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68. We thank especially Y. A. Sidky for collaboration in the design and execution of these studies, B. Houser for excellent administrative assistance, and L. Kubai, L. W. Morrissey, and G. Holbrow for technical assistance. We also thank C. Hughes for help with the graphics, B. Van Nguyen for help with library work, and D. Chandler and G. Burns for help with photography. Our research work was supported by grants IM-102 from the American Cancer Society, PCM 79-22613 from the National Science Foundation, and AI 14607 from the National Institutes of Health.

Biological Control in Agroecosystems

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Crop yields in the United States are reduced by the effects of a variety of pests, including some 160 species of bacteria, 250 kinds of viruses, 8000 species of pathogenic fungi, 8000 species of insects, and 2000 species of weeds (*1*). Weeds are potentially the most damaging pests, followed by insects, plant pathogens, and nematodes (*2*). In spite of mechanized agriculture and advanced technology, losses of about 33 percent of potential production (*3*) or $20 billion annually (*4*) continue. Since 1945, agriculture has come to rely on synthetic chemicals (pesticides) for protection of crops. Usage of such chemicals has increased to over 544 million kilograms annually (*5*). Pesticides are valued for their uniform and rapid effectiveness, ease of application and shipment, and relatively long shelf-life. Unforeseen side effects, such as toxicity to nontarget organisms and induction of resistance in pests, have created a need to produce continually new pesticides, at a current cost of about $18 million each to develop, register, and market (*6*). For each pesticide marketed, more than 10,000 compounds may be screened (*7*) for effectiveness and safety.

Improvements in pesticides such as increased rate of degradation after application and more precise methods of application have made it possible to combine effectively the use of pesticides with other methods of pest control in integrated pest control programs. Public concern for environmental quality has led to increased emphasis on alternative pest management strategies, especially biological control. This is reflected in the fact that fundamental biology and nonchemical control projects accounted for almost 70 percent of the total funds recently budgeted by the U.S. Department of Agriculture (USDA) for pest control research (*8*). Diverse organisms, such as viruses, bacteria, fungi, rickettsiae, protozoa, nematodes, mites, insects, and vertebrates have all been used successfully as pest control agents in classical biological control, augmentative biological control, and conservative or natural biological control (Table 1). Each of these methods is based to a large extent on different ecological principles. In this

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0036-8075/82/0108-0134$01.00/0

Table 1. Integrated pest management concepts and their salient characteristics. These characteristics are not always mutually exclusive.

Objective	Characteristic or use
Classical biological control	Introduction of preferably host-specific, self-reproducing, density-dependent, host-seeking exotic natural enemies adapted to an exotic introduced pest, resulting in permanent control
Augmentative or inundative biological control	Mass propagation and periodic release of exotic or native natural enemies that may multiply during the growing season but are not expected to become a permanent part of the ecosystem
Conservative biological control	Management of the biota of the entire agroecosystem to enhance and conserve existing natural populations of native or introduced natural enemies, such as through use of polyculture, strip cropping, and organic soil amendments
Competitive control	Use of innocuous organisms to increase competition for ecological niches occupied by pests. Such organisms may include hypovirulent strains of parasites; genetic or induced pest-resistant, highly competitive crops; sterile male insects; trap plants to divert pests from crops
Biorational control	Use of behavior-modifying compounds such as pheromones, kairomones, repellents, attractants, antifeedants, and food sprays to attract parasites
Chemical control	Use of natural or synthetic compounds that interfere with metabolism, such as herbicides, fungicides, insecticides, hormones, chemosterilants, growth regulators, and microbial toxins
Cultural control	Management of the agroecosystem by physical techniques such as quarantine, sanitation, rotation, tillage, cultivation, timing of operations, pruning, irrigation, fertilization, weeding, mowing or grazing, crop isolation, scarecrows, light traps, and reduced row spacing

article I discuss these methods of biological control and their integration with other agricultural practices.

An agroecosystem has been defined as "a unit composed of the total complex of organisms in the crop area, together with the overall conditioning environment as modified by the various agricultural, industrial, social and recreational activities of man" (*9*). In ecological terms, early seral or pioneering species (crop plants) are artificially maintained by human activities in an unstable secondary successional state, or disclimax (*10*). This requires energy, equipment, and labor. Of total U.S. energy consumption, 3.4 percent is used on farms; farm chemicals (98 percent as fertilizer) account for only 1 percent (*11*). The agroecosystem represents a complex, mutually interacting network of food chains, forming an artificial food web, which is managed by growers to maximize biomass useful to humans. Any pest control or other agronomic procedure may have repercussions affecting numerous components of the agricultural and socioeconomic environment. Many of these variables are shown in Table 2.

Integrated Pest Management

The integrated pest management (IPM) or integrated pest control concept was developed in an attempt to account for as many as possible of the variables affecting the agroecosystem. The concept was first articulated in 1954 (*12*), and subsequently has been well defined by the United Nations Food and Agriculture Organization (FAO) as "a pest management system that, in the context of the associated environment and the population dynamics of the pest species, utilizes all suitable techniques and methods in as compatible a manner as possible and maintains the pest populations at levels below those causing economic injury" (*13*). Many of the techniques used in various combinations for IPM are summarized in Table 1, where I attempt to rationally stabilize the terminology. Scientists entering biological control from many disciplines tend to use diverse terms that have not been uniformly or explicitly defined; these terms may misleadingly resemble terms used for unrelated practices, or may not accurately reflect the ecological role of the control measure described. For example, "mycoherbicide" (*14*) refers to a plant pathogen used in augmentative biological control; "microbial insecticides" (*15*) and "microbial pesticides" (*16*) are pathogens of insects; and "bioenvironmental control" (*3*) refers to any nonchemical pest management technique.

Some deleterious effects of pesticides in the agroecosystem have been well documented and used to justify biological control; these include development of insecticide resistance by 240 insect species (*17*); resistance to herbicides by weed species or shifts in weed complexes (*18*); resistance to fungicides (*19*); changes in weed flora caused by insecticide-induced changes in insect fauna (*20*); herbicides for weed control indirectly promoting increased insect and pathogen infestations in crops (*21*); toxicity to nontarget organisms such as beneficial insects (*22*) and some vertebrates (*23, 24*); and stimulation of pest reproduction (*22*). However, overall economic benefits to agriculture from the use of pesticides are currently estimated to exceed total losses due to their side effects (*23*).

Summary. Living organisms are used as biological pest control agents in (i) classical biological control, primarily for permanent control of introduced perennial weed pests or introduced pests of perennial crops; (ii) augmentative biological control, for temporary control of native or introduced pests of annual crops grown in monoculture; and (iii) conservative or natural control, in which the agroecosystem is managed to maximize the effect of native or introduced biological control agents. The effectiveness of biological control can be improved if it is based on adequate ecological information and theory, and if it is integrated with other pest management practices.

Alternatives to the use of pesticides (Table 1) are also not without unexpected side effects. As one of many possible examples, the seemingly innocuous close spacing of rows of crop plants for weed control would be expected to result in benefits such as more photosynthetic capacity per hectare and increased competitiveness of crop plants by shading out weed seedlings (*25*); increased humidity and less daily temperature fluctuation beneath the closed crop canopy may result in increased survival of pathogens applied to the crop for biological control of pests (*26*). However, some crop pathogens would also survive better, and circulation of pesticide sprays or dusts to all parts of the crop plants would be impeded (*27*). Closer rows also may decrease soil erosion, compaction, and leaching of nutrients due to attenuation of raindrop impact by the canopy, and this would permit increased populations of both beneficial and harmful soil microbiota. Host and niche location by some migrating crop pests (*28*), and by their searching natural enemies, would be affected. Modified agricultural implements adapted to narrower rows would be needed, as well as new methods of harvest and crop maintenance; if widely adopted, these methods might influence fuel use, labor needs, and ultimately the rural economy.

Classical Biological Control

Classical biological control (Table 1) is a precise method that exploits Vavilov's well-established concept (*29*) of geographic centers of origin and diversity of hosts and of their close relatives. This concept serves to direct scientists efficiently to sources of the most host-specific, and therefore most density-dependent (*10*) and effective, agents for the reduction of populations of introduced pests. Since the control agent, after establishment, becomes a permanent part of the agroecosystem, classical control is most effective against introduced (exotic) perennial weeds or against introduced arthropod pests of perennial crops [see examples in (*30*)]. These perennial plants provide a relatively stable environment that can maintain permanent populations of classical biological control agents for many years. This method has been successfully used since 1863, when the host-specific, originally South American insect, *Dactylopius ceylonicus* Green was introduced into India to control the exotic American cactus *Opuntia vulgaris* Miller. Since then, more than 294 organisms have been introduced worldwide in classical control programs (*30*).

Biological control agents, because they are often carefully selected to be those best adapted to their hosts, usually spontaneously spread throughout much of the host's range, effecting widespread control at relatively little cost. For example, an investment in the 1940's of about $750,000 in research, culminating in the introduction to the United States of host-specific species of European *Chrysolina*, has resulted in benefits totaling more than $100 million to date. The *Chrysolina* beetles have brought about permanent control of the toxic, introduced European range weed, *Hypericum perforatum* L. in California (*31*), and have been introduced elsewhere at nominal cost; economically, they represent a public good. In Australia, 24 million hectares of rangeland in 1925 were infested (12 million hectares were rendered totally useless) by introduced *Opuntia* spp.; the release of the South American moth, *Cactoblastis cactorum* (Berg), after extensive host-specificity testing, permanently reduced *Opuntia* populations to below economically damaging levels (*32*). The relatively high success ratio (55 to 75 percent) in classical biological control of weeds (*32*) and some arthropods (*30*) is often due to the careful prior evaluation of the host's biology and of the roles of pathogens or phytophages under consideration as relatively host-specific control agents. Hazards to nontarget organisms are consequently very low.

To illustrate the extensive research and testing performed before classical biological control is attempted, I will describe the procedures in a typical USDA program for the biological control of an introduced weed.

1) The existing natural enemies, the economic damage, and any beneficial uses of the weed are assessed by the initiating scientist.

2) This information, with basic ecological data provided by the scientist, is reviewed by a panel of scientists from the USDA, U.S. Department of the Interior, Environmental Protection Agency, and U.S. Army Corps of Engineers, representing weed control, entomology, plant pathology, quarantine, forestry, horticulture, wildlife and range management, environmental protection, and waterways, to determine if any major conflicts of interest exist. Because released control agents will disperse, advice is also sought from appropriate Mexican and Canadian scientists.

3) After this review, foreign exploration for natural enemies in and near the weed's homeland (center of origin of the genus) is begun.

4) Studies are conducted of the ecology of the most damaging and selective natural enemies.

5) These candidates are subjected to several years of host-specificity testing. Host-preference tests are conducted first, with crops and other valued plants (especially those related to the weed) being offered as alternative hosts. If the agent attacks only the weed, the agent is subjected to starvation tests, in which it is given no choice other than valued plants; if it fails to feed, survive, or reproduce in the absence of its host weed, it is considered safe for field release in the United States.

6) A report on the agent is reviewed by the interagency scientists, and federal and state quarantine permits for importation and release of the agent are obtained.

7) The agent is screened in quarantine to eliminate its own parasites.

8) The agent is then usually released in field cages for detailed studies of survival and reproduction.

9) The agent is released in the field at relatively undisturbed sites.

10) From these sites the agent spreads spontaneously and is redistributed by participating agriculturists throughout the host's range.

This procedure usually requires 15 to 20 years. For example, more than 350 species of insects and fungi attack the Eurasian thistles of the genus *Carduus*; however, only five of these have proved sufficiently host-specific and damaging to warrant release as classical biological control agents. Foreign exploration was begun in Europe over 20 years ago, yet effective control of these thistles in North America by two of the introduced natural enemies has just begun (*33*). So far, more than 100 host-specific phytophagous insect species have been introduced worldwide for weed control, but none of them have changed hosts or significantly damaged valuable plants, even when their weed hosts have become scarce (*31*).

The host-specificity of natural enemies used for classical control in some situations can be disadvantageous. For example, such natural enemies have not been used effectively against the wide spectrum of opportunistic, vagile pests that attack hosts temporarily occupying disturbed or unstable environments, such as annual row crops. But they have provided permanent control of several perennial weeds and pests of perennial crops.

Augmentative Biological Control

Augmentative biological control (Table 1) has been used since 1884, when the nonhost-specific pathogenic fungus *Metarrhizium anisopliae* Metchnikoff was mass-cultured and disseminated to control *Cleonus* beetles in the Soviet Union (*32*). This method remains popular in the Soviet Union (*34*) and in China (*35*), where the socioeconomic structure, including collectivization of agriculture, integration of research and production, and a large, well organized, labor force permits the successful mass culture and widespread release of augmentative control agents.

In an environment such as that of a crop grown in monoculture, the percentage growth rate of a pest species becomes constant and maximum for existing microclimatic conditions (*10*); this may lead to an exponential population growth or "pest outbreak." To prevent or reduce this population increase, environmental resistance in the form of biotic

Table 2. Some interacting variables that influence the agroecosystem.

Type of variable	Variable and influence
Abiotic	Soil type (minerals, organic molecules, and soil texture) may favor certain crops or weeds; water and ions; amount of light and heat (insolation); day length; atmospheric composition; wind
Soil microflora and microfauna	Saprophytic detritus decomposers; mutualistic mycorrhizae and nitrogen-fixers; pathogens, predators, parasites; antagonists; producers of antibiotics, microbial toxins, and allergens; soil aerators
Weeds (vascular plants)	Competition for light, water, space; toxins to plants (allelopathy) or to animals (allergens, toxins); alternative host for crop pathogens or phytophages; food for beneficial organisms (pollinators, predators, and parasites of pests); direct parasitism [for example, *Cuscuta* spp. (dodder)]; interference with harvest operations; source of natural products such as oils, medicines; source of germ plasm for useful plants
Insects	Phytophages and pollinators of crops, weeds, and other flora; predators and parasites of phytophages and each other; vectors of pathogens of pests and crops; plant host or pest protectors (for example, ants); weed seed dispersers
Pathogens	Obligate or facultative pathogens, such as viruses, spiroplasmas, viroids, rickettsiae, bacteria, protozoa, fungi, and nematodes. Induce disease of crops, weeds, insects, and other organisms
Vertebrates	Wildlife, stock, and humans may use crops and weeds as food; wildlife may spread weed seeds and become vectors or reservoirs of crop, stock, and human parasites and pathogens
Socioeconomic	Energy and materials availability, costs, and materials extraction operations; urbanization, affecting labor and land costs and availability; tax structures affecting land management; crop subsidy payments; agroecological education of grower and consumer; improved communication and computerization for farm management; world population trends; demand for farm products; wildlife conservation; recreation; health regulations

agents must be introduced before the pest population has increased to economically damaging levels. This requires either maintenance of an adequate reservoir of control agents in the unstable annual crop ecosystem (which may be difficult to achieve), or annual mass rearing and releasing of biological control agents before crop damage occurs. Augmentative agents do not usually become a permanently established component of the agroecosystem, but rapid multiplication during the growing season is an important determinant of effectiveness. Success of augmentative pest control by insects is significantly dependent on the total number of individuals released (*36*). Surveys have shown that about 90 percent of introduced insects used as augmentative control agents failed to survive (*32*) or to control pests (*36, 37*). Reports of higher overall success rates (*30, 32*) are misleading because they include results of classical control programs.

Many organisms used for augmentative control are relatively nonspecific, capable of attacking numerous host species within a taxonomic order or family. This wide host range can be advantageous, because each agent can be used to control several pest species; but such agents may also attack related economically neutral native biota (*36, 38*), or beneficial species such as insects used for biological control of weeds (*31*). Other drawbacks, particularly with respect to insects, include the expense of mass rearing and shipment, short shelf-life (relative to pesticides), and difficulty of releasing sufficient numbers at the right time or under suitable conditions for their survival and increase. Facultative pathogens grown in culture (*38*) as well as mass-cultured parasitic insects (*36*) may lose their virulence or effectiveness for field use.

Augmentative control evidently can be cost-effective. Several corporations in the United States are commercially rearing and marketing a number of genera of parasitic wasps, the aphid predator, *Chrysopa carnea* Steph. (*39*), and the insect pathogens *Bacillus thuringiensis* Berliner, *B. popillae* Dutky, *Beauveria bassiana* (Bals.) Vuill. and several nuclear polyhedrosis viruses (*32, 39*). Treatments in which insects are used cost from $24.70 to $29.60 per hectare in orchards to $133 to $2398 per hectare in greenhouses (*39*). For comparison, noncommercial use of *Trichogramma* wasps in the Soviet Union and China cost $0.40 to $1.73 per hectare in 1975 (*39*).

The effectiveness of augmentation could be enhanced by accurately predicting the variables (Table 2) affecting the agroecosystem into which agents are to be introduced. A computerized systems modeling approach (*40*) is needed to adequately predict needs and to optimize and coordinate the use of various combinations of IPM techniques listed in Table 1, including augmentation. Such modeling has been done to some degree of complexity for pasture weeds, the cereal leaf beetle, and pests of cotton, potato, apple, alfalfa, grape, tobacco, and onion (*41*). Professionals such as scouts, consultants, and extension personnel have supplied many of the data for these pilot studies. Since variables will differ among individual farms and fields, it may be necessary to enlist the help of the growers if this approach is to be widely adopted. This should be feasible with training in standard sampling methods and in recognition of the five to ten dominant or "key" pests (*13*) affecting each crop, and with improved on-farm educational and communication facilities. Many growers already use on-farm computer terminals (*42*) and, in self-interest, they are often astute observers of that part of the ecosystem that is in their care. Inadequate access to unbiased pest-control information and to the results of interdisciplinary research has been a factor limiting widespread use of IPM. Those growers who do use IPM techniques have been able to reduce insecticide applications by as much as one-half while maintaining yields equal to those of growers using conventional pesticide application schedules (*41*).

Conservation of Natural Enemies

Another solution to the pest control problem is through habitat management or conservative biological control (Table 1). Instead of attempting to analyze, model, and alter the numerous variables that influence crops grown in monoculture, the grower provides a general environment that permits the survival of a complex biota.

The role of existing natural enemies (natural biological control) in suppressing crop pests was not appreciated until outbreaks of pest insects occurred when their enemies were inadvertently suppressed by insecticides directed at the pest species (*32*). In USDA case studies of organic farms (*11*), crop yields on a per hectare basis were comparable to those on nearby farms where pesticides were used; pests on the organic farms were controlled by crop rotation, tillage, crop spacing, intercropping, mulching, and biological control agents. An important feature of organic farming is the inclusion in the rotation of perennial legume crops of relatively low economic value, such as alfalfa or clover, which provide refuge for beneficial insects and other useful biota while improving the soil.

It is widely believed that ecosystem diversity is associated with long-term stability of included populations (*10*), presumably because a variety of parasites, predators, and competitors is always available to suppress population growth of each species. Dispersal of food plants among other nonhost plants may make migration, host, and mate location, and consequently exponential growth of phytophages or pathogens, more difficult. The local number of insect species is positively correlated with vegetational diversity (*43*); other biota, such as fungi (*44*) are similarly diverse because of the availability of many niches. Vertebrate wildlife is known to benefit from habitat diversity that is increased by providing refugia, ecotones, or transition zones such as hedgerows, woodlots, meadows, orchards, and fallow areas adjacent to crops grown in monoculture. However, advantages to beneficial organisms such as food and shelter for natural enemies of pests and for crop pollinators may be offset by the availability of alternative hosts and hibernacula for crop pests (*28, 31, 45*).

Plants that are related to crop species may attract relatively oligophagous insects away from crops (*46*). Unrelated plants, when grown among crops, provide physical or chemical barriers that interfere with host location by phytophagous insects (*46, 47*) and their predators (*48*). The survival and activity of natural enemies of crop pests are enhanced by manipulating the composition and abundance of other plants growing near or among the crop plants (*49*). The best procedures for each crop and the plants associated with it should be evaluated according to the habitat and host relationships of local pest species (*32, 50*), and the requirements of local beneficial species.

Polyculture, also known as intercropping or mixed cropping, is a traditional agricultural practice in Latin America, Africa, and Asia in which two or more crops are grown simultaneously on the same land. Total combined yields per hectare may exceed those of the same crops when grown in equal density in monoculture (*35, 51*). This synergistic effect or "overyielding" can be due to better light utilization, reduced auto-allelopathy, improved erosion control, humus retention, or nitrogen fixation; a diversity of crop species and genotypes may also reduce pests and thus improve yields (*51, 52*). The use of intercropping to reduce crop disease was first reported (in Europe) in 1767 (*44*). Intercropping with nonhost barrier crops reduces the rate of spread of insect-transmitted phytopathogenic viruses (*53*). Early investigations (*54*) demonstrated the value of intercropped nonhost plants in deterring insect pest invasions and their rapid multiplication. Strip cropping (alternating strips of different crop species) was used to control insect pests in the United States before the advent of insecticides; the avoidance of alternative hosts of pest species in the cropping system was emphasized (*55*), as was the need of beneficial insects for nectar and pollen sources. The use of glabrous (hairless) varieties was recommended because sticky, glandular plant hairs, even though they may protect crops from some phytophagous species, tend to entrap minute species, such as parasitic wasps.

Polyculture is best known in forestry, where most stands are maintained as mixed species. Outbreaks of native pests are most severe where large areas are planted to a single species of tree, or in boreal areas that are naturally occupied by few tree species (*44*). Introduced, spreading pests such as the polyphagous European gypsy moth, *Lymantria dispar* (L.), and the host-specific Dutch elm disease, *Ceratocystis ulmi* Buis., with its European vector, *Scolytus multistriatus* (Marsham) evidently lack effective natural enemies and are not deterred by presumed barriers imposed by the diversity of our North American ecosystem. The great diversity of crops and pests that interact in many polyculture systems throughout the world make it difficult to generalize, but evidence suggests that polyculture may be relatively more successful as a pest control method in areas where native pests, native (natural) biological control agents, and native crops and associated plants (all coevolved and presumably potentially stable) are present. This aspect of biological control warrants further investigation.

The use of polyculture with natural control methods is currently labor-intensive, although technology to alleviate this could be devised. In the United States this system may be most suitable for, and is used to some extent in, the home gardens maintained by 43 percent of households. These gardens produced crops with a retail value of $15 billion in 1980 (*56*). On a larger scale, strip cropping and organic farming may be appropriate for small farms (such as those with annual gross sales of $1,000 to $40,000 each); this would include the 42 percent of all farms in the northeast that locally serve 55 million people. On such farms these methods would help in maintaining productivity per hectare and in reducing environmental stress on this valuable, yet relatively crowded, land (*57*). Part-time farmers (80 percent of all U.S. farmers) have other sources of income (*58*), and therefore they may be most willing to experiment with biological control and polyculture, and to combine these methods with other IPM procedures.

Conclusions

A recent policy statement by the USDA (*58*) specifically recommends reorientation of research and extension to develop new technologies to reduce costs, increase efficiency, and facilitate the economic viability of small to medium-sized farms. Alternatives are required to current chemical-, capital-, and energy-intensive strategies, and greater attention must be paid to remedying deficiencies in our understanding of the agroecosystem.

Classical, augmentative, and conservative biological control are IPM technologies that can help to meet these goals, but they will not be widely adopted by growers until their efficacy is consistently established under field conditions. This requires thorough knowledge of underlying ecological principles and variables to guide their appropriate application in individual agroecosystems. Farming is not only a way of life, but it is also a way of making a living. Therefore, practical pest control methods must be economically viable as well as environmentally compatible.

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59. I thank E. M. Barrows, L. R. Batra, J. Drea, K. Hackett, R. W. Lichtwardt, A. Y. Rossman, and R. M. Sayre for reviewing the manuscript and for providing helpful suggestions.

Scientific Exchanges and U.S. National Security

On 9 October 1981, in a letter addressed to The Honorable Frank Carlucci, Deputy Secretary of the Department of Defense, Mr. William D. Carey, Executive Officer and Publisher of Science, *criticized statements by the Department of Defense concerning scientific exchanges, conferences, and the unclassified, open scientific literature. Mr. Carey's letter and the reply he received from Mr. Carlucci are printed here verbatim.*

I must tell you that the otherwise excellent brochure on *Soviet Military Power* went off the rails badly, in my opinion, in contending (pp. 80–81) that U.S.-sponsored scientific exchanges and scientific communication practices enhance Soviet military power.

I am dismayed to find the Defense Department indicting inter-Academy exchanges, student exchanges, scientific conferences and symposia, and the entire "professional and open literature" as inherently adverse to U.S. military security interests. These normal and well-accepted fora for advancing scientific progress constitute the primary infrastructure of U.S. and worldwide communication in science, and without them the U.S. technology base would go stale very quickly.

The Defense Department should know, by this time, how scientific practice is conducted and how necessary unimpaired communication in science is to advancing the state of the art and improving our own essential capabilities. I find it deplorable to have our Defense Department taking a public and well-advertised stance that exchanges and the open scientific literature constitute still another window of vulnerability and a free asset handed to our principal adversary.

It is also somewhat astonishing to have the Defense Department charging that bilateral U.S.-Soviet scientific and technical exchanges are giveaway channels benefiting Soviet military power. These bilateral exchanges, as you must know, are legitimized by formal intergovernmental agreements initiated by

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