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Transgenic plants for tropical regions: Some considerations about their development and their transfer to the small farmer

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ABSTRACT Biotechnological applications, especially transgenic plants, probably hold the most promise in augmenting agricultural production in the first decades of the next millennium. However, the application of these technologies to the agriculture of tropical regions where the largest areas of low productivity are located, and where they are most needed, remains a major challenge. In this paper, some of the important issues that need to be considered to ensure that plant biotechnology is effectively transferred to the developing world are discussed.

The world's population is expected to double by the year 2050, making food security the major challenge for the next millennium. Food production will have to be doubled or preferably tripled by the year 2050 to meet the needs of the expected 11 billion people, of whom ninety percent will reside in the developing world. The enormity of the challenge is significantly increased by the declining availability of water and the fact that this additional food will have to be produced on existing agricultural land or in regions considered as marginal soils, if we want to preserve the forested regions and the environment as a whole.

Agricultural research and technological improvements are, and will continue to be, required for increasing agricultural productivity. There are numerous ways in which agricultural productivity may be increased in a sustainable way, including the use of biological fertilizers, improved pest control, soil and water conservation, and the use of improved plant varieties, produced by either traditional or biotechnological means. Of these measures, biotechnological applications, especially transgenic plant varieties, probably hold the most promise for augmenting agricultural production and productivity, when properly integrated into traditional systems.

The Case for Genetically Engineered Plants. The effectiveness of transgenic plant varieties in increasing production and lowering production cost has been demonstrated in the cases of virus-, insect-, and herbicide-resistant plants, in which an average increase in production of 5% to 10%, and a saving in herbicides of up to 40% and in insecticides of between $60 to $120 per acre, have been reported in 1996 and 1997 (1). However, these increases in productivity, impressive as they are in terms of their economic and environmental value, will have a limited impact for global food supply. In fact, most of the developments in transgenic crops are aimed either at reducing production costs in agricultural areas that already have high productivity levels or at increasing the value added to the final product by improving, for instance, oil quality. This trend has been stimulated by the current policies of developed countries to limit production of key products such as cereals, meat, and dairy products because of the reductions in international prices of these products, and to reduce the intensive use of fertilizers and pesticides because of their deleterious effects on the environment.

In a global sense, a more effective strategy would be to increase productivity in tropical areas, where an increase in food production is needed and where crop yields are significantly lower than those obtained in developed countries. In tropical areas, the losses caused by pests, diseases, and soil problems are exacerbated by climatic conditions that favor high levels of insect pests and vectors and by the lack of the economic resources to apply insecticides and fertilizers and to purchase high-quality seeds.

In addition to low productivity levels, postharvest losses in tropical areas are very high, again because of climatic conditions that favor fungal and insect infestation and because of the lack of appropriate storage facilities. Despite efforts to prevent preharvest and postharvest crop losses, pests destroy over half of all world production. Preharvest losses caused by insects, the majority of which occur in the developing world, are calculated at around 15% of the world's production.

Using biotechnology to produce transgenic plants that better withstand diseases, insect attack, or unfavorable soil conditions, is not a simple task. There are an estimated 67,000 species of insects worldwide that damage crops and a similar or even higher number of plant pathogens. For instance, in the case of *Phaseolus vulgaris,* over 200 diseases and 200–300 species of insects can affect bean productivity (2). These numbers give an idea of the complexity of the task that scientists face in increasing productivity. There are of course a certain number of diseases and insect pests that can be singled out as the most important constraints for the production of each crop. However, it is also true that when a particular disease or insect pest is controlled, others considered as minor can then flourish, and themselves become major productivity constraints.

One of the major advantages of plant biotechnology is that it can generate strategies for crop improvement that can be applied to many different crops. In this sense, genetically engineered virus resistance, insect resistance, and delayed ripening are good examples of strategies that can benefit many different crops. Transgenic plants of over 20 plant species that are resistant to more than 30 different viral diseases have been produced by using different variations of the pathogen-derived resistance strategy. Insect-resistant plant varieties, using the δ-endotoxin of *Bacillus thuringiensis*, have been produced for several important plant species including tobacco, tomato, potato, cotton, walnut, maize, sugarcane, and rice. Of these, maize, potato, and cotton are already under commercial production. It is envisaged that these strategies can be used for many other crops important for developing countries. Genetically engineered delayed ripening, although tested only on a commercial scale for tomato, has an enormous potential application for tropical fruit crops, which suffer severe losses because they ripen rapidly, and in many developing countries there are neither appropriate storage conditions nor adequate transportation systems to allow their efficient commercialization.

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To date, most of the developments in plant gene transfer technology and the different strategies for producing improved transgenic plant varieties have been driven by the economic value of the species or the trait. These economic values are in turn mainly determined by their importance to agriculture in the developed world, particularly the United States and Western Europe. This economical emphasis is understandable, because important investments are needed to develop, field test, and commercialize new transgenic plant varieties. However, in terms of global food production, it is necessary to ensure that this technology is effectively transferred to the developing world and adapted to the local crops and/or local varieties of crops for which it was originally developed.

Developing improved transgenic versions of local varieties or local crops is not a trivial issue; in most, if not all, cultures, the use of specific crops has a deep social and/or religious meaning. Cultural preservation is just as important as environmental preservation. Cultural aspects of technology transfer need to be considered because simply replacing crops to increase productivity could have an enormously negative effect for certain cultures, and new introductions may not be accepted easily for human consumption.

It is unfortunate that most developing countries do not have sufficient resources to implement the biotechnological capacity needed to solve the major problems that limit agricultural productivity, at least not in the time frame that is required to cope with the increasing demand for food. However, it is in the developing world that biotechnology could have its major impact in increasing crop production, especially in the areas of the world where yields are low because of the lack of technology.

Plant genetic engineering could be considered a neutral technology that in principle does not require major changes in the agricultural practices of farmers in developing countries. Perhaps more importantly, it has the potential to bring about great benefits to the small farmers who lack the economic resources to purchase agrochemicals or prevent postharvest losses because of the lack of storage facilities.

Whether there is time to increase agricultural productivity in the developing world is a question with a complex answer, because there are many factors that need to be taken into account to make this happen. We need to identify and establish mechanisms of technology transfer from developed countries, from both academic institutions and the private sector, to the developing world; there is a need to create a sufficient number of research centers with the capability of acquiring this technology, adapting it to local crops, and developing their own technologies. Seed production facilities must be improved and an effective mechanism implemented to reach subsistence farmers with this new technology. To meet these requirements, several economic, political, and social issues must be dealt with to ensure the general application of plant biotechnology to the agriculture of developing countries. The discussion of these issues goes beyond the scope of this article. However, it is my personal opinion that it will not be technological limitations but rather political and/or economic constraints that will determine how successful we are in supplying food to the hundreds of millions of people who will be malnourished in the next millennium.

Soil Acidity: A Problem for Agriculture in the Tropics. Estimates of the world's potentially arable land resources indicate that only 10.6% of the total land area of the world is cultivated, and about 24.2% is considered cultivable or is potentially arable land (3–5). Of these 2.5 billion hectares of potentially cultivable land, 68% is located in the humid tropics (6). The acid soils of the tropics, especially in the savannas, that historically have resisted permanent settlement and agricultural use are considered to represent the largest remaining potential for future agricultural development (7).

There are problems limiting food production that are specific or more significant to the agriculture of tropical and subtropical regions, but that unfortunately have not been given sufficient importance to deserve being considered priorities in the research being done in developed countries. However, solutions to these problems could significantly contribute to food production in tropical areas. Because many of these problems are common to many developing countries and affect the productivity of a wide spectrum of crops, transgenic strategies to solve them that can be applied to different plant species are urgently needed.

Among the problems common to tropical regions, probably the most important is soil acidity. On a global scale, there are two main geographical belts of acid soils: the humid northern temperate zone that is covered by coniferous forest and the humid tropics, which are (or in some cases were) covered mainly by savanna and tropical rain forest. Soil acidification can develop naturally in humid climates when basic cations are leached from soils but can be considerably accelerated by certain farming practices and by acid rain (8).

Acidic soils comprise about 3.95 billion hectares of the ice-free land or approximately 40% of the world's arable land. Regions with subsoil acidity occupy about 20% of the ice-free land surface. Approximately 43% of the world's tropical land area is classified as acidic, comprising about 68% of tropical America, 38% of tropical Asia, and 27% of tropical Africa (9, 6).

Tropical Acid Soils That Could Be Used for Agriculture. Because a great proportion of forest land is located in acid soils, it is important to remember that not all soils, although potentially arable land, can be used for agriculture. Tropical forests are invaluable with regard to their role in local, regional, and global ecosystems and to the biodiversity found within them (over 90% of plant and animal species live in forest ecosystems). Indiscriminate conversion of tropical forest into agricultural land will have far-reaching ecological consequences, whose effects will certainly outweigh the potential gain in food production. In spite of these consequences, 11 million or so hectares of forest are cleared every year, of which only a small fraction is converted into productive agricultural land, and most of it becomes unproductive grassland (6).

Policies to use acid soils for agriculture should be directed to the acid savannas of the world such as the Cerrado in Brazil, Los Llanos of Venezuela and Colombia, the savannas in Africa, and the largely anthropic savannas of tropical Asia. These acid savannas cover an area of over 700 million hectares (which is approximately 50% of the global area that is currently under cultivation), and their potential in food production for both humans and animals could account for a large portion of that required to satisfy the need of the growing population in the next millennium. There are good examples in Brazil and Asia of successful development of acid savanna into productive land for the cultivation of sugarcane and soybean (6). The use of biotechnology could facilitate enormously the conversion of low-productivity acid savannas into productive cropland.

Aluminum Toxicity. Poor crop productivity and soil fertility in acid soils are mainly caused by a combination of aluminum and manganese toxicity and nutrient deficiencies (mainly deficiencies in P, Ca, Mg, and K). Among these problems, aluminum toxicity has been identified as the most important constraint for crop production in acid soils. Aluminum toxicity problems are of enormous importance for the production of maize, sorghum, and rice in developing countries located in tropical areas of Asia, Africa, and Latin America. Most maize, sorghum, and rice cultivars currently being used are susceptible to toxic aluminum in the soil, and decreases in yield of up to 80% resulting from aluminum toxicity have been extensively reported in the literature (10–12). In particular, maize and sorghum production is severely limited in tropical Africa, where over 45% of the total land area in countries such as Zaire, Zambia, and the Ivory Coast is covered by acidic soils.

In tropical South America, aluminum toxicity is a problem shared by several countries, where about 850 million hectares, or 66% of the region, has acid soils. In Brazil alone, acid savannas with low cation exchange capacity and high toxic aluminum saturation cover 205 million hectares, of which 112 million are suitable for maize and sorghum production (9).

Aluminum has a clear toxic effect on roots, disturbing plant metabolism by decreasing mineral nutrition and water absorption. The most easily recognized symptom of Al toxicity is the inhibition of root growth, and this has become a widely accepted measure of Al stress in plants. Although Al toxicity primarily restricts root growth, given sufficient exposure, myriad different symptoms appear on both roots and shoots that are often mistaken for soil nutrient deficiencies. Therefore, crop production in acid soils is, to a great extent, limited by nutrient uptake deficiency caused by the inhibition of root growth and function that results from the toxic effects of Al (13). Moreover, in some acid soils, plant growth is affected not only by aluminum toxicity but also by low availability of some essential elements such as P, Ca, Mg, and Fe, some of which form complexes with Al and consequently are not readily available for root uptake (14).

It is well documented that many plant species exhibit significant genetic variability in their ability to tolerate Al. Although it is clear that certain plant genotypes have evolved mechanisms that confer Al resistance, the cellular and molecular basis for Al resistance is still poorly understood (13).

Two basic strategies by which plants can tolerate Al have been proposed: (*i*) the ability to exclude Al entry into the root apex and root hairs, and (*ii*) the development of mechanisms that allow the plant to tolerate toxic concentrations of Al within the cell.

Several conceptually attractive hypotheses have been proposed to explain how plants could exclude Al from entering into the root. For example, mechanisms based on alteration in rhizosphere pH, low cell-wall cation-exchange capacity, or Al +3 efflux across the plasma membrane (13). However, experimental evidence from several research groups supports a mechanism that results in Al exclusion from the root apex via the release of Al-binding ligands such as malic and citric acids. When these ligands are released into the rhizosphere, they can effectively chelate Al^{+3} and prevent its entry into the root.

The potential role of organic acid release in Al tolerance was originally proposed by Miyasaka *et al.* (15). Their work showed that the root system of an Al-tolerant snapbean cultivar grown in Al-containing solutions released 10 times as much citrate as an Al-sensitive cultivar grown in the presence of Al. The most complete analysis of the possible role of organic acids as Al^{+3}-chelating molecules in naturally resistant plants comes from the work, done by Delhaize and coworkers (16, 17), using near-isogenic wheat lines differing at the Al tolerance locus (Alt1). These researchers found that, on treatment with Al, tolerant wheat varieties release 5- to 10-fold more malate than do susceptible lines, and that this increased capacity to excrete malate correlated with Al resistance and Al exclusion from the root apex. Because malic acid excretion is located in the root apex, the amount of malic acid excreted depended on the external Al concentration, and the Al tolerance cosegregates with high rates of malate excretion, Delhaize *et al.* (16, 17) proposed that the Alt1 locus in wheat encodes a component of an Al-tolerance mechanism based on the Al-stimulated excretion of malic acid.

The existence of Al-tolerance mechanisms based on the excretion of organic acids has also been reported for plant species other than wheat: citrate in the case of maize, snap beans, and *Cassia tora* (18–20), and oxalic acid for buckwheat (*Fagopyrum esculentum* Moench) (20).

An Example of How Transgenic Plants Could Improve Productivity in Acid Soils. The production of Al-tolerant transgenic plant varieties should be considered an important part of crop management strategies to increase agricultural production on acid soils and to protect forests around strongly acidified industrial regions.

Generation of metal-tolerant plants through genetic engineering has been demonstrated to be a valid approach. For instance, expression of the alpha domain of human metallothionine IA in transgenic tobacco plants confers cadmium resistance (21).

The production of transgenic plants with an increased capacity to produce and/or excrete organic acids that chelate and detoxify Al in the rhizosphere is an appealing strategy to produce Al-tolerant plants. The effectiveness of citric acid in alleviating Al toxicity has also been demonstrated by adding citrate to solutions containing toxic levels of Al, which reverses the inhibition of wheat root growth caused by Al (22). Citric acid forms a strong chelate with Al, typified by a stability constant of 5×10^8 M^{-1}, which is about 700-fold greater than the corresponding value for the malate–Al complex (23).

Citrate overproduction, therefore, appears to be an ideal candidate to produce Al-tolerant transgenic plants. To test whether citrate overproduction could be achieved in transgenic plants and to assess the impact of elevated levels of citrate on aluminum tolerance, our research team produced transgenic tobacco lines that overexpress the citrate synthase from *Pseudomonas aeruginosa* in their cytoplasm (24).

To produce these plants, a chimeric gene, in which the coding sequence of the *P. aeruginosa* citrate synthase gene (25) transcriptionally fused to the ^{35}S promoter from the cauliflower mosaic virus, was introduced into the genome of tobacco plants. Biochemical analysis of these transgenic tobacco lines showed that most of them had elevated levels of citrate synthase and that they contained in their roots 10-fold higher levels of citrate and exuded five times more of this organic acid into the rhizosphere than did their nontransformed siblings.

Because the evidence for the role of organic acid excretion in aluminum tolerance is rather indirect, it was important to determine whether the lines with elevated levels of citrate synthesis and excretion are less or equally susceptible than wild-type plants to phytotoxic concentrations of Al. It was observed that the inhibition of root growth by phytotoxic concentrations of Al is significantly lower in the citrate synthase overproducing lines than in the control (24).

To test whether the same strategy could be used in other plant species, the chimeric gene encoding the bacterial citrate synthase was used to transform papaya plants, a crop that is grown in tropical areas where aluminum toxicity limits its cultivation. It was found that transgenic papaya plants expressing the bacterial enzyme developed roots at concentrations of up to 150 mM Al, whereas the controls failed to do so in concentrations above 50 mM (24).

The finding that in two different plant species an increased capacity to produce and excrete citrate led to Al tolerance suggests that this strategy might be useful in many different plant species.

The production of Al-tolerant plants is just one example of what plant biotechnology could do to improve productivity in developing countries. Drought-tolerant plants or plants with an enhanced capacity to take up nutrients that are present in tropical soils, but that are not readily available for plant nutrition are examples, among others, of technology that could be produced by genetic engineering means, and that could significantly elevate productivity.

Transfer of Technology to Developing Countries. Most of the available technology for producing improved transgenic plant varieties could effectively be used to improve productivity in developing countries. Because most, if not all, of these technologies have been patented and belong to private corporations, a major challenge is to identify and establish the mechanisms to effectively transfer this technology to developing countries. Several avenues could be followed: one would be the training of scientists from developing countries in universities, research institutes, and companies in developed countries; a second one is to assist developing countries in establishing their own facilities for biotechnological research; and the third one is to transfer technology, by means of gene constructs or transgenic plants, from universities or companies to the existing research centers in the developing world.

In terms of training and capacity building, several foundations and government agencies have important programs. Good examples of successful programs of this kind are the rice and cassava programs of the Rockefeller Foundation, the program of the Biotechnology Action Council of the United Nations Educational, Scientific and Cultural Organization (UNESCO) and the International Cooperation (INCO) program of the European Commission, among others. In particular, the success of the Rockefeller rice biotechnology program can be highlighted, which in a few years stimulated biotechnological research for this crop in the U.S. and Europe and facilitated the establishment of rice molecular biology research in many laboratories in many countries in the developing world.

In the short term, the direct transfer of technology may be the most effective strategy to implement plant biotechnology to increase productivity in the developing world. Technology transfer can be done by using end products (transgenic seed) that have been developed for the agriculture of advanced countries. Transfer of end products in some cases will be done anyhow if the market is of value to the companies; however, the use of such seed will probably be limited to intensive agriculture of a nature similar to that for which the transgenic seed was originally developed. It would be more interesting if transgenic seeds were transferred to national breeding programs, which could be used as the basis for developing local varieties better suited to local environment and soil conditions.

Another possibility is to transfer gene constructs to research institutes that have the capacity to introduce this genetic material into local crops or varieties. How to achieve this is still not completely clear, but a number of mechanisms are beginning to be explored. Transferring this technology has some problems; for instance, when royalties can be waived and when not. Perhaps a naive approach would be to reach agreements in which the technology is donated on a royalty-free basis if it will be used only for production aimed at internal markets of developing countries. In cases where export is possible, royalties should of course be paid; if the farmers can export their products, however, they should at least have certain capacities to share their increased income with the providers of the technology.

To be able to meet the needs of developing countries with technology available in public and private institutions in developing countries, a source of easily accessible information will be needed, which preferentially indicates which institutions or companies agree in principle to donate technology. Initial attempts in this direction have been carried out by the International Service for the Acquisition of Agrobiotech Applications (ISAAA). This nonprofit organization is attempting to play the role of an "honest broker," identifying needs in their target countries and assisting a national institution to reach an agreement with the companies that have the technology that can potentially solve the problem. An example of this is the agreement between the Centro de Investigación y Estudios Avanzados in Mexico and Monsanto to develop virus-resistant potatoes for the Mexican market (26). Having a company as a partner makes it more likely that all the steps, from basic research to field evaluation, are carried out successfully. These still-limited initiatives should be significantly enhanced to make sure that plant biotechnology is transferred to developing countries at an adequate pace.

To ensure effective technology transfer, each recipient country must have a research center with the capacity to assimilate the technology and apply it to local crops or local varieties. Although several developing countries, such as Brazil, Argentina, India, and China, have at least some of this capacity, it is clear that not all developing countries have research institutes with sufficient infrastructure and trained personnel to effectively participate in this process. It is therefore urgent that the countries that do not have such capabilities give priority to the establishment of research groups, as well as the regulatory bodies required to assess and approve the use and commercialization of genetically modified organisms.

Even if technology is successfully transferred to developing countries and transgenic varieties are developed for local crops, the problem of getting this technology to the small farmer is still an important challenge. The government of each country needs to implement a system for producing and distributing transgenic seeds and any other input, at low or no cost, to the small farmer. Whether technology transfer to developing countries takes place will, of course, depend on the political will of each national government and the resources required.

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