

Ecological consequences of nuclear war

from S.J. McNaughton, R.W. Ruess and M.B. Coughenour

Simulations of the ecological effects on grassland ecosystems projected from the proposed climatic changes that would follow a nuclear war indicate that temperature and light reductions below ambient mean levels exceeding 10°C and 28%, respectively, are required for severe ecosystem deterioration to occur and that thresholds between promotion and decline are very abrupt.

ESTIMATES of the mass of smoke particles that would be injected into the atmosphere by fires following a nuclear war indicate that the resultant attenuation of light by suspended elemental carbon could substantially increase the optical depth of the atmosphere, producing major, rapid reductions of temperature and incident radiation at the Earth's surface¹, a phenomenon termed nuclear winter². Climatic models using various degrees of structural and dynamic detail have provided diverse predictions of the global climatic effects of atmospheric soot loading, but all are in general agreement that fires of the extent and intensity now reasonably projected to follow a nuclear war that included significant targeting of urban centres would lead to major falls in surface light intensities, temperature and, less certainly, precipitation³⁻⁵. More complex models have tended to predict both a longer duration and a broader geographical scale of climatic effects⁶. Transitory surface temperature reductions of more than 40°C and extended reductions of 20°C below mean ambient levels and light reductions to 0.01 and 0.1 of normal have been predicted. To place these estimates in perspective, the seventeenth century 'little ice age' is believed to have been caused by only a 1°C decline below mean ambient temperature⁷, and major glacial and interglacial periods may involve only 10–15°C peak-to-trough changes⁸. The potential biological and ecological consequences of the climatic changes projected to follow nuclear war could obviously be devastating^{9,10}.

Initial evaluations of the potential ecological effects of nuclear winter have been, of necessity, largely qualitative^{9,10}. Here we present quantitative results obtained by applying a wide range of the climatic effects currently predicted to result from atmospheric soot loading after a nuclear war to a documented, detailed, mechanistic simulation model of grassland ecosystem processes¹¹⁻¹³.

Procedures

We used nuclear winter climatic predictions to modify climatic sub-models of the

Grassland Research and Serengeti Systems Model¹¹⁻¹³, hereafter referred to as GRASS. It combines plant physiological processes; plant growth processes; plant morphometry; shoot demography; and grazing, with carbon, nitrogen, radiation and water sub-models. The principal focus of our research is the grazing ecosystem in the Serengeti region of Tanzania and Kenya¹⁵⁻¹⁸, so both biotic and abiotic parameters were drawn from studies of that ecosystem.

Experimental studies leading to parameter values have previously been documented¹⁹⁻²¹. Because the productivity of cultivation agriculture would probably be severely reduced after a nuclear war, forage agriculture and particularly non-subsidized rangelands, might be major food production systems for human survivors in non-combatant countries, many of which might be located in tropical-to-subtropical locations¹⁹.

We parameterized the GRASS simulations described here for mid-height grasses with a terminal canopy height of 50–150 cm, growing in an equatorial location at an elevation of 1,500 m with a mean annual rainfall of 793 mm and a rainfall-determined growing season of 296 days. We produced rainfall events probabilistically by GRASS and included all microclimatic parameters that might reasonably be modified by decreased light, lower temperatures and modified rainfalls. We ran diurnal variables at 2-h time steps and all others at 2-day time steps. For grazing simulations, we harvested the canopy uniformly to a height of 4 cm above the soil surface every 50 days, the optimum defoliation level for maximum mass yield to grazers in previous simulations¹².

The climatic predictions that have resulted from modelling nuclear war scenarios can be applied to ecological modelling in various ways. We chose the imposition of fixed changes on normal seasonal progression for the entire courses of growing seasons as we wanted to saturate a reasonable climatic factor space with ecological simulations that would produce response surfaces over as broad a range of conditions as was relevant, feasible and interesting.

We ran 90 full growing-season simulations, 45 each under grazed and ungrazed conditions, and modified precipitation by applying fixed percentages of –50, –30, –10, +10 and +30 to each rainfall generated by the weather simulator sub-model of the model. We simulated both increased and decreased rainfall because of the uncertainty of precipitation predictions from climatic modelling⁶. Because light intensity and temperature co-vary upon the injection of smoke into the atmosphere¹⁻⁶, we coupled values for those variables down to near freezing night-time temperatures, which terminated growth. Tropical pasture species are both chilling-sensitive and frost-intolerant, although species with ranges that extend outside the equatorial belt often have cold-tolerant populations in cooler habitats²²⁻²⁴. We did not simulate mean temperature reductions lower than 13°C once initial screening indicated that these temperatures produce periodic night-time frosts.

In addition to control conditions, we performed temperature- and light-intensity reductions at °C/% light combinations of –1°C/–6%; –2°C/–12%; –3°C/–16%; –5°C/–22% and –10°C at light reductions of –28%, –50%, –65% and –88%. The last two light reductions simulated atmospheric optical depths near 1 and 2, which might be widely distributed during post-war periods in non-combatant geographical locations¹⁻⁶. Although we did not apply a time-varying post-war trajectory to climatic variables, the typical seasonal patterns of GRASS were preserved, producing characteristic seasonal progression of precipitation, humidity, cloud cover and other normal weather variables. Control mean temperature was 21°C with a mean diurnal range from 28°C daytime highs to 14°C night-time lows. A given temperature reduction reduced maximum, minimum and intervening 2-h interval temperatures by that fixed amount. We superimposed radiation reductions on diurnal patterns and the cloud cover simulator and then fed them into sub-models of radiation and water balances to affect their performance and the resultant temperatures of plant tissues and

soils. Hence, we simulated total productivity, both above- and below-ground.

Baseline validation

Published data on below-ground primary productivity are scarce and our model produces reasonable outputs when compared with the available data¹¹. More widely available are data on above-ground productivity of ungrazed grasslands. We used three such data sets for a model validation internal to the simulations presented here. Data sets of above-ground primary productivities of ungrazed grasslands have been fit to regressions on annual rainfall for the Serengeti ecosystem¹⁸, eastern and southern Africa²⁵ and the world²⁶. There are many similar fitted curves in the literature but we used these three for baseline comparisons because they are both extensive, relevant to the ecosystem modelled, and have no data overlap.

The most complete data set for 52 worldwide sites²⁶ produces a best fit ($r^2 = 0.51$)-line of $ANP = 0.5(\text{rain}) - 29$, where ANP is above-ground net primary productivity in $\text{g m}^{-2} \text{yr}^{-1}$ and rainfall is in mm. A Serengeti dataset for 20 locations subject to neither excessive drainage nor runoff water influx¹⁸ produces a best fit ($r^2 = 0.48$) line of $ANP = 0.69(\text{rain}) - 102$ and the other African dataset of 33 values²⁵ produces a line ($r^2 = 0.67$) of $ANP = 0.85(\text{rain}) - 20$.

Simulated above-ground productivities of ungrazed grasslands at ambient light and temperatures, and rainfalls less than 900 mm, above which both simulated and measured²⁷ productivities become asymptotic to the abscissa, produces a line ($r^2 = 0.97$) of $ANP = 0.48(\text{rain}) - 48$, as similar to the empirical lines as they are to each other. Together with previous comparisons of model performance with published empirical results¹¹⁻¹⁴, these results indicate that GRASS produces realistic grassland performance over a wide environmental range. Still, the application of post-war climatic predictions, themselves of uncertain surety, to any ecological model is a venture into uncharted predictive realms unamenable to experimental verification. But, where verification is feasible, GRASS performance is in good accord with empirical datasets and the climatic projections considered here deal mainly with conditions close to normal climatic variation, rather than extremes of extended cold, dark conditions.

Aftermath simulations

Our control conditions for simulations are 793 mm of rain at normal light and temperature; our baseline is the rainfall span at unreduced light and temperature. The total, above- and below-ground, simulated productivities of ungrazed grasslands are very sensitive to rainfall near

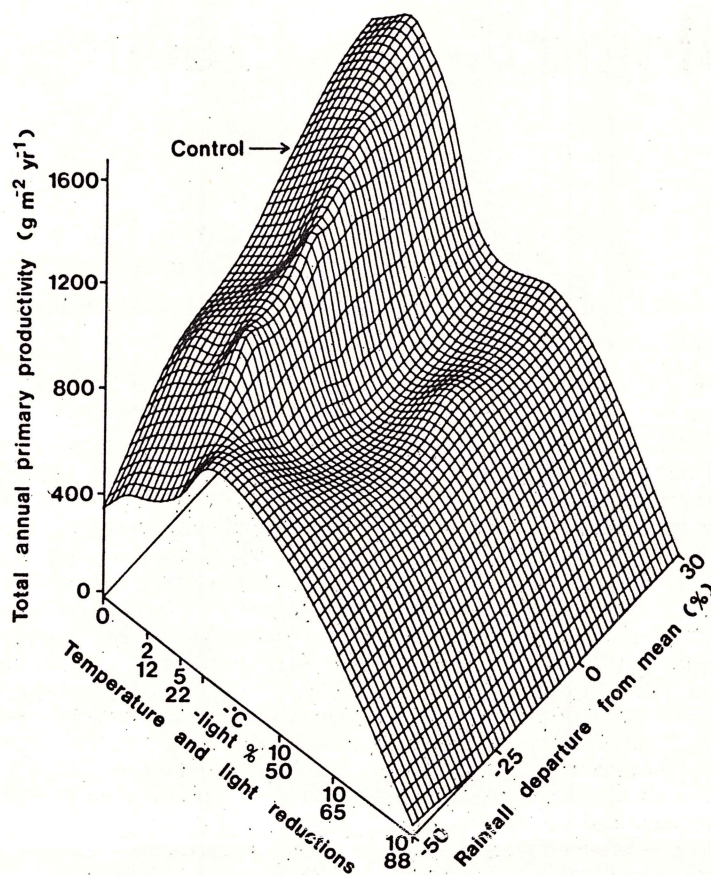


Fig. 1 Simulated total primary productivity in $\text{g m}^{-2} \text{yr}^{-1}$ of ungrazed grasslands in relation to deviations of precipitation and temperature-radiation environments from the long-term mean condition, the indicated by arrow labelled control. Note that the y-axis is linear in light intensity and non-linear in temperature. Data were fitted with the bivariate spline interpolation and graphed with the PROC 3D procedure of the 82.2 enhancements and update release of SAS/GRAPH (SAS Institute, Cary, North Carolina, 1982). Tilt, 60°; rotation, 50°.

normal light and temperature conditions, but are resistant to light and temperature departures from normal until mean reductions approach 28% and 10°C, respectively, below mean ambient levels (Fig. 1). This results in a substantial shelf where primary productivity is near or above control values for moderate climatic changes projected to follow a nuclear war. The upper level of the response surface is twisted by the tendency for cooler, darker conditions to compensate for reduced rainfall.

At the lowest rainfall level, in fact, primary productivity continues to increase at light-temperature reductions that significantly reduce production at higher rainfall levels. Therefore, reduced light and temperature have much greater water-conserving effects at low rainfalls than at higher rainfalls. These environmental interactions were expressed, in part, through compensatory changes in plant water potential, averaged over all shoots. Midway during the growing season, plant water potentials increase from -1.73 MPa at control light/temperature to -0.49

MPa at the 10°C/28% reduction under the lower rainfall conditions. At the highest rainfall conditions, the increase is only from -1.03 to -0.17 in this range.

Plant water potential regulates productivity by influencing net photosynthetic rates and tissue growth rates, and these compensatory interactions are propagated through GRASS performance. In addition, greater rainfalls increase leaf longevity, producing greater average ages of active canopy tissues, which are accompanied by declines in leaf nitrogen content and resultant rates of net photosynthesis. So no simple explanation suffices to explain the twisted response surface; rather, it is a complex consequence of plant growth and metabolic responses to interacting environmental variables. Because of the diagonal crest, productivity at high rainfall levels drops much more precipitously as the more severe region of the factor space is penetrated. The greatly reduced light levels indicate that the grasslands have a broad ability to compensate for light reductions after the initial drop, producing a shelf extending to the light

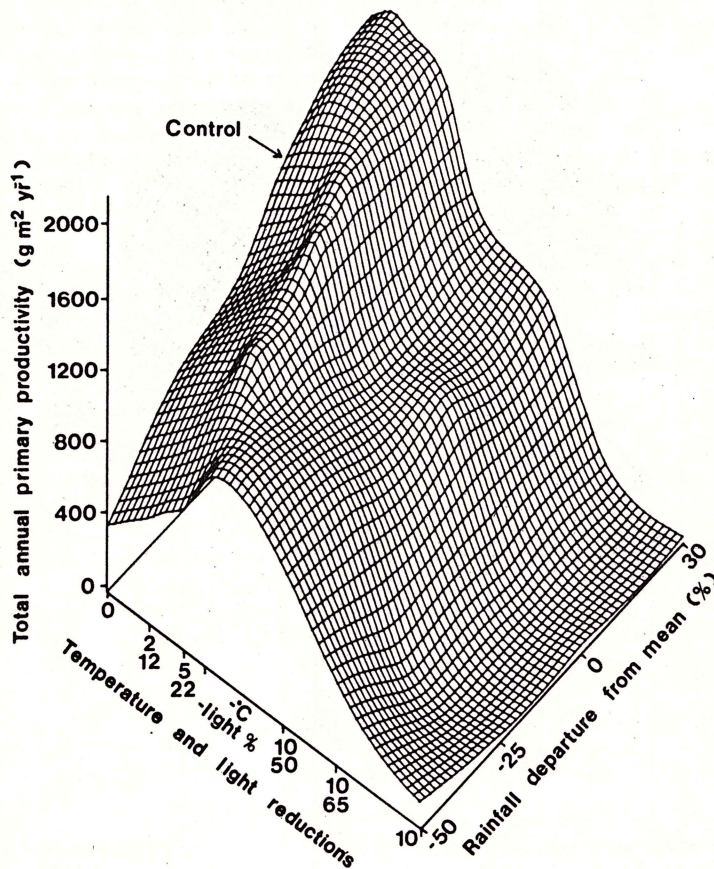


Fig. 2 Simulated total primary productivity in $\text{g m}^{-2} \text{yr}^{-1}$ of grazed grasslands in relation to deviations of precipitation and temperature-radiation environments from the long-term mean condition, indicated by an arrow. Note that the z-axis scale differs from Fig. 1 if comparing the two response surfaces. Data were fitted and plotted as described in Fig. 1 legend. Aspect as in Fig. 1.

intensities produced by an atmospheric optical depth of one. At that optical depth, productivities are 79% of baseline at low rainfall levels, 61% at normal levels, and 46% at the highest simulated rainfall. Beyond an optical depth of 1, however, productivity again plunges precipitously to near zero at an optical depth of 2 and this surface of steeply decreasing primary productivity was rainfall-independent.

More interesting than the obvious fact that severe temperature and light reductions will drive production to zero is the finding that productivities are increased by most simulated post-war light and temperature reductions of moderate extent at a broad range of rainfalls. The minimum productivity on the upper response shelf, equivalent to 41% of control, is produced by the 50% rainfall reduction with no changes in temperature and light. The maximum productivity of the ungrazed simulations, 44% above control, occur at the highest simulated rainfall level accompanied by temperature and light reductions below ambient of 2°C and 12%, re-

spectively. The diagonal crest is produced by the tendency for very minor light/temperature reductions to produce maximum productivities at higher rainfall levels, whereas low rainfall systems continued to exhibit increased productivity at substantial light/temperature reductions. Beyond this crest productivity in low rainfall simulations declined steadily to zero levels, lacking the shelf that occurs at higher rainfalls. These results have important implications for potential yields from water-limited ecosystems in post-war environments.

Grazing stimulates the primary productivities of grasslands at higher rainfall levels but not at low rainfalls; as a consequence, the overall grazed response surface has simpler but much steeper contours (Fig. 2). Primary productivity has a more convex shape under grazed than ungrazed conditions because of higher peaks, steeper contours and more abrupt thresholds. The diagonal crest on the upper shelf is more pronounced because of the tendency for primary production at high rainfall to decline after a slight rise

with minor light/temperature reductions and an extension of the ameliorating range of those reductions at the lowest simulated rainfalls. Net primary productivity is stimulated a maximum of 38% above control conditions by the combination of highest rainfall with a light/temperature reduction of just 1°C and 6%. At baseline conditions, the lowest simulated rainfall reduces the productivity of grazed grasslands to only 28% of the value at control conditions. There is little evidence of a shelf of resistance to light reductions at temperatures above freezing.

Grazed grasslands are generally able to maintain reasonable levels of primary productivities down to a light reduction of 50% below normal, but they are severely inhibited by the reductions produced by an atmospheric optical density of 1. At that level, primary productivities are 19% of baseline at low rainfalls, 12% at normal rainfalls, and 9% at the highest rainfall simulated. Compared with the ungrazed simulation, this result suggests that the trophic web would collapse under conditions still allowing significant primary productivities in ungrazed grasslands.

The ameliorating effects of light and temperature reductions produce steeper responses under grazed conditions over the upper productivity shelf. For example, at control rainfall the productivity of ungrazed systems is 17% below normal at the $10^\circ\text{C}/28\%$ temperature/light reduction. In the grazed ecosystem, in contrast, net primary productivity under those conditions is still 13% above baseline. As a consequence, the descent of productivity as the limiting factor space is penetrated is much more precipitous for grazed than for ungrazed ecosystems.

As grasses must be converted into animal products for uncultivated vegetation in grassland climates to support human populations, secondary productivity is of particular importance to consideration of the potential consequences to humans of climatic changes that might follow a nuclear war. There are two fundamentally different approaches to estimating secondary productivity from model output. The simplest, but perhaps least revealing, is to convert the plant mass consumed by grazers to animal biomass by assuming some conversion efficiency based on animal feeding trials²⁸. That approach assumes that forage quality does not vary across the range of conditions simulated and has the virtue of converting forage consumption per unit area directly into animal yield per unit area.

When we applied a 10% conversion efficiency^{28,29} to animal forage consumption output from GRASS, with that output varying according to both forage amount and its availability due to canopy geometry¹², we found ($r^2 = 0.87$, $P < 0.001$)

that secondary productivity = $0.052 \times$ total primary productivity, the units of productivity are in mass area⁻¹ yr⁻¹ for the 40 environmental combinations above zero. Secondary productivity then, under this assumption, would reproduce the response surface of Fig. 2, but with absolute values 95% lower on a mass density basis.

A second and, we believe, more realistic approach to estimating secondary productivity is to account for differences in forage quality. Both wild³⁰ and domestic³¹ ungulates, particularly in tropical locations, are more often limited by forage quality than by its quantity. Higher mass productivities produced by GRASS are generally accompanied by lower forage quality because nutrients such as nitrogen are diluted by carbon accumulation in plant tissue, consistent with real ecosystems³². Over the range of non-zero conditions simulated here, the relationship between the nitrogen content of forage consumed and the mass of carbon that is consumed is

$$\%N = 1.93 - 0.00386 \text{ gC}$$

where $r^2 = 0.92$, $P < 0.001$ and gC is grams of carbon consumed per square metre of land surface per year.

As a consequence of this negative relationship between forage quality and mass availability, the amount of N consumed was asymptotically related to the amount of forage carbon consumed ($r^2 = 0.86$, $P < 0.001$) with $\text{gN} = (2.27 \ln \text{gC}) - 5.2$ where units are masses of N and C m⁻² yr⁻¹. This conundrum relating forage quality and quantity of further exacerbated by a positive relationship between forage nitrogen content and the digestibility of that nitrogen (ref. 33). Therefore, as a more realistic approach to estimating potential secondary productivities of post-war ecosystems, we multiplied N yield to grazers in gN M⁻² yr⁻¹ by the digestibility of that N predicted from the linear relationship between forage N content and digestibility of N (ref. 33). This yielded digestible gN m⁻² yr⁻¹ consumed by grazers. Additional assumptions that we are unwilling to make at this stage would be required to convert the areal yield of digestible N to animal production, but the shape of the response surface is more likely to reflect the secondary productivity potentials of post-war ecosystems than the simple conversion from Fig. 2.

The quality-based secondary productivity response surface produced by GRASS varies markedly from both primary productivity surfaces (Fig. 3). Maximum secondary productivity, 38% above the control value, is produced at moderate drought and no reduction of ambient light and temperature. Minimum secondary productivity potential outside the severe factor space is at the highest rainfall with temperature-light reductions of 5°C/22%, where the value is only 36% of the control. This response surface is caused by a

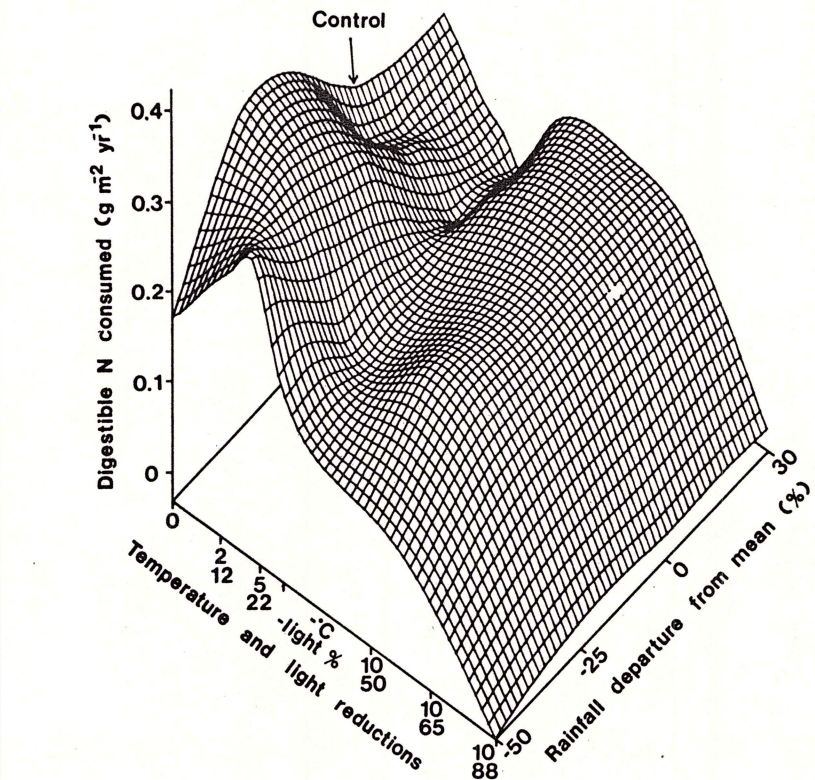


Fig. 3 Simulated yield of digestible N to grazers in g m⁻² yr⁻¹ in relation to deviations of precipitation and temperature-radiation environments from the long-term mean condition, indicated by an arrow. Data were fitted and plotted as described in the legend for Fig. 1. Aspects as in Fig. 1.

greater reduction in plant-carbon assimilation than of nutrient assimilation by mild environmental stress, a phenomenon documented empirically^{34,35} and that GRASS reproduces. As a consequence, there was a pronounced peak of secondary productivity potential at a rainfall reduction to 30% below normal in baseline light and thermal environments. Values drop precipitously around this optimum, particularly at lower rainfall levels and no light/temperature reduction. But the surface is convoluted with folds and pockets, especially as severely limiting conditions are approached. Reduced light levels at non-freezing temperatures produce a broad secondary shelf of slightly increasing secondary productivity potential with a reversal of the rainfall field leading to higher potentials at higher rainfalls. At light intensities above half normal, potential secondary productivity drops sharply to zero. Compared with control conditions, all higher rainfall simulations and all reduced light and temperature conditions under the normal rainfall regime result in secondary productivity potential lower than the control. But many of the climatic conditions predicted to follow a nuclear war, that is, combinations of reduced rainfall with cooler, darker con-

ditions, result in significant enhancements in the yield of digestible N to herbivores.

When compared with the primary productivity simulations and simple extrapolations of secondary productivity from them, these simulations highlight two significant features of ecosystems. First, countervailing processes make it difficult, if not impossible, to optimize all performance standards simultaneously. Second, simple extrapolations are incapable of providing meaningful estimates of the effects of complex biological responses to environmental variation.

Implications

We make no claim for the ultimate accuracy with which GRASS simulations could predict the ecological aftermath of a nuclear war. But we do believe that those projections are fundamentally realistic; that they provide reasonable boundary conditions for severe declines in ecosystem carrying capacity; and that they prudently reflect the ecological conditions that could be expected to occur in many grassland and other water-limited ecosystems following such a war. Primary productivities under both grazed and ungrazed conditions, and secondary productivity potentials, are stimulated by cli-

matic conditions that would be relatively severe under normal conditions, although they can be characterized as mild compared with the more extreme nuclear winter conditions predicted by some models. The abrupt interfaces between stimulatory and degradative effects emphasize the hazards associated with deductions from imprecise climatic predictions.

The sensitivity of our simulations to the countervailing effects of precipitation and radiation-temperature changes within the non-severe factor space indicates that it would be profitable to devote more effort in climatic modelling to precise definitions of the coupling between precipitation and radiation-thermal regimes, perhaps at the sacrifice of global spatial scales where the models are in general, if not precise, agreement. Because climatic effects have post-war meaning only through their ecological effects, more attention to ecological modelling is clearly also warranted.

Our simulations indicate several areas where additional empirical research could contribute fruitfully to a better understanding of both the potential ecological consequences of nuclear war and basic ecological knowledge. We terminated temperature reductions at levels just above those producing periodic nighttime frosts as tropical pasture plants are both chilling sensitive and frost intolerant²²⁻²⁴. However, strains of a widely cultivated tropical grass, *Cynodon dactylon*, have been produced that are tolerant of winter conditions to near 40° N in central North America³⁶, and tropical species with ranges extending outside equatorial locations have frost tolerant genotypes^{22,23}. This suggests that there is sufficient genetic variability in tropical grasses to produce freeze-tolerant genotypes, and natural selection accompanying severe nuclear winter would be intense. If some tolerant genotypes survived as either dormant individuals or as seeds, ecosystem recovery might be possible following even the most severe nuclear winter. We know of no extensive evidence on the freeze tolerance of drought-dormant rather than

actively growing tropical grasses. Nuclear winter during the tropical dry season might not result in extensive plant mortality if drought-hardened individuals are also cold tolerant; information on the relationships between these adaptive traits would allow more realistic estimates of the expected recovery potentials of tropical and subtropical ecosystems if severe nuclear winter penetrated those geographical regions. Information is also limited on the seed banks of tropical soils and the freeze tolerance of those seeds²³. Nuclear winter would expose seeds to cold, dry, dark environments, which in many cases are optimal for increasing seed longevity.

Secondary productivities can also be influenced by many factors in addition to the limitations imposed by food quantity and quality. Radiant heat load³⁷, availability of water, wind speed²⁸, mineral nutrient availability^{31,33} and the shield of veterinary practices protecting both wild and domestic ungulates from potentially epidemic disease^{38,38} could all be modified by post-war conditions. In addition, cold rains accompanying periodic smoke cover and chilling that precipitates water out of the atmosphere might have devastating effects on tropical animals. Realistic estimates of such ecological effects would add precision to estimates of the post-war carrying capacity of ecosystems.

But even with the many uncertainties, we believe that the results of simulations with GRASS have three principal implications for the carrying capacities of ecosystems were a nuclear war to modify climate in the directions now envisaged. First, mild (by the standards of nuclear winter) climatic changes tending to reduce heat loads and evaporative demands of the atmosphere might increase the productivities of many water-limited ecosystems. Such ecosystems occupy major expanses of Earth's surface.

Second, distinctly different conditions lead to performance optima at different levels in the trophic web. Those optima, therefore, cannot be attained simultaneously. Grain production, for example,

would probably track the response surface that we obtained for primary productivities of ungrazed vegetation. Because grassland climates are centres of grain production, increases in precipitation and/or reduced evaporative demands could tend to increase substantially the grain production potential of post-war ecosystems. Animal production, on the other hand, would probably be inhibited by the same conditions.

Third, and, we believe most important, the transition between non-catastrophic (even favourable) environmental changes and those that are calamitous may be extremely abrupt. The presence of those thresholds in all three simulation results suggests that the ecological effects of a nuclear war are very unpredictable and may change drastically over narrow environmental ranges. A population of human survivors in tropical-to-subtropical locations might encounter an increased carrying capacity for certain climatic perturbations only to be plunged into destruction by a seemingly minor drift away from those conditions. Overall, our results emphasize the uncertainty that must be attached to any predictions about the ecology of a post-war Earth, and suggest that ecological unpredictability itself could be one of the most damaging consequences of post-war climatic effects.

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S.J. McNaughton and R.W. Ruess are at the Biological Research Laboratories, Syracuse University, 130 College Place Syracuse, New York 13210, USA; and B.M. Coughenour is at the Natural Resources Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523, USA.

- Crutzen, P.J. & Birks, J.W. *Ambio* 11, 114-125 (1982).
- Turco, T.P., Toon, O.B., Ackerman, T.P., Pollack, J.B. & Sagan, C. *Science* 222, 1283 (1983).
- Covey, C., Schneider, S.H. & Thompson, S.L. *Nature* 308, 21-25 (1984).
- Crutzen, P., Galbally, I.E. & Bruhl, C. *Climatic Change* 6, 323-364 (1984).
- Thompson, S.L. *et al. Ambio* 12, 236-243 (1984).
- Pitcock, A.B. *et al. Environmental Consequences of Nuclear War Vol. 1* (Wiley, Chichester, 1986).
- Parker, G. *Europe in Crisis 1598-1648* (Harvester, Sussex, 1980).
- Heusser, C.J., Streeter, S.S. & Stuiver, M. *Nature* 294, 65-67 (1981).
- Ehrlich, P.R. *et al. Science* 222, 1293-1300 (1983).
- Harwell, M.A. & Hutchinson, T.C. *Environmental Consequences of Nuclear War, Vol. 2* (Wiley, Chichester, 1985).
- Coughenour, M.B., McNaughton, S.J. & Wallace, L.L. *Ecol. Modelling* 23, 101-134 (1984).
- Coughenour, M.B., McNaughton, S.J. & Wallace, L.L. *Ecol. Modelling* 26, 177-201 (1984).
- Coughenour, M.B. *Ecol. Modelling* 26, 203-220 (1984).
- Coughenour, M.B. *Ann. Mo. Bot. Gard.* 72, 852-963 (1985).
- McNaughton, S.J. *Science* 191, 92-94 (1976).
- McNaughton, S.J. *Am. Nat.* 113, 691-703 (1979).
- McNaughton, S.J. *Ecol. Monogr.* 53, 291-320 (1983).
- McNaughton, S.J. *Ecol. Monogr.* 55, 259-294 (1985).
- McNaughton, S.J., Wallace, L.L. & Coughenour, M.B. *Ecology* 64, 307-318 (1983).
- Ruess, R.W., McNaughton, S.J. & Coughenour, M.B. *Oecologia* 59, 253-261 (1983).
- Coughenour, M.B., McNaughton, S.J. & Wallace, L.L. *Afr. J. Ecol.* 23, 179-194 (1985).
- Clements, R.J. & Ludlow, M.M. *J. appl. Ecol.* 14, 551-566 (1977).
- Humphreys, L.R. *Environmental Adaption of Tropical Pasture Plants* (Macmillan, London, 1981).
- Larcher, W. & Baurer, H. in *Physiological Plant Ecology I, Encyc. Plant Phys.* Vol. 12A (eds Lange, O.L., Nobel, P.S., Osmond, C.B. & Ziegler, H.) 403-437 (Springer, New York, 1981).
- Deshmukh, I.K. *Afr. J. Ecol.* 22, 181-186 (1984).
- Lauenroth, W.K. in *Perspectives in Grassland Ecology* (ed. French, N.) 3-24 (Springer, New York, 1979).
- Sims, P.L. & Singh, J.S. *J. Ecol.* 66, 573-597 (1978).
- Garrett, W.N., Bond, T.E. & Kelly, C.F. *J. Anim. Sci.* 19, 60-66 (1960).
- Lodge, G.A. & Lamming, G.E. *Growth and Development of Mammals* (Butterworths, London, 1968).
- Sinclair, A.R.E. *J. Anim. Ecol.* 44, 497-520 (1975).
- McDowell, L.R., Conrad, J.H., Ellis, G.L. & Loosli, J.K. *Minerals for Grazing Ruminants in Tropical Regions* (Univ. Florida, Gainesville, 1983).
- Vitousek, P. *Am. Nat.* 119, 553-572 (1982).
- McDonald, P., Edwards, R.A. & Greenhalgh, J.F.D. *Animal Nutrition* (Longman, London, 1973).
- White, T.C.R. *Oecologia* 22, 119-134 (1976).
- Mattson, W.J. *A. Rev. Ecol. Syst.* 11, 119-161 (1980).
- Beard, J.B. *Turfgrass: Science and Culture* (Prentice-Hall, Englewood Cliffs, New Jersey, 1973).
- Garrett, W.N., Givens, R.L., Bond, T.E. & Hull, J.L. *Proc. Western Sect. Am. Soc. Anim. Sci.* 17, 349-355 (1966).
- Rossiter, R.B. *et al. Vet. Rec.* 113, 459-461 (1983).
- Rossiter, P.B. *et al. Prev. Vet. Med.* 1, 257-264 (1983).