Abstract:

Agriculture may be viewed as a gamble, wherein human society moves increasingly towards a bifurcated biological world: one part specialised in a small number of varieties attuned to high productivity and the other specialised in the maintenance of diversity. This is a gamble in that the widespread existence of genetic diversity has been one part of the mechanism that allowed stability to persist in ongoing relationships within predator-prey systems. The maintenance of stability within these relationships within the agricultural sector will require the steady importation of a flow of resistance from the diversity sector. This indicates the importance of land use considerations in questions of genetic resource management.

In this paper we examine these questions through the analysis of the optimal programme for the management of land use and genetic resources given a bifurcated biological world. We apply some recent techniques developed in the literature on genetic games, so-called “matching allele”-models. These demonstrate that continued investment in the highly productive agricultural sector must be accompanied by a similar investment in the continued flow of genetic information into this sector. We demonstrate that some of the risks created through agriculture can only be insured within the sector, and cannot be provided by a substitute method such as a gene bank system. This requires the dedication of tracts of lands to serve as biodiversity reserves for close and distant relatives of current modern cultivars. At the same time, we show that this investment in reserve lands has not and will not result from decentralized decision-making in agriculture. A number of instruments are available to social planners, however, in order to implement the socially desirable outcomes by changing economic parameters within the farmer’s environment.
1. Introduction

Agriculture as a human endeavor is an interesting gamble from the long term perspective. Assuming that the evolved biosphere was a relatively stable system, the replacement of natural selection by human methods of observation, selection and transportation has created a very different sort of biosphere with very different dynamics. Now there is a very large sector of the biological world that is concentrated in a very small set of species (even varieties). Of course, the reason for the creation of this new sort of biosphere is apparent – it produces more of the sorts of outputs that human societies demand at the least possible cost. At the same time the movement away from the original “steady state” of the evolved biosphere must also have its attendant costs. The stability of the original system must have been based in part upon the breadth of the portfolio of genetic resources of which it was constituted. Displacing this diversity-based system with a uniformity-based one constitutes a fundamental change in the nature of the biosphere. How much can we alter the evolved state of the world without the costs of these alterations overwhelming the benefits of the new system? What sorts of intervention are available to control these costs? The object of this paper is to investigate this trade-off between continued agricultural development and its attendant instabilities, together with the investigation of the forms of intervention best suited to its optimal control.

These are very large questions that might be approached in a variety of ways. We have chosen to base our approach on a framework that has been developed within the recent literature on evolutionary ecology – the analysis of “Red Queen” races in co-evolutionary games and specifically the subset of “matching allele” models that are used within this literature. Ecologists have long regarded Red Queen races as a succinct and useful description of the dynamic interaction between crops and their pests. The basic idea behind this concept is that it situates co-evolving species within a permanent and continuing interchange based on a contest of innovation - each specie changing in non-deterministic ways in order to counter moves on the part of the other – in order for the species to remain in a steady state of ecological fitness (Rosenzweig 1996, Schaffer and Rosenzweig 1978, van Valen 1977). We have used this framework elsewhere to understand the economic significance of ecological processes in agriculture (Goeschl and Swanson 1998). In this paper we will employ Red Queen models of the “allele matching” variety that places this contest of innovation within the context of a matching game.

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2 That is, sets of co-evolved species that maintained relative stability in terms of photosynthetic production.
wherein the prey specie must provide one or more traits that correctly match those previously displayed by the predator in order to remain within the race – these matching alleles are then said to confer “resistance” upon the prey specie against the predator’s existing characteristics (Frank 1997).

The value of this framework is that it allows us to think about the management of genetic resources for agriculture in one very specific way, as the management of an exhaustible resource: the set of traits that had previously co-evolved in the context of a long term predator-prey relationship. Over hundreds and thousands of millennia the set of traits that would have previously been selected and incorporated within a plant variety would be of substantial size, and natural selection would have allowed many different varieties of the same plant specie to co-exist at a given point in time. It would have been this aggregate amount of genetic diversity that would have ensured that “matches” continued to exist at each point in time, and hence that stability prevailed within the system (Scheffer 1997). When human selection began to displace natural selection over a certain portion of the land surface, the benefit to society resulted from the conversion of lands to these selected varieties and the preferred produce they would generate. The implicit cost of this substitution lay in the amount of active management that farmers were required to undertake in order to keep the system in balance. In short, human management of the genetic resource base for agriculture became a substitute method for providing systemic stability, once the natural system for providing stability was displaced (by human determination of land use).  

Therefore, our analysis concerns the optimal program for the management of the genetic resource base that existed at the dawn of the green revolution, some fifty years ago.  

In our analysis, we will assume that the physical genetic resource stock (i.e. the actual availability of seeds) is not in a process of erosion.  

We will also assume that the relevant time-scale renders diversity-increasing mutation irrelevant.  

The reason for these arguable assumptions is that our sole concern shall be the

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3 “Strong epidemics, as far as is known, have always followed some identifiable human activity. Epidemics are largely man-induced” (Zadoks and Schein 1979).

4 The analysis requires a historical reference point for this stock of traits which could be set at a number of points: Before the start of agriculture and the concomitant domestication of crop plants roughly 10,000 years ago (Evans 1993), or before some of the agricultural revolutions which took place in various locations around the globe up to the early 18th century (Holden et al. 1993). The global genetic resource stock which we will treat as the relevant one is that which existed around the point in time for which many crop ecologists agree that the agricultural system was in co-evolutionary balance for the last time, specifically some decades before the onset of the Green Revolution (Scheffer 1997, Barrett 1981, Harlan 1976). This is the relevant endowment of crop and pathogen diversity for the current decision maker because up to this point the evolutionary speed of the agricultural system was sufficiently slow for crop domestication and cultivation to keep pace with pathogens and co-evolution under human intervention to take place (Scheffer 1997, Fry 1982). Any genetic resources lost since then represent sunk costs irrelevant to the determination of the optimal program.

5 This assumption is debatable since the methods used for conservation of the genetic resource base are imperfect. See Brown, Orians, Kunin and Swierzbinski (1988).

6 This is also debatable because a) the relevant time scale for agriculture might be indefinite since discounting might make little sense in a context where the survival of human society is implied; and b) the technological frontier for genetic resource adaptations is rapidly shifting (see Sianesi and Ulph, 1998).
management of the previously evolved set of traits and the “matches” contained therein, once land use is taken into consideration as a choice variable. We examine this question initially from the perspective of two social planners acting jointly: One omniscient with control over the use of the entire surface of the earth concerned with agricultural yield, and the other concerned with the optimal management of genetic resources for society. Then we examine the same question in a more realistic scenario, where land use is determined in a decentralized fashion by a large number of individual “farmers” and government intervention manages for the genetic resource problem. We compare and contrast the socially optimal land use conditions with those that will result from decentralized choice. This demonstrates the nature of the externalities that exist when individuals make choices without consideration of their systemic impacts. Given that decentralized choice in land use will be the general rule, we then examine the policy options for intervention to correct for these externalities. This allows for the consideration of the range of policies being considered for application today, ranging from ex situ (gene bank) storage to the creation of a set of in situ (farming reserve-based) management regimes.

In sum, a steady state between predator and prey species may be conceived of as a matching game, where traits of resistance are the matches that allow the prey to continue in existence. The existence of large scale genetic resource diversity might then be attributable to the need to have a large number of traits in play at any point in time in order to guarantee a “match” and maintain the stability of the system. Agriculture is a gamble in that it represents a move away from the evolved approach to systemic stability, and the increasing substitution of human ingenuity and carefully tuned management for reserve diversity. This paper examines the costs and risks involved in this approach to the bio-sphere, and the optimal policies that should be pursued regarding the management of this genetic resource endowment.

In section two of this paper we introduce the notions of ecological games that we rely upon in the remainder of the work. The basic structures of allele matching models are discussed, their implications for agriculture developed, and the determinants for producing allele matches in agriculture explained. In sections three and four we develop these ideas further in a dynamic model of agricultural production incorporating land use and “allele matches” from the point of view of social interest in agriculture and society’s interest in efficient management of genetic resources. In section three we model the optimal decisions of an ideal social planner in agriculture with respect to land use, use of resistance genes in crops and the import of new resistance conferring allele. This section concerns the use values associated with genetic resources, in particular their productive and epidemiological functions. In section four we show how an optimal genetic resource manager would provide for the demand for resistance genes generated by agriculture through a combination of gene banks and “land reserves” for genetic agriculture. This section deals with the informational values of genetic resource diversity and how this value depends on the use of land for its production. In section five we construct the optimal trade-off between the agricultural and the informational values in terms
of land use and determine the optimal flow of genetic information between the reserves and the intensive sector. In section six we compare the implied optimality conditions for stocks of reserves and flows of matches to those which result from decentralized decision-making, e.g. when land use is chosen initially by a large set of individual farmers. This defines the set of externalities that emanate from decentralized agricultural management regimes that fail to consider their systemic impacts. Section seven concludes with a discussion of the policy implications for optimal interventions based on the existing management regime.

2. Genetic games

Since the seminal work of Felsenstein (1971) and van Valen (1977) on the Red Queen\(^7\), ecologists have tried to establish the conditions under which species may be locked into a continuous evolutionary struggle (Schaffer and Rosenzweig 1978, Roughgarden et al. 1983, Stenseth and Smith 1984, Hofbauer and Sigmund 1988). A typical context for these races is the sort of host-pathogen relationship that exists between crops and their pests.

Recently, evolutionary ecologists have provided the conceptual frameworks for these forms of co-evolutionary relationships which go by the name of “matching allele”-models (Hamilton 1980, Hamilton et al. 1990, Hamilton 1993, Frank 1994, Frank 1996). These models deliver an explanation for the sorts of dynamics that take place in the genetic structures of co-evolving species over time. They have previously been used for modeling host-pathogen relationships in crop epidemiology (Frank 1997).\(^8\)

The purpose of studying matching allele models in our context is that they help us understand better the functional role of genetic diversity in agriculture and to attach use values to different scales of diversity. It is one way in which to think of the sort of resource that genetic diversity constitutes in the context of agriculture.

2.1 Matching allele models

The origins of matching allele models lie within the work of Hamilton (1980, 1990). The basic idea is that both pathogen and host possess an ordered string containing discrete elements of genetic information, and that these strings “match up” in a competitive fashion. This genetic information could be thought of as a “word” with a given number of positions, called \textit{loci}, at which we find

\(^7\) Named after the Red Queen in \textit{Alice in Wonderland}, who said that it was necessary to keep moving just to stand still.

\(^8\) Other applications include the simulation of the differential effects of epidemics on genetically different populations of individuals over time in economics (Epstein and Axtell 1996).
“letters”. The actual letters used to assemble these strings are called alleles. The length of this string, i.e. the number of positions, differs from specie to specie: Crop plants have about 10,000 loci, some of which have identical alleles for all members of the specie, and some of which contain a variety of different alleles at that locus. The proportion of loci with several possible alleles can vary anywhere between 0.17 to 0.86 (Hancock 1992). An average of two to three possible alleles per locus is the norm in crop species. This represents an abundant source of genetic variation.

Figure 1: Genetic string with seven loci

A small subset of the organism’s total genetic information, i.e. a certain number of loci, is involved in co-evolutionary dynamics (Frank 1994, 1996). This means that it is at these positions in the genetic string where we would observe the specie’s evolutionary interchange as a result of interaction with its main ecological counterparts, if this genetic information were easily accessible. This interaction would manifest itself by bringing different alleles to these loci than were there in previous periods. So, for example, we might conceptualize resistance in fig.1 as periodic variation at the loci 2 through 5 – in that these would then present different information in different periods, e.g. locus 3 changing from allele D to alleles A or C.

It is not just the “matching” process that matters but also the specific structures of the alleles that exist at these loci. The alleles conferring resistance have developed over evolutionary history through the continuous interaction between crops and their pests, a process termed “co-evolution” (see e.g. May and Anderson 1983). These alleles are therefore highly specific pieces of information which are used in varying combinations in the population - as a “group” response to changes in the opposing specie - in order to create virulence or resistance.

9 The exact number of loci is unknown for most crop species as this would entail a full-scale genome sequencing. 10,000 is therefore a rough estimate (Gilligan: personal communication). For comparison, humans have about 100,000 loci, while Drosophila, the common fruit fly, has about 4,000.

10 Even assuming that a species has only 20% of its 10000 loci varying, and that there are only two possible alleles at each of these loci, gives a total number of possible permutations of $2^{2000}$. Of course, not every one of these varieties would have potential to resist a pathogen.

11 The actual processes involve an additional level of biochemical recognition: “Resistance occurs only when a pathogen allele produces are particular gene product (elicitor) that can be recognized by a matching host receptor ... If an elicitor-receptor match occurs, then the host induces a defensive response and resists attack. If the same pathogen elicitor is present, but the host produces a non-matching receptor, then the disease develops. Infection also occurs when a pathogen lacks an elicitor that matches the specific host receptor...The pathogen succeeds only when it escapes recognition at all the complementary loci” (Frank 1997, p.8).
Although the actual biochemical mechanisms that bring about resistance or susceptibility in the host are more complicated than presented here, the basic principles can be explained in simple terms. Whether a host is resistant or susceptible to a pathogen is modeled as depending on whether its string “matches” the pathogen’s string with the same letter at least at one point. For example, a host string with five letters such as $ABHCC$ matches a pathogen string $EBBCH$ at the second and fourth loci and is thus said to be resistant. Another variant, e.g. a host with string $CCHBA$, has no match and is thus said to be susceptible. For a crop grown by an agriculturist, this susceptibility translates into yield loss due to disease or infestation.

The evolutionary dynamics of these matching models depend on four factors: (1) The fitness gain associated with being an unmatched pathogen or a matching host relative to the average fitness in the pathogen population; (2) the stochasticity of reproduction; (3) the spatial dimension of reproduction, and (4) the number of pathogen generations per host generation. Focusing on the pathogen, being unmatched enables the parasite to form an infection and to produce offspring. Its capacity to pass on its locally successful information are enhanced by any factors that enhance its ability for incorporating its information in the next generation of pathogens. These factors include initial relative abundance (frequency) and spatial proximity. So in the following generation, an unmatched pathogen is likely to appear in locations close to its previous location by replacing incumbent, matched pathogen. The continuing replacement of nonvirulent strains by the virulent describes the path of an epidemic.

To give an illustration of the pathway of infection described by such matching models, we ran a simulation based on a monoculture with one resistance gene and one pathogen which targets the host. The actual program which gives rise to these figures is reported in the annex. Figures 2 to 5 below give the spatial probability distribution of an unmatched pathogen for a monoculture planted across 500 spatial units. In period one, chance provides that there are only two locations in this space at which pathogens have “un-matched” hosts. This leads to a small focus of infection, which enhances the prospects for supplanting the local “matched” pathogens (Figure 3). The probability of infection then increases over the range of the monoculture as the relative fitness of the “unmatched” genes is greater, and they are replicated throughout the pathogen population (Figure 4). Four periods after the initial infection, there is an average probability of approximately 80% at each location that a virulent

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13 It is customary in these models to work with fixed population sizes, but the framework can be easily expanded into evolution by absolute abundance (Frank 1996, 1997). The epidemiological effects can be seen as working through the spatial effects in combination with the number of pathogen generations per host generation.

14 The probability for mutation is normally introduced as a small constant chance that an allele may be exchanged for a random allele during reproduction.

15 It cannot be excluded that in cases with a small probability, an unmatched pathogen may be replaced. This is not likely to be of great weight, however.

16 The program is based on MatLab. The relative fitness of unmatched pathogens is set at 5. Relative fitness has less of an impact on disease development than the number of pathogen generations per host generation, however.
A pathogen will be present. An epidemic has affected the yield of this crop dramatically, because the unmatched allele has spread throughout the pathogen population on account of its relative fitness.

**Figures 2-5: Spatial development of unmatching pathogens in monoculture**

![Graphs](image)

Period 1

Period 2

Period 3

Period 4

In the simulation, it emerged that the number of pathogen generations per host generation is of crucial importance to the development of the epidemic. This determines the new number of active infections (‘lesions’) on the plant that can then generate the multiple offspring that successively expands in the host area. This is an exogenous determinant of the extent of the epidemic and cannot be altered.

The spatial process of expansion attributes decreasing weights to more distant pathogens and weights are decreasing by factor 2 in distance based on a loose association with epidemic wave theory (Zadoks and Schein 1979).

### 2.2 Applications and Implications

Dynamics of the kind outlined above provide the genetic explanation for the rapid breakdown of resistance of crops (Kiyosawa 1986), for the continuously decreasing yield which crops demonstrate over their useful life (Evans 1993) as well as for the demand for replacement seed for crops in intensive cultivation (Heisey and Brennan 1991).\(^\text{17}\)

\(^\text{17}\) The latter authors estimate for instance that annual yield loss due to genetic advances of pathogens increases by around 1.5 to 2.5% per year.
In unmanaged host populations, these types of processes lead to fairly even distributions of allelic diversity overall, but are characterized by rapid changes at the level of the individual locus. Epidemic fluctuations - although detrimental to the effective population sizes of individual genotypes - are a necessary condition for the host species to successfully counter the fitness gains which accrue to pathogens as a result of their evolving adaptation to the current host population (Frank 1996). Evolutionary stability is therefore attained only at the aggregate level, not at the level of the individual organism or allele.

Matching games generally do not possess pure evolutionary stable strategies (Weibull 1995).\textsuperscript{18} This means in practice that there is no evolutionarily stable monoculture and therefore no fixed genetic combination that society can expect to be able to grow for prolonged periods of time over large tracts of land. It also says that although we can forecast the aggregate trend of the pathogen population’s genetic structure, information about the actual changes at the genetic level are impossible to forecast.

Given the nondeterministic nature of the evolutionary process, it is not possible to forecast which host allele will constitute a match for the next pathogen combination. The existence of a match is not dependent on some intrinsic feature of the allele, but on the particular genetic state of the pathogen population at which the system resides at a given moment. Unmanaged populations can respond to these state changes with an analogous process that allows the appearance of new alleles at those locations where no match has occurred.\textsuperscript{19} The maintenance of stability within this contest would have depended upon the maintenance of a sufficient level of genetic resource diversity within the population – to provide a population-based response to the successful allelic combinations being displayed currently by the pathogen.

Agriculture has substituted human decision-makers for natural selection in the determination of land use (Swanson 1995). Once land use is being determined by decision-makers pursuing an objective function other than maximum fitness, there is the need for a supplementary process for providing resistance.\textsuperscript{20} The long-term stability of the system cannot be assumed once land use is being

\begin{itemize}
\item \textsuperscript{18} This is intuitive from that repeated playing of the same strategy (say ABHCC), even if successful at some point, is necessarily attracting an attack from the competing species. This is an intuitive result from the game of “matching pennies”. Between rational players, this would lead to an equilibrium in mixed strategies with players randomizing over their strategy set. In evolutionary settings with multiple populations however, mixed strategies do not support an equilibrium (Hofbauer and Sigmund 1988, Weibull 1995).
\item \textsuperscript{19} This is a result of the reverse epidemic of resistance that would occur on account of the increased relative fitness of those hosts that match their local pathogen.
\item \textsuperscript{20} Of course one of the subsidiary objectives of a decision maker pursuing another objective, e.g., maximum yields, would have to be the maximisation of resistance; however, there would be many other objectives with which it would now be in competition: minimisation of costs of ancillary inputs (labour, capital), maximisation of consumer preferences (tastes) etc.
\end{itemize}
determined by other considerations. An ancillary problem to the pursuit of low cost agriculture based upon widely planted monocultures must be the provision of a new source for the flow of genetic resources into this system.

The fundamental point about matching models of genetic resources is that they point to the essential resource required for the resolution of this new problem: The resource in question is the set of “match”-generating alleles that have co-evolved in the crop species over the course of many millennia. In the following section, we will explain in more detail how this set of matches was generated, and the determinants of its size and value.

2.3 Production of matches

We will now turn to the development of a set of models for examining how the problems introduced by agriculture may be addressed. The ultimate question that agriculture raises is: how is it possible to integrate the dual objectives of agricultural productivity and genetic resource requirements in the determination of optimal land use? In order to proceed to consideration of these trade-offs, it is first necessary to consider explicitly how land use decisions affect the flow of “matches” into agriculture.

In this model, we will assume that the world’s land area is divided into two distinct areas: 1) an area for intensive agriculture where the objective is the maximisation of crop yields; and 2) a “reserve” area for the supply of a flow of genetic resources into agriculture. The matches are produced by exposing a stock of allelic diversity $F$ to the currently existing diverse pathogen population. The stock $F$ derives from an original endowment of allelic diversity $A$.\textsuperscript{21} We will stick to the usual assumption that there exists a species-area type of relationship between diversity and size of unconverted land (see e.g. Reid 1989, Rowthorn and Brown 1995). If we assume that the initial stock $A$ existed on the entire land endowment before in a fairly uniform distribution, then the stock of allelic diversity in the reserve, $F$, is uniquely defined by the choice of $X$ which is the land devoted to intensive, highly monocultural agriculture:

\[ F = A(1 - X) \]  

We assume that the other part of $A$ as well as duplications of allele which occur in the field are held as a number of accessions, $B$, in a gene bank\textsuperscript{22}. Some of the material will naturally be in use in the intensive sector in the form of resistance conferring alleles, $N$.

\textsuperscript{21} As mentioned in the introduction, $A$ is assumed to be a given number that existed at the time of the onset of the Green Revolution.

\textsuperscript{22} Some staple crops approximate this condition, e.g. rice where about 80,000 samples of the originally 100,000 varieties are reported as accessions in gene banks (Chang 1989).
Let us define two further parameters: One is the degree to which genetic material that exists in the gene bank is duplicated in the reserve. This parameter will be called $f$ with $0 \leq f \leq 1$ and is a measure of the intersection of the allele sets in reserve lands and in the bank. At $f=0$, no allele in the bank has a duplicate in the reserve land while at $f=1$ every allele out of $A$ exists once in the gene bank and once on land. The second parameter is the share of alleles in the intensive sector that is duplicated in the reserve. This parameter we will call $d$ with $0 \leq d \leq 1$ such that $dN$ is the number of resistance alleles which are both in the reserve and in intensive use. Individual crop varieties consist of several alleles. Both parameters therefore capture something of the genetic distance between varieties in intensive use, in the land reserve and in gene banks, since higher levels of duplication are equivalent to having varieties with more similar genetic constitutions.

Then there are two aspects in the production of matching alleles that have to be taken into consideration: One is the production of the quantity of matches. These will be incorporated in plants show no disease during the planting season. Clearly, more matched pathogens translate into higher yield in the reserve sector which can be sold at price $z$. The other is the probability of resistance conferral based on matches: Crops invariably possess very complex genetic structures with a high number of positions at which different alleles reside (see section 2.1). Which of these alleles is the one that has given rise to the resistance observed and can this allele - if found - be easily transferred into an industrial crop? Information about the structure of the individual pathogen and also of the crop is costly to acquire. Information deficiencies discourage the use of genetic material of unknown origin and cause large collections to go unused (Duvick 1984, Goodman 1985).

### 2.3.1 Quantity of matches

The quantity of matches $R$ depends on the values of three variables: (1) The share of labor available in the reserve sector, $1-a$, which measures the amount of information gathering, i.e. observation by farmers, which is undertaken there\(^{24}\); (2) the amount of space allocated to the reserve sector, $1-X$, which has a clear positive relationship with the amount of matches received since it both increases the amount of allelic diversity $F$ and decreases the density at which $F$ has to be planted (thus giving rise to more possible varietal diversity); and (3) the level of duplication of known resistance genes employed in the intensive sector since the use of close relatives can be expected to lead to a higher number of resistant crops as the pathogen population can be expected to exhibit a minimum degree of homogeneity:

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23 The existence of resistance genes in crops against known pathogens already involves long-term statistical experiments or more expensive types of analysis.

24 We will assume $a$ to be constant in this model (or at least to be driven by factors outside this partial system). Some observers have claimed that it is the high labor intensity of traditional agriculture which enabled these cultivation systems to withstand pathogen pressure by using observation to achieve higher rates of fixation of resistance genes that would have naturally occurred (cf. Barrett 1981, Allard 1990, Gliesman et al. 1981).
\[ R = R(a, X, dN) \quad (2) \]
\[ \frac{\partial R}{\partial a} < 0, \]
\[ \text{with} \quad \frac{\partial R}{\partial X} < 0, \]
\[ \frac{\partial R}{\partial (dN)} > 0 \]

There is a clear incentive therefore to plant very closely related crops in the reserve as they are more likely to produce a secure yield. But they are also the most exposed to the changes in the pathogen population and thus - as we will see below - directly linked with the resistance depreciation function of equation (10).

### 2.3.2 Probability of resistance conferral

The quality of information, i.e. the degree to which resistance-conferring alleles can be successfully identified and their transferability to other crop plants assessed, depends upon the ratio of known to unknown alleles in the reserve sector. We will denote this parameter by \( p \) and determine its value as a function of the number of known resistance genes employed in the intensive sector which are also used in the reserve sector and the total amount of allelic diversity in the field. This is a crude, but convenient measure of the degree of genetic distance between modern crops and their relatives in the reserve. Formally then,

\[ \pi = \pi(dN, F) \quad (3) \]

If the ratio is too low, then the plant breeder faces too many unknowns when trying to locate the correct allele among the many unknown alleles. Thus very distant relatives of industrial crop plants may have resistance to pathogens and thus contribute a reliable flow of matches, but it will then be very difficult to locate the allele that is desired for import into the intensive sector (Holden et al. 1993).\(^{25}\) If the number of known alleles is too high, the set of matches produced consists predominantly of those caused by already known alleles. Their contribution in terms of information is nearly zero because the net number of new alleles detected is very low (Goodman 1990). This suggests that there is a ratio \( q^* \) between known and unknown alleles which is optimal such that

\[ q = \frac{dN}{F} \quad \text{and} \quad \pi'(q^*) = 0 \quad \text{and} \quad \pi''(q^*) < 0 \quad (4) \]

\(^{25}\) The problem here consists of the desire to import only the matching allele, and not a lot of other unwanted characteristics from the distant relative. It is a problem of maintaining a flow of information that may extracted at a reasonable cost in terms of yield.
This is equivalent to saying that there exists an optimum of close and distant relatives of modern industrial crops which should be cultivated in the reserve. Useful alleles which are common have mostly been captured by breeders, geneticists and pathologists. They are therefore likely to exist in both land sectors. Rare alleles or specific combinations of rare alleles on the other hand are present only in a few specimens at sufficient frequency (Goodman 1990). So the planting of cultivars with uncommon alleles is impeded by the relative scarcity of rare alleles.

In this section we have explained the basic concepts underlying the use of matching allele models in describing the evolution of crop-pest interaction. We have looked at the implications this has for human decision makers which manage host populations in such evolutionary environments and the consequent demand for resistance alleles for importation into the intensive sector of agriculture. This demand can be predicted to be a permanent need, so long as land use is partially dedicated to an intensive sector. This implies the need for another sector – the reserve sector - in which both the genetic resources are maintained and information on their usefulness is generated. We concluded with a description of the determinants of the value of this sector.

3. Land use and the use of genetic resources

In this section we will look at agriculture from the vantage point of the use values of genetic resources. These values are clearly associated with their use in the intensive part of agriculture where they are used to provide protection from pathogen attack for preferred crop varieties. To establish the socially optimal levels of resistance in agriculture and of monocultural land use, we will begin by assuming a social planner who is not concerned about the type of diversity which brings about the matches in the reserve sector, but only about the rate at which resistance is imported into the intensive sector and the optimal amount of land to be allocated to intensive agriculture.

3.1 Agricultural Production with Genetic Resistance

Imagine a social planner that wants to maximize the long-run food supply of the population using labor and land as input factors. Output is produced in two types of agricultural sectors for reasons which will be explained just below. The agricultural product is therefore

$$Y_t = O_t + O_R$$

(5)

The importance of maintaining individual, non-composite accessions has been emphasized before in the scientific literature for *ex situ* collections (Goodman 1990).
where $O_I$ is the “intensive” sector where varieties with multiple resistance genes are employed, and $O_R$ is the “reserve” sector where a broad set of varieties is held. $O_I$ is produced using labor $a$, land $X$ and a number of resistance genes $N$ against the prevalent pathogen population under a production function which follows the works of Spence (1976), and Dixit and Stiglitz (1977):

$$O_I = (aL)^{1-\beta} \sum_{i=0}^{N} X^\beta_j(i)$$  \hspace{1cm} (6)

where $0 \leq a \leq 1$, $L$ is labor input and $X_j(i)$ is the employment of resistance gene $i$ on the tract of land $j$ and $0<\beta<1$ is the productivity of land in the usual format of a Cobb-Douglas production function. As is evident from the formulation, the production factors have diminishing returns to scale individually, but constant returns to scale in combination.

Resistance genes are used to protect the crops from attack by pathogens of different genotypical form. This is reflected in the additively separable form of the production function since it allows the social planner to characterize each crop by the types of pathogens it is able to resist at the current stage. In this sense, crop varieties with different resistance genes are neither direct substitutes nor direct complements. Adding a new type of resistance gene to the crop allows resistance to a previously unmatched pathogen to take effect. It is easy to see the immediate appeal this formulation has for conceiving of the function which resistance genes serve: They allow to increase expected secure yield by protecting an independent dimension of the crop genetic structure from pathogen risk. Since resistance genes are pathogen specific, they are unlikely to contribute to resistance apart from the locus where they match a particular parasite.

Once a resistance gene has been imported, it can be used as a free good at any chosen scale. This is merely a consequence of dealing with genetic information about an allele characteristic which -once known - can be assumed to be replicable at zero cost. As resistance genes will hence be used across identical range of space in equilibrium (see Barro and Sala-i-Martin 1995), we can simplify the production function to the simple form of

$$O_I = a^{1-\beta} X^\beta N$$  \hspace{1cm} (7)

27 This is in line with the literature on product differentiation in the theory of economic growth (Barro and Sala-i-Martin 1995).
which is the normalized production function solution for \( L=1 \). The reserve sector also produces output valued at unit price \( z \) and linear in the number of *allele matches* \( R \) which occur in the reserve according to

\[
O_R = zR
\]  

(8)

where \( z \leq 1 \) as we assume that varieties in the reserve sector fetch lower prices than the HYV crops with normalized unit price.\(^{28}\) So similar to the intensive sector, we assume that higher resistance translates smoothly into higher output in the sector.

The objective of the social planner is to maximize the following expression using land \( X \) and the level of transfer of resistance-conferring alleles into the intensive sector, \( I \), as control variables:

\[
\max \int_{t=0}^{\infty} e^{-\delta t} Y_t dt \quad \text{where} \quad Y_t = a^{1-\beta} X^\beta N + zR - pI
\]  

(9)

The expression states the maximum of the discounted annual yield from agriculture for an infinite horizon minus the cost of transfer. The parameter \( p \) denotes the price the social planner has to pay for one unit of resistance conferral by the means of importing a matching allele - or a combination of alleles among which resistance is expected to reside.

### 3.2 Dynamic Aspects of Agriculture

In the previous section, we presented an agricultural production function which is capable of reflecting some of the particularities of using resistance genes as a production input, esp. their ability to expand production in independent dimensions and thus to overcome the problem of increasing returns to scale. However, this static picture is only complete when the evolutionary dynamics are taken into consideration. This is because the producer faces a dynamic constraint which affects the level of resistance in intensive agriculture. Its source is the import of resistance by man on the one hand, and the reduction of resistance by pathogens on the other. We will denote this process by

\[
\hat{N} = I - l(X, N)
\]  

(10)

Equation (10) states that the level of resistance changes over time, depending on the input of new resistance genes into the industrial crop by plant breeding and the loss of resistance due to changes in the pathogen population. This loss has two sources: The first is associated with \( X \) and is the epidemiological effect of the amount of land allocated to the cultivation of the industrial crops

---

\(^{28}\) This may be explained by lacking economies of scale in inputs and output or inferior quality. It can be expected that the industrial crop variety is the preferred product, otherwise the returns from incorporating resistance genes into a rival variety would be higher.
(Scheffer 1997, Zadoks and Schein 1979). Epidemic resistance loss, i.e. the positive relationship between the spatial spread of a cultivar and the loss of resistance, is explained by the matching allele models as the result of two facts:

(1) With increasing space more pathogens are given the opportunity to “unmatch” against that of the dominant cultivar (linear relationship) by the means of evolution; and
(2) once a pathogen has come across a combination which is not matched, it is very likely to spread this information very rapidly due to its relatively high fitness in comparison to its neighbors and the equally favorable conditions at neighboring locations in a highly uniform agriculture.

The second source of loss is associated with \( N \): It is the positive relationship between the level of resistance in the monoculture and the expected loss: Pathogen evolution, as outlined in section 2, depends clearly on the average level of pathogen fitness. The lower the average level, the faster a successful recombination can spread since its chance of replacing the incumbent pathogen are proportionately higher. Pathogen evolution thus benefits from generally low levels of competitor fitness.

We can summarize the relationship between the choice for \( X \) and \( N \) therefore in the expressions for the partial derivatives as

\[
I_X = \frac{\partial l}{\partial X} > 0 \quad \text{and} \quad I_N = \frac{\partial l}{\partial N} > 0 \quad (11).
\]

It is a characteristic of these evolutionary systems that there is a proportionate response from pathogens to evolutionary pressure exerted on the population. As a result, we should see the genetic structure of crops in heavy use change constantly as a response to pathogen activity which is confirmed by the rapid turn-over of preferred cultivars which is often due to disease development (see Reid 1989, Heisey and Brennan 1991, Holden et al. 1993).

### 3.3 Social optima of crop resistance and land use

The problem of the social planner is now a completely specified optimal control problem with one state variable, the level of resistance in intensive agriculture \( N \), and two control variables, land use \( X \)

---

29 Empirical research showed that in 62% of diversified agroecosystems pest populations were significantly lower than in monocultures, compared to only 11% where pest population levels were higher (Risch et al. 1983).

30 Basic laws of probability suggest that the more often the dice are cast the more often will a throw result in the desired combination.

31 The rate of recombination is assumed independent from the level of resistance. In models with variable population sizes, the increase in survival probability of a successful recombinant is partially countered by the lower probability of its occurrence. See (Munro 1997).
and resistance transfer \( I \). We will assume that the planner has an infinite planning horizon and employs the social discount rate \( r \).

To construct the optimal path the social planner should choose and how the optimal levels of land use and resistance (and, hence, of the optimal rate of transfer of resistance genes), we apply standard methods of control theory to get a set of first order conditions:

\[
\begin{align*}
\mu &= p \\
N_A^* &= \frac{pl_X - zR_X}{\beta a^{1-\beta} X^{\beta-1}} \quad (12) - (14) \\
X_A^* &= \left[ \frac{p(l_N + r)}{a} \right]^{\frac{1}{\beta}}
\end{align*}
\]

where subscripts of \( l \) and \( R \) indicate partial derivatives. We are therefore able to determine the socially optimal levels of land use and crop resistance for agriculture, \( N_A^* \) and \( X_A^* \). These functions give rise to optimal trajectories which depend crucially on the specification of the loss function and the exact way in which matches will occur as a function of the size of reserve land.

One way of looking at this set of equations - and definitely the easiest for exposition - established by the steady state is to assume linear relationships between the variables involved.\(^{32}\) This is equivalent to specifying the loss function as

\[
I(X, N) = l_N N + l_X X \quad (15)
\]

with constant coefficients \( l_N \) and \( l_X \). The first equation is a switching function for the optimal levels of resistance transfer: The value of the co-state variable, \( \mu \), has to equal the unit price of transfer, \( p \).\(^{33}\) The social planner will meet the condition by adjusting the land use levels, \( X \), and thus the speed at which the system evolves: For increasing prices of resistance, increasingly higher levels of monoculture are necessary to warrant the import of resistance genes as productivity has to keep pace but faces decreasing returns in land. This adjustment is possible only up to the point where all available land is planted to monoculture, i.e. as long as

\[
p \leq \frac{a^{1-\beta}}{l_N + r} \quad (16)
\]

\(^{32}\) This sets the second partial derivatives equal to zero and thus greatly simplifies the otherwise inconclusive analysis.

\(^{33}\) Unless \( p=0 \). In this case the shadow price can be chosen freely to result in optimal conditions.
Above this level, demand for import drops to zero and agriculture moves the point of “self-insurance” where the expected loss from agricultural activity is zero. The more sensitive the system is to evolutionary pressure from resistance, denoted by $l_N$, the lower the choke price lies.

Diagram 2: Agricultural Optimum

Looking at equation (10), it is apparent that the desired level of resistance in the intensive sector, $N^*$, is a function of the epidemiological characteristics of the agricultural system and land use. Resistance levels are socially optimal if the marginal yield gain from expanding monoculture at this resistance level equals the value of the accompanying resistance loss plus the value of output loss in the reserve sector. Resistance level considerations are thus directly linked to questions of optimal land use. As it turns out, this interdependence is reciprocal: The determination of optimal land use can be made on the basis of the level of evolutionary pressure on resistance. If the resistance-induced loss increases linearly with levels of resistance, then $X^*$ is uniquely determined by $N^*$.

The dynamics of this system are depicted in diagram 2 with the isoclines in a $X-N$-space. Under our simplifying assumptions, the system has a unique and stable equilibrium in land use and resistance levels. This implies a constant demand for a flow of resistance-conferring alleles to be employed in the intensive sector which is

$$I^* = I_A^* = I(X_A^*, N_A^*)$$ (17)
If this flow of genetic resistance into the intensive sector is available at the required level of input, then the social planner faces favorable conditions for optimally balancing yield, epidemiological risk and evolutionary dynamics. The reserve sector then serves as an epidemiological barrier and an evolutionary buffer for the management of the system. Note that it is possible to approach the optimum from any arbitrary starting point. This means that from the agricultural point of view, there is no path dependency on previous levels of land use or resistance.

In this section we explained the types of decisions which a social planner who is only concerned with maximizing agricultural output under epidemiological and evolutionary constraints will optimally take. We found that - under simplifying conditions - there exist optimal levels of land use and crop resistance which are reconcilable with the ongoing co-evolutionary interaction between agriculture and its biological predators. These levels require a constant positive rate of import of resistance-conferring alleles into the intensive sector, however. In the next section, we will establish the way in which this flow can be optimally managed from society's point of view.

4. Optimal Genetic Information Management

How will a social planner allocate the genetic resource stock in agriculture faced with choices made in the agricultural sector? As the previous section has shown, there will be a constant demand for a flow of resistance into the intensive sector. This demand can be met out of two sources: Gene banks and reserves which maintain genetic diversity on land. There is a constraint therefore on the social manager of genetic resources in that this demand has to be satisfied by allocating the resource endowment \( A \) in such a way as to safeguard this supply. The purpose of this section is to establish the optimal management decisions taken by the social planner with regards to maintaining this flow over time.

The problem of the resource manager is to maximize the social value of the resource flow minus the costs of producing resistance conferring alleles. To do so, it can manipulate the size of reserve lands and the genetic composition of the reserve sector. Let us assume society’s valuation of resistance genes is determined by the correct shadow price ascribed to it by the social planner in agriculture, \( \mu \). The social benefit is then the volume of resistance transferred multiplied by its social value. The structural constraint in this is that no more resistance can be transferred than is available in the system at any given moment. Taking up the notation developed in section 2.3, society’s benefit can hence be denoted as

\[
S = \mu v \left( R \pi + m B \pi f \right) \quad (18)
\]
where \( 0 \leq v \leq 1 \) is the transferred share out of \( J \), the number of all resistance-conferring alleles, weighted by the probability of resistance conferral, \( \pi \). The components of \( J \) are: Matches received in the reserve, \( R \), the expected share of matches, \( m \), out of the gene bank’s accessions, \( B \), and the degree of duplication between bank and reserve, \( f \). The importance of the probability of resistance conferral is apparent in that it discounts the transfer of alleles down to its effective level. A high degree of duplication between the field and the bank on the other hand enhances the chance of finding a suitable allele \( \textit{ex situ} \) as matches can be searched for “close to” where a match occurred in the reserve. The obvious cost of this is the holding of a higher stock in a bank.

The cost of producing these matches is assumed to be constant per unit, but is not discounted by the quality of information or degree of duplication. This is because costs are invariant to whether the search is successful or not. Therefore the costs, \( K \), are

\[
K = cv(R + mB)
\]

The program the social manager has to optimize therefore is

\[
L = \int_{t=0}^{\infty} e^{-rt} (S - K) dt
\]

s.t. \( (R\pi + mB\pi f) \geq \int \left( X^*_A, N^*_A \right) \)

where the latter is the constraint imposed by meeting the demand for resistance created by the agricultural sector using \( d \) and \( X \) as control variables. Since there is no intertemporal externality involved for the social manager, the static optimum also maximizes the dynamic program. Solving for the first order conditions and simplifying, we can establish two main results.

1. The social manager always maintains the information optimum between reserve and intensive sector. The first order conditions result in the following optimal relationship between the choice of \( d \) and the \( X \),

\[
\frac{\pi d}{R_d} = \frac{\pi X}{R_X}
\]

which states - after rearrangement - that the partial gradients of the probability of resistance conferral, \( \pi \), with respect to \( d \) and \( X \) have to equal that of the quantity of allelic matches, \( R \). So at the optimal point a change in \( d \) should have the same effect as a change in \( X \). But since the signs of the numerator are the same and that of the denominators opposite, by definition, this condition can only hold where \( \pi_d = \pi_X = 0 \).
Therefore

\[ \frac{dN}{A(1 - X)} = q^* \]  \hspace{1cm} (22)

2. The optimal size of reserve lands is determined as

\[ X_I^* = 1 - \left( \frac{I - mB\pi^*}{\pi^* \rho(1 - a)} \right) \leq 1 - \frac{N}{q^* A} \]

where \( \rho = \rho(dN)^* \)  \hspace{1cm} (23)

Equation (23) states that there exists an optimal level of intensive agriculture for the purpose of informational management. Its level is 1 minus the ratio of matches not supplied out of the gene bank over the marginal unit of resistance produced by a unit of land in reserve under optimal information management. Since \( d \) will always adjust to maintain the quality of genetic information at optimal levels, we can make statements about the comparative statics of this point based on the Envelope Theorem: An increase in demand for resistance causes the optimal level of intensive agriculture to go down. This contrasts with the behavior of the agriculturist for whom the opposite rationale holds: Increases in the flow of resistance are generally a consequence of an increase in intensive agriculture.

A combination of information and agricultural management is likely to result in a trade-off at this point. Partial compensation can be accomplished by an exogenous increase in the amount of gene bank stocks and - since the overall stock is constant at \( A \) - the degree of duplication. This is limited though by the range of values the parameters can take (see section 2.3). Alternatively, policies which encourage more farm labor in the reserve sector and thus increase observation of evolutionary responses and enhance their adoption can substitute for an increase in the reserve sector at the expense of intensive agriculture.

At the same time that these exogenous changes can be implemented, there is an upper bound for intensive agriculture. This is because the optimal information management condition that \( \pi = 0 \) requires a minimum of land to be available for “receiving” information about current matching and unmatching by the pathogen population. This is increasing in the amount of resistance held in intensive agriculture and represents the structural constraint of information necessary to keep the system at its optimum. This means that even if it is possible to extend intensive cultivation by exogenous changes to the system - notwithstanding the potential social sub-optimality of such changes - there is a strict maximum for the share of land used for monocultures.

In this section we demonstrated that there is an optimal level and an optimal structure of genetic resource stocks held on reserve lands. The level of land devoted to maintaining crop allelic diversity is mainly determined by the demand for crop resistance created in the intensive sector. Increasing demand is accompanied by an increasing optimal size of the reserve. This demand can partially be met out of allelic diversity maintained in gene banks. It cannot rely exclusively on \textit{ex situ} methods,
however, as information about the current genetic structure of the pathogen population and hence about the expected use values of individual alleles in storage is a necessary production input. This can only be provided by a sufficiently diverse crop population on land. This problem of consequent underutilization of the resource stock due to its basically unknown characteristics is already recognized by practitioners in the field (cf. Goodman 1990, Duvick 1984).

5. The Social Optimum of Conservation and Exploitation

Sections 3 and 4 both determine socially optimal level of land under intensive forms of cultivation, one based on allocation decisions in agriculture where the supply of crop resistance is assumed to adjust to any level, but where epidemiological and evolutionary effects are taken into consideration, denoted by $X_A^*$; the other based on the informational management of the genetic resource endowment for maintaining the flow of resistance from the reserves to the intensive sector, denoted by $X_I^*$. If $X_A^*$ is smaller than $X_I^*$ then there is no trade-off involved between information management and the socially optimal allocation of land: Epidemiological pressure and the evolution of pathogen virulence are sufficient to maintain a share of land where diverse agriculture and production of allelic matches can take place. The desired transfer of resistance does not exhaust the genetic information produced in the reserve and agricultural yield is hence sustainable at the chosen levels. In such a world, no intervention would be needed.

Diagram 3: Social Optimum: Diagrammatic Analysis
It is highly unlikely though that this describes the conditions we observe in agriculture. Firstly, since the onset of the Green Revolution society has been employing technologies other than genetic resistance in order to counter epidemiological threats such as pesticides. These allow the optimal levels of land use to be expanded beyond the levels suggested by this model. So even if there was a social planner, it would be likely to manage these risks in a different, although not necessarily more efficient manner which would involve a substantial expansion of intensive cultivation.

Secondly, society consists of decentralized decision makers who have less incentives than society to take into account the systemic externalities of their land use decisions, a point to which we will return in section 7. We should be more interested therefore in the type of optimal allocation which would result from conflicting land use regimes dictated by agriculture on the one side and resource management on the other.

The most scenario we are most likely to observe will be the one depicted in the diagram 3, where the informational optimum suggests lower levels of intensive land use and crop resistance than determined on the basis of agricultural decision criteria alone. Although the structural constraint is likely to be met by a social planner in agriculture as a result of the internalization of the dynamic effects of agriculture, it is unlikely to fulfill the informational optimum for the reasons mentioned above.

This results in the existence of two optimality conditions for land use which have to be reconciled by suitable adjustments. As is apparent from the factors determining their level, a convergence of levels is possible: A reduction in intensive land use translates into lower level of resistance transfer required from the reserve sector. This in turn relaxes the demand for reserve lands which means that the effects work into opposite directions, $X_I^*$ moving down while $X^*_A$ is moving up. Formally, the optimal level is slightly more unwieldy, and is determined by the equation

$$X^* + \frac{l_N \left(p l_X - zR_X \right)}{\beta a^{1-\beta} \pi^*(1-a)p} X^*^{1-\beta} = \frac{(1-a)p - mBf}{(1-a)p + l_X}$$

which gives $X^*$ only as an implicit transcendental function. The central point however is that the optimal level of intensive land use can be determined on the basis of the relevant parameters and numerically computed. It is also clear from our analysis that its value must lie **between** the optimal levels suggested by agriculture and resource management. Can we expect this level to come about as a result of decision making in agriculture under current conditions?


6. Optimal Biodiversity Management in Agriculture

In the previous section we derived the optimal level for land use which optimizes the trade-off between efficiency in agriculture and the optimal allocation of genetic information. These result not only in socially optimal levels for \( X \), but also for \( N \) and for the optimal rate of transfer of genetic material. This immediately poses the question how these optimal levels are implemented in reality since the social planner which we assumed to effect the allocations does not exist in reality. Land use decisions are taken predominantly through agriculture which is essentially a sector consisting of decentralized decision makers whose choices may or may not coincide with the socially desirable values. At the same time, there exist institutions which currently manage genetic resources. These could be expected to implement choices which are close to those optimal for a social planner. However, these institutions have little control over land use and manage genetic resources almost exclusively through gene banks.

Consequently, we have to ask whether any deviation from the optimum results with a welfare loss to society and if yes, how society can implement the optimal outcome using a minimum number of tools.

The purpose of this section is to show that the non-cooperative solution of independent decision making by farmers leads to a higher degree of intensive agriculture than desirable as well as to a choice of resistance levels which is not reconcilable with the sustainable use of genetic resources. We will model this problem as a simple case of externalities and compare the aggregate of individual decisions with the socially optimal pair of solutions for \( N \) and \( X \).

Assume the farming community consists out of a set of \( W \) identical farmers whose problem is to maximize the net present value of their yield in intensive and diversified agriculture minus expenses for purchasing previously unused resistance genes. Farmers agree with society that the decision horizon should be infinite. The farmers’ discount rate \( \delta \) may differ, however, from the social discount rate denoted by \( r \). Formally,

\[
\max_{t=0}^{\infty} e^{-\delta t} y_t dt \quad \text{with} \quad y_t = \alpha^{1-\beta} x^n + ze - pi \quad (25)
\]
where $\alpha$ is the individual level of labor input, $x$ is the share of land, $n$ the level of crop resistance, and $e$ are the allelic matches produced in the reserve land.\textsuperscript{34} All other parameters are unchanged. We will assume that farmers take into account the epidemiological dynamics of the system when making their choices, but not the effects of evolutionary pressure which arise over the longer term. Similar to the social planner, farmers will not optimize with respect to the stock of biodiversity and the genetic structure of agriculture. Therefore, the dynamic constraint taken into consideration by farmers is

$$
\dot{n} = i - l \left( x_j + \sum_{k \neq j} x_k \right) \quad (26)
$$

which states that the resistance change the individual farmer faces is the number of resistance genes it purchases minus the loss due to monocultural use. For this, the farmer has to take into consideration intensive use of resistance genes by itself as well as by other farmers which it takes as given. Strictly speaking, others’ choices matter only insofar as they use the same resistance genes as the decision maker. But since all farmers will use the same alleles (section 3.1) due to their essentially informational nature, choices will be symmetric and the equation of motion can be given in this simplified form.

Solving the maximization problem for its first-order conditions, we get the following results for the optimal levels of $x$ and $n$ for the individual farmer:

$$
x^* = \left[ \frac{p \delta}{\alpha^{1-\beta}} \right]^{\frac{1}{\beta}} \quad (27)
$$

$$
n^* = \left[ \frac{\delta p}{\beta \alpha} \right]^{\frac{1-\beta}{\beta}} \left( p l_x' - z e_x \right) \quad (28)
$$

Making use of identity assumption and aggregating over all $W$ farmers, we find that for optimal levels of resistance and land use in both models, the non-cooperative outcomes $X^*$ and $N^*$ can be denoted as:

\textsuperscript{34} The scaling is still based on the original norms applied to the social planner’s problem such that the farmer can maximally use $1/F$ for monoculture.
In the non-cooperative case, individuals are only concerned with their own contribution to the epidemiological risk and are not concerned about the source of new matches for the next period. Since the individual contribution to the epidemiological risk is very small, land use decisions will strongly favor intensive agriculture as there are no individual gains from producing matches except for fetching the market price (which is by definition lower than that for HYV). The higher the discount factor \(d\), the more intensive the cultivation of monocultural crops. As agriculture becomes more fragmented, i.e. as \(W\) increases, the amount of land dedicated to epidemiologically risky crops will increase\(^3\) as the individual farmer’s share in the risk becomes smaller. This is because the individual decision maker has diminishing control over the epidemiological pressure applied to the crop and thus accrues less and less benefits from a restraint on intensive use.

Diagram 4: Cooperative versus non-cooperative solution

Comparing the non-cooperative outcome with the socially optimal one, it is apparent that the share of intensive agriculture is greater under a social planner’s regime only if the social discount rate exceeds

\[X^n = \left[\frac{\rho \delta}{a^{1-\beta}}\right]^{\frac{1}{\beta}} \cdot \frac{1}{W^{\beta}}\]

\[N^n = \frac{1}{\beta} (pl_X - zR_X) \left[\frac{\rho \delta}{a}\right]^{\frac{1-\beta}{\beta}} \cdot \frac{1-\beta}{\beta}\]

\(^3\) A countervailing force against this may be individual risk-managing behavior (see Goeschl and Swanson 1996). This may give a lower bound on \(X\).
the private rate and/or if crop resistance caused massive evolutionary dynamics, i.e. certainly more than the suspected 1.5 or 2.5% (Heisey and Brennan 1991). In general it can be safely assumed that

\[ I_N + r < \delta \alpha^\beta W. \]  

(31)

Even if this was not the case for low levels of \( W \), i.e. in case of a high degree of centralized decision making in agriculture involving only few planners, under realistic conditions, this situation rapidly changes to the scenario described in equation (31) such that we can conclude that land use will be generally higher under the decentralized scheme.

Having established this result, it is easy to show that also the level of crop resistance chosen under the social scheme is below the private optimum since with the social level of land use smaller than the individual one,

\[ (W \cdot p \delta)^{\beta-1} > X^s \beta \]

which follows from comparing the equations for \( N_A^s \) and \( N^n \). Since the agricultural optimum, \( N_A^s \), is greater than the social first-best, but smaller than the individual choice \( N^n \), it follows that the social best is also smaller than \( N^n \).

Diagram 4 shows a situation for a high degree of decentralized decision making. The non-cooperative outcome \((X^n, N^n)\) now lies above the socially optimal levels in the region outside the structural constraint \( SC \) which would have to be maintained to receive sufficient information in order to allow public institutions to efficiently screen gene bank accessions for suitable material.\(^36\) At the same time that the information flow cannot be maintained over the long run, the institutions which administer the genetic resource stock have no capacity to limit the maximum size of intensive agriculture which is only constrained by farmers’ own interest in limiting local epidemiological risks. There is therefore no automatic mechanism for communicating society’s interest in the maintenance of non-intensive lands to the individual decision maker.

Since farmers essentially maximize on the assumption that the price of resistance-conferring alleles will remain constant, it is this assumption of non-scarcity which leads them to aim at higher current yields sustained by high inputs of resistance genes. This rate of information transfer cannot be maintained indefinitely, however. It is quite apparent that either the reserve sector that remains runs

\(^{36}\)The under-utilization of material in gene banks can be traced back exactly to the problem of not being able to assess genetic material whose disease context and history is unknown (Duvick 1984).
out of new matches in sufficient numbers to support the yields or that search costs in any reserve of matching alleles held in a gene bank will be soar rapidly due to the lack of information available.

In this section we demonstrated that a decentralized solution to land use decision will result in an agricultural system which places priority on the production objective of the individual farm household. This is achieved at the expense of the long-term need to provide the informational foundations for the detection and conservation of alleles which can confer resistance against adapting pathogens. We have also established that there is no direct way in which society’s interest in the management of epidemiological and evolutionary pressures as well as its interest in optimal information management are reflected in the individual decision maker’s choices. Thus instruments have to be developed which can help implement the socially desirable allocation.

7. Policy Implications

In the absence of coinciding decentralized and socially optimal solutions to land use decisions, it is important to consider the instruments available to a social planner to bring about the desirable outcome.

The formulation of the determinants of $X^a$ suggest basically two avenues, and the consideration of the equation of motion a third. To recapitulate, the non-cooperative outcome for a decentralized agricultural system is

$$X^a = \left( \frac{p \delta}{a^{1-\beta}} \right)^\frac{1}{\beta} \cdot W^{\frac{1}{\beta}}$$  \hspace{1cm} (33)

Short of directly enforcing the optimal levels or of centralizing choice in agriculture, the social planner can choose between three decentralized instruments to bring the level of monoculture into line with the cooperative level: (1) Decreasing the cost of new resistance genes, $p$, (2) decreasing the marginal product of labor in the intensive sector by removing labor from the reserve such that $a$ increases, and (3) subsidizing those types of technological change which increase the productivity of land relative to labor. These policy options are somewhat problematic: In the first case, price subsidies\textsuperscript{37} entail social losses in the plant breeding sector which have to be accounted for. Options (2) and (3) can be expected to have a long reaction time and have structural consequences outside the agricultural sector. Thus they create unfavorable spill-overs into other markets.

\textsuperscript{37} Decreasing the release price is \textit{prima facie} a counter-intuitive policy since one would expect demand for resistance to increase with lower price. But in our two-sector model, the mechanism which drives the farmers’ decisions is the maintenance of equal marginal productivity in both sectors. A lower price for resistance decreases the cash-flow pressure on farmers and thus leads to an expansion of the reserve as a result of the balancing of the two sector at the efficiency frontier.
Apart from implementing optimal land use rules, the level of resistance genes used needs adjusting. The range of instruments available to the social planner thus increases by one, the market price for products from diverse agriculture, \( z \).

\[
N^n = \frac{1}{\beta} (p l_X - z R_X) \left[ \frac{p \delta}{a} \right]^{-\frac{1-\beta}{\beta}} W^{1-\beta} 
\]

With two equations and two unknowns, the system is principally solvable by applying the optimal choices for the price to be charged for allele transfer, \( p \), and for the market price for non-intensive produce, \( z \).\(^{38}\) To determine these levels is a simple algebraic exercise and produces a sufficient result for implementing the socially optimal policy.

A third instrument available to the social planner is to target the level of resistance directly rather than working through the price mechanism. This is effected by setting release quotas for resistance genes to be transferred into the intensive sector. After all, it is the perceived possibility of being able to renew the stock of resistance genes at a constant price and basically unlimited levels which gives the incentives for operating beyond the sustainable level. By setting binding quotas on the release rate, which is accomplished by control over the gene banks and public plant breeding institutions such as CIMMYT and IRRI, this policy not only forces down the level of resistance levels, but also that of monoculture since only a certain amount of loss can be recovered from the gene pool.

The basic idea behind fixed release quotas is that the government can threaten to commit itself to a policy which provides only a certain amount of resistance per year in line with a target loss. This target loss determines a specific level of land use at the current level of crop resistance. If resistance could be rationed individually, farmers would have to suffer the long run consequences of overexploitation in the form of decreasing yields. The obvious problems with this policy are whether this threat is credible given the governments own interest in safeguarding food supply (which would be compromised by a sufficiently large number of farmers deviating from the policy path) and whether individual rationing of genetic material can be effected in reality.

8. Conclusion

In this paper, we developed a perspective on agriculture as a gamble in which humans have supplanted natural diversity by a highly uniform biosphere consisting of man’s most preferred species and, more specifically, varieties. This modification of the biological environment represents a gamble

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\(^{38}\) Curiously, the optimal policy is to decrease the unit revenues farmers receive from diverse agriculture. The reason for this is the effect of portfolio balancing. Increased revenues in the reserve must be accompanied by increased productivity in the intensive sector which can only be achieved by either increasing the level of resistance or the level of land use.
because evolutionary ecology has given reasons to suggest that its impact on the overall stability of the biological system (measured in terms of being able to continue this process) - initially assumed to be neutral - has been unfavorable.

To illustrate a specific aspect of this gamble, the move towards intensive and genetically narrowed agriculture on a large scale, we applied some recent techniques developed in the literature on genetic games. These demonstrated that the continued investment in highly productive agriculture has to be accompanied by a similar investment in ensuring the continued flow of genetic information into intensive cultivation. The reason is that some of risks created through agricultural activity can only be insured within the sector and not substituted for by a third sector such as industry or a gene bank system. At the same time, we showed that why this investment has not and will not result from decentralized decision-making in agriculture. A number of instruments are available to social planners, though, in order to implement the socially desirable outcomes by changing economic parameters in the farmer’s environment.

References:


Annex: MatLab® Simulation program for disease probability curves

% Simulation Program for MatLab Version 4.2b

% This is a simulation program for a monocultural agriculture where two lesions occur in the
% first planting period at random locations.
% The simulation shows the probability landscape for lesions across the agricultural space.
% There are 10 pathogen generations per host generation.
% We show here the case where the cultivation is not changed in response to pathogen virulence.
% After each planting season, the expected number of lesions are registered which then evolve.
% The result shows that after 5 years, the probability of a lesion at practically any location
% on the space is above 90 percent if there is no change in the crop plant.
% Fitness of unmatched pathogen is set at 5, of matched 1. The simulation is fairly robust against
% the relative fitness values chosen within an order of magnitude, however.

clear
clc
clf

space = ones(510,1); %define landscape
new_space = ones(510,1); %define reference landscape
space(round(rand*509)+1) = 5; %random lesions
space(round(rand*509)+1) = 5;

spatial_weights = [0.01 0.02 0.043 0.087 0.17 0.34 0.17 0.087 0.043 0.02 0.01]; %1-dimensional infection
function

figure(3)
axis([0 510 0 1])

coll = 505;
M=moviein(20);

for seasons=1:10, %host generations

    for gen=1:10, %pathogen generations

        for i=6:coll, %check all locations

                limitl=i-5;
                limitr=i+5;

        end

    end

end
neighbours = space(limitl:limitr);
gewichte = spatial_weights .* neighbours';
summe = sum(gewichte);
normgewichte = (1/summe)*gewichte; %unit intervall
new_space(i)= normgewichte * neighbours;
end

l_prob = .25 * (new_space - 1); %construct probability distribution
cumul(gen)=sum(l_prob);
figure(3)
plot(l_prob, 'b')
axis([0 510 0 1])
M(:,gen)= getframe;

space = new_space;
end

figure(2)
plot(cumul,'g+') %plot cumulative fitness of pathogens
% realizations
les = round(cumul(gen));
for b=1:les, %infect new lesions according to probability dist
    loc = round(rand *509) +1;
    if space(loc) > 1, space(loc) = 5;
    else space(loc) = 1;
end
end