Genetic Glass Ceilings

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Transgenics for Crop Biodiversity

Jonathan Gressel

Foreword by

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Dedicated to the memory of Professor Leroy (Whitey) Holm, the person who stimulated me to think differently.

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Foreword

The Needs for Plant Biodiversity: The General Case

Biological diversity (often contracted to *biodiversity*) has emerged in the past decade as a key area of concern for sustainable development, but crop biodiversity, the subject of this book, is rarely considered. Jonathan Gressel's important contribution to the discussion of crop biodiversity in this volume should be considered as part of the general case for biodiversity. Biodiversity provides a source of significant economic, aesthetic, health, and cultural benefits. The well-being of earth's ecological balance as well as the prosperity of human society directly depend on the extent and status of biological diversity. Biodiversity plays a crucial role in all the major biogeochemical cycles of the planet. Plant and animal diversity ensures a constant and varied source of food, medicine, and raw material of all sorts for human populations. Biodiversity in agriculture represents variety in the food supply, allowing choices for balanced human nutrition as well as a critical source of genetic material for the development of new and improved crop varieties. In addition to these direct-use benefits, enormous less tangible benefits can be derived from natural ecosystems and their components. These include the values attached to the persistence, locally or globally, of natural landscapes and wildlife, values that increase as such landscapes and wildlife become scarce. The relationships between biodiversity and ecological parameters, linking the value of biodiversity to human activities, are summarized in part in Table 1.

Biological diversity may refer to diversity in a gene, species, community of species, ecosystem, or even more broadly, the earth as a whole. Biodiversity comprises all living beings, from the most primitive forms of viruses to the most sophisticated and highly evolved animals and plants. According to the 1992 International Convention on Biological Diversity, biodiversity means "the variability among living organisms from all sources including, terrestrial,

Table 1. Primary Goods and Services Provided by Ecosystems

Ecosystem	Goods	Services
Agroecosystems	Food crops Fiber crops Crop genetic resources	Maintain limited watershed functions (infiltration, flow control, partial soil protection) Provide habitat for birds, pollinators, soil organisms important to agriculture Build soil organic matter Sequester atmospheric carbon Provide employment
Forest ecosystems	Timber Fuelwood Drinking and irrigation water Fodder Nontimber products (vines, bamboos, leaves, etc.) Food (honey, mushrooms, fruit, and other edible plants; game) Genetic resources	Remove air pollutants, emit oxygen Cycle nutrients Maintain array of watershed functions (infiltration, purification, flow control, soil stabilization) Maintain biodiversity Sequester atmospheric carbon Generate soil Provide employment Provide human and wildlife habitat Contribute aesthetic beauty and provide recreation
Freshwater ecosystems	Drinking and irrigation water Fish Hydroelectricity Genetic resources	Buffer water flow (control timing and volume) Dilute and carry away wastes Cycle nutrients Maintain biodiversity Sequester atmospheric carbon Provide aquatic habitat Provide transportation corridor Provide employment Contribute aesthetic beauty and provide recreation
Grassland ecosystems	Livestock (food, game, hides, fiber) Drinking and irrigation water Genetic resources	Maintain array of watershed functions (infiltration, purification, flow control, soil stabilization) Cycle nutrients Remove air pollutants, emit oxygen Maintain biodiversity Generate soil Sequester atmospheric carbon Provide human and wildlife habitat Provide employment Contribute aesthetic beauty and provide recreation

Table 1. Primary Goods and Services Provided by Ecosystems (continued)

Ecosystem	Goods	Services
Coastal and marine ecosystems	Fish and shellfish Fishmeal (animal feed) Seaweeds (for food and industrial use) Salt Genetic resources Petroleum, minerals	Moderate storm impacts (mangroves; barrier islands) Provide wildlife (marine and terrestrial) habitat Maintain biodiversity Dilute and treat wastes Sequester atmospheric carbon Provide harbors and transportation routes Provide human and wildlife habitat Provide employment Contribute aesthetic beauty and provide recreation
Desert ecosystems	Limited grazing, hunting Limited fuelwood Genetic resources Petroleum, minerals	Sequester atmospheric carbon Maintain biodiversity Provide human and wildlife habitat Provide employment Contribute aesthetic beauty and provide recreation
Urban ecosystems	Space	Provide housing and employment Provide transportation routes Contribute aesthetic beauty and provide recreation Maintain biodiversity

marine, and other aquatic ecosystems and the ecological complexes of which they are part."[197] It is not a simple task to evaluate the need for biodiversity, in particular, to quantify agroecosystem biodiversity versus total biodiversity.[39,874,1061]

Types, Distribution, and Loss of Biodiversity

Genetic Diversity

In many instances genetic sequences, the basic building blocks of life, that encode functions and proteins are almost identical (highly conserved) across all species. The small unconserved differences are important, as they often encode the ability to adapt to specific environments. Still, the greatest importance of genetic diversity is probably in the combination of genes within an organism (the genome), because the variability in phenotype produced confers resilience and survival under selection. Thus, it is widely accepted that natural ecosystems should be managed in a manner that protects the untapped resources of genes within the organisms needed to preserve the resilience of the ecosystem. Much work remains to be done to both characterize genetic diversity and understand how best to protect, preserve, and make wise use of genetic biodiversity.[880]

The number of metabolites found in one species exceeds the number of genes involved in their biosynthesis. The concept of one gene–one mRNA–one protein–one product needs modification. There are many more proteins than genes in cells because of posttranscriptional modification. This can in part explain the multitude of living organisms that differ in only a small portion of their genes. It also explains why the number of genes found in the few organisms sequenced is considerably lower than anticipated.

Species Diversity

For most practical purposes measuring species biodiversity is the most useful indicator of biodiversity, even though no single definition exists of what is a species. Nevertheless, a plant species is broadly understood to be a collection of populations that may differ genetically from one another to some extent, but whose members are usually able to mate and produce fertile offspring. These genetic differences manifest themselves as differences in morphology, physiology, behavior, and life histories; in other words, genetic characteristics affect expressed characteristics (phenotype). About 1.75 million species have been described and named but the majority remain unknown. The global total might be ten times greater, most being undescribed microorganisms and insects.

Ecosystem Diversity

At its highest level of organization, biodiversity is characterized as ecosystem diversity, which can be classified in the following three categories:

— *Natural ecosystems* (ecosystems free of human activities) are composed of what has been broadly defined as "native biodiversity." It is a matter of debate whether any truly natural ecosystem exists today, because human activity has had an impact on most regions on the earth. It is unclear why so many ecologists seem to classify humans as being "unnatural."

— *eminatural ecosystems* (in which human activity is limited) are subject to some level of low-intensity human disturbance. These areas are typically adjacent to managed ecosystems.
— *Managed ecosystems* can be managed by humans at varying degrees of intensity from the most intensive, conventional agriculture and urbanized areas, to less intensive systems, including some forms of agriculture in emerging economies or sustainably harvested forests.

Beyond simple models of how ecosystems appear to operate, we remain largely ignorant of how ecosystems function, how they might interact with each other, and which ecosystems are critical to the services most vital to life on earth. For example, the forests have a role in water management that is crucial to urban drinking water supply, flood management, and even shipping.

Because we know so little about the ecosystems that provide our life support, we should be cautious and work to preserve the broadest possible range of ecosystems, with the broadest range of species having the greatest spectrum of genetic diversity within the ecosystems. Nevertheless, we know enough about the threat to, and the value of, the main ecosystems to set priorities in conservation and better management. We have not yet learned enough about the threat to crop biodiversity, other than to construct gene banks. Even here we have much to learn, as the vast majority of the deposits in gene banks are varieties and landraces of the four major crops. The theory behind patterns of general biodiversity related to ecological factors such as productivity is rapidly evolving, but many phenomena are still enigmatic and far from understood.[950,1062]

The Global Distribution of Plant Biodiversity

Biodiversity is not distributed evenly over the planet. Species richness is highest in warmer, wetter, topographically varied, less seasonal, and lower elevation areas. Far more species live in temperate regions (per unit area) than in polar ones, and yet far more are in the tropics than in temperate regions. Latin America, the Caribbean, the tropical parts of Asia and the Pacific host 80 percent of the ecological megadiversity of the world.[1100]

Within each region, every specific type of ecosystem supports its own unique suite of species, with their diverse genotypes and phenotypes. In numerical terms, global species diversity is concentrated in tropical rain forests.

Amazon basin rain forests can contain up to three hundred different tree species per hectare. Species and genetic diversity within any agricultural field will be more limited than in a natural or seminatural ecosystem. Nevertheless, agricultural ecosystems can be dynamic in terms of species diversity over time due to management practices. This is often not understood by ecologists who involve themselves in biosafety issues related to transgenics. They still think abaout ecosystems close (or seemingly close) to nature. Biodiversity in agricultural settings can be considered to be important at the country level in areas where the proportion of land allocated to agriculture is high. This is the case in continental Europe, for example, where 45 percent of the land is dedicated to arable and permanent crops or permanent pasture.[329] In the United Kingdom, this figure is even higher, at 70 percent. Consequently, biodiversity has been heavily influenced by humans for centuries, and changes in agrobiological management will influence overall biodiversity in such countries. Innovative thinking about how to enhance biodiversity, in general, coupled with bold action is critical in dealing with the loss of biodiversity.

Centers of biodiversity are a controversial matter, and even the definition of centers of crop biodiversity is still debated. Harlan[468] proposed a theory that agriculture originated independently in three different areas and that, in each case, there was a system composed of a center of origin and a noncenter, in which activities of domestication were dispersed over a span of five- to ten-thousand kilometers. One system was in the Near East (the Fertile Crescent) with a noncenter in Africa, another center included a north Chinese center and a noncenter in southeast Asia and the south Pacific, and the third system included a Central American center and a South American noncenter.[468] He suggests that the centers and the noncenters interacted with each other.

It is widely believed that centers of crop origin should not be touched by modern breeding because these biodiversity treasures are so fragile that these centers should stay free of modern breeding. This is an erroneous opinion, based on the fact that regions of high biodiversity are particularly susceptible to invasive processes, which is wrong. On the contrary, studies show that a high biodiversity means more stability against invasive species, as well as against genetic introgression.[753,1062,1148] The introduction of new predators and pathogens has caused numerous well-documented extinctions of long-term resident species, in particular, in spatially restricted environments such as islands and lakes. However, surprisingly few instances of extinctions of resident species can be attributed to competition from new competing species.

This suggests either that competition-driven extinctions take longer to occur than those caused by predation or that biological invasions are much more likely to threaten species through intertrophic than through intratrophic interactions.[255] This also fits well with agricultural experience, which builds on much faster ecological processes. Many ecologists err by not taking the ephemeral nature of agricultural plant communities into account.[36]

Loss of Biodiversity

Biodiversity is being lost in many parts of the globe, often at a rapid pace. It can be measured by loss of individual species or groups of species, or by decreases in the numbers of individual organisms. In a given location, the loss will often reflect the degradation or destruction of a whole ecosystem. The unchecked rapid growth of any species can have dramatic effects on biodiversity. This is true of weeds, elephants, and especially humans, who, being at the top of the chain, can control the rate of proliferation of other species, as well as their own, when they put their minds to it.

Habitat loss due to the expansion of human urbanization and the increase in cultivated land surfaces is identified as a main threat to 85 percent of all species described as being close to extinction. This threat can increase as so-called marginal langds are planted to biofuel crops. These lands are the last habitats left for many species. The shift from natural habitats toward agricultural land paralleled population growth, often thoroughly and irreversibly changing habitats and landscapes, especially in the developed world. Many from the developed world are trying to prevent such changes from happening in developing nations, to the consternation of many of inhabitants of the developing world who consider this to be ecoimperialism, promulgated by those unable to correct their own mistakes.

Today, more than half of the human population lives in urban areas, a figure predicted to increase to 60 percent by 2020 when Europe and the Americas will have more than 80 percent of their population living in urban zones. Five thousand years ago, the amount of agricultural land in the world is believed to have been negligible. Now, arable and permanent cropland covers approximately 1.5 billion hectares of land, with some 3.5 billion hectares of additional land classed as permanent pasture. The sum represents approximately 38% of the total available land surface of 13 billion hectares.[329]

Habitat loss is of particular importance in tropical regions of high biological diversity where food security and poverty alleviation simultaneously are key priorities. The advance of the agricultural frontier has led to an overall decline in the world's forests. Although the area of forest in industrialized regions has remained fairly unchanged, natural forest cover has declined by 8 percent in developing regions. Ironically, the most biodiverse regions are also those of greatest poverty, highest population growth, and greatest dependence on local natural resources.

Introduced species are another threat to biodiversity. Unplanned or poorly planned introduction of nonnative ("exotic" or "alien") species and genetic stocks can be, in a worst case scenario, is a major threat to terrestrial and aquatic biodiversity worldwide. Hundreds if not thousands of new and foreign genes are introduced with trees, shrubs, and herbs each year.[609,1025] Many of those survive and can, after years and even many decades of adaptation, begin to be invasive. This might be interpreted as increasing biodiversity, but the final effect is sometimes the opposite. The introduced species often displace native species such that many native species become extinct or severely limited.

Biodiversity should still act as biological insurance for ecosystem processes, except when mean trophic interaction strength increases strongly with diversity.[1053] The conclusion, which needs to be tested against field studies, is that in tropical environments with a natural high biodiversity the interactions between potentially invasive hybrids of transgenic crops and their wild relatives should be buffered through the complexity of the surrounding ecosystems. This view is also confirmed by the results of Davis.[255] Taken together, theory and data suggest that compared with intertrophic interaction and habitat loss, competition from introduced species is not likely to be a common cause of extinctions in long-term resident species at global, metacommunity, and even most community levels.

This general case for understanding and enhancing biodiversity should teach us, as Gressel endeavors to do, that the overdependence on so few crop species could be disastrous to world food security. Humans have the capability and obligation to enlarge the cultivated gene pool within insufficiently cultivated species, so that they again can contribute to crop biodiversity.

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Preface

The present volume started out as a journey to write a book on lost crops of the world and how to revive them transgenically to greatly enhance crop biodiversity. The Rockefeller Foundation was kind enough to be host for a month for thought and work at their exquisite facility in Bellagio, Italy, where much of the first draft was outlined and part was written. It immediately became apparent that the object of the journey was naãve insofar as it could not be determined that any crops had really been lost. Conversely, it was discovered that even major crops were precarious in their ability to cope with an ever-changing planet. The journey took on a new direction—to select a representative variety of crops that had reached their genetic ceilings; that is, that have problems that seem intractable to standard breeding but are potentially amenable to further repair by genetic engineering. The choices made are not exhaustive; the aim is not meant to supply a blueprint of how to deal with each crop and constraint. The aim is to present a spectrum of problems using real examples and then to describe how they might be analyzed and dealt with. This is not a recipe for repair but a recipe on how to think about the issues in a book meant for an audience well beyond the molecular community. Purdue University and Professor Gebisa Ejeta provided the quiet necessary for finishing the manuscript.

The amount of literature on underutilized and neglected crops is considerable. Much of it is hyperbole meant to convince people of the potential importance of each such crop but lacking a good analysis of why the crops are underutilized and of the constraints to their cultivation, especially where modern breeding has been ineffective because of a lack of genetic variability in the species. One series of publications stands out, where the missing links are well analyzed, spelled out in a manner that does not require reading between the lines. This is the highly recommended series of more than twenty monographs published by the International Plant Genetic Resources Institution (IPGRI, now called Bioversity International) in Rome on "Promoting the conservation and use of underutilized and neglected crops," The IPGRI and their staff are thanked for providing a copy of this series, although each crop is not examined, as many suffer common problems.

Many of the insights to the problems of the species involved came from an earlier 4.5-day workshop held at the same Rockefeller Foundation facility in Bellagio on ferality in crops, on whether or how transgenic technologies would increase the possibilities of crops becoming feral (published as *Crop Ferality and Volunteerism*).[417] It contains a considerable amount of lore about many crops, some of which is recited again here in a different context, where appropriate. It provided essential information needed for the biosafety analyses described herein for crops and genes in each of the case studies presented.

The author is especially thankful for the discussions, advice, and comments on Chapters 1 through 5 by Klaus Ammann. He kindly wrote a foreword on the general need for biodiversity, to put this book within the larger context, and contributed a few sections (noted in the text) in Chapters 2 and 3 where his expertise far exceeds the author's.

The following people have assisted in gathering the material, analyzing or writing on the following subjects with the author, or providing unpublished information:

— Hani Al-Ahmad on gene mitigation
— Rafael DePrado on silicon inclusions in rice
— Gebisa Ejeta on sorghum and a lot more
— Galo Jarrín on orchids
— Wally Marasas on mycotoxins
— James Ochanda on grain weevils
— Ziv Shani on cellulose modifications
— Bernal Valverde on rice
— Suzanne Warwick on domestication
— Sarit Weissmann and Moshe Feldman on gene flow from wheat
— Aviah Zilberstein on lignin modification

Without their input this book could not have been written, although they cannot be held responsible for the author's mistakes, interpretations, or opinions.

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