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CHAPTER 1

Ecological Principles Relevant to Nuclear War

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1.1 INTRODUCTION

Nuclear war represents the most significant environmental threat of our times. The potential combined effects of reduced temperatures, light, and precipitation, exposure to ionizing radiation and enhanced UV-B, and the release of various toxicants into the environment would result in the short-term devastation, and long-term impairment of recovery for exposed biological communities. In this chapter, some of the ecological principles we feel are necessary to understand the subsequent analyses are introduced.

The ecological principles outlined are very basic ones; we anticipate a readership trained in a broad range of disciplines, including those unfamiliar with the academic discipline of ecology. We include substantial discussion in this chapter on ecophysiology (i.e., the responses of organisms to their environment) because this is relevant to the new understanding of the potential climatic consequences of nuclear war (see Volume I). In particular, the physiological sensitivity of organisms to reduced levels of light and temperature are a key part of the analysis of the potential ecological effects (Chapters 2 and 3) and agricultural effects (Part II) of nuclear war.

Much of the ecological analysis has been organized around major biological units called biomes. In this chapter, we describe the biome concept and discuss some of the environmental–climatic factors that are believed to control biome distribution. A description is also included of the current geographical distribution and productivity of those biomes that are discussed in Chapter 2. Emphasis is given in this chapter to plants because of their controlling influence on ecosystem functions through their role as primary producers. Future reports are needed to address more fully the potential effects on animals. Much more research needs to be done on both plant and animal responses to the types of perturbations possible for the aftermath of a nuclear war. (See Appendix B for a brief listing of research needs.)

Another important element for analysis of the potential ecological consequences of nuclear war concerns recovery processes. As the post-nuclear war environmental extremes ameliorate, ecological communities in devastated regions would begin to reorganize. It is not possible to predict the course of such a succession precisely, but some principles concerning post-perturbation replacement (such as seed banks and germination), relevant successional patterns, and organism strategies are discussed.

1.2. ECOPHYSIOLOGY

1.2.1. Plant Responses to Low Temperatures

The ecological significance of low temperature tolerance, or the lack of it, as a normal response to an environmental stress is well documented by Larcher and Bauer (1981). They point out that for 64% of the Earth's land mass, the mean minimum temperature is below 0°C, and for 48% it is below – 10°C. Forests occupy large areas in Siberia, Alaska, Scandinavia, and Canada, where temperature drops regularly below – 50°C. Tundra species occupy areas further north, where temperatures may not be necessarily more extreme, but where winds increase the winter desiccation problems. An absolute temperature minimum of – 68°C was recorded at Verkhoyansk in lowland Siberia, and one of – 71°C at Olimyakon in eastern Siberia. Larcher and Bauer (1981) noted that absolute minima of – 45°C to – 55°C are reported from Antarctic coastal stations, and temperatures of – 90°C have been reported from continental Antarctica.

Freezing temperatures are clearly a normal event for a majority of the Earth's surface, and adaptations of plants and animals enabling them to live through the normal seasonality of cold in temperate regions reflect this. However, the cold or freezing adaptations generally do not provide protection from temperature extremes well beyond those normally experienced by the organism.

Major patterns of vegetation distribution (i.e., of communities, ecosystems, and biomes) reflect annual and seasonal low temperatures. Each species has its particular temperature limits, but generalized responses occur. For example, the northern latitudinal and altitudinal distributional limits of broad-leaved evergreen woody plants are probably determined by low winter temperatures (Sakai and Wardle, 1978; Larcher, 1981; and Lavagne and Muotte, 1971). Similarly, the northern limits of the temperate deciduous forests of North America and Eurasia correlate well with the threshold for deep supercooling of their tissues; i.e., – 40°C to – 45°C (George et al., 1974; Quamme, 1976; and Rajashekar and Burke, 1978). Using these survival limits of distribution for groups of species against low temperature thresholds, Larcher (1981) used Hoffman's data to construct a world map for vegetation based on five temperature-stress categories. The thresholds are shown in Figure 1.1 using the following categories:

- Zone A: a frost-free zone;
- Zone B: a zone with episodic frosts having lower limits down to – 10°C;
- Zone C: a zone of cold winters, with an average annual minimum of – 10°C to – 40°C. This zone delineates the northern limits of most of the north temperate deciduous forests. Within Zone C, the – 30°C isotherm coincides with the geographic limits of many herbaceous perennial species that are unprotected in winter.
- Zone D: a zone with an average annual minimum temperature below – 40 °C; this zone includes the coniferous boreal and tundra ecosystems;
- Zone E: the polar ice caps, which are substantially devoid of vegetation.

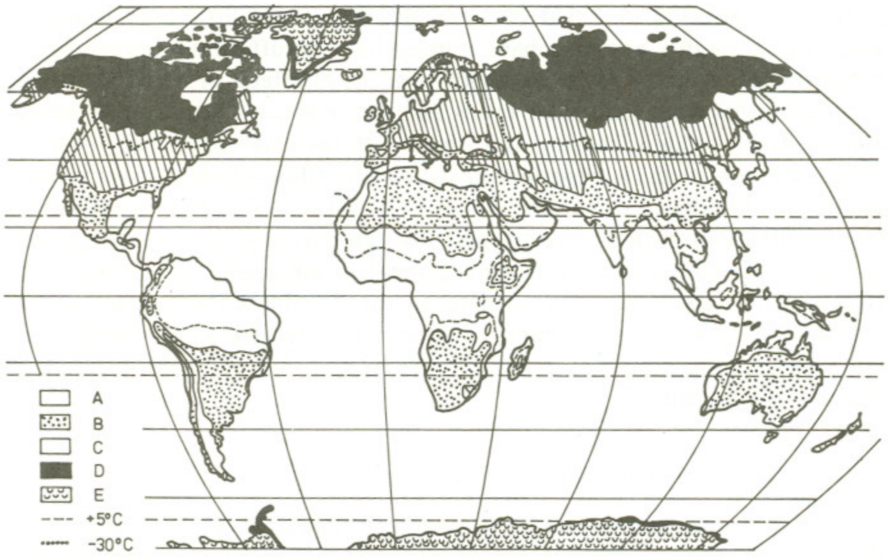

Figure 1.1 Map of low-temperature threshold limiting plant distribution on the Earth. A: frost-free zone; B: zone with episodic frosts down to – 10°C; C: zone with average annual minimum between – 10°C and – 40°C; D: zone with average annual minimum below – 40°C; E: polar ice; - - - : + 5°C lowest temperature isotherm; · · · : – 30°C average annual minimum isotherm. From Larcher and Bauer (1981)

It should follow that if generations of rather rigorous natural selection and adaptation have accommodated plant communities and taxa to their low temperature exposures, then a sudden change in this low temperature exposure might take them beyond their tolerance limits. The climatic disturbances following a nuclear war could cause temperature excursions beyond seasonal or even annual temperature limits. Relatively small ambient alterations applied over many generations can cause the shifting of the boundaries of floras, such as latitudinal shifts during the recent Ice Ages, but short-term events (i.e., applied over time periods of weeks to a few years) might cause local or regional extinctions, without causing latitudinal or altitudinal displacements. The potential for the latter category of climatic perturbations is documented in Volume I and summarized in Appendix C. A more complete description of the types of climatic stresses of biological relevance is provided at the beginnings of Chapters 2 and 4.

Biota respond not only to seasonal and annual mean temperatures, but also to episodic and periodic events. Low temperatures may follow polar air mass intrusions, which on clear nights can cause sudden severe frosts in the temperate region or summer frosts in the boreal region. At high altitudes, frost can occur at any time of the year, even in desert regions. These episodic temperature excursions can take place within a few days or even hours, and plants are damaged or killed because they have very little cold resistance when in the active growth phase if they have insufficient opportunity to enhance their cold tolerance. A major concern of effects of a nuclear war in summer is that both temperate crops and native species would suffer severe damage from sudden freezing at a time when they are most susceptible.

Periodic cold stress is experienced seasonally, allowing plants enough time to adapt gradually (Larcher and Bauer, 1981). Only severe or exceptionally long, continuous periods of extremely low temperatures in winter represent a danger to acclimatized plants. This generalization applies to the ecological effects of a nuclear war commencing in the Northern Hemisphere winter months; i.e., the ability of plants to survive and regrow when climate subsequently ameliorated would be affected by the intensity and duration of extreme temperatures.

1.2.1.1. Chilling-Sensitive Plants

Many sensitive plants can be damaged or killed at temperatures above the freezing point, by what is commonly termed chilling. This phenomenon has long been recognized (e.g., Molisch (1896) reported that in 1844, Hardy found that in tests on 56 tropical species, 25 were killed at 1°C to 5°C).

Chilling temperature is defined as any temperature sufficiently cool to produce injury, but not cold enough to freeze the plant. In most cases the plants do not suffer chilling injury until the temperature drops below +10

°C. For warm temperate, sub-tropical, or tropical plants, the possibility of temperatures being reduced to +10°C for days or weeks during a nuclear war-induced climatic event seems possible (Volume I, Pittock et al., 1985). In some cases, severe damage can occur at temperature exceeding +10°C; for example, flowering rice and sugar cane suffer damage at 15°C (Adiv, 1968; Tsunoda et al., 1968; Levitt, 1977). (See the discussion on rice in Chapter 4.)

As with frost damage, the intensity and duration of chilling are critical to the damage, as are intrinsic features of the plant species. This is illustrated in Figure 1.2 for chilling exposure of *Saintpaulia* leaves to temperatures from 7°C to 1°C for 1 to 72 hours. At 1°C, irreversible damage occurred within minutes of exposure, while 12-hour exposure caused death of all leaves. In contrast, an 8-hour exposure to 5°C was needed before damage occurred, and more than 48 hours exposure was needed to damage more than 50% of the leaves irreversibly.

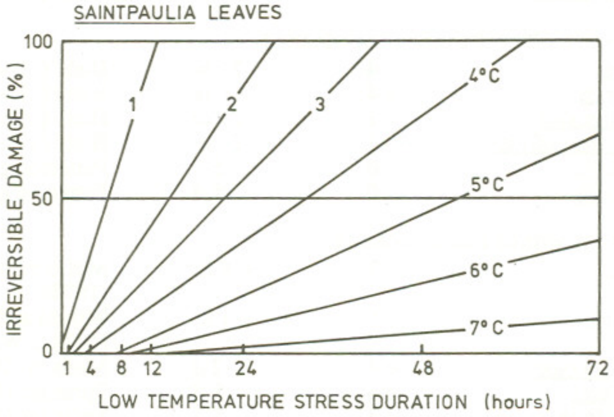

Figure 1.2 Dose dependence of chilling injury in leaves of *Saintpaulia*, Rhapsody strain. The duration of low temperature exposures required to cause various percentages of irreversible injury are shown. From Larcher and Bauer (1981)

Chilling excursions, such as the friagems in Brazil and Amazonia, are known to have devastating effects on native tropical flora and tropical or sub-tropical crops. Larcher and Bauer (1981) noted that certain tropical rainforest plants and mangroves, many cultivated and ornamental plants of tropical origin, tropical seagrasses, tropical C_4 fodder grasses, and vegetables of tropical origin suffer visible injury after exposure to chilling temperatures (Table 1.1). This table clearly shows the extreme sensitivity of many mangrove species, including *Avicennia* and *Rhizophora*, to temperatures from 1 °C to 4°C for as little as 24 hours (Larcher and Bauer, 1981).

TABLE 1.1.

SUSCEPTIBILITY TO LOW TEMPERATURE STRESS FOR LEAVES OF CHILLING-SENSITIVE CORMOPHYTES [a]

Species	Chilling injury at °C	Duration of chilling at the indicated temperature	Reference
1. WOODY PLANTS IN THEIR NATURAL HABITAT (PUERTO RICO)			
Guarea guara	4	24 hr	Biebl (1964)
Marcgravia sintenisii	4	24 hr	Biebl (1964)
Avicennia nitida	3	24 hr	Biebl (1964)
Marcgravia rectiflora	0.5-1	24 hr	Biebl (1964)
Cecropia peltata	0.5-1	24 hr	Biebl (1964)
Rhizophora mangle	0 - 1	24 hr	Biebl (1964)
Psychotria berteriana	0 - 1	24 hr	Biebl (1964)
2. HERBACEOUS PLANTS IN THEIR NATURAL HABITAT			
Pilea obtusata	< 4	24 hr	Biebl (1964)
Ruellia coccinea	< 4	24 hr	Biebl (1964)
Psychotria uliginosa	1	24 hr	Biebl (1964)
Peperomia hernandifolia	0 - 1	24 hr	Biebl (1964)
Passiflora edulis	0	5 d	Patterson et al. (1976)
Passiflora edulis	0	25 d	Patterson et al. (1976)
3. CULTIVATED PLANTS OF TROPICAL ORIGIN			
Phalaenopsis	7	< 8 hr	McConnell and Sheenan (1978)
Episcia reptans	5	1 hr	Wilson and Crawford (1974); Wilson (1978)
Eranthemum tricolor	< 4	2 d	Molisch (1897)
Impatiens sultani	< 3	1.5 d	Spranger (1941)
Peperomia arifolia	< 3	1.5 d	Spranger (1941)
Schismatoglottis pulchra	< 3	2 d	Spranger (1941)
Scindapsus pictus	4.5	< 4 d	McWilliams and Smith (1978)
Maranta leuconeura	4.5	4 d	McWilliams and Smith (1978)
Begonia stigmatosa	< 4	5 d	Molisch (1897)
Piper decurrens	< 3	5 d	Spranger (1941)
Peperomia argyrea	< 4	5-7 d	Molisch (1897)
Lycopersicon esculentum	< 5	> 6 d	Seible (1939)
Eranthemum tuberculatum	< 4	11 d	Molisch (1897)
Zebrina pendula	< 5	> 14 d	Seible (1939)
4. TROPICAL SEAGRASSES			
Syringodium filiforme	2	1 hr	McMillan (1979)
Thalassia testudinum	2	4 hr	McMillan (1979)
Halodule wrightii	2	1 d	McMillan (1979)

[a] Data from Larcher and Bauer (1981).

Despite the widespread use of maize (*Zea mays*) in temperate regions, it is very susceptible to chilling injury in various ways. For example, Crevecoeur et al. (1983) studied physiological and ultrastructural effects on the germination of kernels under sub-minimal temperatures. When exposed to chilling lasting for more than 6 to 8 days, the ability of maize embryos to resume growth declined. After a 26-day chilling period, all embryos had died. Significant ultrastructural changes also occurred, with the nucleolus becoming fibrillar and unusual ribonucleoprotein granules appearing, in addition to large decreases in chromatid transcription. By extrapolation, one month of a nuclear war-induced chilling that occurred after seeds were sown in the spring would be enough to devastate maize crops, even without the occurrence of freezing temperatures

Hodgins and Van Huystee (1985) found that maize seedlings exposed to 12°C for 6 days were unable to synthesize chlorophyll, even though fully illuminated. However, when subsequently returned to 28°C, chlorophyll synthesis was restored, though the seedlings had etiolated (i.e., become elongated, pale, and thin) by this time. Biochemical examination of seedlings at different stages of the 12°C chilling showed an accumulation of chlorophyll precursors but an absence of aminolevulinic acid, an essential factor in the synthesis of the porphyrin ring of the chlorophyll molecule. Thus, chilling at a temperature as high as 12°C causes potentially debilitating metabolic disorders in maize, even though this temperature is a good deal higher than the point of freezing-induced death.

Any low temperature excursions which caused chilling in tropical regions and which persisted for even a few days would have devastating effects. Freezing temperatures would be worse, since most low altitude tropical plants have no mechanism for avoiding ice crystal formation within cells and would be killed. Ripening fruits of both tropical and sub-tropical plants are also especially susceptible to cold.

1.2.1.2. Differences in Freezing Resistance and Killing Temperatures

The tolerance of all plants to low temperatures is increased at lower tissue water content (Kappen and Lange, 1970a; Lipman, 1936; Mazur, 1969). In an air-dry state, most microorganisms, mosses, algae, lichens, and ferns are able to survive extreme temperatures (e.g., immersion in liquid nitrogen). Bacteria and yeast are especially able to tolerate very low temperatures, though abilities vary a great deal. There is a cryophile microbial flora that is best adapted to low temperatures, just as there are other groups that can tolerate very high temperatures. Dried seeds are also able to tolerate low temperatures, with tolerances at the maximum in dried conditions.

The crucial survival factor for many organisms would be whether they were dry or wet, growing or dormant at the onset of nuclear war-induced climatic extremes. Dry seeds are characteristic of grasslands and other temperate ecosystems, especially for weedy species. The seeds and fruit of the tropical rainforest species, in contrast, are predominantly fleshy, enhancing sensitivity to freezing. On the other hand, the compilation of data from Larcher and Bauer (1981) (Table 1.2) emphasizes the remarkable cold tolerances of many groups of organisms and indicates that many plant species would survive if in a dried condition. Even tropical mosses and ferns showed chilling tolerance, and temperatures from between 0°C to – 7°C were necessary to kill them (Biebl, 1964, 1967). Clearly mosses and many ferns have remarkable tolerances irrespective of geographic origin.

It should also be noted that some permanently ice-covered lakes occur in the Canadian arctic; yet, in the waters beneath the ice, phytoplankton, zooplankton, bacteria, and fungi exist. Also, the well-known phenomenon of ice-algae occurs in polar marine waters, where attached to the bottom of the ice-pack and often embedded in the ice itself at temperatures of – 4°C and at very low light levels, an annual prolific colonization by unicellular diatoms and chrysophytes regularly occurs. Often these ice algae peak in productivity before spring break-up of the ice pack occurs (Aragno, 1981). Thus, a well-adapted algal flora can exploit cold environments with low light and short summers, and life is possible at about 0°C for a wide variety of microorganisms and functions. Other examples include fungal pathogens that infect alpine fir trees and grow under snow cover, and algae and fungi that grow on or through the melting snow pack (Aragno, 1981).

Larcher and Bauer (1981) used data from many sources (Tables 1.3 and 1.4) to analyze the potential frost resistance of many species of plants. These were also analyzed according to their ecosystem of origin. Not surprisingly, tropical and sub-tropical plants are largely susceptible to freezing throughout their lives. Most of these species are unable to frost harden, so that their freezing point lies between – 1°C to – 3°C. Markley et al. (1982) point out that few species, except mangroves and seagrasses, are distributed from the tropics into temperate coastlines. McMillan (1979) studied three of the seagrasses (*Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*) collected from the western tropical Atlantic. All three showed leaf and plant damage to various degrees when exposed to chilling temperatures, with populations of more tropical origin showing the most chilling damage and those from more temperate populations showing the least injury at 2°C to 4°C. Similarly, tropical mangroves are more sensitive to low temperatures than are sub-tropical species.

The C_4 grasses and the sugar cane relatives from Australia, New Zealand, and the Pacific tropical and sub-tropical areas are very sensitive (Rowley et al., 1975; Ivory and Whiteman,1978; Miller, 1976). Another group of extremely sensitive plants are those growing in warm temperate coastal regions where frosts are very rare. The tropical lianas and epiphytes are typically

TABLE 1.2

POTENTIAL COLD RESISTANCE OF ALGAE, LICHENS, AND MOSSES IN THE HYDRATED STATE[a]

Plant and habitat	Injury below indicated temperature (°C)	Reference
1. ALGAE		
Arctic seas	-8 to -28	Biebl (1968, 1970)
Intertidal	-2 to -4	Biebl (1968, 1970)
Sublittoral		
Temperate seas		
Intertidal Chlorophyceae	-8 to -25	Terumoto (1964); Biebl (1958,
Phaeophyceae	-40 to -60	Parker (1960) 1972)
Rhodophyceae	-7 to -8 (-70)[b]	Biebl (1939, 1958); Terumoto (1964); Migita (1966)
Sublittoral	-2 to +4	Biebl (1958, 1970)
Tropical seas		
Intertidal	-2 to +11	Biebl (1962)
Sublittoral	+3 to +14	Biebl (1962)
Arctic and Antarctic freshwaters		
Cyanophyceae	-70 to -196	Holm-Hansen (1963)
Phycophyta	-15 to -30	Holm-Hansen (1963); Biebl (1969)
Temperate lakes		
Cyanophyceae	(-25) -70 to -196	Holm-Hansen (1963)
Phycophyta	-2 to -20	Terumoto (1964); Duthie (1964); Biebl (1967); Schölm (1968)
Tropical lakes	n.d.[c]	
Hot springs	[+15 to +20][d]	Soeder and Stengel (1974); Brock (1978)
Epiphytic and epipetric algae	-70 to -196	Kärcher (1931); Edlich (1936)
Soil algae	-25 to -196	Holm-Hansen (1963)
Snow algae	ca. -40	Göppert (1878)
2. LICHENS		
Arctic, Antarctic	-80 to -196	Kappen and Lange (1972); Riedmüller-Schölm (1974)
Desert, High mountains	-78	Kappen and Lange (1970b, 1972)
Temperate zone	-50 and below	Kappen and Lange (1972)
3. MOSSES		
Arctic	-50 to -80	Riedmüller-Schölm (1974)
Temperate zone		
Marchantiales	-5 to -10	Clausen (1964), Dircksen (1964)
Jungermanniales	-10 to -15	Clausen (1964), Dircksen (1964)
Musci (Hydrophytes)	-8 to -20	Irmscher (1912), Dircksen (1964)
Musci (bogs)	-7 to -15	Dircksen (1964)
Musci (forest floor)	(-10) -15 to -35 (-55)	Irmscher (1912); Dircksen (1964); Hudson and Brustkern (1965); Antropova (1974)
Musci (epiphytic, epipetric)	-15 to -30	Irmscher (1912)
Humid tropics	< 0 to -7 (-16)	Biebl (1964, 1967)

[a] Data from Larcher and Bauer (1981).

[b] Exceptional values indicated by parentheses.

[c] n.d. No experimental data available.

[d] Estimated from growth limitations indicated by brackets.

TABLE 1.3

POTENTIAL FROST RESISTANCE OF HERBACEOUS VASCULAR PLANTS[a]

Plant group	Frost resistance (lowest temperature (°C) sustained without lethal injury)			Reference
	Leaves	Shoot apex	Subterraneous organs	
1. PTERIDOPHYTES				
Tropical ferns	0 to -2			Biebl (1964)
Temperate ferns	-13 to -25		-7 to -12	Kappen (1964)
Subarctic (*Lycopodium*)	-80			Riedmüller-Schölm (1974)
2. GRAMINOIDS				
Tropical and subtropical grasses	-1 to -4	-4 to -6		Rowley *et al.* (1975); Ivory and Whiteman (1978)
Temperate grasses	-20 to -25	-5 to -30	-7 to -20	Till (1956); Fowler *et al.* (1977); Fuller and Eagles (1978); Noshiro and Sakai (1979)
Steppe grasses	n.d.[b]			
Alpine sedges	(-70)[c]	(-70)	(-70)	Kainmüller (1975)
Arctic graminoids	n.d.			
3. HERBACEOUS DICOTYLEDONS				
Tropical herbs	-1 to -2			Biebl (1964)
Meadow plants	-15 to -25	-10 to -20	-5 to -15	Schnetter (1965); Noshiro and Sakai (1979),
Temperate forest herbs	-10 to -20	10 to -20	-7 to -11	Till (1956)
Geophytes	-5 to -12	ca. -10	-7 to -14	Till (1956); Goryshina (1972); Lundquist and Pellett (1976)
Halophytes	-10 to -2	ca. -20	-10 to -20	Kappen (1969); Maier and Kappen (1979)
Winter-annual desert plants	-6 to -10			Lona (1963)
Arctic and alpine rosette and cushion plants	-20 to -50	-30 to -50	-20 to -60	Ulmer (1937); Sakai and Otsuka (1970); Kainmüller (1975)
Tropical high mountain plants	-7 to -12			Larcher (1975)

[a] Data from Larcher and Bauer (1981).

[b] No experimental data available.

[c] Parentheses denote exceptional values.

very sensitive to frost. It seems a general phenomenon, however, that during seasonally dormant or inactive periods, such as droughts in tropical systems and winter in temperate systems, plant freezing tolerance is greater, and such ecosystems are more resistant to cold temperatures than ecosystems that are constantly moist and warm. It should also be emphasized that in ecosystems with very little seasonal temperature variation, as in many evergreen tropical areas, sudden temperature drops would likely be devastating because of lack of adaptation. The generalization that ecosystems can tolerate normally experienced extremes, but not extremes for which there is little previous experience, seems to be true for low temperature, as it is for drought, darkness, hurricanes, and other climatic extremes.

Having said this, it also needs to be recognized that substantial differences occur within and across species, even within an ecosystem at a specified location. The individual can alter its response somewhat, provided it is not killed outright by the first exposure to the new (surprise) circumstances. Further, population-level accommodations can occur if there is a diversity of tolerances among the individuals in the population. The hardening and acclimation of temperate forest trees on a seasonal basis is one clear example. Some cold adaptation has also been demonstrated in sub-tropical grasses (e.g., *Paspalum dilotatum* and *Evengrostis curvula*) (Rowely et al., 1975), as well as in citrus species growing in Florida (Yelenosky, 1975).

Sudden freezes have led to disasters to the citrus groves of Florida on numerous occasions this century, seemingly most frequent over the past decade. This is an example of a semi-tropical crop grown beyond the limits if its normal range, and provides a dramatic demonstration of the disaster which a nuclear war could bring to agricultural systems everywhere and to ecosystems in the tropics and sub-tropics should frost occur, especially if chilling temperatures were prolonged.

The acclimation or hardening of plants to tolerate low temperatures is reversible and temporary. If, for example, some sub-tropical species were to acclimate to chilling conditions, the acclimation might be of little value in the climatic conditions after a large-scale nuclear war, as the acclimation would be lost as temperatures increased, and the plants would be just as sensitive to damage from subsequent chilling as they were to the first.

Subterranean organs generally are less adapted to very low temperatures than are plant parts exposed at or above the soil surface. This is illustrated in Table 1.3. It is not normally disadvantageous, however, since the substantial insulating properties of soils ameliorates air temperatures within a few centimeters of the surface. Low growth forms and lack of trees or shrubs in exposed arctic and alpine areas, together with the development of belowground perennating (over-wintering) and storage organs, emphasize this point. The classification by Raunkiaer (1909, 1928) indicated that both latitudinal and altitudinal vegetation types change in relative abundance based

TABLE 1.4

POTENTIAL RESISTANCE OF WOODY PLANTS TO LOW TEMPERATURES AND FROST[a]

	(lowest sustained temperatures without lethal injury) (°C)		
Plant group	Leaves	Buds	Flower buds
1. TROPICAL REGIONS			
Forest and fruit trees	+4 to -3	down to -5	
Tropical palms	(-1)[b] -3 to -5	[-3 to -5][c]	
Lianas	+4 to 0		
Mangroves	+4 to -4		
2. SUBTROPICAL REGIONS			
Evergreen trees and shrubs	(-2) -4 to -6 (-8)	-6 to -12	
Drought and deciduous trees		ca. -14	
Subtropical palms	-5 to -12	down to -14	
3.MARITIME-TEMPERATE REGIONS			
Conifers	-10 to -20	-10 to -25	(-10)
Arcto-tertiary flora	-10 to -15	-8 to -15	
Evergreen broad-leaved trees and shrubs	-7 to -15 (-20)	-10 to -18	down to -17
Mediterranean scherophylls	-5 to -12 (-15)	-8 to -18	-10 to -16
Warm-temperate deciduous trees		-15 to -30	-15 to -30
Ericaceous heath shrubs	-15 to -30	-20 to -30	-15 to -25
4. REGIONS WITH SEVERE WINTERS			
Conifers	-40 to -70 (-196)	-30 to -70 (-196)	
Temperate deciduous trees		-25 to -35 (-60)	-25 to -40
Boreal deciduous trees		-30 to -80 (-196)	
Arctic and alpine dwarf shrubs	-30 to -50 (-80)	-20 to -40	

[a] Data from Larcher and Bauer (1981).

[b] Parentheses denote exceptional values.

[c] Brackets denote estimations from observations of occasional frost injury

TABLE 1.4 continued

Plant group	Stem	Roots	References
1. TROPICAL REGIONS			
Forest and fruit trees		down to -5	Biebl (1964); Sakai (1972,1978b,c)
Tropical palms			Biebl (1964); Smith (1964); Larcher (1980b)
Lianas			Biebl (1964)
Mangroves			Biebl (1964); McMillan (1975)
2. SUBTROPICAL REGIONS			
Evergreen trees and shrubs		-6 to -15	Larcher (1971); Layton and Parsons (1972); Sakai (1972, 1978b); Yelenosky (1977)
Drought and deciduous trees		-15 to -20	Larcher (1971); Sakai (1978b)
Subtropical palms			Larcher (1980a); Larcher and Winter (1982)
3. MARITIME-TEMPERATE REGIONS			
Conifers	-15 to -30	-10 to -20	Parker (1960); Larcher (1954, 1970); Sakai and Okada (1971); Havis (1976); Sakai (1978b)
Arcto-tertiary flora	-8 to -18		Sakai (1971)
Evergreen broad-leaved trees and shrubs	-10 to -20	-7 to -9	Sakai (1972); Havis (1976); Sakai and Wardle (1978);Sakai and Hakoda (1979)
Mediterranean sclerophylls	-8 to -22[d]		Larcher (1954, 1970); Sakai (1978b)
Warm-temperate deciduous	-20 to -40[d]		Larcher (1970); Sakai (1971, 1972, 1978b,c); Sakai and Weiser (1973); Kaku and Iwaya (1978)
Ericaceous heath shrubs	-15 to -35	-10 to -20	Till (1956); Havis (1976); Sakai and Miwa (1979)
4. REGIONS WITH SEVERE WINTERS			
Conifers	-50 to -196	-20 to -35	Pisek and Schiessl (1947); Parker (1962); Sakai and Okada (1971);Havis (1976); Sakai (1978a,1979)
Temperate deciduous trees	-30 to -50[d]	-15 to -25	Till (1956); Pisek (1958);Parker (1962); Sakai (1972,1978c); Sakai and Weiser (1973); George et al. (1974)
Boreal deciduous trees	down to -196		Sakai (1965); Sakai and Weiser (1973); Sakai (1978c)
Arctic and alpine dwarf trees	-30 to -50	-10 to -30	Ulmer (1937); Pisek and Schiessl (1947); Sakai and Otsuka (1970);Riedmüller-Schölm (1974); Larcher (1977).

[d] Stem resistance limited by deep supercooling of xylem.

on the position of perennating buds (meristems surviving dormant periods). In tropical evergreen ecosystems, the great majority of species have buds well above the ground, whereas in seasonal forests, a mixture of woody perennials or herbaceous perennial (phanaeophytes and hemicryptophytes) occurs (Figure 1.3), with annual species surviving during the cold or drought seasons as well-protected dry seeds. In cold polar regions, the perennating buds are at or below the ground surface. This life-form sequence along climatic gradients is to a large extent based on progressive protection of vital meristems against cold and drought. It means that cold-temperate and polar ecosystems are at least partially pre-adapted (by chance) to the climatic disturbances that a nuclear war could impose.

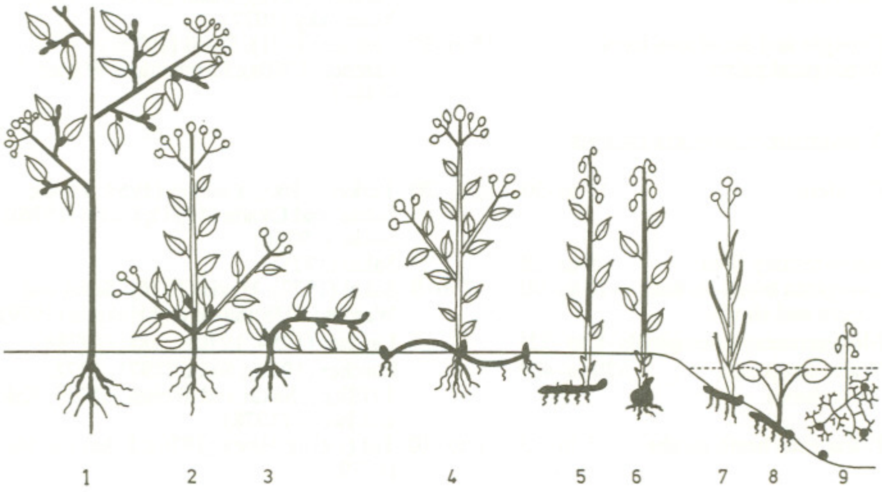

Figure 1.3 The relative positions of the perennating parts of four life forms. (1) Phanerophytes, (2–3) Chamaephytes, (4) Hemicryptophytes, and (5–9) Cryptophytes. The persistent axes and surviving buds are shown in black. From Raunkiaer (1934)

1.2.1.3 Acclimation and Hardening

Hardening is a sequential process, as described in Tumanov (1962), Weiser (1970), Kacperska-Palacz (1978), and Tyurina et al. (1978). Initial hardening is achieved at temperatures from 0°C to 5°C, which makes it possible for moderate frosts to be survived. Subsequent, sustained frosts lead to complete hardiness, in those plant species capable of developing it, so that the plants achieve their limits of freezing tolerance. At this stage of hardening, woody boreal species (e.g., *Abies*, *Picea*, *Pinus*, *Salix*, *Betula*, and *Ribes*) are resistant to extreme temperatures, even including immersion in liquid nitrogen (– 196°C). Some herbaceous plants of the northern woods, tundra, and high mountains also exhibit unlimited freezing tolerance.

Differences between hardened and unhardened plants are striking in their temperature limits (Table 1.5). Cold periods occurring during the winter can induce additional cold-tolerance within a few days for plants already hardened. However, dehardening by warming to above-freezing, especially if temperatures suddenly rise to greater than + 10°C in winter in cold temperate regions, takes place even faster, being completed within 1–2 days of persistent warm temperatures This phenomenon leads to premature bud break and subsequent frost damage to shrubs and trees. A lack of continuous below-freezing temperatures following a nuclear war could cause this

TABLE 1.5

KILLING TEMPERATURES FOR PLANTS IN THE FROZEN STATE[a]

	Killing temperature (°C) when frozen		
Species	Unhardened	Hardened	Reference
Potato tuber	-2		Maximov (1914)
Red beet root	-2		Maximov (1914)
Wheat		-12, -15	Tumanov and Borodin (1930)
Cabbage	-2	-6, -20	Levitt (1939) Kohn and Levitt (1965)
Vaccinium vitis idea	-2	-22	Ulmer (1937)
Erica carnea	-4	-19	Ulmer (1937)
Sempervivum glaucum	-3	-25	Kessler (1935)
Rhododendron ferrugineum	-4	-28	Ulmer (1937)
Globularia nudicaulis	-4	-19	Ulmer (1937)
Globularia cordifolia	-4	-19	Ulmer (1937)
Saxifraga caesia	-4	-30	Ulmer (1937)
Homogyne alpina	-4	-18	Ulmer (1937)
Saxifraga aizoon	-4	-19	Ulmer (1937)
Hedra helix	-5	-18	Kessler (1935)
Rhododendron hirsutum	-5	-29	Ulmer (1937)
Saxifraga cordifolia	-5	-19	Kessler (1935)
Carex firma	-6	-30	Ulmer (1937)
Pinus mugo	-6	-41	Ulmer (1937)
Empetrum nigrum	-6	-29	Ulmer (1937)
Juniperus nana	-8	-26	Ulmer (1937)
Pinus cembra	-9	-38	Ulmer (1937)
Pinus cembra	-10	-40	Pisek (1950)

[a] Data from Levitt (1980).

phenomenon, especially in more southerly latitudes, such as 30°N–40°N. Examples of the seasonal and shorter term changes in freezing tolerances are shown in Figures 1.4–1.6 .

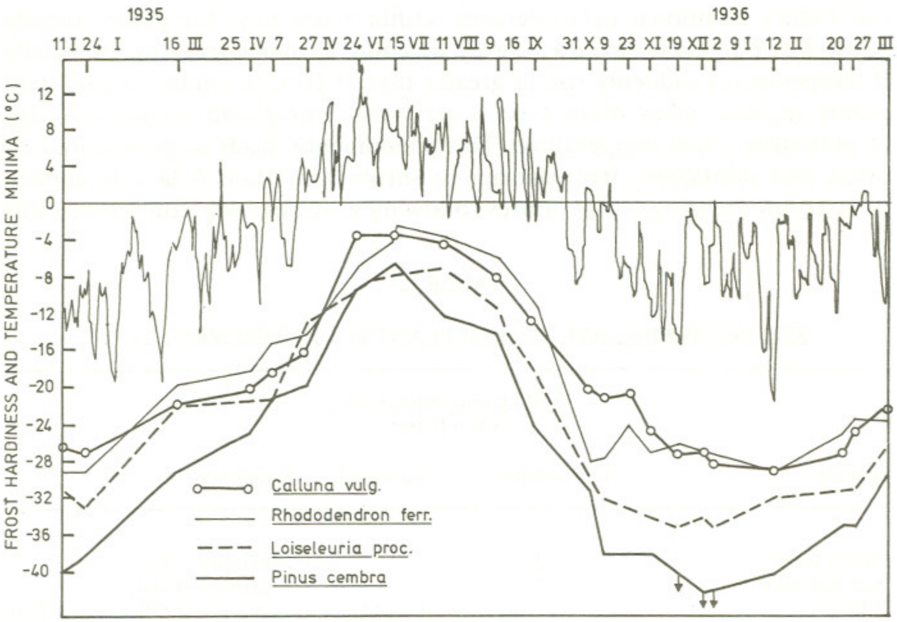

Figure 1.4 Seasonal changes in freezing tolerance of four evergreen species compared with the daily temperature minima. From Levitt (1972)

Cannell (1985) noted that frost hardening is an active metabolic process and that there is abundant evidence that complete hardening of temperate woody species occurs only if the plants receive a sequenced change in conditions from long, warm days ⇒ short, warm days ⇒ short, cool days ⇒ short, frosty days. All steps in the sequence are essential. If the short, warm day (autumn) step is omitted, then the trees do not harden fully. In autumn before the second stage of hardening is induced by decreased daylengths, the difference between ambient temperatures and the hardiness of the shoots (defined by the killing temperatures for that time of the year) can be less than during the summer, indicating an increased vulnerability to frost damage. This is illustrated by Figure 1.7 (Timmis, 1978), which shows that in the absence of the short, warm days, both in spring and autumn while active growth occurs, hardening is insufficient to prevent damage at temperatures as high as −3°C to −10°C. Other examples of this induction of cold hardiness are shown in Figures 1.8 and 1.9.

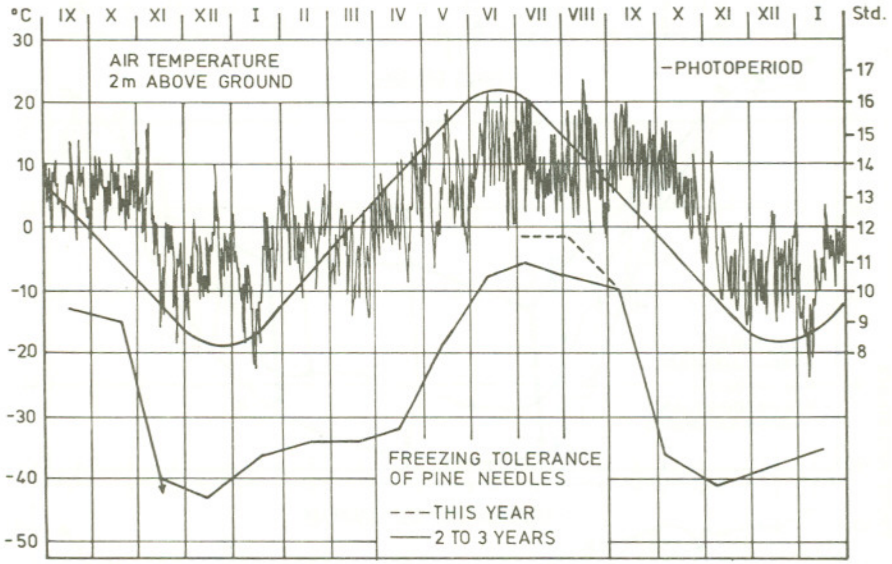

Figure 1.5 Seasonal changes in air temperature (daily extremes), photoperiod (upper curve), and freezing tolerance (lower curve) of pine needles, from September 1965 to January 1967. From Levitt (1972)

Though the hardening sequence described by Cannell (1985) needs to be met both in the correct order and for the appropriate minimum length of time, there is some evidence that acclimation can be achieved in the early autumn. Simonovitch (1982) noted that, for black locust (*Robinia pseudoacacia*) growing at about 45°N latitude, the triggering effects of cool night temperatures or shortening daylengths are completed by mid-September; these effects are instrumental in promoting cessation of growth, leaf senescence, and the migration of nutrients and metabolites needed for the final process of bark cell hardening. Over a 15-year period, these trees attained winter hardiness of bark tissues at almost the same time each year, despite the occurrence in some years of moderately warm conditions. Simonovitch et al. (1975) suggested that an endogenous clock mechanism in bark cells drives the hardening reaction to completion in the autumn, to a considerable extent irrespective of light or low temperatures. Many of the black locust bark cells that were maintained for 5 weeks in the dark at 10°C were able to survive immersion in liquid nitrogen, indicating that extreme hardiness was attained (Figure 1.10). Under normal conditions, these trees do not reach total tolerance to liquid nitrogen by mid-October.

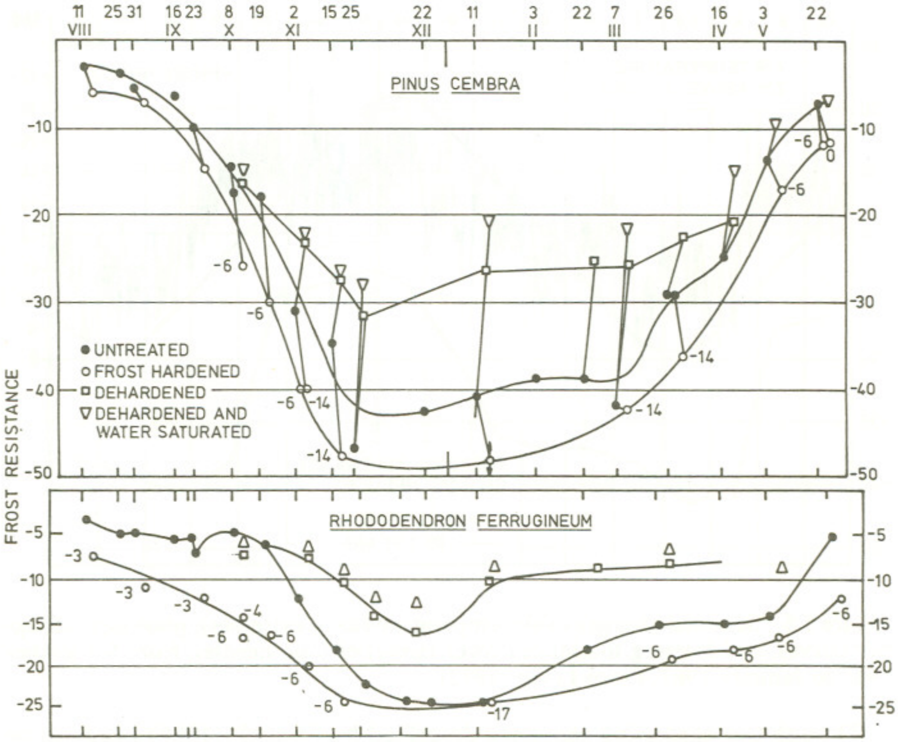

Figure 1.6 Seasonal course of the *actual* frost resistance in the habitat, the *potential* resistance after cold hardening, and the *minimal* resistance after artificial dehardening of leaves of *Pinus cembra* and *Rhododendron ferrugineum* from the alpine timber line in Europe. The difference between minimal and potential frost resistance is a measure of the degree to which the state of hardening can be influenced by weather conditions. From Larcher and Bauer (1981)

In terms of potential acute temperature drop following a nuclear war, severe damage to Northern Hemisphere temperate forest trees would be likely if this drop occurred before September; however, later in the autumn, the most northerly forested ecosystems of the boreal regions might be either already winter hardened or could continue to harden, even as smoke- and dust-induced darkness occurred. On admittedly limited data, it can be suggested that if a nuclear war-induced climatic disturbance commenced in mid-September, then forests in eastern North America and Europe north of 50°N latitude would already be winter acclimated. Likewise, if an acute, extreme temperature excursion commenced in mid-October, forests above

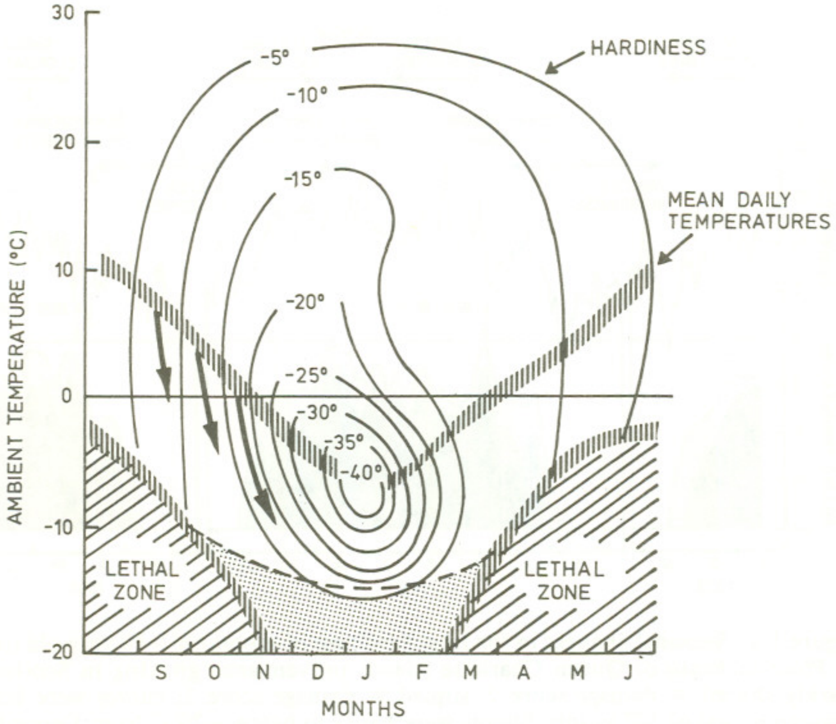

Figure 1.7 Relation between seasonal changes in ambient air temperature and development of hardiness. If premature cooling occurs in September–October, before hardening has developed fully, then exposure to −10°C to −20°C can be lethal. Adapted from Timmis (1978)

45°N would be acclimated; those north of 40°N would be well on their way to acclimation and might be able to complete it, thus avoiding frost damage, so long as temperatures did not drop immediately to lows of −20°C to −40°C.

Though northern temperate trees, such as oak, black locust, spruce, and beech, are frost hardened in a sequence which involves a daylength or photoperiod trigger, not all woody species are initiated in this way. Eucalyptes and other woody angiosperm genera of the Southern Hemisphere have evolved frost tolerance mechanisms to survive brief and occasional frost (down to about −8°C to −16°C) and resume growth within a few days of warm weather recurring (Paton, 1978, 1982, and unpublished data). The photoperiodic insensitivity of *Eucalyptus* is notable for the rapidity with which hardening or dehardening can occur, compared with Northern Hemi-

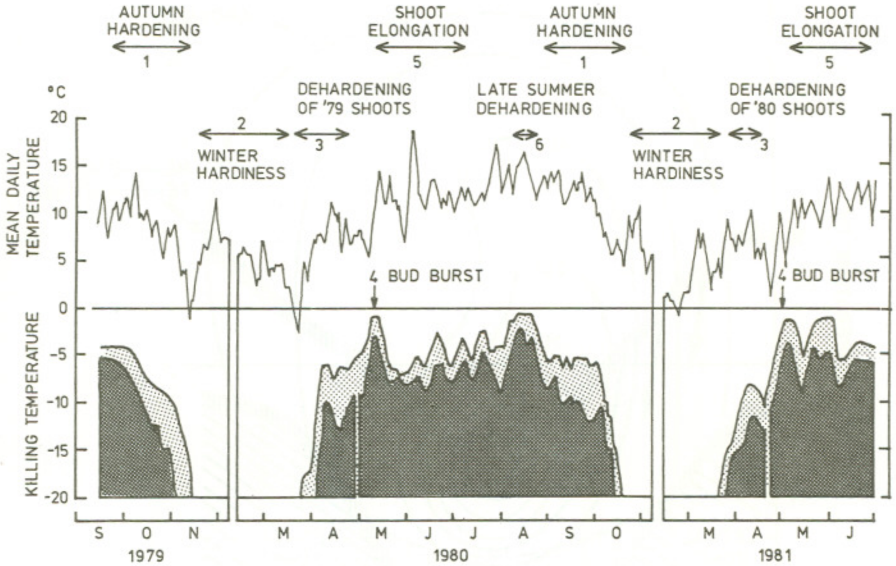

Figure 1.8 Seasonal changes in the frost hardiness of shoots on 7–10 year-old trees of *Picea sitchensis* of Queen Charlotte Islands provenvance growing in Scotland. Darkly shaded = damage score 2; stipled = damage score 1; curves were fitted through a total of 302 points. Shoots were hardy to below −20°C from December to February. Mean daily temperatures have been smoothed by taking 3-day moving means. From Cannell and Sheppard (1982)

sphere trees. They have not evolved either the deep supercooling mechanism, which would allow them to tolerate to −40°C, or the dehydration freezing tolerance mechanism, which would allow even greater cold tolerances. Since *Eucalyptus* is very widely planted in many parts of the world, frost tolerance is a factor to be considered. For example, large plantations of *E. viminalis* were killed in southern U.S.S.R. in 1950 when temperatures dropped to −13°C for several days. In the 1970s, severe frost damage occurred in Northern California and in Brazil.

The geographic distributions of species, genera, and families are at least partially determined by minimum temperatures (Yoshie and Sakai, 1982); woody plants from different geographic locations (and climates) exhibit large and gradual (clinal) differences in freezing resistance. Oohata and Sakai (1982) reported data for winter hardiness of 48 species of pine (*Pinus*) from a wide range of latitudes and for 9 species of the subgenus *Strobus*. Several species were uninjured at −80°C while others, such as *Pinus caribaea*, were damaged at temperatures below −9°C, and *P. leiophylla* and *P. lawsonii* at

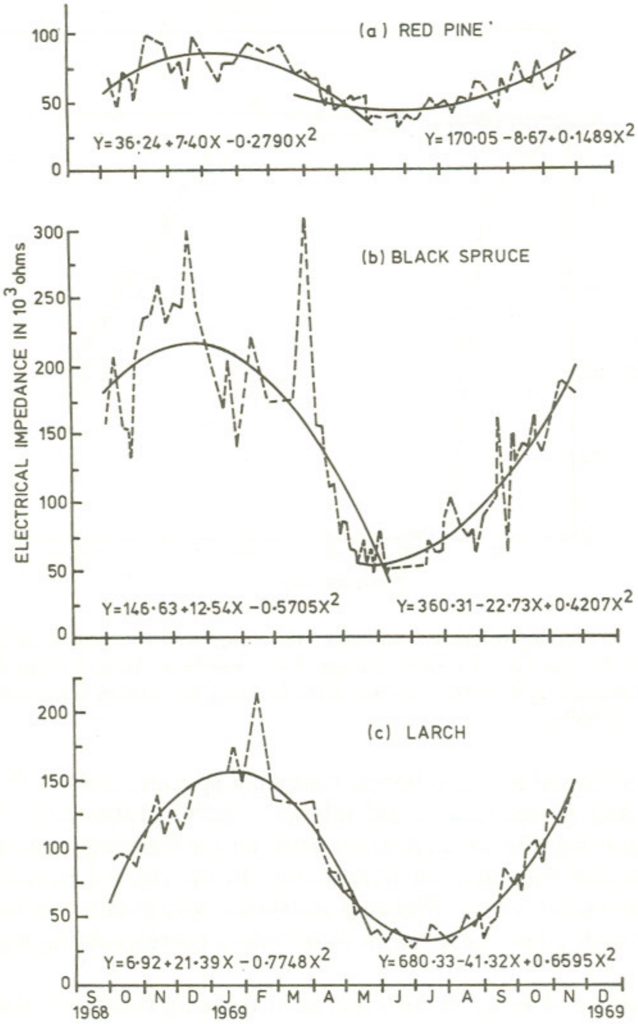

Figure 1.9 Electrical impedance trends for (a) red pine, (b) black spruce, and (c) larch. The electrical impedance increased gradually during October and November in the pines and rapidly in the other species. It remained relatively unchanged during the winter months. In April and May, the impedance decreased gradually in the pines and drastically in the other species, to a minimum. In August, the impedance started to increase again. The two second-degree curves were calculated from the October 1968–July 1969 and June–November 1969 measurements. The curves indicate the trends, and the measured data demonstrate the variations that were encountered from one week to the next. The reading at each date is based on an average of five trees, with two measurements per tree. From Glerum (1973)

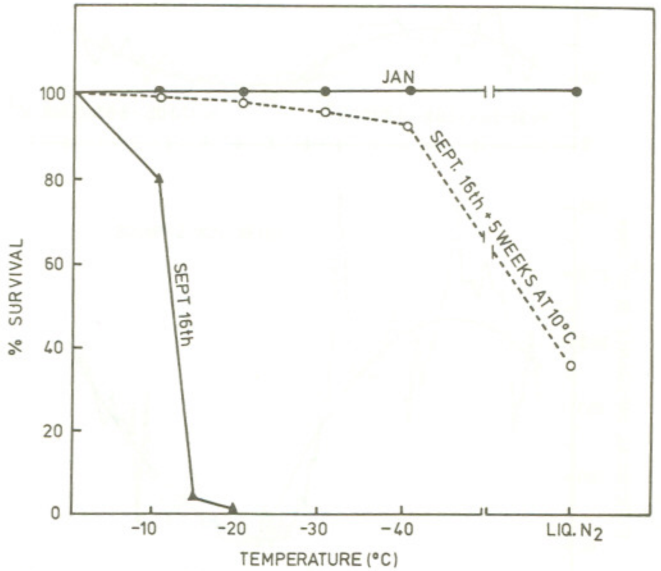

Figure 1.10 Freezing tolerance of bark of sections of the trunk of black locust tree on Sept. 16; on Oct. 17 after storage for 5 weeks at 10°C in the dark; and in January; measured in terms of survival after freezing to various temperatures. From Siminovitch (1982)

– 8°C. Some boreal and sub-boreal Canadian species, such as *P. banksiana*, *P. strobus* and *P. resinosa*, could tolerate – 80°C (Table 1.6). Figure 1.11 shows a highly significant correlation between the freezing resistance of each pine species and the mean air temperature in the coldest month within the natural distribution range. Freezing resistance was greatest in these species from areas with a low mean warm index and a corresponding high negative cold index.

Intraspecific and ecotypic differences in freezing resistance and in timing of cold hardening in the autumn also occur. Northern populations harden earlier than those from southern and coastal regions (Smithberg and Weiser, 1968). These facts suggest that winter minimal temperatures and frost intensity are important selective factors in species adaptations to cold climates.

Differences in life form allow for differences in freezing resistance, as demonstrated by Yoshie and Sakai (1982) (Table 1.7). They found that the hardiest winter buds are the woody shrubs and trees with the over-wintering buds located well above the ground (phanerophytes). Subterranean organs of hemicryptophytes, which have buds at the soil surface, are much hardier

TABLE 1.6

FREEZING RESISTANCES IN PINUS SPP.[a]

Pinus species		Mean Warmth Index (°C/month)	Mean Cold Index (°C/month)	Mean Air Temp. of Coldest Month (°C)	Freezing Resistance (°C)
1. SUBGENUS STROBUS					
SUBSECT.:					
Cembrae	P. koraiensis	43	-78	-15	-70
	P. pumila	20	-116	-18	-70[b]
	P. cembra	24	-53	-7	-70[b]
Strobi	P. strobus	62	-41	-7	-80[b]
	P. monticola	47	-21	-1	-80[b]
	P. ayacahuite	95	0	10	-15
	P. peuce	51	-35	-6	-40
	P. griffithii	71	-17	-2	-35
Cembroides	P. cembroides	113	-1	8	-12
Gerardianae	P. bungeana	81	-34	-7	-30
2. SUBGENUS PINUS					
SUBSECT.:					
Leiophyllae	P. leiophylla	105	0	10	-8
Canarienses	P. canariensis	57	-1	7	-22
Sylvestres	P. resinosa	55	-52	-9	-80[b]
	P. nigra	81	-11	1	-40
	P. mugo	44	-27	-4	-70[b]
	P. densiflora	86	-15	0	-60
	P. insularis	179	0	15	-7
	P. merkusii	211	0	20	-10
Australes	P. palstris	156	0	9	-18
	P. taeda	147	-1	8	-23
	P. elliottii	165	0	10	-22
	P. caribaea	221	0	20	-9
Ponderosae	P. ponderosa	60	-32	-4	-26
	P. engelmannii	120	0	8	-15
	P. michoacana	134	0	12	-10
	P. lawsonii	155	0	14	-8
Contortae	P. banksiana	38	-100	-20	-80[b]
	P. contorta	30	-51	-7	-75[b]
	P. clausa	195	0	14	-14
Oocarpae	P. radiata	92	0	9	-13
	P. patula	100	0	9	-15
	P. greggii	114	0	8	-15

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[a] Data from Oohata and Sakai (1982).

[b] Uninjured at the lowest temperature indicated.

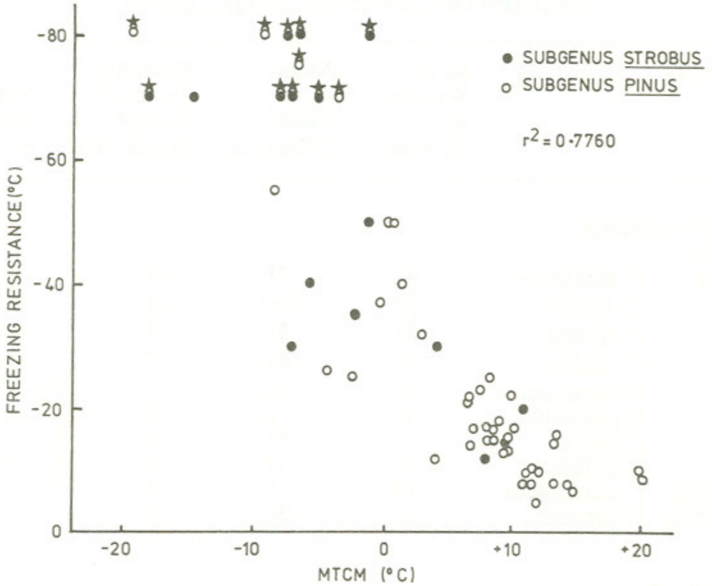

Figure 1.11 Relation between freezing resistance of each pine species and mean air temperature in the coldest month (MTCM) at the natural distribution range. Star = uninjured at the lowest temperature. From Oohata and Sakai (1982)

in those plants growing at the edge of forests than in plants well within the forest. Differences in hardiness of subterranean organs among different life forms and microhabitats were found to be much greater in Japan than in Scandinavia (Till, 1956). Yoshie and Sakai (1982) accounted for this by the much more severe winter experienced at Hokkaido than at Gottingen.

1.2.1.4 Supercooling and Dehydration—Mechanisms of Frost Hardening

Plant structures that can survive extreme low winter temperatures do so by two primary mechanisms that involve either tolerating or avoiding ice formation (Levitt, 1980). Cells that survive by tolerance dehydrate intracellularly in the winter, and extracellular water freezes without injuring the living cellular constituents. In mid-winter, such plant tissue is extremely hardy, and can withstand immersion in liquid nitrogen (– 196°C) without injury (Sakai, 1960). In contrast, plant cells that survive by avoidance of ice formation do so by supercooling of the tissues. A supercooled solution remains liquid below its equilibrium freezing point (Becwar and Burke, 1982) and is said to be deep supercooled when it remains liquid to the low temperature limit for supercooling, the homogeneous nucleation temperature for the solution. This is about −40°C for plant solutions and sets the lower limit on winter hardiness in supercooling plants.

Becwar and Burke (1982) noted that in terms of ecological significance, most eastern deciduous forest trees of North America have tissues that can supercool. Their northern distribution limit closely parallels the −40°C average annual minimum temperature isotherm for North America, at which temperature tissues freeze and are injured. In contrast, boreal forest trees of more northerly latitudes, where −40°C temperatures occur regularly, survive freezing by tolerating the ice that forms, a mechanism which is not limited by extreme low temperatures. Much of the ice damage problem is avoided by dehydration of tissues. Becwar and Burke (1982) reviewed literature on the mid-winter hardiness of timberline or treeline species of Europe, Japan, and America. Treeline minimum average temperatures were reported to be consistently between −40°C and −43°C.

It is apparent from this that if a nuclear war-induced climatic disturbance were to occur after winter hardening, even the worst scenarios would not likely cause death of the northerly boreal forest species, especially coniferous ones with an ice-tolerance dehydration system. However, if winter temperatures went much below −40°C in areas where supercooling predominates (e.g., in the eastern deciduous forests of the United States, at the higher altitudes in the Rocky Mountains, and in the mountains of northern and central Europe), then those woody species could be severely harmed or fatally damaged. Even in that case, however, the cambial cells at the base of the trunk are often best protected by soil and thicker bark, so that coppicing or adventitious shoots might be produced at the base of surviving trees, allowing eventual recovery.

The possibility of a nuclear war pushing temperatures below the tolerance limits of timberline species in either winter or summer seems a real one. The timberline is at about 3400 m over a very wide and heterogeneous area. Becwar and Burke (1982) suggested that the environment on passing through the timberline changes gradually, but the plants respond discontinuously to the gradient of worsening environmental factors. That is, a small change in a single environmental factor can cause severe plant stress damage. Such responses to temperature stresses are well known. For example, Engleman spruce twigs survive prolonged winter exposure at −35°C, but are injured after brief exposure to −45°C (Becwar et al., 1981); wheat leaves survive prolonged exposure to −1°C, but are killed after brief exposure to −17°C (Gusta et al., 1975).

The differential distribution of the two major mechanisms of freezing tolerance are illustrated for North America in Figure 1.12. Rajashekar and Burke (1978) pointed out that conifers and deciduous species of the northern boreal forest cover large areas of Canada, Alaska, and Northern Eurasia,

TABLE 1.7

FREEZING RESISTANCE OF DORMANT BUDS, LEAVES, RHIZOMES, AND ROOTS[a]

Species	Freezing Resistance (°C)			
	Dormant Buds	Leaves	Rhizomes	Roots
1. Phanerophytes				
Quercus mongolica var. *grosseserrata*	-20			
Juglans ailanthifolia	-30			
Carpinus cordata	-17			
Cornus controversa	-25			
Cercidiphyllum japonicum	-25			
Fraxinus sp.	-25			
Tilia maximowicziana	-30			
Magnolia kobus var. *borealis*	-25			
Sorbus alnifolia	-25			
Acer mono var. *mayrii*	-15			
Acer palmatum var. *amoenum*	-25			
Hydrangea petiolaris	-20			
2. Chamaephytes (Forest Floor)				
Daphne pseudo-mezereum var. *jezoensis*	-20	-7		-5[b]
Pachysandra terminalis	-20	-20	-7	-5[b]
Euonymus fortunei var. *radicans*	-20	-20		-10
Lycopodium obscurum	-20	-20		
Lycopodium serratum var. *serratum*	-20	-15, -20		-10
Pyrola secunda	-17	-15	-5	
Pyrola incarnata	-15	-15	-7	
Pyrola alpina	-15	-12	-5	
Pyrola renifolia	-12	-12	-5	
Oxalis acetosella	-12	-7	-5	-5
Tripterospermum japonicum	-15	-5		
3. Chamaephytes (Forest Margin)				
Lycopodium clavatum var. *nipponicum*	-25	-15, -25		

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[a] Data from Yoshie and Sakai (1982).

[b] Injured at indicated temperature.

TABLE 1.7 continued.

Species	Dormant Buds	Freezing Resistance (°C) Leaves	 Rhizomes	 Roots
4. HEMICRYPTOPHYTES (Forest Floor)				
Tiarella polyphylla	-10	-7	-10	-5
Agrimonia pilosa	-10		-7	-5[b]
Maianthemum dilatatum	-10		-5	-5
Chamaele decumbens	-5[b]		-5[b]	-5[b]
Sanicula chinensis	-5		-5	-5[b]
5. HEMICRYPTOPHYTES (Forest Margin)				
Oenothera sp.	-12	-12		-7, -12
Miscanthus sinensis	-7		-7	-7
Filipendula sp.	-12		-10	-5[b]
Solidago virga-aurea	-12		-10	-10
Plantago asiatica	-10		-10	-10
Trifolium pratense	-5		-5[b]	-5[b]
Petasites japonicus var. *giganteus*	-5		-5[b]	-5[b]
Leibnitzia anandria	-7		-7	-5
Artemisia montana	-10		-7	-7
Artemisia japonica	-12		-12	-12
Anaphalis margaritacea	-7		-7	-7
Sanguisorba tenuifolia var. *alba*	-7		-7	-5
Lysimachia vulgalis var. *davurica*	-7		-7	-7
6. GEOPHYTES (Forest Floor)				
Phryma leptostachya var. *asiatica*	-5[b]		-5[b]	-5[b]
Cacalia delphiniifolia	-5[b]		-5[b]	-5[b]
Cacalia auriculata var. *kamtschatica*	-5[b]		-5[b]	-5[b]
Sceptridium multifidum var. *robustum*	-5	-17	-5[b]	-5[b]
Lilium cordatum var. *glehnii*	-5[b]		-5[b] (bulb)	-5[b]
Adoxa moschatellina	-5[b]		-5[b]	-5[b]

Figure 1.12 Hardiness zone map of North America. The map is divided into three hardiness regions. Region A has average annual minimums below – 40°C and extreme minimums much lower. Region B has finite probability of – 40°C minimums. Region C has very little probability of – 40°C. Deep undercooling trees only occur in the very southern parts of region A; however, they dominate the forests in regions B and C. Adapted from Rajashekar and Burke (1978)

and do not deep undercool. Most deciduous species native to the eastern deciduous forest, which covers the eastern half of the U.S.A., do deep undercool. Such deep undercooling trees dominate the forests in regions B and C, where the probability of temperatures of −40°C occurring is low. Hence, we estimate that should a major nuclear war cause winter temperatures to plunge below −40°C for extended periods or below −50°C for brief periods, then the native species would simply not be able to survive. If even temperatures of −20°C were reached in latitudes below about 34°N for the United States, the native vegetation would not be adapted to survive, except for alpine species.

1.2.2. Responses of Plants to Low Light

The acute phase of post-nuclear war climatic disturbances outlined in Volume I could be sufficiently severe that in Northern mid-latitudes, light could be reduced by 90% or more. Even as conditions subsequently ameliorated during a chronic period, light reductions by 5% to 10% could occur. This decreased light would be accompanied by lower temperatures. Since productivity of green plants, the essential primary producers for all natural and agricultural ecosystems, is achieved through light-mediated photosynthesis, significant reduction of light would cause a reduction in photosynthesis and possibly alter other related physiological processes.

The more severe temperature excursions of the acute phase following a summer nuclear war could lead to a sudden onset of temperatures well below freezing. Since it is at just such a stage in the post-war climate that accompanying light levels would be minimal, it is important to recognize for terrestrial ecosystems that it is the low temperatures which would have the predominant acute period effects. If grasslands and temperate forests were subject to subfreezing temperatures, it would matter little with regard to vegetation whether darkness or full sunlight prevailed. For many animals however, the intensity of light and number of daylight hours would be important to finding food.

In aquatic systems, light, rather than temperature, determines productivity rates and reduced light levels would cause an almost linear reduction in photosynthesis. If low light were to be prolonged, the normal trophic interactions and successional and seasonal patterns of species replacements would be severely altered. Light would become the dominant controlling factor.

1.2.2.1. Plant Responses to Prolonged Light Reductions

Much research over the past 50 years has demonstrated the great difference among and within species in their ability to grow in deep shade versus in open habitats exposed to direct solar illumination. Many plants, especially forest species, normally grow under deeply shaded conditions, with light intensities of 10% to ≤1% of that reaching the upper canopy. Similarly, in tall grasslands, low growing species and the basal leaves of grasses typically occur at very low light intensities.

Grime (1979) suggested that shade is only important in climatic regimes conducive to the development of dense canopies. In normally functioning ecosystems, shade frequently coincides with the high temperatures and humidities of tropical and sub-tropical climates year-round, or temperate regions during summer, and with conditions of mineral nutrient depletion associated with the development of a large biomass. It is likely, therefore, that many plant characteristics described as shade adaptations are, in fact, more related to simultaneous tolerance to shade, high temperatures, and mineral nutrient stress. This being the case, a low light intensity accompanied by low temperatures imposed as a consequence of a nuclear war would probably present a novel climatic event.

Few plant species are able to survive continuous low light conditions because of limitations in photosynthesis. Beneath dense tree canopies, especially canopies composed of evergreen species, herbaceous species are sparse, and, consequently, vertical light gradients are less pronounced near the forest floor. Ability to compete for light under such circumstances is likely to be of secondary importance compared with an ability to tolerate shade.

The effects of shade upon growth rate and morphology of plants have been examined by many researchers (e.g., Burns, 1923; Blackman and Rutter, 1948; Grime and Jeffery, 1965; Loach, 1970). In general, plants in shaded conditions produce less dry matter, develop larger internodes and petioles, and produce larger, thinner leaves. However, species differ considerably in their responses. Loach (1970) and others have shown that greatest plasticity (i.e., ability to alter leaf shape and size) occurs in those species for which deep shade is an unusual or transitory occurrence, whereas those species or populations which occur in continuous deep shade do not make such leaf morphological adjustments.

Grime (1966) and Grime and Hunt (1975) found in comparative studies that shade-tolerant herbs and tree seedlings show a consistent, slow growth rate, which is genetically determined (Mahmoud and Grime, 1974). Shade-tolerant plants are better able to exploit shaded locations by having rapid photosynthetic fixation of carbon at low light intensities, coupled with lower respiratory rates; plants that require full sunlight respire more rapidly, but photosynthesize at the same or lower rate than the shade-tolerant species. If a nuclear war caused reduced light intensities for prolonged periods, the shade-tolerant plants would be at an advantage compared to those species from open habitats. However, this general statement needs qualification, since low light would be accompanied by low temperatures, which would reduce respiration rates. Nevertheless, the advantage of shade-tolerant species would probably remain, if they and shade-intolerant species are equally metabolically slowed by lowered temperatures.

An unresolved issue for botanists is how long species could tolerate low light levels and which species might prevail. Very little literature exists on plant survival in the dark. The study by Hutchinson (1967) emphasized the remarkable tolerance of some species to this unnatural condition. He examined the comparative ability of 25 native species from the U.K. to survive in complete darkness and considered the effects of soil nutrition, air temperature, and the influence of seed size on survivorship. Survivorship was also examined relative to the habitat in which the species normally occur. These included open habitats, short grasslands, tall herb and grassland sites, and woodlands. Species varied in seed weight by up to 70-fold. Data are given in Tables 1.8 and 1.9.

On nutrient-poor soil at low temperatures (5°C–7°C), longevity was greatest. The woodland grass *Deschampsia flexuosa* survived in the dark for 280 days as seedlings, after being grown in the light for 20 days, and for 252 days when initially grown for 40 days in the light. On nutrient-sufficient loam, longevity was less. In contrast, species from open and lightly shaded habitats survived about 50 to 60 days under the same circumstances at 5°C to 7 °C. This indicates that even very young seedlings might be able to survive low temperatures and low light for a number of months. However, higher temperatures (15°C–17°C) were found to result in decreased survivorship, presumably because of higher metabolic activity and concomitant higher respiratory loss.

Based on this limited data base, woodland species would appear be at a distinct advantage in temperate regions. The general response within a habitat category is that the slower the growth, the longer the survival. Plants on nutrient-poor soils survive longer than on nutrient-sufficient soils. This could have implications for agricultural crops, which would normally be planted on fertile soils. Species from tall herb and tall grassland communities are intermediate between the woodland and open community types in their longevity, and grasses are generally more persistent than dicotyledons. Particularly on infertile acidic soils, seedlings were found to be capable of remarkable persistence and resumed normal healthy growth when light conditions improved. This could be relevant to the change from acute to the chronic climatic phase after a nuclear war.

In tropical regions, the severity of any climatic change as a result of a nuclear exchange is anticipated to be much less than in the mid-latitudes of the Northern Hemisphere. Deep shade as a result of reduced sunlight is unlikely. However, since the ground flora of evergreen tropical forest are adapted to life in uniform deep shade, no effect from light reductions would

TABLE 1.8

LONGEVITY OF SEEDLINGS GROWN IN DARKNESS[a], [b]

Species	Acidic Soil			Calcareous Soil			
	Pre-treatment period		R.G.R.[c]	Pre-treatment period		R.G.R.[c]	Mean survival time
	0 days	30 days		0 days	30 days		
Anagallis arvensis	28	28[d]	0.56	18	18	0.60	23
Arabidopsis thaliana	40[d]	43	0.17	30	43	0.63	39
Hordeum murinum	44	39	0.55	44	43	0.52	42
Lotus corniculatus	45	48	0.31	35[d]	48	0.39	44
Scabiosa columbaria	45	36[d]	0.19	39[d]	31[d]	0.33	38
Thlaspi arvense	24	22	0.37	25[d]	17	0.56	22
Ulex europaeus	49[d]	47	0.22	64	38	0.12	48
Brachypodium pinnatum	54[d]	42	0.29	28	49	0.41	43
Utrica dioica	44	38	0.41	39[d]	35	0.36	39
Zerna erecta	44	68	0.21	45	75	0.25	58
Brachypodium syllvaticum	104	67	0.24	97	58	0.40	82
Deschampsia caespitosa	55[d]	58	0.81	62[d]	59	0.60	57
Geum urbanum	50	70	0.50	48	57	0.63	56
Hypericum hirsutum	45	64	0.47	40	44	0.57	49

[a] Data from Hutchinson (1967).

[b] The longevity (days) of seedlings of fourteen species grown on two contrasting soils in continuous darkness after being grown in the light for 0 or 30 days at 15°C. Longevity is given as the time from commencement of dark treatment until 100% death occurred. The mean survival time of each species is also given as the mean of its longevity on both soils and after both pre-treatment periods. The relative growth rates were measured over the first 28 days from germination. The soils used were a phosphorus-deficient colluvial soil, pH 5.8, from exposed Old Red Sandstone ledges at Jedburgh, Roxburghshire; and a brown-calcareous soil, pH 7.3, from the North Downs, which was both phosphorus and nitrogen deficient.

[c] Relative growth rate. [d] Seedlings attacked by fungi.

be likely, even with a decrease by 50%. Unfortunately, the shade might be accompanied by low temperatures which would be very damaging to tropical ecosystems (see Chapter 2).

1.2.2.2. Effects of Shade on Photosynthesis

Many species and ecosystems have a fine balance between net primary production and the needs for food reserves to last through seasonally cold winters or dry seasons; there is a similar balance between net primary production and the high respiratory rates in tropical and sub-tropical ecosystems. Ecosystem maintenance depends directly on adequate photosynthesis which, in turn, depends upon adequate light, both in quantity and quality. Disruption of photosynthesis by attenuation of incident sunlight, as is possible during an acute climatic disturbance phase after a nuclear war, would have serious consequences that would propagate through foodchains, including those upon which humans depend. Primary production would be reduced roughly in proportion to the degree of light attenuation, assuming the plants were actively growing, and assuming, perhaps unrealistically, that the plants remained otherwise undamaged.

The relationship between increasing incident light (quantum flux density) and rate of photosynthesis is illustrated for two ecotypes of the European goldenrod (*Solidago virgaurea*) (Figure 1.13). One ecotype was collected from a sunny, open field and the other from a shaded woodland (Björkman and Holmgren, 1963). Photosynthetic response increased linearly with increasing light intensities at low levels. The shade-tolerant ecotype was able to photosynthesize more rapidly than the sun ecotype at lower flux densities. However, the sun ecotype was able to maintain the linear relationship at higher light intensities than the shade-tolerant ecotype. Thus, at fluxes above 500 $\mu E \cdot m^2 \cdot sec^{-1}$, it photosynthesized more rapidly. Full sunlight is well above photosynthetic saturation level of an isolated ecotype, largely because of restrictions in quantity of chlorophyll available for interception. For shade-tolerant ecotypes, light intensity could be decreased further before direct reductions in photosynthesis would ensue.

The photosynthetic rate responses to light intensity also differs among species (Figure 1.14) in their ability to photosynthesize at high light intensity and in their ability to adapt (Björkman, 1981). Those that cannot adapt or have a limited ability would be at a disadvantage if significant light attenuation followed a major nuclear war. Adaptation would not be immediate, perhaps requiring a few weeks. A key factor then, would be how long an acute phase light attenuation would last. Further, synergisms with accompanying reduced temperatures are largely unknown.

Berry (1985) suggested that about 3% of total incident sunlight energy is stored in the form of chemical bonds in plants under optimal conditions

TABLE 1.9

LONGEVITY OF SEEDLINGS GROWN IN DARKNESS ON DIFFERENT SOILS[a,b]

A. At 5°C-7°C	Acidic Soil Pre-treatment period		Loam Pre-treatment period		Mean survival time
	20 days	40 days	20 days	40 days	
Betula pubescens	50	100	56	51	64
Erophila verna	Failed		43	100	72[c]
Galium aparine	60	10	74	65	52
Hieracium pilosella	140	146	63	65	108
Koeleria gracilis	233	220	81	220[d]	189
Arrhenatherum elatius	170	197	140	209	179
Betonica officinalis	Failed		230	138	184[c]
Deschampsia flexuosa	281	252	133	240	227
Digitalis purpurea	146	169	75	187	144
Zerna ramosa	190	188	152	210	185

[a] Data from Hutchinson (1967).

[b] Longevity is given as the time (days) from initiation of the dark treatment until 100% seedling death occurred. The seedlings were grown for 20-40 days in the light prior to dark treatment. The mean survival time of each species at each temperature is also given as the mean of its longevity on both soils and after both light treatments. The relative growth rates were measured over the 42 days following germination. The soils used were a fertile loam from Newcastle University Experimental Gardens, pH 5.6, and an alluvial silt from Gosforth, Northumberland, pH 3.8, which was highly infertile and produced symptoms of heavy metal toxicity in several species.

[c] Mean survival time on loam only.

[d] Seedlings attacked by fungi.

TABLE 1.9 continued

B. At 15°C-17°C	Acidic soil			Loam			
	Pre-treatment period		R.G.R.[e]	Pre-treatment period		R.G.R.[e]	Mean survival time
	20 days	40 days		20 days	40 days		
Betula pubescens	50[d]	68	0.43	20[d]	48[d]	0.53	47
Erophila verna	Failed		-	20	33[d]	1.12	27[c]
Galium aparine	43[d]	10	0.08	40[d]	40[d]	0.40	33
Hieracium pilosella	39[d]	40	0.23	18	16[d]	0.83	28
Koeleria gracilis	63[d]	68	0.24	38[d]	40[d]	0.89	52
Arrhenatherum elatius	48	46	0.08	40[d]	57[d]	0.73	48[c]
Betonica officinalis	Failed		-	64[d]	74[d]	0.63	69[c]
Deschampsia flexuosa	90[d]	89[d]	0.16	42[d]	64[d]	0.74	71
Digitalis purpurea	57[d]	28[d]	0.08	33[d]	65[d]	0.70	46
Zerna ramosa	50[d]	65[d]	0.14	38[d]	50[d]	0.54	52

[e] Relative growth rate.

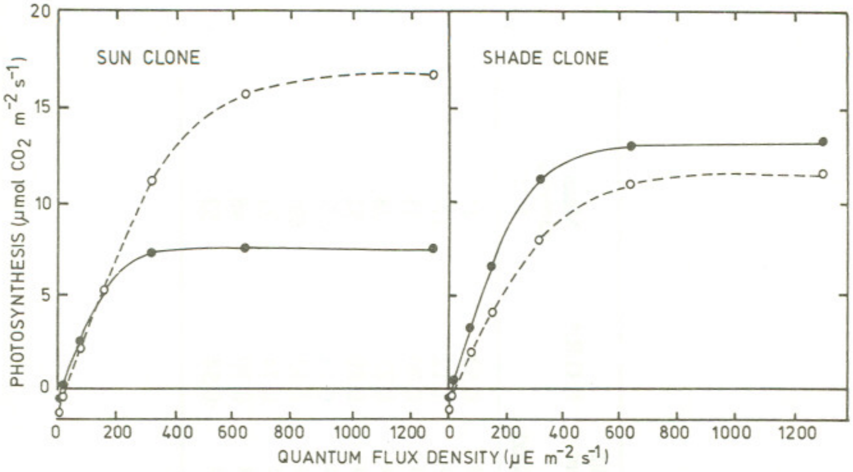

Figure 1.13 Rate of photosynthesis as a function of incident quantum flux density in clones of sun and shade ecotypes of *Salidago virgaurea*, grown at 6.6 (•) and 33.1 (o) μE m^{-2} day^{-1}. Measurements were made at 320 μbar O_2, and a leaf temperature of 22°C. From Björkman (1981)

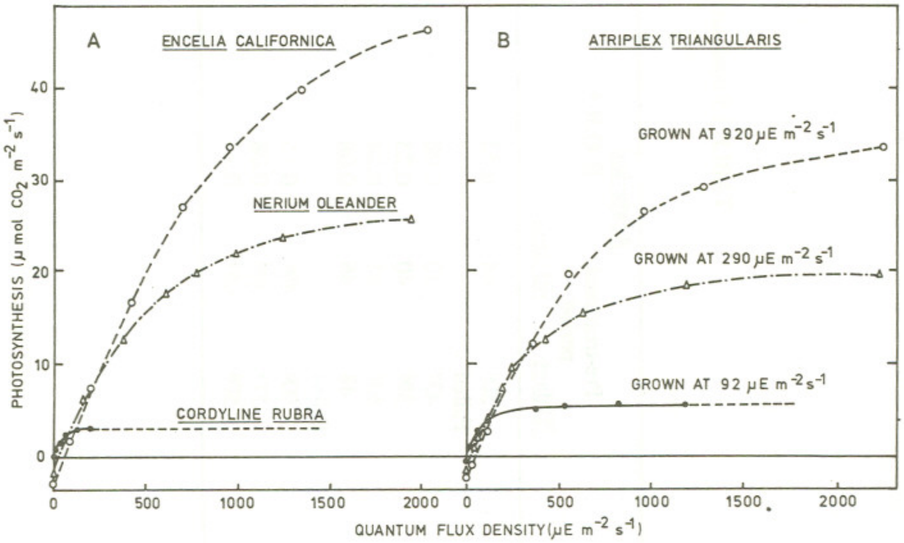

Figure 1.14 Rate of net photosynthesis as a function of incident quantum flux density (400–700 nm) for A: the sun species *Encelia californica* and *Nerium oleander rubra*, grown under natural daylight (approx. 40 μE m^{-2} day^{-1}), and the shade species *Cordyline rubra* grown in its native rain forest habitat (0.3 μE m^{-2} day^{-1}); and B: the sun species *Atriplex triangularis*, grown under three different light intensity regimes. All measurements were made in air of normal CO_2 and O_2 partial pressures and a leaf temperature of 25°C or 30°C. From Björkman (1981)

and that the photosynthetic efficiency is reduced at increasing light levels approaching saturation. Net primary production rates are always lower, however, than photosynthetic carbon fixation rates because some of the captured energy is needed to provide maintenance for the plants or to offset energy losses to grazing by animals, pathogens, and other factors.

Since the linear relationship between absorbed light and photosynthesis only holds at lower light intensities, it is important to consider how much light is needed for saturation in natural vegetation stands. Studies have been done on individual leaves and on canopies *in situ*. Light interception is a function of spatial arrangements of many overlapping leaves in a forest or a grassland. Some light is transmitted through leaves, while other is reflected or absorbed. As the light intensity decreases with depth in the canopy, the characteristics of the leaves change, such that they require less light for saturation (Figure 1.15). The light response of the whole forest canopy is

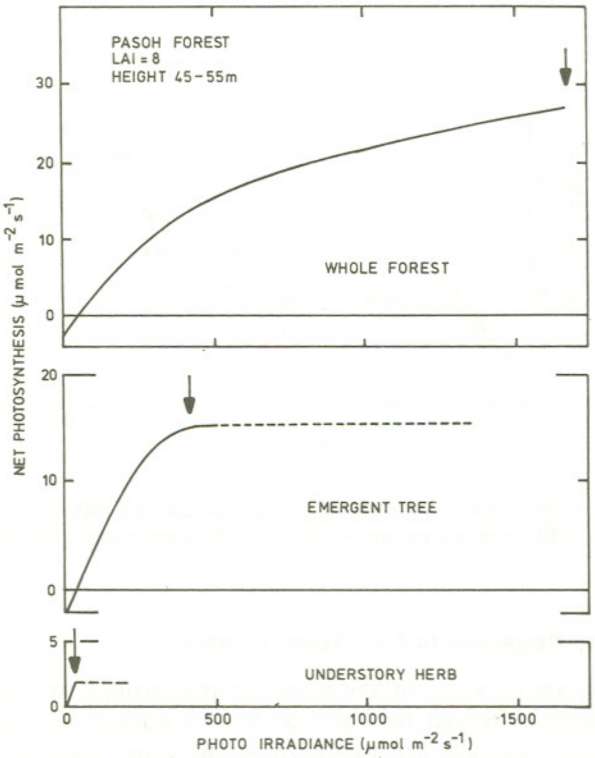

Figure 1.15 Effect of canopy depth and light saturation on photosynthesis as determined for a whole forest, for individual emergent trees, and for understory herbs. From Harwell (1984)

a sum of the responses of all the leaves to the light levels that penetrate to their micro-habitats (Berry and Downton,1982). The net result is that it takes much higher light to saturate the entire canopy than for any single component (Figure 1.15).

Leaf area index (LAI; i.e., the amount of leaf surface area present per unit area of ground) is also an important factor. LAI is a composite of all species and takes account of overlapping leaves; it is determined by the phenological (developmental-seasonal) stage and is affected by limitations of water and nutrients. In water- or nutrient-deficient ecosystems, fewer leaves are formed; thus, the leaf area index is reduced, and the maximum ecosystem interception of light for photosynthesis is reduced. In these areas, much of the incident sunlight strikes the soil and is not available for photosynthesis. In such situations, a reduction in light to the individual plant would directly reduce photosynthesis (Figure 1.16).

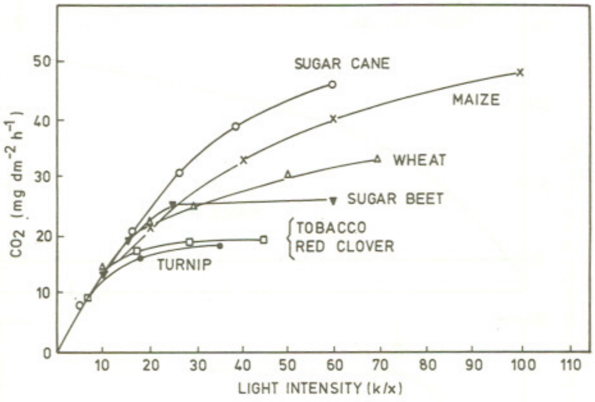

Figure 1.16 Light response curves of photosynthesis for different crop plants. Attached leaves, CO_2 concentration = 0.03 vol. %; temperature = 20°C. From Stoy (1965)

1.2.3 Animal Responses to Low Temperatures [1]

The responses of some of the major animal groups to low temperature stress and their potential for survival after a nuclear war are considered in this section. Animals are subjected to the same kinds of climatic seasonal fluctuations as are plants, and similarly many animals are adapted

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[1] This section prepared by K. Meema.

to cold temperature extremes, which enable them to survive winter conditions in northern latitudes and in alpine areas. Animals exposed to freezing temperatures avoid lethal freezing of body tissues by either behavioral or physiological mechanisms. Some terrestrial insects and frogs, however, are able to allow their body tissues to freeze and thaw with no adverse effects. Animals may be divided into two groups according to their ability of regulate their body temperatures; homeotherms (birds and mammals), which maintain their internal body temperature at a relatively constant value by metabolic processes regardless of environmental temperature fluctuations, and poikilotherms (all other animals), which have body temperatures that vary according to ambient environmental temperatures. It would be expected that homeotherms that are not adapted to cold temperatures would suffer more severely in the event of reduced temperatures following a nuclear war than their poikilothermic counterparts, since they must maintain a high internal temperature. If, however, temperatures dropped below freezing in areas not usually experiencing such temperatures, both groups would be in danger of body tissue freezing.

1.2.3.1 Freezing Tolerance of Terrestrial Insects

Since terrestrial insects of temperate and polar regions must normally survive sub-freezing temperatures, a number of behavioral and physiological responses to these temperatures have developed. Apart from those insects that avoid cold temperatures by migration, two groups of insects that are not injured during their overwintering in either the dormant or diapause stage have evolved mechanisms similar to plants, specifically: 1.) insects which are freeze-sensitive but prevent ice formation in their tissues, and 2.) insects able to tolerate the freezing of their extracellular fluids (e.g., beetles, flies, wasps) (Storey and Storey, 1983). The majority of insects overwinter using the latter strategy.

Freeze-sensitive insects prevent the formation of ice through the use of cryoprotectant (anti-freeze) compounds (e.g., glycerol and sorbitol), which aid in the supercooling of body fluids and elimination of ice nucleation sites in the body (e.g., emptying of the gut contents). Glycerol both lowers the freezing point of tissues and increases supercooling (Cloudsley-Thompson, 1970) and is the most prevalent cryoprotectant. Supercooling temperatures in the larvae of the Canadian hymenopteran *Bracon cephi* were found to vary in direct proportion to the glycerol concentrations (Salt, 1959). The cues for hibernation are important, since these cryoprotectants are produced before hibernation.

The mechanism of freeze tolerance is similar to that of plants and some microorganisms and can be remarkable in its extent. For example, the gall fly larva is able to withstand temperatures of −40°C during winter. The insect is able to control the amount of ice formation and protect the cells from dehydration and osmotic damage (Storey and Storey, 1983). Freeze-tolerant species decrease free cellular water, which would otherwise form lethal ice crystals, by expelling this free water to extracellular spaces or by increasing bound water through the action of cryoprotectants. These cryoprotectants also lower the freezing point of intracellular water and increase osmotic pressure to prevent cellular dehydration (Storey and Storey, 1983). Again, the most common cryoprotectant is glycerol, which is synthesized in response to cooling. Sorbitol, however, is produced in response to temperatures of 5 °C to −8°C, the supercooling point. It is interesting to note that species that are freeze-tolerant in the winter are able to withstand low temperatures in the summer by supercooling to an extent beyond that which occurs in the winter. This implies that freeze-tolerance is a seasonal response, similar to hardening in plants.

1.2.3.2 Freezing Resistance in Freshwater Fishes

Freshwater systems could be expected to cool significantly following a nuclear war, and surface ice could result. Freshwater fish are not in great danger of freezing, as the freezing point of freshwater is nearly 0.5°C above the freezing point of their body fluids (DeVries, 1971). However, in lakes that did freeze to the bottom, fish would be in danger of freezing. Some species can normally avoid freezing by burrowing into the mud at the bottom and overwintering in an inactive state (Nikolsky, 1963). The greatest danger of lowered temperatures for freshwater fish is the decrease in dissolved oxygen content of the water brought on by the complete coverage and formation of surface ice to a considerable depth. Fish not in the inactive, semi-dormant state (i.e., with normal oxygen consumption rates) and some fish with limited oxygen requirements are in danger of suffocation from a reduced oxygen supply. This winter kill frequently occurs during severe winters in lakes that do not normally freeze over.

1.2.3.3 Response of Amphibians to Cold Temperatures

Most amphibians (with the exception of freeze-tolerant terrestrial frogs) avoid freezing temperatures by the behavioral mechanism of burrowing deep into the soil or mud, or they remain at the bottoms of lakes and ponds where the minimum temperature is usually 4°C. Brattstom (1970) suggested that cold may be the factor that restricts certain species to the tropics; this is supported by evidence that amphibian cold-tolerance increases with latitude. Thus, many amphibians in the tropics might not be able to tolerate the chilling associated with the lowered temperatures possible after a nuclear war. Those in temperate climates, which normally have to survive seasonal fluctuations, might not have the instinct, the proper environmental cues, or proper sequence of environmental cues to survive a rapid and substantial decrease in temperature.

Drought conditions would affect the ability of this group to survive, since water loss, respiration, and breeding activity depend on humidity and the availability of surface moisture.

1.2.3.4 Freezing Resistance in Frogs

Terrestrial frogs that hibernate on the land (e.g., *Hyla versicolor*, *H. crucifer*, and *Rana sylvatica* [Schmid, 1982], and *Pseudacris triseriata maculata* [MacArthur and Dandy, 1982]) are the only known vertebrates that can withstand the freezing of extracellular fluid. This freezing appears to occur when the ambient temperature is lowered to approximately −2°C, and the animals are able to survive several days at temperatures as low as −6°C (Storey and Storey, 1984). Tadpoles are reported to survive in frozen shallow waters for several days. During freezing, the extracellular fluids and blood are frozen, and breathing and heartbeat cease. Though tissues rely on degradation of endogenous substrates locally for cellular energy, the anoxia tolerance of tissues, particularly those in the brain, probably determines the length of time in the freezing state (Storey and Storey, 1984). The accumulation of metabolic wastes and end products must also be tolerated.

Both glycerol and glucose have been found to act as cryoprotectants in the tissues and urine of these frogs. Interestingly, the rapid synthesis of these cryoprotectants is in direct response to exposure to subzero temperatures, in contrast to the production of cryoprotectants during an acclimation period in freeze-tolerant insects (Storey and Storey, 1983). This appears to be a mechanism of conservation; if the temperatures do not drop to below freezing, the cryoprotectant is not produced, and the animal does not have to convert excess glucose to glycogen in the spring.

Photoperiod is not a triggering mechanism for cryoprotectant production in frogs, although burrowing may be. Since these frogs live in northern latitudes, they burrow under the leaf litter and snow, which offer protection from extremely cold temperatures. Frogs are unable to survive temperatures of −30°C. The question remains as to whether frogs would have the instinct to burrow if the temperature dropped in the summer.

1.2.3.5 Response of Reptiles to Cold Temperatures

The number of species of reptiles, including snakes, declines markedly along a gradient from the tropics to temperate latitudes. Lizards, alligators, crocodiles, turtles, and tortoises are scarce or absent in cold temperate regions. Reptiles survive in cold temperate climates by behavioral adaptations to maintain their body heat at levels that allow them to be active during spring, summer, and autumn, and by hibernation during winter.

Most reptiles, such as land tortoises, diurnal snakes, and lizards, primarily gain heat from solar insolation, using it to attain body temperatures at which activities can be performed. The changes in body posture and contours enable maximization of insolation striking the surface of the animal. Many snakes in cold temperate regions hibernate in well-insulated locations during the cold winters. Sudden temperature decreases with accompanying decreases in solar insolation following a nuclear war would be devastating to these animals.

1.2.3.6 Responses of Birds to Cold Stress

Avifauna are particularly vulnerable to cold stress because of their high metabolic requirements. In most situations, their high mobility allows for avoidance of cold temperatures. However, some birds can effectively regulate their body temperatures, even under severe cold conditions. For example, Veghte (1964) found that body temperatures of the gray jay remained unchanged between January (temperatures as low as −40°C) and July (average temperatures 15°C).

Behavioral responses to cold include postural changes and plumage adjustment, as well as movement into sheltered areas. The latter response is not as widely used as with mammals, since birds do not hibernate. However, willow ptarmigan do burrow in the snow, and cavities in trees are used by woodpeckers. Dawson and Hudson (1970) have reviewed the anatomical adaptations that conserve heat in birds living in northern climates, which include heavier plumages than in those birds that migrate, and countercurrent vascular flow in unfeathered areas of birds. Larger digestive capacity in some boreal finches increases the storage capacity of food.

Muscular thermogenesis (i.e., shivering) was suggested to be the major means of thermoregulation by West (1965), who studied the relationship between electrical activity of muscles and ambient temperature. Non-shivering thermogenesis, demonstrated by many mammalian species, does not appear to be used (Dawson and Hudson, 1970).

Environmental parameters can influence the basal metabolic rate of some bird species. Some northern species are able to maintain higher metabolic rates in winter than in summer. For example, evening grosbeaks and house sparrows that have been cold acclimated are able to maintain higher metabolic rates under severe cold stress than those of the same species that have not been acclimated (Hart, 1962). Basal metabolic rate of the northwest crow was about 20% higher in winter than in summer in Alaska. However, other species, such as yellow bunting (Wallgren, 1954), cardinal (Dawson, 1958), and gray jay (Veghte, 1964), have basal metabolic rates which do not vary with the seasons. Acclimation appears to be important in some species, since experiments show that birds exposed to low temperatures increase their metabolic activity, thermogenic capacity, and cold resistance within 1 to 4 weeks (Dawson and Hudson, 1970). Furthermore, Chaffee et al.(1963) found that exposure of various sparrows to 1°C for 7 weeks caused an increased in the size of the heart, kidney, and liver, and an increase in myoglobin content. Increased thyroid activity has also been found (Miller, 1939).

1.2.3.7 Responses of Hibernating Animals

Both acclimation and hibernation may be used as mechanisms to tolerate cold temperatures in hibernating mammals. Acclimation may occur before hibernation, but this is not necessary. Typical physiological changes occurring during acclimation include: lowered oxygen consumption, increased non-shivering thermogenesis, decreased shivering, and increased quantity of unsaturated fats (which remain more fluid at lower temperatures than saturated fats).

Hibernation is the state of inactivity in mammals with accompanying physiological changes, such as lowered body temperature and decreased heart rate. It is triggered by different environmental cues or other mechanisms in different animals. The woodchuck (*Marmota monax*), for example, requires food deprivation before it will hibernate (Davis, 1967). Other animals respond to decreases in temperature, changes in photoperiod, or a combination of these factors. For example, a short photoperiod and low temperatures induce hibernation in the arctic ground squirrel (*Spermophilus undutatus*) (Drescher, 1967). There are also differences in the intensity of environmental cues needed to induce hibernation. Some species are able to enter into hibernation without external cues, but in response to an internally regulated annual circadian rhythm (Hudson, 1973). These species include many of the ground squirrels (e.g., *Citellus* and *Spermophilus*), the hedgehog (*Erinaceus europaeus*), many chipmunk species (e.g., *Tamias striatus* and *Eutamias* spp.), and the bat *Myotis lucifugus* (Hudson, 1973). In the event of an unnatural, sudden drop in temperature, those species that hibernate in response to internal cues would perish if the climatic conditions were severe and hibernation were not induced.

Hudson (1973) concluded that the cue for periodic arousal from the torpid state of mammals during hibernation relates to their excretion requirements. However, the triggers for complete arousal from hibernation are likely to be as complex as the mechanisms which induce hibernation. Squirrels wake at intervals to feed in winter months. Those animals dependent on temperature increases for complete arousal would be the most likely to survive a nuclear war-induced climatic perturbation, since this would ensure that they would not be aroused during periods of severe cold.

1.2.3.8 Responses of Non-Hibernating Mammals to Cold Temperatures

Non-hibernating mammals living at northern latitudes or in alpine areas must be able to tolerate cold temperatures either on a nightly or seasonal basis. In regions that experience severe temperatures, such as the arctic, mammals cannot rely strictly on increased metabolic heat production through increased food consumption. The obvious way in which many mammals are able to withstand cold temperatures is through insulation provided by fur; arctic animals have coats much thicker than those animals of comparable size in the tropics. Those that are not able to coat themselves sufficiently with fur because of size constraints spend much of their time in borrows beneath insulating snow.

The extremities of animals tend to be less well covered in fur to facilitate movement. The temperature gradient present within the limbs result from either vasoconstriction (Adams,1963) or a countercurrent vascular system, which prevents rapid loss of heat from the body. In this system, warm arterial blood loses heat to cool venous blood as it is returned back to the heart. A review of the literature concerning countercurrent blood flow may be found in Whittow (1971).

Other adaptations to cold temperatures include: increased heat production by shivering and increased shivering efficiency; increased peripheral vascularization; increased total blood volume; and altered neuronal and hormonal levels (Adams, 1971).

1.2.3.9 Survivability

Despite the adaptations that enable various groups of animals living in temperate regions to cope with low temperatures, these will not necessarily ensure that they would be able to survive the climatic conditions after a nuclear war. The timing of the nuclear war would be a major factor in survivability of many groups, the least damage occurring in the winter, when many animals would be in a dormant state or acclimated to lowered temperatures. The key factors in determining survivability are : 1.) the cues that control acclimation and hibernation/dormancy; and 2.) the need and availability of food sources during the period of reduced temperatures and thereafter. For example, insects that are freeze-tolerant and respond directly to decreases in temperature would be able to survive the period of cold. However, it is essential that they feed once temperatures increased (Storey, pers. comm.).

Since temperature is not often the only cue for hibernation and dormancy, it is unlikely that many species that are sensitive to freezing temperatures would be protected by going into hibernation. The length of time for acclimation would also be important, especially since the acute decrease in temperature is predicted to be sudden. Animals with migratory instincts not reliant solely on temperature decreases, and those animals living in warmer climates, would be unlikely to survive major cooling events because they would not have the behavioral or physiological adaptations characteristic of cold-hardy animals. Migratory birds and mammals might well suffer severely, as the appropriate triggers for migration would not likely be present.

Many migratory birds in the Northern Hemisphere travel from the tropics or sub-tropics to temperate regions. Even for those used to arriving in polar regions while ice is still on the sea or land, a prolonged, unmelted snowpack could cause catastrophic losses of young or of unhatched eggs. Many of these species (e.g., ducks, geese, ravens, sandpipers, and plovers) could be greatly reduced in numbers if sub-freezing temperatures prevented the normal cycle of food availability in spring or summer. A premature southward migration because of nuclear war-induced freezing could equally leave the birds with insufficient food reserves to make the return northerly migration, or could leave young to die. Catastrophe could occur if the normal stop-over areas for resting or feeding, in mid-latitudes, were under the influence of nuclear war-induced climatic alterations.

For migratory animals such as caribou or reindeer, the timing for the seasonal migrations is critical in terms of food supply and arrival in calving grounds. Predation is also a factor which is dependent on the vigor of the herds and on the availability of stragglers and of unprotected young. Native human populations harvest these herds for essential protein. It is entirely conceivable that a sudden onset of an acute climatic phase after a nuclear war could severely and perhaps fatally disrupt the balances and migratory instincts.

1.3 PLANT STRATEGIES RELEVANT TO NUCLEAR WAR [1]

1.3.1 Introduction

The task of predicting the effect upon the planet of a major nuclear war would be greatly simplified if the now rapidly evolving models of world climate and its potential disruption by nuclear war could be complemented by general models of the functional characteristics of the world's ecosystems. At present, ecologists are sharply divided in their assessment of the feasibility of devising predictive models of ecosystem and community functioning and response to perturbation. In consequence, whereas several ecosystem models are used in assessing the potential consequences of nuclear war (Chapter 2), another approach preferred by many ecologists is to concentrate upon those systems and organisms for which detailed information is available. This section explores the alternative approach using existing knowledge and theory,

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[1] This section based on a paper prepared by J.P. Grime.

which are now sufficient to allow some general predictions of variation in sensitivity and resilience in biota. The concepts developed here rely heavily upon 'strategy' theories (Ramenski, 1938; Grime, 1978) of ecological specialization, and they are illustrated mainly by reference to terrestrial plants. However, most of the principles can be readily adapted to fungi (Pugh, 1980), algae (Dring, 1982), and animals (Greenslade, 1983). Reference will be made to three types of plant strategies: 1.) primary strategies of established (mature) plants; 2.) strategies of growth response to temperature; and 3.) regenerative strategies.

1.3.2 Primary Strategies of Established Plants

One approach that has been used to summarize the main types of ecological specialization in the established phase of plant and animal life-histories (Ramenski, 1938; Grime, 1974) is to define three primary ecological strategies, each corresponding to habitat conditions characterized by reference to the quantity and continuity of resource supply (Table 1.10).

TABLE 1.10

CONDITIONS OF RESOURCE SUPPLY ASSOCIATED
WITH THREE PRIMARY STRATEGIES[a]

STRATEGY	RESOURCE SUPPLY
Ruderal (ephemeral)	Temporarily abundant
Competitor	Continuously abundant but subject to local and/or progressive depletion as resources are exploited
Stress-tolerator	Continuously scarce

[a] After Grime (1979)

For plants, it has been recognized that the extreme conditions favoring either competitors, stress-tolerators, or ruderals (i.e., weedy species) form only part of the range of environments occurring in nature. The full spectrum of habitat conditions and their associated strategies can be described as a unilateral triangle (Grime, 1974), in which the relative importance of competition, stress, and disturbance is represented by three sets of contours. This model allows recognition of not only the three extremes of plant specialization described above, but also a range of intermediate strategies associated with less extreme equilibria among stress, disturbance, and competition. A review of the full implications of the model has been presented elsewhere (Grime, 1979). Essential features of the primary strategies are summarized in Table 1.11, which also draws attention to the features of plants most relevant to predictions of sensitivity to nuclear war-induced climatic disturbances and to the potential for recovery.

1.3.3 Strategies of Growth Response to Temperature

Since both the acute and chronic phases following a major nuclear war could involve depressions of temperature, it is desirable to examine existing knowledge of plant responses to temperature. Considerable research has been conducted on: 1.) the relative cold-hardiness of species of different geographical distribution and origins, and 2.) the efficiency of C_3 and C_4 and CAM photosynthetic systems under various temperature regimes. Although these types of studies provide information relevant to the post-nuclear war analysis, further insights are required. In order to devise adequate predictions of plant survival and recovery, it is necessary to assess the extent to which growth (i.e., the construction of plant tissue through division and expansion of cells) would be disrupted by altered climate. In particular, we need to differentiate between plants that would remain dormant and those that would continue to grow or would initiate growth during the period of low temperature and insolation following a nuclear war, although possibly with severe penalties. This growth would commence after the sub-freezing phase ended, since growth is obviously temperature limited.

Grime (1983) suggested that some predictions of how plants would respond to lowered temperatures can be obtained by reference to recent theories relating the amount of DNA in plant cell nuclei (known as the nuclear DNA content of plants) to the climatic conditions to which their growth has been attuned by natural selection.

Differences in nuclear DNA content exist on a broad geographical scale. Whereas plants of low nuclear DNA content are ubiqituous, species with high values appear to be restricted to regions in which cool temperatures are experienced during the growing season. The data are consistent with the hypothesis that climate has operated upon nuclear DNA content, especially through differential sensitivity of cell division and cell expansion to low temperatures.

At one extreme are the vernal geophytes with massive DNA contents. In these plants, growth at cold temperatures in the early spring is achieved mainly by expansion of large cells formed during warm conditions of the previous summer, rather than by cell division. The other extreme corresponds to the wide range of vascular plants in which growth is restricted to relatively warm conditions. Natural selection for rapid rates of plant development by both cell division and cell expansion appears to have resulted in

TABLE 1.11
CHARACTERISTICS OF PLANT STRATEGIES AS RELEVANT TO RESPONSES TO NUCLEAR WAR[a,b]

		COMPETITIVE	STRESS-TOLERANT	RUDERAL
•o	Life-forms	Herbs, shrubs, and trees	Lichens, bryophytes, herbs, shrubs, and trees	Herbs, bryophytes
	Morphology	High dense canopy of leaves. Extensive lateral spread above and below ground	Extremely wide range of growth forms	Small stature, limited lateral spread
o	Life-span	Long or relatively short	Long - very long	Very short
•o	Longevity of leaves and roots	Relatively short	Long	Short
	Leaf phenology	Well-defined peaks of leaf production coinciding with periods of maximum potential productivity	Evergreens, with various patterns of leaf production	Short phase of leaf production in period of high potential productivity
o	Reproduction	Established plants usually reproduce each year	Intermittent reproduction over a long life-history	Prolific reproduction early in life-history
o	Proportion of annual production devoted to seeds	Relatively small	Small	Large
•	Perennation	Dormant buds and seeds	Stress-tolerant leaves and roots	Dormant seeds
o	Maximum potential relative growth-rate	Rapid	Slow	Rapid

[a] After Grime (1979).

[b] Code indicates the following:

o - particularly relevant to recovery

• - particularly relevant to susceptibility in the acute phase.

•o - particularly relevant to both susceptibility in acute phase and to recovery.

TABLE 1.11 continued.

		COMPETITIVE	STRESS-TOLERANT	RUDERAL
o	Photosynthesis and uptake of mineral nutrients	Strongly seasonal, coinciding with long continuous period of vegetative growth	Opportunistic, often uncoupled from vegetative growth	Opportunistic, coinciding with vegetative growth
•	Acclimation of photosynthesis, mineral nutrition and tissue hardiness to seasonal change in temperature, light and moisture supply	Weakly developed	Strongly developed	Weakly developed
•o	Storage of photosynthate and mineral nutrients	Most photosynthate and mineral nutrients are rapidly incorporated into vegetative structure but a proportion is stored and forms the capital for expansion of growth in the following growing season	Storage systems in leaves, stems and/or roots	Confined to seeds
•	Defense against herbivory	Often ineffective	Usually effective	Often ineffective
	Litter decomposition	Rapid	Slow	Rapid
•o	Associated regenerative strategies[c]	V, S, W, B_s	V, B_j, W	S, W, B_s
o	Role in secondary successions in productive habitats	Relatively early	Late	Early

[c] Key for regenerative strategies (see Table 1.12): V - vegetative expansion, S - seasonal regeneration in vegetation gaps, W - numerous small, widely dispersed seeds or spores, B_s - persistent seed or spore bank, B_j - persistent juveniles.

reductions in cell size, cell cycle length, and nuclear DNA content. The vernal geophytes could be at an advantage if chronic decreases in temperature were to be sustained over several growing seasons. However, many arctic and alpine species are of the second type, i.e., with small cells, short cell life cycles, and low DNA content. This type is best able to exploit abrupt and brief opportunities for growth.

1.3.4 Regenerative Strategies

The regenerative strategies of plants can be considered for insights into effects of nuclear war. Five major types of regenerative strategies are distinguished in Table 1.12, which contains a brief description of the seed bank types (discussed later in this chapter) and habitat conditions with which each strategy appears to be associated. When these concepts are used in predictions of nuclear war-induced effects, it is necessary to bear in mind that

TABLE 1.12

FIVE REGENERATIVE STRATEGIES OF WIDESPREAD OCCURRENCE IN TERRESTRIAL VEGETATION[a]

STRATEGY	HABITAT CONDITIONS TO WHICH STRATEGY APPEARS TO BE ADAPTED
Vegetative expansion (V)	Productive or unproductive habitats subject to low intensities of disturbance
Seasonal regeneration in vegetation gaps (S) (seed banks transient)	Habitats subjected to seasonally predictable distrubance by climate or biotic factors
Regeneration involving persistent seed or spore bank (B_s)	Habitats subjected to spatially predictable but temporally unpredictable disturbance
Regeneration involving numerous widely despersed seeds or spores (W) (seed banks usually transient)	Habitats relatively inaccessible (cliffs, tree trunk, etc.) or subjected to spatially unpredictable disturbance
Regeneration involving persistant juveniles (B_j) (seed banks transient or non-existent)	Unproductive habitats sunjected to low intensities of disturbance

[a] After Grime (1979).

TABLE 1.13
TRENDS IN ECOSYSTEM SUCCESSIONAL DEVELOPMENT[a]

ECOSYSTEM ATTRIBUTES	DEVELOPMENTAL STAGES	MATURE STAGES
Community Energetics		
Gross production/community respiration (P/R ratio)	greater or less than 1	approaches 1
Gross production/standing crop biomass (P/B ratio)	high	low
Biomass supported/unit energy flow (B/E ratio)	low	high
Net community production	high	low
Food chains	linear, predominantly grazing	weblike, predominately detritus
Community Structure		
Total organic matter	small	large
Inorganic nutrients	extrabiotic	intrabiotic
Species diversity - variety	low	high
Species diversity - equitability	low	high
Biochemical diversity	low	high
Stratification and spatial heterogeneity (pattern diversity)	poorly organized	well organized
Life History		
Niche specialization	broad	narrow
Size of organism	small	large
Life cycles	short, simple	long, complex
Nutrient Cycling		
Mineral cycles	open	closed
Nutrient exchange rate between organism and environment	rapid	slow
Role of detritus in nutrient regeneration	unimportant	important
Selection Pressure		
Growth form	for rapid growth	for feedback control
Production	quantity	quality
Overall Homeostasis		
Internal symbiosis	undeveloped	developed
Nutrient conservation	poor	good
Stability (resistance to external perturbations)	poor	good
Entropy	high	low
Information	low	high

[a] Based on Odum (1969).

some plant species and genotypes exhibit several of the regenerative strategies listed in Table 1.13. This fact is relevant to assessments of both sensitivity and potential for recovery. Two of the strategies (V and B_s) would likely favor resistance during an acute phase of extreme temperatures, since these categories often involve, respectively, the maintenance of dormant buds and dormant seeds at or below the soil surface.

1.3.5 Susceptibility During an Acute Phase Following a Nuclear War

The extent of the mortalities suffered by particular plant populations during extreme temperature decreases would depend upon many factors, including geographical location, season, intensity and rate of onset of low temperatures, plant physiology, and plant strategy. Assessing the effects of frost damage from an abrupt drop in temperature would rely primarily upon existing physiological data dealt with in detail elsewhere in this volume. Predictions of frost and fire damage would vary considerably according to the season at which the event occurred, with greatest mortality if the perturbation occurred during the growing season.

Several additions or refinements to physiologically based predictions are suggested by strategy concepts. The most important of these derives from major differences in the relative sensitivity of established plants and their propagules. An extensive literature (Brenchley, 1918; Brenchley and Warrington, 1933; Chippendale and Milton, 1934; Crocker, 1938; Major and Pyott, 1966; Went, 1969; Zobel, 1969; Marks, 1974; Symonides, 1978; Thompson, 1977; Grime, 1981; Grandstom, 1982; Keddy and Reznicek, 1982; Cavers, 1983; During and ter Horst, 1983; Conn et al., 1984; Nakagoshi et al., 1983) shows that plants that exploit habitats subject to spatially predictable disturbances (e.g., arable fields, pastures, marshland, heathland, savannah, chaparral, taiga, secondary tropical forest) tend to accumulate large reserves of spores or seeds (known as seed banks), which persist either in the soil or, more rarely, attached to the parent plants. The propagules form an inconspicuous but extremely resistant component of many plant populations in vegetation types where cycles of destruction and regeneration are a normal feature of the vegetation dynamics. Ungerminated seeds, especially in temperate regions and where they have not imbibed water, are relatively resistant to temperature fluctuations. Along with any surviving shoot bases and rhizomes, seeds could be expected to confer resilience on populations, even in circumstances if there were large-scale mortality of the established vegetation (Section 1.4).

Transient seed banks, which occur for many species, provide a less certain means of survival. A large number of trees, shrubs, and grasses are known to regenerate each year by producing a single crop of seeds, which after a short period on the soil surface, germinate synchronously in a particular season.

Quite clearly, timing of the climatic disturbance in relation to season would determine whether populations dependent upon this type of regeneration would suffer catastrophic mortalities.

If widespread destruction of the established vegetation occurred in response to chilling, fire, or other perturbations, the most vulnerable plants would likely be those in which regeneration relies wholly upon a bank of juveniles (seedlings, sporelings, or saplings). This type of regeneration is particularly characteristic of ferns, gymnosperms, primitive families of woody angiosperms, and in primary tropical rainforest; it is also common in a wide range of slow-growing plants of late successional vegetation. In many of these plants, seeds or spores are produced only intermittently and tend to germinate with little delay. Recovery of systems having seedling banks, rather than seed banks, would be exceedingly vulnerable to extreme perturbations, in which the adult and regenerative components would be killed simultaneously.

1.3.6 Recovery After an Acute Phase

The vegetation recovery processes after a nuclear war would be considerably affected by the severity and differential effects of the initial perturbations. If the impacts were severe, the greatest risks of total extinction would be expected in relatively stress-tolerant species, including many of the late successional dominant forest trees of temperate and tropical forests. On first inspection, this prediction may seem paradoxical, since many of the temperate forest trees normally endure considerable climatic extremes in their natural habitats. If the impacts of the acute phase were restricted to effects of low temperature and reduced insolation experienced in the winter by acclimated plants, high survival could be expected. However, this is the most optimistic of the range of possible scenarios; at the other extreme could be situations in which a summer perturbation might eliminate (at least locally) the many species in which there is no capacity for re-sprouting and in which seed banks are transient or non-existent.

If mass destruction of the established vegetation in temperate regions occurred (e.g., from an extreme climatic disturbance in summer), the early phases of recovery would likely be similar to those familiar in large areas of deforested and derelict landscape. For example, in many parts of ex-industrial sites in northern England at the present time, late successional trees, shrubs, herbs, and cryptograms are quite localized; many areas of wasteland succession remain suspended indefinitely at a low diversity stage of competitive-dominance by a relatively small number of mobile, early successional herbs and shrubs (Grime, 1979). The lack of seed banks, poor dispersal ability, slow-growth, and delayed reproduction of late-successional species (Table 1.11) could be expected to retard the process of recovery. A state of suspended recovery is often apparent in areas of severe industrial devastation, such as around major smelters and in heavily industrialized regions of Europe (Amiro and Courtin, 1981).

The species that could be expected to expand fastest after nuclear war-induced severe disturbances would almost certainly include those herbs and shrubs that possess several different types of regenerative strategies. These are plants which have shown a formidable ability to survive disturbance as underground buds or seeds, and to disperse widely over the landscape, to colonize open ground, and subsequently to monopolize extensive areas by prolific seeding or clonal expansion.

In addition to the truncation of the succession to forest, there might occur aspects of recovery peculiar to the post-nuclear war conditions. For example, during the later part of an acute phase, when temperatures and insolation might be adequate for growth but remained depressed from normal, plants that are normally capable of winter or spring growth (including many geophytes and grasses of high DNA content) might commence growth in conditions which would lead to etiolation, wasteage of storage reserves, and susceptibility to fungal attack. Although this might not cause mortalities directly, it would likely play a significant role in the competitive interactions that would determine the composition of recolonizing communities.

An additional and more unpredictable element to be accommodated in the recovery assessment would be the potential population explosion of insect herbivores in the absence of avian predators and applications of insecticides. Particularly since the ruderal and competitive early successional plants are weakly defended (Coley, 1983; see Table 1.11), this could have devastating effects on the early recovery process and might lead to the temporary emergence of some unfamiliar vegetation dominants. It is possible, therefore, that succession could follow an erratic course until populations of insect parasitoids and returning insectivorous birds became re-established and stabilized.

Many ecosystems experience considerable year-to-year variation in climate without major repercussions, and it is therefore tempting to propose that the major effects of climate on vegetation following a nuclear war would be those arising from extreme temperature excursions during an acute phase. While this might apply to many ecosystems, some possible exceptions exist. For example, vegetation types established in a Mediterranean climate might well survive an acute phase as bulbs or dormant seeds; however, the life cycles of most of the geophytes and grasses of Mediterranean climates are closely adapted to alternating wet-cool and hot-dry seasons, both of which processes are essential to plant development. Physiological studies of these processes (e.g., Hartsema, 1961) suggest a degree of developmental inflexibility that could lead to failure if the climate remained variable into a chronic phase.

1.3.7 Summary

From plant strategy concepts the following may be concluded concerning terrestrial vegetation sensitivity and recovery potential:

1.) Resistance to damage from low temperature and insolation during an acute phase would be greatest in stress-tolerant plants of unproductive habitats or late successional communities, but these same plants would face the highest risk of local extinction if there were widespread destruction of the established vegetation.

2.) Survival and recovery would be enhanced in plant populations maintaining a persistent bank of buds or seeds within the soil.

3.) Resilience would be greatest in vegetation where cycles of destruction and regeneration are already a normal feature of the vegetation dynamics.

4.) Where severe vegetation damage occurred in temperate and tropical regions, recolonization would involve the mobile, early-successional herbs and shrubs that currently dominate derelict ex-industrial or ex-agricultural landscapes, where succession could remain truncated indefinitely over extensive areas.

5.) Initial loss of predators (especially insectivorous birds) could lead to severe damage of the recovering vegetation by insect outbreaks; this could lead to erratic and unusual patterns of vegetation development.

6.) Species normally capable of winter or spring growth in cold conditions (many geophytes and grasses) could continue or commence shoot expansion during the post-nuclear war conditions; this would have deleterious effects and reduce their competitive ability in relation to plants which remained inactive.

7.) Where there is protracted disruption of seasonality, such as for the wet-cool, dry-hot seasonal pattern of Mediterranean climates, severe effects could be expected in plants with determinate life-cycles.

1.4 SEED BANKS AND REGENERATION

1.4.1 Occurrence of Seed Banks

If nuclear war were to result in large-scale mortality to plants in an ecosystem, then the long-term consequences to that ecosystem would depend to a great extent on the ability of individual species to regenerate. This would involve the attributes exemplified in post-fire successions, such as the ability to survive extreme physical conditions and to regenerate from buds or belowground perennating organs that have survived buried in the soil. Another factor in regeneration would be the ability to repopulate an area as a consequence of seeds remaining viable until conditions became suitable for germination. Species that would seem pre-adapted include those that already experience severe climatic stress and normally have seed banks which persist and accumulate in the soil following dispersal from the parent plants.

The possession of a sizeable seed bank is an adaptation for survival during unfavorable conditions, often of a seasonal nature, e.g., droughts, freezing, severe cold, or low light. Other ecosystems do not have sizeable seed banks, and most seeds germinate soon after release. In comparing transient and persistent seed banks, it seems clear that a majority of the seeds of persistent seed banks are deeply buried, which helps the viability of seeds because of lower soil temperatures, darkness, or increased CO_2 levels, each of which may inhibit germination.

Some species (e.g., willow [*Salix*]) have seeds that are viable for only a few days after dispersal. Others have seeds with thick seed coats and large food reserves that can persist for decades (e.g., some legumes). Selective pressures within habitats seem to have played a large role in seed persistence. The best-documented examples of species which accumulate large seed reservoirs in the soil are the ruderals (weeds) of arable fields (Brenchley and Warington, 1930; Roberts, 1970). Such ruderals appear in large numbers when the habitat is disturbed, for example by plowing.

Large seed banks are particularly characteristic of shrubs and perennial herbs occurring in habitats subjected to intermittent damage by fire (Grime, 1979). In addition, large seed banks occur in shore-line habitats, in species colonizing seasonally water-logged grasslands, and in many natural grasslands. In vegetation subjected to summer drought, persistent seed banks are accumulated by both perennial herbs and winter annuals (King, 1976; Thompson, 1977).

1.4.2 Regeneration from a Seed Bank

Those species with a substantial seed bank buried in the soil would be at an advantage in recovery following destructive freezing temperatures or extensive fires following a nuclear war. Species that lack a seed bank are especially common in wet tropical evergreen ecosystems, where seedling banks are more common (see Chapter 2 for discussion of specific ecosystem responses). Regeneration from banks of persistent seeds in shrubs and trees in those ecosystems would be restricted to species associated with frequently disturbed habitats.

The closed-cone pines (e.g., in California, the New Jersey Pine Barrens, and the Appalachians) and the jack pine stands of the North American boreal forests provide an unusual addition to the seed bank species. It has been shown that the seed-containing cones, which often persist on the trees for years, are specifically adapted to release their seeds after periodic destruction by fire (Vogl, 1973). The actual forest stands are often short-lived (30–75 years) and composed of even-aged trees. Release of seeds from the cones occurs when the cones open upon exposure to high temperatures, which destroy the resins which normally keep such cones closed. Soon after a fire, enormous numbers of pine seedlings appear. Such adaptations might be advantageous to regeneration after a nuclear war, following fires directly caused by the nuclear war, or fires in stands killed by climatic stresses, which in turn increases the fuel load available to burn.

Seed banks of tundra and boreal forests, as well as those in most subtropical and tropical ecosystems, have received very little attention. McGraw (1980) collected soil from a cottongrass (*Eriophorum vaginatum*) tussock tundra in Alaska and determined the distribution, abundance, and germination patterns of buried viable seeds. Seeds of *Carex bigelowii*, *E. vaginatum*, and *Ledum palustre* were abundant, and smaller amounts of other species were also present. Buried seeds were found to a depth of 21 cm below the soil surface. When exposed to favorable conditions, germination took place initially rapidly then more slowly. Another interesting example of a tundra plant with a persistent seed bank is that of *Lupinus articus* seed, estimated to be 10,000 years old, which was recovered from permanently frozen lemming burrows and found to be viable (Porsild et al., 1967).

1.4.3 Regeneration by Vegetative Means

Many plant species produce new shoots vegetatively, such as from stolons, rhizomes, tussocks, or suckers; spreading by runners; splitting of bulbs; or by coppicing. After fires in frequently burned ecosystems, vegetative recovery is often rapid, often involving species with perennating organs at or below the surface, with protected apical meristems (e.g., bulb- and corm-forming species in prairies, grasslands, chaparral, and Mediterranean habitats). Grasses have an intercalary meristem located at or below the soil surface, between the root and leaf blade, which enables them to re-sprout after defoliation by fire, grazing, mowing, cutting, or air pollution. Often ruderal and post-fire colonizers combine effective widespread dispersal by wind-borne seeds (e.g., fireweed [*Epilobium angustifolium*], and hawkweeds [*Hieracium* spp.]), with effective vegetative spread as soon as seedlings are established. Such pioneer colonizers can be expected to be effective in regenerating after a nuclear war.

Some woody species have a high capacity to coppice, i.e., produce new shoots from dormant buds located near the base of the plant, or to produce suckers. Trees such as aspen, other poplars, willows, fir, and maples regenerate in this way after the trunk or branches are cut or burned.

1.5 COMMUNITY SUCCESSION

Plant communities are subject to temporal changes, both in species composition and in the relative importance of constituent life-forms. Such changes may be described as successional or, in some cases, cyclical. Successions may occur over very long time periods, or they may be typically interrupted at a certain stage, such as when fire occurs in pine forests and the forest is turned back to an earlier successional stage. Primary succession involves primitive soils or bare ground exposed for the first time; pioneer plants move in, generally with dispatch. Primary succession occurs on rock surfaces, on foredunes of sand-dunes, on muds and sediments of infilling lakes, and on exposed glacial moraines and tills as glaciers retreat. Secondary succession involves recolonization after an existing plant community is destroyed and soils are exposed. Secondary successions occur on abandoned agricultural fields; after fires in forests, chaparral, and grasslands; and following clear-cutting, extensive hurricane damage, and other major disturbances.

Odum (1971) characterized the maturation and development of ecosystems as a strategy of increased control of the physical environment, which provides the biota with maximum protection from environmental perturbations. The culmination of this dynamic and largely predictable (unidirectional) process of community-controlled modification of the environment can be a stabilized ecosystem. In the course of a succession, biomass increases, species diversity increases, food chains become more complex, vertical stratification develops, detritus and organic matter increase, nutrient cycling becomes tighter as less nutrients are lost from the system, while long-lived and larger organisms enter the system and niche differentiation accelerates. This is further explained in Table 1.13.

Given all of these processes and changes leading in the common direction of enhanced stability, we need to determine as best we can the effects of nuclear war-induced perturbations which, in the short term at least, would likely cause instability. We need to examine which ecosystems have particular resistance to such stresses and what the prospects are for regeneration of the systems. This analysis is described in Chapter 2 for several biomes. Clearly, those ecosystems which are regularly subject to stresses such as fire, clearance, and grazing are likely to have species components in them that may respond better to nuclear war-induced stresses than other ecosystems, where such interventions are unknown or so rare as to be beyond the life spans or generation times of key (dominant) components.

While the particular paths of regeneration and post-nuclear war succession cannot be predicted with certainty, it seems most likely that they would follow known paths in ecosystems where disturbance is a regular phenomenon. We might anticipate greater long-term damage, other things being equal, in those systems unaccustomed and therefore probably unadapted to major disturbance (Chapter 2). For the former systems, we predict no surprises, but for the latter (e.g., for cactus deserts, evergreen rain forests, and mangrove swamps) confident predictions become more difficult.

1.6 WORLD BIOMES

1.6.1 Introduction

Biome is a general term used to identify a biotic community type, dominant over broad geographical regions. There are a number of classification systems used in categorizing and naming biomes, several of which are widely accepted. In all but a few cases, the name given to a biome reflects in some way the geographic placement and overall structure of the plant community present, and frequently gives some indication of climate. Thus we see terms such as 'north temperate deciduous forest', or 'tropical desert scrubland'.

Temperature and precipitation to a very large extent determine the distribution of terrestrial ecosystems in complex ways, yielding a broad range of identifiable communities. Because variation in climate is less pronounced near the equator, vulnerability to changes in environmental conditions increases with decreasing latitude. Thus, nuclear war in northern latitudes might cause smaller or briefer climatic disturbances in equatorial latitudes, but the biota of those regions are not adapted to even moderate changes in light, temperature, or precipitation regimes beyond the normal diurnal or seasonal fluctuations. For example, evergreen wet tropical rainforests in lowland areas experience almost no seasonal temperature change.

1.6.2 Distribution of Biomes

A simple classification of biomes can be made by comparing regional temperature and moisture regimes and relating these climatic factors to the general physiognomy of the plant community (Figure 1.17). No single climatic variable can be used to classify terrestrial biomes; for example, several biomes receive about the same amount of annual precipitation but differ greatly in mean annual temperature. The climatic effects of nuclear war could alter the atmosphere so that temperature and precipitation regimes characteristic of northerly, dry, cold biomes would extend to more temperate, mesic biomes.

Temperature and precipitation influence biological activity in a number of different ways. For plants, temperature and precipitation can be combined as indices that reflect the potential availability of moisture for primary production (Figure 1.18). Tropical forests, north temperate forests, and tundra are similar when compared on the basis of moisture availability, but potential evapotranspiration is much higher in tropical forests. This separation is

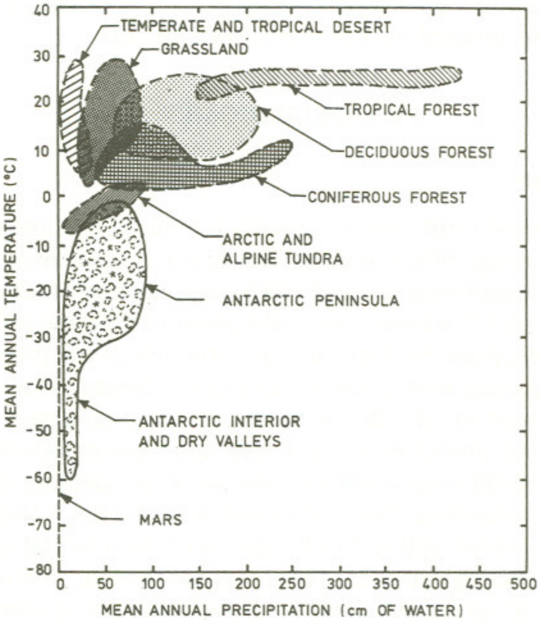


Figure 1.17 Terrestrial biomes in relation to mean annual temperature and precipitation

largely influenced by the temperature regime across the latitudinal range occupied by these biomes. In contrast, desert shrublands and grassland biomes occur in areas of low moisture availability and high potential evapotranspiration.

The importance of precipitation and evapotranspiration to net primary production (the amount of photosynthetic carbon fixed by plants minus that respired by plants or consumed by animals) can be seen in Figure 1.19. Net primary production (NPP) increases almost linearly up to about 1,000 $mm \cdot yr^{-1}$ of precipitation, with a plateau in response above about 1,800 $mm \cdot yr^{-1}$. What is not shown in these figures is that for some ecosystems, evapotranspiration may exceed precipitation, causing water stress and limiting primary production. Thus, moderate decreases in average temperatures of 1°C to 2°C if occurring *alone* can increase potential primary productivity. But cooler average growing season temperatures could well occur with increases in freeze frequency, damaging plants before seed maturation.

There are several ways to combine climatic indices to describe the distribution of major biotic communities (see Emanuel et al., 1985). A simplified vegetation map of the world is shown in Figure 1.20. Of course, this

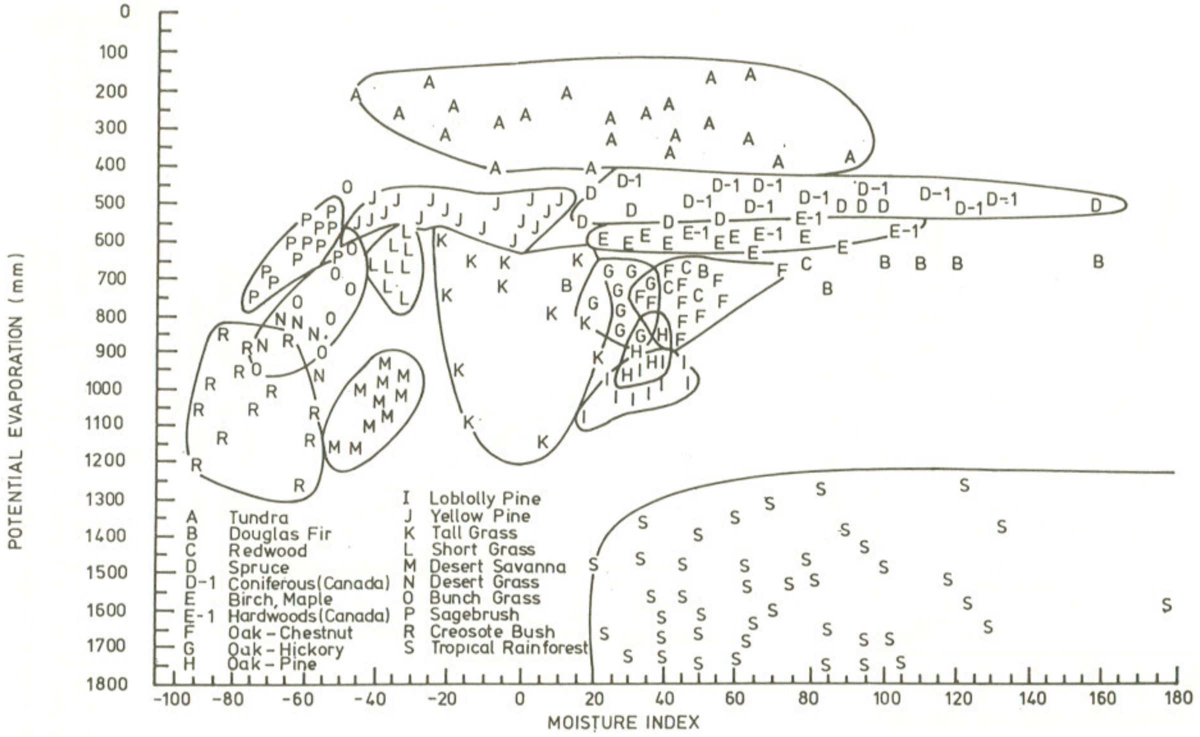
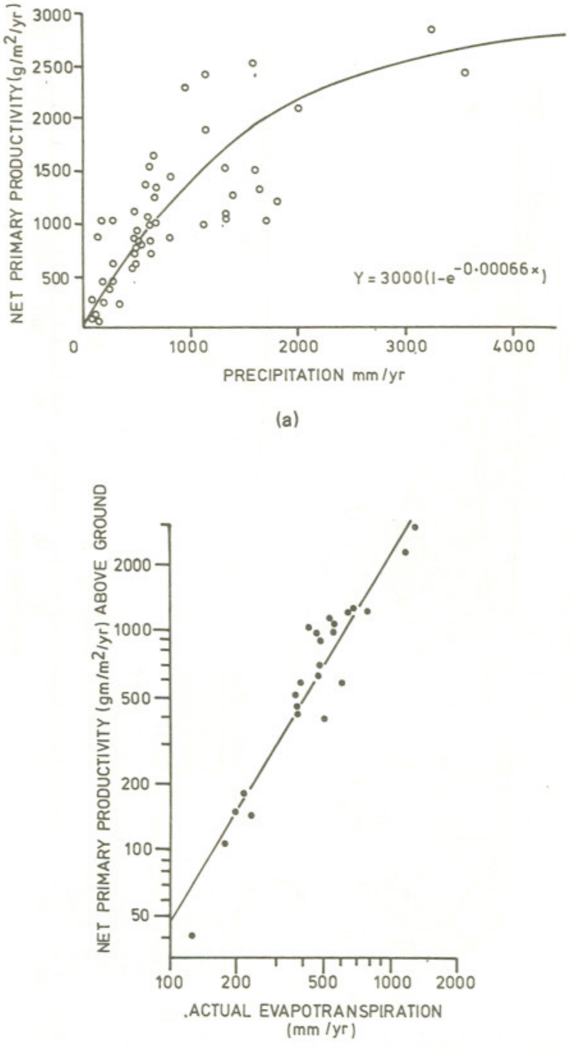


Figure 1.18 Relation between distribution of communities and climate, where climate is defined as potential evapotranspiration, and a moisture index. The moisture index is calculated as follows:

$$\text{Moisture Index} = \frac{\text{Annual Water Surplus–Annual Water Deficit}}{\text{Annual Potential Evapotranspiration}} \times 100$$

From Carter and Mather (1966)



(a)

(b)

Figure 1.19 A: Net primary productivity, above and below ground, in relation to mean annual precipitation. From Lieth (1973). B: Net primary productivity in relation to actual evapotranspiration. From Whittaker (1975)

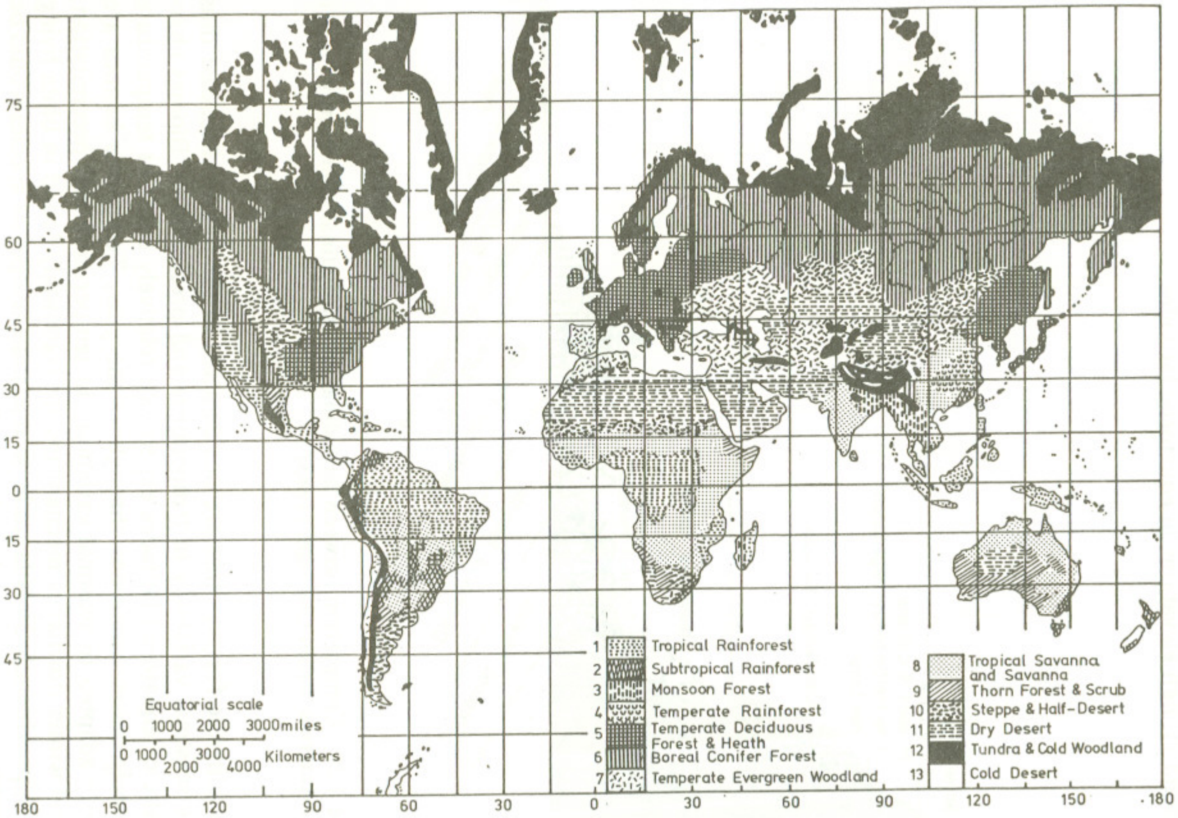


Figure 1.20 Terrestrial biomes of the Earth. From Dansereau (1957)

broad-scale depiction does not resolve elevational variation in biome type, as illustrated in Figure 1.21. Thus, an increase in latitude is similar to an increase in elevation, so that biomes characteristic of northern latitudes can be found at high elevations in equatorial latitudes.

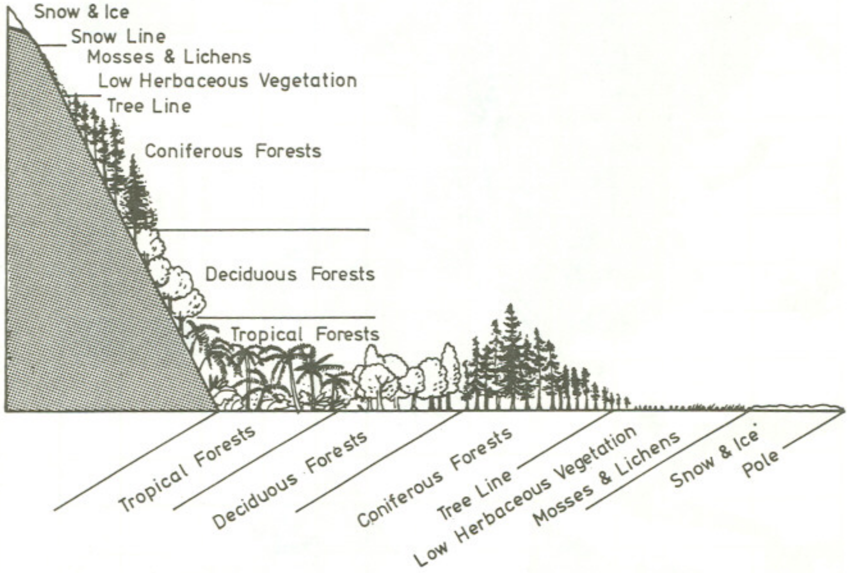


Figure 1.21 Comparison between latitudinal and altitudinal community types in North America. From Clapham (1983)

Two climatic features that are not depicted in the figures discussed thus far are seasonal variability in temperature and precipitation. Biomes characteristic of equatorial latitudes experience relatively constant temperature and precipitation conditions throughout the year. Temperate biomes are variously adapted to seasonal variability in temperature and precipitation. Fall and winter dormancy mechanisms are commonly found in biota living above approximately 30°N latitude, so that some temperate species would be susceptible to the climatic disturbances following a nuclear war only during the growing season, while subtropical and tropical species would be highly vulnerable during the entire year.

1.6.3 Production within World Biomes

Table 1.14 summarizes information on the areal extent and biological productivity of major world biomes. Extreme desert, rock, sand, and ice cover the greatest proportion of the Earth's land surface (16%), yet account for less than 1% of the biological production. Tropical rainforest covers about 11% of all land surface, but accounts for the greatest proportion of terrestrial net primary production (32%), plant biomass (42%), and animal biomass (33%) of any single biome type. Species diversity (richness) is also highest in the tropics.

Open ocean is the predominant marine biome type (Table 1.14). However, all of the other marine biomes shown contribute proportionally more to total marine net primary production, plant biomass, and animal biomass than their areal extent would predict. Thus, continental shelf, estuarine, upwellings, and reef systems are more productive per unit area than is open ocean.

Although marine systems account for 71% of the Earth's surface, only 32% of the net primary production occurs in these ecosystems, and less than 1% of the plant biomass is found there. In contrast, about 50% of the world's animal biomass is found in marine systems, reflecting the dynamic relationship that exists between consumers and primary producers. That is, a relatively small amount of plant biomass supports a large consumer component, because of rapid turnover and high net primary production by the plants that are present. As a result, changes in marine production capacity can rapidly cascade through the food chain having second- and third-order effects on consumers, such as zooplankton and pelagic fishes, and even shorebird populations (e.g., El Niño of 1982–83).

1.6.4 Soil Factors

One final factor of potential importance to the agricultural and ecological responses to the perturbations after a nuclear war is that of soil type. The behavior of radionuclides, for example, would be strongly influenced by the physical and chemical properties of soils, the presence or absence of a permafrost, the height of the water table, and the level of microbial activity in the soil. These features of soils, as well as the soil types themselves, are substantially determined by climatic conditions, as illustrated in Figure 1.22.

Rates of nutrient cycling and litter decomposition would affect radionuclide pathways and retention time. Actual rates of evapotranspiration in comparison with inputs of water from precipitation and other sources would determine whether leaching into groundwater or runoff to watersheds would predominate, or whether an upward evaporative movement prevailed, with associated long retention times.

TABLE 1.14

REPRESENTATIVE PRODUCTION AND BIOMASS SUMMARIES FOR BIOMES OF THE EARTH[a]

Ecosystem Type	Area 10^6 km^2 (% world total[b])	NPP g•m^{-2}•year^{-1} (%world total[c])	Mean Plant Biomass kg•m^{-2} (% world total [c])	Animal Consum. 10^6 t•year^{-1}	Animal Product. 10^6 t•year^{-1}	Animal Biomass 10^6 t (% world total[c])
TERRESTRIAL						
Tropical rainforest	17.0 (11.4%)	2200 (32.5%)	45 (41.6%)	2600	260	330 (32.8%)
Tropical seasonal forest	7.5 (5.0%)	1600 (10.4%)	35 (14.1%)	720	72	90 (9.0%)
Temperate evergreen	5.0 (3.4%)	1300 (5.7%)	35 (9.5%)	260	26	50 (5.0%)
Temperate deciduous	7.0 (4.7%)	1200 (7.3%)	30 (11.4%)	420	42	110 (10.9%)
Boreal Forest	12.0 (8.1%)	800 (8.3%)	20 (13.1%)	380	38	57 (5.7%)
Woodland & shrubland	8.5 (5.7%)	700 (5.2%)	6 (2.7%)	300	30	40 (4.0%)
Savannah	15.0 (10.1%)	900 (11.7%)	4 (3.3%)	2000	300	220 (21.9%)
Temperate grassland	9.0 (6.0%)	600 (4.7%)	1.6 (0.8%)	540	80	60 (6.0%)
Tundra & alpine	8.0 (5.4%)	140 (0.96%)	0.6 (0.3%)	33	3	3.5 (0.3%)
Desert & Semi-desert scrub	18.0 (12.1%)	90 (1.4%)	0.7 (0.7%)	48	7	8 (0.8%)
Extreme desert & rock, sand and ice	24.0 (16.1%)	3 (0.06%)	0.02 (< 0.1%)	0.2	0.02	0.02 (<0.1%)
Cultivated land	14.0 (9.4%)	650 (7.9%)	1 (0.8%)	90	9	6 (0.6%)
Swamp & marsh	2.0 (1.3%)	2000 (3.5%)	15 (1.6%)	320	32	20 (2.0%)
Lake & Stream	2.0 (1.3%)	250 (0.4%)	0.02 (< 0.1%)	100	10	10 (1.0%)
Total Continental	149 (29%)	773[b] (68%[d])	12.3[b] (99.8%[d])	7810	909	1005 (50.2%[d])

[a] Data from Whittaker (1975).

[b] Averaged separately for terrestrial and marine biomes

[c] Based on world net production or biomass for terrestrial and marine biomes separately.

[d] Based on terrestrial + marine totals.

TABLE 1.14 continued

Ecosystem Type	Area 10^6 km^2 (% world total[b])	NPP g•m^{-2}•year^{-1} (%world total[c])	Mean Plant Biomass kg•m^{-2} (% world total [c])	Animal Consum. 10^6 t•year^{-1}	Animal Product. 10^6 t•year^{-1}	Animal Biomass 10^6 t (% world total[c])
MARINE						
Open ocean	332.0 (92%)	125 (75.5%)	0.003 (25.6%)	16,600	2,500	800 (80.2%)
Upwellings	0.4 (0.1%)	500 (0.4%)	0.02 (0.2%)	70	11	4 (0.4%)
Continental shelf	26.6 (7.4%)	360 (17.5%)	0.01 (6.9%)	3,000	430	160 (16.0%)
Algal beds & reefs	0.6 (0.1%)	2,500 (2.9%)	2 (30.8%)	240	36	12 (1.2%)
Estuaries	1.4 (0.4%)	1,500 (3.8%)	1 (35.9%)	320	48	21 (2.1%)
Total Marine	361 (71%)	152[e] (32%[d])	0.01[b] (0.2%[d])	20,230	3,025	997 (49.8%[d])
WORLD TOTALS	510	333	3.6	28,040	3,934	2002

[c] Based on world net production of biomass for terrestrial and marine biomes separately.

[e] Weighted by system.

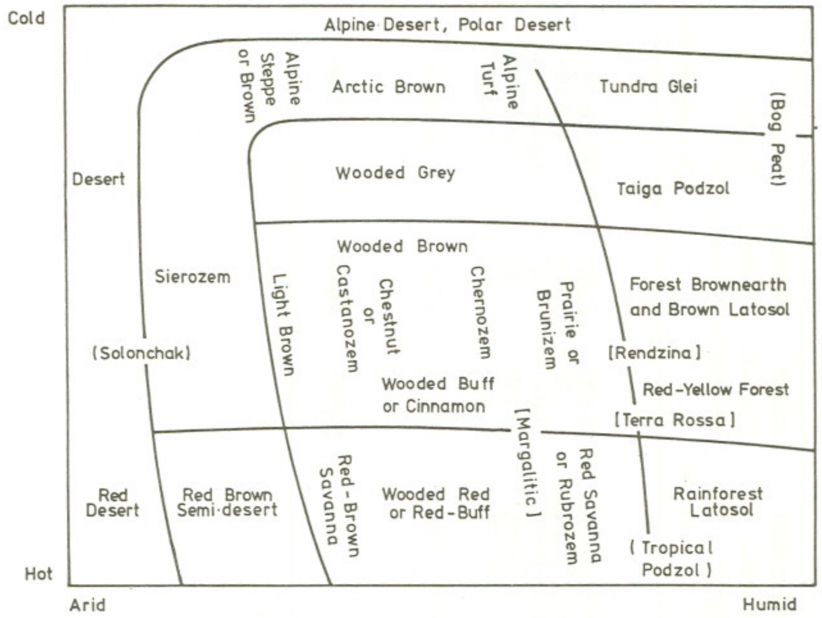


Figure 1.22 Great soil groups in relation to climate. Zonal great groups are shown by relative positions along climatic gradients of humidity on the horizontal axis, and temperature on the vertical. In intermediate climates, both grass dominated and nongrass communities are written on the vertical; soils formed by woodlands and shrublands (or, in the arctic, in tundra) are written on the horizontal for the same climates. Certain nonzonal great soil groups are also shown; those formed with impeded drainage or special conditions of water movement in parentheses. Terminologies and numbers of great soil groups vary among authors. Forest brown earths as used here include more than one group in most classifications; brown latosols occur in tropical mountain forests. From Whittaker (1975)

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