

- Brown, C. J. (1985). The status and conservation of the Cape vulture in SWA/Namibia. *Vulture News*, **14**, 4–15.
- Brown, C. J. (1986). Biology and conservation of the lappet-faced vulture in SWA/Namibia. *Vulture News*, **16**, 10–20.
- Brown, C. J. (1988). Scavenging raptors on farmlands: what is their future? *Afr. Wildl.*, **42**, 103–5.
- Brown, L. H. (1966). Observations on some Kenya eagles. *Ibis*, **108**, 531–7.
- Brown, L. H. & Cade, T. J. (1972). Age classes and population dynamics of the bateleur and the African fish eagle. *Ostrich*, **43**, 1–16.
- Clancey, P. A. (1964). *The Birds of Natal and Zululand*. Oliver & Boyd, Edinburgh.
- Cramp, S. & Simmons, K. E. L. (eds.). (1980). The birds of the western Palearctic, Vol. 2. Oxford University Press, Oxford.
- Giess, W. (1971). A preliminary vegetation map of South West Africa. *Dinteria*, **4**, 1–114.
- Hickey, J. J. (1952). Survival studies of banded birds. *U.S.D.I. Spec. Sci. Rep. Wildlife*, No. 15.
- Hustler, K. & Howells, W. W. (1986). A population of tawny eagles in the Hwange National Park, Zimbabwe. *Ostrich*, **57**, 101–6.
- Hustler, K. & Howells, W. W. (1987). Breeding periodicity, productivity and conservation of the martial eagle. *Ostrich*, **58**, 135–8.
- Liversidge, R. (1984). The importance of national parks for raptor survival. *Proc. Pan-Afr. Ornith. Congr.*, 5th, 589–600.
- Mendelsohn, J. M. (1978). A study of the black-shouldered kite *Elanus caeruleus*. PhD thesis. University of Natal, Pietermaritzburg.
- Mundy, P. J. (1982). *The Comparative Biology of Southern African Vultures*. Vulture Study Group, Johannesburg.
- Newton, I. (1979). *Population Ecology of Raptors*. T. & A. D. Poyser, Berkhamsted.
- Piper, S. E., Mundy, P. J. & Ledger, J. A. (1981). Estimates of survival in the Cape vulture *Gyps coprotheres*. *J. Anim. Ecol.*, **50**, 815–25.
- Smeenk, C. (1974). Comparative ecological studies of some East African birds of prey. *Ardea*, **62**, 1–97.
- Snyder, N. F. R. & Wiley, J. W. (1976). Sexual size dimorphism in hawks and owls of North America. *Ornith. Monogr.*, **20**, 1–96.
- Steyn, P. (1973). Observations on the tawny eagle. *Ostrich*, **44**, 1–22.
- Steyn, P. (1982). *Birds of Prey of Southern Africa*. David Philip, Cape Town.
- Tarboton, W. R. & Allan, D. G. (1984). The status and conservation of birds of prey in the Transvaal. *Transvaal Mus. Monogr.*, No. 3.
- Watson, R. T. (1986). The ecology, biology and population dynamics of the bateleur eagle *Terathopius ecaudatus*. PhD thesis. Johannesburg, University of the Witwatersrand.



Kirtland's Warbler Habitats: A Possible Early Indicator of Climatic Warming

Daniel B. Botkin, Douglas A. Woodby & Robert A. Nisbet

Department of Biological Sciences and Environmental Studies Program,
University of California, Santa Barbara, California 93106, USA

(Received 28 February 1990; revised version received and accepted 7 June 1990)

ABSTRACT

If the projections of global climate models are correct, jack pine Pinus banksiana forests in central Michigan, managed as the primary nesting habitat for the endangered species Kirtland's warbler Dendroica kirtlandii, will soon be growing at a significantly slower rate than they have in the recent past. As a result, these forests may become unsuitable as habitat for the warbler within 30–60 years. This projection is based on results from a global climate model applied to a forest growth model. The robustness of these predictions is discussed. Measurement of tree growth in these forests could provide some of the earliest evidence of biological effects of climatic warming due to an increase in greenhouse gases in the atmosphere.

THE IMPORTANCE OF THE KIRTLAND'S WARBLER AS A CASE STUDY OF GLOBAL WARMING EFFECTS

It has been suggested that climatic shifts brought on by global 'greenhouse' warming may lead to local habitat changes and possible extinction of species with highly restricted ranges (Peters & Darling, 1985; Botkin & Nisbet, 1990). In part, this would be a result of rapid movement of climatic zones. For example, in the mid-latitudes of eastern North America, climate zones are predicted to move northward several hundred kilometers over the next century (Zabinski & Davis, 1989) at approximately ten times the rate characteristic of the Holocene and Pleistocene (Schneider, 1989), so that present vegetation types may be replaced by those characteristic of more

southern regions (Botkin *et al.*, 1989). But this effect could be made worse by the patchiness of the contemporary landscape, within which habitats of endangered species have become ecological islands locally isolated from one another. The extent to which global warming might affect extinction rates of endangered species has, however, only been a subject for qualitative speculation.

In this paper we present quantitative projections of the effects of global warming on an important example in biological conservation: the Kirtland's warbler *Dendroica kirtlandii*, an endangered species which nests only in the lower peninsula of Michigan (Fig. 1).

The Kirtland's warbler, the object of considerable management effort and scientific study, provides an important example of the possible impacts of global warming on endangered species. It was the first song bird subject to a complete census, and the population history of this species is comparatively well-known (Mayfield, 1960; Walkinshaw, 1983). The numbers dropped



Fig. 1. Map of Michigan's lower peninsula showing the past breeding range of Kirtland's warbler (1975-85) and the distribution of the Grayling sand soil type. Adapted from Byelich *et al.* (1985). □, townships with Kirtland's warbler nests; ■, Grayling sand.

from an estimated 432 males in 1951 (Mayfield, 1953) to just 201 males censused in 1971 (Mayfield, 1972), recovering only to 212 males censused in 1989 (J. Weinrich, pers. comm.). This rapid decline had two important results: it stimulated scientific study of the species and led to a management plan for its conservation that is now underway.

In the 1960s, it was posited that the most important cause for the drastic decline of the Kirtland's warbler population was the loss of its breeding habitat, jack pine *Pinus banksiana* stands in central Michigan, and that the decline in jack pine was the result of fire suppression (Byelich *et al.*, 1985). As a result, formal management plans based on the need for forest fire and the advice of experts, and first initiated in the late 1950s, were expanded in the early 1970s and continue today to promote recovery of the warbler (Byelich *et al.*, 1985). These plans include extensive habitat management through controlled burning to increase the area of young jack pine. Possible rapid climate change raises questions as to the outcome of this habitat management.

Jack pine, as a fire-dependent species, requires periodic fires for regeneration (Fowells, 1965). Trees of this species are intolerant of shade, and seedlings and saplings are unable to grow under a forest canopy. Cones open and release seeds only after they have been heated in a forest fire. Thus, without fire jack pine does not germinate and, if it could, would not grow within a mature forest. Like many other species of pine, it has persisted in areas subject to frequent, recurring fires. For example, in northern Minnesota the average fire recurrence in jack pine habitats prior to the 20th century was in the order of 15-30 years (Heinselman, 1981). With fire suppression in the 20th century, fire recurrence in the same area has decreased to as long as 800 years (Hall *et al.*, in press).

Given this information, there are three reasons why quantitative projections of the decline of the Kirtland's warbler habitat due to global warming would be useful. The first is to signal the potential loss of an endangered species as a result of global warming, which may require new and unique management efforts to prevent. Second, we propose that monitoring growth of jack pine may provide early evidence of a biological effect of global warming. Third, the projections may be useful to those concerned about the potential climatic effects on endangered species in general. While the habitat requirements of the Kirtland's warbler are unique, the specificity of these requirements are typical of many endangered species, and in this and other ways the effects of global warming on the Kirtland's warbler are representative of the problems to be faced by many other endangered species that depend on forests for habitat.

Because of the longevity of trees, changes in forest composition might occur slowly relative to climatic change (Smith, 1965; Davis & Botkin, 1985).

However, global climate models project that mid-latitudes will undergo rapid, pronounced warming (Manabe & Stouffer, 1980; Ghan *et al.*, 1982; Hansen *et al.*, 1983, 1988; Manabe & Wetherall, 1987; Schlesinger & Mitchell, 1987; Schlesinger & Zhao, 1988). The sensitivity of forests to these changes may vary with many environmental factors, including the present climate regime and soil conditions.

Jack pine occurs throughout a large part of North American boreal forest (Fowells, 1965; Botkin & Simpson, 1990). However, the Kirtland's warbler nests only in young (6–21 year old) jack pine stands and almost exclusively where these grow on a single soil type, Grayling sands—a coarse sand found only at the southern edge of the jack pine's range in the northern lower peninsula of Michigan (Byelich *et al.*, 1985) (Fig. 1). Hence the concern is that, if jack pine fails to regenerate in this area, the warbler will be unable to find suitable habitat elsewhere in North America, and will become extinct.

CLIMATE PROJECTIONS

To explore the consequences of projected rapid climatic warming for jack pine in Michigan, we used climate projections for a transition from current conditions to that under twice CO₂ atmospheric concentration from the GISS general circulation model of NASA Goddard Space Flight Center, New York (Hansen *et al.*, 1983). Those projections are based on a smooth transition in CO₂ concentrations over a 90-year period starting in 1980. Monthly temperature and precipitation from this model were used as input to a revised version of the JABOWA forest model (Botkin *et al.*, 1972; Davis & Botkin, 1985; see below).

The 1951–80 weather records from Grayling, Michigan served as the 'normal' climate, applied in repeating sequence to project climate for 1980–2070. A greenhouse-gas induced warming climate was projected by modifying these records as follows. Ratios between the GISS 'normal' steady-state CO₂ conditions and gradually enhanced CO₂ conditions were calculated for mean monthly temperature and total monthly precipitation (R. Jenne, NCAR, pers. comm.). These ratios were then multiplied by the actual mean monthly temperature and precipitation at Grayling, Michigan. The climate model projects a great increase in temperature and overall slight increase in precipitation (temperature and precipitation patterns for 'normal' and 'global warming' climates are shown in Fig. 2). The large increase in temperature produces a large increase in evapotranspiration that, in spite of an increasing rainfall, leads to drier soils. Both the warming of the air temperature and drying of the soils can affect tree growth in reality as well as in the model.

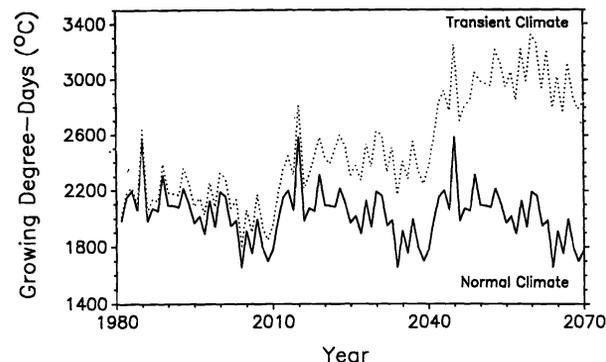


Fig. 2. Projected pattern of growing degree-days (°C) from 1980 to 2070 for 'normal' and global warming 'transient' climates. The normal pattern is the 1951–80 temperature pattern repeated. The global warming pattern is that for 1951–80 modified by the projections of the NASA GISS climate model (Hansen *et al.*, 1983, 1988). See text for explanation.

The forest model

The forest model is a well-established stochastic model (Botkin *et al.*, 1970, 1972) previously applied to problems of climate change (Davis & Botkin, 1985; Solomon & West, 1987; Botkin *et al.*, 1989) and modified by us to include improved methods of modeling soil moisture dynamics and tree responses to soil moisture conditions (Botkin & Levitan, 1977), and nitrogen requirements of trees (Aber *et al.*, 1979), as well as parameters to characterize 33 major tree species of the North American boreal and northern hardwood forests (Botkin *et al.*, 1989). Details of the model's equations and algorithms are given in those papers and are expanded in a new book (Botkin, in press); here the model is described briefly for those readers unfamiliar with it and information is provided concerning aspects of the model especially relevant to the jack pine in the Kirtland's warbler habitat.

The forest model simulates the process of forest growth by calculating the regeneration of each species, in terms of the number of new stems added to a plot each year, and the growth and mortality of individual trees on annual time steps on small 10 × 10 m plots. The annual growth in height and diameter of each tree is a result of life-history characteristics for each species and its species-specific response to the simultaneous environmental limitations of light, air temperature, soil moisture, soil nutrient conditions and stand crowding. In our newest version of JABOWA, a complete water balance is calculated for each month which depends on the monthly rainfall and temperature, soil depth, soil moisture holding capacity (which in turn is

a function of the average soil particle size), and depth to the water table (Botkin *et al.*, 1989). The modeled responses of growth to each of these factors is based on the long history of research on the physiology of vegetation in general and woody plants in particular (see, for example, Kramer and Kozlowski, 1960, 1979; Kozlowski, 1971).

In reality, and as projected by the model, only a subset of the 33 tree species are actually able to grow under the conditions found in the jack pine plains of Michigan's northern lower peninsula due to environmental constraints. That area is colder and drier and has poorer soil fertility than most surrounding areas. Typical dominant tree species in these areas include jack pine, white pine *Pinus strobus*, red pine *P. resinosa*, and trembling aspen *Populus tremuloides*.

The temperature response function is of particular concern for the simulations considered here. In the model, the response of trees to temperature is a parabolic function of heat tolerance, as suggested by the extensive literature of the response of woody plants to temperature (Helmers, 1962; Kramer & Kozlowski, 1960; Botkin *et al.*, 1972, 1989). Heat tolerance (HT_i) for species i , expressed as annual growing degree-days, is estimated by summing daily temperatures above 4.4°C, so that

$$HT_i = \frac{4(DD - DD_{\min,i})(DD_{\max,i} - DD)}{(DD_{\max,i} - DD_{\min,i})^2}$$

where DD = growing degree-days during the current year at the site; $DD_{\min,i}$ = value at the southern end of the range of species, and $DD_{\max,i}$ = value at the northern end of the range of species.

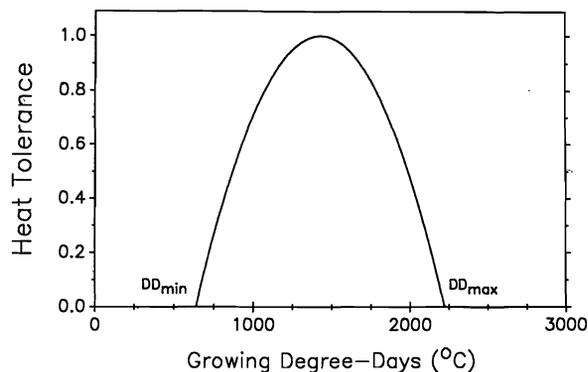


Fig. 3. The heat tolerance curve of jack pine used in the forest model. DD_{\min} and DD_{\max} are the lower and upper growing degree-day limits as derived from range maps.

Growing degree-days is the sum of the days \times °C above 4.4°C under the annual curve of temperature.

Because of the lack of laboratory data on the growth responses of jack pine and other species, the cold and warm temperature limits of a species (where the temperature growth response is zero) are calculated as the average growing degree-days at the observed current geographic northern and southern limits of the species. As a result, the growth falls off rapidly as the borders of the range of a species are approached. The hypothesized growth response for jack pine is shown in Fig. 3.

Reproduction is limited by the same environmental constraints that affect tree growth. In the model, mortality is a stochastic function of the maximum possible age of each species, and the risk of mortality increases for trees that are growing poorly. Fires are common on the jack pine plains of Michigan, and these are simulated by killing all trees every 30 years in rough concordance with the managed disturbance frequency (Byelich *et al.*, 1985).

RESULTS: DECLINE OF JACK PINE HABITAT

Under the normal climate, simulations indicate that jack pine increases steadily between each fire, just as has occurred in the past (Fig. 4(a)). For these conditions, the model's projections are realistic, based on the known natural history of the species (Fowells, 1965). Surprisingly, the response of jack pine to the transient climate due to global warming is almost immediate. By the projected year 1985, basal area of jack pine (the cross-sectional area of tree stems) is significantly lower under transient climate conditions than under normal climate ($p > 0.95$; t -test). As the climate changes, other tree species are predicted to become dominant. By year 2040, quaking aspen *Populus tremuloides* and oaks *Quercus* spp. are dominant, but only small stems of oaks are common by year 2070 (Fig. 5). Although aspen and oak come in to replace jack pine, a mature forest never develops; the low basal area indicates an open woodland of small stems. Thus, the model projects that a forest subject to projected global warming and composed solely of the native species now present in the area would not persist throughout the next century.

How robust are these projections? The most vulnerable part of the model is the estimation of parameters for specific equations that relate tree growth and regeneration to environmental conditions. Of particular concern are the parameters for the temperature response of jack pine. Under the normal climate regime at Grayling near the Kirtland's warbler habitat, simulated growth of jack pine is highly sensitive to the estimated heat tolerance of the species. In fact, the temperature regime of Grayling, Michigan is only slightly

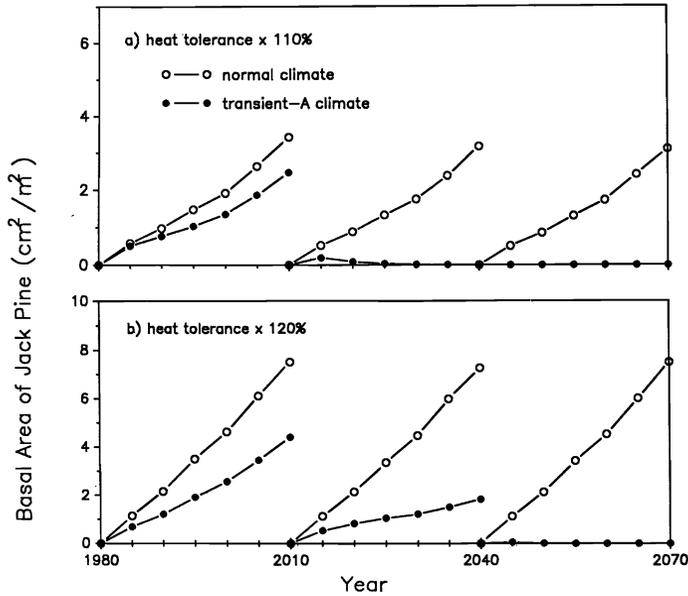


Fig. 4. Projected basal area of jack pine *Pinus banksiana* near Grayling, Michigan under normal climate (○) and transient-A climate (●) for the 90 year period 1980–2070, representing three periods of growth between controlled burns. (a) Basal area projections with thermal tolerance (maximum growing degree-days) of jack pine increased by 10% and (b) by 20%. Basal area is the cross-sectional area of the tree stems, summed by species for all trees in a sample. The soil particle size is a coarse sand to represent the Grayling sand where the Kirtland's warbler nests. Soil moisture holding capacity is defined as 50 mm of water per meter depth of soil. Soil depth is 0.4 m; depth to the water table is 1 m; nitrogen content of the soil is 42 kg ha⁻¹. Initial conditions are a clearing with no trees but adequate seeds available for regrowth of any of the species for which the climate is suitable.

cooler than the estimated maximum tolerated by jack pine, and our initial simulations failed to allow normal growth without increasing our estimate of jack pine's heat tolerance. Realistic growth in diameter of jack pine was achieved with an upper heat tolerance boosted by 10% to 2222°C growing degree-days, and this estimate served as our control. This suggests that the actual geographic range of jack pine is greater than that generally observed in the 20th century, or that ecotypes of the species that occur near the southern edge of the range have a greater temperature tolerance than the average for the species.

We tested the sensitivity to error in estimation of jack pine's heat tolerance

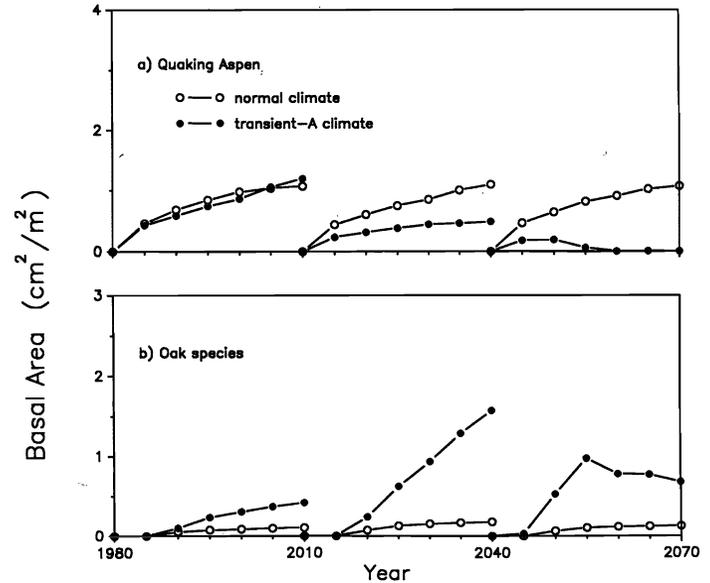


Fig. 5. Projected basal area of (a) quaking aspen *Populus tremuloides* and (b) oaks *Quercus* spp. under normal climate and transient-A climate scenarios. Conditions are as given for Fig. 4(a). Oak species include red oak *Q. rubra* and white oak *Q. alba*.

by increasing the maximum tolerance an additional 10% to 2444°C growing degree-days. Even with this more extreme heat tolerance, statistically significant reductions in basal area are projected to occur within the first five years (by 1985) after an initial fire ($p > 0.95$; t -test). Stark reductions in jack pine growth are still predicted to occur in the second 30-year period (after 2010) (Fig. 4(b)), so that the extent of the decline, but not the timing, is delayed.

As mentioned earlier, the model includes responses of trees to soil water as well as to air temperature. In another application of the model, oak-dominated woodlands near Mt Pleasant, Michigan responded more to changes in soil moisture than in air temperature (Botkin *et al.*, 1989). In this case the woodlands are nearer to the prairie-forest border and maps of presettlement vegetation show patches of prairie intermixed with oak forests. The oaks are not near their southern temperature limits but are near the western boundary for soil moisture for tree growth. Thus, the model suggests that whether soil moisture or air temperature changes will dominate the impact of global warming on forests depends on site

conditions and the biogeography of the tree species. The Kirtland's warbler habitat is so near the southern temperature limit of jack pine that in this case the temperature response overwhelms other effects.

DISCUSSION AND CONCLUSIONS

Results indicate that, in spite of the longevity of trees, jack pine forests that are the habitat of the Kirtland's warbler might respond surprisingly rapidly to the projected global warming. The quickness with which jack pine might decline, and therefore, the speed with which the breeding grounds of the warbler might disappear, suggests that the warbler may be subject to a greatly increased risk of extinction. This in turn implies that managers of that habitat may need to consider the implications of global warming, so that management plans might be adjusted before the species undergoes another serious decline. The plans might be modified to include: breeding of hybrids of jack pine with greater tolerance for warmer and drier conditions; more emphasis on studies to understand breeding habitat selection by the Kirtland's warbler; additional attempts to transfer breeding pairs of the warbler to habitats to the north; additional emphasis on the monitoring of diameter increment of jack pine as a measure of global warming and as an indication of the likely success of the present management program. Ultimately, if a rapid decline is observed in the growth of jack pine and if other indications of global warming become evident, then the utility of continued fire management of the Kirtland's warbler habitat near Grayling, Michigan would have to be reconsidered. Emphasis could be placed on fire management at the northern edge of the breeding habitat presently utilized by the warbler and in areas adjacent to these and just to the north, as a way of promoting the northward migration of the species.

The swiftness of the response suggests that jack pine stands managed as habitat for the Kirtland's warbler could be monitored to provide one of the earliest biological indicators of global climate warming. If jack pine trees on which the warbler depends undergo a rapid decline, then we might conclude that the effects of global warming are underway. If jack pine continues to grow as well as it has in the past in these habitats, then there would be no significant indication in that locale of a biological effect of global warming. To test this possibility, diameter increments of jack pine could be measured, and increments laid down since 1980 could be compared to those produced earlier. Measurements would have to be done in a way that eliminated variation due to local competitive effects.

The projected responses of these stands are much more rapid than for other stands in the Great Lake States for which we have made projections,

including boreal forests of the Boundary Waters Canoe Area, Minnesota and oak woodlands of southern Michigan (Botkin *et al.*, 1989). In part, the rapidity of the response of the jack pine woodlands of Michigan seems to be the result of the sensitivity of tree growth to temperature conditions at the borders of geographic ranges of trees. In addition, the frequent burning, which removes the protection of soils, seedlings, saplings and mature trees, hastens the response to climate change. From this one can see that populations of short-lived species can be expected to respond more rapidly to climate change than long-lived species, just as frequently disturbed forests will respond more rapidly than infrequently disturbed forests (Davis & Botkin, 1985). Finally, population responses are likely to be more rapid in areas recently cleared and undergoing regeneration than in older forests, because mature trees can persist longer during a climatic change than can seedlings and saplings (Botkin *et al.*, 1989). Jack pine stands now actively managed as the primary nesting habitat for the Kirtland's warbler meet all of these criteria, and for these reasons may be sensitive indicators of a rapid climatic change.

Climate projections must be viewed with caution. Current climate models do not consider some potentially important factors. For example, thermal inertia of upper ocean levels and mixing with deeper waters, which are not taken into account, may delay global warming one or more decades (Schneider & Thompson, 1981). Indicators which might separate the signal of warming from the noise of normal weather variation, and which could be monitored over time to serve as verification of projections, have been lacking. It is therefore important to determine whether the projected decline of jack pine is robust with respect to severity of the climate change. To investigate this robustness, some additional tests were conducted. Temperature and precipitation ratios equal to 25, 50 and 75% of the transient ratios were used to create three climate scenarios intermediate between the normal and transient-A climates, mimicking a slower climatic change. Even in these cases, significant differences from normal growth are evident by year 1985 in both the 50 and 75% transient climates, and by 1990 in the 25% transient climate (Fig. 6; $p > 0.95$, t -test). Drastic reductions in growth of jack pine are evident by 2040 for all but the 25% transient climate, and this mildest scenario still results in drastic declines by 2070. The projected declines are drastic because the projected climate change is so severe and because the Kirtland's warbler management areas lie at the extreme southern end of the jack pine range.

Results are restricted to effects of climate change. No other independent human-induced effects on tree growth were taken into account, such as acid rain and gaseous oxidants. Nor were direct effects of CO₂ increases on jack pine considered. Laboratory experiments show that fertilized and irrigated

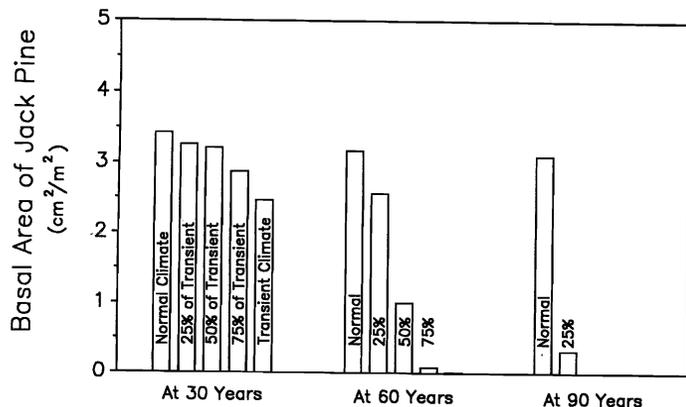


Fig. 6. Projected basal area of jack pine near Grayling, Michigan at the end of three 30-year periods following simulated burns under five climate scenarios. Projections are for a normal climate (left hand bar for each 30-year period), transient-A climate (right hand bar), and three intermediate climates representing 25, 50 and 75% of the difference in mean monthly temperature and precipitation values between the normal and transient climates. Soil conditions are as in Fig. 4.

plants undergo great increases in production under CO_2 -elevated atmospheres (Funsch *et al.*, 1970; Kramer, 1981; Tolley & Strain, 1984; Sionit *et al.*, 1985; Teskey & Shrestha, 1985; Hollinger, 1987), leading some scientists to conclude that declines in forest composition during the next decades would not occur (Wigley *et al.*, 1980). We do not expect this effect to be significant for two reasons: heat tolerance, which the forest model projects will be the primary factor limiting growth of jack pine in the Kirtland's warbler habitat as climate changes, would prevent any substantial response to CO_2 (Botkin & Nisbet, 1990); and as we have shown elsewhere (Botkin *et al.*, 1973), competition among trees for light in a mixed species forest buffers the forest against CO_2 fertilization. With competition limited by temperature, light, and soil fertility, the direct response to CO_2 fertilization is likely to be insignificant. Simulations reported elsewhere (Botkin & Nisbet, 1990) indicate that direct effects of carbon dioxide fertilization lead to no significant change in projections.

Some scientists have speculated that an increase in CO_2 concentration would lead to greater water-use efficiency by trees. Stomata need to be open a shorter time. Seedlings grown under high CO_2 atmospheres might have a lower stomatal density than those grown under ambient conditions. However, we have found no study that allows the determination of a quantitative relationship between CO_2 concentration and the soil water balance in a way that could be incorporated into the forest model. Thus, the

possibility remains untested that an increase in water-use efficiency would reduce the impacts of global warming on trees. While we believe that this response is unlikely to make a significant difference in the results we have reported in this paper, studies should be done to improve our understanding of the relationship between CO_2 concentration in the air, water-use efficiency by trees, and the soil water budget.

The accuracy of the projections also depends on the accuracy and realism of the forest model. In almost 20 years of use, the model has been shown to be realistic and accurate for those cases where data exist that can be used for validation (Botkin *et al.*, 1973; Botkin, 1981). However, the results obtained here suggest that certain specific field and laboratory studies would enhance our acceptance of the results. For example, physiological studies of the response of jack pine to increasing temperature would be valuable, as would field research on the observed temperature tolerances of jack pine ecotypes. Laboratory studies to improve our understanding of the effects of an increase in CO_2 concentration on water-use efficiency and on the soil water budget would also be valuable.

In spite of these limitations, the projections raise a warning that climate change could have rapid impacts on the habitats of endangered species, and that the management of such habitats might need revision in light of a projected global warming.

ACKNOWLEDGEMENTS

We thank J. Bergengren for assistance with computer programming. This research was supported by the US Environmental Protection Agency, the National Science Foundation, the Pew Charitable Trusts, and the Andrew J. Mellon and Pearl Chase Foundations. The information in this report does not necessarily reflect the view of any funding agency and no official endorsement should be inferred from it. We also thank the staff of the Department of Natural Resources, State of Michigan, for their help with field research.

REFERENCES

- Aber, J. D., Botkin, D. B. & Melillo, J. M. (1979). Predicting the effects of different harvesting regimes on productivity and yield in northern hardwoods. *Can. J. For. Res.*, **9**, 10-14.
- Botkin, D. B. (1981). Causality and succession. In *Forest Succession: Concepts and Applications*, ed. D. C. West, H. H. Shugart & D. B. Botkin. Springer-Verlag, New York, pp. 36-55.
- Botkin, D. B. (in press). *The Ecology of Forests: Theory and Evidence*. Oxford University Press, New York.

- Botkin, D. B., Janak, J. F. & Wallis, J. R. (1970). A simulator for northeastern forest growth: a contribution of the Hubbard Brook Ecosystem Study and IBM Research. *IBM Res. Rep.*, No. 3140, Yorktown Heights, NY.
- Botkin, D. B., Janak, J. F. & Wallis, J. R. (1972). Some ecological consequences of a computer model of forest growth. *J. Ecol.*, **60**, 849-72.
- Botkin, D. B., Janak, J. F. & Wallis, J. R. (1973). Estimating the effects of carbon fertilization on forest composition by ecosystem simulation. In *Carbon and the Biosphere*, ed. G. M. Woodwell & E. V. Pecan. US Department of Commerce, Washington, DC, pp. 328-44. (Available from NTIS, Springfield, VA, as CONF-720510).
- Botkin, D. B. & Levitan, R. E. (1977). Wolves, moose, and trees: an age-specific trophic-level model of Isle Royale National Park. *IBM Res. Rep. Life Sci.*, RC 6834.
- Botkin, D. B. & Nisbet, R. A. (1990). Direct effects of carbon dioxide on forest growth, unpublished report to EPA Office of Policy, Planning and Evaluation.
- Botkin, D. B., Nisbet, R. A. & Reynales, T. E. (1989). Effects of climate change on forests of the Great Lake States. In *The Potential Effects of Global Climate Change on the United States*, ed. J. B. Smith & D. A. Tirpak. US Environmental Protection Agency, Washington, DC, EPA-203-05-89-0, pp. 2-1-2-31.
- Botkin, D. B. & Simpson, L. G. (1990). Distribution of biomass in the North American boreal forest. In *Global Natural Resource Monitoring and Assessments: Preparing for the 21st Century*, Vol. 3, ed. F. G. Cini. American Society for Photogrammetry and Remote Sensing, Falls Church, Virginia, pp. 1036-45.
- Byelich, J., DeCapita, M. E., Irvine, G. W., Radtke, R. E., Johnson, N. I., Jones, W. R., Mayfield, H. & Mahalak, W. J. (1985). *Kirtland's Warbler Recovery Plan*. US Fish & Wildlife Service, Rockville, Maryland.
- Davis, M. B. & Botkin, D. B. (1985). Sensitivity of cool-temperate forests and their fossil pollen record to rapid temperature change. *Quatern. Res.*, **23**, 327-40.
- Fowells, H. A. (1965). *Silvics of Forest Trees of the United States*. *Agric. Hdbk*, No. 271, US Government Printing Office, Washington, DC.
- Funsch, R. W., Mattson, R. H. & Mowry, G. R. (1970). Carbon dioxide-supplemented atmosphere increases growth of *Pinus strobus* seedlings. *For. Sci.*, **16**, 459-60.
- Ghan, S. J., Lingaas, J. W., Schlesinger, M. E., Mobley, R. L. & Gates, W. L. (1982). A documentation of the OSU two-level atmospheric General Circulation Model. *Climate Research Institute Report, Oregon State University, Corvallis*, No. 35.
- Hall, F. G., Botkin, D. B., Strebel, D. E., Woods, K. D. & Goetz, S. J. (in press). Large scale patterns in forest succession as determined by remote sensing. *Ecology*.
- Hansen, J., Russell, G., Rind, D., Stone, P., Lebedeff, S., Ruedy, R. & Travis, L. (1983). Efficient three-dimensional global models for climate studies, Models I and II. *Monthly Weather Rev.*, **111**, 609-62.
- Hansen, J., Fung, I., Lacs, A., Rind, D., Lebedeff, S., Ruedy, R. & Russell, G. (1988). Global climate changes as forecast by Goddard Institute for Space Studies three-dimensional model. *J. Geophys. Res.*, **93**, 9341-64.
- Heinselman, M. L. (1981). Fire and succession in the conifer forests of northern North America. In *Forest Succession, Concepts and Applications*, ed. D. C. West, H. H. Shugart & D. B. Botkin. Springer-Verlag, New York, pp. 374-405.

- Helmets, H. (1962). Temperature effect on optimum tree growth. In *Tree Growth*, ed. T. T. Kozlowski. Ronald Press, NY, pp. 275-87.
- Hollinger, D. Y. (1987). Gas exchange and dry matter allocation responses to elevation of atmospheric CO₂ concentration in seedlings of three tree species. *Tree Physiol.*, **3**, 193-202.
- Kozlowski, T. T. (1971). *Growth and Development of Trees*, 2 vols. Academic Press, New York.
- Kramer, P. J. (1981). Carbon dioxide concentration, photosynthesis, and dry matter production. *BioScience*, **31**, 29-33.
- Kramer, P. J. & Kozlowski, T. T. (1960). *Physiology of Trees*. McGraw-Hill, New York.
- Kramer, P. J. & Kozlowski, T. T. (1979). *Physiology of Woody Plants*. Academic Press, New York.
- Manabe, S. & Stouffer, R. S. (1980). Sensitivity of a global climate model to an increase of CO₂ concentration in the atmosphere. *J. Geophys. Res.*, **85**, 5529-54.
- Manabe, S. & Wetherald, R. T. (1987). Large-scale changes in soil wetness induced by an increase in carbon dioxide. *J. Atmos. Sci.*, **44**, 1211-35.
- Mayfield, H. F. (1953). A census of the Kirtland's Warbler. *Auk.*, **70**, 17-20.
- Mayfield, H. F. (1960). *The Kirtland's Warbler*. Cranbrook Institute of Science, Bloomfield Hills, Michigan.
- Mayfield, H. F. (1972). Third decennial census of Kirtland's Warbler. *Auk.*, **89**, 263-8.
- Peters, L. R. & Darling, J. D. S. (1985). The greenhouse effect and nature reserves. *BioScience*, **35**, 707-17.
- Schneider, S. H. (1989). *Global Warming: Are we Entering the Greenhouse Century?* Sierra Club Books, San Francisco.
- Schneider, S. H. & Thompson, S. (1981). Atmospheric CO₂ and climate: importance of the transient response. *J. Geophys. Res.*, **86**, 3135-47.
- Schlesinger, M. E. & Mitchell, J. F. B. (1987). Model projections of the equilibrium climate response to increased carbon dioxide. *Rev. Geophys.*, **25**, 760-98.
- Schlesinger, M. E. & Zhao, Z.-C. (1988). *Seasonal climate changes induced by doubled CO₂ as simulated by the OSU atmospheric GCM/mixed-layer ocean model*. Climate Research Institute Report, Oregon State University, Corvallis.
- Sionit, N., Strain, B. R. & Helmets, H. H. (1985). Long-term atmospheric enrichment affects growth and development of *Liquidambar styraciflua* and *Pinus taeda* seedlings. *Can. J. For. Res.*, **15**, 468-71.
- Smith, A. G. (1965). Problems of inertia and threshold related to postglacial habitat changes. *Proc. R. Soc. Lond., Ser. B*, **61**, 331-42.
- Solomon, A. M. & West, D. C. (1987). Simulating forest ecosystem responses to expected climate change in eastern North America: applications to decision making in the forest industry. In *The Greenhouse Effect, Climate Change, and US Forests*, ed. W. S. Shands & J. S. Hoffman. The Conservation Foundation, Washington, DC, pp. 189-217.
- Teskey, R. O. & Shrestha, R. B. (1985). A relationship between carbon dioxide, photosynthetic efficiency and shade tolerance. *Physiol. Plantarum*, **63**, 126-32.
- Tolley, L. C. & Strain, B. R. (1984). Effects of CO₂ enrichment on growth of *Liquidambar styraciflua* and *Pinus taeda* seedlings under different irradiance levels. *Can. J. For. Res.*, **14**, 343-50.

- Walkinshaw, L. H. (1983). *Kirtland's Warbler: The Natural History of an Endangered Species*. Cranbrook Institute of Science, Bloomfield Hills, Michigan.
- Wigley, T. M. L., Jones, P. D. & Kelley, P. M. (1980). Scenario for a warm, high CO₂ world. *Nature, Lond.*, **283**, 17–21.
- Zabinski, C. & Davis, M. B. (1989). Hard times ahead for Great Lakes Forests: A climate threshold model predicts responses to CO₂-induced climate change. In *Potential Effects of Global Climate Change on the United States: Appendix D—Forests*, ed. J. B. Smith & D. A. Thirpak. Office of Policy, Planning and Evaluation, US Environmental Protection Agency, Washington, DC, pp. 5-1–5-19.



Minimum Estimate of the Number of Bottlenose Dolphins *Tursiops truncatus* in the Moray Firth, NE Scotland

P. S. Hammond

Sea Mammal Research Unit, c/o British Antarctic Survey,
High Cross, Madingley Road, Cambridge CB3 0ET, UK

&

P. M. Thompson

Department of Zoology, University of Aberdeen,
Tillydrone Avenue, Aberdeen AB9 2TN, Scotland, UK

(Received 4 September 1989; revised version received 1 June 1990;
accepted 19 June 1990)

ABSTRACT

*The Moray Firth contains one of the best known resident groups of bottlenose dolphins *Tursiops truncatus* in UK waters. However, despite concerns over the fate of these animals, few data exist on the size or status of this or other small cetacean populations around Britain. In August 1989, a coordinated survey was carried out around the coast of the Moray Firth to obtain a minimum estimate of the number of bottlenose dolphins present in the area. A minimum of 62 dolphins was counted during the survey, including at least seven calves. Most animals were observed in the inner part of the Moray Firth, particularly in the narrow mouths of the Cromarty, Beaully and Inverness Firths. These results show that coordinated land-based surveys can provide a useful first estimate of the population size of coastal small populations.*

INTRODUCTION

Bottlenose dolphins *Tursiops truncatus*, Montagu are distributed widely throughout the world's warm and temperate oceans, occurring in both oceanic and coastal groups (Leatherwood & Reeves, 1983; Martin, 1990).

79