Tree Productivity Models based on Annual Ring Widths for Contemporary and Subfossil Scots Pine in Ireland

A. McNALLY and G. J. DOYLE

Botany Department, University College, Belfield, Dublin 4.

ABSTRACT

Ring width series from *Pinus sylvestris* L. are used to compute empirical growth functions for a number of sites, including two subfossil pinewood sites. These empirical functions are corrected for non-proportionality of annual ring width and stem volume increment. Significant correlations between stem diameter and tree productivity allow the corrected curves to be interpreted as current, mean tree productivity on each site. The trends evident in the productivity curves correspond with reported changes in pine productivity with age.

A comparison of relative productivity on the sites sampled indicates that trees growing on mineral substrates achieve higher current annual production than trees growing on peat at all ages. The rate of increase is also greater, and maximum productivity is achieved in older trees on mineral soils. Minimum relative productivity occurred in subfossil pines which grew on a midland raised bog. The observed differences in productivity are primarily attributed to differences in soil nutrient status and drainage.

It is suggested that productivity curves might be used in conjunction with information on stand density, and calibrated with quantitative productivity data to yield estimates of absolute stand productivity. This would be particularly useful in the study of subfossil woodlands where direct measurements are not possible.

INTRODUCTION

Efficient forest management requires an accurate knowledge of tree performance under specific environmental conditions in order that timber yields may be reliably forecast (Jonnson 1978). Because of extended crop rotations, the acquisition of the required data by experimental means, or by direct observation is a lengthy and expensive procedure. This paper describes an approach for reconstructing tree productivity based on simple empirical models.

Scots pine (*Pinus sylvestris* L.) was studied at a number of locations in order to relate differences in tree productivity to site conditions. Subfossil pine timbers excavated from midland raised bogs allow performance of native trees growing on peat to be assessed and thus provides a benchmark for comparison with contemporary introduced trees on similar sites.

Productivity of individual trees is strongly correlated with tree diameter at breast height, or various transformations of this

IRISH FORESTRY, 1985, Vol, 42, No. 1:33-43.

parameter such as basal area, or girth class (Heinsdijk 1975, O'Neill and DeAngelis 1981, Ovington and Madgwick 1959). Since stem diameter is the sum of annual radial increments, these can be used in deriving a model of current tree productivity with age. Derivation of the model involves computing empirical growth functions for trees on each site, and correcting these functions for the decrease in ring width which results merely from an increase in stem diameter, and which is not related to any changes in tree productivity.

Sites

Scots pines were sampled at seven sites encompassing a wide range of environmental conditions. The sites, along with some relevant data, are listed in Table 1. All the living trees sampled grew in unmanaged stands of low densities. *Pinus sylvestris* was dominant at all sites except Knocksink, where hardwoods, particularly *Quercus petraea* (Matt.) Liebl., predominated.

Trees sampled at Glashabaun and Ballycon were subfossil pine timbers. Radiocarbon dating and related pollen-stratigraphical analyses revealed that these timbers represented sub-Boreal pinewoods which existed on midland bog surfaces between 2000-1500 BC (McNally and Doyle in 1984 a, 1984 b).

Materials and Methods

Living trees were sampled by taking three increment cores at breast height (1.3m) using a Pressler borer. Subfossil timbers were sampled by cutting cross-sections with a power saw. When dry, samples were prepared for measurement using standard surfacing techniques (Stokes and Smiley 1968).

Ring widths were measured in units of 0.01mm along each of three radii per tree using a graduated moving stage and low power dissecting microscope with a cross-hairs fitted in the ocular (McNally and Doyle 1981).

Empirical Growth Functions

A mean ring series was based on all the individual radial series measured at each site. These mean site ring widths for the first 90-100 years of growth are plotted against cambial age in Fig 1. High frequency (year to year) ring width variation has been cancelled in the averaging process. Such variation is largley associated with changes in the annual climatic regime, in particular with temperature fluctuations from year to year (McNally 1983). The remaining variance is mostly associated with increasing stem diameter and development features common to all the trees (Fritts 1976).

Table 1. List of sampling sites with concise details of site conditions. Slope is given in degrees.

Sites	Trees	Grid. Ref.	Alt. (m)	Slope	Aspect	Soil
Scalp, Co. Dublin	Live	O215 200	180 — 210	50	WSW	Shallow quartz sand
Knocksink, Co. Wicklow	Live	O220 178	120	45	SSW	Red-brown boulder clay
Glencullen, Co. Wicklow	Live	O151 218	330 — 360	25	SW	Shallow Peat (0.5m) on granite
Black Valley, Co. Kerry	Live	V880 805	150	30	NW	Well-drained podzolic
Timahoe, Co. Kildare	Subfossil	N740 330	75	0	—	Peat (1.75m)
Glashabaun, Co. Offaly	Subfossil	N668 291	75	0	—	Peat (1.75m)
Ballycon, Co. Offaly	Subfossil	N550 268	75	0	—	Peat (0.75m)

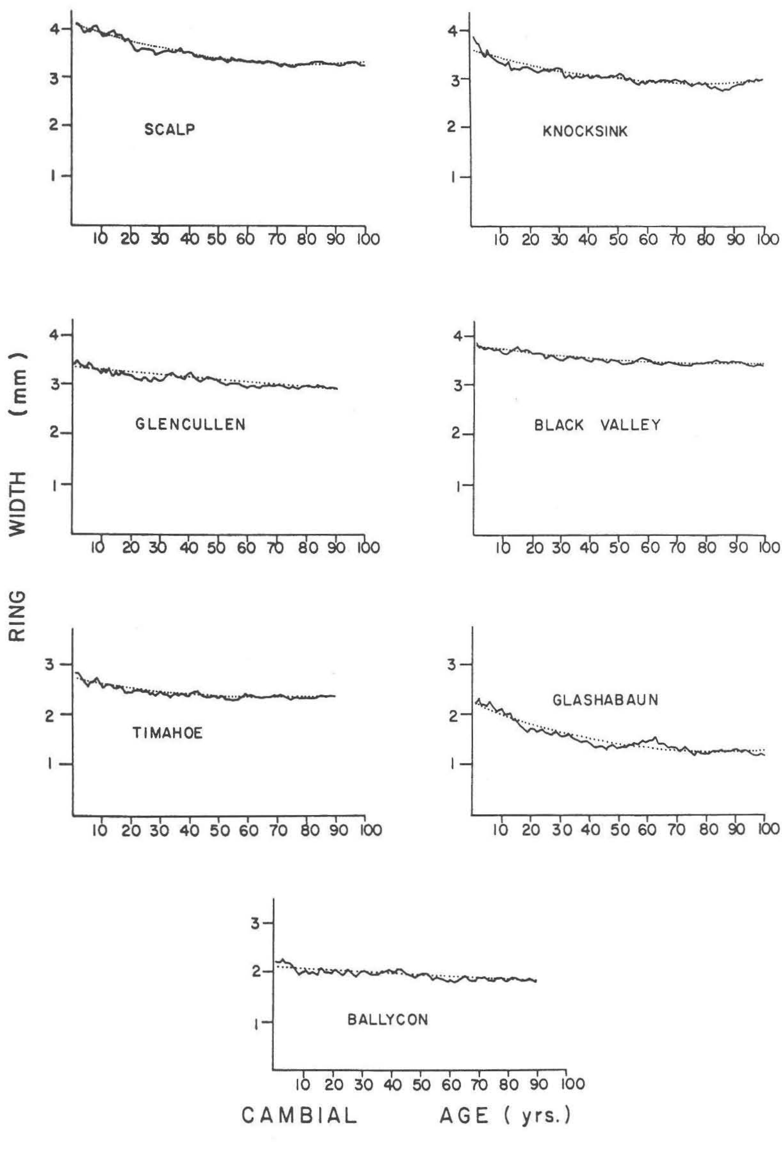

Fig 1. Empirical growth trends for each site obtained by averaging absolute ring width (mm) for increasing cambial age classes. The dotted lines in each plot are polynomial or single regression approximations of the growth trend. The equations for these curves are listed in Table 2.

These empirical growth trends have been approximated by fitting either orthogonal polynomial curves or straight lines with negative slopes (Graybill 1982). The equations for these curves are listed in Table 2, and constitute the empirical growth function for each site. Although they provide an index of changing tree productivity they are not readily interpreted because of proportionality constraints associated with the radial growth pattern.

Table 2. Empirical growth functions obtained by fitting polynomial or linear regression functions to mean ring series (0.01mm) for each site. The number of radial series on which the mean series are based (n), and the length of the series in years (yrs) are listed for each site. $y^{\prime}$ in each function is the predicted ring width in units of 0.01mm, and x is year number (i.e. cambial age) ranging from 1 to yrs.

Sites	Empirical Function	n	yrs
Scalp	$y^{\prime} = 411.24 - 2.09x + 0.0123x^2$	21	100
Black Valley	$y^{\prime} = 381.98 - 0.84x + 0.0050x^2$	9	100
Knocksink	$y^{\prime} = 359.33 - 1.78x + 0.0113x^2$	24	100
Glencullen	$y^{\prime} = 335.00 - 0.51x$	12	90
Timahoe South	$y^{\prime} = 275.45 - 1.14x + 0.0084x^2$	15	90
Glashabaun	$y^{\prime} = 221.37 - 2.33x + 0.0140x^2$	123	100
Ballycon	$y^{\prime} = 209.25 - 0.34x$	18	90

Constant Productivity Model

Ring width provides a linear measure of the amount of timber added to the tree bole each year. However, even if the amount of timber produced (measured either as volume, or cross-sectional area increment) remained constant, ring width would decrease exponentially with increasing distance from the pith, or increasing cambial age (Fritts 1971).

Assuming that the annual increment is a constant c, the total cross-sectional area after t years of growth is

$$ct = \pi r_t^2 \qquad \text{Eq. 1}$$

where r_t is the radius of the tree bole after t years. Thus, the cross-sectional area after 1 year of growth is

$$c = \pi r_1^2 \qquad \text{Eq. 2}$$

Substituting for c in equation 1 yields

$$\pi r^2_1 t = \pi r^2_t$$

which may be rewritten as

$$r_t = r_1 (t^{1/2}) \qquad \text{Eq. 3}$$

that is, bole radius after t years of growth (r_t) is a function of the initial radius (r_1). The expressions thus far have dealt with total bole radius. Ring width, or annual radial increment (k), in any year can be calculated by using equation 3, as the difference between two successive years (t and t+1). So

$$k = r_1 \left[(t+1)^{1/2} - (t)^{1/2}\right] \qquad \text{Eq. 4}$$

i.e. the difference between the radius of the bole in year t+1 and year t. This expression relates ring width in any year to the initial radius (r_1) and to cambial age (t). It assumes that annual production, as measured, by cross-sectional area increment of the bole at breast height, remains constant.

Tree Productivity

The constant productivity function (equation 4) is used to correct the empirical growth functions for the non-linearity effects of radial growth. The initial radius (r_1) for each site is read from the empirical growth curves in Fig 1. Each of these r_1 values is entered into equation 4 and used to generate values for k for years 1-90 (or 100). These values are plotted, along with the empirical curves in Fig 2.

The difference between the empirical growth curve (e) and the curve based on equation 4 (constant productivity curve, k) is a direct measure of the current annual wood production in tree boles on the various sites (Fig 2). As the annual wood increment in the bole represents a sizeable fraction of, and is strongly correlated with total productivity (O'Neill and DeAngelis 1981), the derived curves (e – k) allow comment on the mean tree productivity at each of the sites. While they do not show productivity in absolute terms, they can be used to assess patterns of changing (current annual) productivity with tree age, and to compare the relative productivities on different sites. Hereafter they are referred to as "productivity curves".

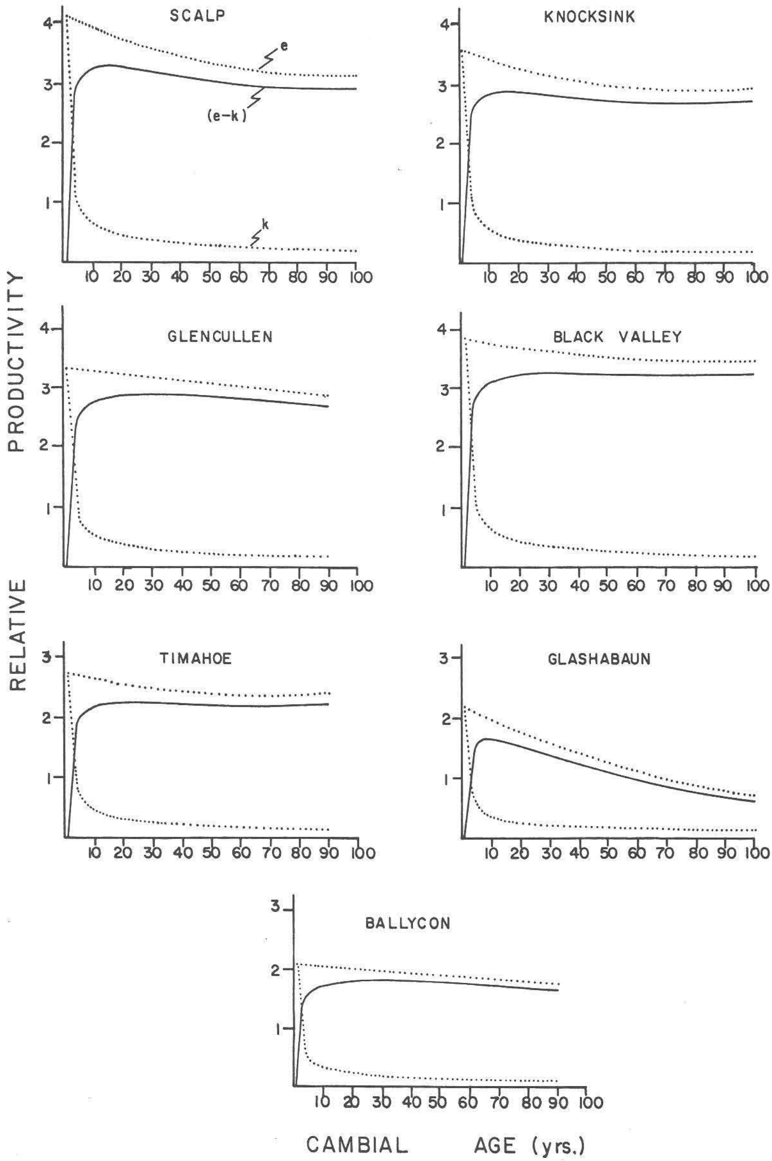

Fig 2. Plots of empirical growth functions (e) listed in Table 2, and constant productivity functions (k) based on equation 4 for each site. The curve labelled (e – k) in each plot is obtained by difference. It shows the current annual productivity corrected for non-proportionality due to linear ring width measurements of stem volume increment.

General Features of Productivity Curves

All the curves indicate a rapid increase in productivity during the early years of growth, reaching an absolute maximum between cambial ages of 10 and 30 years (Fig 2). If it is assumed that it takes 10 years for a pine sapling to reach breast height (Borthwick 1906), the real tree age is estimated at 20-40 years. This initial phase of rapid growth reflects the development and expansion of the sapling foliage and root system. This greatly increases its capacity for exploitation of soil nutrients, for assimilation and photosynthate production. Litter production, foliage dry weight and surface area, and current annual accumulation of organic matter reach absolute maxima in Scots pine between 10 and 30 years of age (Ovington 1959, Ovington and Heitkamp 1960). This is reflected by the maxima in the productivity curves over this same interval (Fig 2).

After the initial rapid increase in growth, the curves generally indicate a gradual decrease in current annual productivity. These observations are in general agreement with those of Ovington (1957) who found that current annual dry matter increment in *Pinus sylvestris* reached a maximum at 28 years of age and then declined. Such a decline in productivity with age is attributable to a number of causes. Nutrient deficiencies usually become marked at ages of 20-30 years, and even earlier on peat, when there is a maximum nutrient requirement (Carlisle and Brown 1968, Gunia 1967, McVean 1963a). Scots pine generally develops the flat crown typical of the species as it matures, and the current annual increment of leaves becomes constant after approximately 20 years (Carlisle and Brown 1968). However, the photosynthetic capacity of needles decreases with increasing tree age as well as with increasing needle age (Zelawski 1967). Therefore a reduction in total tree productivity would be expected.

Since the general trends exhibited by the deduced productivity curves are substantiated by the published observations on productivity/age relationships in *P. sylvestris* cited above, these curves are accepted as accurate records of current mean tree productivity on the sites studied. They are used as the basis for intersite comparisons of relative tree productivity.

Relative Site Productivities

Comparison of curves for all sites clearly indicates that tree productivity is greatest on sites with mineral substrates, or in the case of Glencullen, where the shallow peat substrate permits root access to mineral subsoils.

The reduced productivity of trees growing on peaty sites is attributable to the relative nutrient deficiency of such soils (McVean

1963b) allied with decreased nutrient assimilation by roots under conditions of reduced aeration (Brown *et al* 1966), and possibly accentuated by reduced mycorrhizal infection (McVean 1963a).

Amongst the peatland sites, relative productivity is greatest at Timahoe South, is intermediate at Ballycon, and least at Glashabaun. The higher productivity of contemporary pines at Timahoe South is probably due to the existence of improved soil conditions connected with ongoing commercial exploitation of adjacent peatlands and associated artificial drainage. Although the depth of peat underlying these contemporary trees and the subfossil Glashabaun pines is approximately the same (1.75m), the latter trees grew near the centre of an intact, undrained bog system where rooting conditions were probably less favourable. The subfossil trees at Ballycon however, grew on shallower peats near the margin of the then intact bog, and mean annual tree productivity was intermediate between Timahoe South and Glashabaun.

The productivity curve for the Glashabaun trees indicates that early tree growth was slowest on this site, and that limiting site conditions resulted in an early inflection of the productivity curve. Subsequently there is a pronounced decrease in annual production with increasing tree age. This suggests that the low concentration of available nutrients is sufficient to sustain early growth, but becomes limiting as the trees increase their demands on the nutrient reserves over the first 20-30 years (Carlisle and Brown 1968).

Fig 3 shows a mean productivity curve for the sites with mineral substrates (Scalp, Knocksink, Black Valley and Glencullen) compared with a mean curve for the bog sites (Timahoe South, Ballycon and Glashabaun). It is obvious that mean relative productivity is higher at all stages of growth on the mineral sites, and that the initial rate of increase is also greater. The productivity begins to decline somewhat earlier on the bog sites, and decreases more rapidly with age.

The curves presented are based on a number of trees from each site. Therefore, they provide an index of mean site productivity, integrating the effects of competition, density, nutrient availability, drainage etc. If combined with estimates of tree density and calibrated using stochastic relationships between total tree or above ground productivity and basal area, they could be used to estimate total site productivity. It would then be possible to compare absolute stand productivity between subfossil and contemporary woodlands.

The trees sampled in this study occurred in unmanaged stands at relatively low densities. Therefore the differences observed in

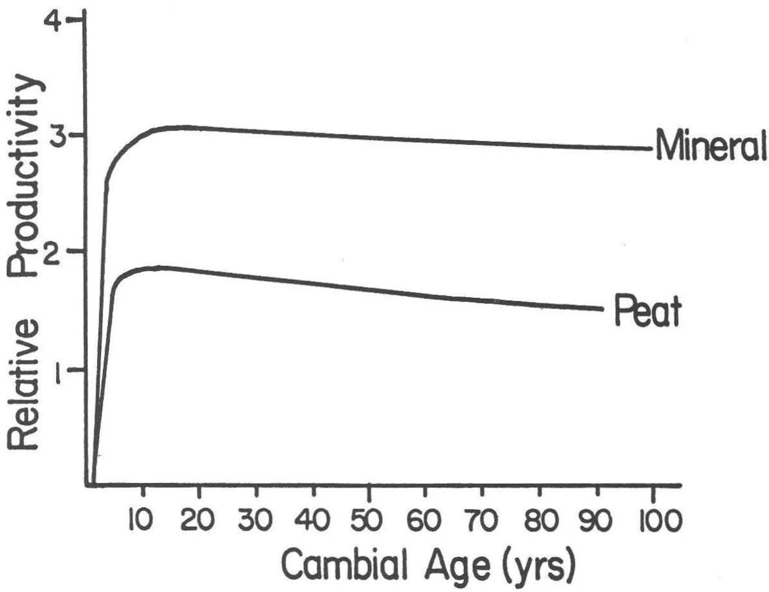

Fig 3. Mean current annual productivity curves for mineral substrates (based on four sites), and for peat substrates (based on three sites).

current annual productivity curves are mainly due to differences in site nutrient status, drainage conditions and, in the case of subfossil and contemporary woodlands, possibly to differences in the regional climatic milieu. Intraspecific competition at high tree densities is unlikely to have accounted for the different rates of annual radial increment and productivity.

REFERENCES

BORTHWICK, A. W. 1906. The life history of *Pinus sylvestris*. Trans. R. Engl. Arboricultural Soc. 6:205-223.

BROWN, A. H. F., CARLISLE, A. and WHITE, E. J. 1966. Some aspects of the nutrition of Scots pine on peat. Physiology in Forestry. Suppl. to Forestry 39:78-87

CARLISLE, A, and BROWN, A. H. F. 1968. Biological flora of the British Isles. *Pinus sylvestris* L. J. Ecol. 56:269-307.

FRITTS, H. C. 1971. Dendroclimatology and dendroecology. Quatern. Res. 1(4):419-449.

FRITTS, H. C. 1976. Tree-rings and climate. Academic Press, London.

GRAYBILL, D. A. 1982. Chronology development and analysis. *In* Hughes, M. K., Kelly, P. M., Pilcher, J. R. and LaMarche Jr., V.C. (Eds.). Climate from tree rings. 21-28. Cambridge University Press, Cambridge.

GUNIA, S. 1976. Mineral nutrition. *In* Bialobok, S. and Zelawski, W. (Eds.). Outline of physiology of Scots pine. (Translated from Polish). 119-151. Polish Academy of Sciences, PWN.

HEINSDIJK, D. 1975. Forest assessment. PUDOC, Wageningen, Netherlands.

JONNSON, B. 1978. A growth model as a basis for long-term forecasting of timber yields. *In* Fries, J., Burkhart, H. E. and Max, T. A. (Eds.). Growth models for long-term forecasting of timber yields. 119-137. Publication FWS-1-78. School of Forestry and Wildlife Resources, Virginia Polytech. Inst. and State University.

McNALLY, A. 1983. A dendrochronological study of contemporary and subfossil Scots pine in Ireland. Ph.D. thesis, National University of Ireland.

McNALLY, A. and DOYLE, G. J. 1981. Tree-ring series: a valuable source of ecological and environmental information. Irish For. 38(1):7-18.

McNALLY, A. and DOYLE, G. J. 1984a. A study of subfossil pine layers in a raised bog complex in the Irish midlands. I. Palaeowoodland extent and dynamics. Proc. R. Ir. Acad. 84B: 57-70

McNALLY, A. and DOYLE, G. J. 1984b. A study of subfossil pine layers in a raised bog complex in the Irish midlands. II. Seral relationships and floristics. Proc. R. Ir. Acad. 84B: 71-81.

McVEAN, D. N. 1963a. Growth and mineral nutrition of Scots Pine seedlings on some common peat types. J. Ecol. 51:657-670.

McVEAN, D. N. 1963b. Ecology of Scots pine in the Scottish Highlands. J. Ecol. 51:671-686.

O'NEILL, R. V. and DeANGELIS, D. L. 1981. Comparative productivity and biomass relations of forest ecosystems. *In* Reichle, D.E. (Ed.) IBP 23: Dynamic properties of forest ecosystems. 411-449. Cambridge University Press, Cambridge.

OVINGTON, J. D. 1957. Dry matter production by *Pinus sylvestris* L. Ann. Bot. N.S. 21: 287-314.

OVINGTON, J. D. 1959. The circulation of minerals in plantations of *Pinus sylvestris* L. Ann. Bot. N.S. 23:229-239.

OVINGTON, J. D. and HEITKAMP, D. 1960. The accumulation of energy in forest plantations in Britain. J. Ecol. 48:639-646.

OVINGTON, J. D. and MADGWICK, H. A. I. 1959. Distribution of organic matter and plant nutrients in a plantation of Scots pine. Forest Sci. 5:344-355.

STOKES, M. A. and SMILEY, T. S. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago.

ZELAWSKI, W. 1967. Gaseous exchange and water balance in needles. *In* Bialobok, S, and Zelawski, W. (Eds.). Outline of physiology of Scots pine. 31-96. (Translated from Polish) Polish Academy of Sciences, PWN.