

Predicting the relative sensitivity of forest production in Ireland to site quality and climate change

Christine L. Goodale^{1,*}, John D. Aber¹, Edward P. Farrell²

¹Complex Systems Research Center, Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, New Hampshire 03824, USA

²Department of Environmental Resource Management, University College Dublin, Agriculture Building Belfield, Dublin 4, Ireland

ABSTRACT: Most model-based predictions of climate change effects on forest ecosystems have used either potential or static descriptions of vegetation and site, removing the effects of direct management or land use. In this paper we use a previously developed and validated model of carbon and water balances in forest ecosystems (PnET-II) to assess the relative sensitivity of forest production in Ireland to predicted climate change and to ambient variability in site quality. After validating the model against measured productivity for 2 sets of stands, we ran the model using existing variation in site quality, represented as differences in foliar N concentration, and also for predicted changes in climate and atmospheric CO₂. Resulting variations in productivity were compared with those due to potential errors in the specification of input parameters and to variation in current ambient climate across the region. The effects on net primary production (NPP) and wood production of either ambient variation in climate or predicted changes in temperature, precipitation and CO₂ are quite small (0 to 30%) relative to the effects of ambient variability in site quality (up to 400%). The range of possible variation in other user-specified physiological parameters resulted in changes of less than 10% in model predictions. We conclude that site-specific conditions and management practices result in a range of forest productivity that is much greater than any likely to be induced by climate change or CO₂ enrichment. We also suggest that it is essential to understand and map spatial variability in site quality, as well as to understand how the productive capacity of landscapes will change in response to management and pollution loading, if we are to predict the actual role that climate change will play in altering forest productivity and global biogeochemistry.

KEY WORDS: Regional modeling · Validation · Foliar nitrogen · Sitka spruce

1. INTRODUCTION

Direct disturbance by management and indirect disturbance through altered atmospheric chemistry and climate have been identified as 2 primary change agents for forest ecosystems globally (Vitousek 1994, Galloway et al. 1995). While many different ecosystem models have been used to predict the effects of changes in climate and atmospheric chemistry (e.g. VEMAP Members 1995), most use potential or static descriptions of vegetation and site so that the effects of direct management or land use on forest ecosystems have not been considered. Given this limitation, it is

not known how direct human manipulation of the landscape can alter the predictions derived from simulations using potential or regionally averaged soil and vegetation conditions. Without this understanding, we cannot know how well current model simulations will represent actual ecosystem response. The availability of these data would allow us to examine how site characteristics or direct human manipulation influences forest productivity.

Ireland is currently experiencing a rapid change in land use through a vigorous program of reforestation, mainly with exotic conifers (Anonymous 1994). Management practices used in the establishment of plantations range from planting alone to intensive site preparation including drainage of peatlands and fertilization (Farrell 1990b, Farrell & Boyle 1990). Extensive re-

*E-mail: christy.goodale@unh.edu

gional datasets are available on the soils and climate of Ireland (Gardiner & Radford 1980, Goodale et al. 1998), and production data are also available for a large number of plantation sites (see below).

In this paper we apply a previously developed and validated model of carbon and water balances in forest ecosystems (PnET-II) and a model of climate variation in Ireland (companion article in this issue; Goodale et al. 1998) to predict the growth of coniferous forest plantations in Ireland. We use existing variation in site quality resulting from differences in soil type and management practices, represented as differences in foliar N concentration, in conjunction with predicted changes in climate and atmospheric CO₂, to assess the relative sensitivity of these systems to site management and climatic and atmospheric change.

2. BACKGROUND

2.1. History of forestry in Ireland

Temperate deciduous forests once covered most of Ireland, but centuries of use for timber and charcoal production left the island with only 1.4% forest cover by 1905 (McEvoy 1954, 1958). Specimen plantings of exotic conifers in the 19th century suggested the potential for very high growth rates, and reforestation initiatives, restricted initially to low-fertility soils unsuitable for agriculture, were begun early in this century. Exotic coniferous species (primarily *Picea sitchensis*, *Pinus contorta*, *Picea abies*, and *Pinus sylvestris*) were used primarily, and they currently make up 90% of Ireland's plantations (Anonymous 1994). Sitka spruce (*P. sitchensis*) covers over half of the forested land in Ireland (Anonymous 1994).

The early suggestions of high potential productivity have been proven correct. Ireland's average rate of potential softwood production is more than double that of France and more than triple that of Sweden and Finland (Carbonnier 1991). This, combined with changes in agricultural subsidy policies within the European Economic Community, have made forestry an increasingly attractive alternative to traditional agriculture (Conway 1991, Kearney 1991). Planting rates have accelerated rapidly over the past decade, and forests now cover 8% of the Republic of Ireland (Anonymous 1994).

Methods used for stand establishment in Ireland differ widely depending on site conditions (Farrell 1990b). Blanket peats in the west of Ireland are generally plowed for drainage, with planting occurring on the overturned turf above the lowered water level in the furrow. The use of phosphorous fertilizers has increased with time on this site type. Minerotrophic

raised bogs in the central lowlands are used as a fuel source for electricity generation. Plantation establishment on this site type has been limited to date, but may increase in the future, and generally involves planting only, without site preparation.

2.2. Models of forest productivity in Ireland

Potential forest yield in Ireland (yield class, expressed in m³ ha⁻¹ yr⁻¹) is currently determined with empirically derived height, age, and growth relationships developed by the Forestry Commission of the United Kingdom (Edwards & Christie 1981). This value represents expected volume production at the time of maximum mean annual increment. The British models have never been fully tested under Irish conditions, and it has been suggested that they may underestimate the growth of Sitka spruce in Ireland (Anonymous 1994). Empirical yield models also cannot be used to predict the effects of changes in environmental conditions, and in fact these models may lose reliability as environmental conditions change over time (Bossel 1991, Mohren & Burkhart 1994, Spiecker et al. 1996). Change can result either from alterations in climatic and atmospheric conditions or from management practices that affect fertility or site quality.

2.3. Predicted climate change

While there is emerging scientific consensus that climates will warm over much of the Earth over the next several decades (Kattenberg et al. 1996), the degree of warming and effects on the timing and distribution of precipitation are still subject to debate. Predictions of climate change in Europe have been developed from general circulation models (GCMs) and from mesoscale models nested within GCMs, and have either included or ignored the effects of sulfate aerosols in moderating the effects of greenhouse gases. Without the aerosol correction, GCM runs presented in the most recent report of the Intergovernmental Panel on Climate Change (IPCC) suggest a 4.0 to 4.5°C increase in temperature across Ireland in a double CO₂ environment (Kattenberg et al. 1996), and a change in precipitation of -0.3 to +1.0 mm d⁻¹. The nested mesoscale models, which give greater spatial specificity to predictions, suggest a 3.5 to 4.5°C increase in temperature, and an increase in precipitation of 0 to 1 mm d⁻¹ (Giorgi et al. 1992, Marinucci & Giorgi 1992).

The predicted net effect of increasing sulfate aerosols in the atmosphere is a reduction in solar radiation penetration to the Earth's surface, and a partial

compensation for warming due to increased greenhouse gases (Mitchell et al. 1995, Trenberth et al. 1996). With the sulfate aerosol corrections included, changes in mean temperature for Ireland predicted by the Hadley Centre GCM range from +1 to +3°C depending on season, while changes in precipitation are predicted to vary seasonally from -10 to +10 mm mo⁻¹ (Mitchell et al. 1995, <http://www.cru.uea.ac.uk/link/>).

Global warming is expected to increase minimum temperatures more than maximum temperatures, shrinking the diurnal temperature range (Kattenberg et al. 1996, Nicholls et al. 1996). This has the important primary effect of lengthening the growing season in spring and fall and increasing nighttime respiration rates. It also has the secondary effect of reducing vapor pressure deficit (VPD) and reducing transpiration if minimum nighttime temperature is assumed to approximate the dewpoint temperature.

2.4. Physiological effects of CO₂ enrichment

To date, most work on the direct effects of CO₂ on trees has been performed in short-term studies on seedlings in CO₂-enriched growth chambers. While most of these studies have demonstrated increases in photosynthesis and water use efficiency, the magnitude of change is highly variable, and many feedbacks must be quantified before scaling up in space or over time (Eamus & Jarvis 1989, Bazzaz 1990). Increases in photosynthesis may not be sustained over time due to down-regulation of photosynthesis through end product inhibition or limitations by light or nutrient levels (Bazzaz 1990). Evidence from whole ecosystems in response to CO₂ enrichment suggests different responses in different systems. Northern tundra systems demonstrated no long-term direct response to CO₂ enhancement (Oberbauer et al. 1986), while growth was enhanced in a nutrient-enriched estuarine marsh (Curtis et al. 1989a, b). Feedbacks between CO₂ and nutrient availability are difficult to predict. Availability may be increased by enhanced photosynthesis and allocation of carbon to roots, augmenting soil exploration, or increasing allocation to mycorrhizae. However, increases in the C:N ratio in foliage could decrease both photosynthetic rate (Reich et al. 1995) and nutrient mineralization (Bazzaz 1990).

Water use efficiency has consistently been shown to increase in a doubled-CO₂ environment, although the magnitude of

increase can vary from 20 to 160% (Eamus & Jarvis 1989, Woodward et al. 1991, Polley et al. 1993, Pitelka 1994). Water use efficiency may increase due to increased photosynthesis and/or reduced stomatal conductance. In Sitka spruce seedlings, doubling CO₂ concentration caused water use efficiency to double (Townend 1993).

3. METHODS

3.1. Model structure

PnET-II (Fig. 1) is one of a number of published, physiologically based models designed to predict forest growth through calculations of processes such as photosynthesis and transpiration (e.g. Pastor & Post 1986, Running & Coughlan 1988, Raich et al. 1991, McMurtrie et al. 1992). While more complex than the empirically based models currently in use in Ireland, physiological models offer the potential to capture and predict more accurately the effects of changes in climate and site quality. PnET-II differs from many models in that input parameters are determined directly from the literature with no attempt to calibrate the inputs to achieve measured outputs. Data on predicted variables [e.g. net primary production (NPP), wood production, transpiration, water yield] are not used in

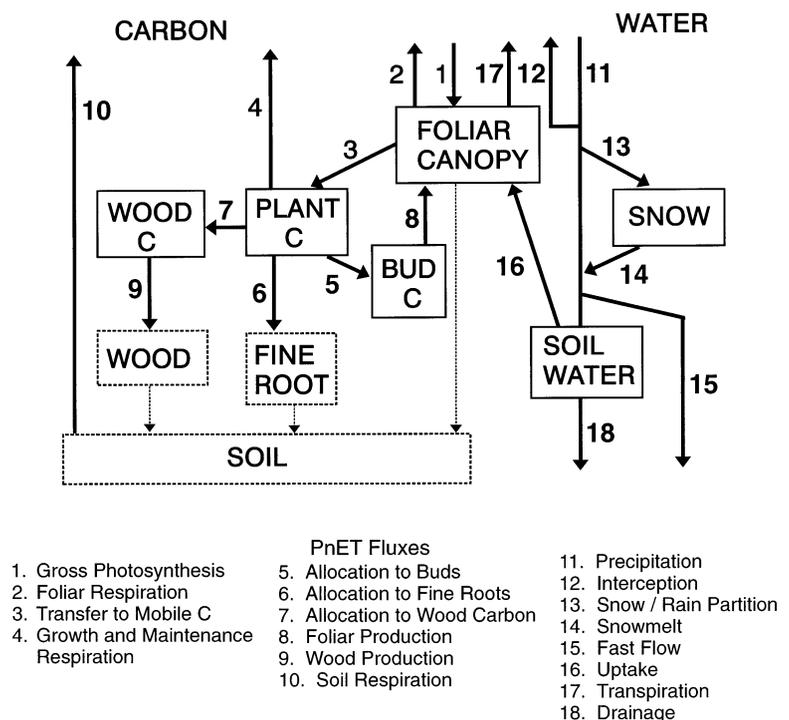


Fig. 1. Structural diagram of the PnET-II model (Aber et al. 1995). PnET-II does not explicitly track accumulation or litter production of wood and roots (dashed boxes)

any way to determine the inputs. This lack of calibration allows the model to be tested against the independent output variables listed above to assess the accuracy of model function.

PnET-II was designed to predict monthly carbon and water balances using relatively few inputs, so that it can be run within the data constraints of a geographic

information system (GIS). Required site variables include vegetation type, plant-available soil water holding capacity (WHC), and average monthly climate data (maximum and minimum temperature, precipitation, and solar radiation). The original PnET (Aber & Federer 1992) was validated against measured data from 10 widely distributed temperate and boreal forest

Table 1. Input parameters required by the PnET-II model. Starred values (*) vary with vegetation type and are listed in Table 2

Name	Definition and units	Value
Canopy variables		
<i>k</i>	Canopy light attenuation constant (no units)	*
FolNCon	Foliar nitrogen content ($\text{g}_N \text{g}_{\text{leaf}}^{-1}$)	*
FolReten	Foliage retention time (yr)	*
SLWMax	Specific leaf weight at top of canopy (g m^{-2})	*
SLWDel	Change in SLW with increasing foliar mass above leaf layer ($\text{g m}^{-2} \text{g}^{-1}$)	*
GDDFolStart	Growing degree days at which foliar production begins	*
GDDFolEnd	Growing degree days at which foliar production ends	*
GDDWoodStart	Growing degree days at which wood production begins	*
GDDWoodEnd	Growing degree days at which wood production ends	*
FolRelGrowMax	Maximum relative growth rate for foliage (yr^{-1})	0.3
Photosynthesis variables		
AmaxA	Intercept of the relationship between foliar N% and max. photosynthesis rate ($\text{nmol CO}_2 \text{g}_{\text{leaf}}^{-1} \text{s}^{-1}$)	*
AmaxB	Slope of the relationship between foliar N% and max. photosynthesis rate ($\text{nmol CO}_2 \text{g}_{\text{leaf}}^{-1} \text{s}^{-1}$)	*
BaseFolRespFrac	Respiration as a fraction of maximum photosynthesis	0.1
HalfSat	Half saturation light level ($\text{mmol PAR m}^{-2} \text{s}^{-1}$)	200
AmaxFrac	Daily Amax as a fraction of early morning instantaneous rate	0.76
PsnTOpt	Optimum temperature for photosynthesis ($^{\circ}\text{C}$)	*
PsnTMin	Minimum temperature for photosynthesis ($^{\circ}\text{C}$)	*
RespQ10	Q_{10} value for foliar respiration (factor of respiration increase per 10°C temperature change)	2.0
Water balance variables		
DVPDA	Coefficients for determining DVPD, a photosynthesis multiplier ranging from 0 to 1. $\text{DVPD} = 1 - \text{DVPDA} \times \text{VPD}^{\text{DVPDB}}$	*
DVPDB		*
PrecIntFrac	Fraction of precipitation intercepted and evaporated	*
WUEConst	Constant in the equation for water use efficiency (WUE) as a function of vapor pressure deficit (VPD): $\text{WUEConst} (\text{mg}_{\text{CO}_2} \text{g}^{-1} \text{H}_2\text{O kPa}) = \text{WUE} \times \text{VPD}$	10.9
FastFlowFrac	Fraction of water inputs lost directly to drainage	0.1
<i>f</i>	Soil water release parameter (d^{-1})	0.04
Carbon allocation variables		
CFracBiomass	Carbon as a fraction of foliage mass	0.45
RootAllocA	Intercept of the relationship between foliar and root allocation	0
RootAllocB	Slope of the relationship between foliar and root allocation	2
GRespFrac	Growth respiration, as a fraction of allocation	0.25
RootMRespFrac	Ratio of fine root maintenance respiration to biomass production	1
WoodMRespA	Wood maintenance respiration as a fraction of gross photosynthesis	0.07
PlantCReserveFrac	Fraction of plant C held in reserve after allocation to bud C	0.75
MinWoodFolRatio	Minimum ratio of carbon allocation to wood and foliage	*
Soil respiration variables		
SoilRespA	Intercept of relationship between mean monthly temperature ($^{\circ}\text{C}$) and soil respiration ($\text{g}_C \text{m}^{-2} \text{mo}^{-1}$)	27.46
SoilRespB	Slope of relationship between mean monthly temperature ($^{\circ}\text{C}$) and soil respiration ($\text{g}_C \text{m}^{-2} \text{mo}^{-1}$)	0.06844
Wood yield conversion variables		
BoleFrac	Bolewood as a percent of total woody NPP	*
Density	Wood density (g cm^{-3})	*

ecosystems. PnET-II (Aber et al. 1995) contains a revised photosynthetic routine which has been validated against daily whole-canopy CO₂ exchange data from eddy-correlation measurements from the Harvard Forest, Petersham, Massachusetts, USA (Aber et al. 1996) and improved plant allocation and soil respiration terms.

The core relationship in PnET is the linear correlation between maximum photosynthesis and foliar nitrogen content observed across and within many plant species (Field & Mooney 1986, Mitchell & Hinckley 1993, Reich et al. 1995). PnET-II uses this relationship to predict maximum photosynthesis for a specified foliar N concentration. Sub-optimal conditions of temperature, light, humidity, or water availability determine realized net photosynthesis. The model simulates whole-canopy photosynthesis by combining estimates of potential net photosynthesis with a photosynthetic light response curve and an equation for light attenuation through the canopy. Potential photosynthesis determines transpirational demand, which is fulfilled as long as sufficient soil water exists. Respiration, growth, and carbon allocation terms determine partitioning of photosynthate to roots, foliage, and buds. Wood production is derived from the carbon left over after allocation to all other carbon pools, including stored reserves (see Aber et al. 1995 for complete model description).

Two additional terms (BoleFrac and Density) were added to PnET-II to convert the units of estimated wood production from weight of all woody material (g m⁻² yr⁻¹) to volume increment of bolewood (m³ ha⁻¹ yr⁻¹). The added terms did not affect calculations of physiological processes, but allowed comparison of predictions between PnET-II and the existing empirical yield models.

3.2. Model parameterization

Three types of parameters are required to run PnET-II (Table 1): (1) physiological parameters that are held constant for all forest types; (2) physiological parameters that vary with vegetation type (Table 2); and (3) site-specific parameters that vary with location, such as climate, soil WHC, and elevation. Values for parameters held constant for all vegetation types are described in Aber et al. (1995, 1996). Parameter values spe-

cific to the simulations reported here were not calibrated, but determined from literature review of published measurements of Sitka spruce physiology and physical properties. If published data sources could not be found for sites in Ireland or Northern Ireland, reports were sought for sites in Scotland, England, or Wales. This selection procedure made the parameters as site-specific as possible but should not be confused with calibration, which involves choosing sets of input parameter values which optimize fits of predicted values with measured data. Non-calibrated models require that careful attention be paid to determining parameter values, so we describe this process in detail here.

AmaxA, AmaxB, MinWoodFolRatio. Of the parameters that change with vegetation type (Table 2), AmaxA, AmaxB, and MinWoodFolRatio are held constant within the general vegetation types of broadleaf deciduous or evergreen coniferous. AmaxA and AmaxB describe the intercept and slope, respectively, of the relationship between potential photosynthesis (Amax; nmol CO₂ g_{leaf}⁻¹ s⁻¹) and foliar N (% dry weight). One photosynthesis/foliar N relationship is used to for needle-leaved evergreen species, and a steeper one is used for broad-leaved deciduous species (Reich et al. 1995, Aber et al. 1996). MinWoodFolRatio is the lowest ratio of wood production to foliar production allowed, representing the minimum

Table 2. List of values for PnET-II variables that vary with vegetation type (starred values in Table 1). Aber et al. (1996) describes the data sources for hardwoods, pine, and red spruce/balsam fir values. The Douglas-fir parameters are from a previous version of PnET (Aber & Federer 1992) which had slightly different parameter requirements. Data sources for Sitka spruce values are described in this paper

Parameter	Hardwoods	Pine	Red spruce, Douglas-balsam fir	Douglas-fir	Sitka spruce
AmaxA	-46.0	5.3	5.3		5.3
AmaxB	71.9	21.5	21.5		21.5
MinWoodFolRatio	1.5	1.25	1.25		1.25
FolNCon	2.4, 1.9	1.2	0.8		1.8
<i>k</i>	0.58	0.5	0.5	0.4	0.5
SLWMax	100	200	170	135	275
SLWDel	0.2	0.2	0	0	0.06
FolReten	1	2.25	4	4.5	2.6
PsnTMin	4	4	0	0	0
PsnTOpt	24	24	20	20	19
DVPDA	0.05	0.05	0.05	0.21	0.21
DVPDB	2	2	2	1	1
PrecIntFrac	0.11	0.15	0.15	0.15	0.30
GDDFolStart	100	900	300		650
GDDFolEnd	900	1600	1400		1500
GDDWoodStart	900	900	300		650
GDDWoodEnd	1600	1600	1400		1500
BoleFrac					0.64
Density					0.34

investment in new xylem tissue to support new foliar production.

Foliar nitrogen content (FolNCon). FolNCon is the canopy-averaged percent of nitrogen in dry foliage ($\text{g}_N \text{g}_{\text{leaf}}^{-1}$). Foliar N may vary within a stand due to needle age (Hom & Oechel 1983) or canopy position (Brooks et al. 1994). These differences should be integrated to obtain a value for the whole canopy.

Foliar nitrogen values varied dramatically in the managed Sitka spruce plantations of Ireland and the United Kingdom (Table 3), most likely due to the wide range of site types and treatments of the Sitka plantations. Several of these sites were studied specifically because they were nitrogen deficient (poorly aerated peatlands or peaty sites with strong *Calluna vulgaris* competition for N), while the higher foliar N values were the result of site treatment (fertilization or aeration).

Foliar nitrogen values are particularly variable on peatland sites, where N availability is strongly affected by fertilization (Farrell 1985, 1990a) and drainage (Schaible & Dickson 1990). Deficiencies of both P and N limit the growth of Sitka spruce on blanket peats in western Ireland (Farrell 1985, 1990a). Data from sites in the U.S. and the tropics indicate that the relationship between foliar nitrogen and pho-

tosynthesis weakens when phosphorus is limiting (Reich & Schoettle 1988, Reich et al. 1994). Phosphorus deficiency inhibits efficient use of nitrogen by white pine (*Pinus strobus*) at P:N ratios below 0.10 to 0.14 (Reich & Schoettle 1988). As the P:N ratios for many of the Sitka spruce sites are also in this range (Table 3), productivity at these sites may be limited by phosphorus availability.

PnET-II should be run using site-level, canopy-averaged foliar N data where these measurements exist. Where foliar N measurements were not available, a default value of 1.8% was used. This value was the median foliar N concentration of 3 years' worth of regional surveys of current-year foliar chemistry throughout Ireland (McCarthy 1993). We expect this measure to over-represent FolNCon for 2 reasons: first, the average foliar N content of the whole canopy is generally slightly lower than that of the current year foliage; and, second, most Sitka spruce stands in Ireland are fairly young, so reported foliar N concentrations may be somewhat higher than if the stands were mature. The magnitudes of these biases are not known.

Canopy light attenuation (k). The canopy light attenuation constant, k , describes the decrease in light levels with canopy depth according to the equation:

Table 3. Reported foliar nitrogen contents ($\text{g}_N \text{g}_{\text{dry foliage}}^{-1}$) and foliar P:N ratios from Sitka spruce plantations in Ireland and the United Kingdom

Foliar %N	P:N ratio	Stand age (yr)	Soil type	Site	Source
1.8 2.1 1.5	0.10 0.09 0.10	Varied	Varied	Mean of at least one sample from each of 25 plots in Ireland for 1988, 1989, and 1990, respectively	McCarthy (1993)
1.6 1.3	0.12 0.23	35 36	Peat	1991 and 1992 measurements at Cloosh Forest, Co. Galway, Ireland	Farrell et al. (1994)
1.9 1.6	0.11 0.10	32 33	Podzol	1991 and 1992 measurements at Roundwood Forest, Co. Wicklow, Ireland	Farrell et al. (1994)
1.8	0.07	30	Peat/gley	Mean of 8 trees; Co. Wicklow, Ireland	Carey & O'Brien (1979)
1.0 1.2 1.3 1.6	0.12 0.11 0.11 0.10	17	Peat	Study on effects of peat drainage patterns on forest growth; Cam Forest, Northern Ireland	Schaible & Dickson (1990)
1.1–1.5	0.10–0.21		Blanket peat	Seven years of measurements averaged over plots subject to varied N and P fertilizer treatments; Glenamoy, Co. Mayo, Ireland	Farrell (1990a)
0.6 0.8 1.2 1.2	0.14 0.14 0.10 0.09	12 19 32 50	Peat/gley	Culloden, Inverness, Scotland Inchnacardoch, Fort Augustus, Scotland Mean of 6 sites across Scotland Kirkten Glen, Scotland	Miller et al. (1993)

$$I_i = I_0 e^{-k(\text{LAI}_i)} \quad (1)$$

where I_i is the solar radiation received at level i in the canopy, I_0 is radiation at the top of the canopy, and LAI_i is the total leaf area index ($\text{m}^2 \text{m}^{-2}$) above canopy layer i . Measurements of k for Sitka spruce in Scotland range from 0.43 to 0.58 (Norman & Jarvis 1972, Jarvis et al. 1976, Jarvis 1981, Jarvis & Leverenz 1983), with a median value of 0.5. PnET-II used a value of 0.5 for k for Sitka spruce. This is the same k value determined for several other conifers native to the northwestern United States (Pierce & Running 1988, Pierce et al. 1994).

Specific leaf weight (SLWMax and SLWDel). Sun leaves at the top of the canopy usually have a greater specific leaf weight (g m^{-2}) than shade leaves at the bottom. SLWMax represents the maximum foliar specific weight at the top of the canopy (g m^{-2}), and SLWDel ($\text{g m}^{-2} \text{g}^{-1}$) represents the change in foliar specific weight with canopy depth, where canopy depth is the foliar mass above a given layer ($\text{g}_{\text{leaf}} \text{m}_{\text{ground}}^{-2}$).

Foliar specific leaf weight data from two 16- to 20-yr-old Sitka spruce stands in Scotland were used to calculate SLWDel values of 0.063 (Norman & Jarvis 1972) and 0.056 $\text{g m}^{-2} \text{g}^{-1}$ (Ford 1982), and so SLWDel was set at 0.06 $\text{g m}^{-2} \text{g}^{-1}$ for Sitka spruce. Maximum foliar specific weights in the Scottish stands were approximately 260 g m^{-2} (Norman & Jarvis 1972) and 290 g m^{-2} (Ford 1982). SLWMax was set at 275 g m^{-2} .

Length of foliar retention (FolReten). FolReten represents the mean number of years that trees retain their foliage. At the end of each growing season, PnET-II 'drops' $1/\text{FolReten}$ of the calculated foliar mass. While Sitka spruce can retain some of its foliage for 4 or more years (Norman & Jarvis 1972, Watts et al. 1976, Harcombe et al. 1990), only a small portion of Sitka spruce foliage reaches this age (Norman & Jarvis 1972, Watts et al. 1976). Measurements of the abundance of foliage in different age classes in 20- to 25-yr-old Sitka spruce in Scotland (Norman & Jarvis 1972, Watts et al. 1976) indicate that Sitka spruce drops 38 to 39% of its foliage per year, resulting in an average foliar retention time of 2.6 yr. This value ignores any changes in foliar retention time brought about by pest attacks (e.g. spruce aphid).

Temperature controls (PsnTMin and PsnTOpt). PsnTMin and PsnTOpt are, respectively, the minimum and the optimum daytime temperatures for photosynthesis. PnET-II uses these 2 parameters to describe a parabolic response of photosynthesis to temperature. Although detached Sitka spruce shoots have demonstrated low levels of instantaneous photosynthesis at -5 to -6°C (Ludlow & Jarvis 1971, Neilson et al. 1972), significant photosynthesis is unlikely to occur during months with mean daytime temperatures of -5 to

-6°C , when much colder minimum temperatures adversely affect photosynthesis. PsnTMin was set at 0°C .

Optimum temperatures for photosynthesis in Sitka spruce can vary from 10 to 22°C , depending on provenance and time of year (Ludlow & Jarvis 1971, Neilson et al. 1972), but the most common optimum temperature for Sitka spruce is 19°C (Neilson et al. 1972), so PsnTOpt was set at 19°C .

Humidity controls (DVPDA and DVPDB). The coastal Pacific Northwest region of the United States and Canada—the natural range of Sitka spruce—experiences mild wet winters and warm dry summers. Tree species native to this region have evolved to close their stomata in response to both soil drought and high vapor pressure deficit (Running 1976, Waring & Franklin 1979). DVPDA and DVPDB are empirically-derived coefficients that describe the effect of vapor pressure deficit (VPD, kPa) on photosynthesis. PnET-II calculates the effect of VPD on photosynthesis by multiplying potential photosynthesis by DVPD, a scalar ranging from 0 to 1, which is calculated as:

$$\text{DVPD} = 1 - \text{DVPDA} \times \text{VPD}^{\text{DVPDB}} \quad (2)$$

Estimates of DVPD were derived from measurements of the effects of VPD on photosynthesis in well-watered Sitka spruce seedlings (Watts & Neilson 1978, Sandford & Jarvis 1986). Maximum photosynthesis was assumed to occur at the lowest VPD treatment, and subsequent increases in VPD were presumed to be the only cause of decreased photosynthesis (Fig. 2). Regression coefficients derived from the Sandford & Jarvis (1986) data ($\text{DVPD} = 1.00 - 0.21 \text{VPD}$; $R^2 = 0.99$, $p < 0.001$) exactly matched the linear VPD effect previously determined for Douglas-fir and lodgepole pine (Table 2), and so DVPDA and DVPDB were set to these values.

Interception of precipitation (PrecIntFrac). PrecIntFrac represents the percent of monthly precipitation intercepted by the canopy. Rainfall interception in Ireland and the United Kingdom ranges from 25 to 49% of total annual rainfall (Table 4). Although the oldest plantation has the highest interception value, no other trend between interception and age was apparent. PrecIntFrac was assigned a value of 30%, the median of the interception fractions listed in Table 4. Measured rainfall interception values for Sitka spruce were substantially higher than for the other vegetation types that PnET-II has considered (Table 2).

Growing degree days (GDDFolStart, GDDFolEnd, GDDWoodStart, GDDWoodEnd). GDDFolStart, GDDFolEnd, GDDWoodStart and GDDWoodEnd are growing-degree-day controls on the start and end of foliage and wood production. PnET-II calculates growing

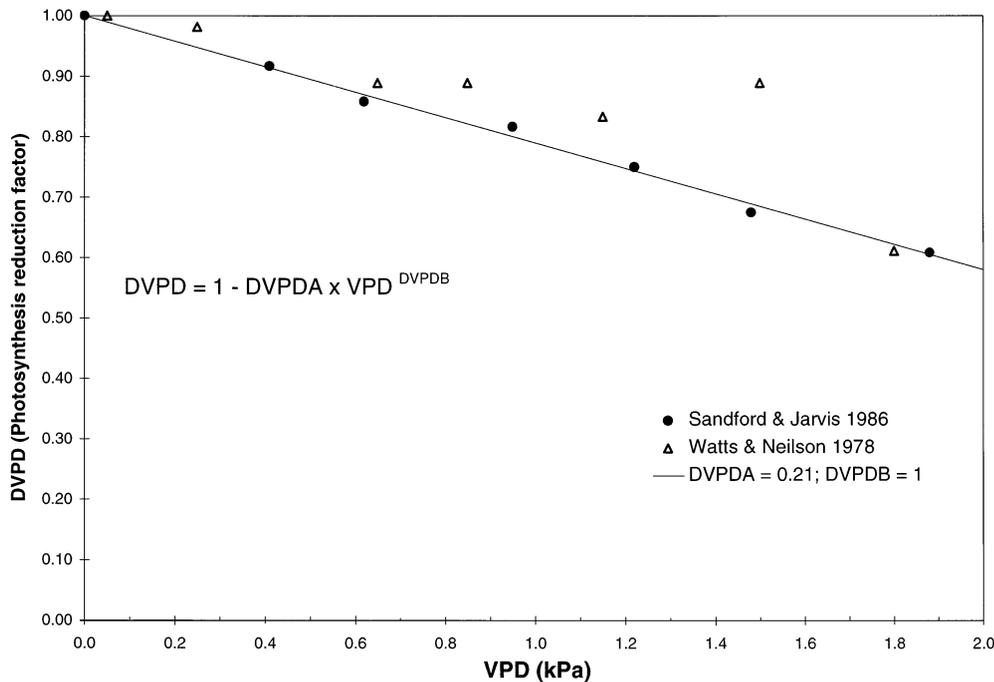


Fig. 2. Effect of vapor pressure deficit (VPD) on DVPD, a photosynthesis reduction factor. VPD effects on photosynthesis are estimated by multiplying potential photosynthesis by DVPD

degree days as the accumulated mean temperature above 0°C from January 1. The timing of wood production (GDDWoodStart and GDDWoodEnd) is assumed to correspond with the timing of foliage production (GDDFolStart and GDDFolEnd).

Bud burst in Sitka spruce has been shown to correspond with degree days above 5°C accumulated after February 1 and the number of chilling days less than 5°C after November 1 (Cannell & Smith 1983). Estimates of GDDFolStart were approximated from these data, and ranged from 600 to 750 with an average of 650.

Table 4. Reported canopy interception as a fraction of total annual rainfall from Sitka spruce plantations in Ireland and the United Kingdom

Interception (%)	Stand age (yr)	Site location	Source
47	20	Glenturk, Co. Mayo, western Ireland	Farrell (1990a)
38	33	Roundwood Forest, Co. Wicklow, eastern Ireland	Farrell et al. (1994)
22	36	Cloosh Forest, Co. Mayo, western Ireland	Farrell et al. (1994)
30	14	Rivox, Greskine Forest, Dumfriesshire, southern Scotland	Ford & Deans (1978)
29	25	Kielder Forest, Northumberland	Anderson & Pyatt (1986), from Johnson (1990)
49	63		
25	29	Plynlimon, United Kingdom	Hudson (1988), from Johnson (1990)
28	50	Kirkten Glen, Highland Scotland	Johnson (1990)
33	18	Cloch, Glentress Forest, southeastern Scotland	Teklehaimanot et al. (1991)

Dates of Sitka spruce bud and shoot elongation have been reported for sites in Argyll, Scotland (Cannell & Willett 1975) and Moffat Forest, Scotland (Ford et al. 1987). Both studies report temperatures only for the growing season. January to May growing degree days were approximated from long-term (1941 to 1970) average temperature measurements at weather stations in western Scotland. Estimates of GDDFolStart at the 2 sites were 700 to 750, and GDDFolEnd was 1400 to 1600. For all Sitka spruce model runs, GDDFolStart and GDDWoodStart were set to 650; GDDFolEnd and GDDWoodEnd, to 1500.

Wood production conversion factors (BoleFrac and Density). BoleFrac and Density were added to PnET-II to convert wood production estimates from woody NPP ($g_{\text{biomass}} m^{-2} yr^{-1}$) to stem volume increment ($m^3 ha^{-1} yr^{-1}$). BoleFrac represents the fraction of all

Table 5. Estimates of BoleFrac for Sitka spruce and other coniferous species. BoleFrac represents the fraction of all woody net primary production (branches, woody roots, bolewood, bark) allocated to stemwood and bark, and may be represented by allocation patterns of woody biomass

Species	BoleFrac	Stand age (yr)	Site location	Source
<i>Picea sitchensis</i>	69%, NPP	18	Scotland	Ford (1982)
<i>Pinus nigra</i> var. <i>maritima</i>	60%, NPP	36	Scotland	Miller & Miller (1976)
<i>Abies amabilis</i>	51%, NPP 64%, NPP	23 180	Oregon, USA	Grier et al. (1981)
<i>Pseudotsuga menziesii</i>	78%, NPP, biomass	} Old growth (~450)	Oregon, USA	Grier & Logan (1977)
<i>Tsuga heterophylla</i>	57%, NPP, biomass			
<i>Thuja plicata</i>	52%, NPP, biomass			
<i>Picea sitchensis</i>	64%, biomass	30	Co. Wicklow, Ireland	Carey & O'Brien (1979)

woody NPP (woody roots, bark, branches, and bolewood) allocated to bolewood and stem bark.

Measurements from a highly productive Sitka spruce stand indicate that 69% of total woody NPP is allocated to bolewood (Ford 1982). No other NPP data were found for Sitka spruce, but patterns of NPP allocation in other conifers and biomass allocation in Sitka spruce suggest that the high-productivity stand allocates a rather large percentage of woody NPP to the stem (Table 5). Data for several western U.S. conifers indicate that woody NPP and biomass allocation patterns were essentially identical (Grier & Logan 1977), and so PnET-II used the more conservative estimate of bolewood allocation derived from biomass allocation patterns observed by Carey & O'Brien (1979), and BoleFrac was assigned a value of 0.64.

Density is the density of bolewood (g cm^{-3}) used to convert from stem weight to volume. Most reported estimates of Sitka spruce density were between 0.3 and 0.4 g cm^{-3} (Gholz 1982, Jarvis & Leverenz 1983, Harcombe et al. 1990, Dewar & Cannell 1992). Young Sitka spruce can have densities up to 0.6 g cm^{-3} , but wood density decreases with age (Cannell et al. 1983). According to UK forest mensuration charts, density varies inversely with growth rate (Hamilton 1985, from Dewar & Cannell 1992). A density of 0.34 g cm^{-3} was used to correspond with Ireland's mean yield class of 16 $\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$ (Carbonnier 1991, Anonymous 1994).

Climate and soils data. To validate PnET-II against measured forest production values, and to perform sensitivity analyses appropriate for the range of conditions in Ireland, we needed site-level data on climate and soil WHC for those sites where production data were available. Climate data (average monthly maximum and minimum temperature, precipitation and radiation) were derived from a statistical model developed for Ireland to describe the spatial and elevational variation of average monthly climate for the period

1951 to 1980 (Goodale et al. 1998). Sites were located within a 1 km resolution GIS based on a digital elevation model (DEM) of the same scale developed for this project, and climate data obtained using the spatial model.

In order to estimate plant-available soil WHC, the 1:575 000 General Soil Map of Ireland (Gardiner & Radford 1980) was digitized and converted to a raster system with 1 km^2 grid cells to overlay the DEM described above (Fig. 3). Each of the map's 44 soil associations was assigned an estimated WHC value (J.

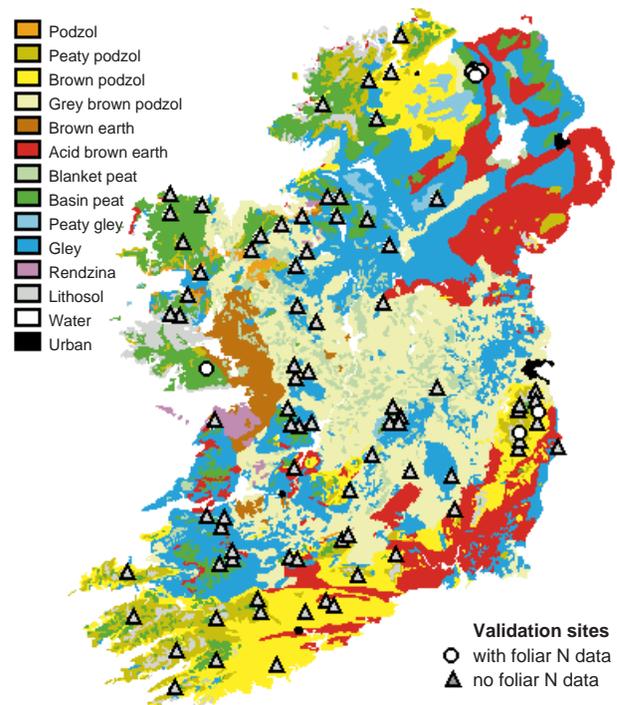


Fig. 3. Principal soils of Ireland used to map approximate soil water holding capacity (from Gardiner & Radford 1980), with locations of stands used for validation

Collins pers. comm.). For example, peatlands were assigned high WHC values (16 cm) while lithosols were assigned low values (2 cm). This approach enabled general characterizations of major differences in soil water, but was an approximation at best.

3.3. Validation

PnET-II's predictions of annual wood production ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$) were compared with estimates of yield class for 2 sets of stands: 7 stands from the literature with published foliar N values (Table 6), and 82 stands from the Irish Forestry Board (Coillte Teoranta) without foliar N data. For both sets of stands, elevations were estimated to within 30 m (100 feet) from 1:126 720 ($\frac{1}{2}$ inch : 1 mile) maps published by the Ordnance Survey of Ireland. Climate data were obtained from the climate models described above based on the latitude, longitude and elevation of each site (Goodale et al. 1998). WHC values were estimated from the stand's location within the GIS soil WHC data layer. For the 7 stand set, measured foliar N values were used, with one exception. Foliar N:P ratios at the Glenmalure site exceeded the critical 10:1 ratio, suggesting a phosphorus limitation. PnET-II was run for this site with both the measured foliar N concentration (1.8%) and an 'effective' foliar N concentration of 1.2%, 10 times the foliar P concentration. For the 82 stand set where foliar N data were not available, runs were performed using default values of 1.1% and 1.8% for all sites.

3.4. Sensitivity analyses and predictions

We used different sets of input parameters and a standardized set of site locations to assess the relative

sensitivity of PnET-II predictions of NPP and wood production to predicted changes in climate and currently occurring variations in site quality. For each simulation presented below, PnET-II was run for the same subset of 830 locations randomly selected from a GIS for Ireland (Goodale et al. 1998). Soil WHC and elevation were determined for each site by location within the GIS, and the selected pixels had elevation and WHC distributions identical to those of the full GIS. Ambient climate conditions were determined for each pixel using regional climate models (Goodale et al. 1998). Sensitivity to climate change was determined by altering temperature and precipitation for each pixel as predicted by the Hadley Centre GCM. Sensitivity to site quality was determined by varying foliar N concentration across the range of values measured in Ireland (Table 3). Results were compared with predicted sensitivity to errors in parameter estimation and to the current range in ambient climate and site quality conditions.

Climate and CO₂. An ambient control and 5 climate change scenarios were run for each of 3 different foliar N concentrations (0.9, 1.5 and 2.1%). The first 4 climate change runs consisted of changes in individual parameters: symmetric and asymmetric temperature changes, precipitation changes, and the effects of CO₂ enrichment on water use efficiency. A fifth run incorporated changes in temperature, precipitation and water use efficiency all at once. For the first temperature change run (symmetric temperature increases) both daily maximum and minimum temperature were increased by the same amount (Table 7) using seasonal sulfate-corrected predictions obtained from the Hadley Centre GCM (Mitchell et al. 1995, <http://www.cru.uea.ac.uk/link/>). In the second run (asymmetric temperature increases), changes in minimum temperature accounted for two-thirds of the

Table 6. Site descriptions of the 7 locations with published foliar N data. Age, elevation, foliar N and yield class were provided for all sites. The foliar N value in parentheses is an 'effective' foliar N value based on phosphorus limitation. WHC values were estimated from descriptions of soil type

Site	Age (yr)	Elevation (m)	Mean foliar N%	Est. WHC (cm)	Yield class ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$)	PnET-II wood volume increment ($\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$)
Cloosh ^a	35	102	1.47	16	18	18
Roundwood ^a	38	395	1.76	10	16	17
Glenmalure ^b	33	350	1.80 (1.21)	14	14	21 (10)
Cam Forest 1 ^c	17	250	1.04	14	6–8	7
Cam Forest 2 ^c	17	250	1.24	14	12	10
Cam Forest 3 ^c	17	250	1.28	14	14–16	10
Cam Forest 4 ^c	17	250	1.55	14	20	16

^aFarrell et al. (1994), ^bCarey & O'Brien (1979), ^cSchaible & Dickson (1990)

Table 7. Climate change predictions used in tests of sensitivity of forest production. Values are from the Hadley Center GCM (Mitchell et al. 1995). Predictions are from a model experiment in which the effects of sulfate aerosols are combined with effects of increases in greenhouse gases. Winter is December, January and February; spring is March, April and May; summer is June, July and August; and fall is September, October and November. Distribution of temperature change between maximum and minimum assumes that 2/3 of the change in mean temperature is due to increases in minimum temperature

Climate parameter	Season			
	Winter	Spring	Summer	Fall
Mean temp. (°C)	+2.1	+1.8	+2.1	+2.3
Max. temp. (°C)	+1.1	+0.9	+1.1	+1.2
Min. temp. (°C)	+3.2	+2.7	+3.2	+3.5
Precip. (cm mo ⁻¹)	+0.6	+0.6	-0.3	+0.6

change in mean temperature, while maximum temperatures were increased only slightly (Table 7). Both methods result in the same increase in monthly mean temperature, but have different effects on nighttime respiration and on VPD. In the third run, precipitation was altered seasonally according to the Hadley Center predictions in which precipitation increased in all seasons except summer, when it decreased (Table 7). These monthly changes were added to the monthly climate values for each of the 830 pixels in the subset of the Irish DEM used for these analyses.

In the fourth run, we simulated the physiological effects of CO₂ enrichment by increasing water use efficiency only, as in previous applications of PnET-II (Aber et al. 1995). This may underestimate actual sensitivity to enrichment as potential increases in photosynthesis are ignored. Essentially, this assumes that nutrient limitations will lead to a down-regulation of photosynthesis, leaving only the water use efficiency effects in place (see discussion in Section 2 above).

The fifth climate change run combined the effects of changes in precipitation, temperature and CO₂ enrichment. This run represents the prediction for the combined effects of the changes described here on forest production in Ireland across a range of site qualities.

Site quality. To determine sensitivity to site quality, summarized in these simulations as foliar N concentration, we varied foliar N from 0.9% to 2.1% N (Table 8) to capture most of the measured range in this parameter in Ireland and Scotland.

Potential errors in physiological parameters. In addition to foliar N, each of the vegetation parameters discussed above was varied across the range of published values (Table 8), with the exception of DVPDA and DVPDB, FolReten, and PsnTMin for which the variation could not be assessed from the studies available. PsnTMin was varied $\pm 2^\circ\text{C}$, and the other 3 parameters were varied $\pm 10\%$. Sensitivity indices were cal-

culated as the percent change in productivity (NPP or wood growth) divided by the percent change in the parameter value.

Ambient soil and climate. The effects of spatial variation in current climate and soil conditions on NPP or wood production are captured as variation around the mean for each of the runs performed.

4. RESULTS AND DISCUSSION

4.1. Validation

PnET-II's predictions agreed fairly well with published yield class estimates of production where foliar N data were available (Fig. 4). Wood production estimates for 6 of the 7 sites fell within 5 m³ ha⁻¹ yr⁻¹ of the actual yield classes, which are generally reported in 2 m³ ha⁻¹ yr⁻¹ classes. The Glenmalure site was predicted more accurately with the 'effective' foliar N value equal to 10 times the phosphorus concentration, than by actual foliar N. This suggests that nutrient limitation by elements other than nitrogen may be represented by 'effective' N concentrations based on critical N:element ratios. Additional data from sites with foliar N and P values would provide a more rigorous test of the model.

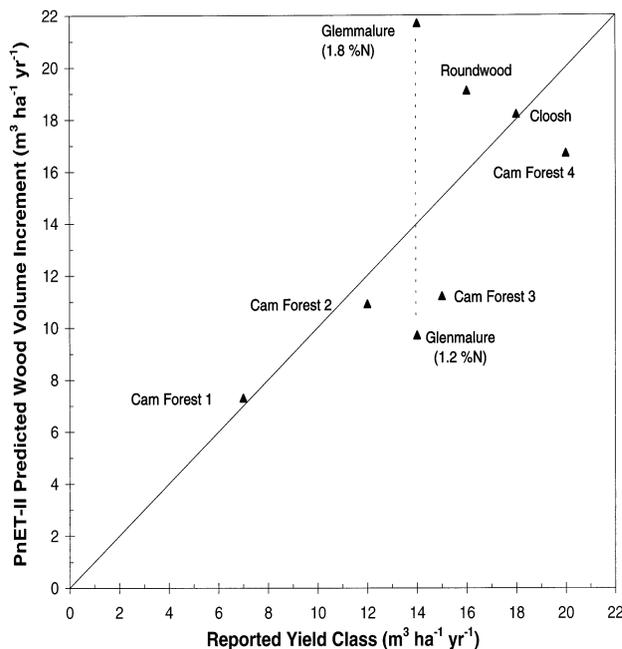


Fig. 4. PnET-II predictions of annual wood volume increment compared to yield class estimates at 7 sites with published foliar N and yield class data (Table 6)

Yield class at the 82 Coillte Teoranta sites with no available foliar N data averaged $16.5 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$. PnET-II generally overpredicted mean wood production ($21.5 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$) when foliar N was set to 1.8% at all sites and underpredicted wood production ($8.8 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$) when 1.1% was used instead (Fig. 5). The differences between PnET-II and Coillte wood production estimates did not follow any discernible pattern with respect to elevation, age, estimated WHC, estimated soil type, calculated temperature, or calculated precipitation. The effect of wind in reducing potential Sitka spruce growth was estimated from empirical relations developed in Scotland (Worrell & Malcolm 1990a, b) and an existing wind zonation map for Ireland (Miller 1986), but this index also failed to explain the discrepancy between Coillte Teoranta and PnET-II growth estimates. Based on the more successful results where foliar N values were known (Fig. 4) and the results of sensitivity analyses below, we believe that actual stand-level variation in foliar nitrogen status, were such data available, would explain much the observed variation in yield class.

Yield class is not a direct measurement of tree volume growth, but an index of a stand's predicted maximum mean annual growth rate ($\text{m}^3_{\text{bolewood}} \text{ ha}^{-1} \text{ yr}^{-1}$), generally expressed in increments of $2 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$. These empirical models have not been tested in Ireland, and their validity may not continue at sites experiencing environmental change (Bossel 1991, Mohren & Burkhardt 1994, Spiecker et al. 1996). Thus, errors may occur in either PnET-predicted or 'observed' yield class.

Wood growth is also one of the most difficult processes for the PnET model to predict accurately, in that the model allocates carbon to wood only after all other plant demands are met. As a residual term, wood production is the least constrained term in the stand carbon balance and is particularly sensitive to changes in the system's carbon economy.

4.2. Sensitivity analyses

The effects on NPP and wood production of either ambient variation in climate and soil WHC or predicted increases in temperature, precipitation and CO_2

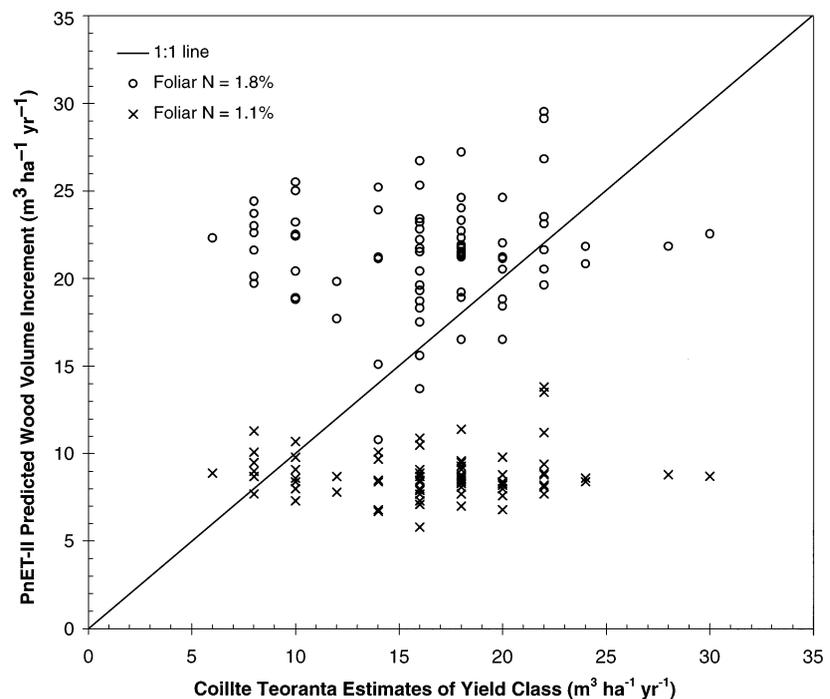


Fig. 5. PnET-II predictions of annual wood volume increment compared to yield class estimates for 86 sites across Ireland. Foliar N data were not available for individual stands, and so PnET-II used default values of 1.8 and 1.1%

are quite small relative to the effects of ambient variability in site quality represented as changes in foliar N concentration (Fig. 6).

Climate and CO_2 . Among climate change runs, predicted differences in NPP were always less than 9% (Fig. 6). This is less than the variability due to variation in ambient climate and soil conditions. Differences in wood production between climate change treatments were greater than differences in NPP as PnET-II gives allocation priority to foliage and roots, and lower priority to wood. Still, these differences never exceeded 30% and generally were less than 15%. Differences were accentuated at higher foliar N concentrations. In general, those treatments which increased the length of the growing season (temperature increases) increased wood production. The asymmetric temperature increase resulted in an even longer growing season, and hence even more wood production, than the symmetric increase. The asymmetric temperature change also decreased VPD and so increased water use efficiency as described above. However, increased water use efficiency alone was only important at the highest foliar N level, where the higher rate of photosynthesis, and hence transpiration, resulted in a small amount of water stress. The combined effects of predicted increases in temperature, precipitation and CO_2 are predicted to be minor for forests in Ireland (Fig. 6,

Table 8. Mean sensitivity of model predictions of net primary production (NPP, g m^{-2}) and wood volume increment ($\text{m}^3 \text{ha}^{-1}$) to changes in 12 vegetation parameters for 830 randomly-selected sites. Each parameter value was varied according to the range of published data values. The sensitivity index is the ratio of the percent change in model predictions to the percent change in the input parameter. OM: organic matter

Standard value	Tested value	% Change			Sensitivity index	
		NPP		Yield class	NPP	Yield class
		Standard value: 2101 g OM m^{-2}	Standard value: 25 $\text{m}^3 \text{ha}^{-1}$			
Foliar N = 1.8	0.9	-50%	-47%	-67%	0.95	1.33
	1.2	-33%	-28%	-45%	0.83	1.34
	1.5	-17%	-12%	-20%	0.72	1.20
	2.1	17%	9%	16%	0.57	0.97
$k = 0.5$	0.43	-14%	7%	5%	-0.53	-0.35
	0.57	14%	-8%	-6%	-0.54	-0.44
SLWDel = 0.06	0.056	-7%	<0.1%	<0.1%	-0.04	0.01
	0.063	5%	<0.1%	<0.1%	-0.03	-0.01
SLWMax = 275	260	-6%	-3%	-3%	0.61	0.48
	290	6%	3%	2%	0.55	0.34
FolReten = 2.6	2.3	-12%	-3%	-11%	0.22	0.95
	2.9	12%	2%	8%	0.16	0.72
GDDStart = 650	550	-15%	<0.1%	1%	-0.03	-0.05
	750	15%	<0.1%	-1%	-0.03	-0.04
GDDEnd = 1500	1400	-7%	<-0.1%	<-0.1%	<0.01	<0.01
	1600	7%	<0.1%	<0.1%	<0.01	<0.01
PsnTMin = 0	-2		5%	8%		
	2		-8%	-11%		
PsnTOpt = 19	17		-1%	<0.1%		
	21		<0.1%	-2%		
DVPDA = 0.19	0.19	-10%	2%	2%	-0.16	-0.23
	0.23	10%	-1%	-2%	-0.15	-0.22
PrecIntFrac = 0.33	0.22	-33%	2%	3%	-0.07	-0.10
	0.49	48%	-6%	-7%	-0.12	-0.15
BoleFrac = 0.64	0.59	-8%	0%	-8%	0.00	1.00
	0.69	8%	0%	8%	0.00	1.00
Density = 0.34	0.3	-12%	0%	-12%	0.00	1.00
	0.4	18%	0%	18%	0.00	1.00

rightmost bar in each group). Overall, changes in NPP or wood production induced by changing temperature, precipitation and water use efficiency separately or in combination were no more than 30% of ambient (control run) values, assuming no feedback between climate change and site fertility.

Changes in NPP and wood production are not always proportional in PnET-II. Conditions of water stress result in lower allocations to foliage in the following year and hence higher proportional allocation to wood. Thus the increase in NPP in the water use efficiency run at 2.1% foliar N relieves water stress, leading to higher allocations to foliage, with less of an effect on wood production.

Site quality. In contrast to the small changes predicted in response to climate change, a 2-fold increase in NPP and a 4-fold increase in wood production are predicted over the measured range of foliar N concen-

trations values currently existing in the field (Fig. 6). The range of values for yield class predicted over the measured range of foliar N concentrations is in agreement with the range of measured yield class values for Ireland (Fig. 5).

Physiological parameters. A comparison of model sensitivity to foliar N and other physiological parameters also emphasizes the potential importance of site quality relative to potential errors in specification of these parameters (Table 8). Not only is the model extremely sensitive to small differences in foliar nitrogen (sensitivity indices of 1.0 or more), but Sitka spruce foliar N contents also vary widely from site to site (Table 3).

Following foliar nitrogen content, foliar retention time, maximum specific leaf weight, and the light attenuation constant were the next most critical model parameters, although production estimates changed

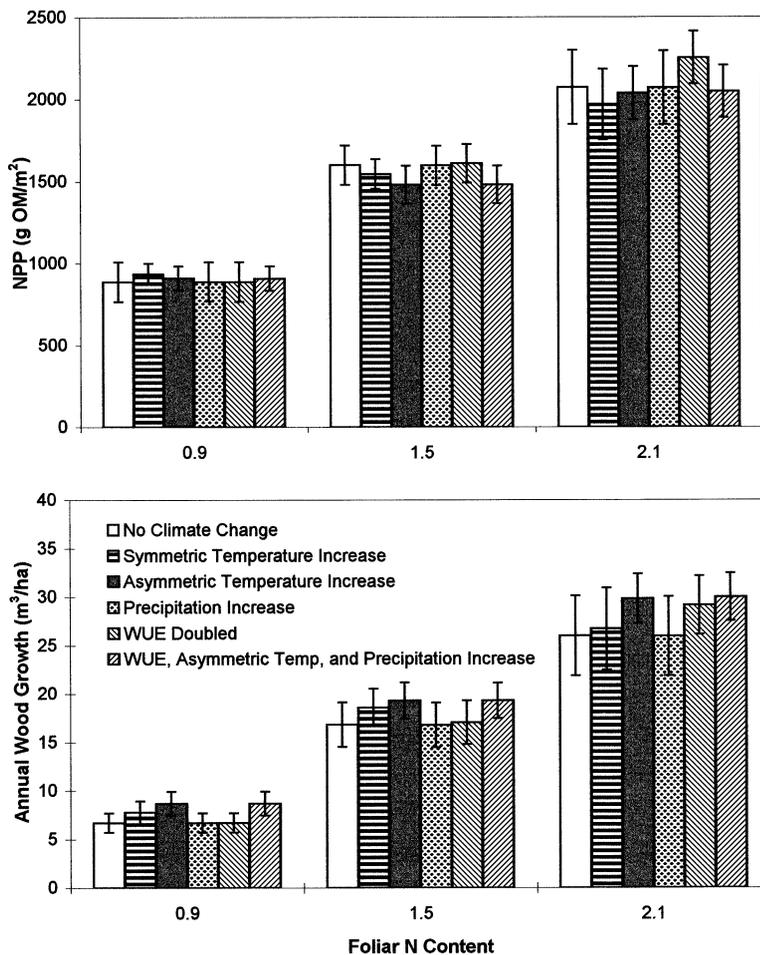


Fig. 6. PnET-II predictions of NPP ($\text{g organic matter m}^{-2}$) and annual wood volume increment ($\text{m}^3 \text{ha}^{-1}$) under current and changed climates at 3 different levels of foliar nutrition. In the first climate change scenario, maximum and minimum temperatures were increased equally (symmetric temp. increase), and in the second, minimum temperatures were increased more than maximum (asymmetric temp. increase). See text for more complete description. Bars represent mean (± 1 SD) values for 830 1-km² pixels randomly selected from the Irish GIS

by 11% or less due to observed variability in measurements of these parameters (Table 8). Decreasing foliar retention time decreases wood production more than overall NPP (Table 8), because faster leaf turnover demands additional carbon allocation to leaves. NPP remains high, but little carbon remains for wood production.

Changing the minimum temperature required for photosynthesis by 2°C affected production far more than changing the optimum temperature did. Lowering the critical minimum threshold for photosynthesis (PsnTMin) increased NPP and wood production by extending the growing season to the late fall and early spring. Variation in phenology parameters had very minor effects on production, confirming that the rough values determined for these parameter values

were adequate under these circumstances.

Considering the wide range of interception values observed (Table 4), interception impacts on production were quite small. Precipitation intercepted by the canopy is assumed in the model to evaporate and not contribute to soil water storage. This result indicates that water availability did not generally limit forest production in PnET-II runs.

Variation of BoleFrac and Density values did not affect predictions of NPP, but they did affect estimates of wood volume increment. Varying either BoleFrac or Density caused direct, uniform changes in the predicted wood volume increment at all pixels. Errors in specifying these 2 parameters could consistently bias predictions by up to 20%.

Ambient soil and climate. Standard deviations for each individual run average less than 10% of the mean (Fig. 6), and represent the variability resulting from variation in ambient soil WHC and climate conditions across Ireland. This source of variability is relatively minor due to Ireland's maritime climate.

5. CONCLUSIONS

Site-level foliar N concentration was the most sensitive parameter in this analysis of potential forest production in Ireland. Site-to-site variation in foliar chemistry may be due to natural differences in site fertility (Körner 1989, Martin & Aber 1997) or plantation management practices (Farrell 1990a, b, Farrell & Boyle 1990, Schaible & Dickson 1990). We conclude that these site-specific treatments, in combination with previous site history, result in a range of forest productivity that is much greater than any likely to be induced by climate change or CO₂ enrichment. Eamus & Jarvis (1989) drew a similar conclusion.

This result has global implications. Many models of regional NPP fail to include any index of N availability or site quality. Many of those models that do consider site quality use single default values of N availability for whole ecosystem types or regions (e.g. McGuire et al. 1992, Aber et al. 1995, VEMAP Members 1995, although Parton et al. 1993 provide an exception), which may strongly over- or under-represent the productivity of a large region (e.g. Fig. 5) particularly

where land use practices or forest management have induced differences in site quality. Additionally, these models use parameters from ecosystem study sites chosen to represent relatively undisturbed, mature or equilibrium conditions, or are calibrated to data sets developed at these sites. Direct effects of human management on site quality may impact forest productivity and carbon storage far more than the indirect effects resulting from an altered atmosphere, and so models must begin to incorporate the broad-scale effects of land management on forest productivity. This may be possible through the use of remote sensing of foliar chemistry (Matson et al. 1994, Martin & Aber 1997) or the incorporation of disturbance history into existing biogeochemical models (Aber et al. 1997). If we are to predict the actual role of climate change in altering forest productivity and global biogeochemistry, we must consider site quality—its spatial variability, controlling factors, and response to management and pollution loading.

Acknowledgements. Mr Peter Dodd provided yield class data from Coillte Teoranta. Dr Jim Collins of the Department of Crop Science, Horticulture, and Forestry at the University College Dublin (UCD) provided soil water estimates for the soils of Ireland, and Julian Aherne of the Forest Ecosystem Research Group at UCD assisted with digitizing. Drs C. A. Federer, R. Congalton, and several anonymous reviewers provided constructive comments on drafts of this manuscript. Research for this paper was from a thesis submitted to the Graduate School at the University of New Hampshire as part of the requirements for completion of a Master of Science degree. Financial support was provided by the U.S. EPA and the National Science Foundation's International and Long-term Ecological Research Programs.

LITERATURE CITED

- Aber JD, Federer CA (1992) A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia* 92:463–474
- Aber JD, Ollinger SV, Driscoll C (1997) Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecol Model* 101:61–78
- Aber JD, Ollinger SV, Federer CA, Kicklighter DW, Melillo JM, Lathrop RGJ, Ellis JM (1995) Predicting the effects of climate change on water yield and forest production in the northeastern U.S. *Clim Res* 5:207–222
- Aber JD, Reich PB, Goulden ML (1996) Extrapolating leaf CO₂ exchange to the canopy: a generalized model of forest photosynthesis validated by Eddy correlation. *Oecologia* 106:257–265
- Anderson AR, Pyatt DG (1986) Interception of precipitation by pole-stage Sitka spruce and Lodgepole pine and mature Sitka spruce at Kielder Forest, Northumberland. *Forestry* 59:29–38
- Anonymous (1994) Pathway to progress: a programme for forest research & development. National Council for Forest Research and Development, University College Dublin, Dublin
- Bazzaz FA (1990) The response of natural ecosystems to the rising global CO₂ levels. *Annu Rev Ecol Syst* 21:167–196
- Bossel H (1991) Modelling forest dynamics: moving from description to explanation. *For Ecol Manage* 42:129–142
- Brooks JR, Hinckley TM, Sprugel DG (1994) Acclimation responses of mature *Abies amabilis* sun foliage to shading. *Oecologia* 100:316–324
- Cannell MGR, Sheppard LJ, Ford ED, Wilson RHF (1983) Clonal differences in dry matter distribution, wood specific gravity and foliage 'efficiency' in *Picea sitchensis* and *Pinus contorta*. *Silvae Genet* 32:195–202
- Cannell MGR, Smith RI (1983) Thermal time, chill days and prediction of budburst in *Picea sitchensis*. *J Appl Ecol* 20:951–963
- Cannell MGR, Willett SC (1975) Rates and times at which needles are initiated in buds on differing provenances of *Pinus contorta* and *Picea sitchensis* in Scotland. *Can J For Res* 5:367–380
- Carbannier L (1991) Ireland—forestry; the potential. In: Mollan C, Maloney M (eds) *The right trees in the right places: The proceedings of a conference on forestry and the environment held at the Royal Dublin Society on October 17–19, 1990*. Royal Dublin Society, Dublin, p 48–55
- Carey ML, O'Brien D (1979) Biomass, nutrient content and distribution in a stand of Sitka spruce. *Ir For* 36:25–35
- Conway A (1991) Ireland—agriculture; the prospects. In: Mollan C, Maloney M (eds) *The right trees in the right places: The proceedings of a conference on forestry and the environment held at the Royal Dublin Society on October 17–19, 1990*. Royal Dublin Society, Dublin, p 42–47
- Curtis PD, Drake BG, Leadley PW, Arp W, Whigham DF (1989a) Growth and senescence of plant communities exposed to elevated CO₂ concentrations on an estuarine marsh. *Oecologia* 78:20–26
- Curtis PD, Drake BG, Whigham DF (1989b) Nitrogen and carbon dynamics in C₃ and C₄ estuarine marsh plants grown under elevated CO₂ in situ. *Oecologia* 78:297–301
- Dewar RC, Cannell MGR (1992) Carbon sequestration in the trees, products and soils of forest plantations; an analysis using UK examples. *Tree Physiol* 11:49–71
- Eamus D, Jarvis PG (1989) The direct effects of increase in the global atmospheric CO₂ concentration on natural and commercial temperate trees and forests. In: Cragg JB (ed) *Advances in ecological research*. Academic Press, London, p 1–55
- Edwards PN, Christie JM (1981) Yield models for forest management. Forestry Commission Booklet No. 48. HMSO, London
- Farrell EP (1985) Long-term study of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) on blanket peat. 2. Water-table depth, peat depth and nutrient mineralisation studies. *Ir For* 42:92–105
- Farrell EP (1990a) Aspects of the nitrogen cycle in peatland and plantation forest ecosystems in western Ireland. *Plant Soil* 128:13–20
- Farrell EP (1990b) Peatland forestry in the Republic of Ireland. In: Hanell B (ed) *Proceedings of Biomass Production and Element Fluxes in Forested Peatland Ecosystems*. Swedish University of Agricultural Sciences, Dept of Forest Site Research, Ulmea
- Farrell EP, Boyle G (1990) Peatland and forestry in the 1990's. *Ir For* 47:69–78
- Farrell EP, Cummins T, Boyle GM (1994) Intensive monitoring of forest ecosystems in Ireland. Final report. Forest Ecosystem Research Group Report Number 13. Department of Environmental Resource Management, University College Dublin

- Field C, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: Givnish TJ (ed) *On the economy of plant form and function*. Cambridge University Press, New York, p 25–55
- Ford ED (1982) High productivity in a polestage Sitka spruce stand and its relation to canopy structure. *Forestry* 55(1):1–17
- Ford ED, Deans JD (1978) The effects of canopy structure on stemflow, throughfall and interception loss in a young Sitka spruce plantation. *J Appl Ecol* 15:905–917
- Ford ED, Deans JD, Milne R (1987) Shoot extension in *Picea sitchensis*. I. Seasonal variation within a forest canopy. *Ann Bot* 60:531–542
- Galloway JN, Schlesinger WH, Levy H II, Michaels A, Schnoor JL (1995) Nitrogen fixation: anthropogenic enhancement-environmental response. *Global Biogeochem Cycles* 9:235–252
- Gardiner MJ, Radford T (1980) Ireland general soil map. National Soil Survey, An Foras Taluntais, Dublin
- Gholz HL (1982) Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. *Ecology* 63:469–481
- Giorgi F, Marinucci MR, Visconti G (1992) A $2\times\text{CO}_2$ climate change scenario over Europe generated using a limited area model nested in a general circulation model. 2. Climate change scenario. *J Geophys Res* 97:10011–10028
- Goodale CL, Aber JD, Ollinger SV (1998) Mapping monthly precipitation, temperature, and solar radiation for Ireland with polynomial regression and a digital elevation model. *Clim Res* 10:35–49
- Grier CC, Logan RS (1977) Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecol Monogr* 47:373–400
- Grier CC, Vogt KA, Keyes MR, Edmonds RL (1981) Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Can J For Res* 11:155–167
- Hamilton GJ (1985) Forest mensuration handbook. Forestry Commission Booklet No. 35. HMSO, London
- Harcombe PA, Harmon ME, Greene SE (1990) Changes in biomass and production over 53 years in a coastal *Picea sitchensis* - *Tsuga heterophylla* forest approaching maturity. *Can J For Res* 20:1602–1610
- Hom JL, Oechel WC (1983) The photosynthetic capacity, nutrient content, and nutrient use efficiency of different needle age-classes of black spruce (*Picea mariana*) found in interior Alaska. *Can J For Res* 13:834–839
- Hudson JA (1988) The contribution of soil moisture storage to the water balance of upland forested and grassland catchments. *Hydrol Sci J* 22:1602–1616
- Jarvis PG (1981) Production efficiency of coniferous forest in the UK. In: Johnson CB (ed) *Physiological processes limiting plant productivity*. Butterworths, London, p 81–107
- Jarvis PG, James GB, Landsberg JJ (1976) Coniferous forest. In: Monteith JL (ed) *Vegetation and the atmosphere*. Academic Press, London, p 171–240
- Jarvis PG, Leverenz JW (1983) Productivity of temperate, deciduous and evergreen forests. In: Lange OL, Osmond CB, Ziegler H (eds) *Physiological plant ecology*. IV. Springer-Verlag, New York, p 234–280
- Johnson RC (1990) The interception, throughfall and stemflow in a forest in Highland Scotland and the comparison with other upland forests in the U.K. *J Hydrol* 118:281–287
- Kattenberg A, Giorgi F, Grassl H, Meehl GA, Mitchell JFB, Stouffer RJ, Tokioka T, Weaver AJ, Wigley TML (1996) Climate models—projections of future climate. In: Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (eds) *Climate change 1995: the science of climate change*. Cambridge University Press, Cambridge
- Kearney B (1994) Agriculture, forestry, and the environment in the year 2025. In: Mollan C, Maloney M (eds) *The right trees in the right places*. The proceedings of a conference on forestry and the environment held at the Royal Dublin Society on October 17–19. Royal Dublin Society, Dublin, p 56–63
- Körner C (1989) The nutritional status of plants from high altitudes. *Oecologia* 81:379–391
- Ludlow MM, Jarvis PG (1971) Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) I. General characteristics. *J Appl Ecol* 12:879–892
- Marinucci MR, Giorgi F (1992) A $2\times\text{CO}_2$ climate change scenario over Europe generated using a limited area model nested in a general circulation model. 1. Present day seasonal climate simulation. *J Geophys Res* 97:9989–10009
- Martin ME, Aber JD (1997) High spectral resolution remote sensing of forest canopy lignin, nitrogen, and ecosystem processes. *Ecol Appl* 7:431–443
- Matson P, Johnson L, Billow C, Miller J, Pu R (1994) Seasonal patterns and remote spectral estimation of canopy chemistry across the Oregon transect. *Ecol Appl* 4:280–298
- McCarthy R (1993) Monitoring forest condition in Ireland. *Ir For* 50:21–34
- McEvoy T (1954) A review of Irish forestry. *Ir For* 11:20–27
- McEvoy T (1958) Forestry in Ireland. *Adv Sci* 56:307–316
- McGuire AD, Melillo JM, Joyce LA, Kicklighter DW, Grace AL, Moore B III (1992) Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Global Biogeochem Cycles* 6:101–124
- McMurtrie RE, Leuning R, Thompson WA, Wheeler AM (1992) A model of canopy photosynthesis and water use incorporating a mechanistic formulation of leaf CO_2 exchange. *For Ecol Manage* 52:261–278
- Miller HG, Miller JD (1976) Effect of nitrogen supply on net primary production in Corsican pine. *J Appl Ecol* 13:249–256
- Miller JD, Cooper JM, Miller HG (1993) A comparison of above-ground component weights and element amounts in four forest species at Kirkton Glen. *J Hydrol* 145:419–438
- Miller KF (1986) Windthrow hazard in conifer plantations. *Ir For* 43:66–78
- Mitchell AK, Hinckley TM (1993) Effects of foliar nitrogen concentration on photosynthesis and water use efficiency in Douglas-fir. *Tree Physiol* 12:403–410
- Mitchell KFB, Johns TC, Gregory JM, Tett ASFB (1995) Climate response to increasing levels of greenhouse gases and sulphate aerosols. *Nature* 376:501–504
- Mohren GMJ, Burkhardt HE (1994) Contrasts between biologically-based process models and management-oriented growth and yield models. *For Ecol Manage* 69:1–5
- Neilson RE, Ludlow MM, Jarvis PG (1972) Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) II. Response to temperature. *J Appl Ecol* 9:721–745
- Nicholls N, Gruza GV, Jouzel J, Karl TR, Ogallo LA, Parker DE (1996) Observed climate variability and change. In: Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (eds) *Climate change 1995: the science of climate change*. Cambridge University Press, Cambridge, p 132–192
- Norman JM, Jarvis PG (1972) Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) III. Measurements of

- canopy structure and interception of radiation. *J Appl Ecol* 9:375–398
- Oberbauer SF, Sionit N, Hastings SJ, Oechel WC (1986) Effects of CO₂ enrichment and nutrition on growth, photosynthesis, and nutrient concentration of Alaskan tundra plant species. *Can J Bot* 64:2993–2999
- Parton, WJ, Scurlock JMO, Ojima DS, Gilmanov TG, Scholes RJ, Schimel DS, Kirchner T, Menaut JC, Seastedt T, Garcia Moya E, Kamnalrut A, Kinyamario JI (1993) Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochem Cycles* 7:785–809
- Pastor J, Post WM (1986) Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2:3–27
- Pierce LL, Running SW (1988) Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer. *Ecology* 69:1762–1767
- Pierce LL, Running SW, Walker J (1994) Regional-scale relationships of leaf area index to specific leaf area and nitrogen content. *Ecol Appl* 4:313–321
- Pitelka LF (1994) Ecosystem response to elevated CO₂. *TREE* 9:201–239
- Polley HW, Johnson HB, Marino BD, Mayeux HS (1993) Increase in C₃ plant water-use efficiency and biomass over Glacial to present CO₂ concentrations. *Nature* 361:61–64
- Raich JW, Rastetter EB, Melillo JM, Kicklighter DW, Steudler PA, Peterson BJ, Grace AL, Moore B III, Vorosmarty CJ (1991) Potential net primary productivity in South America: application of a global model. *Ecol Appl* 1:339–429
- Reich PB, Kloeppel B, Ellsworth DS, Walters MB (1995) Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia* 104:24–30
- Reich PB, Schoettle AW (1988) Role of phosphorus and nitrogen in photosynthetic and whole plant carbon gain and nutrient use efficiency in eastern white pine. *Oecologia* 77:25–33
- Reich PB, Walters MB, Ellsworth DS, Uhl C (1994) Photosynthesis-nitrogen relations in Amazonian tree species. I. Patterns among species and communities. *Oecologia* 97:62–72
- Running SW (1976) Environmental control of leaf water conductance in conifers. *Can J For Res* 6:104–112
- Running SW, Coughlan JC (1988) A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecol Model* 42:125–154
- Sandford AP, Jarvis PG (1986) Stomatal responses to humidity in selected conifers. *Tree Physiol* 2:89–103
- Schaible R, Dickson DA (1990) Effects of drainage intensity and planting position on the growth and nutrition of second rotation Sitka spruce on shallow peat. *Ir For* 47:19–27
- Spiecker H, Mielikainen K, Kohl M, Skovsgaard G (1996) Growth trends in European forests. Springer-Verlag, Heidelberg
- Teklehaimanot Z, Jarvis PG, Ledger D (1991) Rainfall interception and boundary layer conductance in relation to tree spacing. *J Hydrol* 123:261–278
- Townend J (1993) Effects of elevated carbon dioxide and drought on the growth and physiology of clonal Sitka spruce plants (*Picea sitchensis* (Bong.) Carr.). *Tree Physiol* 13:389–399
- Trenberth KE, Houghton JT, Meira Filho LG (1996) The climate system: an overview. In: Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (eds) *Climate change 1995: the science of climate change*. Cambridge University Press, Cambridge
- VEMAP Members (1995) Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO₂ doubling. *Global Biogeochem Cycles* 9:407–737
- Vitousek PM (1994) Beyond global warming: ecology and global change. *Ecology* 75:1861–1876
- Waring RH, Franklin JF (1979) Evergreen coniferous forests of the Pacific Northwest. *Science* 204:1380–1386
- Watts WR, Neilson RE (1978) Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) VIII. Measurements of stomatal conductance and ¹⁴CO₂ uptake in controlled environments. *J Appl Ecol* 15:245–255
- Watts WR, Neilson RE, Jarvis PG (1976) Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) VII. Measurements of stomatal conductance and ¹⁴CO₂ uptake in a forest canopy. *J Appl Ecol* 13:623–638
- Woodward FI, Thompson GB, McKee IF (1991) The effects of elevated concentrations of carbon dioxide on individual plants, populations, communities, and ecosystems. *Ann Bot* 67:23–38
- Worrell R, Malcolm DC (1990a) Productivity of Sitka spruce in northern Britain. 1. The effects of elevation and climate. *Forestry* 63:105–118
- Worrell R, Malcolm DC (1990b) Productivity of Sitka spruce in northern Britain. 2. Prediction from site factors. *Forestry* 63:419–428

Editorial responsibility: Brent Yarnal,
University Park, Pennsylvania, USA

Submitted: September 10, 1996; Accepted: November 3, 1997
Proofs received from author(s): March 30, 1998