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CHAPTER 2

Vulnerability of Ecological Systems to Climatic Effects of Nuclear War

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2.1 INTRODUCTION

The potential perturbations to ecological systems that could result from a large-scale nuclear war include: 1.) direct effects of nuclear detonations; 2.) climatic disturbances; 3.) other global-scale disturbances such as fallout and enhanced UV-B; and 4.) localized disturbances such as air and water pollution.

The direct effects involve initial ionizing radiation (i.e., gamma rays and fast neutrons emitted from the fireball) and thermal radiation, each of which initially is limited to a relatively small area around a nuclear explosion. As discussed in Harwell (1984), the effects of blast are insignificant to the Earth's ecosystems in areal extent. Areas affected by initial ionizing radiation are even smaller than for blast for the size of nuclear warheads in current arsenals and, thus, these effects are also unimportant to ecosystems. Thermal radiation does offer the potential for greater ecological damage insofar as targets in grasslands and forests (e.g., missile silos) could have nuclear bursts that initiate fires in those systems. This issue is discussed further in Chapter 3.

The *indirect* effects on ecosystems of nuclear war cannot be so easily dismissed, however. The remainder of this chapter addresses the vulnerabilities

TABLE 2.1

ESTIMATES OF CLIMATIC RESPONSES TO NORTHERN HEMISPHERE SUMMER AND WINTER NUCLEAR WARS[a]

A. SUMMER WAR

REGION	PHASE ACUTE (1ST FEW WEEKS)	INTERMEDIATE (1-6 MONTHS) (DEGREES C. BELOW SEASONAL AVERAGE)	CHRONIC (1-FEW YEARS)
N. Hem. Mid-Latitude Cont. Interiors	-15 to -35 under dense smoke[b]	-5 to -30	0 to -10
N. Hem Sea Surface[c] (Ice Free)	0 to -1	-1 to -3 and local anomalies	0 to -4 and local anomalies
Tropical Cont. Interiors	0 to -15	0 to -15	0 to -5
Coastal Areas[c]	0 to -5 very variable unless offshore wind, when: -15 to -35	0 to -5 very variable unless offshore wind, when: -5 to -30	0 to -5 variable
N. Hem. & Tropics Small Islands[c]	0 to -5	0 to -5	0 to -5
S. Hem. Mid-Latitude Cont. Interiors	initial 0 to +5 then 0 to -10 in patches	0 to -15	0 to -5
S. Hem. Sea Surface[c] (Ice Free)	0	0 to -2	0 to -4
S. Mid-Latitude Coastal Areas	0	0 to -15 in offshore winds	0 to -5
S. Hem. Small Islands	0	0 to -5	0 to -5

[a] From Volume I, Pittock et al. (1985).

[b] Smoke clouds with an absorption optical depth of 2 or more, remaining overhead for several days.

[c] These figures are climatological average estimates. Local anomalies may exceed these limits, especially with respect to changes in oceanic behavior, such as upwelling or El Niño-type anomalies.

B. Winter Nuclear War

Region		Phase	
	Acute (1st few weeks)	Intermediate (1-6 months)	Chronic (1-few years)
	(Degrees C. below Seasonal Average)		
N. Hem Mid-Latitude Cont. Interiors	0 to -20 under dense smoke[b]	0 to -15	0 to -5
N. Hem Sea Surface[c] (Ice Free)	0	0 to -2 and local anomalies	0 to -3 and local anomalies
Tropical Cont. Interiors	0 to -15	0 to -5	0 to -3
Coastal Areas[c]	0 to -5 very variable unless offshore wind, when: 0 to -20	0 to -5 very variable unless offshore wind, when: 0 to -15	0 to -3
N. Hem. & Tropics Small Islands[c]	0 to -5	0 to -5	0 to -5
S. Hem. Mid-Latitude Cont. Interiors	0	0 to -10	0 to -5
S. Hem. Sea Surface[c] (Ice Free)	0	0 to -1	0 to -1
S. Mid-Latitude Coastal Areas	0	0 to -10 in offshore winds	0 to -5
S. Hem. Small Islands	0	0 to -5	0 to -5

of ecosystems to the types of climatic disturbances that have been characterized as possible after a large-scale nuclear war. Chapter 3 is concerned with other local- and global-scale disturbances to ecosystems.

In analyzing the potential vulnerability of ecosystems to climatic disturbances, the effects were related to categories of stresses rather than to specific values for temperature, light, and precipitation reductions predicted from particular simulations by atmospheric scientists. In that regard, the estimates of the effects on the biological systems of Earth would not be strictly dependent on resolution of the uncertainties in the atmospheric projections, which continue to be updated following new analyses, and which are often scenario dependent. Designing classes of stresses, with alternatives among them to cover the range of possible climatic impacts, was considered sufficient for most of the purposes and uncertainties associated with the biological analyses.

The stresses considered follow the values provided by Volume 1 (summarized in Table 2.1); additional discussion of this approach is given at the beginning of Chapter 4. The resistance of an ecosystem type to an environmental perturbation, such as temperature decreases, was matched with assumed exposures to that parameter that the ecosystem would experience under various scenarios. It is this combination of considerations that is important to establishing the vulnerabilities of ecosystems to the perturbations that could result from a nuclear war.

The analyses were based upon a variety of considerations. For the more extreme stresses possible in the acute phase after a large-scale nuclear war, physiological-level information (discussed in Chapter 1) formed the primary basis for estimates of effects, since it was felt that the first-order effects on organisms would dominate the early responses of the systems to physical stresses. These estimates were primarily accomplished in the various technical workshops that specifically addressed the potential effects on ecosystems in the Northern temperate, tropical, and Southern temperate regions of the world, reaching as broad a consensus as possible among the workshop participants as to the probable responses of the ecosystems to perturbations. Notes from these workshops, prepared discussion papers, additional information from the literature, and discussions with specialists collectively provided much of the information base for the following discussions.

For lesser perturbations, such as those during a chronic period of climatic disturbances, or following a relatively mild acute climatic disturbance, a number of computer simulation models were additionally drawn upon. These were developed to analyze the productivity and components of particular ecosystem types as functions of the physical environment. It was felt that the lesser stresses examined do not exceed the bounds for which these models are reasonably reliable, a situation not the case for extreme, acute stresses. Many of these models provide conservative estimates of chronic-phase ecosystem response (i.e., underestimates), because potential acute-phase alterations of ecosystem structure and composition were not considered where perennial organisms dominate. These simulations are a useful guide to potential ecosystem sensitivity, and as simulations of possible effects of milder climatic disturbances. Simulations cannot provide precise predictions of ecosystem biomass, productivity, or species composition changes following a nuclear war. However, the model results are useful as a guide to the type of responses that could occur, even with relatively small climatic disturbances.

The analyses that follow, then, are based on a suite of approaches: physiological information, historical analogs, simulation and statistical analyses, and expert judgment. Because of the great complexity of ecosystems across the global landscape and the temporal and spatial complexity of potential nuclear-war induced climatic disturbances, it is not possible uniquely to characterize the effects on ecosystems. A biome approach has been chosen as an appropriate level for generalization of potential effects. In separate sections that follow, Northern Hemisphere temperate terrestrial ecosystems, aquatic ecosystems, tropical ecosystems, and Southern Hemisphere extra-tropical ecosystems are addressed.

It should be noted that the ecosystem discussions emphasize effects on the primary producers, in large part because those components are fundamental to the total ecosystem and are often especially vulnerable to the types of perturbations considered here. Estimates of effects on fauna are largely based on those mediated through changes in food supplies. Further study of effects on trophic structures and of indirect effects on species propagated through the complex interactions of ecosystems is required.

2.2 POTENTIAL EFECTS ON NORTHERN TEMPERATE TERRESTRIAL ECOSYSTEMS

2.2.1 Potential Effects on Arctic and Boreal Ecosystems [1]

2.2.1.1 Estimation of Vulnerabilities to Acute Climatic Disturbances

This discussion is concerned with landscapes north of about 65°N latitude, including the northern taiga (forests), lichen-woodland, tundra, and other more northern arctic ecosystems. This area is characterized by very small human populations, essentially no agricultural development, and

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[1] Note: much of this section follows from the Toronto working group on ecosystems effects, chaired by L.C. Bliss, and from the discussion papers prepared for the workshop by Bliss and by J.Svoboda and H.W. Taylor

limited human impacts on ecosystems. Humans are primarily supported by natural animal populations, and therefore their diets are predominantly protein rather than fiber and carbohydrates, as found in the diets of most human populations. In this regard, maintenance of the natural ecosystems, especially the total productivity of the plant communities and the persistence of particular food- source animal populations, is essential for maintenance of the indigenous human population.

The taiga, i.e., a boreal (subarctic) ecosystem, typically forms cold-limited needle-leaved forests across climatic ranges extending around the Earth in the northern parts of North America and Eurasia. These circumpolar ecosystems occupy about 10×10^6 km^2 of the Earth's surface. Tundras do not have trees, and are characterized by the dominance on a more local scale of shrubs, grasses, herbs, mosses, and lichens. With low levels of temperature and precipitation, these semi-arid landscapes demonstrate characteristics of deserts.

If acute nuclear-war induced climatic disturbances were to occur in the *autumn or winter*, the effects would be considerably mitigated. From water relation studies of black spruce in Alberta (van Zindern Bakker, 1974) and the Northwest Territories of Canada (Black and Bliss, 1980), and studies of Jack pine in northeastern Alberta (Mayo et al., 1980), it appears that boreal conifers conduct little if any photosynthesis during this period, probably because their root systems are not active. Thus, a reduction in temperature and associated light levels in an acute response during this period would not reduce primary production directly in northern forests and arctic ecosystems since the plants would be dormant.

The separate question of freeze-induced mortalities of the plant species seems not to be a major problem for a winter-onset war, although sudden severe temperature decreases could cause frost cracks and increased disease susceptibility. In the dormant state, most arctic and boreal vegetation could withstand temperatures down to − 50°C to − 70°C or below, well under the minimal temperatures expected in a post-nuclear war environment. In addition, the landscapes are usually covered by snow and ice, which provide a protective blanket for understory plants and components of the soil subsystems.

A winter-onset war could also affect an ecosystem by delayed impacts, specifically by the extension of winter temperatures into the following spring and summer. Again in the case of tundra ecosystems, these effects would appear to be small for the plants. There are few field data from the low arctic to indicate how shrubs or other dominants would respond to a summer with little or no plant growth as a result of an unusually prolonged winter season. However, many arctic species have been maintained in cold laboratory environments for 12 to 24 months, brought out of dormancy, and subsequently resumed normal growth. By extrapolation, one can assume the same would be the case in the aftermath of post-war climatic disturbances that occurred in the winter season and under the conditions in which the environment did not warm sufficiently to release the plants from the cold-hardened state. Plants in the high arctic would be little affected if they experienced no summer at all. For instance, in 1964 there were large areas in which snowmelt did not occur until early August, yet the arctic plants survived and flowered in the following year (Savile, 1972). It is less clear what the effects would be if a very brief summer were to be experienced, followed by early initiation of the following winter.

Effects on arctic animals would be much more pronounced than effects on plants, although less than on animals in biomes at lower latitudes in the Northern Hemisphere. Extending the length of the winter period might be a major cause of animal mortality, especially for birds and for mammals that do not hibernate. Resident bird populations would probably survive increased winter cold, although population reductions of up to one-third seem possible. Large herbivores would be more susceptible to population reductions, especially if temperature reductions extended into May and June. In that instance, winter foraging for food of low nutritional value would be extended into periods of calving and lactation, and temperature effects could lead to increased mortality among newborn populations. Carnivores such as foxes and wolves would also be adversely affected, although with a greater delay period; increased food supplies would occur initially as their prey species experienced increased mortality, but eventually the reduced secondary production would propagate to reduced carnivore production. Small mammals would be less affected by maintaining themselves under a snow pack, unless they consumed all of their food within their home range before productivity could be restored. The decomposer system, by contrast, would probably not experience long-lasting effects.

Effects on boreal and arctic ecosystems from nuclear-war induced climatic disturbances occurring in the *summer* could be far more significant. The impact of reductions of temperature below freezing on actively growing tissues of trees, shrubs, graminoids, and forbs would be considerable. Little is known about the level of cold hardiness of arctic plants in the summer. Studies by Somers (1981) on *Salix arctica* at 75°N and by Sakai and Otsuka (1970) on alpine species in Japan suggest that arctic plant species may tolerate temperatures of $-5°C$ to $-10°C$ during the growing season. If temperature and light reductions occurred gradually over a two-week period or longer, an additional increase in cold hardiness might be induced, further minimizing freezing damage to plants. However, more rapid reductions in temperatures would not allow acclimatization; in that instance, it is not clear what proportion of the tundra plant community would be killed.

For lichen-woodlands and taiga, a drop in summer temperatures would kill the new growth of conifers (e.g., *Larix*, *Pinus*, *Picea*, and *Abies*) and deciduous trees and shrubs (e.g., *Populus*, *Betula*, *Alnus*, and *Salix*). Unless summer temperatures dropped below – 10°C, the older needles of the conifers and the older branches of the deciduous species would largely survive. If subfreezing temperatures were experienced, high mortality of the plant community could be expected; however, individual trees and shrubs could survive, and for many species, resprouting of new growth from the shoot base could occur for perhaps 10–20% of the populations (e.g., for shrubs, black spruce, Jack pine, poplars, and birches). Dwarf shrubs and the graminoids would survive if temperatures dropped more gradually, especially if they were covered by a protective snow blanket prior to severe temperature reductions. This snow cover would prevent rapid freezing of the soil subsystem, providing time for cold hardiness of root systems to develop. Lichens and mosses would be little affected.

In the tundra, arctic shrubs, grasses, and forbs would all be considerably affected by the combination of cold and reduced light levels if occurring in the summer, but the plant communities would largely survive, although recovery rates might be quite slow. Shrubs would be most severely affected, with extensive dying back to ground level; most graminoids, herbs, and dwarf shrubs would survive. In the high arctic (>70°N latitude), early onset of snows in August are seen to force the plants into early dormancy, and the systems survive. Arctic species function normally in summer temperatures of only 3°C to 10°C, and they maintain at least a limited level of cold hardiness in summer (low temperature limits are about – 5°C to – 10°C) (Somers, 1981). The potential initial reduction in light and temperatures following a nuclear war could trigger an increase in cold hardiness, down to – 20°C to – 30°C within 7 to 10 days. Arctic plants are relatively long-lived (20 to 100+ years), and the loss of seed production for one or two years would have little impact on the survival of many plant species. Although in general some seed banks are present, even in the high arctic, certain dominant species (e.g., *Carex aquatilis*, *C. bigelowii*, *C. stans*, *Alopecurus alpinus*, *Luzula confusa*, and *L. nivalis*) produce little or no ripe seed each year. Should populations of these dominants be eliminated over large areas, recolonization would be very slow, and forage for large herbivores would be severely reduced. There are very few ruderal or pioneer species in the arctic to initiate succession. Thus, plant reestablishment would result from resprouting and from species in the soil seed bank.

In general, survival of arctic animals would be reduced if the plants upon which secondary production is based were damaged, killed, or buried in snow. If animals are unable to replace energy reserves over the summer season, increased mortality would ensue after a few months. Large herbivores would require a growing season of about two months prior to the onset of a nuclear war-triggered cold period in order to gain enough energy reserves to last through the subsequent period of 8 to 10 months with only limited foraging. Invertebrate populations would be reduced by direct mortality, but the species would not be eliminated, since most species require more than one year to complete their life cycles, and immature stages (e.g., eggs, larvae, pupae, and nymphs) could survive within the soil and litter until the following growing season. Large mammal populations could survive extreme climatic disturbances for a number of months, but only a few large and small herbivore populations could survive until the next summer, and then only provided that they were already located in a highly favorable winter-grazing habitat. Should surface vegetation be sealed in ice, small mammals and large mammals would be eliminated from large areas (Fuller et al., 1977; Miller et al., 1975). In these circumstances birds, both migratory and resident, could be eliminated. The soil fauna and flora would survive essentially intact.

2.2.1.2 Vulnerabilities to Chronic Climatic Disturbances

The considerations thus far have dealt with the response to an extreme acute period of climatic disturbances affecting arctic and boreal ecosystems in the winter or the summer. We next consider effects on arctic ecosystems from potential chronic reductions in temperature, light levels, and precipitation. In order to help evaluate the vulnerability of these ecosystems to chronic temperature decreases, these discussions focus on average temperature reductions of about 3°C below normal, persisting throughout the growing season. These are partially based on the estimations of effects on arctic ecosystems from the Little Ice Age (Andrews et al., 1976; Dyke, 1978, 1979) and on many years of observation of the effects of unusually cold or warm summers on the phenology and plant growth in the arctic (Svoboda, 1982).

A decrease in the average temperature by 3°C would probably result in delayed or incomplete snowmelt, resulting in a shallower or absent biologically active layer in the soil. Reduced average temperatures could be expected to result in a delay in ice break-up in river and lake systems and an earlier incidence of freezing in the following fall. There would be a decreased number of degree-days above freezing, upon which primary production is dependent. Old unmelted snow would result in firn formation, an initial phase of ice crust formation, if the chronic effects lasted longer than a single year.

The lack of snowmelt or ice break in the Arctic Ocean could also result in an increased albedo throughout the year, with subsequent increased loss of radiant energy from the arctic regions. Note, however, that this effect would be mitigated if sufficient particulates from a disturbed atmosphere were to be deposited on top of the ice cover. It is unclear from the atmospheric analyses how prevalent such a particulate cover on these regions would be. One analysis (Warren and Wiscombe, 1985) indicated that there might be sufficient smoke and soot from a perturbed atmosphere to result in significant reduction in the albedo of Greenland and arctic sea ice. Further, they suggested that upon melting each year, the deposited polluted layer would become reexposed and, therefore, repeatedly reduce the albedo. Subsequent snowfall would again increase the albedo until the next snow melt. This could affect both the nature and timing of the snowmelt process and extend the climatic responses in time.

Climatic alterations could result in the vascular plants of boreal and low arctic regions experiencing a prolonged period of winter dormancy and concomitant delayed initiation of the growing season by up to a month. Thus, most of the life cycle would develop after the summer solstice, a period of declining solar irradiation, adding a further limitation to the solar radiation already decreased by smoke. Growth of plants would probably begin, but the normal life cycles might well not be completed. In general, in highly seasonal ecosystems the life cycles of the constituent plants must coincide with cycles of the physical environment. If buds break dormancy too early, they are killed by frost; likewise, if they are delayed too long in appearance, there would be insufficient time for the life cycle to be completed and for fruits to ripen. The chronic climatic disturbances could result in sporadic occurrence of flowering, or incomplete fruit development. If the chronic phase lasted for several years, these effects would be more severe (Dahl, 1985).

Considerable enhancement of the extent and frequency of fires could occur if large-scale die-off of taiga trees occurred during an acute period, and fuel moisture conditions permitted. Low arctic animal populations would probably be severely affected because of a general shortage of food resources from reduced primary production. Predators and scavengers might temporarily have an increased food supply, but the decline in carnivore populations would eventually follow the decline in herbivores.

Within boreal forests there are herb and shrub species that rapidly recolonize sites disturbed by fire or tree harvest (e.g., fireweed, grasses, willows, and birches). These species would be present in the seed bank following disturbance and would facilitate recolonization of denuded lands.Resprouting of woody species, as discussed previously, would also enhance plant succession.

In the high arctic, the chronic reductions in temperature and light could result in snow cover for the entire summer, and vegetation would not grow. Snow cover would enhance long-term plant community survival if the plants did not break out of dormancy and cold hardiness. However, under such conditions all land-bound vertebrates could starve within a few months. The bird populations would also be severely affected by the loss of breeding grounds, as they would not be able to return to their nesting sites, nor would they be able to find adequate food.

2.2.1.3 Inferences from Previous Modelling Studies

These estimates of the potential effects of nuclear war on arctic ecosystems are reinforced by some previous analyses of tundra ecosystem models under simulated conditions of reduced temperatures (Cooper et al., 1979). Two separate tundra models were analyzed. The first was a model of the physical processes affecting photosynthesis rates for individual plant leaves and, by extrapolation, primary production (Miller and Tieszen, 1972). The model shows that plant production is almost totally temperature- and insolation-dependent, and that soil moisture is not a major limiting factor, at least for the wet soils of the Barrow, Alaska area, for which the model was calibrated. Other data show the importance of temperature in controlling photosynthesis rates (Hartgerink and Mayo, 1976; Addison and Bliss, 1984).

The model results reported by Cooper et al. (1979) approximate a 25% reduction in primary production for each 2°C drop in temperature. Field data, however, do not support this model. Over a three-year period, mean weekly temperature and total degree-days over a 50-day growing season changed 3-fold, yet plant production within two communities changed less than 10% (Bliss, 1977). This illustrates that current models can be helpful in explaining responses of individual species, but community and ecosystem responses may be quite different. A major factor is the role of food reserves (carbohydrates and fats) in perennial species. This limits the usefulness of these simulation models to plants that store limited food resources. Other, more useful ecosystem models for arctic systems were not available for evaluating potential effects of nuclear war.

2.2.2 Potential Effects on Forest Ecosystems [2]

2.2.2.1 Vulnerabilities to Acute Climatic Disturbances

The second major class of ecosystems that were considered includes the deciduous and coniferous forests that occur in the temperate regions of the Northern Hemisphere. The deciduous forests of North America, Europe, and Eastern Asia are broad-leaved, consisting of oak, maple, beech, birch, and ash, and many other species of trees, including mixtures of conifers. These ecosystems are characterized by relatively high species diversity and productivity. Temperate coniferous forests occur in a variety of regions and climates, ranging from dry, fire-maintained ecosystems to the massive forests found in the cool maritime climate of the Pacific Northwest region of North America.

One particular consideration for the temperate Northern Hemisphere forests is that they are located in the probable latitudinal bands of the nuclear war itself. Thus, these systems could experience more intense climatic

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[2] The discussions in this section are based primarily on the conclusions of the ecosystems working group at the Toronto conference, chaired by L.C. Bliss.

disturbances than other ecosystems, and there would be a greater input of other stresses, such as radiation, pyrotoxins, particulates, and toxic gases. These are independently considered elsewhere (Chapter 3), but the potential for synergisms should always be kept in mind.

The possible effects from acute reductions in temperature and light would be considerably less if imposed in winter as compared to in the summer. For the more northern and mountainous deciduous and coniferous forests, the trees would be in a state of winter dormancy. Substantial undercooling would permit bud primordia to survive unfrozen to temperatures of about −40°C (see further discussion in Chapter 1 of cold-hardiness of temperate species). Thus, trees would not suffer substantial mortality from the direct effects of cold. In these areas, snow cover might protect the understory plant species as well. In southern coniferous forests, the trees would be much less cold hardy, especially pines, and a substantial fraction of the trees, shrubs, and herbs would be killed, at least back to ground level. Subsequent snow associated with the initial stages of nuclear war-induced climatic changes might provide protection to the understory species. Reduced light levels would not affect coniferous plants much or deciduous plants at all because of the reduced rates of photosynthesis during these periods.

A variety of factors would influence the survival and recovery of mammal and bird populations following a winter-onset war. Northern animals might tolerate climatic stress better, but southern populations might encounter higher levels of food availability because of the existence of less snow cover than in northern areas. Severe climatic disturbances could reduce primary productivity, possibly to levels insufficient for maintaining animal populations. Although decomposer activity is reduced by decreasing temperatures, climatic stresses would probably not eliminate many decomposer organisms (soil invertebrates, bacteria. and fungi). Similarly, mycorrhizal infection of tree roots might decrease under reduced temperatures, but the resistance of mycorrhizal spores and inoculum to stress would prevent those species from being eliminated. In general, these forest ecosystems have a diversity of species well adapted to colonization following major disturbances.

One possible climatic response to a summer-onset nuclear war is the occurrence of subfreezing temperatures, brought on very rapidly in combatant-zone latitudes. Sudden freezing would be expected to result in widespread loss of the current season's foliage. However, that alone is not expected to cause long-term effects for the trees, as some forests can experience large foliage losses from insect consumption and continue to survive into the next season. Aboveground tree mortality from reduced temperatures could also occur. Among the deciduous species (e.g., oak, maple, beech), some might be able to resprout in the next warm growing season. If temperatures remained below freezing for two or more months, however, most species of trees could survive only in very low numbers (below 10%), if at all. If temperatures remained below freezing for weeks to months, many shrubs would be killed outright, and the tops of all herbaceous species would be killed. Significant losses of nutrients might occur in forests with high levels of tree mortality, because of reduced uptake and immobilization of nutrients. This effect could be particularly important in regions of normal or increased precipitation.

Large and small mammals could be eliminated because of insufficient food, coupled with extremes of temperature. Likewise, other than a few hardy winter residents, birds would probably be killed. The soil subsystems, however, would remain essentially intact.

In subsequent years, those forests that had experienced substantial mortality of at least the aboveground portions of the trees could be subject to great increases in insect outbreaks. Fire could also be extensive in these systems, thereby extending ecosystem stresses well into the future following the acute phase, even if there were no chronic climatic effects. The relatively high density of viable seeds in these types of forests promotes recovery of a forest community after perturbation. However, the combinations of perturbations and the probable propagation of indirect effects throughout the ecosystem indicate that it is not possible to describe precisely the extent or ultimate effects of these potential post-war perturbations.

2.2.2.2 Vulnerabilities to Chronic Climatic Disturbances

The vulnerability of forest ecosystems to potential chronic conditions, i.e., temperature reductions of a few degrees, light reductions of 5–20%, and precipitation reductions of up to 50%, are more difficult to characterize. It is clear that chronic temperature reductions could result in delayed growing season initiation and an earlier onset of winter; further, the variance in temperature could result in episodes of near- or sub-freezing temperatures being experienced well into a growing season. This would result in the increased mortality of plants and, especially, in the interruption of the normal life cycles of plants. However, if subfreezing temperatures were not experienced within a growing season and if the precipitation were not reduced substantially, reductions in temperature alone could result in *increased* primary productivity in those forests that are at least partially limited by soil moisture stress. On the other hand, photosynthesis and respiration rates would *decrease* with reduced temperatures; thus, the integrated effect of these processes would be difficult to predict. A mechanistic simulation model could be used to explore this problem. In the event of reduced precipitation, there could be a substantially increased incidence of fires, which would have a considerable effect on forests not accustomed to experiencing a high fire frequency. Reduced light levels associated with the chronic phase could be expected to reduce productivity in many forests.

2.2.2.3 Results from Previous Modelling Studies

For deciduous forests, there are simulation models that can be used to look more carefully at the effects of the chronic perturbations and the propagation of those effects throughout the ecosystem and over time. One set of such simulations was reported in Harwell (1984). The FORNUT model (Weinstein, 1983) was designed to test the effects of environmental perturbations on the primary productivity and species composition of Eastern deciduous forests of the United States (Harwell and Weinstein, 1982; Weinstein and Shugart, 1983). The version used for these simulations was calibrated to the mixed conifer-hardwood forest of the Southern Appalachian Mountains based on data from eastern Tennessee. FORNUT is based on the forest-gap replacement concept, in which simulations monitor the birth, growth, and death processes for individual trees.

The results of the FORNUT simulations should not be interpreted as predictions of species composition or ecosystem characteristics following a nuclear war. The model was not initialized with conditions appropriate for a forest severely damaged by acute-phase climatic or other disturbances. The model is more appropriately evaluated as part of an analysis of forest sensitivity to relatively mild climatic stresses, potentially occurring in an acute phase in some regions or a chronic phase elsewhere. With severe acute disruptions, FORNUT simulations would probably greatly underestimate effects and the time required for forest recovery. On the other hand, simulating chronic stresses lasting for 5 years may overestimate the consequences of shorter-term chronic perturbations.

Results from the FORNUT simulations are shown in Figure 2.1. The 0°C case is the control simulation, demonstrating the successional development of the forest over the fifty-year period, beginning with the forest as currently constituted. Chronic temperature reductions were imposed for the first five years of the simulation, with subsequent return to normal temperature conditions for the remainder of the simulation period. During that period, the total biomass of the control forest trees increased by about two-thirds. Simulations of an average 3°C drop resulted in an initial decrease in biomass by about 25%, with return to the unstressed trajectory in about three or four decades. By contrast, reductions in average air temperatures of 6°C led to an 80% reduction in the biomass of the forest, with the peak loss occurring a few years *after* the temperatures had returned to normal. Moreover, the reductions in biomass had not returned to normal conditions by the end of the simulation period; i.e., even 50 years after temperatures returned to pre-war levels, the forest biomass would be less than one-half its value had there not been the chronic stress lasting for the first five years. A similar pattern ensued after a 9°C reduction in temperature.

Another set of simulations was conducted to evaluate the effect of reduced

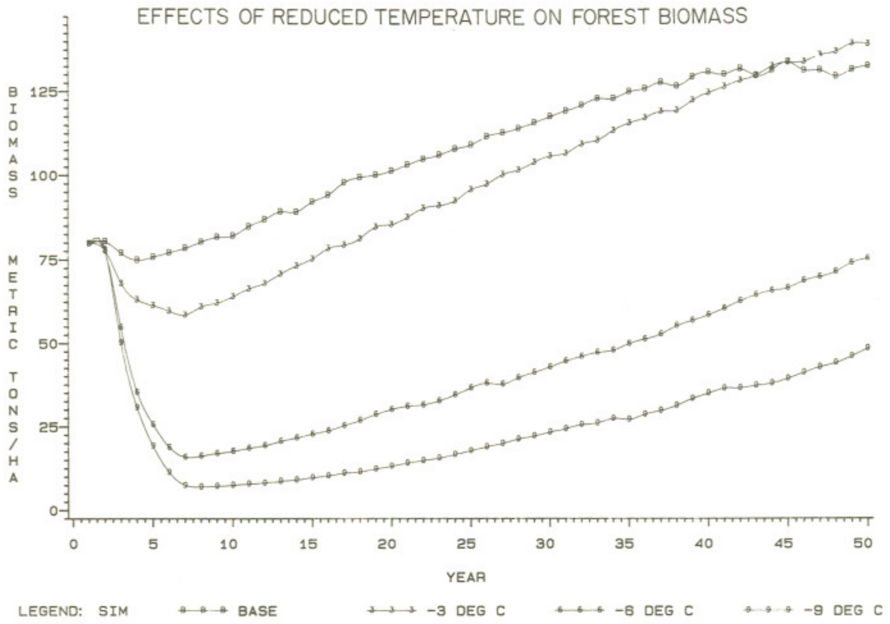

Figure 2.1 Effects of reduced air temperatures on forest biomass. Reductions in average annual air temperatures imposed for first five years at levels of 0°C (base case), 3°C, 6°C, and 9°C. Simulations performed using FORNUT model. From Harwell (1984)

precipitation on the forest structure and productivity if that co-occurred with a 6°C decrease, again having the stresses last only for the first 5 years of a 50-year simulation (Figure 2.2). As in the other simulations, no account was taken of the effects from the acute period of nuclear war stresses. Three simulations were run, with reductions in precipitation by 0%, 10%, and 25%. The results indicate that for this forest, primary productivity is far more sensitive to a 6°C reduction than to precipitation reductions. Simulations were also conducted to test the effect of reduced insolation on the forest with and without a simultaneous reduction in precipitation. Figure 2.3 indicates that a 25% reduction in precipitation alone is about equivalent in effect to a 50% reduction in insolation lasting for one year (a situation *not* expected to be an outcome of nuclear war), and these in turn are only somewhat greater in effect than the 3°C reduction if that occurred alone (Figure 2.1).

The FORNUT model was also examined for species compositional effects from the chronic stresses. The model maintains number, size, and age information for each individual tree in the simulation plots. These were used to estimate the biomass levels for the dominant tree species at the end of

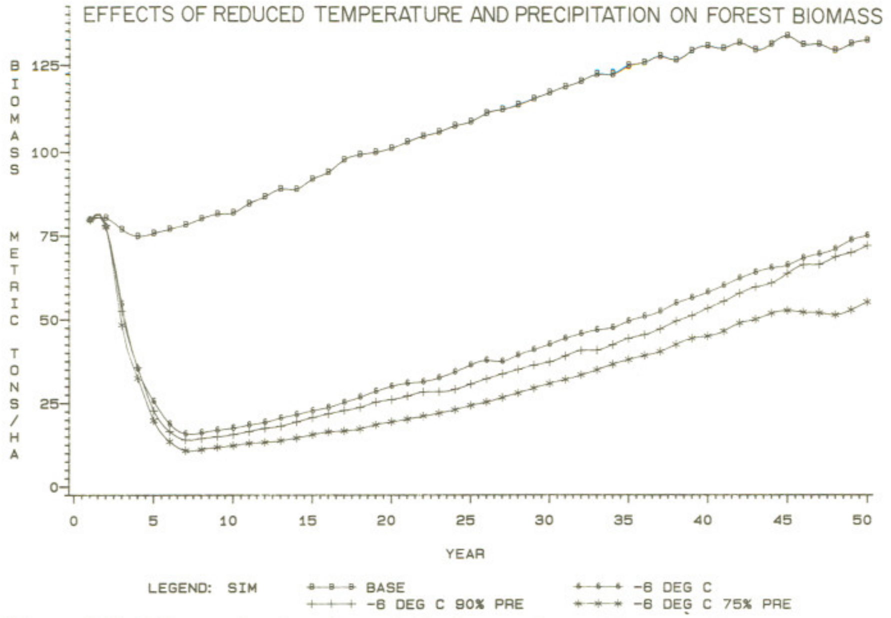

Figure 2.2 Effects of reduced precipitation on forest biomass. Air temperatures reduced by 0°C and 6°C, and precipitation reduced 0%, 10%, and 25% for first five years. Simulations performed using FORNUT model. From Harwell (1984)

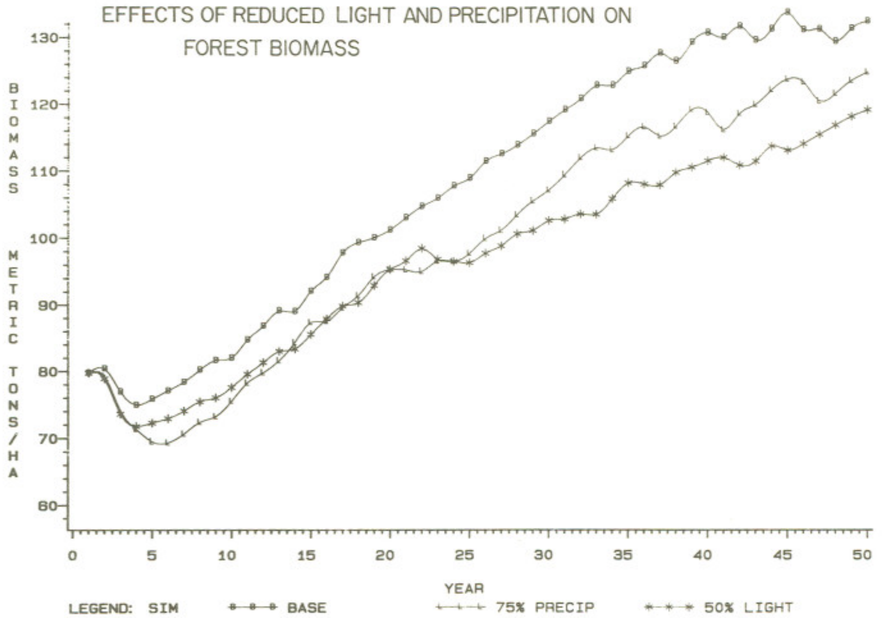

Figure 2.3 Effects of light and precipitation reductions on forest biomass. Reduction of 75% for precipitation imposed for first five years only; reduction of 50% for light imposed for first year only. Simulations performed using FORNUT model. From Harwell (1984)

the fifty-year simulation period for the control forest simulation and for simulated temperature reductions of 3°C, 6°C, 9°C (Figure 2.2), and a 25% precipitation reduction, and a 50% reduction in insolation (Figure 2.5), each acting independently. Compositional changes were limited for the 3°C case, with only sourwood (*Oxydendron arboreum*) being eliminated from the forest. However, a 6°C or a 9°C reduction resulted in a relative increase in red maple (*Acer rubrum*), ash (*Fraxinus americana*), and black cherry (*Prunus serotina*), but a loss of hickory (*Carya glabra*), tulip poplar (*Liriodendron tulipifera*), blackgum (*Nyssa sylvatica*), sourwood (*Oxydendron arboreum*), and oak (*Quercus prinus*). The responses are roughly correlated with the geographical ranges of the tree species: those species distributed over a wide latitudinal range tended to increase, while species with a more restricted southerly distribution were reduced or eliminated. In contrast, reductions in either precipitation or insolation were found to have no significant effect on the composition of the dominant trees in the forest.

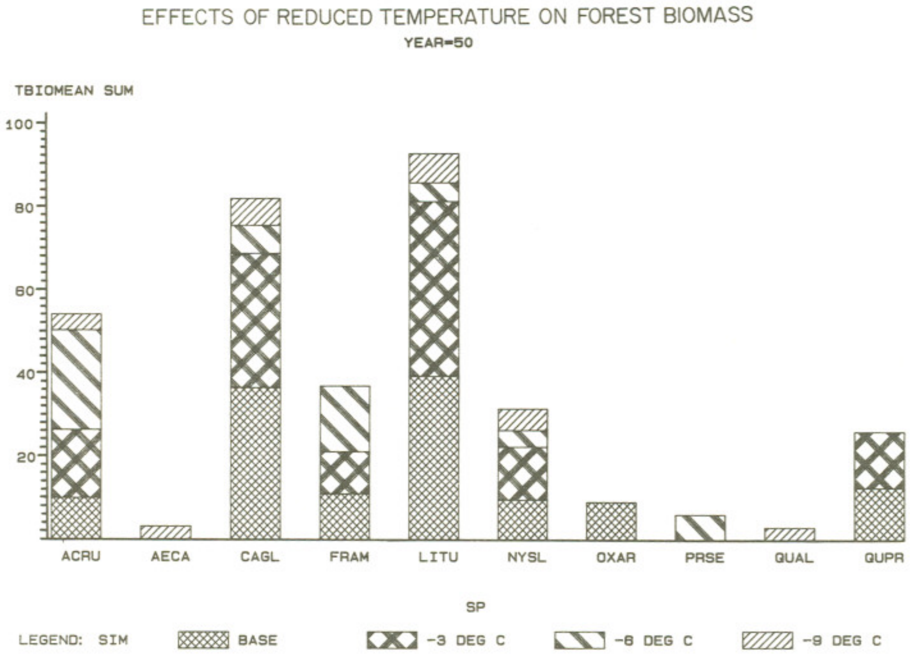

Figure 2.4 Effects of reduced air temperature on forest composition. Biomass values reported for species at fifty years, with temperature reductions occurring only for first five years. Species code: AECA, *Aesculus octandra*; ACRU, *Acer rubrum*; CAGL. *Carya glabra*; FRAM, *Fraxinus americana*; LITU, *Liriodendron tulipifera*; NYSL, *Nyssa sylvatica*; OXAR, *Oxydendron aboreum*; PRSE *Prunus serotina*; QUAL, *Quercus alba*: OUPR, *Quercus prinus*. From Harwell (1984)

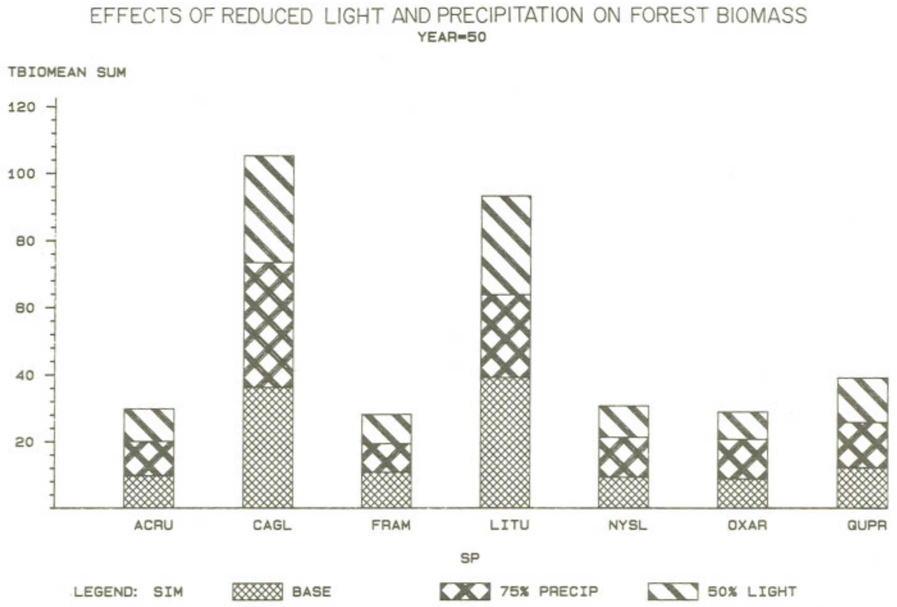

Figure 2.5 Effects of 50% light and 75% precipitation reductions on forest biomass. Reductions for first five years only. Simulations performed using FORNUT model. Species code as in Figure 2.4. From Harwell (1984)

These simulations (Harwell, 1984) are illustrative of the types of effects that could occur on the plant components of forested ecosystems following possible chronic stresses associated with nuclear war. First, there is the potential for long-term reductions in *primary productivity* lasting for decades after the perturbations ceased and the climate returned to normal. This expectation of slow recovery is related only to chronic stresses, and does not include the probably much more marked forest alterations in response to the acute stresses. It also does not include the likelihood of increased fires during the same period. Either case would considerably retard the projected rates of recovery, as would human exploitation. Second, changes in the species *composition* of the forest could occur under some of the stress conditions; these changes reflect the propagation of effects through the mechanism of species interactions, as trees more sensitive to temperature or other reductions became replaced by more hardy species. Third, although the model does not link the forest to the animal communities associated with it, the reductions in productivity could be expected to translate into at least as great a reduction in secondary productivity, and the shifts in species composition among plants is both an indicator of and an initiating factor in animal community alterations. Indeed, experience would suggest that the animal populations would undergo more significant impacts than indicated for the relatively stable tree community.

2.2.3 Potential Effects on Temperate Grassland Ecosystems [3]

2.2.3.1 Vulnerabilities to Acute Climatic Disturbances.

Temperate grasslands occur in large areas of the moderately dry and continental climates of North America and Eurasia. They are dominated by graminoids and herbs that die back to ground level each year, with relatively few shrubs and trees found only in riparian habitats. Landscapes that naturally would be grassland have been extensively modified by human activities, mostly for agricultural crops and grazing. Thus, relatively little of the original grassland ecosystems continue to exist, and these have largely been depleted of their original large herbivores.

As with other ecosystems, the effects of potential acute climatic stresses associated with nuclear war are first considered. The major grasslands of the Northern Hemisphere are at the latitudes of potential nuclear war targets, and they are in areas where the maritime influence on the climate is minimal. Thus, these ecosystems could experience rapid onset of severe climatic disturbances. In addition, being concentrated in the continental, nuclear war zone, these ecosystems would likely be subject to additional stresses such as radiation, fire, pyrotoxins, air pollutants, and human exploitation.

Following a *winter* nuclear war, the effects of reduced temperature and light levels during the acute phase would not initially reduce primary productivity, which is low or nonexistent during this season. However, delayed effects, such as a reduction in average temperatures extending into the following summer months, could delay or inhibit plant productivity. The effects of immediate temperature reduction on the large mammals could be severe, with perhaps 25–75% mortality because of cold temperatures, potentially increased initial snowfall, and reduced access to forage. Small mammal mortality would not be nearly so large because of aestivation. Resident birds would be severely affected. However, the soil subsystem would remain essentially intact. In general, the impact on the plant community, even in southern grasslands, would be far less than the impacts on the large mammal and bird populations.

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[3] This section is based in part on discussions of the ecosystem working group at the Toronto conference, L.C. Bliss chairman. The section on simulation modelling of grasslands under simulated post-nuclear war conditions was largely written by J.K. Detling and J.D. Hanson.

Following a Northern Hemisphere *summer* nuclear war, grasslands throughout North America (i.e., from Alberta and Saskatchewan to New Mexico and Arizona), as well as grasslands throughout the U.S.S.R. and Asia, could be severely affected if low temperatures and limited light occurred during the peak of the growing season. Essentially all aboveground portions of grasses and shrubs would be killed to ground level, and belowground components could experience significant mortality (perhaps 20–50%), depending on the intensity of cold events and their duration. Grasses are well adapted to tolerating drought conditions during the growing season (Wilson and Sarles, 1978; Redmann, 1971), but not freezing episodes.

All large herbivore populations would be severely reduced by the low temperatures and loss of food supplies, especially if plant biomass was covered by snow or ice. Small mammals and bird populations would also be eliminated or reduced to very low densities. The possible sudden onset of cold would not allow animals that normally aestivate to attain the level of cold tolerance typical of winter conditions. Invertebrates would suffer high mortalities among adults, but most species would survive through their egg and larval stages.

2.2.3.2 Vulnerabilities to Chronic Climatic Disturbances

In the case of possible chronic climatic stresses, reduced precipitation, light, and temperature would lead to reduced primary production. Laboratory studies of North American grass species indicate that a 5°C shift in daytime temperature may result in anything from a negligible change in production to a doubling or halving in production. Similar trends regarding the effects of temperature on above- and belowground production of *B. gracilis* (C_4) and *Agropyron smithii* (C_3) from the shortgrass prairie were reported by Kemp and Williams (1980). Thus, relatively small changes in temperature could have profound effects on total plant production and hence food availability and forage quality, as well as total protein yield available.

The seed bank in grassland soils is adequate to permit reestablishment of most species. Ruderal species are less abundant in grassland ecosystems than in forest ecosystems, therefore, plant succession dominated by pioneer species is less important than in forests. With the disruption in agriculture, the large tracts of previously cultivated lands would be dominated by weedy annuals for a number of years .

2.2.3.3 Results from Modelling Studies

Ongoing modeling studies at USDA-ARS in Fort Collins, Colorado and laboratory experiments in the Natural Resource Ecology Laboratory at Colorado State University were used to evaluate potential sensitivities to reductions in temperature and light. The initial simulations were done to evaluate the potential effects of chronic stresses following a nuclear war, i.e., conditions following the first few months. The direct effects of a possible extreme acute phase were *not* included in the initial simulations. Other runs that did include acute effects are reported later. These model results should not be interpreted as predictions of post-war grassland conditions, but as analyses of sensitivities to the stresses considered.

A recently developed grassland model, SPUR (Simulation of Production and Utilization of Rangelands), was used to evaluate the potential effects of several combinations of reductions in light and temperature on primary production and plant standing crops for a shortgrass prairie site. As depicted in Figure 2.6, the SPUR model (Hanson et al., 1983) simulates the flow of carbon and nitrogen from the atmosphere through rangeland plants.

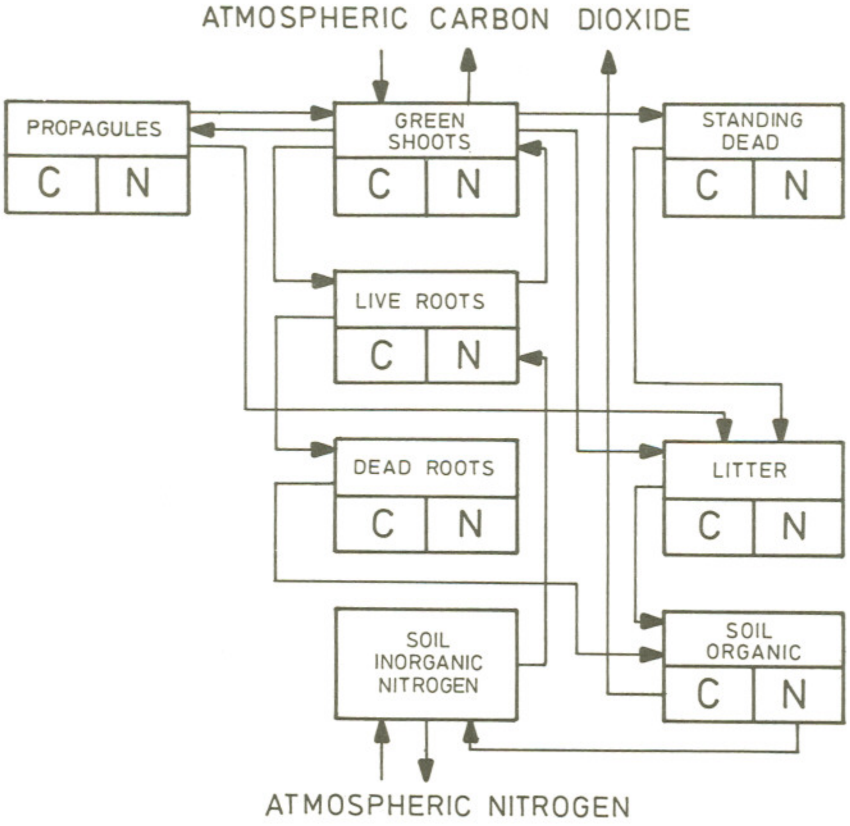

Figure 2.6 Carbon (C) and nitrogen (N) flow diagram for the plant growth component of the SPUR grassland model. Based on Hanson et al. (1983)

The initial set of simulations consisted of running the model for an entire year, using one of four different light levels (normal solar radiation and 25%, 50%, or 75% reductions), and four different temperature combinations (normal maximum and minimum daily temperatures, and 3°C, 6°C, or 9°C reductions in these values), based on weather data from the Pawnee Site in north-central Colorado for 1972. No changes in precipitation were included in these simulations.

The sensitivity of primary productivity to temperature decreases (Figure 2.7) is considerably less than seen for deciduous forests, as shown by the FORNUT simulations, described previously. The result using the SPUR model for grasslands is quite consistent with the results reported in Cooper et al. (1979), where 6% reduction in primary productivity was projected for each degree C reduction in temperature over the range of 0–4°C reductions. The decreased soil moisture stress in grasslands under reduced temperature conditions and associated reduced rates of evapotranspiration mitigated somewhat the effects of reduced temperatures on photosynthesis rates. The model results suggest that the principal effect of a decrease in temperature of 5°C (Figures 2.8 and 2.9) would be a shortening of the growing season for both C_3 and C_4 grasses. A 2–3 month reduction in the length of time that live (green) grasses would be available to consumers would have serious consequences for animal production, winter survival, and fecundity.

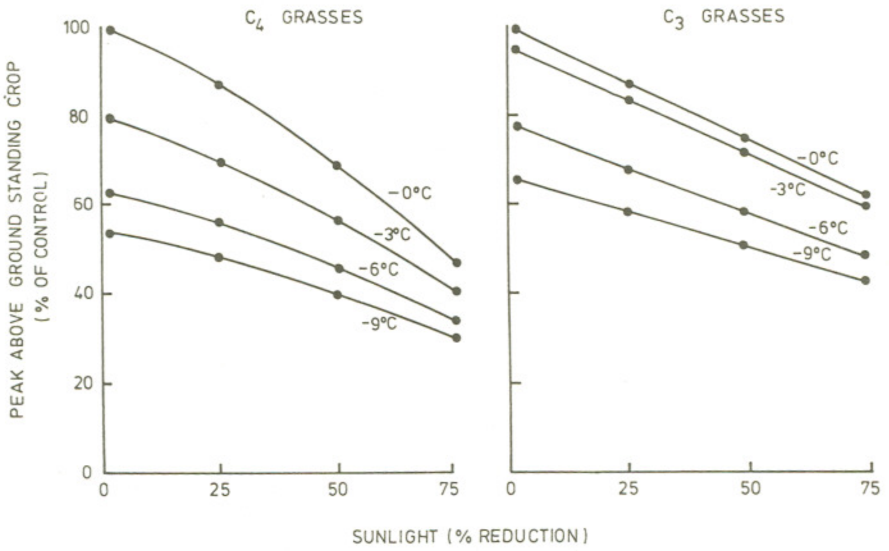

Figure 2.7 Simulated peak aboveground standing crop of C_3 and C_4 grasses at various reductions in temperature and light from observed values. Hanson et al., unpublished

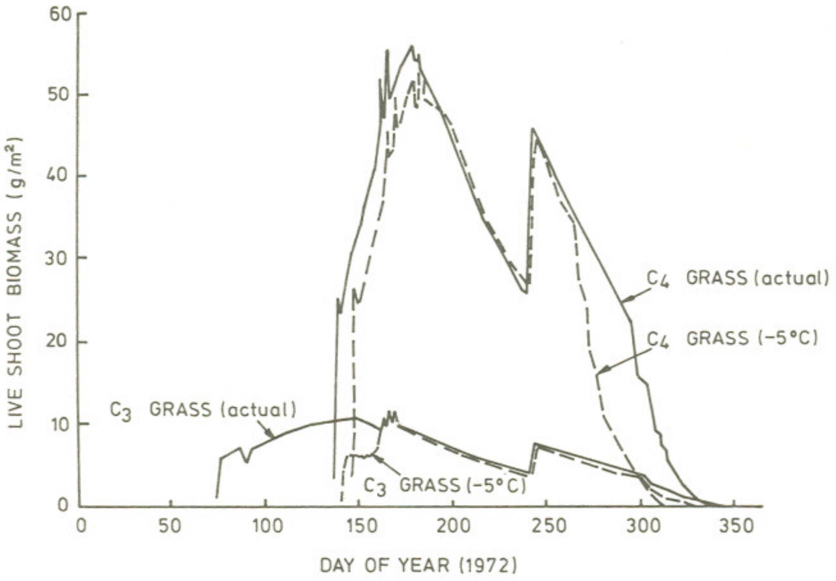

Figure 2.8 Simulated live shoot biomass dynamics of C_3 and C_4 grasses under actual measured temperatures for 1972 and with a 5°C decrease in temperature at the Pawnee grassland site

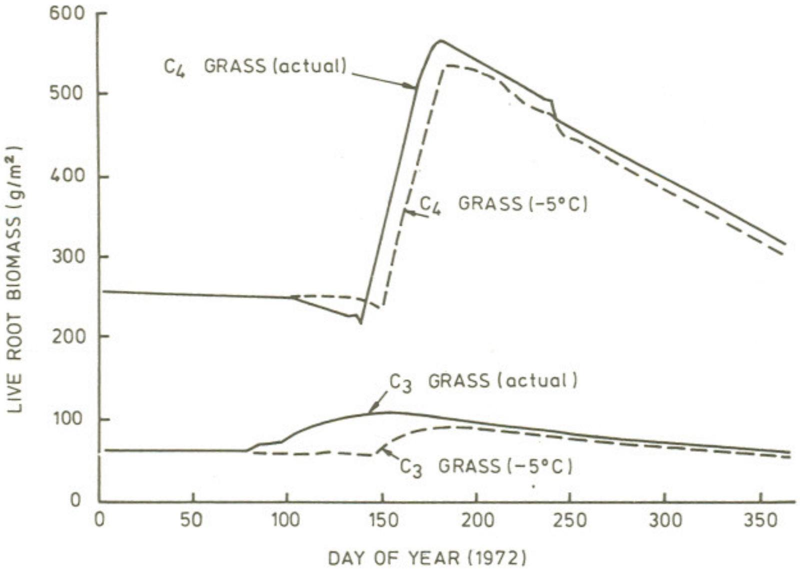

Figure 2.9 Simulated live root biomass dynamics of C_3 and C_4 grasses under conditions specified in Figure 2.8

A great deal of caution must be exercised in evaluating the results of these initial simulations. For example, no attempt was made to simulate increased plant death, which might be expected to be particularly high should episodes of severe climatic disturbances occur during the growing season. That is, the reductions in productivity predicted by these SPUR simulations occurred as a result of reduced photosynthetic activity for each plant rather than the actual loss of plants or their offspring. Also, as many models of perennial grass growth have shown (e.g., Detling et al., 1979), production in a given year is highly dependent upon the size of the perennating live biomass (e.g., crowns, stolons, rhizomes). In these simulations, no reductions in the primary producer state variables were made; hence, annual productivity might well be far less than predicted in the model runs. The set of simulations discussed below in part accounts for these factors.

Results of the first-year simulations indicated that a nuclear war on 1 January could reduce peak aboveground live standing crop more than an

TABLE 2.2

PEAK ABOVEGROUND LIVE PLANT STANDING CROP (g BIOMASS m^{-2})[a]

PLANT FUNCTIONAL GROUP	NOMINAL SITUATION	ACUTE ON DAY 1	ACUTE ON DAY 182
	YEAR 1		
C_4 Grasses	37.8	38.0	37.8
C_3 Grasses	12.6	4.7	12.6
Warm Season Forbs	3.8	11.6	3.8
Cool Season Forbs	10.3	0.7	10.3
Dwarf Shrubs	16.1	13.1	16.1
TOTAL	80.6	68.1	80.6
	YEAR 2		
C_4 Grasses	46.0	38.5	31.0
C_3 Grasses	11.9	7.2	9.1
Warm Season Forbs	10.9	9.5	9.2
Cool Season Forbs	9.6	3.2	2.8
Dwarf Shrubs	13.0	11.5	9.8
TOTAL	91.4	69.9	61.9

[a] From simulations by J.K. Detling and J.D. Hanson using the SPUR model.

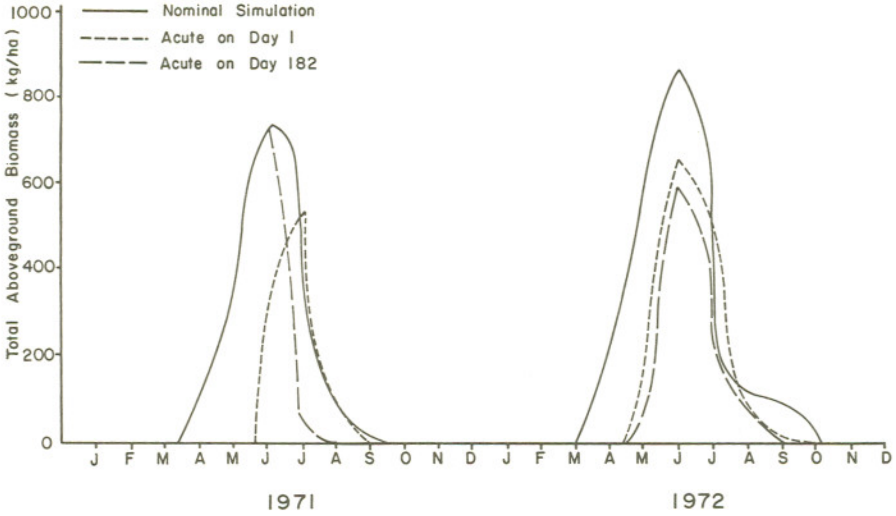

Figure 2.10 Simulated aboveground plant biomass for grassland under normal conditions and with climatic perturbations beginning on 1 January and 1 July. Simulations by Detling and Hanson using SPUR model

exchange conducted on 1 July (Table 2.2 and Figure 2.10). This result is somewhat misleading, however, because the peak biomass during 1971 was attained prior to 1 July (nearly all photosynthesis had occurred before that date [Table 2.3]) as a result of the extended summer drought and, thus, occurred *before* the climatic disturbances from a summer-onset nuclear war was assumed to begin. More importantly, as Figure 2.10 indicates, the aboveground live biomass immediately fell to near zero levels in the aftermath of a summer-onset nuclear war because of plant mortality. These near-zero levels remained until the second growing season. By contrast, the SPUR simulations suggest that primary productivity could recur during the first growing season after the winter-onset nuclear war.

In these nuclear war scenarios, the period of time during which live aboveground biomass was present was greatly reduced (Figures 2.10, 2.11, 2.12). This reduction in the growing season duration would be of particular significance to surviving grazing animals whose nutritional needs could best be met by consuming nutritionally superior live forage. Also, in years in which normal weather patterns would have favored a greater amount of late season growth, such growth would likely be completely eliminated following a midsummer nuclear exchange and reduced following a mid-winter exchange.

The abiotic section of the SPUR model simulates soil erosion losses on the

TABLE 2.3

ANNUAL ABOVEGROUND NET PHOTOSYNTHESIS (g BIOMASS m^{-2})[a]

PLANT FUNCTIONAL GROUP	NOMINAL SITUATION	ACUTE ON DAY 1	ACUTE ON DAY 182
	YEAR 1		
C_4 Grasses	197	240	193
C_3 Grasses	93	7	92
Warm Season Forbs	4	28	4
Cool Season Forbs	24	1	24
Dwarf Shrubs	58	39	57
TOTAL	376	315	370
	YEAR 2		
C_4 Grasses	266	155	129
C_3 Grasses	73	46	16
Warm Season Forbs	27	9	19
Cool Season Forbs	11	6	2
Dwarf Shrubs	17	12	2
TOTAL	394	228	168

[a] From simulations by J.K. Detling and J.D. Hanson using the SPUR model.

8000-hectare Pawnee Site. Following a simulated nuclear exchange, soil erosion losses from the site were estimated to be from 22 to 27 times greater during the year of the nuclear war than in nominal simulations. During the second year following the simulated nuclear war, the soil erosion losses continued to be greater than in the nominal simulation, but they were considerably less than the soil erosion losses of the first year. Soil losses were markedly greater in the second year following a summer-onset nuclear war than following a winter-onset nuclear war.

As with other simulation models, the results from these analyses need to be treated carefully. For example, this model is unable to simulate changes in species composition within any of the individual plant functional groups. It is possible that one species in a functional group might be largely replaced

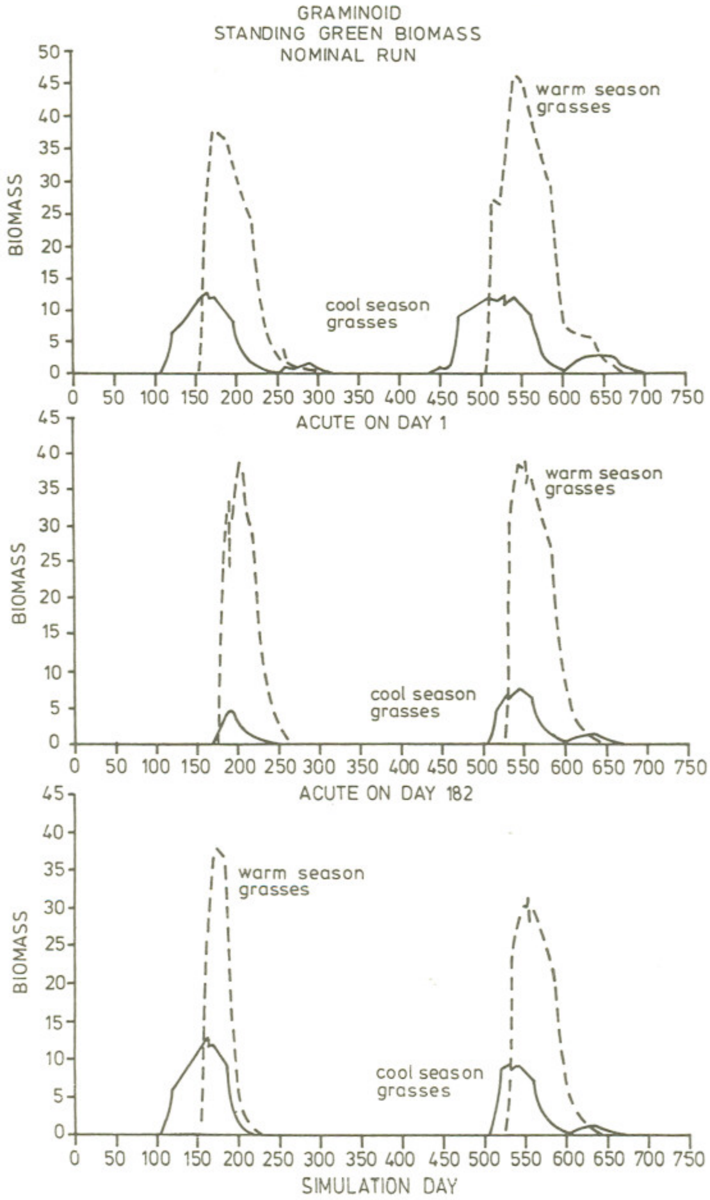

Figure 2.11 Simulated aboveground biomass for grassland ecosystem warm season and cool season grasses under normal conditions and with climatic perturbations beginning on 1 January and 1 July. Simulations by Detling and Hanson using SPUR model

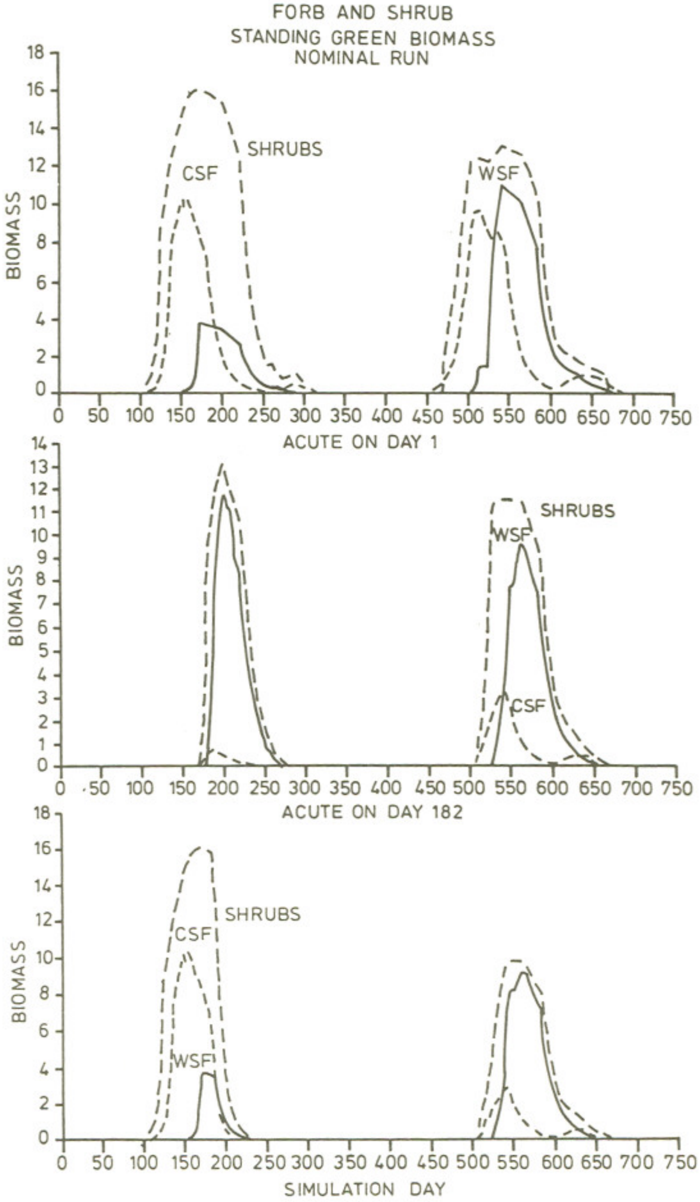

Figure 2.12 Simulated aboveground biomass for grassland ecosystem forbs and shrubs under normal conditions and with climatic perturbations beginning on 1 January and 1 July. Simulations by Detling and Hanson using SPUR model

by another less nutritional or desirable species. The model does not purport to handle the animal populations with the degree of reliability as the plant components. Changes occurring indirectly as a result of other factors (e.g., fire enhancement, human activities, loss of herbivores, loss of insect predators, and many other examples) could translate back into effects on primary production and community composition in ways not addressed by the simulations. Additionally, indications are that how the reduction in the average temperature over a growing season is imposed in a simulation can have a large effect on the results of the simulation. For example, a 3°C reduction in every daily maximum and minimum is likely to give quite different results from having most days with a lesser reduction, but a few days with much colder episodes. This issue was found to be very important for the simulations of agricultural productivity (Chapter 4), but for grassland ecosystems the effects of such temporal climatic variability have not yet been simulated.

2.2.4 Potential Effects on Arid and Semi-arid Ecosystems [4]

2.2.4.1 Introduction

The arid and semi-arid ecosystems of the temperate regions of the Northern Hemisphere include a wide variety of types, ranging from arctic to subtropical in distribution (Whittaker, 1975). Arctic-alpine semi-arid ecosystems occur above the timberline limited by latitude or elevation; these systems have been included in previous discussions. Cool semi-arid ecosystems are typified by the landscapes of the Great Basin in the United States, between the Cascade and Rocky Mountains, and in broad reaches of central Asia such as the Gobi. They are characterized by drab gray scrub, with the most widespread communities dominated by sagebrush (*Artemisia* spp.) and perennial grasses.

In more southerly areas, warm semi-arid ecosystems occur, characterized by open scrub of creosote bush (*Larrea divaricata*) with smaller shrubs and cacti. These ecosystems are widespread in North America, and through large areas in Northern Africa, the Arabian Peninsula, and India. In the warm semi-arid ecosystems, there has not been the convergence to a dominant plant form, as is the case for the cool semi-arid regions and other biomes (Whittaker, 1975). Animals in these ecosystems include a relatively rich diversity of reptiles (especially lizards and snakes), small mammals, and birds, and these ecosystems are often utilized to support large herds of beef

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[4] This section is drawn primarily from the discussions of the ecosystems working group at the Toronto conference, chaired by L.C. Bliss.

cattle, sheep, or goats. By contrast, true deserts are characterized by very low species diversity of animals, and occur primarily in subtropical regions. Essentially no plant community exists for those regions where the precipitation is less than 2 cm per year, and sparse vegetation occurs between 2 and 5 cm of precipitation per year. True deserts are characterized by the nature of the ground surface (e.g., sand, stony desert pavements, salt crust, and barren rock). These ecosystems occur in the Northern Hemisphere in Northern Africa, the Arabian Peninsula, and in parts of the Southwestern United States.

2.2.4.2 Vulnerabilities to Potential Acute Climatic Disturbances

Considering first the vulnerability of these ecosystems to an acute climatic response to a nuclear war that occurred in the *winter*, in the cool semi-arid regions it is expected that reductions in temperature would not have a great impact on the plant communities, since these systems usually experience cold temperatures, with some snow, each winter. The shrubs and grasses in these ecosystems are cold hardened, probably to levels similar to tundra ecosystems, since the lack of a deep snow cover subjects the plants to more extreme temperatures than would be experienced under a snowpack. The hot deserts, however, could be significantly affected by climatic alterations in the winter, since many of the constituent plants in these ecosystems are not cold hardened. Nobel (1982) reported on the low temperature tolerance and cold hardiness of cacti, including 14 species in North America and 4 species from South America. Cacti from southern Arizona and California are cold hardy to −6°C to −9°C; cacti from high, semi-arid grasslands in Wyoming are cold hardy to −20°C. This suggests that cacti could survive temperature reductions of 5°C to 15°C in the winter, and might be able to cope with subfreezing temperatures even in the summer. Some shrubs would survive, although mortality could exceed 75%.

Large animals would be reduced in numbers, and most birds would die. Small mammals in the warm semi-arid ecosystems would suffer, since they would have reduced food supplies and since they do not aestivate, unlike their cool desert counterparts. Most invertebrates, and other species in the soil subsystems, would survive in either the cool or warm semi-arid ecosystems.

In the event of a *summer*-onset nuclear war, subfreezing temperatures and light reductions occurring in an acute phase would result in very large effects on either cool or warm semi-arid ecosystems. High plant mortality would occur. If temperatures did not reach below the freezing point, plants could probably survive, but photosynthesis would be substantially reduced. Animal populations would suffer high mortality initially from extreme temperatures, and recovery would be impeded because of insufficient food availability resulting from the loss of primary production. The soil subsystem would remain intact. In subsequent periods, when temperatures returned to near-normal levels, nutrients would be released in a pulse, as decomposition and recycling processes would suddenly increase because of the increased substrate. Plants would eventually resprout or would grow from germination within the seed bank, which would be largely unaffected by the acute perturbations. Annual species are common, but a group of true successional, ruderal species is quite limited. Plant reestablishment is largely limited to perennial grasses, shrubs, and cacti.

2.2.4.3 Vulnerabilities to Potential Chronic Climatic Disturbances

The vulnerability of semi-arid ecosystems to the chronic effects of a nuclear war would be dominated by effects on precipitation rather than effects on temperature. For these ecosystems, the results reported in Cooper et al. (1979) suggest that reducing temperature by a few degrees gives an effect similar to the mechanism seen in grasslands, where productivity reductions were found to be less than for other types of ecosystems because of the reduced levels of evapotranspiration associated with reduced temperatures. However, in the case of the semi-arid ecosystems, reduction in evapotranspiration and concomitant reduction in moisture stress typically more than compensates for reduction in temperature, so that there would likely be a net increase in primary production in response to the reduction in temperature by a few degrees. The analyses reported in Cooper et al. (1979) indicated that about a 3% increase in primary production would occur per degree decrease in average temperature over the range of +3 to −3°C difference from normal temperatures. On the other hand, if a reduction in precipitation of 25% to 50% also occurred, as believed to be possible after a nuclear war, then reduced primary production would ensue. However, even in those circumstances, the major ecosystem components would survive, since these ecosystems are largely adapted to prolonged periods of drought, and most of the organisms would compensate by shifts in the timing of their life cycles.

Ecosystems of arid lands contain few plant species that are truly successional and thus changes in species composition following major climatic disturbances would relate to shifts in the relative importance of species. Semi-arid ecosystems should be less sensitive to episodes of extreme temperature, since the biota often experience large drops in temperature during a single diurnal cycle in the summer months and, thus, are better adapted to brief temperature excursions than, e.g., forests. Therefore, the way in which an average temperature reduction would be imposed (i.e., uniformly versus episodic) would cause less sensitive effects for deserts and semi-arid ecosystems than for most other ecosystems.

2.3 POTENTIAL EFFECTS ON AQUATIC ECOSYSTEMS

2.3.1 Effects on Marine and Estuarine Ecosystems [1]

2.3.1.1 Introduction

Marine ecosystems cover the major portion of the Earth's surface (71%, Sverdrup et al., 1942), and, thus, are tremendously diverse and spatially extensive. For our purposes, marine ecosystems include: open ocean ecosystems, including surface pelagic and deep pelagic ecosystems; deep ocean and continental shelf benthic ecosystems; near-shore marine ecosystems; littoral ecosystems, including coral reefs, mud flats, and sandy beaches; and estuarine ecosystems. Vulnerability effects are separately considered for marine ecosystems in the Northern Hemisphere, in the tropics, and in the Southern Ocean. In each case, there are different levels of potential nuclear war-induced perturbations to consider, different sensitivities and resiliences of the ecosystems, and different degrees of importance to humans of consequences on the ecosystems.

An initial consideration is simply that much less is known about marine ecosystems than about terrestrial ecosystems, having both fewer data and a poorer understanding of basic processes. There have not been the sorts of experimental manipulations of most types of marine ecosystems as with their terrestrial counterparts, and observations in the field are more difficult and expensive to make. Existing ecosystem models of marine systems, although useful in characterizing what is known and what information is needed to understand these ecosystems, have limited predictive capabilities, even within more normal ranges of physical parameters than would be the case after a nuclear war. Moreover, there has to be a translation of the effects of nuclear war on the atmosphere into effects on the physical conditions of aquatic ecosystems. This is necessary in part because such changes in the physical conditions of bodies of water with significant water masses would be mediated and subject to a considerable time delay compared to the atmospheric conditions. And it is necessary in part because in coastal regions, the influxes of cold air, freshwater runoff, and sediment loadings from land areas are likely to be highly variable in intensity, spatial extent, and duration; these influxes alter the hydrodynamic features of vertical mixing and advective transport of fluids and suspended matter, which in turn affect temperature and light distributions. Nevertheless, enough is understood so

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[1] The discussions in this section are based on the marine working group considerations at the Toronto conference, J.R. Kelly rapporteur, and on discussion papers developed for SCOPE-ENUWAR by J.M. Teal; A. Seymour; D.W.H. Walton; A. Spitzy, V. Ittekkot, and E.T. Degens; and by G.J. Kelly and S.W. Jeffrey. The Narragansett Bay Model simulations were conducted by J. McKenna.

that initial estimates of the effects on marine systems of nuclear war can be made, with more known about near-shore than open-ocean ecosystems.

Many types of marine ecosystems are light limited, so that reductions in solar insolation may be more important to primary production than in terrestrial ecosystems. Some marine ecosystems are also nutrient limited, so that alterations in nutrient cycling processes can be quite consequential. The trophic structures of marine ecosystems are typically based on unicellular plants with rapid turnover in individuals and in their constituent elements, the same elements often recycling many times within the producer communities. These factors should be kept in mind in the following discussion.

2.3.1.2 Vulnerability of Open Ocean Ecosystems to Potential Climatic Disturbances

In this section, effects on pelagic and benthic ecosystems are considered. Pelagic systems contain plankton and larger swimming animals. Oceanic phytoplankton account for about 90% of total ocean primary production. Light and nutrients are limiting, and both must be co-located for photosynthesis to proceed at significant levels (Figure 2.13; Bunt, 1975).

The deep pelagic ecosystem is totally heterotrophic, dependent on food from outside sources, especially settling plankton and particulates from near-surface pelagic ecosystems. The deep pelagic systems contain distinctive ani-

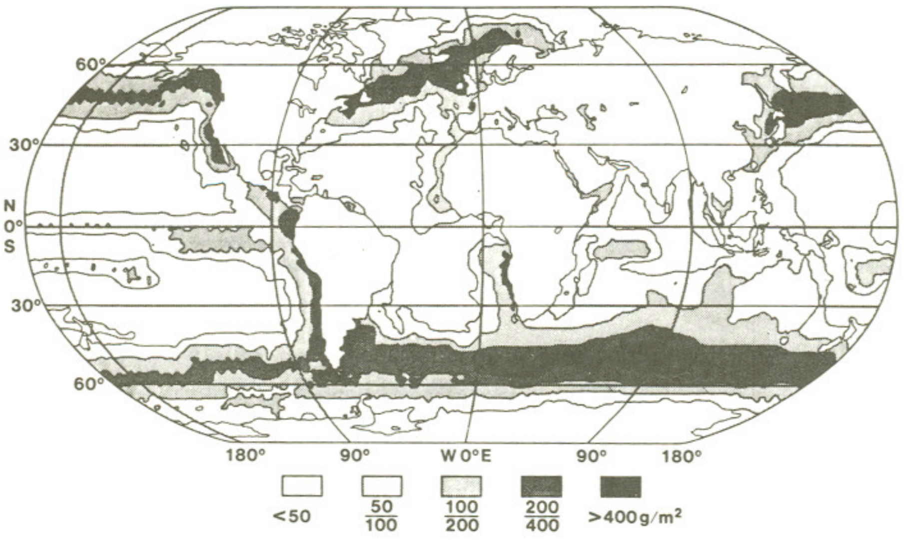

Figure 2.13 Primary productivity pattern of the oceans. Ranges mapped in g dry matter m^{-2} yr^{-1}. After Bunt (1975)

mal populations, including colonial protozoans, carnivorous crustaceans, and larger vertebrates. Benthic communities are also heterotrophic and cover the continental shelf and deep ocean. They consist of bacteria and animals living on or in the ocean bottom mud, and, on continental shelves, extensive algal communities supporting abundant herbivores and associated carnivores.

The first consideration of the potential effects of nuclear war on open ocean ecosystems is that they are well buffered against temperature changes. It might be possible for the sea-surface temperatures to be decreased by a degree or two in response to prolonged nuclear war-induced climatic perturbations, but larger water temperature reductions are not anticipated for the open oceans. Laboratory experiments indicate that phytoplankton would continue to grow under such temperature reductions (Figure 2.14). The nektonic (i.e., swimming) organisms in the pelagic oceans would not experience any major effects from a few degrees reduction in temperature, except that where behavioral patterns were finely tuned to ambient temperatures, some effects might occur.

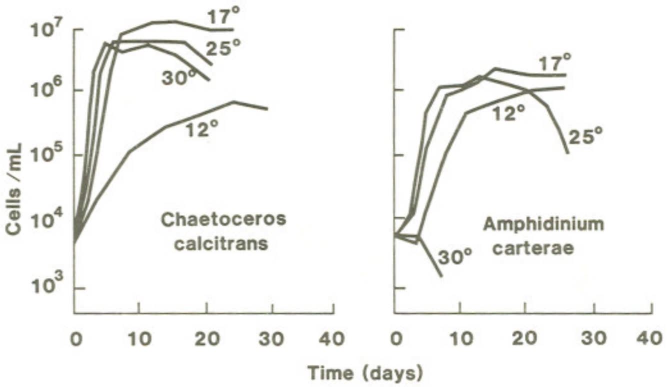

Figure 2.14 Growth in culture of two unicellular marine algae at various temperatures. Similar temperature tolerances were observed with seven other examined species. From Wilson, M.K., Kelly, G.J., and Jeffrey, S.W., unpublished

These projected minor temperature changes for the open ocean water would not extend very deeply into the water column, certainly not down to the level of the benthos. The animals in the lower water and benthic regions are also not sensitive to small reductions in temperatures, even if these could occur in response to climatic changes. Thus, one would not expect *any* direct effects from water temperature changes for either the pelagic or benthic biological communities in the open oceans. The potential for indirect effects, especially changes in ocean currents and in thermocline depths and stability (see Luyten et al., 1983a,b), however, does warrant further consideration.

Reduction in light levels, on the other hand, could significantly affect the primary productivity of pelagic ecosystems. Phytoplankton exist at depths to which irradiance is reduced to 1–10% of surface levels, in the range of 10 to 200 μEinsteins m^{-2} sec– 1 (Richardson et al., 1983). If this were reduced by 95% or more for a period lasting up to several weeks, growth for most algal species would effectively cease, since the remaining irradiance would fall below the light compensation point. That value is defined as the amount of light input at which photosynthetic carbon dioxide fixation is just sufficient to compensate for the loss of carbon dioxide through respiration by the plant organism (Figure 2.15). With a 95% reduction in incident solar radiation at the surface, the light compensation point, which normally occurs at the lower boundary of the euphotic zone, would be raised much closer to the surface (Figure 2.16). Consequently, light would not be limiting above the new compensation point. However, nutrients, which are relatively homogeneously mixed within the water column above the thermocline, would not be available at the depths to which light penetrated; e.g., in Figure 2.16, the depth to the compensation point would decrease from 110 m to about 10 m, reducing the water volume and associated nutrients available for photosynthesis by an order of magnitude. This much thinner layer of light availability would require an additional influx of nutrients, such as from upwelling, to maintain the levels of primary productivity.

Recent work suggests that significant levels of photosynthesis can continue for some species in the open ocean when the light levels are greatly reduced, even down to the extreme levels postulated for the post-nuclear

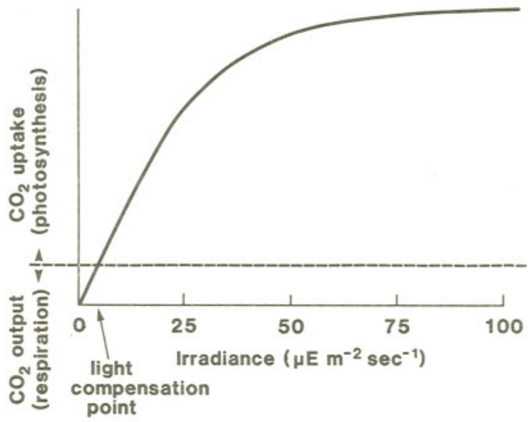

Figure 2.15 Idealized curve for effect of solar irradiance on phytoplankton growth. The light compensation point is about 5μE m^{-2} sec^{-1}. From Wilson, M.K., Kelly, G.J., and Jeffrey, S.W., unpublished

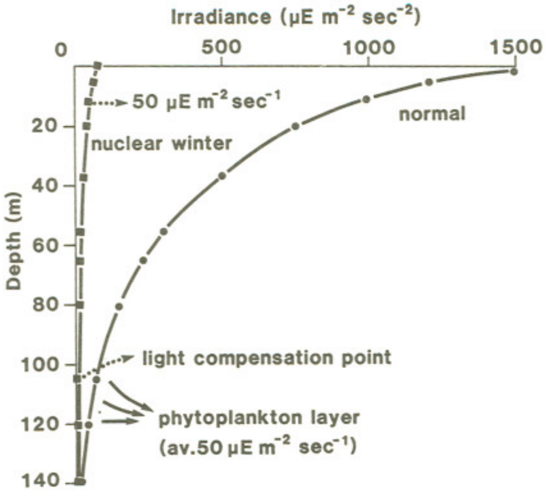

Figure 2.16 Light penetration and phytoplankton growth in the ocean. The 'normal' curve is for relatively transparent waters of the Coral Sea (Jeffrey et al., 1982), where depth profiles of phytoplankton Chlorophyll *a* are maximal at about 100–120 m (Jeffrey, S.W., and Hallegraeff, G.M., unpublished). The 'nuclear winter' curve is constructed using solar irradiance values equal to 5% of those on the normal curve

war situation (Jenkins and Goldman, 1985). However, it is not clear how widespread this phenomenon is and whether or not it could compensate for the reduction in primary productivity associated with plankton that require higher intensities of incident sunlight. Thus, potential for a compensatory mechanism does exist, but would require replacement of much of the phytoplanktonic community by low-light tolerant species of phytoplankton, which may be present locally. In general, reducing solar input by 95% for periods of weeks or more would greatly reduce phytoplankton photosynthesis and reproduction, and the biomass of the primary producers would largely disappear, as their cells would not be replenished even though grazing and mortality would continue, perhaps even at higher than usual rates.

Whether or not particular phytoplankton populations would survive would depend on their capability to exist heterotrophically, to photosynthesize at low-light levels, or to become encysted until more favorable environmental conditions returned. At the most extreme light reduction scenarios, e.g., reduction to 1% of normal lasting for months, the phytoplankton standing crop would be insufficient to support heterotrophic populations, and the question of species survival rather than just population size would become central. Survival of diatoms for three months in darkness has been recorded (Garrison, 1984), and the formation of spore or cyst stages that can survive for months or even years has been documented for several groups, including diatoms and dinoflagellates. Indeed, polar species have for millenia survived darkness that lasts for months. Thus, it is probable that plankton communities would recover (i.e., not go extinct) after light levels returned to normal, with a relative increase in low-light tolerant species, species that encysted, and populations that were transported by currents into the depleted regions.

If the phytoplankton biomass in the pelagic regions of the Northern Hemisphere were severely depleted following an acute reduction in insolation, it is probable that the zooplankton that feed on phytoplankton would decrease in numbers, as would the larval fish that feed on the zooplankton. This is because these relatively small organisms do not have the energy reserves to carry them for long periods of time without food inputs; baleen whales, on the other hand, which feed on phytoplankton and zooplankton, would not likely suffer mass mortality if the plankton populations recovered over the space of several months.

It is not clear how intermediate-sized heterotrophic populations, such as the pelagic fishes, would respond to a loss of the primary producer base. If the plankton food sources were lost for a long enough period, mortality of fish from insufficient food might occur. However, many of these species might find alternative food sources, and many could endure prolonged periods without food. One factor to consider is the potential for feedback between limited phytoplankton resources and increased herbivory by the zooplankton. In coastal waters, this could lead to increased loss of phytoplankton populations (i.e., those that survived the physiological problems of insufficient light might be subject to an increased rate of consumption by herbivores); however, in open ocean ecosystems, zooplankton populations tend to starve to death, in large part because of the lower density of plankton populations.

If fish larval life stages were eliminated but the adults did not experience substantial direct mortality, then the overall population impacts would depend on the longevity of the species and the number of years for which adults are reproductively viable. Projections of fish population responses are highly uncertain; current models are not good predictors of fish population size based on estimating effects of the physical environment on recruitment, since the relationships between larval survival and adult recruitment are poorly understood. Some generalities can be identified, however. Species such as cod, which ordinarily produce significant year classes every year, would suffer a relatively small reduction in total population, since individual adults are long-lived, on the order of 10 years. Thus, complete loss of an age class would constitute only a 10% reduction in the total population. On the other hand, species such as haddock, which produce a significant year class only every 7–10 years (i.e., essentially only once in the adult population's life cycle), could either not be affected (i.e., if the perturbations occurred in a year for which there were not a major production of new juveniles), or could be devastated (i.e., if the nuclear-war induced perturbations eliminated the total new year class). In that case, the species itself could be in jeopardy, depending on the spatial extent of the larval die-off. In general, however, ocean fisheries would not experience total elimination from climatic perturbations; indeed, many species might actually experience significant increases in numbers following a reduction in the human fishing pressure, which is now the principal cause of mortality for the adult fish of many species. Such an increase in fish populations occurred during the years of World War II, apparently for this reason (Cushing, 1975; Gulland, 1974).

The impacts on pelagic ecosystems from a potential *chronic* reduction in light levels by 5–20% and air temperatures by one degree or so do not appear to be significant. Once light levels returned to a substantial fraction of normal, the phytoplankton and zooplankton populations would recover rather quickly, albeit perhaps with different dominant species. The populations of larger animals of the euphotic and deep pelagic regions would survive essentially intact. Thus, long-lasting acute effects, if any, would not extend into the chronic period, and the potential levels of stress at that time are considered to be insufficient to cause substantial reductions in primary or secondary production by direct mechanisms.

On the other hand, indirect effects from altered oceanic circulation patterns could substantially alter the spatial distribution of upwellings and, therefore, of high productivity. For example, the recent El Niño was associated with alterations in oceanic circulation patterns that resulted in decreased upwelling off the coast of Peru, resulting in a collapse of that nation's anchovy fishery. El Niño is a good example of how relatively small sea surface temperature changes can be linked to a decrease in the strength of trade winds. Much larger alterations in wind strengths and directions would likely be possible in the chronic phase of a post-nuclear war world in response to differential temperature effects between the Northern and Southern Hemispheres, and between oceanic and continental regions. Thus, ocean fisheries are vulnerable to indirect effects, mediated via changes in oceanic circulation, both with respect to their magnitude and variability, and with respect to the predictability of location of this potential food source by human survivors. Moreover, disturbances of ocean currents have been known to last for years and to interfere with fisheries for years or decades thereafter.

Effects of climatic alterations on the benthic ecosystems well away from continents would be minimal. During the acute or the chronic periods, there would be no change in the light regime experienced by benthic biota, since they already exist in the dark. There would also be no change in the temperatures at the bottom, since the upper water mass would totally absorb these temperature changes before they could be felt by the benthos. Thus, effects on benthic ecosystems would be limited to indirect effects propagated by changes in the biological productivity of the upper pelagic systems.

Mortality of plankton in an acute period could lead to a temporary increase in food inputs to the benthos; however, the standing crop of plankton is small relative to total annual production. Therefore, receiving the brief, small pulse of additional organic inputs from planktonic die-off would be more than compensated for by the decrease in inputs in subsequent periods. Another factor is that fine particles in the upper layers of the ocean have settling velocities that are too slow to overcome turbulent mixing in the waters. These do not accumulate in the water column, however, since there is a biologically mediated formation of aggregates heavy enough to sink. Two mechanisms are involved: 1.) fecal pellet formation by zooplankton; and 2.) formation of organic-rich flocs, consisting of minerals glued together by organic matter derived from metabolic activities of phytoplankton (Kranck and Milligan, 1980; Honjo, 1982; Deuser et al., 1983). Mass mortality in planktonic populations could substantially alter this source of sedimentation to the benthos.

It is not clear how much reduction in the total resource base inputs (i.e., direct plankton and plankton-mediated inputs) would actually be felt by demersal fish and benthic invertebrates, nor what their capability is to withstand temporary reductions in food. Since the energy for benthic ecosystems comes seasonally from the surface, with rapid enough response so that that seasonality can be seen in the benthos (Deuser et al., 1983), one could expect that these organisms are adapted to surviving periods without food inputs and, therefore, would be essentially unaffected by nuclear-war induced perturbations.

2.3.1.3 Vulnerability of Coastal Ocean Ecosystems to Potential Climatic Disturbances

Pelagic and benthic regions closer to the continents are different from open ocean systems because of the proximity to terrestrial systems. The pelagic systems are more influenced by nutrients, sediments, and other inputs from terrestrial systems, and are thereby generally of higher productivity than their more open ocean counterparts. They are also more subject to anthropogenic influences. The coastal benthos is subject to considerably less constancy than deep ocean benthos, with fluctuations in light, temperature, and particulate and other organic inputs.

In the context of the potential consequences of nuclear war, the coastal pelagic ecosystems are subject to the same sorts of light limitations and effects as discussed for open oceans. In addition, however, the near-shore pelagic ecosystems could experience a greater temperature effect, because of the shallowness of the water and because of influence of runoff from freshwater systems. Moreover, coastal systems could experience increased storminess and thereby experience turbulence, increased sedimentation, and increased mixing. The sediment load could add to light limitation problems; increased mixing and turbulence, along with enhanced nutrient inputs from terrestrial systems and from near-shore upwelling, would tend to increase primary productivity where sufficient light was available.

Coastal production in normal winter is apparently quite large and proceeds most rapidly at low light levels (Glibert et al., 1985), including levels typical of what is projected for atmospheric disturbances. Primary production, in that case, would not be as adversely affected if the phytoplankton populations could adapt to the unusual timing of an apparent winter. The animal populations would survive as long as the food remained sufficient. Thus, there is the potential for greater resistance to the stresses associated with climatic alterations than is the case for open oceanic pelagic ecosystems.

Tropical coastal marine ecosystems are much more sensitive to changes in both light and temperature. In general, the range of temperature tolerances in tropical waters is narrow, only about one-half the range found in temperate regions. These tropical ecosystems do not have an elevated maximum temperature; the upper limits are typically not much higher than in the temperate counterparts. Rather, the minimum temperature limits are usually at higher values, and tropical marine species have reduced cold tolerance (Zieman, 1975). For example, coral reefs are ecosystems that are restricted to the warmer oceans of the world where winter temperatures do not drop below 20°C and where depths typically do not exceed 50 m (Moore, 1966). Some corals depend on their symbiotic relationships with zooxanthellae for survival, and these corals have been shown to die after only about 30 days in the dark; other coral reefs recovered after exposure to dark for 60 days, and still others are not light sensitive at all (i.e., not dependent on the algae) (Franzisket, 1970; Lang, 1971). Coral reefs can also be damaged by temperatures of about 15°C , which was seen to kill staghorn corals in the Persian Gulf after only a 9-hr exposure (Shinn, 1976). In addition, corals are especially sensitive to increased levels of UV-B radiation, particularly those corals exposed or nearly exposed to the air at low tides (Harriott, 1985), as well as increased sedimentation. In short, it is probable that effects on coral reefs from nuclear-war induced perturbations would be among the most widespread and severe for marine ecosystems. Similarly, shallow-water tropical seagrass ecosystems are quite vulnerable to temperature reductions (Zieman, 1975, 1982).

The coastal benthic ecosystems that are partially autotrophic would likely have that source of production eliminated, as insufficient light would reach the bottom because of atmospheric darkening and water murkiness. It has been discovered that attached benthic algae live and grow at depths where less than 0.1% of the surface light penetrates (Littler et al., 1985); since these plants are close to the limits of tolerance, they would seem to have only a limited ability to withstand additional reduction in light. Strictly heterotrophic benthic ecosystems would experience the same types of effects as seen in open ocean benthic ecosystems, specifically the temporary loss of organic inputs from the pelagic systems above. Direct effects from light and temperature changes would not be noticed on the benthic systems. However, increased sediment loadings from terrestrial runoff could reach the benthos, carrying with it increased inputs of organics, toxic chemicals, and radionuclides.

Truly coastal areas such as beaches, mud flats, and salt marshes would be subject to much greater extremes of perturbations than the other ocean systems, especially with respect to temperature reductions, perhaps experiencing subfreezing temperatures for periods of time. Intertidal areas could likewise experience subfreezing temperatures at regular intervals (i.e., when exposed to the air). The consequences of extremes of temperatures would depend on the season, location, salinity, and tide strength. In winter in high latitude coasts, these conditions are normally accommodated, but most mid- and low- latitude coastal zones do not experience subfreezing temperatures; in that situation, mortality of surface-dwelling organisms would be likely, but those organisms that routinely burrow into sand or sediments would be at least partially protected. As another example, mangrove ecosystems which form the tropical protection for soft-sediment coastlines are unable to withstand freezing even briefly, although they would have sufficient energy reserves to withstand prolonged periods without solar light. (See discussion in Section 2.4.2.6). Mangroves and other coastal ecosystems are also especially vulnerable to intense coastal storms, which can move sediments and coastline profiles on a large scale (Kuhn and Shepard, 1981, 1983; Emery and Kuhn, 1982).

Fish populations in coastal waters that do not normally experience cold temperatures are vulnerable to substantial mortality from brief episodes of cold temperatures. Subfreezing episodes in coastal waters of Florida and Texas provide clear examples of this effect on low- and mid-latitude areas throughout the year, and, perhaps, on more northerly ecosystems in the summer. A 5-day freezing episode in Texas left many adult fish killed, with an apparent correlation between the extent of mortality and the rapidity of onset of freezing (Gunter and Hildebrand, 1951; see also, Storey and Gudger, 1936; Storey, 1937; Gunter, 1941). In the Florida Keys, an unusually cool month of January, with minimum air temperatures in the range of 4–10°C, led to widespread fish mortality across many species (Miller, 1940; Galloway, 1941); another cold event in Tampa Bay, Florida, with air temperatures rapidly falling to – 7°C and water temperatures down to 10°C, resulted in a fish kill, especially for subtropical and tropical species (Rinckey and Saloman, 1964). In most cases, adult fish mortality seems to occur at a greater rate for the larger species and larger individuals within a species (Snelson and Bradley, 1978) and for the shallower water areas (Dahlberg and Smith, 1970). This evidence suggests that near-shore fisheries in tropical and sub-tropical waters, and in temperate waters in the summer, are substantially vulnerable to episodes of cold temperatures, especially in bays and other shallow-water bodies that would be most directly accessible to human survivors. An additional factor to consider is that for many commercial fish species, their eggs or larvae live near the surface, and, thus, would experience increased stresses related to temperature, UV-B, radiation, toxic chemicals, and other stresses.

2.3.1.4 Vulnerability of Estuarine Ecosystems to Potential Climatic Disturbances

For those saline ecosystems that are more closely linked to freshwater and terrestrial ecosystems, i.e., estuarine ecosystems, many of the same considerations apply as discussed for the near-shore coastal waters; however, estuarine ecosystems would likely be subject to even greater stresses, particularly with respect to temperatures and surface runoff. One aspect not previously thought to be of significance for marine ecosystems discussions is the effect of potentially reduced precipitation, resulting in decreased inputs of fresh water into estuaries and, therefore, leading to increased salinities in the upper sections of these ecosystems.

Considering first salt marshes and intertidal wetlands, these ecosystems are dominated in their plant community by a few species of grasses, especially *Spartina*. This is a C_4 plant, adapted to high light levels; primary productivity decreases essentially in direct proportion to decreased insolation. In addition, survival of the plants in the summer can be a problem in the dark; the plants can survive for only a few weeks if the underground part of the marsh system, with its warm sediments, continues to respire rapidly while temperature and light effects prevent the aboveground portions from photosynthesizing (Hartman, 1984). The effect would depend on the precise timing of the onset of climatic perturbations, with a summer occurrence of extreme climatic disturbances resulting in a large-scale die-off of the plant community.

Such a die-off would propagate to the animal community and would lead to increased sediment load being exported from the marsh ecosystems. This sedimentation, along with increased resuspension associated with potentially increased storminess, would cause smothering of shellfish and other benthic organisms before the waters cooled sufficiently for these organisms to become dormant and, therefore, resistant to suffocation. The increased sediment load would inhibit light penetration, further reducing photosynthesis. Fish that depend on the wetlands for nursery areas could suffer loss of the year class; waterfowl and shorebirds could be affected by the loss of food as well as by the physical environmental stresses.

Other estuaries are also vulnerable to climatic perturbations. Most estuaries in the Northern Hemisphere are closely associated with human populations, and therefore could experience fallout and other direct effects from local nuclear detonations in combatant countries. Increased run-off in the early periods, associated with fires, habitat destruction, an initial pulse of precipitation, and other factors, would carry a substantial load of pollutants, which tend to accumulate in estuaries (Meade, 1972). Current anthropogenic pollutants, such as aromatic hydrocarbons, are transported into estuarine and near-shore sediments (Hoffman et al., 1984), and benthic organisms accumulate these compounds (Farrington et al., 1980), and their partial metabolic products (McElroy, 1985). Increases in these inputs would reduce the value of shellfish and other fisheries in these areas of closest proximity to humans, although tidal wetlands themselves are relatively resistant to pollution damage (Valiela et al., 1984).

Since it appears that estuarine ecosystems are both more vulnerable to nuclear war effects than other marine ecosystems and of greater importance to humans, a simulation model was used to look more closely at the responses of a major estuarine ecosystem, the Narragansett Bay in Rhode Island. The Narragansett Bay Model (Kremer and Nixon, 1978) simulates the flows of energy and materials among the compartments of the Bay, as shown in Figure 2.17 (see Chapter 2 appendix for model description).

Harwell (1984) reviewed simulations using the Narragansett Bay Model reported in Kremer and Nixon (1978) (i.e., simulation runs not done to simulate nuclear war climatic disturbances) for implications about those conditions. These simulations showed that the model ecosystem is sensitive to alterations in the seasonal patterns of water temperatures, that rapid reduction in primary and secondary production would follow from reductions in sunlight, and that rapid recovery of plankton production would occur when the physical conditions ameliorated.

In the present analyses, the Narragansett Bay Model was used to simulate the Bay under physical conditions of climatic perturbations. A series of simulations was conducted to represent: 1.) the acute onset of air temperature reductions of 5°C and 10°C lasting for two months, coupled with 90% reductions in insolation; nuclear war-induced climatic disturbances occurring in January and in July were simulated, and in another simulation, a July onset of acute climatic disturbances (lasting two months) was directly followed by the onset of chronic conditions (3°C /13% light reduction); and 2.) a chronic climatic perturbation period, with air temperatures and light levels reduced for the entire simulation period by 1°C /5%, 3°C /13%, and 5°C /16%, respectively. The simulations were conducted on the entire Bay, but results reported only for the area in the upper reaches of the Bay.

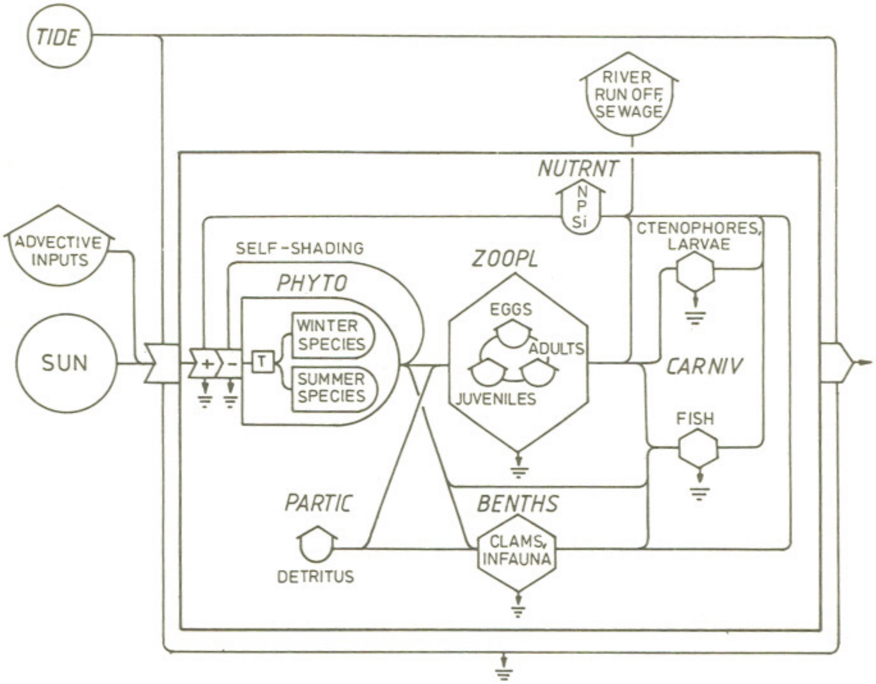

Figure 2.17 Energy flow diagram and conceptual framework for the simulation model of the Narragansett Bay ecosystem. After Kremer and Nixon (1978)

Figures 2.18a,b show how the water temperature and light levels were applied to the two acute scenarios. (The slight difference in second and third year temperatures are an artifact of the air/water temperature conversion process.) These represent the forcing functions for the simulations shown in Figures 2.18c,d. The phytoplankton production graph (representing net primary productivity) shows that phytoplankton production is vulnerable to a summer disruption in climate. By contrast, a January simulation resulted in an initial time lag in the development of the initial phytoplankton bloom during the spring, but by summer, when the temperature and light levels had returned to normal in this simulation, there were no effects on the phytoplankton production or dynamics. By the second and third year, no effects were seen to carry over from simulated acute stresses which lasted two months in the first year. (Note: The increased rates of phytoplankton production in the second and third years reflect an artifact in the modelled increase in temperature during that part of the simulation, and, therefore, they do not represent a nuclear war-induced response.)

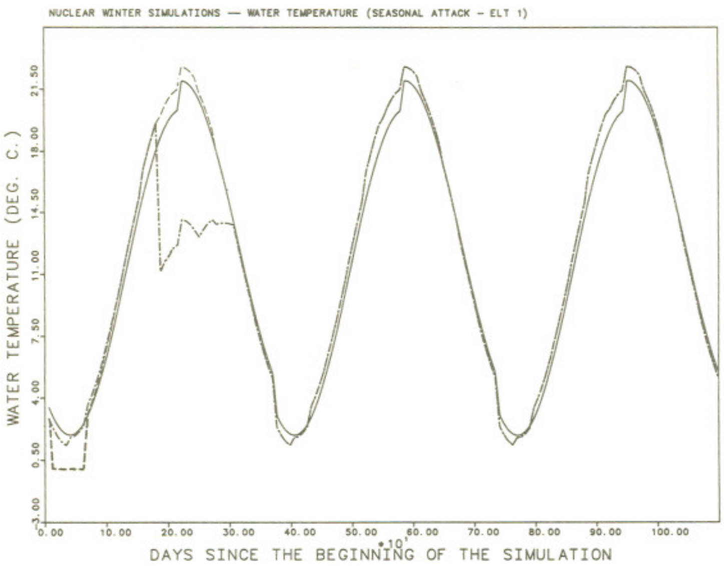

Figure 2.18a Water temperatures used in the Narragansett Bay Model simulations for normal (solid line), winter (dashed line), and summer (dash–dot line) acute climatic alterations. Temperatures were reduced by 5°C and 10°C for two months for winter and summer simulations respectively. Simulations conducted by J. McKenna

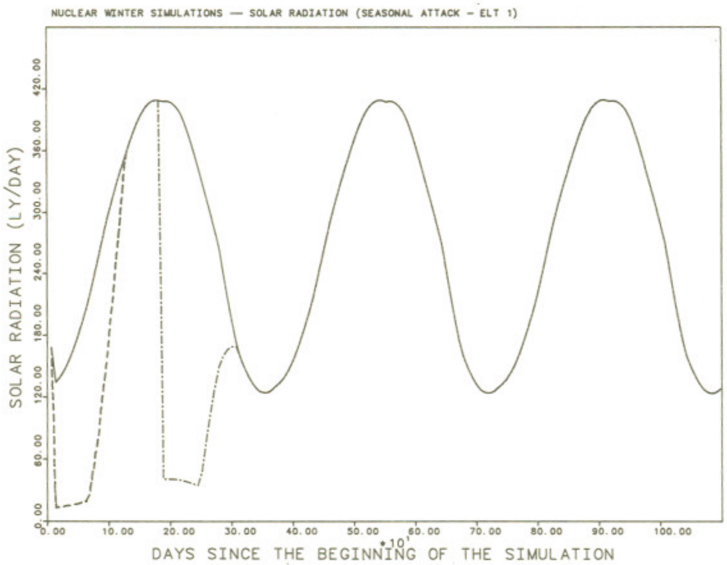

Figure 2.18b Solar insolation used in the Narragansett Bay Model simulations for normal (solid line), winter (dashed line), and summer (dash–dot line) acute climatic alterations. Light levels were reduced by 90% for two months

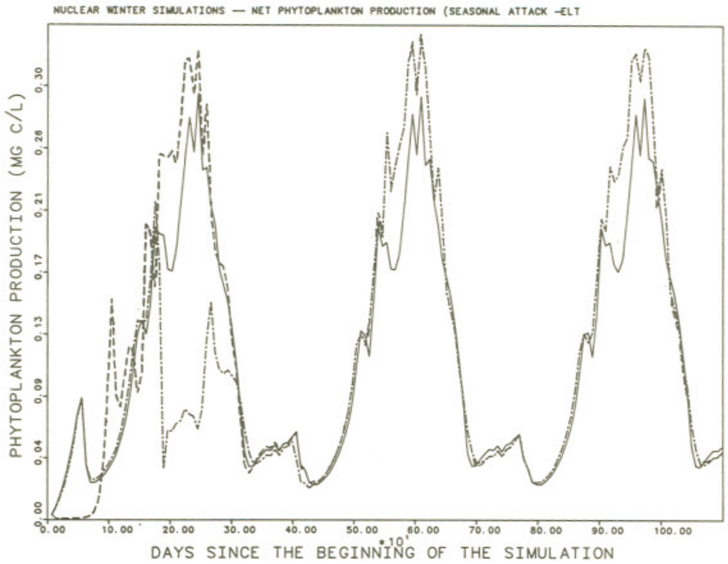

Figure 2.18c Simulated phytoplankton biomass (expressed as mg C l^{-1}) for Narragansett Bay Model. Simulations of normal (solid line), winter (dashed line), and summer (dash–dot line) acute climatic alterations

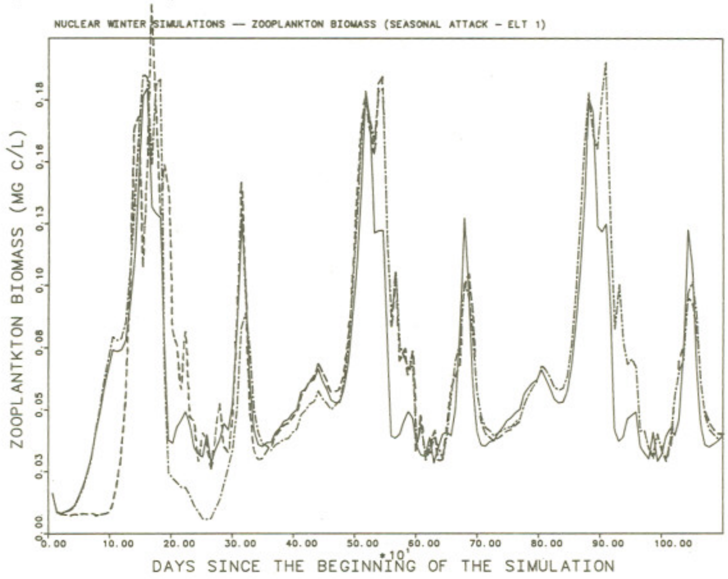

Figure 2.18d Simulated zooplankton biomass (expressed as mg C l^{-1}) for Narragansett Bay Model. Simulations of normal (solid line), winter (dashed line), and summer (dash–dot line) acute climatic alterations

For this simulation, the zooplankton population experienced a considerably less marked effect during the first year, and no effect in subsequent years (again after accounting for the temperature discrepancies). Climatic disturbances beginning in the winter were seen to delay the growth of the zooplankton populations the following spring, reflecting the delay in phytoplankton blooms; an initiation of climatic effects in the summer resulted in a time delay from its normal pattern before the zooplankton population reduction in the fall, and a more substantial drop in the population levels at the minimum periods the following winter.

It is clear from these simulations that the recovery rates after acute stress would be very rapid, and that there is no carryover effect into following years. The simulations of the chronic period, however, show that effects last as long as the stresses are imposed. Figures 2.19a,b illustrate the water temperature and light regimes imposed during the simulation for three levels of a chronic condition, as described above. The effects on the phytoplankton production are shown in Figure 2.19c. From this it can be seen that there is only a slight difference from the mild chronic case (1°C /5%) compared with the control run, but the middle and high chronic runs resulted in significant reductions in primary productivity, with rates at maximum production

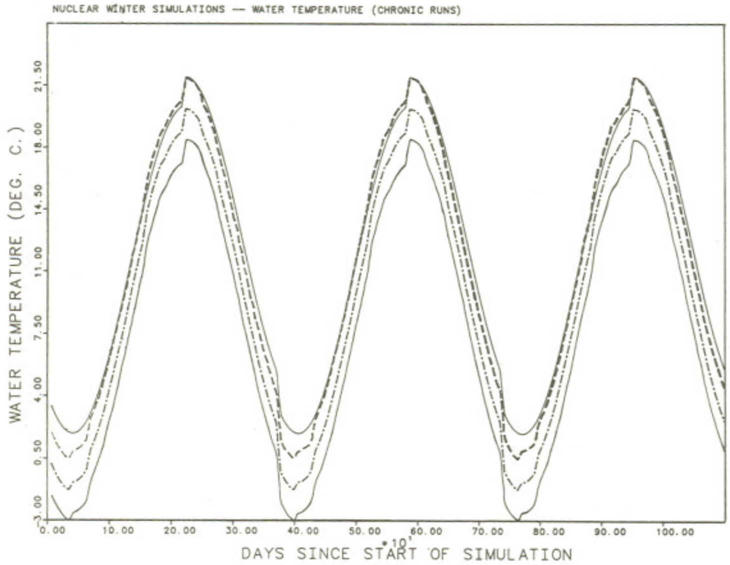

Figure 2.19a Water temperatures used in the Narragansett Bay Model simulations for chronic climatic alterations for normal air temperatures (solid line), and for air temperatures reduced by 1°C (dashed line), 3°C (dash–dot line), and 5°C (thin solid line)

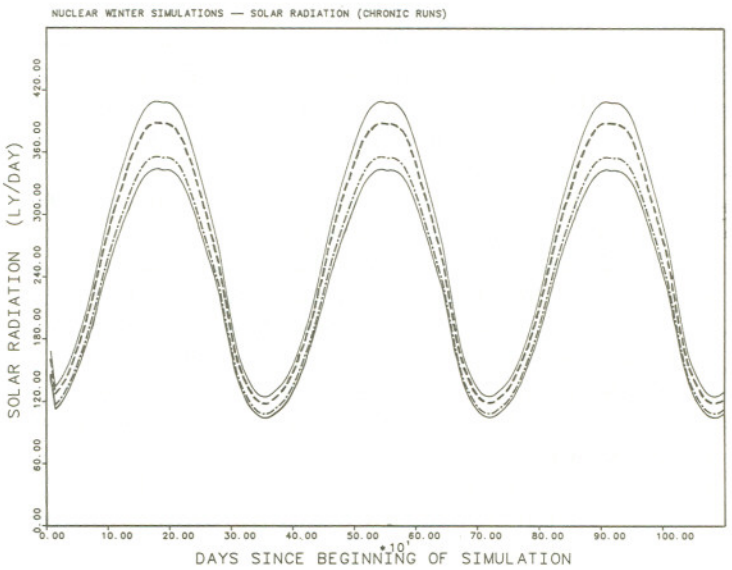

Figure 2.19b Solar insolation used in the Narragansett Bay Model simulations for chronic climatic alterations for normal (solid line), and for solar insolation reduced by 5% (dashed line). 13% (dash–dot line), and 16% (thin solid line)

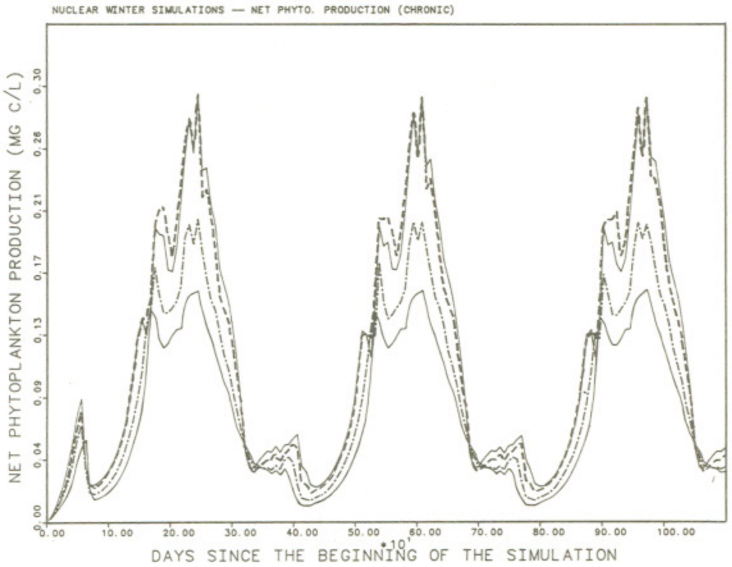

Figure 2.19c Simulated phytoplankton biomass (mg C l^{-1}) for chronic simulations of Narragansett Bay Model specified in Figures 2.19a, b

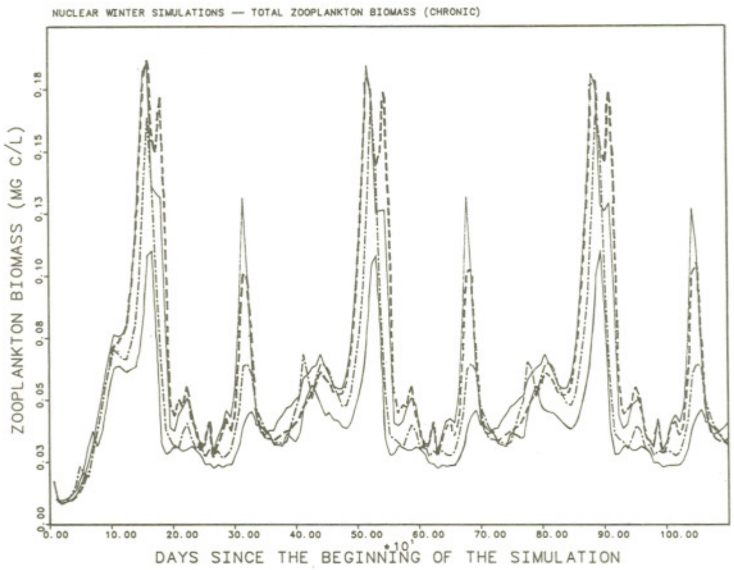

Figure 2.19d Simulated zooplankton biomass (mg C l^{-1}) for chronic simulations of Narragansett Bay Model specified in Figures 2.19a, b

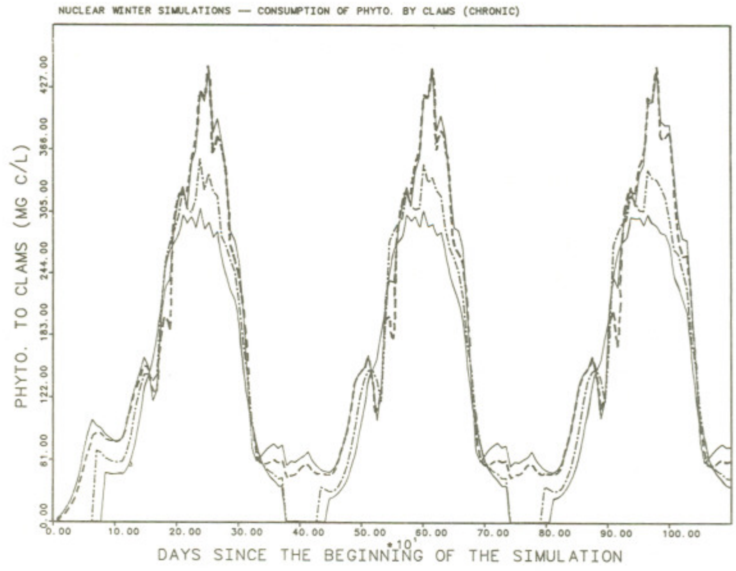

Figure 2.19e Simulated consumption rate (mg C l^{-1} day^{-1}) of phytoplankton by clams for chronic simulations of Narragansett Bay Model specified in Figures 2.19a, b

being decreased by one-third to one-half, respectively. Note that there are no effects on the seasonality of the primary production; this is because the sinusoidal patterns of temperatures and light are maintained in the chronic runs. However, the timing of the initiation of population growth is delayed under chronic stresses, and the onset of the fall decline in production is accelerated.

Zooplankton population levels again show little sensitivity to a mild chronic case (Figure 2.19d), and while there is a noticeable effect in the medium chronic case, the effect is much greater in the high chronic case, indicating a nonlinear response to increased perturbation. Seasonality does not appear affected, but the same effect on the duration of the high biomass periods is seen as in the case of the phytoplankton. An interesting aspect is that the normal second population growth period in the late fall is more sensitive to the chronic stresses than the summer growth period.

Figure 2.19e shows how the consumption rate for clams feeding on phytoplankton is affected by the chronic conditions. This reflects primarily the temperature-dependent function that controls clam filtration rates, as illustrated by the nonlinear response during the winter for the medium and chronic case; this is because of a threshold in the model for a minimum temperature for clam activity. Comparison of this graph with Figure 2.19c indicates that the reduction in phytoplankton production does not translate into a proportional decrease in clam feeding on phytoplankton; however, that may be an artifact of the particular formulation of clam consumption in the model as controlled by abiotic versus biotic factors.

The final set of Narragansett Bay Model simulations involved an acute perturbation beginning in July and lasting two months, and followed by a high chronic perturbation (Figures 2.20a,b). For the phytoplankton, the first year (Figure 2.20c) followed very closely the pattern seen in the previous acute climatic simulation imposed in July (Figure 2.18c). By the second year, the phytoplankton production rates followed very closely the rates seen in the high chronic simulation (Figure 2.19c). Likewise, the zooplankton population levels in the first year (Figure 2.20d) were the same as in the July acute case (Figure 2.18d), then followed quite closely the zooplankton biomass response seen in the high chronic only simulation (Figure 2.19d). These results clearly show no carryover effect across time from an acute to a chronic phase, again indicating a very rapid recovery response for the estuary ecosystem as a whole.

Some caution should be used in extrapolating from these simulations. While the model is reasonably well validated against real data for the Narragansett Bay (Kremer and Nixon, 1978), it is site specific and, therefore, may not reflect conditions in other estuaries, particularly those at different latitudes. Secondly, the model did not include the additional stresses on the Bay that could ensue from nearby detonations, increased sedimentation loading,

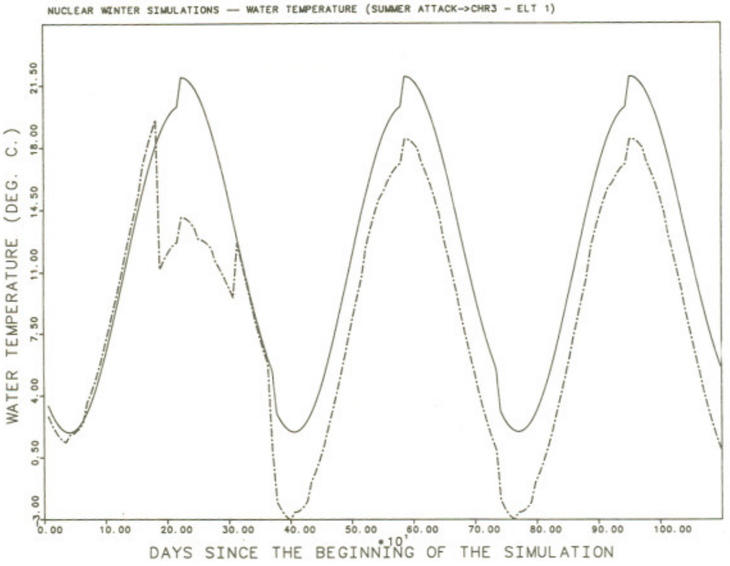

Figure 2.20a Water temperatures used in the Narragansett Bay Model simulations for the acute-chronic case, with acute (10°C) decrease in air temperatures beginning 1 July for two months, then chronic decrease by 3°C (dashed line). Normal water temperatures shown by solid line

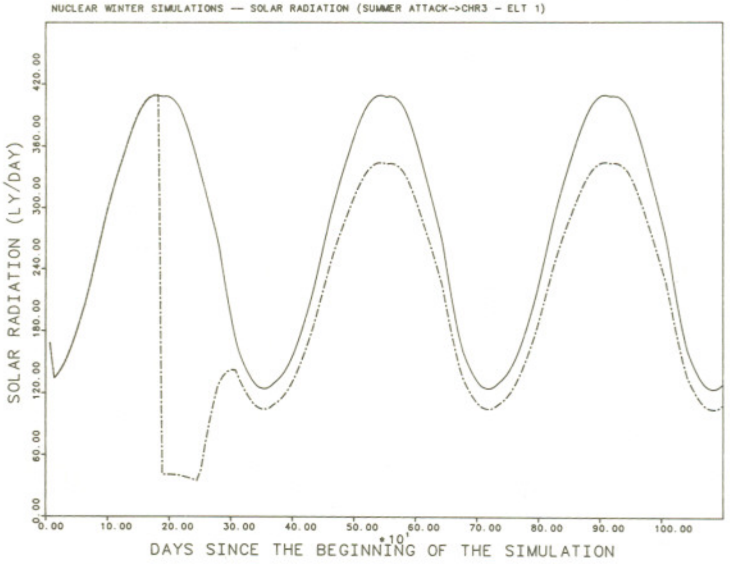

Figure 2.20b Solar insolation used in the Narragansett Bay Model simulations for the acute-chronic case, with acute decrease by 90% beginning 1 July for two months, then chronic decrease by 13% (dashed line). Normal solar insolation shown by solid line

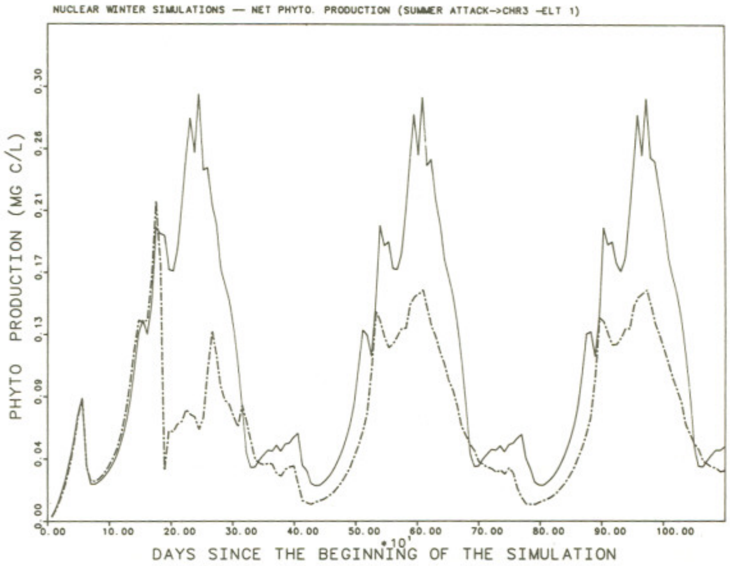

Figure 2.20c Simulated phytoplankton biomass (mg C l^{-1}) for the acute-chronic simulation specified in Figures 2.20a, b

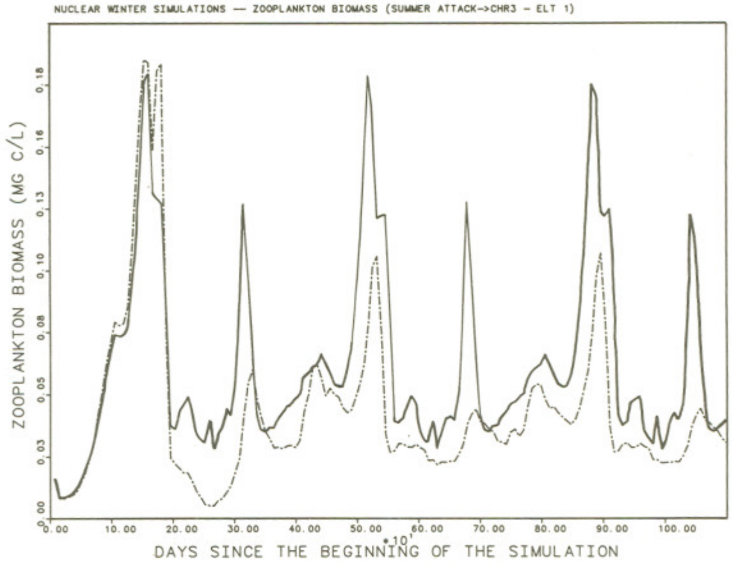

Figure 2.20d Simulated zooplankton biomass (mg C l^{-1}) for the acute-chronic simulation specified in Figures 2.20a, b

burdens of toxic chemicals, increased coastal storminess, and other physical disturbances. These could alter the response patterns, especially the recovery processes. Nevertheless, these simulations are instructive in evaluating the potential vulnerability of estuarine ecosystems to nuclear war.

2.3.2 Potential Effects on Freshwater Ecosystems [1]

2.3.2.1 Vulnerabilities to Potential Climatic Disturbances to Surface Water Systems

Freshwater ecosystems include lentic ecosystems (i.e., ponds and lakes) and lotic ecosystems (i.e., streams and rivers). These ecosystems range in scale from very small farm ponds to the Great Lakes, and from intermittent streams to the Amazon River. Figure 2.21 illustrates the major changes that could occur to the terrestrial hydrologic cycle in response to possible atmospheric changes following a nuclear war. In general, both reduced temperatures and reduced precipitation would lead to early reductions in the amount of liquid water stored at the surface in rivers and lakes. Groundwater would be much slower to change, and any alterations would be much slighter. Groundwater might be used as a drinking water source for humans, but only if there continued to be energy available to pump groundwater to the surface. Freezing of more readily available surface waters is, therefore, a very important question for humans and for other animals. It is useful to divide attention between those lakes and streams that normally experience freezing annually versus those freshwater ecosystems that never freeze over. Lakes store most of the Earth's fresh surface water; river channels contain relatively little water at any one time (Table 2.4); therefore, this discussion will concentrate on lakes.

The characteristics of lakes depend on their size, nutrient inputs, substrate, bedrock, surrounding watershed, precipitation, and a host of other factors. A discussion of the physical and chemical attributes of lakes is given in Rawson (1961); Brylinsky and Mann (1973); Margalef (1978); Forsberg and Ryding (1980); and Kalff and Knoechel (1978). The relationships between the physicochemical characteristics and the constituent biological communities are discussed in Jonasson (1970); Larkin and Northcote (1970); and Colby et al. (1972). Similar characterizations for stream ecosystems are presented in Horwitz (1978); Moyle and Li (1979); and Payson (1982).

The key issue for freshwater ecosystem responses to climatic disturbances is the possible reduction in temperature and, secondarily, the reduction in

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[1] The discussions in this section are based on the freshwater working group at the Toronto conference, J.R. Kelly rapporteur, and on a discussion paper prepared by A. Keast. Model simulations were performed by V.M. Ponomarev, V.V. Ivanishchev, and V.V. Mikhailov.

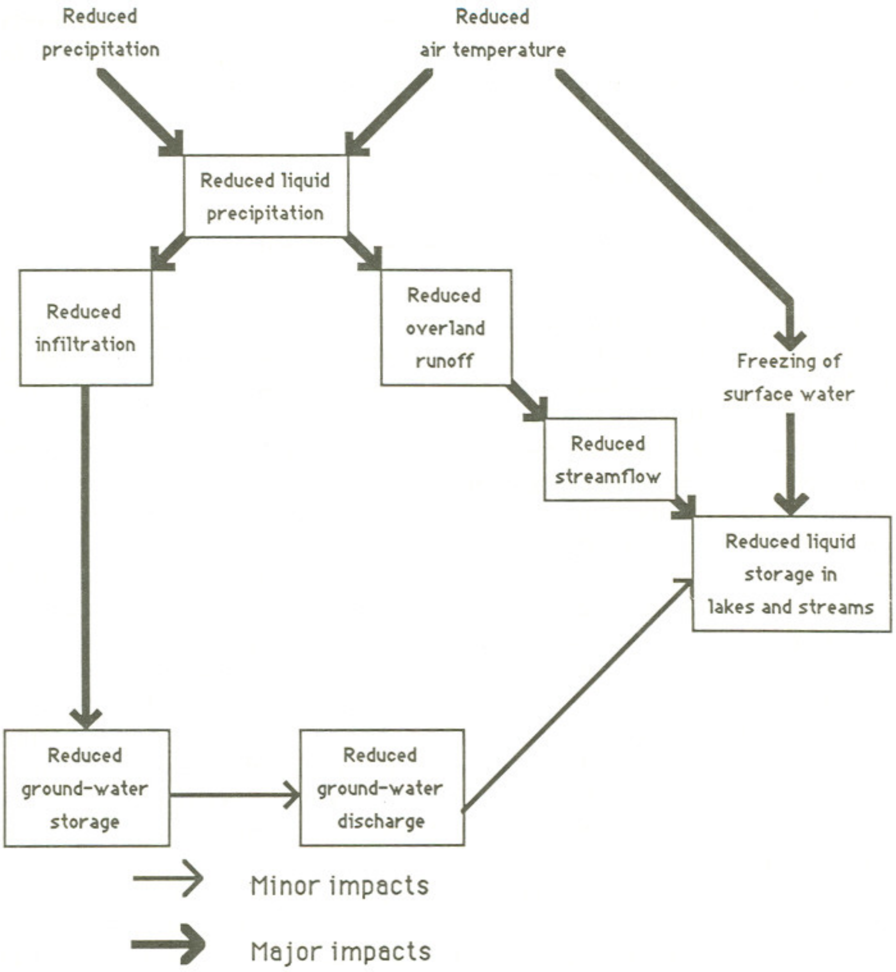

Figure 2.21 Potential mechanisms for climatic disturbance effects on the hydrologic cycle

insolation. Temperature alterations are dampened considerably from the changes experienced by terrestrial ecosystems because of the high specific heat of water, especially for large bodies of freshwater. However, freshwater ecosystems are subject to potential adverse temperature impacts, unlike the situation in the open ocean ecosystems. It is instructive first to examine the temperature changes and responses of the normal ecosystems.

Air temperatures below freezing for long periods of time can produce a thick layer of ice. The thicker the ice, the greater the difficulty in breaking

TABLE 2.4

SELECTED COMPONENTS OF THE NORTHERN HEMISPHERE WATER BALANCE[a]

COMPONENT	EUROPE	ASIA	NORTH AMERICA
Average water stored, rivers (km^3)	80	565	250
Inputs (km^3yr^{-1})			
from overland runoff	2090	10,660	5290
from ground water	1120	3750	2160
Outputs (km^3yr^{-1})	3210	14,410	7450
Average water stored, lakes (km^3)	2027	27,782	25,623
Average water stored, reservoirs (km^3)	422	1350	950

[a] From U.S.S.R. Committee for the International Hydrologic Decade (1977, 1978).

it and the longer the duration of the ice cover, restricting human access and potentially leading to anoxia under the ice cover, which could be lethal to some aquatic organisms. Thick ice on a shallow lake can tie up a significant fraction of its volume; this is another important measure of the impact of ice on freshwater ecosystems.

Soviet scientists have compiled statistics about lake sizes, which include surface area and total volume information, summarized in Table 2.5 (U.S.S.R. Committee 1977, 1978). One pattern to note is that the largest number of lakes, and, therefore, the most widely distributed and accessible to humans, is the category of the smallest and shallowest lakes, which would be most subject to having a substantial proportion of the volume tied up in ice. Table 2.6 shows calculated lake area and volume statistics.

This discussion focuses on lakes that routinely freeze over as instructive in how these ecosystems respond to freezing, and treats the other category of lakes in terms of sensitivity to freezing as similar to the summer lakes of northern climates. The characteristics of the lakes of eastern Ontario are noted as representative of temperate lakes, since the ranges of physical, chemical, and biological conditions among lakes globally are far too diverse for consideration in this study.

TABLE 2.5

DISTRIBUTION OF FRESHWATER LAKE AND RESERVOIR VOLUMES AND AREAS[a]

AREA CLASS (km^2)	EUROPE			ASIA			NORTH AMERICA		
	No.	(km^2)	(km^3)	No.	(km^2)	(km^3)	No.	(km^2)	(km^3)
>10000	1	17,700	908	4	92,670	23,200	8	327,280	24,322
1000 - 10,000	26	74,989	995	21	67,070	3128	22	73,185	1258
100 - 1000	23	9618	479	36	16,760	520	17	7252	214

[a] Data summarized from U.S.S.R Committee for the International Hydrologic Decade (1977, 1978); Tamrazyan (1974); and Bowen (1982).

TABLE 2.6

DISTRIBUTION OF LAKE VOLUME BY DEPTH FOR DIFFERENT SIZE CLASSES

LAKE AREA	PERCENTAGE OF TOTAL VOLUME[a] ABOVE GIVEN DEPTH					PERCENTAGE OF HEMISPHERE[b]	
Size Class Lake (km^2)	0.5m	1.0m	1.5m	2.0m	2.5m	Area	Volume
$>10^4$	0.5%	0.9%	1.3%	1.8%	2.2%	22%	86%
10^3- 10^4	2.0%	4.0%	5.8%	7.6%	9.2%	11%	10%
10^2- 10^3	1.4%	2.8%	4.2%	5.5%	6.8%	2%	2%
10 - 10^2	14%	27%	38%	49%	58%	12%	0.8%
1 - 10	28%	50%	68%	81%	91%	19%	0.6%
<1	56%	88%	100%	100%	100%	35%	0.5%

[a] Calculations were made by assuming that lakes are shaped like elliptic sinusoids, whose volume is stated by: $V = 1.456\,abz$; a and b = radii, z = maximum depth.

[b] Size statistics summarized from U.S.S.R. Committee for the International Hydrologic Decade (1977) for lakes over 100 km^2 area; from Tamrazyn (1974) and Bowen (1982) for smaller lakes.

Northern lake ecosystems are subject to an extensive cover of ice (1.5–2.0 m), extending from November or December until April or May, alternating with periods of open water. Most of the biological activity, including photosynthesis, feeding, growth, reproduction, and decomposition occur during the open water period. Those activities that do continue through the winter months tend to operate at much reduced rates. With spring ice melt, water warming is accelerated until it reaches a maximum in August, from which it returns to freezing by the end of the year. Plant growth commences in May, with the greatest biomass being achieved from late July until early September (Craig, 1976). The spring and summer period is also characterized by rapid buildup in the animal populations, with fluctuations in population levels thereafter.

Fish populations typically begin breeding in the spring and continue through the summer. There is a marked temporal component to this, with different species undergoing reproduction at different times, thereby reducing direct competition for food among the young of the year. Breeding times are determined by temperature and day lengths (Keast, 1977). All fish species in these Northern lakes follow a consistent metabolic pattern, however. The annual cycle requires that they restore body energy reserves following the winter period of low food availability and low temperatures; feed, grow, and reproduce during the summer; and lay down body fat as energy reserves for the succeeding winter. There is probably little resistance to changes in the physical parameters controlling the development of these stages.

Disruption in any of the life history phases would lead to at least the loss of a new age class, and severe perturbations would lead to the loss of adults. The consequences of the former depend on the longevity of the adults and the number of age classes in the population at any point in time; for instance, if a fish lives and reproduces for 5 years, then the loss of a new age class would not devastate the population, whereas loss of an age class in a shorter-lived species or in one that only reproduces once, would have far more serious effects. Likewise, stresses that result in direct mortality of the adults could lead to at least local extermination of a population.

Biological impacts would follow from freezing of the water in freshwater ecosystems during the spring-summer for temperate lakes, or any time for more southerly lakes. Thus, the extent of freezing likely to be experienced is one factor in analyzing the potential effects of climatic disturbances on freshwater ecosystems. Calculations performed by Pacenka, reported in Harwell (1984), indicate that freshwater ecosystems of the Northern Hemisphere would freeze in response to climatic disturbances associated with a large-scale nuclear war, with ice thicknesses forming to 0.5–1.2 m, depending on the specific scenario of nuclear war. However, these calculations were based on a hemispherically and annually averaged temperature and, therefore, did not account for the effects of seasonality, either of the temperature reduction itself, or of the base normal temperature to which the decrements were applied. Further, the calculations did not account for differences across latitudes or in mid-continental versus coastal areas. Therefore, the actual extent of freezing that would be experienced following a climatic disturbance requires further analysis.

One basis for evaluating potential effects on lake ecosystems is the study by Ponomarev et al. (1984), done for the SCOPE–ENUWAR project. These researchers used the Lake Ecosystem Simulation Model developed at the U.S.S.R. Academy of Sciences Leningrad Research Computer Center. This model is being developed and validated for evaluating the dynamics of lake ecosystems and their constituent species, the relationships between lakes and their watersheds, and the effects of industrial development on lakes. The model consists of three biotic compartments (phytoplankton, zooplankton, and detritus) linked to nitrogen, phosphorus, sediment, dissolved oxygen, air temperature, insolation, and radiation factors (Figure 2.22). The simulation of severe climatic perturbations was done by reducing air temperatures by 15°C within 20 days, returning to a 5°C deficit by about the 120th day after a nuclear war occurring in either February or July; concomitant reductions in insolation were imposed in the simulations.

Results from the February nuclear war are shown in Figure 2.23, where the normal and hypothetical climatic alteration curves are shown for water temperature, insolation, phytoplankton biomass, zooplankton biomass, detritus biomass, and mineral-to-organic nitrogen ratio. The phytoplankton population in these ecosystems demonstrates a rapid decrease from a rather high normal level in the winter; this population recovers rapidly after insolation levels return to normal by the end of the summer, even though temperature levels at that time are still significantly depressed. This suggests that phytoplankton biomass is more sensitive to light level reductions than to temperature reductions. The zooplankton population suffers an immediate decline and does not recover within a year, presumably because of the loss of food resources. The development of anoxia in the water is predicted in the model to occur from an increase in the detritus, which contributes to increased respiration rates and depletion of dissolved oxygen at a time when photosynthesis is suppressed.

Effects from climatic alterations imposed on the July simulation are more dramatic and long-lasting (Figure 2.24). The recovery of temperatures and insolation would occur in this scenario just at the onset of the normal winter period, thereby prolonging the total period of low light and temperature levels. This results in the essential loss of phytoplankton activity for an entire year, with associated loss of zooplankton. However, the model results indicate rapid recovery of phytoplankton and zooplankton populations upon resumption of insolation at normal levels the following summer.

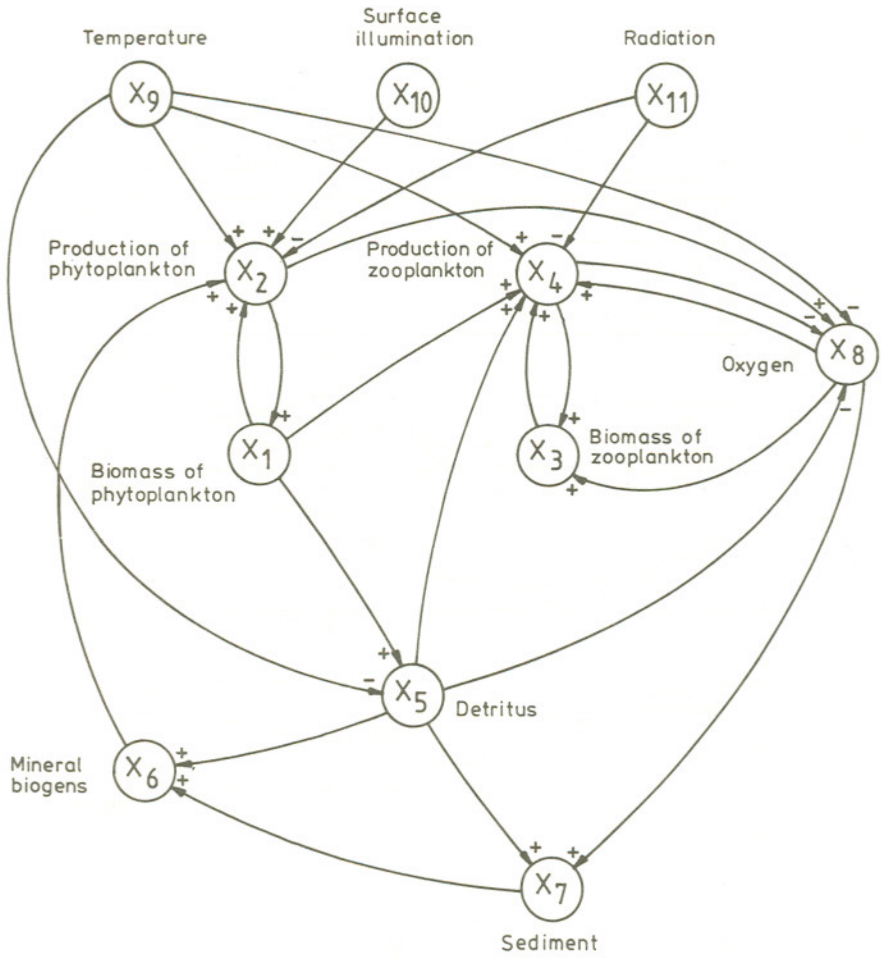

Figure 2.22 Conceptual framework for the Soviet lake ecosystem model. After Ponomarev et al. (1984)

These simulations are instructive for characterizing the response of lake ecosystems with respect to energetics and material flow. A simulation that takes into account the populational responses of primary and secondary producers, including the life cycle dynamics of fish and other fauna, has not been done. These considerations, by necessity, were addressed in the ENUWAR workshops in qualitative discussions among appropriate experts. The pattern of biological responses developed by these groups follows.

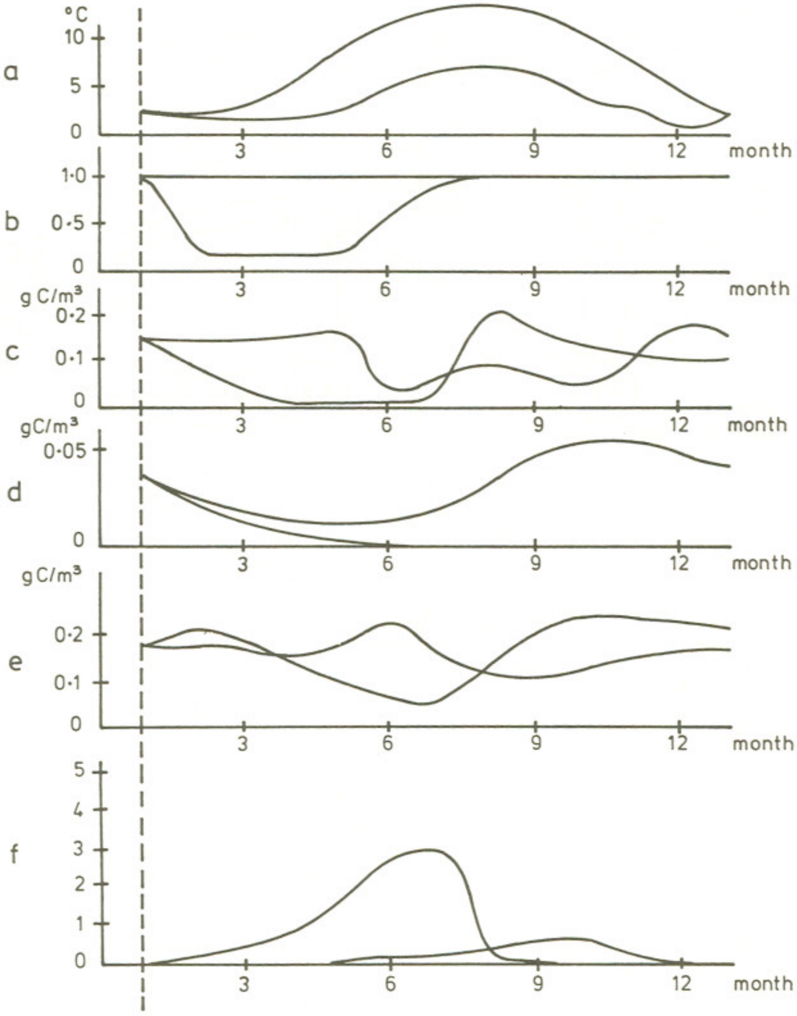

Figure 2.23 Dynamics of major lake ecosystem components after a February war. a—mean lake water temperature; b—relative surface insolation level; c, d, e—biomass of phytoplankton, zooplankton, and detritus (g C m^{-3}; f—mineral to organic nitrogen ratio. After Ponomarev et al.(1984)

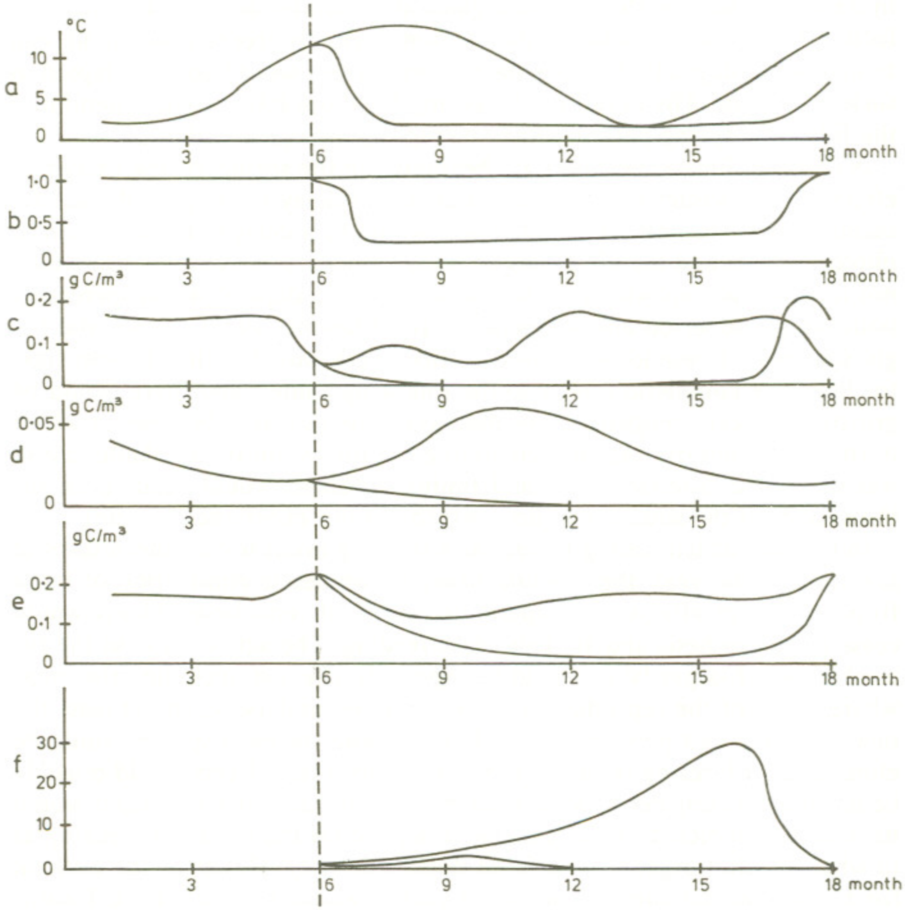

Figure 2.24 As in Figure 2.23 for a July war. After Ponomarev et al. (1984)

If nuclear war-induced climatic disturbances were to occur in the winter in regions where the lakes normally were near freezing, ice cover thickness could increase. With minimal temperature decrease, this might have no effect, but in greater temperature declines, the increased ice thickness, especially coupled with lower insolation levels, could reduce ongoing photosynthesis and associated oxygen levels to the point where phytoplankton could die and the ecosystem could become anoxic. In shallow lakes, freezing could occur to the bottom, killing most of the biota in the lake. In streams that normally experience some freezing, a winter-onset war could result in the formation of anchor ice, i.e., ice forming at the bottom even though the entire water column was not frozen. Such a situation could also result in death to many of the stream organisms. A winter acute disturbance affecting freshwater ecosystems that do not normally freeze over could lead to marked biological effects, as the species present would not be adapted to such conditions. The duration of freezing for those lakes would extend into the following spring period, totally disrupting biological activities.

A chronic climatic perturbation beginning in the spring, or the carryover effect from a winter-onset nuclear war, could delay melting of the ice remaining from the normal winter. There would be a delay in the initiation of photosynthesis and the life cycles of many animals. For example, fish would not initiate their spawning cycles, since these are dependent on increasing both the photoperiod and temperature (de Vlaming, 1972). If they did begin spawning, it would be delayed so that there would be insufficient time for life cycle completion prior to the following winter, and there would be greatly enhanced competition for limited resources across fish species which normally did not overlap in their timing but for whom the available season was shortened. Similar delays and timing problems would occur even for those lakes in the southern regions which did not experience freezing.

In the case of late spring freeze, or a freezing event for southern lakes at any time of the year, there would likely be wholesale elimination of biota from the direct effects of temperature and light reductions. Plants would cease photosynthesis and animals cease feeding. The active areas in the littoral zones of larger lakes would be especially affected, including the areas where much of the reproductive cycle would be underway, and at least the new age class, and perhaps the total populations, of most species would be eliminated. If freezing occurred in summer, however, effects would possibly be less immediately deleterious, since many of the sensitive life stages would have been completed; the effect would depend on the extent of freezing as to whether adult organisms suffered direct mortality. However, the outlook for those who did survive the initial period would be poor, since insufficient feeding would likely have occurred to store enough body fat to get through the following winter. The duration of effects would be particularly important the following spring.

Climatic disturbances during the fall would appear to be the least consequential for northern freshwater ecosystems, since the organisms would have passed the reproductive stages and feeding requirements of the current year and would have already initiated acclimation to winter conditions (Weiser, 1973). For more southerly lakes and streams, however, the effects would still be severe, because those ecosystems would not have begun winter acclimation.

The longer-term factors affecting freshwater ecosystem recovery include the potential loss of fish species in individual lakes, for which recolonization is a large problem because of isolation from other sources. The invertebrate, phytoplankton, and decomposer populations, however, even if they had suffered widespread mortality, should recover once the climatic conditions returned to near normal. Nevertheless, the ecosystem as a whole could continue to show residual effects for long periods of time, including the possibility of some irreversible effects.

2.4 POTENTIAL EFFECTS ON TROPICAL ECOSYSTEMS [1]

2.4.1 Introduction

The potential responses of tropical ecological and agricultural systems to climatic disturbances after nuclear war were discussed at the SCOPE–ENUWAR tropical workshop. Though there was a focus on American tropical and sub-tropical systems, it was felt that many of the discussions and conclusions could be extrapolated to tropical systems in Asia, Australia, and Africa.

In order to have a framework for considering effects on tropical systems, probable responses of a number of key tropical ecosystems were examined. Similar to the temperate ecosystem analyses, a set of perturbations was considered to establish the *vulnerability* of tropical ecosystems to the types of climatic alterations possible after a nuclear war, rather than analyzing a single particular scenario. Vulnerability to reduced temperature was examined for a severe acute phase, characterized by freezing temperatures occurring for brief periods, and for chronic temperature declines of 1°C to 5°C for extended periods of time. Precipitation declines of 25%, 50%, or more were considered. The effects of light reductions of up to 90% in an acute phase and 1% to 10% in a chronic phase were considered. For each of these physical disturbances, no prediction is made that it necessarily would occur at a particular location or in a particular time period.

Since many tropical systems have seasonal rains, climatic perturbations occurring both in wet and dry seasons were examined. Temperature and light seasonality in the tropics would be of limited significance because of the even daylight-night hours and the general limited temperature fluctuations on a monthly or annual basis. Near sea level, the mean monthly air temperature at most tropical stations is between 20°C to 30°C in every month of the year. Mean temperature fluctuates from day to day around the monthly mean in response to local synoptic weather patterns, but the changes are less

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[1] This section is based primarily on the tropical ecological working group discussions at Caracas, Venezuela, chaired by T.C. Hutchinson.

frequent and less abrupt in the tropics than in temperate latitudes. Diurnal temperature fluctuations are even further reduced within the forest than out in the open or above the canopy. The diurnal fluctuations in temperature may be larger and more important to plant growth and animal activity than monthly fluctuations in temperature. The adaptation to this constancy of temperature makes biotic systems more vulnerable to extreme episodic temperature excursions. These are nearly always declines, and in the case of the friagems extending into Amazonia they can cause severe damage.

Major mountain ranges are found in the tropics, especially in South and Central America, and at sufficiently high altitudes these have either ice or snow fields. The decrease in temperature attributable to altitude is about 0.6 °C per 100 m, in the lowest 1.5 km (Monteith, 1977). At the higher altitudes frosts are often a daily event (e.g., in Mount Kilimanjaro in Africa or in the puna and paramo regions of the Andes). The altitudinal zonation of vegetation on these mountains in general parallels the latitudinal zonation.

The annual range in daily solar insolation is much smaller in the tropics than in temperate latitudes. Annual insolation ranges from about 8GJ m^{-2} on the margins of the subtropical deserts to 5GJ m^{-2} in wet equatorial regions. Daylength is just over 12 hours throughout the year at the equator and ranges from 10.6 to 13.7 at latitude 25° . While the range of daylength is also much less than in temperate regions, the development of tropical crops and native vegetation is nevertheless related to changes in day length.

Rainfall may be uniform and high (e.g., in coastal regions of evergreen forests or in central continental regions such as Zaire and Amazonia), or it may be strongly seasonal (e.g., the extreme seasonality of the monsoons of Asia and Africa). In some higher altitude forests, much precipitation occurs by contact with clouds and fogs, allowing the development of cloud forests. Seasonal droughts are characteristic of tropical grasslands, savannahs, and deciduous forests. Deciduous trees are numerous in the rainforests in all parts of the tropics and are present even in climates with an almost uniformly distributed rainfall (e.g., in Singapore and in the New Hebrides) (Richards, 1966). As the precipitation limit of the rainforest is approached, the proportion of deciduous species gradually increases, first in the upper, then in the lower stories.

The following sections focus on several ecosystem types occurring in the tropics. The estimates of potential vulnerabilities are based primarily on the direct effects of climatic disturbances on the ecosystems. It should be kept in mind for ecosystems in general, and particularly for tropical ecosystems, that indirect effects would likely be widespread, affecting species not vulnerable to direct effects and extending ecosystem effects over time. Further, the potential for synergisms is very high, but predictions are very tenuous. Consequently, the vulnerability of tropical ecosystems to specific perturbations is likely to be greater than projected here.

2.4.2 Vulnerabilities of Tropical Ecosystems to Potential Climatic Disturbances

2.4.2.1 Evergreen Tropical Rainforest

The evergreen tropical rainforest is characterized by a lack of seasonality in temperature, rainfall, light intensity, and photoperiod. Light intensity declines sharply through the canopy strata to ground level. These forests have a very uniform environment and great species richness and diversity in both plants and animals. The three major evergreen rainforest areas are in: 1.) South and Central America and the Caribbean, 2.) the Indo-Malayan region, and 3.) central Africa. Perennial plants dominate, and annuals are very rare. Soil types differ considerably, but are often deep, ancient soils leached by high rainfall and with a poor nutrient status. Major nutrients are often deficient in the soils, and nutrient turn-over and litter decomposition are very rapid. Epiphytes are abundant, increasing in frequency at higher altitudes as relative humidity rises. Pollination is predominantly by insects or birds, rather than the wind-pollination typical for temperate trees. Many animals are arboreal.

In considering the vulnerabilities of these ecosystems to near- or subfreezing episodes, it was felt that *all* photosynthetic aboveground plant tissues would be killed rapidly, as tropical plants are very sensitive to chilling. They neither chill- nor frost-harden as do temperate plants, nor do they have the genetic-physiological capacity to acclimate to such extremes. In contrast, reductions of a few degrees in a chronic situation would not likely have major impacts on these ecosystems. The critical phenomenon for tropical lowland ecosystems would be the occurrence of episodes of low temperatures.

If a freezing event were short, i.e., up to a week, then *some* limited recovery could be expected through aboveground sprouting, coppicing, or production of adventitious buds on the trunks and stems. The position of the apical meristems of tropical species well above the ground put them in a most exposed position (phanerophytes), and protective bud scales are absent. Many tropical palms would be killed also because of their exposed meristem, though some of the palms would be able to regenerate from underground rhizomes. Bamboo and other species that sprout from below or near the ground would be better able to survive and regenerate because of the insulation provided to their meristems.

Most forest trees and shrubs in evergreen tropical forests have limited seed banks, and those seeds that are present are primarily of the current year and lack a dormant phase. These seeds are often fleshy or contained within fleshy fruit. Seeds in the soil could be killed because they are not deeply buried or covered with a thick litter layer. The drought- and cold-resistant seeds typical of grasslands, savannahs, and temperate systems are largely absent. Instead of a seed bank, the forest floor often contains a seedling bank. Seedlings and saplings are cold sensitive, so that future reserves would be killed by freezing episodes along with the parent trees.

Those seeds that might survive brief extremes of temperatures belong to pioneer species. Secondary species occur in small numbers in natural openings, such as where large trees have fallen and opened the canopy (Richards, 1966). Such naturally weedy species have adaptations that enable them to exploit open situations, and they often can regenerate from rootstocks. Palms with hard seeds may also be able to regenerate even if the parents are killed. The amount of moisture available for seed imbibition could be important. If the seeds were at low temperatures in wet soils, then their viability would decrease considerably.

The limited regeneration after an acute temperature decline would yield only a small fraction of the former species diversity. For example, Chevalier (1909) reported that the secondary forests of the Ivory Coast, after clearance and burning, consisted of about 30 species of trees, while that of the virgin forest consisted of 250–300.

When extensive clearing occurs in evergreen tropical forests, recovery can be very slow. For example, savannah occurs in extensive areas adjacent to evergreen forests for which the climate is appropriate for evergreen forests (e.g., Sumatra and Venezuela), but such forests do not occur because fire prevents successional development. Similarly, in Guiana and Belize, thorn forests and dwarf forests are believed to be secondary as a result of ancient human interference. These successional forests are composed of fast-growing but short-lived species, which would add to the instability of the recovery process.

Most of the secondary forest species would be at an advantage in a recovery phase after a nuclear-war induced climatic disturbance, since they can regenerate in high light conditions, whereas many of the virgin forest species require low light levels. Since most evergreen tree and shrub species would be killed in a freezing episode, there would be high light intensities at the forest floor and a substantial accumulation of dead wood and organic matter.

Reliable models are lacking for predicting animal responses during an acute freezing phase. The effects of freezing or chilling would be severe on animals that are accustomed to warm, constant environments. Since most rainforest animal species are arboreal, they would not survive in areas experiencing total devastation of the forest trees. Generally, larger animals would be most vulnerable to cold temperatures. Large carnivores are the most likely to survive during the short term, since there would be plenty of meat (carcasses) available. Hibernating animals do not have an advantage since hibernation is physiologically complex and cannot be induced without the proper environmental cues. Most soil-dwelling insects or those that are not food specialists might survive even extreme temperatures. Fruit-eating bird species, comprising the majority of the rainforest avifauna, have high metabolic requirements and would die where their food source was destroyed. Bird species that occur or are able to migrate to coastal areas, where the temperature extremes are not expected to be as severe, would have better survival rates. Migratory birds would have the capability of moving to a better climate, though this response is felt to be tenuous as migratory instincts might miscue.

2.4.2.2 Deciduous (Seasonal) Forests

Tropical deciduous forests occur at the margins of evergreen rainforest, where seasonal rains prevail, and in areas experiencing monsoons. Such rainforests occur in India, Burma, Indochina, East Africa, North Australia, and South America. Annual drought, characteristic of such forests, affects the vegetation in a number of ways. Most trees lose their leaves during the dry season. The duration of this leaf loss depends upon soil moisture; for example, along river banks where moisture is plentiful, leaf loss is reduced. Even in the deciduous forest, a number of evergreen species occur (Vickery, 1984). These evergreen species have small, leathery leaves, which are often are highly toxic to consumers and which are similar to leaves on Mediterranean species, in contrast to the large leaf forms of the deciduous species. In Australia, where this forest is extensive inland in the northeast, merging into savannah and thornscrub, the ground flora is often of tussocky C_4 grasses with high root:shoot ratios (3:1 to 10:1), and forest species include large evergreen *Eucalyptus* species. In South America in the zone between the deciduous and evergreen forests, the upper tree story is made up of deciduous thick-trunked *Bombidaceae*, while the lower stories are still evergreen, so that the forests can be termed tropical semi-evergreen (Walter, 1973).

The stratification of the canopy is simpler, and since more light reaches the ground, the shrub layers are thicker than for rainforests. Most herbs produce their leaves and flowers during the wet season, and survive the drought period in dormancy, often as bulbs, corms, or tubers. Annuals complete their life cycle in the wet season, and their seeds lie dormant in the soil through the drought. Many of the deciduous forest trees flower at the end of the dry season, enabling ripening of fruit and seeds to occur when water is plentiful. Bird and insect pollination predominates. Epiphytes are much less common than in the evergreen forests.

During the dry season tropical deciduous forests are very susceptible to fire. Most trees have evolved thick and often deeply fissured bark as an adaptation to fire.

Extreme temperature reductions during the wet season would be as devastating for seasonal forests as they would be at any time for evergreen tropical rainforests. If cold temperatures occurred during the dry season, many tree species would be dormant and without leaves. Herbaceous species might survive as underground perennating organs. Thus, overall effects of freezing would not be as great as during the wet season, but extinction of sensitive species could still occur. If the freeze were prolonged or repeated during the growing season, there could be death of virtually all existing vegetation. For the chronic period, the deciduous forest species are expected to be more hardy than those of the evergreen forest because temperature and drought fluctuations are both greater in these systems. With a drop of a few degrees, most plant species would survive intact, but at more extreme chronic temperature reductions, some species would grow very poorly and might experience chill damage.

Recovery would be more rapid in deciduous tropical forests than in evergreen forests because of better seed survival, a larger seed bank, and better sprouting ability. If frosts occurred when the trees were flowering at the end of the dry season, an entire seed year could be lost, along with the pollinators. There are features of drought tolerance which would also enhance frost (or chilling) tolerances (Ivory and Whiteman, 1978a, 1978b). Many of the grasses would have intact seed banks, and the trees have deep tap roots, especially on sandy soils. Similarly, thick, fire-tolerant bark would enhance frost-tolerance. In areas which experience ground fires frequently, the vegetation would be better pre-adapted to the acute phase of climatic disturbances. Recovery, as a result of re-sprouting, coppicing, adventitious shoots, and stolons, would occur as it does for many species in the post-fire phase. The deep roots of the deciduous trees and shrubs would also provide some protection and enhance recovery.

Animals would suffer a high mortality from chilling and freezing events, especially if they occurred in the wet season when species would be active and arboreal. In the dry season, many animals stay closer to the water and would be less vulnerable. Some, such as armadillos and a few rodents, would be protected by burrowing. Homoiothermic animals might die from chilling if they became wet before freezing occurred. Long-term continuation of reduced temperatures could lead to gradual replacement of animal species.

Birds inhabiting the deciduous rainforest could suffer the same stresses as those in the evergreen forest. The omnivorous, wide-ranging species, such as vultures, would have the best chance of survival. The insects of the deciduous forest would have a better chance of survival than in tropical rainforests, since in the dry season their eggs are able to survive low temperatures and the metabolic activity of the adults can slow down.

Vulnerability to reduced light levels is much less than the vulnerability to temperature reductions, so that even a large decrease in light accompanying acute temperature reductions would be merely an additional stress factor for vegetation. A maximum light reduction of 10% during a chronic perturbation probably would not result in major effects.

Tropical deciduous forest ecosystems are often fire-adapted. Germination of many seeds are favored by fires, and the longevity of the seed bank is greater than in the evergreen forest. In South America, for example, palms are fairly long lived and produce drought-tolerant, thick-walled seeds. If fires occurred in the growing season, the seed bank would lose one year of input, which for some species could be a very high percentage. If most vegetation were killed in an extreme temperature episode, the subsequent fuel load would be high. If the precipitation were also reduced, then fires would be a certainty. Such fires could be much more severe than those normally experienced, eliminating the remaining aboveground surviving shoots and seedlings. High temperatures at the soil surface could destroy the seed bank. If fires occurred after a chronic temperature phase, the fuel load on the ground would be much less. Fires under these circumstances would be similar to those occurring normally in the deciduous forests, and the fire adaptation of the plants would enable many or most to survive.

An extreme situation of prolonged periods of very low levels of precipitation could turn the deciduous forest into a desert within a few years. A smaller decrease in precipitation might allow for some acclimation of species, but with considerably slower growth and with xeric species being favored. The distribution of precipitation is an important consideration, both spatially and temporally. Lower precipitation would be less of a factor here than a similar percentage drop in evergreen forest.

2.4.2.3 Montane–Cloud Forest

Orographic precipitation occurs as air masses ascend mountainous areas. Dry seasons occurring in the lowlands become shorter with increasing altitude, or disappear altogether. Also, temperature decreases, and clouds and fog drift through the trees on a daily basis, maintaining a very high humidity. These conditions result in montane–cloud forests, characterized by a two-story structure. Cloud forests are found between 1000 m and 2500 m, but up to 3400 m in some regions.

The continuous fogs cause low direct light intensities, so the ground flora are not as rich as in the evergreen lowland forest. Temperature is lower but almost constant. Such climate conditions encourage the growth of epiphytes. Bamboos in Asia and Africa are the dominant species of the wet low slopes of cloud forests, while *Selaginella* covers open ground. Tree ferns are also numerous in South America, southern Asia, and New Zealand. Walter (1973) notes that in many tropical mountain regions, the wettest altitudinal belt is characterized by palms or dense bamboo stands.

In the montane–cloud forest, the great majority of the trees are evergreen, and rather few are buttressed. Some trees are very large, especially at lower altitudes. At very high altitudes, the trees become dwarfed and gnarled with twisted branches, forming elfin forests. At higher altitudes, conifers enter the community. As the trees are eliminated, a shrub zone occurs, narrow in altitudinal range. The treeline may be determined by precipitation or the occurrence of frost at high elevations, where temperatures can drop below freezing point at night for a few hours (Walter and Medina, 1969).

An extreme temperature drop to below freezing would be devastating. Most trees and shrubs would be killed within a few days as the cold penetrated the trunks and caused ice formation in the tissues. The shallow roots of many species could be killed by the cold. However, leaf litter is greater in these forests than in evergreen forest, so that some soil protection might be provided. Erosion on steep slopes would be substantial. The upper slope parts of these forests are likely to be more cold-adapted than lower areas and also better adapted to reduced precipitation and humidity. Species with coppicing potential and those with seeds having a thick protective coat would be at an advantage in regeneration.

The consequences of ambient drops in temperature during the chronic phase of climatic disturbances would most impact root systems. The length of the chronic phase and its severity would ultimately determine the amount of altitudinal destruction of forest taking place because of soil mean temperature effects alone. At the timberline, roots require a soil temperature of 7–8°C. If an ambient drop of 5°C occurred, treeline species would die. For those mid-altitude cloud forest species which require root-soil temperatures of 10°C–12°C, then clearly more dramatic declines would be expected in the forests.

For montane-cloud forest systems under chronic perturbations, there could be severe damage at timberline even if the ambient temperature were reduced by less than 5°C. The timberline would probably shift down by 800 m with a 5°C decrease in temperature. Since light would likely be decreased along with temperatures, many of the plants requiring insolation for heating the rocks and soils in which they live would suffer from further decreases in their ambient temperature. Further from the timberline, species would not suffer such extremes. However, erosion on steep slopes could be severe.

Many animal species in these ecosystems are quite vulnerable to subfreezing temperatures; e.g., in Central and South America, no monkeys occur above 2500 m, suggesting thermal intolerance to low temperatures. Burrowing animals such as the agouti would probably survive if the acute phase were not prolonged. Large predators, such as the ocelot and jaguar, could be able to migrate to more favorable conditions. Tree-dwelling animals such as sloths and monkeys would be particularly vulnerable, just as in evergreen forests. Birds in the cloud forest are fairly specialized, often feeding on fruit and restricted in altitudinal range. If their food supplies were destroyed by frost and cold, many birds would perish.

Since a 30–40% decrease in precipitation is within the normal variability of this ecosystem type, vegetation can tolerate a decrease of 30% for up to a year. The epiphytic community would be the most vulnerable. A 30% decrease in incidence of fog could have a significant effect in a dry cloud forest, since it is dependent on frequent episodes of moisture. A long-term reduction in temperature by a few degrees coupled with reductions in precipitation would result in significant damage within one or two years and a drastic change in species composition over longer periods.

Greater decreases in precipitation would increase the risk of fire. The frequency of fires would increase as a result of human activities. Fires would cause large-scale erosion on slopes and loss of seed banks.There is a high percentage of plants with fleshy fruit in the tropical cloud forest and their seed would be destroyed by fire. Further, the seedling bank, which is relied upon for recovery processes, is particularly vulnerable to fires.

The recovery of the cloud forest after extensive fires would be most rapid in the valleys because of increased moisture availability. Erosion on the slopes would favor the invasion of grasses and shrubs rather than cloud forest species, which require greater soil depths. Palms would not re-sprout, though the ability of their seeds to survive might be high.

2.4.2.4 Tropical Alpine Systems

In the wet tropics, the alpine region (páramo) is almost perpetually wet, misty, and cold, with frequent night frosts and seasonal precipitation. The plants are adapted to continuous freezing and thawing cycle, primarily relying on supercooling. During the flowering season, the upper soil layers warm during the day to temperatures above the annual mean. A rocky habitat is more favorable for this than a wet, cold soil.

Tropical alpine ecosystems would not be totally devastated by an acute phase reduction in temperatures; some of the vegetation might be able to withstand up to a 7–8°C drop. Those species that presently tolerate a 15°C diurnal cycle through cold-temperature avoidance mechanisms would be able to survive a 10–15°C drop. Those plant species that supercool could not withstand these temperature drops. The duration of the temperature drop would have to be brief for plants to survive; for instance, after three days, the meristems would suffer because they are adapted to daily freezing or thawing, not to continuous freezing.

If precipitation were severely reduced, fires could occur, as they now do on occasion in the lower páramo. However, fuel loads would be low, and fires are less likely in tropical alpine ecosystems than in almost any other tropical ecosystem. The puna and lower pramo might recover in some areas from fires, because most of the reproductive organs are in the soil.

Tropical alpine areas would not suffer greatly during the chronic phase in terms of survival, since supercooling ability of plants increases with lower availability of resources, though growth rate may be decreased. Aggressive, weedy alpine species might be able to colonize areas where other vegetation was lost. If much vegetation were lost, the possibility of landslides and avalanches increases. Freezing of the alpine watershed could occur with a temperature drop of 10°C at high altitudes.

It is anticipated that many endemic animals (e.g., vicuña, alpaca, llama, chinchilla, and vizcacha) would migrate from areas of temperature extremes. However, the specialization in feeding behavior of these animals might limit their survival in areas with a different plant composition. For example, condors, which are found from sea level to 5000 m, should be able to migrate to areas with accessible food; on the other hand, high-altitude flamingos, giant coots, and plovers might be able to move down, but they require open water for feeding and would not survive for more than a few days without food.

2.4.2.5 Tropical Grasslands and Savannahs

Tropical grasslands and savannahs are widely distributed in South America, Australia, Africa, and Indo-Malaysia. The transition from open forest with grassy undergrowth (savannah-woodland) to true savannah is gradual. In many cases savannahs and grasslands are of anthropogenic origin from grazing, burning, and shifting cultivation; some are quite ancient. Indeed, the ease of burning and clearance for agriculture currently results in an expansion of these ecosystems.

Annual rainfall in the tropical grasslands varies from 75 mm to over 1500 mm and is generally seasonal. Grasses can utilize the water of the wet season very effectively. At the end of the rainy season when water becomes scarce, transpiration continues until the leaves and usually the entire aerial shoot system dies. Only the root system and the terminal growing point of the shoot survive. This intercalary meristem (between the root and the shoot) is well protected during the ensuing drought by the many layers of dried-out leaf sheaths. The high rainfall of many savannahs, such as the llanos of Venezuela, is more characteristic of deciduous tropical forests. Trees are present in natural savannahs if there remains sufficient water at the end of the rainy season to support maintenance of tree and shrubland roots through the following dry season. In some areas where savannah occurs, but where the climate is typical of deciduous tropical forests, the determining factor in savannah establishment is soil type. This is the case in the very extensive llanos area of Venezuela and Colombia, where a hard lateritic crust is formed between 30–80 cm depth, cemented by ferric hydroxide.

The mean temperature of the tropical grasslands varies between 22–28°C, with greater seasonal fluctuations than in the forested regions. In higher altitude grasslands, such as in East Africa and Australia, cool or cold nights are common. In Australia, the presence of woody species (*Acacia* and *Eucalyptus*) offers a more forested appearance than occurs elsewhere in the world under similar climatic conditions because of the tolerances to drought and fire of these genera.

Grazing by livestock in tropical grasslands reduces foliar leaf area, thereby reducing evapotranspiration and increasing soil moisture content. This allows shrubs and trees to colonize. Since thornbushes are able to tolerate grazing, grazed grasslands have a strong tendency to change to secondary thornscrubs, as in Australia, Africa, and South America, as well as in warm temperate regions such as Texas in the southern U.S. If a higher human population density occurs in these areas, the bush is often used for fuel, and overuse eventually leads to desert conditions.

Other factors affecting the composition of the grasslands and savannahs are grazing by large herbivores, such as the wildebeest and antelopes of East Africa and kangaroos in Australia, and the frequent occurrence of fires in the dry season. Deliberate annual fires set just before the wet season have a large influence on species composition of tropical grasslands, especially when this is followed immediately by cattle or sheep grazing.

A few days of sub-freezing temperature during the wet season would kill aboveground plant tissues. The dominant C_4 grasses are unable to tolerate temperatures much below freezing, and some suffer chilling injury at +2°C to +4°C (Ivory and Whiteman, 1978a, 1978b). As temperatures ameliorated, herbs and grasses would re-sprout from rhizomes and crowns, and the trees and shrubs by coppicing. If the freezing occurred in the dry season, damage to grasses might be very limited because of protected and insulated meristems. If the freezing or severe chilling were to occur for more than a few days, then all vegetation could be expected to die. Some regeneration could be expected from seed banks. These systems are much more vulnerable to temperature variations than to changes in light, so that acute decreases in light levels are not likely to add to effects on these ecosystems.

Large mammals, especially grazing animals, could die from loss of heat (body chilling) and lack of food if severe temperature decreases occurred during the wet, growing season. Carnivores would have a better food supply, consisting of carcasses, than herbivores. If acute temperature decreases did not last more than a few weeks, carnivores might survive. However, if heavy rains occurred at temperatures near freezing point, then chilling effects might predominate. Adult insects would die from subfreezing episodes, but survival of the eggs and diapausing insects in the dry season would be likely. Reptiles, amphibia, and many birds would die in an acute phase. If more favorable areas are within reach, then mobile species might survive.

Because of the potential support to surviving human populations by grasslands, the sensitivity of Serengeti grassland ecosystems to potential chronic phase temperature and light reductions was simulated with a previously developed computer model (Coughenour et al., 1984). These simulation results apply only to grasslands not severely damaged by acute phase climatic disturbances. The results must not be interpreted as predictions of post-nuclear war productivity levels in Serengeti grasslands, but should be used in conjunction with other judgments of potential responses.

Baseline production in the simulated grassland is about 350 gC m^{-2} yr^{-1}, with 900 mm of annual precipitation. The combined effects of reducing mean temperature 5°C or less and reducing insolation 6–22% below normal were seen in the simulations to *increase* primary productivity. This pattern was observed whether or not grazing was included in the model. These simulated climatic alterations tend to decrease moisture stress, but decreased precipitation levels could greatly reduce productivity.

In most savannahs, water supply is the limiting factor. A reduction in overall annual precipitation of 25%, 50%, or more would cause substantial reduction in primary production. If seasonality were lost but overall amounts of precipitation were maintained, production would still be reduced, as endogenous dormancy reduces the ability to benefit from dry season rains. Shrubs and trees would benefit, but grasses would suffer. If this occurred, the system would move towards a desert ecosystem, especially if 50% or greater reduction in precipitation occurred. The last decade in the Sahel of North Africa demonstrate this effect of decreased precipitation. In grasslands and savannahs with greater than 1000 mm rainfall per year, the effects of decreased precipitation would be less. Maintenance of reduced rains for a number of years would have major effects, causing changes in species composition and ultimately threatening survival of the ecosystem.

Subtropical grasslands and savannahs in Africa and South America might be the least affected of the terrestrial ecosystems, because plants are more cold tolerant and drought resistant, and there is a reservoir of C_3 plants which can maintain net production under cooler, lower light conditions (McNaughton and Medina, 1985). The sensitivity of tropical grasslands is substantially larger, but the dry season adaptations and the temperature fluctuations, especially in higher altitude ecosystems such as in East Africa, enhance their probability of survival. Grassland-savannah ecosystems in general are more robust to climatic stresses than are evergreen tropical forests, montane–cloud forests, or mangroves.

Tropical grasslands often have a history of burning by humans and are adapted to fire. The frequency of natural tropical grassland fires initiated by lightning is much rarer than in the temperate ecosystems because of the high precipitation which usually accompanies storms (Rundel, 1981). Decreased precipitation, if occurring post-nuclear war, would increase the fuel combustability of grasslands, and the probability of large-scale burns would be high. These fires, however, would be cooler than forest fires, protecting the belowground tissues from damage. Recovery would be initiated by perennial grasses, which are extremely fire resistant because they renew growth from the protected leaf bases of old leaves. Fire resistant seed germination would be the second step in the process of recovery.

A severe drop in chronic temperatures could cause chilling and even frost damage to occur in some seasons, and C_4 grasses would have reduced rates of photosynthesis. Respiration might not be so reduced. Consequently, a moderate to severe reduction in net primary production could occur, leading to collapse of the trophic food web. As a consequence, subsequent rains would allow species to regenerate from the seed bank, but there would be an increase in ruderal species. In all chronic phases, some animals would survive, but overall diversity and biomass would be drastically reduced.

2.4.2.6 Mangroves

Mangrove swamps are a striking feature of tropical and sub-tropical coastal systems, occurring from about 35°N to 38°S in all parts of the world. Generally, they develop on sediments deposited in sheltered estuaries, inlets, and bays, especially in the leeward side of islands and off-shore reefs. They are subject to periodic flooding by tidal waters and are usually intersected by a dendritic creek system. Mangrove swamps are woody communities dominated by the stilt-rooted and pneumatophore-bearing mangrove shrubs and trees. They are the equivalent of the salt marshes of the temperate regions. Productivity in mangroves is normally very high.

More than 50 different mangrove species occur, with members of the genera *Rhizophora* and *Avicennia* being the most widespread. A zonation occurs as one moves from open water towards the coast. The sediment gradually rises in elevation, and changes in species accompany this rise (Macrae, 1968). Salinity, light, exposure and nutrient status alter along this sequence. Because of evaporation, the most saline habitats are at the in-shore edge of the swamps. Most mangrove species have unusual morphological and physiological adaptations to their extreme habitat, which include special organs that assist in oxygen supply in the anaerobic sediments; the production of viviparous, specialized shoots which are finger-like seedlings detached from the mangroves; and the ability to grow by anchoring in mud. The roots of mangroves are able to exclude most of the salt, and the little that enters is stored in vacuoles and excreted through the roots. The plants are succulent, have high internal osmotic pressures in their cells, and contain aerenchymatous tissues.

Mangrove swamps are very important feeding and nursery grounds for shellfish and fish, and their waters teem with life. They also export large amounts of carbon to the sea in the form of detritus (Heald, 1969; Odum, 1969), which is essential in the food chains of estuarine and commercial fisheries. Mangrove swamps are also important feeding areas for birds and numerous crustaceans and are the home of many species of fiddler crabs and aquatic mammals, such as manatee.

Towards the latitudinal margins for mangrove swamps, the species diversity of plants is reduced. For example at the northerly limit in Florida, it is reduced to one species (*Avicennia nitida*), while in temperate Australia, it is reduced to two species (Rodriguez, 1975).

Pannier and Pannier (1977) pointed out that the southern limits of mangrove ecosystems is about 4°S on the Pacific coast of South America, while it is about 28°S on the Atlantic coast. They found that while temperature tolerance was a key factor in this, the pressure of an annual rainy season in the Atlantic was critical.

Four factors are involved in mangrove distributional limits and occurrences. These are: 1.) thermal tolerance; 2.) photoperiodic sensitivity; 3.) precipitation fluxes; and 4.) impact of storms (Pannier, 1985). The distribution of mangroves is thermally limited worldwide. Many species are unable to withstand any frost, and many are susceptible to chilling injury. Annual temperatures of 24.5°C to 26.5°C are normal. *Avicennia nitida* can tolerate temperatures to −4 or −5°C for short periods, while the lower limit for *Rhizophora racemosa* is 19°C, below which temperature the salt-root barrier breaks down and chloride concentration instantly increases in the roots. Mangroves favor a 12-hour photoperiod. If exposed to long days, the root-salt barrier is broken, allowing high salt levels to develop in the roots, killing them. A number of studies on the temperature tolerances of particular species have emphasized the inability of all species except *Avicennia nitida* to tolerate any frost at all, and the general extreme sensitivity of mangroves to low temperature (Pannier and Pannier, 1977; McMillan, 1975, 1979; Lugo and Zucca, 1977). Temperature is also important to the induction of roots on the new shoots [illegible] hypocotylar bud development. Roots need to be formed very quickly to [illegible] the stick- or finger-like seedlings or they will be washed away. At lower temperatures, seedling establishment may fail, since lower temperatures cause an increase in root induction time, as well as lowering the percentage of bud development of the seedlings.

Annual rains are necessary to allow seedling establishment. The importance of adequate rainfall for mangroves (1700–2000 mm year^{-1}) was noted by Pannier and Pannier (1977). Jennings and Bird (1967) ascribe Australia's lack of extensive swamps and marshes to the general aridity of Australian estuaries and to low run-off coefficients and the few perennial rivers, which flood only spasmodically, releasing less fluvial sediments than elsewhere. Any decrease in precipitation would decrease the input from rivers, so that salinities would increase, which could adversely affect all species. *Avicennia nitida* would be least affected by this, but this is uncertain as there are reports of temperature decreases lowering salinity tolerances of several species (Lugo and Zucca, 1977). If in an acute or chronic phase after a nuclear war precipitation were reduced by 25% to 75%, this would prevent re-establishment of damaged or devastated mangrove swamps.

Two main factors are responsible for the destruction of mangroves during coastal storms: 1.) the physical destruction and uprooting of the outer zones of the mangroves; and 2.) increase in sedimentation. Both sudden heavy sedimentation or removal of sediments can kill mangroves. In Florida, damage from a storm which struck the Everglades in 1934 is still visible after 50 years. If the coastal storms were to be increased in intensity after a nuclear war, mangrove ecosystems would be very much at risk, irrespective of reduced temperature and rainfall. A key factor in recovery is the occurrence of the floating regenerative viviparous units. Without these, recovery is not possible.

Mangroves have burned in southern Florida during droughts, such as in 1985. They are replaced by herbaceous vegetation and recovery is slow, with encroachment from the periphery of the burned areas. During severe droughts, the organic soils may also burn.

During a chronic phase of climatic perturbations, mangrove ecosystems might well be the most sensitive of tropical systems to temperature decreases, enhanced coastal storm activity, and reductions in precipitation. Mangrove species cannot cold harden, and they are thus especially susceptible to frost. They do not have seed banks, nor do they have dry, thick-coated seeds. Many species are dependent on water levels, sedimentation, and precipitation for production of live regenerative viviparous propagules, which are very vulnerable to frost and cold. This vulnerability makes recovery unlikely or, at best, very slow. The mangrove systems in the tropics grow in low stress areas with respect to temperature. If the temperature falls on average 5–10°C, this would have a very severe impact at all latitudes, with some fish kills and disruption of food chains. In an acute phase with temperatures falling to near- or sub-zero for a few days, there would be complete mortality for low latitude mangroves, even at temperatures as high as at +5°C. At higher latitudes and at the latitudinal extremes of distribution of mangroves, there would be general die-back, except for *Avicennia* which might survive if the freeze is for just a few days. There would be widespread mortality of fish, shellfish, and plankton in the shallow waters. *Avicennia* might be able to resprout from any living basal wood. If the temperature fell 1–3°C from ambient, then there would be a reduction in productivity, and some species would be adversely affected, especially as regards reproduction.

The susceptibilty of the mangrove ecosystems to reduced precipitation, with the resulting changes in salinity, would affect reproduction and the ability of mature mangroves to survive. Increased storms would cause extensive damage and allow flooding of low-lying coastal areas. This would be accentuated by the occurrence of weakened plants following temperature declines. Mangrove ecosystems, if disturbed on a large scale by severe perturbations, tend to have slow recovery rates, as evidenced by the current devastated state of mangrove ecosystems in Vietnam over a decade after cessation of military applications of herbicides (Netter, 1985).

2.5 POTENTIAL EFFECTS ON SOUTHERN HEMISPHERE ECOSYSTEMS

2.5.1 Vulnerability of Terrestrial Ecosystems to Climatic Disturbances [1]

2.5.1.1 Introduction

Northern Hemisphere and tropical ecosystems might experience nuclear war-induced climatic effects from a war occurring any time of the year, although seasonality is believed to be an important consideration. For the Southern Hemisphere, the importance of seasonality is more marked, with current projections of acute effects occurring in the Southern Hemisphere only following a nuclear war initiated in the Northern summer. A Northern winter-onset nuclear war, on the other hand, does not appear to offer the potential for altered atmospheric circulation patterns to result in significant transport of particulates into the Southern Hemisphere (see Volume I of this report; see also, Pittock, 1985; Pittock and Nix, 1985a).

Another important difference between the Southern and Northern Hemisphere potential climatic effects is the reduced intensity of both acute and chronic stresses, a result of two factors: 1.) the nuclear war is hypothesized to occur largely or totally in the Northern Hemisphere and, thus, the smoke and soot would be initially limited to Northern latitudes; and 2.) the Southern Hemisphere has a much larger proportion of its area covered by ocean (about 80%), so that temperature buffering from the high specific heat of water is much greater. Further, because the transport of the smoke clouds across hemispheres would require alteration of atmospheric circulation patterns on a massive scale and the movement of particulates across several thousands of kilometers, there could be a noticeable time lag before effects occurred. The final difference in potential climatic effects that should be kept in mind is the possibility of changes in monsoonal circulation patterns, a factor noted to have potentially devastating effects on tropical systems.

The net effect of these considerations is the projections of possible acute

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[1] The information in this section is primarily based on the biological working group discussions at the Melbourne conference, M.J. Salinger, chairman, and on the synopses of the discussions prepared by Salinger and by N. Cherry.

and chronic stresses on the Southern Hemisphere following a summer- and winter-onset nuclear war, as indicated in Table 2.1. These projections have a great deal of uncertainty associated with them; thus, all estimations of the effects on Southern Hemisphere ecosystems must be treated as preliminary and tentative. This is especially true for the projections of precipitation anomalies, which appear to be a very important potential effect for Southern Hemisphere ecosystems. In evaluating the vulnerability of ecosystems to these types of stresses, as in the Northern Hemisphere evaluations, possible climatic disturbances have been categorized to include brief periods of subfreezing temperatures, along with reduced sunlight (described as an acute situation), and to include a few degree reduction in average temperatures, with associated 5–20% reductions in insolation. The vulnerability to large (up to 50%) reductions in precipitation was also considered. As previously, such perturbations are *not* projected to occur at any particular probability level or over any particular spatial extent; rather, these are chosen for understanding the vulnerability of Southern Hemisphere ecosystems to classes of perturbations after a large-scale nuclear war, categorized on the basis of biological importance.

The land areas that fall in this region include southern Africa, southern South America, Australia, and New Zealand. Our deliberations focused on the latter two countries as the topic of the Melbourne, Australia, workshop. It is believed that the environmental stresses and responses in southern Africa would be similar to those experienced in Australia, but extra-tropical ecosystems of Africa or South America have not been specifically analyzed.

2.5.1.2 Potential Vulnerabilities of Australian Ecosystems

Considering Australia as representing effects on continental areas, it is clear that the important concerns for the Southern Hemisphere extra-tropics are dominated by grasslands/rangelands, discussed in detail in the agricultural section (Chapter 4), and by oceans, discussed below. Only the effects on forests, deserts, and freshwater ecosystems are briefly considered here.

Terrestrial ecosystems in Australia are largely xerophytic, i.e., the plant and animal communities are adapted to periods of low water availability. Trees and other forest plants typically have sclerophyll leaves, characterized as being tough, evergreen, relatively small, and broad. The warm semi-arid scrub ecosystems in Australia, having evolved in isolation, do not have the succulents of parallel ecosystems on other continents; spiny tussock grasses (spinifex, *Triodia*) predominate. Other terrestrial ecosystems in Australia include the cool semi-arid deserts and true, extreme deserts.

It is felt that none of these ecosystems would be sensitive to brief periods of reduced temperatures and light levels in an acute period and that none is vulnerable to longer, milder climatic disturbances of a chronic phase. This is supported by research on the transportability of several Australian plant species considered for export in cool storage on ocean-going ships (Brunsdon et al., 1984). This research indicated that many such plant species could withstand low temperatures (1°C to 10°C) if simultaneously kept in dark containers, with survival significantly greater at the 10°C level.

The effects of prolonged periods of reduced precipitation, such as possible in the chronic phase after a nuclear war, were also felt to be within the bounds of what the forests and semi-arid and arid ecosystems could absorb without significant effect, since these ecosystems routinely are subjected to prolonged periods of reduced precipitation.

Effects on freshwater ecosystems in Australia would also appear to be limited, in that the temperature reductions do not seem likely to remain below freezing for long enough periods for these ecosystems to freeze. Water availability for humans and other animals might become limiting in the case of prolonged periods of precipitation being reduced by half, but this would not be a problem in the short term because of the current water storage capacity in reservoirs.

2.5.1.3 Potential Vulnerabilities of New Zealand Ecosystems

Effects on the ecosystems of New Zealand and Tasmania could be more marked with respect to temperature reductions. Many of New Zealand's indigenous species are both drought- and frost-sensitive. It is felt that brief temperature excursions near or below freezing could result in plant mortality on a substantial scale. The probability of such events would seem to be diminished in general for New Zealand compared to Australia, because of a greater influence on the weather and climate by the ocean, and, therefore, a dampening of temperature excursions; however, the greater range of altitudes and the more temperate climate of New Zealand suggest that a smaller decrease in average temperatures would be needed to attain near freezing conditions. Clearly, the effects of acute temperature reductions in New Zealand cannot be projected without better resolution of the physical stresses likely to be encountered.

Effects of reduced precipitation on New Zealand ecosystems would become a problem in those areas where precipitation fell below 100 cm annually, with a reduction in primary production likely in those circumstances. Freshwater streams in particular would be adversely affected by major reductions in precipitation. However, precipitation in New Zealand is largely controlled by the direction of winds from the ocean, with a strong orographic component to the distribution of rainfall across the landscape. Knowing the direction and intensity of the on-shore winds in the aftermath of a markedly altered atmosphere is below the level of resolution of climatic projections currently available, and again predictions of ecological effects on New Zealand are tentative. New Zealand ecosystems would appear to be as vulnerable to subfreezing temperatures, half-normal precipitation, and other more extreme climatic perturbations as are comparable ecosystems in the Northern Hemisphere (New Zealand Ecological Society, 1985; Royal Society of New Zealand, 1985); however, the extremes of climatic disturbances do not currently seem plausible to occur in New Zealand after a Northern Hemisphere nuclear war.

2.5.2 Potential Effects on the Southern Ocean and Antarctica [2]

The Southern Hemisphere global weather patterns are dominated by two features—a vast expanse of ocean and the Antarctic continent with its associated sea ice cover. It is the Antarctic and the winter sea ice which seem likely to be the critical feature in any response to nuclear war-induced climatic disturbances in the region.

The Antarctic ice sheet, with an area of about 14×10^6 km^2, contains about 90% of the global freshwater (Walton, 1984). Any major long-term changes in its mass balance would have world-wide effects on sea level and more local effects on Southern Hemisphere heat balance and weather system dynamics.

The Southern Ocean surrounding the continent supports a biologically rich marine ecosystem, and it is significant both in its likely role as an atmospheric CO_2 sink and in its interactions with temperate and tropical ocean waters to the north. Antarctic bottom water, formed in the Southern Ocean, influences deep oceanic temperatures on a global scale. Each winter a large part of the Southern Ocean is covered by seasonally formed sea ice, which is at a minimum in February and increases five-fold in area to a maximum in October. This increases the total ice cover (i.e., including Continental ice) in the Southern Hemisphere from about 17×10^6 km^2 to about 34×10^6 km^2. Sea ice cover shows considerable annual variation, both in extent and duration. Changes in either would have a major effect on marine communities in the Southern Ocean.

An attempt was made by Budd (1975) to relate sea ice changes to air temperatures. Using 60°S as the mean position of the maximum extent of sea ice, Budd suggested that a decrease of 1°C in mean annual air temperature would shift the limit north by about 1° latitude. Using the longest run of Antarctic meteorological data (from Laurie Island, South Orkney Islands) to estimate local temperature effects on ice duration, it was calculated that a decrease of 1°C in mean annual temperature would increase sea ice longevity by about 70 days at that latitude (70°S). However, more recent analyses of these temperature data and sea ice extent (Raper et al., 1984) suggest that the

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[2] This section was primarily written by D.W.H. Walton.

relationship is more complex and that continental Antarctic sea ice trends cannot be reliably inferred from the Laurie Island data.

Recent studies by Takahashi et al. (1984) suggest that the Southern Ocean waters south of the Antarctic Convergence may well act as a sink for over 30% of global industrial CO_2. Gordon (1979) suggested that the area of ocean and sea ice south of the Antarctic Convergence may act as the heat exchanger for the entire Earth's oceans, providing a major area for heat loss to balance heat inputs elsewhere. A crucial feature of this is the area of cold open water within the sea ice in winter, since this accounts for the highest rates of cooling and gas exchange. Large polynya (i.e., open water areas within ice formations) are therefore of considerable importance to global dynamics. Current satellite photographs indicate that at least 25% open water exists within the sea ice even in late winter and up to 60% open water within the ice pack in summer (Keys, 1984), in sharp contrast to the Arctic Ocean, where over 95% is generally frozen.

If the Southern Ocean is defined as the area from the Antarctic continent north to the subtropical convergence (about 49°S), it has an area of about 36×10^6 km^2 and encompasses about 10% of the total world oceanic area. Within this area, ice-free land is very limited (the Antarctic has only 1–2% ice-free areas), and all terrestrial ecosystems are closely marine related. The marine trophic food webs may be much simpler than elsewhere, with Antarctic krill occupying the critical position in many areas, and copepods in others. There are relatively few predator species, primarily marine mammals, and land biota are very depauperate because of the combination of long-range dispersal problems and extreme climatic stress. Nutrient transfer from sea to land is principally by birds and aerosols, and nutrients may be limiting to survival of terrestrial biota.

The Antarctic marine flora, like that of other major oceans, consist almost entirely of phytoplankton (Heywood and Whitaker, 1984). Ice-associated species of phytoplankton are important, being found throughout the whole depth of ice in the Weddell Sea, and forming dense and rich communities beneath the fast ice. Many of the phytoplankton are well adapted to low light levels, down to 0.1% of incident noon insolation (about 0.25 $W\ m^{-2}$). This level of light occurs to depths of 40–200 m of ocean water and about 2 m of sea ice. Most species are obligate psychrophiles, with a sharp metabolic fall-off above 10°C, although they seem to be operating at suboptimal temperatures in the Southern Ocean environment. Limited available evidence suggests that primary production is no greater than in other oceans, with the exception of the Arctic Ocean.

Because of the nature of the trophic structure, organisms and processes initially most critically affected by changes in sea ice dynamics following a nuclear war would be phytoplankton and krill (Everson, 1984). If reductions in temperature and insolation were to reach the Southern Ocean in the austral summer, and if these were substantial, the sea ice growth in the fall could begin earlier and extend farther north than normal. Duration of sea ice could, in a positive feedback mechanism, lead to a minimal summer season the following year and further enhance winter conditions. However, if temperature effects were to reach the Southern Ocean in the austral winter, only a slight increase in sea ice cover would be expected, and the end of the following summer might see a return to normal sea ice conditions.

The effects of prolonged sea ice cover would likely be complex. If the proportion of open water within the sea ice pack were substantially below normal, the Antarctic Convergence would be shifted north, and the open water period in summer would be reduced. These could lead to a northward shift of cold water between the Antarctic and Subtropical Convergences, possibly with a reduction in the width of this zone. In the worst case, there could be a reduction in the Antarctic penguin and seal populations because of a loss of breeding grounds and a reduction in food supply, and a shift in the habitat of petrel and albatross populations to areas further north. However, since these animals are long-lived, the maximum impact would likely be loss of an age class rather than of the entire population. Only extreme prolonged climatic changes would result in the loss of a substantial portion of the adult population

It is not yet clear what the physical stresses on the ecosystems in the most southern parts of the Earth would be in the aftermath of a nuclear war, but the range of possible perturbations outlined in Volume I does not imply that a sufficiently long temperature depression would ensue that would permanently alter the Southern Ocean and Antarctic ecosystems, because of: 1.) rapid recovery times of effects on plankton and krill; 2.) the resistance, longevity, and spatial extent of the populations of the larger organisms; and 3.) the adaptations of many organisms to low light and temperature levels. Antarctica and the Southern Ocean seem likely to survive nuclear war-induced climatic disturbances largely unscathed. However, the role of the Southern Ocean and its sea ice cover in global dynamics does offer the possibility of longer-term and larger-scale effects on other parts of the Earth.

APPENDIX

The Narragansett Bay Model (Kremer and Nixon, 1978) simulates the flows of energy and materials among the compartments of the Bay, as shown in Figure 2.17. A hydrodynamical model is necessary as an input to the ecological model, since many of the important parameters for the latter are controlled by the hydrodynamics. In the model, solar input is the driving energy source for the phytoplankton primary producer compartment, using a daily time step and including effects of the diel cycle.

Primary production is calculated based on a function of maximal potential growth, which is decremented in response to less-than-optimal physical parameters. The relationships with light are based on a time and depth integration of a photosynthesis/light response that includes surface inhibition and self-shading. Nutrient limitations are based on a Michaelis-Menten (1913) function assuming the most-limiting nutrient only; the nutrients simulated include ammonia, oxidized forms of nitrogen, phosphate, and silicate.

The primary producers are split into two physiological groups, with specific values for each for temperature and nutrient responses, half-saturation constants, nutrient content, and nutrient:carbon ratios. The zooplankton compartment consists primarily of herbivorous copepods found in the Bay, and is separated into compartments for eggs, juveniles, and adult life stages. Adults consume phytoplankton, detritus, and zooplankton eggs and juveniles in a density-dependent manner as a function of temperature. Egg release and development are functions of temperature. Seasonality is imposed on predators, especially involving ctenophore and fish populations. A benthos compartment is included, which receives inputs from the plankton; clams actively filter the water at a temperature-dependent rate. Benthos also regenerate nutrients into the water column by releasing ammonia, phosphate, and silicate at temperature-dependent rates. Finally, a chemical nutrient compartment is incorporated in the model, providing a critical feedback loop connecting all other compartments and adding inputs from anthropogenic sources.

Water temperatures were calculated as a function of the assigned reduction in air temperatures, according to a linear regression analysis of the air/water temperature relationships seen in Narragansett Bay from a 20-yr record of weekly mean water temperatures and climatological data from Newport, RI, for the same periods. The relationships applied were:

$$T_w = 1.34736 + 0.880516\,T_a \qquad (r^2 = 0.974) \qquad \text{warming period}$$
$$T_w = 3.24267 + 0.868082\,T_a \qquad (r^2 = 0.982) \qquad \text{cooling period}$$

where:

T_w = water temperature (°C)
T_a = air temperature (°C).

The high r^2 values indicate a close correlation between air temperatures and water temperatures; the shift in warming versus cooling period relationships was instituted on 1 August of the simulated years.

These temperature analyses and the model simulations were done by J. McKenna, of the Graduate School of Oceanography, University of Rhode Island, for the SCOPE–ENUWAR project.

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