# Stand structure and dynamics of four native Scots pine (*Pinus sylvestris* L.) woodlands in northern Scotland

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*Summary*

Stands in four native pinewoods (Glenmore, Black Wood of Rannoch, Glen Garry and Glen Affric) dominated by Scots pine (*Pinus sylvestris* L.) with contrasting management histories and climates were assessed for differences in age, structure and dynamics. Tree age, height, diameter at breast height (d.b.h.), basal area, stem density and *x*, *y* coordinates were used to compare the recruitment of trees (>1.3 m height, >7 cm d.b.h.), saplings (>1.3 m height, <7 cm d.b.h.) and seedlings (<1.3 m) following disturbance events and protection from browsing. There was a 20-year lag between localized intensive cultivation and tree recruitment on sites that were protected from deer browsing (Glenmore and Glen Garry). Recruitment was low in sites with disturbance but no protection (Black Wood of Rannoch). The oldest population, Glen Affric, showed signs of initial intense recruitment followed by a long period of nil recruitment. Abundant standing dead trees were recorded only in Glen Affric, and prolific birch and rowan only in Glen Garry. Managers should consider localized intense cultivation in conjunction with a complete reduction in browsing pressure for rapid seedling recruitment and increased structural diversity.

## Introduction

Forests dominated by Scots pine (*Pinus sylvestris* L.) used to cover extensive areas of the north-central highlands of Scotland reaching a maximum distribution of 1.5 million ha some 4400 years ago (McVean and Ratcliffe, 1962; Bennett, 1995). These forests formed the most westerly fringe of the distribution of Scots pine in Europe (Ennos, 1991) and are considered genetically unique from the European populations due in part to the pattern of recolonization following the last glacial period 10,000 years ago (Kinloch *et al.*, 1986). Exploitation and unsustainable management over many centuries reduced this area to a remnant population of ~19,759 ha in the late twentieth century (Mason *et al.*, 2004b).

Many of the stands in our remnant native pinewoods have developed as a consequence of the interventions of managers in previous decades. Exploitative fellings (Strachey, 1911; Steven and Carlisle, 1959), conversion to deer forests


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(Watson, 1983) and felling during the First and Second World Wars (Mason *et al.*, 2004b) have all had an influence on the structure and composition of the resource we have now. Current managers are faced with the two challenges of expanding the area of native pinewood and restoring their natural diversity of composition and structure to meet the requirements of the UK Biodiversity Action Plan (Anonymous, 1994, 1995). Unfortunately, there is little information on the natural structure and dynamics of Scottish pinewoods. Areas of uncertainty include the mixture of tree species present in a natural pinewood, the frequency of natural regenerated seedlings and their spatial recruitment into the mature stand. It is also unclear whether there are major differences in the dynamics of pinewoods in these western fringe populations in Scotland compared with European populations, and whether differences occur between the more oceanic areas of western Scotland compared with drier parts of eastern Scotland.

The required increase in core pinewood area and increase in the diversity of composition and structure are to be met by encouraging natural regeneration from existing parent trees, both within the stand and in areas adjacent to it. Previous studies have shown that direct manipulation of the vegetation and soil through weed control and/or cultivation will increase regeneration recruitment (Booth, 1984; Low, 1988; Worrell, 1990) but that control of browsing is essential for successful establishment (Miles and Kinnaird, 1979a, b). Although these researchers demonstrated an increase in recruitment in disturbed sites, the interaction between cultivation and browsing reduction has not yet been fully explored. Scott *et al.* (2000) showed that a period of 20–25 years was required from germination for trees to reach 1.5-m height on a suitable site in the Ballochbuie pinewood, but no one has related the effects of cultivation and browsing control to the long-term development in stand structure.

Several authors have put forward their views on pinewood dynamics in Scotland. McVean (1964) suggested that mixed stands of birch and pine with rowan were much less common than pure woods, and this is supported by more recent studies (Edwards and Mason, 2000). Miles (1985) concluded that birch and aspen tended to establish more rapidly after fire than Scots pine, but the longer lived pines become predominant until the next fire. Steven and Carlisle (1959) quote Michie (1901) when discussing pinewood dynamics in Ballochbuie, saying pine had a tendency only to regenerate in the open so that these woods gradually move across the landscape over time ('shift their stance'). The implication is that in Scotland pine does not readily regenerate under its own canopy.

This paper reports on the age structure and size distributions of four different stands of native Scots pine, which have been under non-intervention management for at least 50 years. The effects of a reduction in browsing levels by fencing and locally intensive site cultivation upon natural regeneration recruitment are also considered.

## Materials and methods

Stand-level assessments were completed in four research plots located in four native pinewood stands that form a climatic gradient from east to west across northern Scotland. All stands occur within large native pinewoods owned by the Forestry Commission, and have been under non-intervention management for varying periods of time. Figure 1 shows the general location of each woodland site.

### *Glenmore*

This stand is located within Glenmore Forest Park, at an altitude of 320–350 m a.s.l. Soils are predominately leached and compacted outwash sands and gravels, with varying depth of peaty humus (15–45 cm) overlying fluvio-glacial deposits on Central Highland granulites. The vegetation layer is dominated by tall (40–70 cm), dense *Calluna vulgaris* (L.) Hull, *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L. with a deep (10–20 cm) bryophyte layer. The topography is generally level with only slight hummocks causing changes in micro-topography. Mean annual precipitation is between 1000 and 1100 mm.

In 1930, Forest Research established an experimental reserve in which trials were established looking at the influence of cultivation on recruitment of natural regeneration within a native pine stand. Eight types of disturbance were compared

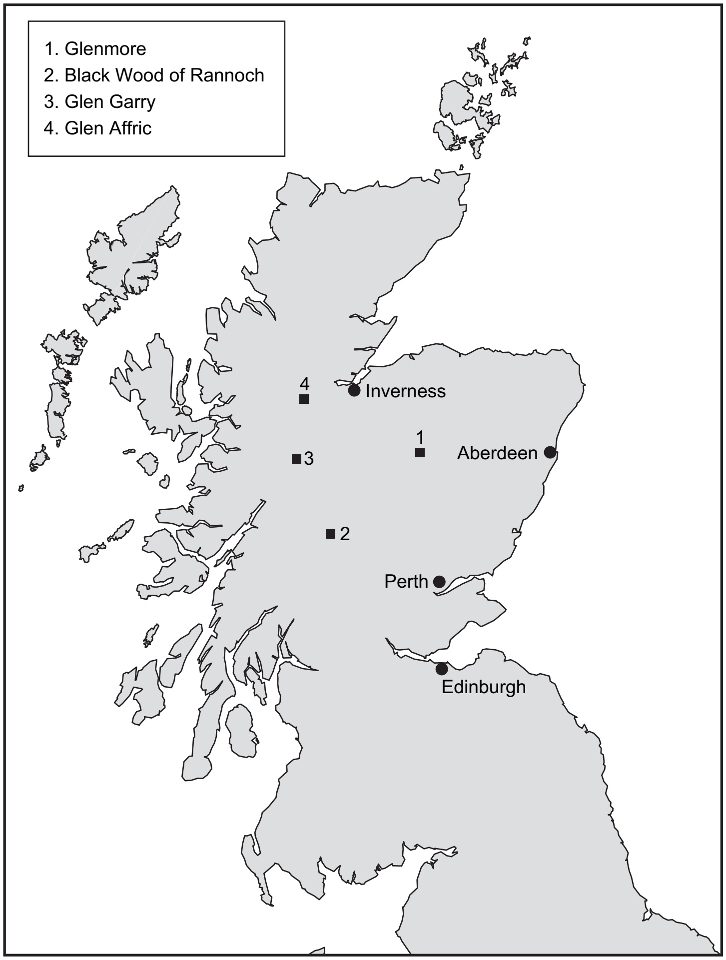


*Figure 1*. The geographic location of each of the four native Pinewoods assessed in this paper: Glenmore, Black Wood of Rannoch, Glen Garry and Glen Affric.

ranging from simple vegetation manipulation to localized intense ground cultivation (Henman, 1961). Prior to Forest Research involvement, Glenmore had been subject to a series of selective fellings, and grazing by sheep and deer, that had left a stand of relatively widely spaced mature trees. From 1930 onwards, the area was fenced against browsing animals, and allowed to develop without further intervention. The fence was removed in 1982. Assessments have been carried out at intervals since establishment, particularly monitoring the recruitment of seedlings and saplings within the plot. The most recent assessments were completed in 2000 within a 0.80-ha plot.

### *Black Wood of Rannoch*

The stand in the Black Wood of Rannoch is part of a native Scots pine reserve on the southern shores of Loch Rannoch in the Tummel Valley, Perthshire. It has a northerly aspect and mean elevation of 250 m a.s.l. Soils are predominately podsols on moranic knolls with poorly flushed peaty gleys in between. Basic geology is undifferentiated gneisses and schists of Dalradian series, with deep layers of glacial drift material. The vegetation layer is dominated by short, dense *C. vulgaris* (L.) Hull with an associated deep (10–20 cm) bryophyte layer, with sporadic patches of *V. myrtillus* L., *V. vitis-idaea* L. and *Pteridium aquilinum* (L.) Kuhn. Mean annual precipitation is between 1200 and 1300 mm.

Ownership of the Black Wood of Rannoch has changed periodically through the centuries, with periods of felling and overgrazing being common (Edwards and Mason, 2000). The last extensive felling episode occurred in 1940–1941 by the Canadian Forestry Corps, when only the best trees were removed, and the small or poor form individuals were left. Areas of the Black Wood of Rannoch were identified for monitoring in 1948, when several large (0.85 ha) plots were located (Arkle and Nixon, 1996). The site was not fenced and no further interventions or management operations, except deer control, have taken place. Assessments were completed in 1995 in a 0.85-ha plot (Arkle and Nixon, 1996).

### *Glen Garry*

Located to the south of Loch Garry, the Glen Garry stand has a north-easterly aspect and elevation range of 180–200 m a.s.l. Soils are shallow peats with exposed rocks on the western half, and deeper peats and a moranic knoll on the eastern half. Basic geology is undifferentiated schists. Vegetation is dominated by tall (40–90 cm) *V. myrtillus* L. and *V. vitis-idaea* L. with *C. vulgaris* (L.) Hull and associated deep (10–20 cm) bryophyte layer. Mean annual precipitation is between 1900 and 2100 mm.

Prior to the 1930s, Glen Garry had been subject to periodic fellings and the forest was open to grazing by sheep and deer. In 1927, it was purchased by the Forestry Commission, and in 1929, part of the area was established as an experiment. This experimental area was fenced in early 1929 and has remained fenced ever since. The stand was subject to a 'seed tree' felling later in 1929 leaving ~100 trees $ha^{-1}$ to encourage seeding and open the stand for the establishment of natural regeneration. No further management operations have taken place.

Twenty-three of the original seed trees were wind-blown in years immediately following the seed tree felling; 69 remained standing. These were described as 'not very healthy' and did not produce prolific seed until 1944. The area was divided into three sections, with each section then allocated a different basal treatment. One had all brash removed, the second had the brash evenly spread over the area and the third was to have parallel strips cultivated to expose the mineral soil and mix the humus layer. This latter treatment was never applied. Crown die back in the seed trees was recorded in the early 1930s shortly after felling. All tree, sapling and seedling assessments were completed in 2004 in a 0.96-ha plot.

### *Glen Affric*

The plot in Glen Affric is located on the south of Loch Beneveian at the western end of the loch. It is gently sloping with a north-easterly aspect and elevation range of 245–250 m a.s.l. Soils are predominately peaty podsols on well-drained moranic knolls with poorly flushed peat on flatter ground between. An area of deeper peat forms a bog woodland on the lower slopes just outside the north-east corner of the plot. Basic geology is undifferentiated gneisses and schists of Dalradian series, with deep layers of glacial drift material. The vegetation layer in Glen Affric is predominately *C. vulgaris* (L.) Hull dominated with small patches of *V. myrtillus* L. and *V. vitis-idaea* L. Mean annual precipitation is between 2000 and 2200 mm.

The past history of this stand is the least well known of the four in this paper. However, it has been recorded that sawlogs were being floated down the rivers Cannich and Glass (Steven and Carlisle, 1959) to a sawmill above the Kilmorack Falls, and it is likely that some fellings have taken place at intervals throughout its history. The area has been a pinewood reserve since purchase in 1951 by the Forestry Commission.

A deer fence once enclosed a large area of Glen Affric, which would have included the area now occupied by our plot; however, the research plot was never individually fenced or disturbed since 1951. All assessments were completed in 2004 within a 1.0-ha plot.

### *Data collection and analyses*

Within each stand the following information was recorded: tree species; tree total height; tree diameter at 1.3 m (d.b.h.); tree $x$, $y$ coordinates and tree age. Tree age was assessed by collecting increment cores from a height of 1.0 m above ground level, which were mounted onto wooden batons and prepared for annual ring counting using the standard techniques described by Stokes and Smiley (1968). Increment cores were only collected from trees with a d.b.h. >10 cm. Seedling and sapling locations and height and d.b.h. details were also recorded. A tree is a woody plant >1.3 m height and >7 cm d.b.h., saplings are >1.3 m height but <7 cm d.b.h. and seedlings <1.3 m height.

Tree $x$, $y$ coordinates were used to create the distribution maps. Height, d.b.h. and age data were converted in class groups before plotting. Data were subject to basic descriptive analyses using Minitab (2000), while Genstat (2005) was used to calculate Pearson's correlation coefficients, significance values and regression equations.

## Results

### *Glenmore*

The distribution of trees, saplings and seedling in Glenmore (Figure 2a) was directly linked to the establishment of the experiment in 1930 and tree fellings prior to that date. There is now a mosaic of older trees embedded with groups of younger trees, saplings and seedlings recruited into ground cultivation sites. More recruitment of trees and saplings can be seen in canopy gaps in conjunction with localized intensive ground cultivation than in areas with a dense overstorey or no ground cultivation.

Tree and sapling height (Figure 3a) and tree and sapling d.b.h. (Figure 4a) appeared to follow a negative exponential curve or 'J-curve' distributions. This plot had the greatest density of pine trees and saplings and highest density of seedlings between the four plots assessed (Table 1). Mean tree d.b.h. was the lowest (23.6 cm) and this plot had the least percentage of trees with a d.b.h. > 50 cm. The trees in Glenmore were the shortest of the four sites with the lowest mean height (10.9 m) and the smallest maximum tree height (22.0 m) (Table 1).

Glenmore tree age distribution was bimodal, with a small first peak at around 200 years and a second much greater peak at around 50 years (Figure 5a). Between these dates, there was a gap in the number of trees recorded, reflecting a lack in recruitment over this period. Only 7.7 per cent of trees aged were >200 years old.

There was a significant correlation between tree age and d.b.h. ($P < 0.00$, Figure 6a), between age and height ($P < 0.001$, Figure 7a) and between height and d.b.h. ($P < 0.001$, Figure 8a). Age *vs* d.b.h. and age *vs* height show aggregation of points in two distinct groups, while height *vs* d.b.h. shows an exponential increase.

### *Black Wood of Rannoch*

In contrast, at Black Wood of Rannoch, the distribution of trees, saplings and seedlings (Figure 2b) indicates a gradient of tree classes on site, with the oldest at the northern end of the plot and younger trees towards the southern end. Seedlings and saplings were most abundant in the open areas where tree density was low. There were a lack of standing dead trees or broadleaved species at this site.

Tree heights (Figure 3b) form a normal distribution about a mean height of 15.7 m. A second peak was beginning to form corresponding to the saplings that have been recently recruited. The tree of largest d.b.h. (117.7 cm) found in this study was located in this plot, and there was the second greatest percentage of trees with a d.b.h. >50 cm (27 per cent) (Table 1). The d.b.h. distribution (Figure 4b) was slightly skewed around a mean of 42.7 cm, with a long tail towards larger sizes. This plot also had the greatest basal area of pine trees of the four studied, but had fewest saplings (26 stems $ha^{-1}$) and the second lowest tree density (158 stems $ha^{-1}$) (Table 1).

Although the second oldest tree of the four plots was located in this plot (273 years), this was an isolated individual; the distribution of age clearly indicates a skewed distribution about a mean age of 129 years, with more young trees than older ones (Figure 5b). There was a significant correlation between tree age and d.b.h. ($P < 0.001$, Figure 6b), between age and height ($P < 0.01$, Figure 7b) and between height and d.b.h. ($P < 0.001$, Figure 8b).

### *Glen Garry*

In Glen Garry, young pine tree recruitment was generally located within canopy gaps following

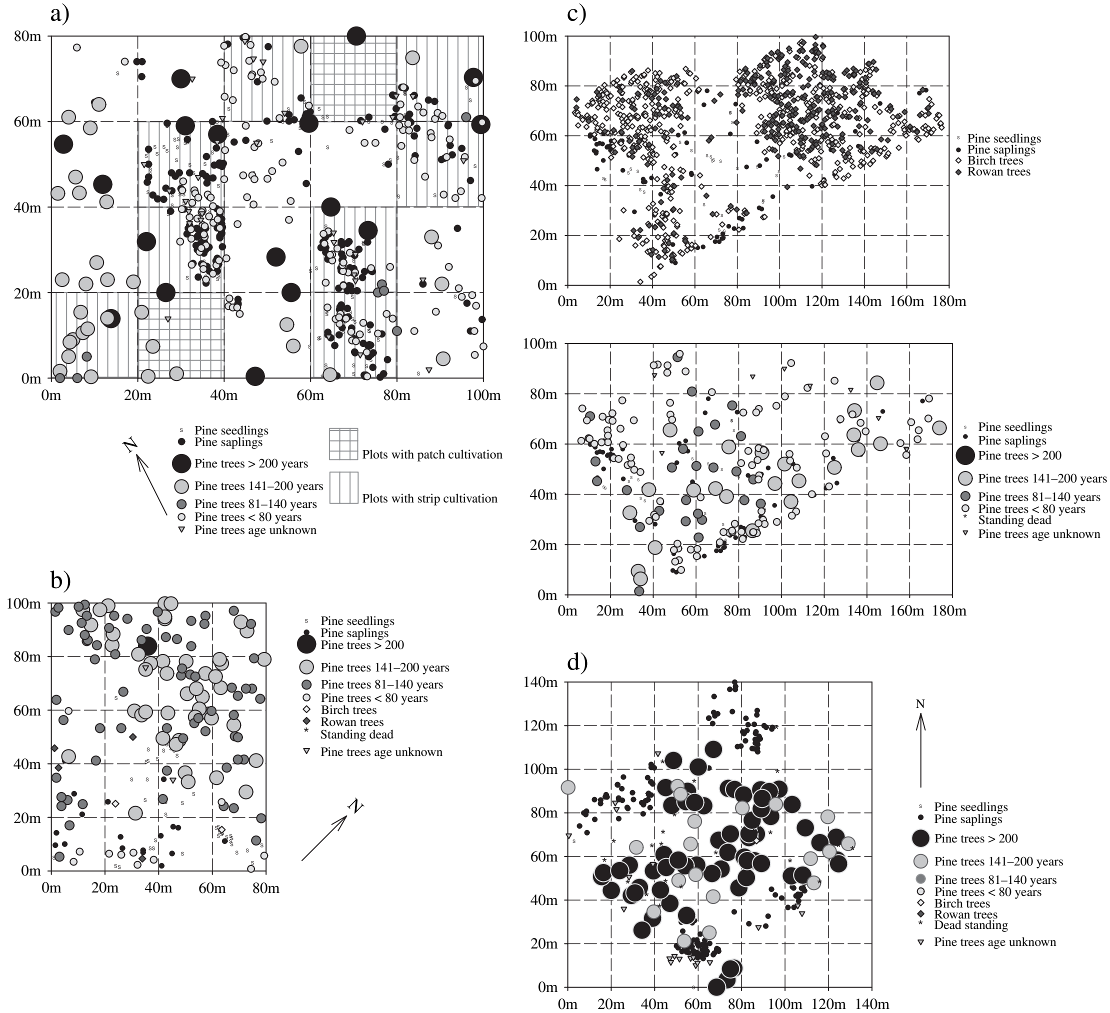


*Figure 2*. Distribution maps of trees, saplings and seedlings for plots in (a) Glenmore, (b) Black Wood of Rannoch, (c) Glen Garry and (d) Glen Affric. The upper graph for the Glen Garry plot shows only birch trees, rowan trees, pine saplings and pine seedlings. The lower graph shows pine trees and pine saplings only.

site cultivation, and had developed a distribution similar to that seen in Glenmore; however, it was 'masked' by the extensive recruitment of birch (*Betula pubescens* Ehrh.) and rowan (*Sorbus aucuparia* L) across most of the site (Figure 2c). Both birch and rowan trees were densest in the more open areas of pine canopy where the density of mature pine trees was lowest. An observation made in 1957 following a site visit to the experiment stated both birch and rowan seedlings were densest and most vigorous on the moist soils originally dominated by grasses. Pine seedlings were irregular in distribution, and estimated to be from seedlings germinating between 1930 and 1935.

Scots pine tree height distribution in Glen Garry was a flattened distribution about a mean of 15.1 m. It had the tallest tree of the four sites at 27.4 m, and an even distribution of other tree

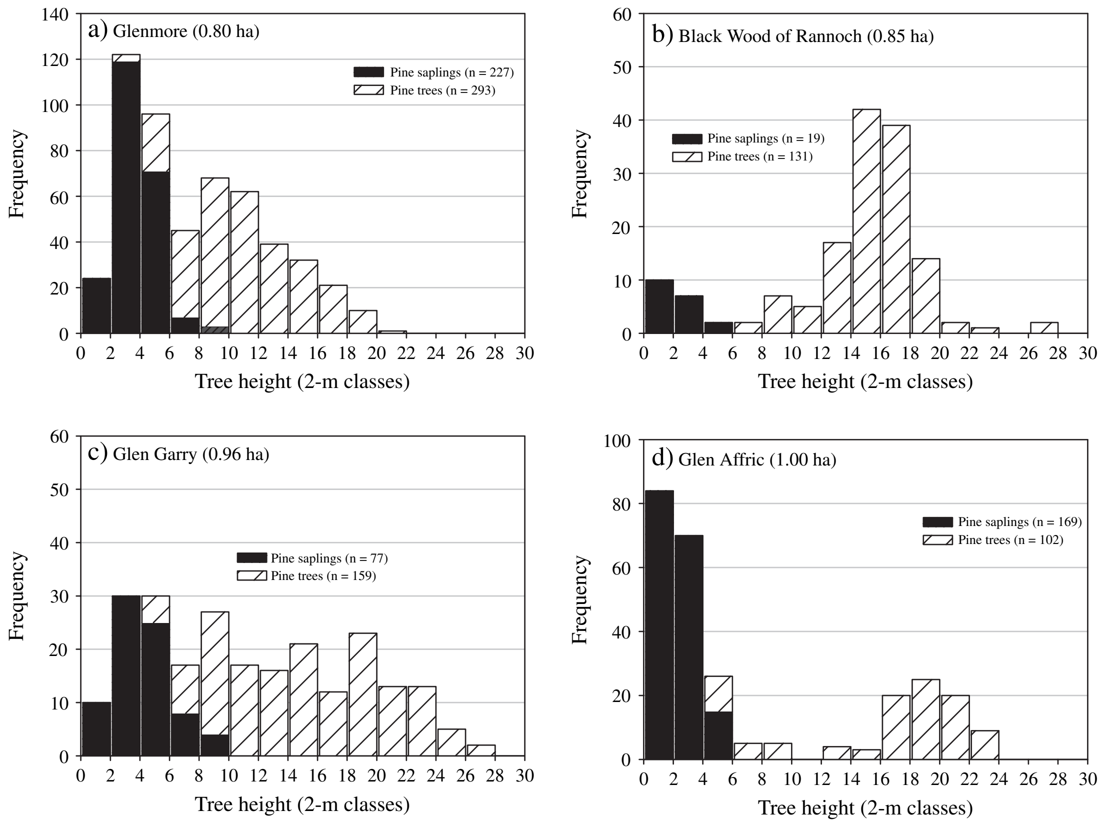


*Figure 3*. Histogram of tree height of Scots pine in the four plots in (a) Glenmore, (b) Black Wood of Rannoch, (c) Glen Garry and (d) Glen Affric. Note the different scales used and the break in axis in Glen Affric graph. *n* = number of observations.

heights (Figure 3c). Scots pine saplings form a normal distribution by themselves.

The shape of the diameter distribution of the pine trees approaches that of a negative exponential curve, with a greater proportion of small diameter trees than larger ones (Figure 4c). Glen Garry had the second lowest percentage of trees >50 cm d.b.h. (19 per cent), and the lowest total basal area of pine (15.3 $m^2$ $ha^{-1}$). However, if the basal area for birch and rowan trees were added, the total basal area for the site was 26.1 $m^2$ $ha^{-1}$, the largest of all four sites (Table 1). Glen Garry also had the greatest density of trees when all three species were accumulated (1156 stems $ha^{-1}$).

The age distribution of pine trees in Glen Garry was clearly bimodal, with one peak at ~140 years corresponding to the mature trees left on site following felling, and the second left skewed peak at 50 years corresponding to the pine cohorts following cultivation (Figure 5c). Mean tree age was the lowest of all four sites (74 years) as was the maximum age of trees on this plot (173 years). This was the only site with no trees >200 years.

There was a significant correlation between tree age and d.b.h. ($P < 0.001$, Figure 6c), between age and height ($P < 0.001$, Figure 7c) and between height and d.b.h. ($P < 0.001$, Figure 8c). The regression curve between height and diameter had an $r^2$ value of 0.75 (Table 2); although significant, there was too much scatter in the data above 15 m height and 30 cm d.b.h. to be of predictive value.

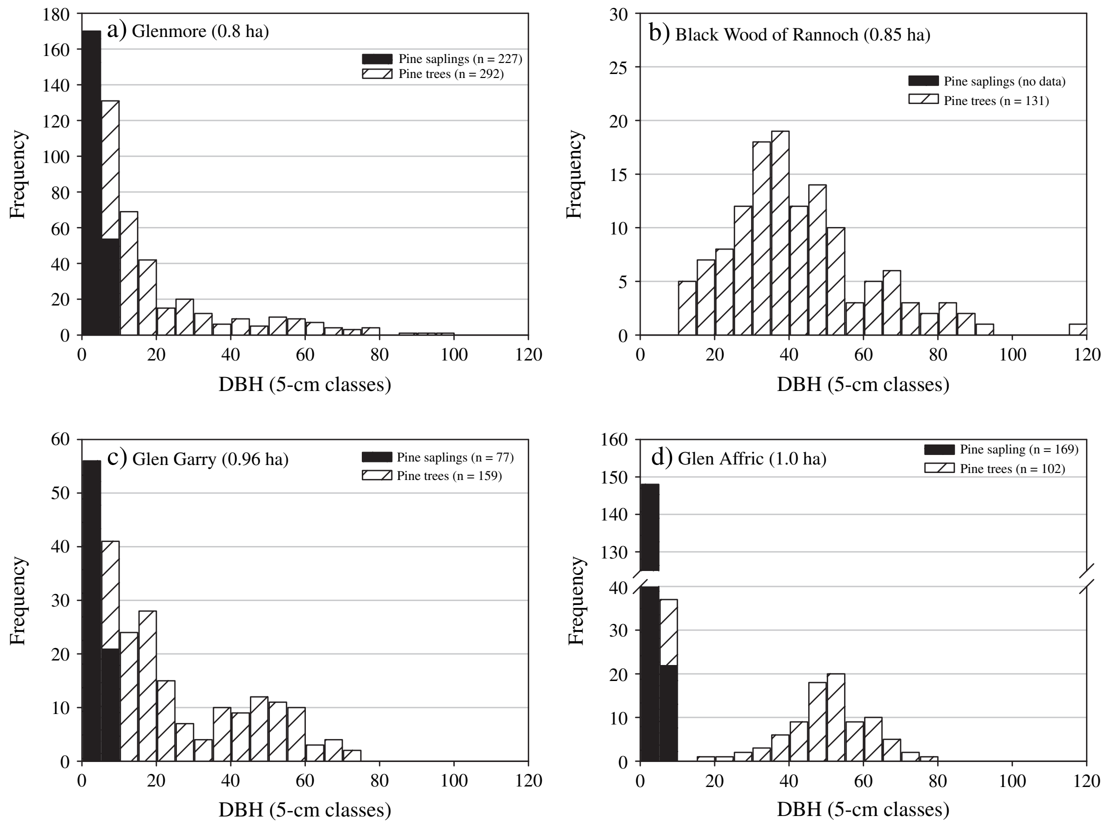


*Figure 4*. Histogram of Scots pine tree d.b.h. (cm) in the four plots in (a) Glenmore, (b) Black Wood of Rannoch, (c) Glen Garry and (d) Glen Affric. Note the different scales used and the break in axis in Glen Affric graph. *n* = number of observations.

### *Glen Affric*

In Glen Affric, the majority of the older trees were located within a broad swath through the central area of the plot. This was the only plot with significant numbers of standing dead trees (34 stems $ha^{-1}$) which were located among the mature trees (Figure 2d). Saplings were concentrated at the edges of the plot principally in small groups, which tend to be located within gaps in the overstorey canopy. No seedlings were found beneath the central area dominated by the older overstorey trees.

Tree height had a normal distribution; the inclusion of the sapling data alters this to a bimodal distribution (Figure 3d). Glen Affric trees have the greatest mean height (16.3 m) of the four populations.

Pine tree diameters were normally distributed (Figure 4d) around a mean of 44.4 cm, which was the greatest mean d.b.h. of the four populations (Table 1). When sapling diameters were included in this histogram, it showed as a single peak of small material. This population had the greatest number of trees >50 cm d.b.h. (46 per cent) (Table 1).

Glen Affric had the oldest mean age (225 years) and the oldest recorded individual tree (278 years) but the distribution of ages was skewed with a long left-hand tail (Figure 5d). It had the greatest number of trees > 200 years (74.7 per cent) but none younger than 140 years. The absence of any young trees was striking, and indicates a lack of recruitment over a long period until the sapling cohort developed.

*Table 1*: Tree, sapling and seedling data for the four populations in this study

| Stand Name | Tree d.b.h. (cm) | | Tree height (m) | | Tree age (years) | | | Basal area ($m^2$ $ha^{-1}$) | | | Stem Density ($ha^{-1}$) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | % >50 cm | Maximum | Mean | Maximum | Minimum | Mean | Trees | Saplings | Total | Trees | Seedlings | Saplings | Dead |
| Glenmore | 23.6 | 13.0 | 22.0 | 10.9 | 231 | 19 | 87.6 | 20.7 | 0.3 | 21.0 | 372 | 167 | 283 | 0 |
| Black Wood of Rannoch | 42.7 | 27.0 | 27.0 | 15.7 | 273 | 33 | 129 | 22.5 | – | 22.5 | 158 | 26 | 23 | 0 |
| Glen Affric | 44.4 | 46.0 | 23.6 | 16.3 | 278 | 141 | 225 | 18.4 | 0.1 | 18.5 | 103 | 2 | 170 | 34 |
| Glen Garry (SP) | 29.6 | 19.0 | 27.4 | 15.1 | 173 | 23 | 74 | 15.2 | 0.1 | 15.3 | 167 | 32 | 80 | 1 |
| Glen Garry (Bi) | 12.5 | 0 | 21.8 | 11.4 | – | – | – | 8.7 | – | – | 652 | 0 | 0 | 0 |
| Glen Garry (Row) | 8.8 | 0 | 14.5 | 8.9 | – | – | – | 2.1 | – | – | 337 | 0 | 0 | 0 |
| Glen Garry (all species) | | | | | | | | 26.0 | 0.1 | 26.1 | 1168 | 39 | 80 | |

Only in Glen Garry have separate details for Scots pine (SP), birch (Bi) and rowan (Row) been given.

The basal area of trees in Glen Affric was the second lowest of the four plots (18.5 $m^2$ $ha^{-1}$). Tree density (103 stems $ha^{-1}$) was the lowest of all four plots, and seedling numbers were the lowest recorded with only two located within the 1-ha plot. There were significant numbers of saplings (170 stems $ha^{-1}$).

This plot was the only one to show a significant negative correlation between tree age and diameter ($P = 0.001$, Table 2, Figure 6d), and although the correlation between tree age and height was also negative (Figure 7d), it was not significant (Table 2). The plot of tree height against diameter showed a significant correlation ($P < 0.001$, Figure 8d).

## Discussion

Spatial recruitment of pine seedlings and saplings across all four sites has not been uniform, instead the pattern is irregular and closely associated with both canopy gaps and areas of cultivation. More recruitment of young trees (<80 years) into the canopy has occurred where the stand density is lowest. The overall result is an increase in structural diversity in the stand, which is most pronounced in those that were cultivated and least in those that were left to regenerate naturally. The abundance of standing dead trees within the matrix of older live trees in the Glen Affric plot indicates that there has been recent mortality in this stand, which has not been recorded in any of the other stands. This increased natural mortality is most likely a result of inter-tree competition among those that form the main component of this stand (Oliver and Larson, 1996) and suggests that there has been less direct management and anthropomorphic disturbance at this site compared with the three other stands studied. Although the dead trees in Glen Affric were not aged, it is likely the increase in sapling recruitment and the mortality of overstorey trees are closely linked. An increase in tree death will lead to a lower canopy density, increasing the light intensity at the forest floor (Mason *et al.*, 2004a), which is known to influence Scots pine seedling height growth and survival (Chantal *et al.*, 2003; Mason *et al.*, 2004b). This natural process is reproduced artificially by site cultivation directly

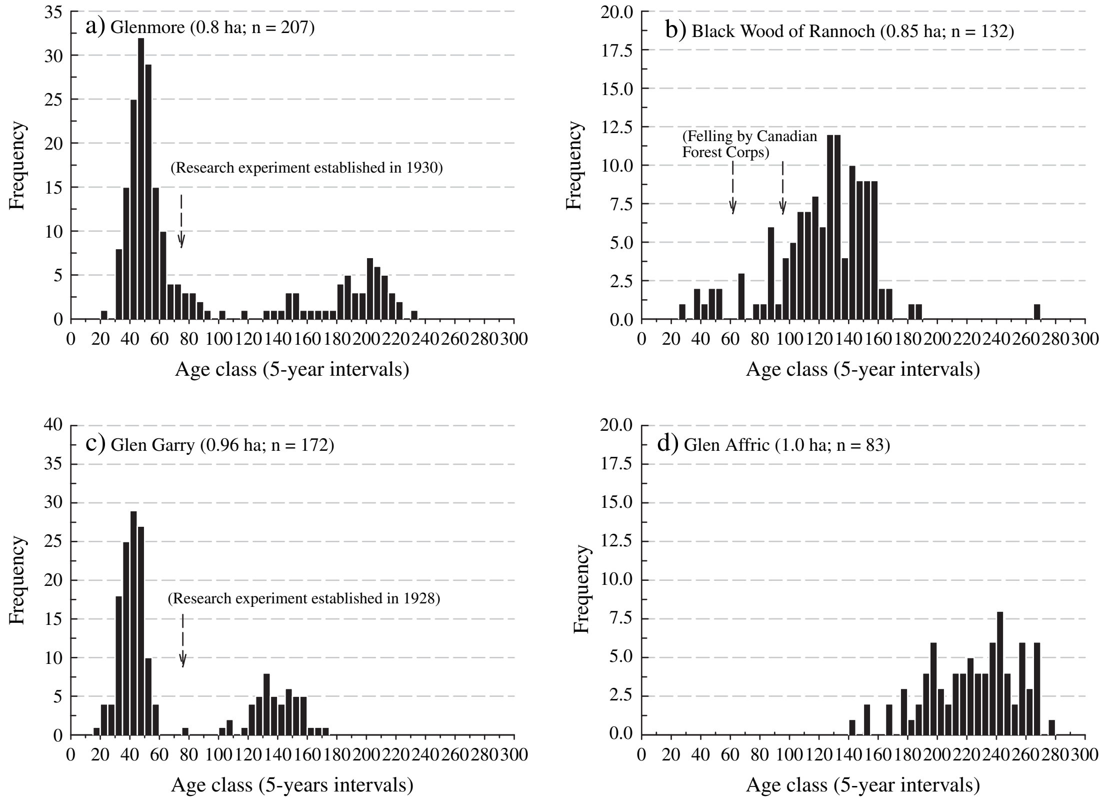


*Figure 5*. Histogram of Scots pine tree ages in the four plots in (a) Glenmore, (b) Black Wood of Rannoch, (c) Glen Garry and (d) Glen Affric. Note the different scales used. *n* = number of observations.

following a reduction in stand density, and is regularly practised in Sweden (Karlsson, 2000; Karlsson and Örlander, 2000) and Finland (Valkonen *et al.*, 2002) to increase seedling recruitment in Scots pine stands.

The Glen Affric trees form the oldest population of the four in this study, with a much greater mean age (225 years) and larger minimum age (141 years) for those trees cored. However, even these trees are younger than the oldest recorded age of Scots pine of 550 years in Scotland (Bartholomew *et al.*, 2001) or 700 years in Sweden (Engelmark *et al.*, 1994). The bimodal age profiles in Glenmore and Glen Garry (Figure 5) are similar in shape to Scots pine dominated stands in Latvia (Brumelis *et al.*, 2005) and to pine in mixed Norway spruce–Scots pine stands in Fennoscandia (Pennanen, 2002; Wallenius *et al.*, 2002). However, in the mixed spruce–pine stands fire is the main disturbance factor influencing mature tree mortality and regeneration recruitment, and may influence the upper age of the trees recorded (Wallenius, 2002; Wallenius *et al.*, 2002). The influence of fire history on Scottish populations is unknown and spruce is not a natural component of our pinewoods.

The lack of older trees in the profiles of Rannoch and Glen Garry (Figure 5b and c) reflect the fellings that occurred prior to the sites being redesignated as pinewood reserves and managed under non-intervention regimes. Abundant younger trees are recorded only in those sites (i.e. Glenmore and Glen Garry) that have undergone intensive cultivation and browsing protection (Figure 5a and c). This peak in the age profile is not seen in the other two sites as neither was subject to the

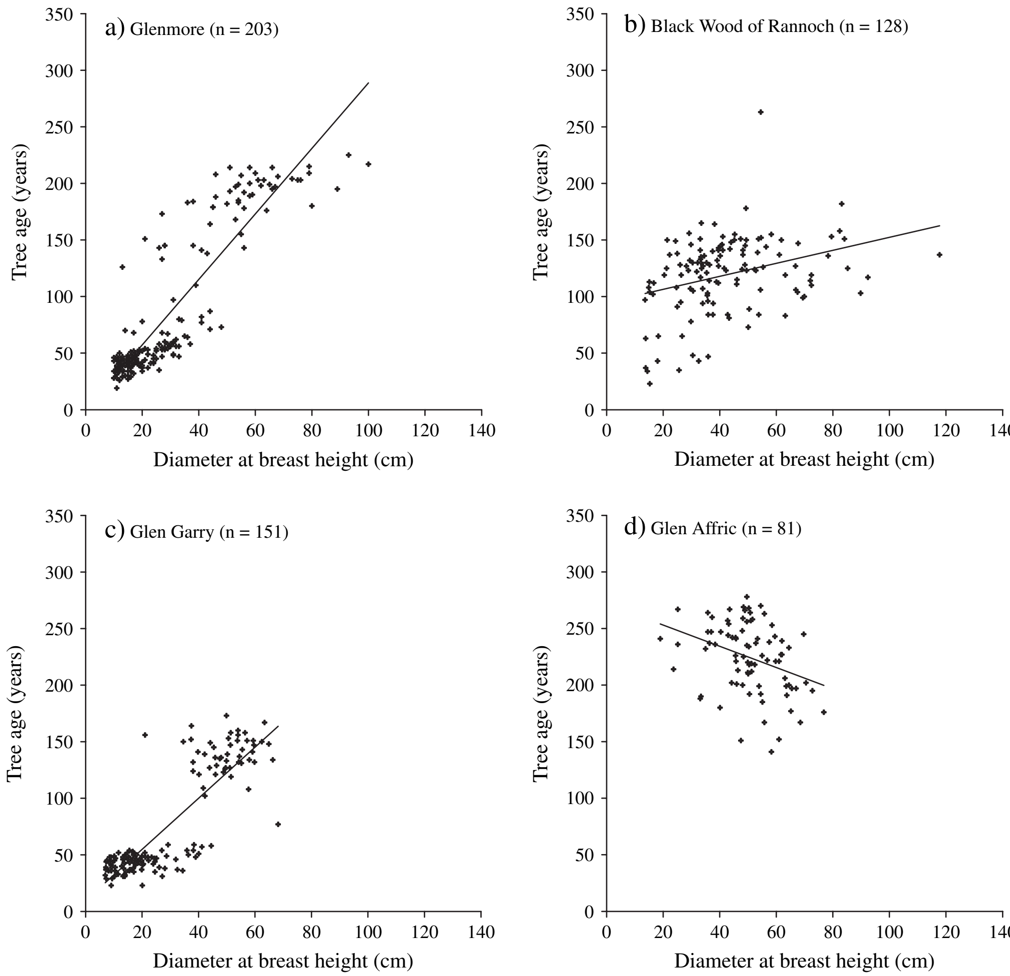


*Figure 6*. Scatter graphs of Scots pine tree age and tree d.b.h. for the four plots in (a) Glenmore, (b) Black Wood of Rannoch, (c) Glen Garry and (d) Glen Affric. *n* = number of observations.

same management operations. The slower recruitment seen in Rannoch (Figure 5b) following less intense cultivation is much less pronounced, but younger trees are recorded in the profile.

In the two plots that were deliberately disturbed and fenced (Glenmore and Glen Garry), the lag between the cultivation events in 1930 and 1928, and the peak in tree recruitment, is ~20 years and 17 years, respectively. Since these sites were fenced, the lag is not due to deer browsing holding seedlings back from development, as suggested for other areas by Gormley (1995), but is attributable to the slow growth of pine seedlings under these conditions. Subsequent to this lag, there is an extended 'recruitment' phase, which appears to last about 30 years. Over this period, 'new' seedlings are recruited into the understorey and add to the developing structure of the stand. The resulting age profile is very characteristic and is replicated in the d.b.h. profiles as a negative exponential or 'reversed J-curve' distribution with numerous young or small d.b.h. trees and a decreasing number of older or larger d.b.h. trees.

This profile suggests steady recruitment over a period of time (Hett and Loucks, 1976; Engelmark

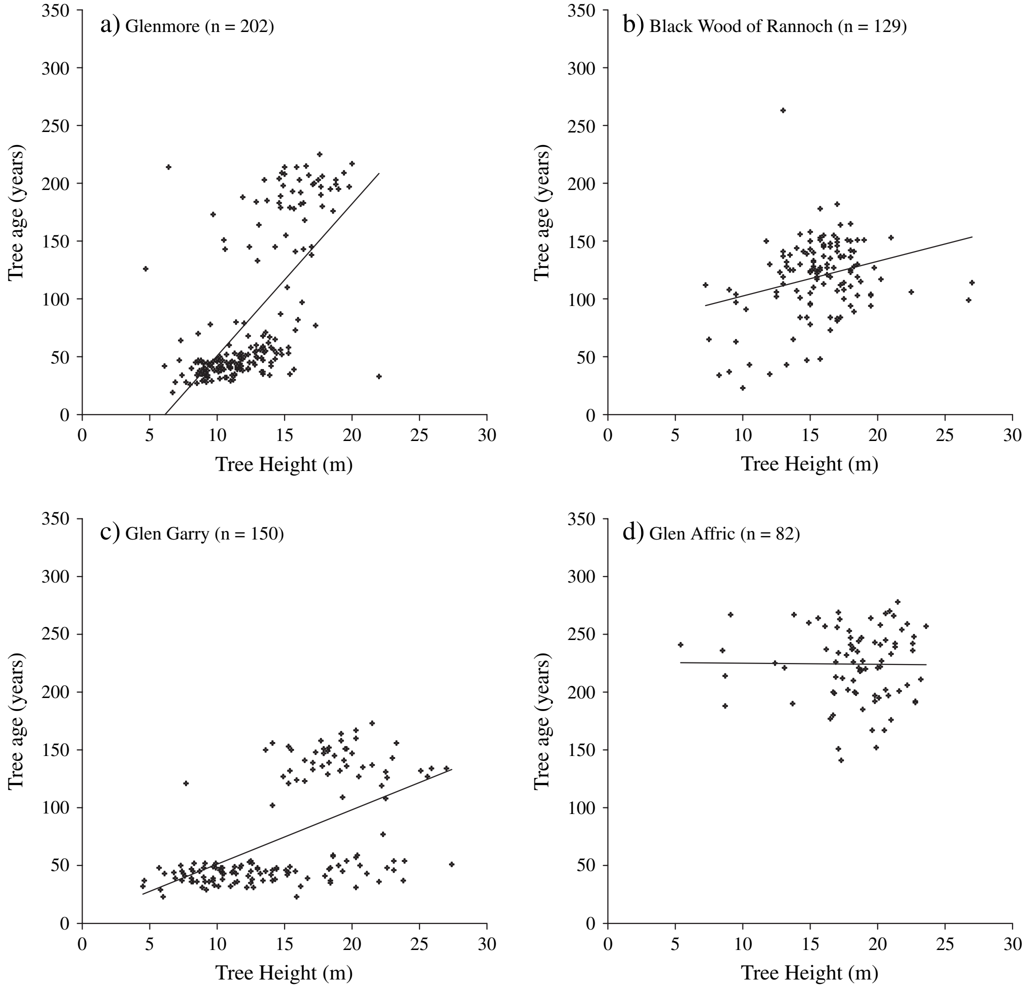


*Figure 7*. Regression graphs of Scots pine tree age plotted against tree height for the four plots in (a) Glenmore, (b) Black Wood of Rannoch, (c) Glen Garry and (d) Glen Affric. $n$ = number of observations.

*et al.*, 1994); however, because of the management history of these plots, it is known that the majority of the recruitment occurred over a relatively short period following a deliberate event. Increment cores are removed from trees at a height of ~1.0 m above ground level, giving an age for the tree when it reached that height, and is not an indication of the date when the tree was recruited. The slow growth indicated above shows that 20 years may elapse on good sites between seed germination and the tree reaching a height that would be recorded by the collection of increment cores. This lag is similar to that predicted by Scott *et al.* (2000) for pine regeneration being recruited onto good pine sites. The exponential decay seen in Glenmore and Glen Garry probably reflects this slow-growth period and not a long period of gradual recruitment. This profile only indicates the high structural diversity in the wood. Although the Black Wood of Rannoch also suffered some disturbance, it was never as locally intense as Glenmore or Glen Garry, and there was no fence protection. Both the age and d.b.h. profiles for Rannoch are

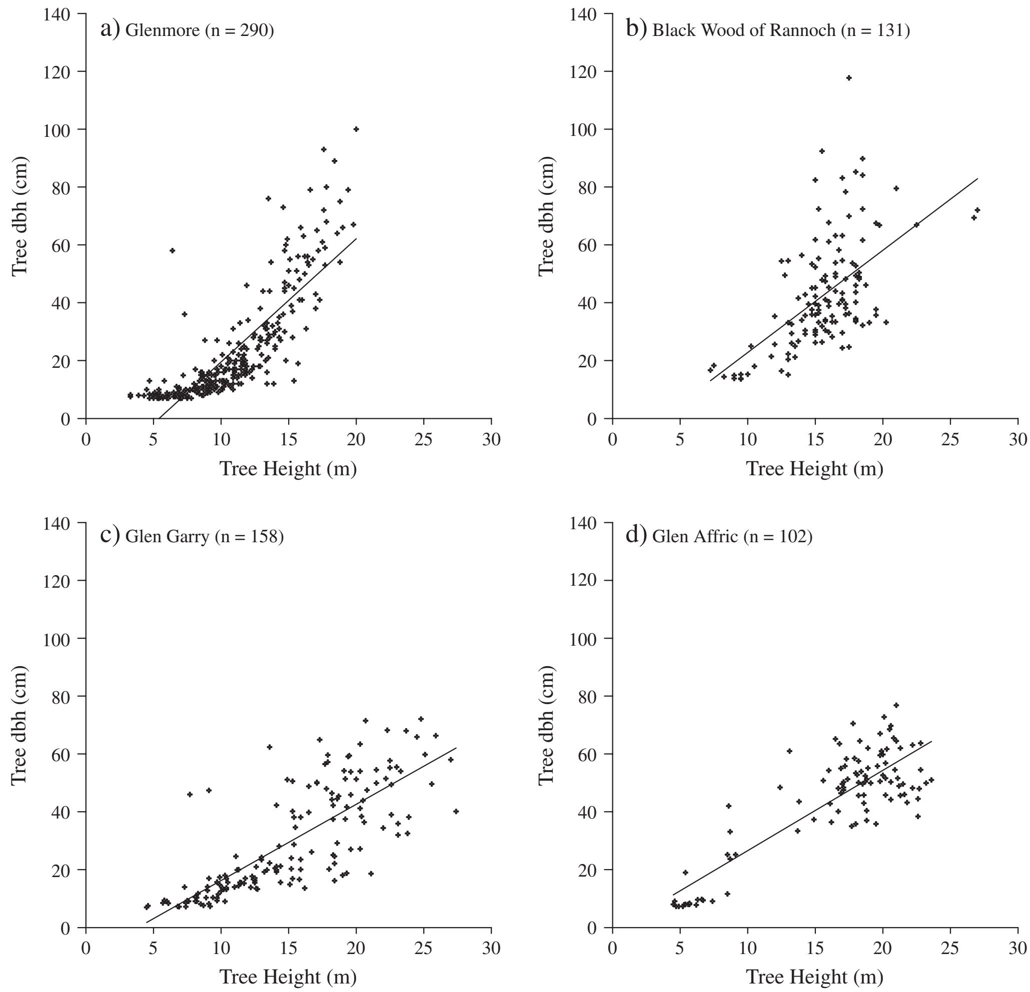


*Figure 8*. Regression graphs of Scots pine tree d.b.h. plotted against tree height for the four plots in (a) Glenmore, (b) Black Wood of Rannoch, (c) Glen Garry and (d) Glen Affric. $n$ = number of observations.

different to those for Glenmore and Glen Garry, indicating that although some recruitment has occurred it is substantially less than in other plots.

Despite high ($P < 0.01$) and very highly ($P < 0.001$) significant Pearson's correlation coefficients between tree age and d.b.h. for Glenmore, Rannoch, Glen Garry, and Glen Affric or tree age and height for Glenmore, Rannoch and Glen Garry, the predictive value of the equations are limited by the large residual variation in the data. Neither tree height nor tree d.b.h. can be used to calculate the age of pine trees in any of these populations with accuracy; this is similar to the findings of other researchers in Scottish pinewoods (Nixon and Cameron, 1994; Arkle and Nixon, 1996; Goucher and Nixon, 1996).

Close examination of Figure 6a and c and Figure 7a and c shows an aggregation or grouping of scatter points corresponding to the two main age classes in each population (Figure 5a and c). In each case, it appears possible that a separate regression line could be fitted independently through both groupings. This is most clearly

*Table 2*: Tabulated values of significance and $r^2$ for all regression comparisons made between age, height and d.b.h. for the four study populations

| Population | Comparison | Pearson's correlation coefficient | Significance ($P$ value) | $r^2$ | Equation |
|---|---|---|---|---|---|
| Glenmore | Age *vs* d.b.h. | 0.895 | 0.000 | 0.80 | Age = −2.2288 + 2.9902 d.b.h. |
| | Age *vs* height | 0.717 | 0.000 | 0.51 | Age = −101.493 + 14.9138 height |
| | d.b.h. *vs* height | 0.819 | 0.000 | 0.67 | d.b.h. = 23.0118 + 4.2548 height |
| Black Wood of Rannoch | Age *vs* d.b.h. | 0.327 | 0.000 | 0.10 | Age = 94.878 + 0.57481 d.b.h. |
| | Age *vs* height | 0.278 | 0.002 | 0.07 | Age = 72.376 + 3.006 height |
| | d.b.h. *vs* height | 0.573 | 0.000 | 0.33 | d.b.h. = −12.575 + 3.5337 height |
| Glen Garry pine | Age *vs* d.b.h. | 0.863 | 0.000 | 0.74 | Age = 13.4537 + 2.16769 d.b.h. |
| | Age *vs* height | 0.593 | 0.000 | 0.34 | Age = 6.03775 + 4.59205 height |
| | d.b.h. *vs* height | 0.866 | 0.000 | 0.75 | d.b.h. = −6.73023 + 2.42975 height |
| Glen Garry birch | d.b.h. *vs* height | 0.722 | 0.000 | 0.52 | d.b.h. = −0.6562 + 1.13854 height |
| Glen Garry rowan | d.b.h. *vs* height | 0.408 | 0.000 | 0.16 | d.b.h. = 4.95354 + 0.426923 height |
| Glen Affric | Age *vs* d.b.h. | −0.345 | 0.001 | 0.11 | Age = 271.828 − 0.98963 d.b.h. |
| | Age *vs* height | −0.011 | 0.923 | 0.00 | Age = 225.995 − 0.095078 height |
| | d.b.h. *vs* height | 0.964 | 0.000 | 0.93 | d.b.h. = −3.99828 + 2.9135 height |

seen in Glen Garry (Figure 7c), where the younger newly recruited trees apparently have a greater height for their age than the mature overstorey trees. It is possible that in these two populations the presence of a mature overstorey, of seed-bearing parent trees, has altered the growth pattern of the natural regeneration recruited below as a result of the cultivation events. As a result, there is greater variation in structural diversity than the other two plots. Further investigation of the growth curves in each of these stands is needed before more detailed conclusions can be drawn.

In all but two instances (Table 2), the relationship between tree age and tree d.b.h. or tree height and the relationship between tree d.b.h. and tree height are positive. It is expected that with increasing age both tree d.b.h. and tree height would increase. However, the data in Glen Affric show a relationship in which the younger trees in this woodland have larger diameters than older trees (Figure 6d). This can also be seen in Figure 7d, where the scatter of regression points suggests trees 15 m in height can range in age between 145 and 260 years and that tree height is not related to tree age. However, it is likely that the absence of younger and smaller regeneration in Glen Affric in both these graphs has given rise to relationships that although statistically valid appear to be in contradiction to those relationships presented in the three other graphs. Non-linear regressions could also be fitted to the data points and new relationships computed, however, that are beyond the scope of this paper.

Analyses of the pollen record for pine tree presence in the Glen Affric pinewood strongly implies trees have only occupied this part of Glen Affric for the last 400–500 years (Shaw, this publication). If accepted, then older trees in Glen Affric are probably the first Scots pine trees to grow on this site in several thousand years. The age profile and regression relationships reflect the pattern of new pine tree recruitment onto a previously non-wooded site. The skewed distribution results from a decrease in tree recruitment over time as the site became fully occupied and space for further tree recruitment or growth decreased. This would also explain the negative age–diameter relationship as the older earliest recruited trees onto the site would have altered the site conditions, making it initially more suitable for further recruitment. As the stand developed, the younger trees to be recruited would then have had better conditions in which to grow and this is reflected in their growth rates. It clearly shows the long time periods over which recruitment, mortality and further recruitment of pine trees occur.

The substantial recruitment of birch and rowan in Glen Garry did not occur in any other population (Figure 2a–d), and masks the less obvious trends with the pine seedlings, saplings and young trees (<80 years). Miles and Kinnaird (1979a) expected stands of pine to be regenerated only following an interphase of predominance of other species, and that birch would occur as a successional stage after the destruction of a pine woodland by fire or felling. In Glen Garry, we have both these processes occurring. The fellings in 1928 stimulated the recruitment of birch, rowan and pine seedlings, and given the protection of the fence, all three species thrived and formed the dense multi-species structure we have now. It is likely that few seedlings, particularly of the broadleaved species, would have survived if protection had not been given as grazing appears to prevent the continued development of seedlings (Kinnaird, 1974; Raspé *et al.*, 2000; Palmer and Truscott, 2003). Rowan and birch regeneration are occurring in other similar plots within the Black Wood of Rannoch (C. Edwards, unpublished data), but the level of recruitment is slow and the density of seedling very low over the entire site. Only when site cultivation and fence protection have occurred together have prolific rowan and birch seedlings been recruited into the Black Wood of Rannoch (Edwards and Dixon, 1994).

The lack of broadleaved recruitment in the Black Wood of Rannoch and Glen Affric is almost certainly due to a lack of cultivation and protection from browsers, but this fails to explain why the plot at Glenmore, which was cultivated and protected, does not exhibit prolific regeneration of either of these broadleaved species. Suitable seed-bearing trees of both broadleaved species can currently be found in the locality but the frequency of trees in the 1930s, when the site was cultivated, is unknown.

## Conclusion

As seen in Glen Affric, pinewood stand dynamics must be considered as operating over a long-term time frame. We suggest that 300 years is a minimum period over which a stand will progress from the seeding stage to the opening of the canopy through natural tree mortality and recruitment of seedlings, saplings and trees to diversify the structure. During this period, stand structural diversity is likely to be low until inter-tree competition begins to alter the canopy and light conditions and seedling recruitment occurs. Achieving these changes over shorter time periods will require direct manipulation of the stand by thinning in combination with cultivation and reductions in browsing pressure. Species composition in these pinewoods can also be influenced by management operations. More broadleaved species can be encouraged into the stand, but will be dependent on local seed-bearing trees being present when cultivation operations are carried out and on an adequate level of protection being provided to young seedlings to allow development into mature trees.


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