

Wet Woods Restoration Project

The Age Structure of Scots pine bog woodlands



A.R. Anderson and K.I.M. Harding
Forest Research, Forestry Commission

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Summary

The age structure of Scots pine (*Pinus sylvestris* L.) bog woodland was investigated at four sites in NE Scotland to clarify whether these examples of the habitat are stable or transient. Individual tree age cannot be predicted from general equations relating age to height or diameter. The sampling sites at Pitmaduthy Moss, Abernethy Forest and Inshriach Forest had been severely impacted by human activities, some of which were reflected in the age structure of the pine population. Most of the Monadh Mor site was apparently undisturbed. The site at Abernethy Forest supported 'bog pines' up to 335 years old and a ground flora including *Sphagnum fuscum* and abundant *Sphagnum austinii*. This combination suggests that the site has supported open bog woodland for several centuries. These results are consistent with a process of bog woodland development on bogs in response to natural or anthropogenic disturbance. Tree growth rates and branching may be used as indicators of the degree of alteration caused by the disturbance and of whether the site is likely to succeed to closed-canopy woodland.

Introduction

Scots pine bog woodland consists of stunted Scots pine trees on peaty ground with the ground vegetation essentially that of a bog. Tree density can vary; examples range from bogs with scattered stunted trees to open pinewoods. The size of the trees also varies, stunted implying slow-growing rather than small. A distinction is sometimes made between genuine bog woodland, in which the growth rate and density of tree cover are constrained by low nutrient availability, and tree invasion of damaged bogs, where drying of the peat has increased nutrient availability, allowing rapid growth and eventual development of closed canopy woodland.

Bog woodland is listed as a priority for conservation in the EU Habitats Directive. The UK Biodiversity Action Plan includes Scots pine (*Pinus sylvestris* L.) dominated bog woodland in the Habitat Action Plan for Wet Woodland, stating that in the UK it is confined to Scotland (UK Biodiversity Group, 1998). So the need to conserve examples of the habitat is clear. Little is known, however, about its biological status. One view, that it is a climax vegetation type on bogs in Scotland's small boreal vegetation zone, conflicts with the alternative that it is a transient phase of a secondary succession triggered by anthropogenic disturbance.

A review of forested wetlands in western Europe concluded that pinewoods on ombrotrophic bogs represent a climax community under recent climatic conditions (Wiegers, 1990). Banner, Pojar and Rouse (1983) found pollen evidence in Canada for a natural succession from forest to bog woodland (muskeg). They explained this and the apparently contradictory evidence of earlier reports of the opposite succession by concluding that vegetation is a dynamic complex that responds to changes in climate. A bog woodland phase has occurred during climatically-induced successions both from forest to bog and from bog to forest.

In Scotland, stunted Scots pine may have grown on the surface of raised bogs ever since their formation, becoming denser during dry climatic periods and declining as a wetter climate returned (Godwin, 1956). Ombrotrophic wooded bogs are thought to have been fairly widespread and common during a mid-Holocene period from 7000 to 4000 BP, especially during relatively dry climatic periods (MacKenzie and Worrell, 1995). Prior to this, bogs would have been rare in Scotland because most mires were at an early stage in their development and their vegetation was minerotrophic (*i.e.* they were fens, not bogs). After 4000 BP, the cooler, wetter climate favoured paludification, which would have reduced the occurrence of wooded bogs. MacKenzie and Worrell (1995) concluded that Scotland's climate is marginal for the growth of natural tree stands on ombrotrophic bogs, except in the Eastern Highlands, where the more continental climate is favourable.

Age structures of Scots pine populations on undisturbed Swedish mires showed that pine recruitment patterns varied among mires (Ågren and Zackrisson, 1990). They distinguished three types of dynamics. A reverse-J shaped age class distribution indicated populations that had maintained a fairly constant rate of recruitment. Other unimodal age class distributions reflected a wave-like regeneration pattern, possibly resulting from interactions between different tree age and size classes. Where multimodal age class distributions were evident, the timing of the peaks of colonisation coincided among sites, suggesting that these populations had experienced periods of abundant regeneration, probably due to climatic fluctuations.

Freléchoux *et al.* (2000a, 2000b) studied bog pine (*Pinus uncinata* Ramond var. *rotundata* (Link) Antoine) communities on sites affected by drainage and nearby peat cutting in the Swiss Jura. The communities ranged from open, wet bog with uneven-aged, scattered, small trees (0-5 m) to dense, relatively young (<150 years old) and even-aged stands of tall trees (10-15 m). Pollen studies suggested that all the communities had existed since the development of the bogs and could be considered to be climatic climax communities. However, succession in response to drainage and peat cutting had altered their distribution, with the denser types spreading inwards from the bog edges and developing near peat cuttings and the sparser types spreading onto formerly treeless central parts.

This paper describes a study of the age structure of Scots pine dominated bog woodland at four sites included in the EU LIFE Wet Woods Project. The aims of the study were:

1. To characterise these bog woodlands in terms of tree cover density, composition and coning, as a record of UK examples of the habitat.
2. To determine relationships between tree size (diameter and height) and age with a view to allowing age to be estimated without coring.
3. To determine the age structure of the pine populations at these sites and from it determine whether these bog woodlands are long-standing, stable communities as reflected by a reverse-J shaped age class distribution or transient communities originating from discrete, climatically or humanly triggered regeneration episodes.

Materials and methods

Four bog woodland sites were sampled (Table 1). A time-series of aerial photographs of each site was used to select fairly uniform, sparsely wooded sampling areas. At each site up to three sample plots, in the form of belt transects, were used to determine tree ages and map the composition and structure of the bog woodland (Table 1). All the transects except Aber T2 and T3 represented part of the gradient from bog edge to bog centre. Aber T2 represented a gradient from a peat cutting face to the bog centre and Aber T3 did not represent any obvious gradient. Additional small samples of larger trees (Table 1) were aged (a) in an attempt to establish the maximum age of trees growing on the bog near the transects, (b) to establish the age of trees growing on cutover bog (Aber S2) or (c) to provide a mineral soil comparison from adjacent non-bog ground.

The rarity of bog woodland in Britain necessitated sampling for age determination by increment cores, leaving the trees unharmed and minimising disturbance. In each transect a single 5 mm increment core was taken in a south/north orientation, 20-30 cm above ground, from every tree with a basal diameter of >2 cm.

A tree size/age classification suited to the stunted trees in these bog woodlands was devised. Tree within the transects were classed as cored trees (i.e. stem diameter >2 cm at coring height), seedlings (i.e. obviously young with stem diameter <2 cm at coring height), small old trees (i.e. apparently old with stem diameter <2cm at coring height) or dead. The height and location was recorded for all individuals. For cored trees, diameter and peat depth (where measurable), were recorded. Trees bearing cones at the time of sampling (August 1999 for Inshriach, June 2000 for Pitmaduthy and Monadh Mor, October 2000 for Abernethy) were also noted.

The number of annual rings was counted under a microscope after gluing the core into a wooden holder and paring it down to provide a smooth longitudinal section. About half the cores did not include the central rings so the number of missing rings was estimated. A transparent acetate sheet marked with concentric rings of uniform width selected to match the inner-most ring widths of the core was aligned over the core so that the radii of curvature of its rings matched those of the core's inner-most rings. The number of missing rings was then counted. This method assumed that the rings missing from the core were circular and the same width as the inner-most ones present in the core.

At each of three of the sites (Pitmaduthy, Monadh Mor and Inshriach) 10 trees between 0.5 and 1.3 m tall were destructively sampled to determine the number of years growth at the root collar. Discs taken at the root collar had 3 ± 1.4 (SE) more annual rings than counted from the increment core. To compensate for error in root collar estimation, we decided upon a standard addition of 5 years to convert core age to tree age.

Tree age class distributions were prepared using 20-year age classes to give reasonable numbers within classes. The inclusion of seedlings and older trees too small to core required an assumption that seedlings of stem diameter less than 2 cm were less than 20 years old and that older trees with a diameter less than 2 cm were

20-39 years old. These assumptions were borne out by the limited destructive sampling undertaken.

The relationship between a tree's age and the probability of it bearing cones at the time of sampling was examined for the samples containing at least 7 coning and 7 non-coning cored trees. The probability of coning for individual trees in these samples was assumed to increase with age according to an S-shaped probability v age curve. The logit function of the probability of coning was regressed against age to best fit each sample to the model. The age at which trees had a 50 % probability of bearing cones was estimated using the ED50 procedure used to estimate the effective dose of a drug from the responses recorded in dosage trials.

Results

Bog woodland composition and physical structure

The spatial distribution of tree species and size/age classes for the transects is presented in map form in Fig. 1 and densities are summarised in Table 2. Scots pine was the dominant species on all transects. Birch (*Betula* spp.), mostly downy (*Betula pubescens* Ehrh.), varied in frequency among the sites and was absent from the Abernethy site. One seedling each of lodgepole pine (*Pinus contorta* Douglas ex Loudon), Sitka spruce (*Picea sitchensis* (Bong) Carr), grey willow (*Salix cinerea* L.), rowan (*Sorbus aucuparia* L.) and European beech (*Fagus sylvatica* L.) was encountered.

The transects varied in density of tree cover, even within sites (Table 2). In general the trees were fairly evenly distributed throughout the transect. The first 10 m of Monadh Mor T1 was dominated by one large Scots pine which appeared to have suppressed tree establishment nearby (Fig. 1). The nearest pine seedling was 5 m away.

Abernethy T1 had a patchy tree distribution (Fig. 1), reflecting an apparent ecotone from the bog edge, where there were large trees but no seedlings, through a zone of smaller trees with increasingly frequent seedlings, to a zone with no large trees but frequent seedlings (Fig. 2). Inshriach Transect 1 had a patchy tree distribution related to the ground vegetation. The distinct large treeless patch supported wet *Sphagnum cuspidatum* lawn.

At Abernethy, T3 and the middle part of T1 had a two-tiered structure with a scatter of trees over 5 m tall and frequent seedlings up to 0.6 m tall among the field layer (Fig. 2). Fire scars dating from about 1918 on almost all the large trees suggest that a fire may have killed trees below a certain size, accounting for the lack of intermediate sized trees.

Relationship between density of tree cover and ground vegetation

Transects with greater cover of *Eriophorum vaginatum* than *Calluna vulgaris* (Table 1) had higher tree densities than the others and included birch (Table 2). This apparent vegetation effect cannot easily be separated from a between-sites effect since all the transects with greater cover of *Calluna* than *Eriophorum vaginatum* were at Abernethy. However, among the three Abernethy transects, Transect 2, which had the

least cover of *Calluna*, had a higher density of cored trees (*i.e.* trees with stem diameter >2 cm at coring height) than the others.

Relationships between age and tree height and diameter

Relationships between tree height and age and tree diameter and age are summarised in Table 3. Five out of ten bog woodland samples had R^2 values greater than 0.5 for the relationship between age and height while only four out of twelve had $R^2 > 0.5$ for age vs diameter. Two out of four dry ground (mineral soil) samples had $R^2 > 0.5$ for age vs diameter. Diameter growth rates were higher for trees growing on the adjacent dry ground than for trees in the transects (Fig. 3). Of the additional samples, Pitmaduthy S1 and Abernethy S1, both growing on a primary bog surface, resembled the transects, while those on cutover bog, *i.e.* at Abernethy S2 and Inshriach S1, had medians closer to those of the mineral soil samples than those of the transects.

Age structure

Tree age was not related to distance along the transects, suggesting that recruitment had not occurred recently through gradual edge-inward colonisation of the mires.

All transects except Abernethy T3 had a predominance of trees in the youngest two age classes (Fig. 4). All had a unimodal age class distribution, peaking in either the 0-19 or the 20-39 age class except Abernethy T1 and Abernethy T3. The former peaked in the 0-19, 140-159 and 200-219 classes while the latter peaked in the 0-19 and 140-159 classes. Monadh Mor T1 and T2 and Inshriach had fewer trees in the 0-19 age class than in the 20-39 class, indicating that recruitment had decreased and/or that mortality for the youngest age class has increased.

Pitmaduthy T1 and S1 were only 200 m apart but had very different age structures (Fig. 5). The absence of trees older than 50 years in T1 and its abundance of younger trees contrasted strongly with the wider age range, from 24 to 134 years, of S1, few of which were younger than 50. T1 had a significantly greater ($p < 0.001$) lifetime mean height growth rate than S1 (Fig. 5) but this may only reflect the age difference, rather than any site-related growth difference, between the two populations. T1 also contrasted with S1 in having wetter ground conditions with greater Sphagnum cover, birch present and *Drosera anglica* absent.

Abernethy S1, one of the additional samples used to determine the maximum age of trees in the vicinity of the transects, had one tree of 335 years old, markedly older than the others. This tree, near the centre of the bog, had a basal diameter of 24 cm, a height of 7 m, a crown diameter of 4 m and a crown depth of 2 m. It contrasted with the two largest trees in Abernethy T1, both near the edge of the bog. Around 210 years old, they had attained heights of 13 and 14.5 m and a diameter of 56 cm.

Cone production

All the transects contained some pines bearing cones (Fig. 1). They were spread along the transects, except Abernethy T2, in which only two such trees were present. For those samples with at least 7 cone-bearing and 7 non-cone-bearing trees, only three fitted the S-shaped coning probability v age model well enough to give a meaningful estimate of the age at which an individual tree had a 50 % likelihood of bearing cones. The 95 % confidence intervals for this age were: Pitmaduthy T1: 20-31 years; Pitmaduthy S1: 50-94 years; Inshriach T1: 34-49 years.

Discussion

Vegetation dynamics in these bog woodlands

Many interacting factors influence vegetation dynamics on bogs, including seral succession, climatic fluctuation, herbivory and anthropogenic disturbances such as fire, drainage, peat cutting, tree cutting, nutrient deposition and alteration of water flow paths. Impacts on the ground vegetation can alter its composition and structure, and hence the quality of seedbed and substrate for early growth of pine. Tree canopy shade can suppress regeneration. The tree layer may increase rainfall interception, altering the water balance and hence surface dryness.

For three of the four sites studied we can identify specific disturbance factors which have strongly influenced the degree and type of tree cover in the transects. Air photos show that all the large trees disappeared from the western part of Pitmaduthy Moss, including T1 but excluding S1, between 1946 and 1959, presumably in a timber harvesting or bog clearing operation, partly accounting for the difference in age structure between T1 and S1. The abundance of younger trees in T1 compared with S1 probably reflects the contrasting ground conditions, which suggest that at T1 the upper peat may have been removed.

There is indisputable fire-scar evidence for a fire in about 1918 at Abernethy even though no historical documentary evidence is known to us. This fire most likely killed the small trees. All those surviving from 1918 were over 30 years old then, with one 17 year old exception. The fire does not seem to have precipitated a wave of regeneration, or if it did they have not survived. The oldest surviving post-fire trees were not established until almost 50 years later except for one established 9 years after the fire on the cutover part of the bog. The reason for this delay in regeneration is unclear. Pine regeneration may have been suppressed by heavy deer browsing or prevented by dense *Calluna* regeneration on the burned surface. The peat cutting activity on the north-eastern part of the bog may have gradually dried the surface of the main plateau sufficiently for eventual successful pine regeneration.

The presence of an eroded peat face beside the Inshriach bog and a peat depth of only 5-75 cm indicates that the bog had been entirely cut over. The trees on it ranged from 11 to 54 years old, confirming that this bog woodland has developed recently on a secondary peat surface. The seeds will almost certainly have originated from the forest adjacent to the bog, which was planted around 60 years ago. Despite the high degree of anthropogenic disturbance at this site, the remarkably shallow layer of peat remaining and its recent origin, the bog woodland is similar in some respects to longer-standing examples. Both the height and diameter growth rates of the pines are slow (1-4 mm diameter per year in T1 compared with 3-5 mm per year on the

adjacent dry ground) and apparently constrained by the soil conditions. Most of the trees are markedly stunted and cones are small.

Monadh Mor is the least disturbed site. Water table rise, the cause unknown, had caused paludification of a wooded area of the mire before 1990 (Mackay, Redgate and Holmes, 1999). A central dome of drying, ombrotrophic bog, fringed by cutting faces, indicates former peat cutting activity but it is unlikely that our sites, some distance away, have been affected. Drainage and afforestation of land adjacent to the mire may have altered the timing and amount of runoff reaching the mire. The transects both had shallow peat (~0.5 m) at the near end and deeper peat (1.1 m for T1; 3.1 m for T2) at the far end. This may account for the dominance of the old tree at the near end of T1 and the similar old trees in that vicinity in sample S1, also on shallow peat, but is not reflected in the tree cover in T2. Both transects had few trees over 50 years old, suggesting either a high mortality rate or a spread of trees onto these areas during the last half century.

The Abernethy Forest site has had Scots pine growing on the bog on peat several metres deep for over 200 years and at least one tree in the central part of the bog has grown there for 335 years. The abundance of *Sphagnum austinii* and *S. fuscum* in the bog suggests that open bog conditions have prevailed there for a long time. These species, particularly *S. austinii*, are vulnerable to disturbance and have been lost from many formerly occupied bogs in Britain (Daniels and Eddy, 1990). They require a relatively open habitat and are most often found on the deepest, wettest parts of nutrient-poor bogs (Hill *et al.*, 1992), the areas least likely to have tree cover. Our small sample of trees from the cutover area at the north end of the bog, Aber S2, indicates that the peat cutting began at least 150 years ago and at least part of the present face was probably last cut about 130 years ago. This site provides evidence of long-lived bog woodland but its origin cannot be unequivocally ascribed to nature or to the effects of peat cutting. Scots pine bog woodland has occupied at least part of the site in spite of fire and peat cutting affecting it within the last 150 years.

Predicting tree age from height or diameter

The results clearly showed that age could not be predicted from height or diameter using a single predictive equation that would apply to all sites or even to the whole of a single site. However some of the samples gave useful predictive equations applicable to the vicinity of the sample area (Table 3). A further sampling of one or more sites could be used to test the variability of the age vs height and age vs diameter relationships within a site.

Natural or not?

The question of whether Scots pine bog woodland occurs ‘naturally’ in Britain is academic and irrelevant. The whole of Britain has been affected by man so we have no ‘natural’ habitats if natural is taken to mean unaffected by man. There is no doubt that genuine bog woodlands do exist and European Union legislation requires that some examples be protected. This study has shown that a natural process of bog woodland development has occurred at some sites in response to disturbances, whether ‘natural’ or anthropogenic. The process is the same as that suggested by Godwin (1956), whereby tree cover fluctuates with climatic variation and mirrors the results of Frelechoux *et al.* (2000 a, 2000b) for *Pinus uncinata* in Switzerland.

The findings from the Abernethy site show that bog woodland development does not necessarily lead, at least in the 200-300 year term, to the development of closed canopy pinewood. Many man-altered lowland raised bogs in Britain have, however succeeded to closed-canopy pinewood or birchwood and man has, by deliberate afforestation, created productive forests on bogs. So there seems to be a critical threshold of disturbance or alteration below which bog woodland development may occur but above which succession to closed-canopy woodland follows. Growth of individual trees may be one of the best indicators of whether this threshold has been reached. Straight, vigorous growth and regular branching may indicate that the site has been altered beyond the threshold and will succeed to closed canopy woodland whereas slow, stunted growth probably indicates that a bog woodland community will persist.

Conclusions

Our results highlight the scarcity of bog woodlands undisturbed by human activities. They also show that various types of human disturbance can be tolerated by bog woodland. Some of our most highly regarded examples of Scots pine bog woodlands have developed on sites subject to strong human disturbance. We cannot be certain whether, in the long term, the disturbances identified at the study sites will cause a succession from bog woodland to closed canopy pinewood but it looks unlikely.

Conflicts may arise in future between the HAP objectives of restoring bogs and creating or restoring wet woodlands. In some cases partial failure to restore treeless, open bogs may result in the creation of bog woodlands.

There are few, if any, Scots pine bog woodlands in Britain that have only been affected by 'natural' disturbance. Human disturbance has made it impossible to ascertain whether bog woodland would have occurred as a climatic climax on the sites we studied. However the Abernethy site provides evidence of a very long-lived bog woodland community. Bog woodland can, it seems, be a long-lived, stable, natural habitat.

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Table 1.

Details of the sampling sites and the various samples. The main samples, in the form of belt transects and named T1, etc. were used to determine the bog woodland age structure. Supplementary samples, named S1, etc. were used to determine the maximum tree age in the vicinity of the transects. Dry ground samples, D1, etc. were from nearby mineral soil ground, serving as a reference with which to compare the bog woodland samples.

Site	Grid Ref.	Sample	Size (m)	n	Age range	Vegetation
Pitmaduthy Moss	NH7777	Pit T1	4 x 35	47	13-50	<i>Eriophorum vaginatum</i>
		Pit S1		20	24-134	
		Pit D1		10	41-72	
Monadh Mor	NH5953	Mon T1	4 x 35	32	19-97	<i>Eriophorum vaginatum</i>
		Mon S1		10	66-106	<i>Eriophorum vaginatum</i>
		Mon T2	4 x 30	20	18-51	
Abernethy Forest	NH9918	Aber T1	4 x 100	13	125-215	Calluna/ <i>Eriophorum</i>
		Aber S1		8	121-335	
		Aber D1		6	47-129	
		Aber T2	4 x 90	17	20-33	Trichophorum/ <i>Calluna</i>
		Aber S2		5	73-146	
		Aber D2	6	64-71	<i>Calluna vulgaris</i>	
		Aber T3	12 x 75	21		99-173
Inshriach Forest	NH8604	Insh T1	4 x 45	50	11-51	<i>Eriophorum vaginatum</i>
		Insh S1		7	48-54	
		Insh D1		7	42-53	

Table 2.

Tree density by imposed size class for the sample transects.

Transect	Tree density within transect (stems per ha)										
	Cored trees		Seedlings		Old small trees		Dead		All trees		Pines with cones
	Pine	Birch	Pine	birch	pine	birch	Pine	birch	pine	birch	
Pit T1	2929	357	786	1071	143	143	429	0	4286	1571	1357
Mon T1	3500	71	1357	143	214	71	71	71	5143	357	714
Mon T2	1667	0	1250	500	583	500	0	0	3500	1000	1000
Aber T1	300	0	2075	0	0	0	0	0	2375	0	300
Aber T2	528	0	1111	0	444	0	167	0	2250	0	56
Aber T3	233	0	144	0	44	0	11	0	433	0	100
Insh T1	2778	0	722	111	222	0	833	0	4556	111	722

Table 3.

Linear regression relationships between (a) tree height and age and (b) tree diameter and age. Equations are given for relationships with $R^2 > 50\%$.

	(a) Height (m) v age			(b) Diameter (cm) v age		
	<i>n</i>	R^2	Regression equation	<i>n</i>	R^2	Regression equation
<u>Transects</u>						
Pit T1	47	55	Ht = 0.05 x Age + 0.28	46	64	Diam = 0.23 x Age – 0.32
Mon T1	32	83	Ht = 0.09 x Age – 0.58	32	80	Diam = 0.56 x Age – 10.95
Mon T2	20	12		20	25	
Aber T1	13	43		13	39	
Aber T2	17	0		17	6	
Aber T3	21	56	Ht = 0.04 x Age + 0.12	21	31	
Insh T1	50	74	Ht = 0.09 x Age – 1.17	50	63	Diam = 0.29 x Age – 3.10
<u>Bog pine samples</u>						
Pit S1	20	85	Ht = 0.04 x Age + 0.11	20	65	Diam = 0.23 x Age – 2.63
Mon S1	10	12		10	42	
Aber S1				8	6	
Aber S2	5	0		5	10	
Insh S1				7	2	
<u>Dry ground samples</u>						
Pit D1				10	55	Diam = 0.63 x Age – 9.00
Aber D1				6	30	
Aber D2				6	78	Diam = 0.41 x Age + 5.77
Insh D1				7	27	

Figure captions

- Fig. 1.** Maps showing the distribution of trees on the transects by species and size/age class. The transects are ordered as in Table 2, with Pitmaduthy T1 at the top and Inshriach T1 at the bottom.
- Fig. 2.** Tree heights along the transects. Transect order as in Table 2. The full length of the vertical (y) axis on all transects represents 15 m.
- Fig. 3.** Box and whisker diagrams representing the distribution of lifetime mean diameter growth rate within the samples. The box represents the interquartile range, cut in two at the median value. The whiskers represent the range of values excluding any outliers, which are shown by asterisks. Outliers are here defined as values outside the interquartile range by a distance of more than 1.5 times the interquartile range.
- Fig. 4.** Age class distributions for the transects (order as in Table 2). Each vertical axis represents 100 % of the trees and seedlings within the transect. Seedlings are assumed to be in the age class 0-19 years and small old trees are assumed to be in the 20-39 years class.
- Fig. 5.** Variation of height growth rate with age at Pitmaduthy Moss for T1 (crosses) and S1 (circles).

Figure 1: Maps showing the distribution of trees on the transects by species and size/age class. The transects are ordered as in Table 2, with Pitmaduthy T1 at the top and Inshriach T1 at the bottom.

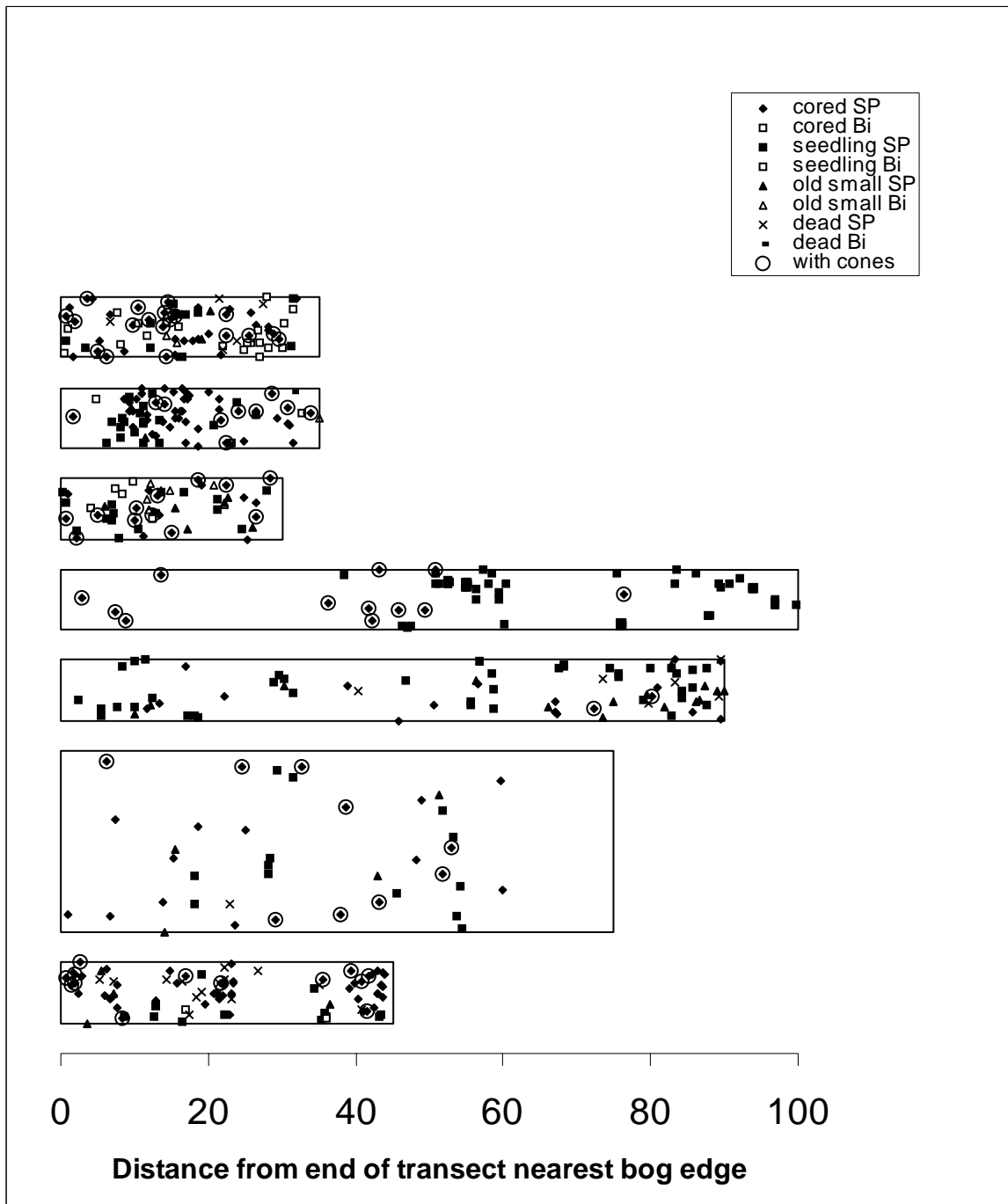


Figure 2: Tree heights along the transects. Transect order as in Table 2. The full length of the vertical (y) axis on all transects represents 15 m.

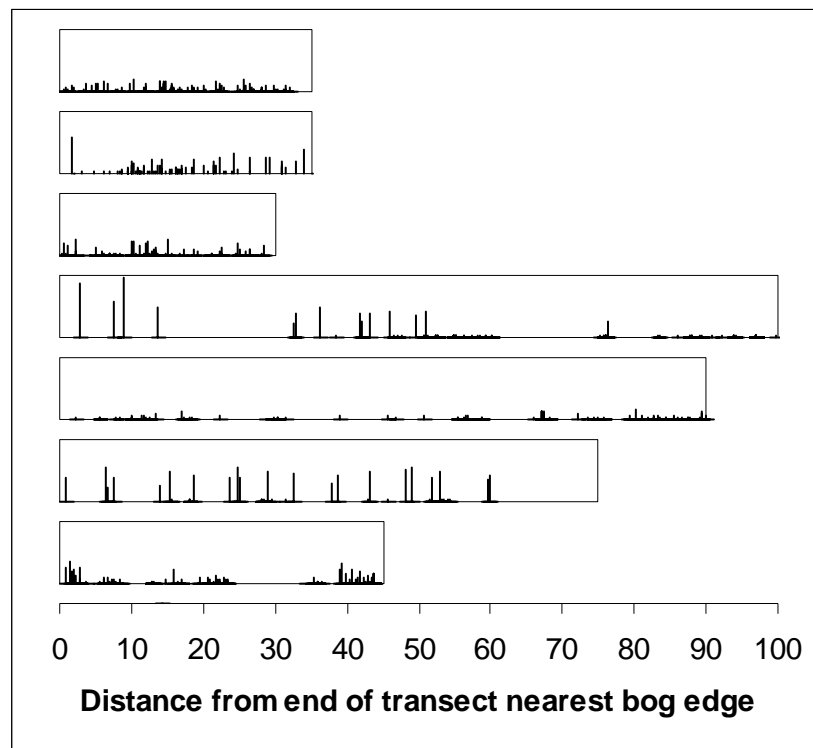


Figure 3: Box and whisker diagrams representing the distribution of lifetime mean diameter growth rate within the samples. The box represents the interquartile range, cut in two at the median value. The whiskers represent the range of values excluding any outliers, which are shown by asterisks. Outliers are here defined as values outside the interquartile range by a distance of more than 1.5 times the interquartile range.

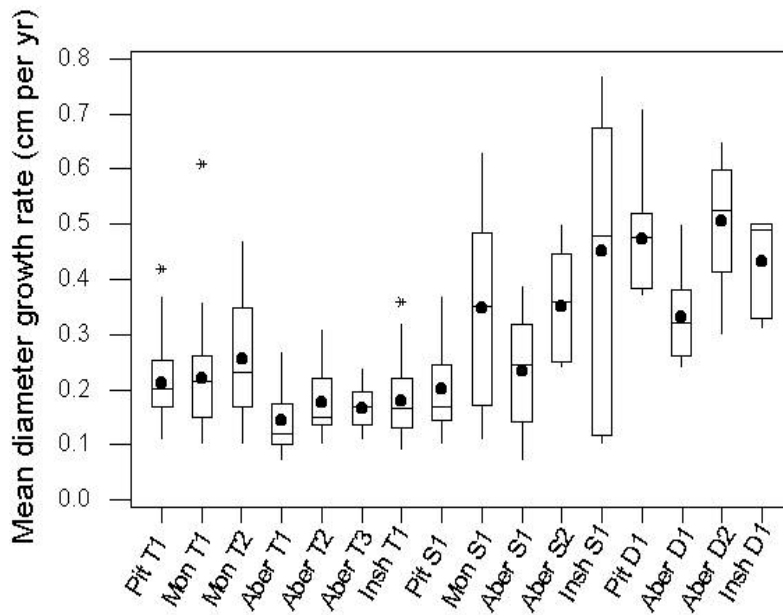


Figure 4: Age class distributions for the transects (order as in Table 2). Each vertical axis represents 100 % of the trees and seedlings within the transect. Seedlings are assumed to be in the age class 0-19 years and small old trees are assumed to be in the 20-39 years class.

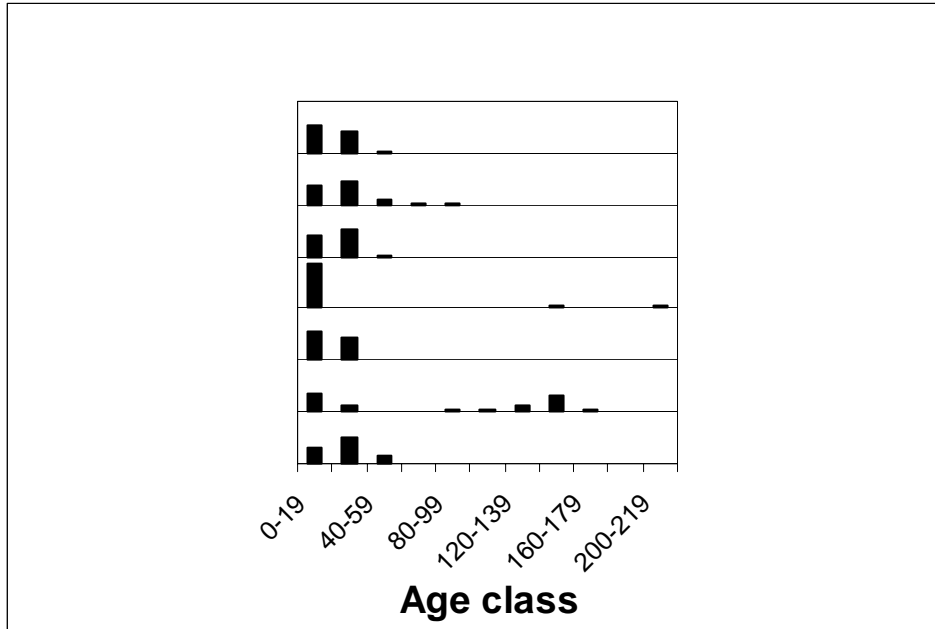


Figure 5: Variation of height growth rate with age at Pitmaduthy Moss for T1 (crosses) and S1 (circles).

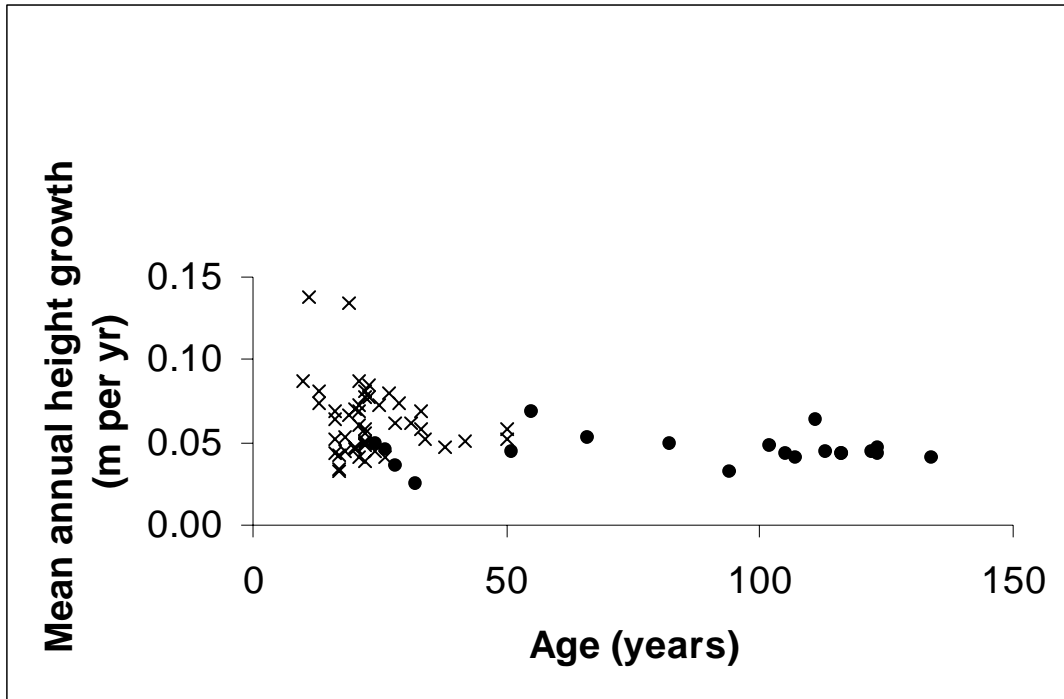


Photo captions

1. Bog woodland at Monadh Mor
2. Stunted Scots pine at Abernethy
3. Bog woodland of recent origin at Inshriach

1. Bog woodland at Monadh Mor



2. Stunted Scots pine at Abernethy



3. Bog woodland of recent origin at Inshriach

