_{2,4} &= TAW_{2,3} \times L_4 \times P_4 \times O_4 \times E_4 \times W \end{aligned}$$

$$Annual\ growth\ rate = Log\left(\frac{TAW_{2,4}}{TAW_{1,4}}\right) = 3.163268$$