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Long-term monitoring and management of Langley Wood

A minimum-intervention National Nature Reserve

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Long-term monitoring & management of Langley Wood: a minimum-intervention National Nature Reserve

E. P. Mountford[1], G. F. Peterken[2] & D. Burton[3]

[1]Ecoscope Applied Ecologists, c/o 17 Butler Road, Wem, Shropshire SY4 5YP
[2]Beechwood House, St. Briavels Common, Lydney, Gloucestershire GL15 6SL
[3]English Nature, Cherry Lodge Farm, Shrewton, Salisbury, Wiltshire SP3 4ET

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Keith Kirby, English Nature

Preface

This report is part of the RENFORS project - REgeneration of Native FORest Stands for timber production and environmental value - funded by the European Communities Directorate-General for Agriculture as a collaborative project between teams in Sweden, Denmark, Italy and Great Britain (Contract FAIR PL95-0420). Field recording (in 1996) and analysis were carried out by the author under the general supervision of Dr. George Peterken.

The study transects were established in 1986 by Christa Backmeroff as part of a programme of studies on long-term changes in unmanaged woodland National Nature Reserves. This programme was initiated with funding by the Nature Conservancy Council (NCC) under the supervision of G. F. Peterken, then of the Chief Scientist's Directorate of NCC.

The records of the initial condition were included in a report held by English Nature (Backmeroff 1987). Copies of both sets of records and the report are held by EPM and GFP.

David Burton, English Nature Site Manager, provided the section on managing Langley Wood.

Acknowledgements

Langley Wood was maintained for many decades as a semi-natural woodland by Mr. Nigel Anderson and his family. It is currently a National Nature Reserve managed by English Nature in association with Mr Anderson. We are grateful for the information and guidance provided by Mr Anderson on several occasions. Nigel Cowling, Anne Hargreaves, Albert Knott, John Lobb and Linda Smith helped with the 1996 field survey.

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Summary

Changes in unmanaged semi-natural stands in Langley Wood NNR were quantified between 1986-96 by means of two permanent transects. Over 5700 stems and seedlings were recorded. The stands had long been treated as coppice-with-standards, but after the last coppicing between 1920-1940, had been allowed to develop mostly by natural processes. By 1986 birch-oak-hazel, birch-oak, lime-oak, and wet birch-ash stands had developed. The most abundant trees were oak from retained standards, maiden birch, lime and hazel from stump sprouts, ash from recent advanced regeneration, and hawthorn from stump sprouts and seedling regeneration.

Changes since c1940 and between 1986-96 were typical of the stem exclusion stage of stand development. The canopy remained largely closed. Stand basal area increased. Living stem density decreased. The girth of surviving stems increased. Smaller diameter stems tended to grow more slowly, occupy lower strata, show more dieback, and suffer higher mortality rates than larger ones. However by 1996 two stands had progressed into the understorey re-initiation stage of development. Hazel-birch-oak stands had recently recruited new stems, individuals, and seedlings, mostly of hawthorn and hazel. Wet birch-ash stands had amassed numerous ash seedlings since about 1960. No re-initiation was observed in the lime-oak and birch-oak stands.

Contrasts were observed between 1986-96 in the performance of major woody species. Lime gained in importance, through low mortality of mainly small-girth stems, rapid growth of large-girth survivors, and the exclusion of other nearby species. Nevertheless many lime stems remained in the sub-canopy and understorey. Birch increased little in importance, due to lower survival, windblow of many larger trees, and poor growth of large girth survivors, but it still remained the most numerous canopy tree. Oak continued to dominate in terms of basal area, through low mortality and high average growth of retained standard trees. Ash began to assert itself, as large trees survived and some of the numerous suppressed saplings grew vigorously into the sub-canopy. Hazel increased its domination of the underwood, through low mortality of mainly small-girth stems, high average growth of survivors, and much regeneration from stools and new seedlings. Hawthorn increased slightly in numbers, through low mortality, stem recruitment, and the establishment of small seedlings, but growth of surviving stems was poor. Three exotic species, rhododendron, sweet chestnut, and sycamore, failed to regenerate successfully, but large existing individuals developed vigorously.

Grey squirrels bark-stripped several sycamore and beech. The largest of three sycamores was badly debarked and the only two medium-size beeches that died between 1986-96 were killed following severe debarking. Fast growing beech poles were especially vulnerable to debarking.

Stem debarking by deer was very small-scale, mainly effecting small hazel stems <10cm gbh, although lime had the greatest percentage damage.

Most standing and fallen dead wood was small and large material remained extremely scarce. Slow-decaying oak and fast-decaying birch accounted for most of the volume. Accumulations remained low compared to undisturbed virgin forests, but similar to comparable near-natural woodland in Britain. Turnover of standing material was high and decay appeared rapid.

1. Introduction

Restoring natural conditions has become one of the main aims of nature conservation in British woodlands (Peterken 1996). Several large semi-natural woodlands have been designated as 'minimum-intervention' so that natural processes and structures can be allowed to develop freely. Under these conditions large old trees and dead wood should accumulate. Diversity will be generated by natural disturbances, and natural patterns of tree growth and mortality will prevail.

Such reserves provide an invaluable research resource; natural processes can be studied; natural structures quantified; environmental change detected; and, by comparison with managed stands, the ecological effects of forestry can be quantified. Woods assigned to minimum-intervention indefinitely are thus reference points, or controls, forming an essential scientific basis for nature conservation. In the United States, such places are known as Research Natural Areas.

Unfortunately, few semi-natural woods in Britain fit with the requirements for minimum-intervention management (Peterken 1996; Kirby and Reid 1997). Most are too small or ill-shaped, they present problems in controlling invasive exotic species, some rare resident species can deteriorate under the new regime, revenue will be lost from timber sales, and the site owners and local public can object to proposals.

Sustaining monitoring is difficult too. The work is long-term and often falls prey to human failings before coming so. The initiators lose interest, get promoted, or are offered other contract work. Fashions in science and conservation change. Financial support is fickle. The records are lost or forgotten and institutions are reformed or disbanded. Even those studies that have lasted for 25 years or more have often done so by the skin of their teeth (Peterken and Backmeroff 1988).

Langley Wood (declared a National Nature Reserve in April 1998) is a good example of a reserve suitable for minimum-intervention management. Single blocks of over 200ha of ancient, semi-natural woodland are rare enough, but even among these Langley Wood is outstanding. It has a large number of woodland types; the vascular flora is amongst the richest of any wood in southern England; it includes many rare and localised species of flowering plants; the bryophyte and epiphyte flora is likewise rich and includes notable species; and the invertebrate and bird fauna are both exceptionally rich. Bordering the New Forest, it is effectively an 'ungrazed' (by stock) version of the Forest woodlands. Many of the trees appear to be 200 years old or more.

The wood contains features of near-natural forest which are rarely found together elsewhere in England. These include areas of oak-lime woodland - the original condition of much natural woodland in the English lowlands. The epiphyte flora and dead wood fauna (including a range of saproxylic species) occur with a relatively ungrazed woodland ground flora: normally these components of natural forest survive separately in wood-pasture and coppices respectively.

Unlike most other large woods, Langley had only small areas of plantation. Where exotic tree and shrub species were present, they were limited and controllable. The owner had controlled the numbers of grey squirrels and deer.

Accordingly, the wood was regarded as a prime candidate for management as a minimum-intervention reserve with the aim of restoring the wood to as near a wholly natural condition as is possible in a cultural landscape. Under such a regime, it would remain rich in wildlife, but it could also function as a scientific resource. If the development of the wood was studied, we could learn about the structure and dynamics of natural woodland and use Langley as a baseline for measuring the influence of management on other woods.

With this in mind, Langley Wood became part of a programme of long-term studies in unmanaged near-natural woodland reserves, which includes several other NNRs, such as Lady Park Wood in the Lower Wye Valley, Monks Wood in Cambridgeshire, Clairinsh Island in Loch Lomond, and Wistman's Wood on Dartmoor (Peterken and Backmeroff 1988). Transects were set out and recorded in 1986, and now, 10 years later, we have been able to repeat the recording and measure recent changes. This work formed part of the European Union funded RENFORS project which specifically intends to; (i) identify the variables that control the species diversity of trees and forest flora and fauna (biodiversity) at the regeneration phase; (ii) develop silvicultural measures that favour biodiversity at the regeneration phase; (iii) experimentally test measures in traditionally managed mature stands; and (iv) analyse the economic and biodiversity implications of the systems developed.

As it happened, the wood largely avoided the great storms of 1987 and 1990, so changes have been small and predictable. Eventually, however, it is likely that changes will be more dramatic, and the recording over the first ten years will then provide a useful baseline against which the effects of future storms, drought, snowfalls, etc., can be measured.

2. Description of Langley Wood

Situation, status & management

Langley Wood (national grid reference SU 2220) covers 219 hectares and is situated on the edge of the New Forest perambulation, between the villages of Redlynch and Hamptworth, south-east Wiltshire (Figure 1). It is designated as a Site of Special Scientific Interest with Nature Conservation Review Grade I status, and is leased by English Nature as National Nature Reserve from the family trust established in 1987 by Mr. Nigel Anderson of Hamptworth Lodge.

History

Langley Wood is a remnant of the lime-dominated mixed broadleaved woodland that covered most of lowland England about 5000 years ago. The wood became part of the Royal Forest of Melchet about 1000 years ago, but appears always to have remained outside the boundary of the New Forest and its intensive grazing history. Thereafter, probably beginning in the 14th century and continuing until the 19th century, the original wood pasture management appears to have been progressively replaced by inclosure for coppicing. Numerous enclosure banks and ditches still remain throughout the wood today. Oak standards, some of which were described as very large trees indeed, were maintained in both the wood pasture and coppice systems.

Coppice-with-standards management declined about 100 years ago, but some coupes were cut up to about 1940. Thereafter management in much of the wood was limited to the removal of dead trees and fallen timber for firewood, and the maintenance of ditches and access rides. Otherwise a few areas were block felled and then conifers planted. Accordingly large areas of the wood have remained relatively undisturbed for many decades.

Topography, geology & soils

Langley Wood is situated on gently undulating ground, dissected by several small stream valleys. The local geology is mainly Pleistocene drift sands and gravels overlying London Clay. Although the soils are complex, depending on local hydrology and the type of drift material present, in general they are slowly permeable, seasonally waterlogged, slightly acid, fine loamy and fine silty soils over clay, often with brown subsoils.

Vegetation

Most of the wood is covered by mixed broad-leaved woodland, with pedunculate oak *Quercus robur*, hazel *Corylus avellana*, and birch *Betula pendula/pubescens* the most abundant tree species. The oak typically occurs as a large standard tree, and in some areas sessile oak *Quercus petraea* replaces the pedunculate form. Maiden birch form canopy trees both between the oaks and exclusively in some larger areas of the wood. Hazel forms a dense underwood layer in much of the wood. Ash *Fraxinus excelsior*, usually as maiden trees, and lime *Tilia cordata*, from strongly developed large coppice stools, locally replace the oak and birch. Alder *Alnus glutinosa* predominates along the wetter valley bottoms, whilst sweet chestnut *Castanea sativa* and sycamore *Acer pseudoplatanus* have invaded some portions of the wood, although management is now reducing their extent. Other minor tree species include aspen *Populus tremula*, beech *Fagus sylvatica*, field maple *Acer campestre*, goat/grey willow *Salix caprea/cinerea*, hornbeam *Carpinus betulus*, wild cherry *Prunus avium*, and yew *Taxus baccata*.

Underwood shrubs are prolific in much of the wood, and apart from hazel, include alder buckthorn *Frangula alnus*, blackthorn *Prunus spinosa*, crab apple *Malus sylvestris*, dogwood *Cornus sanguinea*, field rose *Rosa canina*, guelder rose *Viburnum opulus*, hawthorn *Crataegus monogyna*, and holly *Ilex aquifolium*. Some dense patches and scattered bushes of rhododendron *Rhododendron ponticum* are currently being eliminated.

The distribution of Peterken (1993a) stand types in the wood has been mapped (see Figure 13.6 in Peterken 1996). Much is covered by hazel-pedunculate oak woodland (Peterken stand type 6Dc), with several large patches of birch-pedunculate oak woodland (type 6Db). Hazel-ash (type 3A) and ash-maple woodland (type 2Aa) are found where the soils are more base-rich, whilst valley alder woodland (types 7A, 7Ba) occupies the wetter ground beside streams. The few patches of birch woodland (types 12A, 12B) indicate sites where oaks were felled long ago. An ecologically complex area is found where a patch of oak-lime woodland (type 5A, 5B) occurs in the west of the wood.

The ground vegetation includes a wide variety of species, many of which are indicators of a long history of woodland continuity. The most common species are bluebell *Hyacinthoides non-scripta*, bramble *Rubus* spp., butcher's broom *Ruscus aculeatus*, creeping soft grass *Holcus mollis*, dog violet *Viola reichenbachiana*, hairy woodrush *Luzula pilosa*, pignut *Conopodium majus*, wood anemone *Anemone nemorosa*, wood spurge *Euphorbia amygdaloides*, and yellow archangel *Lamiastrum galeobdolon*. Where soils are light and most acid, bracken *Pteridium aquilinum* predominates, with bilberry *Vaccinium myrtillus*, heath bedstraw *Gallium saxatile*, honeysuckle *Lonicera periclymenum*, wavy hair-grass *Deschampsia flexuosa*, and wood sage *Teucrium scorodonia* commonplace.

There are small localised populations of many uncommon species, including cow-wheat *Melampyrum pratense*, hay-scented buckler-fern *Dryopteris aemula*, lesser skullcap *Scutellaria minor*, lily-of-the-valley *Convallaria majalis*, loose-spiked wood sedge *Carex strigosa*, narrow leaved buckler-fern *Dryopteris cartusiana*, orpine *Sedum telephium*, prickly shield-fern *Polystichum aculeatum*, soft shield-fern *Polystichum setiferum*, Solomon's seal *Polygonatum multiflorum*, southern woodrush *Luzula forsteri*, and wild daffodil *Narcissus pseudonarcissus*.

The most common ferns are of broad buckler fern *Dryopteris dilatata*, hard fern *Blechnum spicant*, lady fern *Athyrium filix-femina*, and scaly male fern *Dryopteris affinis*. Ground mosses can account locally for much of the ground vegetation; amongst the most common species are *Eurhynchium praelongum, Hypnum cuppressiforme*, *Mnium hornum, Polytrichum formosum, Pseudoscleropodium purum,* and *Thuidium tamariscinum*. The site is also very rich in lichen species, with many uncommon species represented, including *Lobaria pulmonaria, Parmelia crinita, Thelopsis rubella, Bacidia biatorina* and *Schismatomma quercicolum*. Of the 119 lichen taxa recorded about one quarter are good indicators of a long history of woodland continuity.

3. Managing for minimum intervention

This section describes the objectives, rationale and practice of managing Langley Wood as a minimum intervention National Nature Reserve, and the role within this of long-term recording.

Current philosophy and management aims

Langley Wood has been included in a proposed network of 20-30 large semi-natural woodlands in England retained under a minimum intervention policy (Kirby and Reid 1997). This approach is desirable for some semi-natural woods where nature conservation is a priority. Preliminary criteria for selecting such sites are (Peterken 1996; Kirby and Reid 1997):

- large area (preferably >100ha)
- compact shape
- little recent treatment or unnatural disturbance
- few introduced species and no highly invasive ones
- no major external deleterious factors operating (eg agricultural spray drift).
- not noted for rare or unusual species that depend on management for their survival
- stable ownership
- diversity of age structure.

An ecological appraisal of Langley Wood showed that it possessed most of the desirable attributes (Peterken 1993b), with the main features of nature conservation interest being:

- the large area of ancient woodland (>200 ha) and its situation in an even larger area of woodland;
- the variety of woodland types with a relatively natural distribution;
- the abundance of old-growth stands;
- the proximity to the New Forest.
- the diverse structure resulting from its varied past management, mainly as coppice with standards, but with some areas of abandoned wood pasture and progressive enclosure from wood pasture to coppice.
- the diverse flora and fauna, including many rare species, many types indicative of ancient woodland, and many saproxylic types.

The large-size, occurrence within a well-wooded landscape, and near-natural conditions make Langley an ideal candidate for minimum intervention management. The majority of wildlife will be resilient to short term potentially damaging events, such as a large natural disturbance event or a mistaken management policy. Nevertheless, the near-natural status remains at threat from invasive non-native species in surrounding woodland, such as sycamore and grey squirrels.

Accordingly, the key management aims are to:

- Seek to maintain and restore past-natural woodland on the basis that the wood is already more or less in this condition - i.e. retain woodland of native trees and genotypes from local stock, but eliminate introduced species by undertaking an initial programme of restoration work.
- Allow the woodland to develop through natural processes - ie allow natural seedling or coppice regeneration following man-made or natural disturbances, rather than planting.
- Designate a substantial minimum-intervention area where a predominantly mature natural woodland structure will be maintained as habitat for saproxylic species, accepting that a wide-scale natural disturbance could singly level a large part of it.
- Treat features in the wood generally as naturally as possible - i.e. no additional draining or fertilising, but protect the boundary banks.
- Initiate a programme of long-term monitoring in the minimum-intervention area for the study of natural processes.
- Outside the minimum-intervention area consider encouraging diversity by introducing wood pasture and coppice areas.

All the main management aims have been implemented, except the introduction of wood pasturage and a large coppice area. These regimes could be applied without compromising the integrity of the minimum-intervention area (Peterken 1993b), but they have been curtailed for two reasons:

- David Sheppard, English Nature's Invertebrate Ecologist, recommended that the majority of the wood be retained as closed canopy woodland with widened rides and clearings providing additional habitat (Sheppard, 1989). He advised against a return to coppice with standards in part of the wood because this regime would be potentially catastrophic for a number of resident rare invertebrates that are thought to require large areas of closed canopy woodland for their survival.
- The reintroduction of coppice and wood pasture would present a large management input for only a moderate wildlife benefit. It was therefore decided to put any plans to introduce livestock to a part of the wood on hold and restrict coppice work to a buffer zone, where naturalised species exist, and along widened rides. This will have an added benefit because cutting non-natives on a short rotation should curtail their capacity to seed into the minimum-intervention area. In addition, large areas of open space have already been generated by selective felling of non-natives (see below), and more will be created by the final harvest of conifers. This should, along with 5 hectares of coppice on the adjacent Loosehanger SSSI, cater for important open space species, such as pearl-bordered and small pearl-bordered fritillary butterflies.

Current management programme

A programme to eliminate non-native species and restore semi-natural conditions is now well under way. The methods and experiences gained are outlined below.

Rhododendron control

The method recommended by J. Parkin, R.S.P.B. Reserve Warden at Dinnet Wood National Nature Reserve (pers. comm.), has been adopted and refined to control *Rhododendron ponticum.* Wherever possible bushes are spot sprayed with glyphosphate herbicide. Large blocks have been cleared and burnt up using a hymac and a bulldozer with a drott bucket. Isolated clumps which are too tall to spray and inaccessible for tracked machines, have been cleared by cutting back with chainsaws and burning the material by hand. No attempt has been made to stump treat the cut rhododendron. The regrowth has been left for about three years, then spot treated with glyphosphate herbicide and left to rot down *in situ.* Parkin recommends burning off the dead rhododendron to speed up the recolonisation of ground flora and trees. In Langley, this has not been necessary because sprayed rhododendron stands have generally colonised quickly with large numbers of birch seedlings.

Conversion of conifer plantations

Small blocks of conifer plantation are scattered through the wood. All of these were in the closed canopy stage when English Nature took over the management of the wood. It was generally agreed that the best course of action was to thin the conifer to gain some income, then harvest when markets were good or when the reserve becomes short of open habitat. The exception to this has been where young conifer plantations lie adjacent to tracks. Here the conifers have been clear felled to leave wide rides, which have then been managed to provide a range of grassland, scrub, and coppice habitats. Native pioneer species, especially birch, have been quick to regenerate in most of the areas cleared of young conifers.

Reduction of naturalised species

Control of invasive naturalised species that have the capacity to seed into the non intervention area has been a priority. A stand of sycamore has been clear felled, an area with thick sycamore understorey and some canopy trees has been removed, and sweet chestnut has been selectively felled in two areas and thinned in a third. Their remains a number of areas of advanced regeneration sycamore and some canopy trees of both sycamore and sweet chestnut. It is intended to leave a few old chestnuts close to a public path, but otherwise to gradually remove the remaining trees and spot spray any regeneration close to or in the minimum intervention area. Sycamore and chestnut in the buffer zone are to be coppiced on short rotation.

Seed harvesting of some of the native trees in Langley has been carried out by a specialist nurseryman and a local community nursery. Some of seedlings grown from this may be planted in cleared areas where natural regeneration is likely to be composed mainly of naturalised species.

Deer control

Four species of deer are resident in significant numbers; fallow, sika, roe and muntjac. Apart from the need to control deer to minimise damage to crops and young trees on neighbouring land, it is important to keep numbers down to mimic near-natural conditions in which regeneration occurs naturally in areas where the canopy breaks up. The owner of the wood retains the right to cull deer and the bulk of activity occurs along rides and in large cleared areas. Part of a ride has been coppiced to a depth of 15m as an area suitable for culling.

Grey squirrel control

English Nature is obliged under the terms of its lease to control squirrels in Langley Wood. At present control is undertaken in June using selective hoppers baited with warfarin-impregnated wheat. Hoppers are placed close to neighbouring plantation woodland where squirrel damage is likely to occur. At present there is no attempt to control numbers in the interior of the wood. The minimum intervention technique outlined by Kenward and Dutton (1996) may be adopted in the future to help reduce damage in neighbouring plantations.

Maintenance of infrastructure

English Nature's lease in Langley Wood stipulates that the network of ditches and rides must be maintained annually. Care is taken to minimise this unnatural disturbance. A local contractor is employed on a call out basis to clear ditches by hand, remove fallen timber blocking the rides and paths, and swipe the vegetation along the rides. All timber removed from the ditches and rides is placed close to where it fell. The rides are cut once with a chain flail after the ground vegetation has flushed in the spring. English Nature and Hamptworth Estate trialed the use of tractor driven swipes using chain and knife flails. The action of the chain flail was considered more appropriate because it tended to bruise and flatten vegetation (akin to the trampling caused by herds of deer or cattle), and was more robust over rough ground.

Public relations and visitors

Public access to minimum-intervention reserves require special consideration. Two public paths cross the wood. Visitor number are low and the limited car parking means numbers are unlikely to increase greatly. The public paths have been way marked and the owner has actively dissuaded people from leaving paths. The wood seems likely to remain relatively undisturbed by visitors.

With such a high potential for dead, dying and dangerous trees, annual inspections are made of all trees lining public paths and road sides. In 1997, a minimum amount of tree surgery was carried out to ensure public safety. Such work will probably be required about every decade.

Unfortunately, the selective felling of chestnut close to the public road caused a local outcry and attracted attention from the national media. However, the thinning operation carried out the following year was also next to a public path and this caused very little concern. To help inform the public, a bimonthly information sheet outlining recent management and notable wildlife is pinned to the two entrance signs to the wood. Other encapsulated sheets explaining forestry operations are hung close to forestry work sites where they are crossed by a public path. The Site Manager gives guided walks and talks to local community groups.

Survey and monitoring

The minimum-intervention areas are seen as both a mature habitat and a scientific resource in which natural processes can be studied and comparisons can be made with managed woodland. Recording and analysis are therefore essential if this potential is to be realised.

Two transects were established in 1987 as a basis for long-term recording of stand structure and composition. A further transect is planned in the western section of the wood. The transects are marked out with metal posts that have remained undisturbed and intact for ten years. The only problem encountered has been one of health and safety, with the owner of the wood tripping up on the posts. The data from the transects has proved useful in measuring changes in the stands and the impact of natural disturbances. They show what recruitment is occurring, what changes in the canopy and understorey layers are going on, what effect grey squirrels and deer are having, and just how competitive invasive non-natives are. This information has provided an invaluable guide to understanding and making management proposals for the wood.

Two 50x50 metre deer exclosures were erected at opposite ends of the wood in 1998. The plots and adjacent controls have been surveyed using the National Vegetation Classification methodology, carabid beetles have been surveyed, and fixed point photographs taken. Data from these will help gauge the general impact that the current deer population is having and what changes may occur if future deer numbers are reduced.

English Nature is currently helping to develop generic targets used to assess the condition of habitats which are considered to be of national or international importance. Langley Wood is likely to be selected as one of the sites used to attempt to validate generic targets for woodland habitat.

Otherwise, surveys of lichens, bryophytes, higher plants, fungi (limited), flies, moths, birds have been carried out in the past. It is hoped that follow up surveys will be undertaken, as these could help ascertain what impact the present management policy is having.

Funding

English Nature provides the majority of funds for the upkeep of Langley Wood. Bids for essential, programmed, and enhancement work are submitted annually. An enhancement bid for funds to set up a third long-term transect has been deferred until 1998/99.

Revenue made from wood sales is important. Thinning of the conifer plantations and sales of sweet chestnut have helped pay for a significant part of estate work. Otherwise, the Forestry Authority Woodland Grant Scheme has helped pay for some of the woodland restoration works through an area payment of £35/ha under the Special Management Grant. Encouragingly, this is due to change in 1998/99 when targeted payments for specific works such as rhododendron clearance will replace the flat rate payment.

The European Commission has funded the recent surveying of the long-term monitoring transects. There is also a possibility that future funds for research and restoration could be found from other EU projects, such as LIFE, from the National Lottery schemes, or perhaps the forestry industry for research into natural woodland processes. Any increase in funding to facilitate research and survey work would help promote the site as an unmanaged, old growth forest.

4. Recording & analysis

Permanent transects

The baseline record for long-term monitoring at Langley Wood was undertaken in August 1986. Christa Backmeroff established two permanent 20m-wide transects that extend for 365m and 273m (Figure 2). The transects cross a range of stand types that were probably last disturbed by coppicing between 1920-1940 (pers. comm. Nigel Anderson). Along the transects, 1.12ha were accurately mapped on to scaled charts with the following detail recorded (Backmeroff 1987):

- the location, species and status (as standing alive, leaning alive, fallen alive, crown healthy, crown-dead, or dead) of all trees attaining 1.3m height;
- the girth at breast height 1.3m (gbh) of all living and dead stems attaining 5cm gbh and many below 5cm gbh, measured to the nearest cm using a tape; for rhododendron only the area covered was recorded;
- the orientation of leaning and fallen living stems;
- sketches of the position of fallen dead logs (criteria not specified);
- the location of salient features (eg woodbanks);
- notes on the ground flora composition and photographs of each section.

The transects were surveyed again between 23rd September and 10th October 1996, but the total area recorded was extended to 1.276ha to include all transect sections. The following data was collected:

- the vertical position of canopy gaps as viewed from the ground and notes on their disturbance origin and amount of understorey filling;
- the species and status (as standing alive >1.3m height, fallen alive >1.3m height, standing alive <1.3m height, or dead) of all trees attaining 1.3m height and established seedlings <1.3m height; recruiting stems since 1986 and established seedlings were identified and accurately plotted; complex multi-stemmed stools were individually sketched;
- the girth at breast height 1.3m (gbh) of all living stems attaining 3cm gbh and all dead stems attaining 5cm gbh, measured to the nearest 0.5cm using a tape; for rhododendron only the area covered was recorded;
- for all living stems attaining 1.3m height; (i) a description of their general form; (ii) quantification of crown position based on four stratificatory layers (*canopy* = in uppermost layer and not overtopped, *sub-canopy* = just below and mostly overtopped by the canopy layer, *understorey* = below sub-canopy layer, *ground* = mostly <2m height); (iii) quantification of crown size, relative to the canopy position and potential for the species, based on five categories (*very large, large*, *medium*, *small*, or *very small*); (iv) quantification of the extent of visible crown dieback, defined relative to crown size, and based on five categories (*very severe*, *severe*, *moderate*, *part*, or *none*); (v) a brief description of the extent of any trunk debarking;

- for all living beech stems attaining 1.3m height quantification of grey squirrel stem debarking below and above 2m based on the five-point scale used by Mountford (1997a); *4 = very severe* (ring-barked), *3 = severe* (>50% bark removed), 2 = *moderate* (10-50% bark removed), *1 = limited* (<10% bark removed), and *0 = none* (e.g. 2/3 = moderate damage below 2m/severe damage above 2m)

- for dead standing stems attaining 1.3m height their approximate height and a brief description of their condition

- for fallen dead stems an assessment of their quantity and status using the line transect method of Warren and Olson (1964); 21 line transects, each 20m long, were positioned across the middle of each 30m-long transect section; the diameter or girth (to nearest cm) of fallen dead stems attaining 5cm diameter (where they crossed the line) were measured with a tape, and the degree of rot (as solid, part rotten, rotten or very rotten along the whole stem), amount of residual bark (as percentage on whole stem), and the probable source of origin recorded; in addition all fallen dead logs attaining 1m length and 12.5cm diameter at their largest end were plotted but these were not included in the analysis.

Analysis

The data set provided a large volume of information concerning the fate of over 5700 stems. To facilitate sorting, statistical analyses, and long-term storage, the information was put on a Microsoft Excel spreadsheet.

Most of the data appeared unambiguous and most stems recorded in 1986 were relocated with confidence. However difficulties were associated with large, complex, multi-stemmed and forked stools, especially of hazel, where stem relocation was difficult. Also in some instances recording errors and omissions occurred. In dealing with these errors, small gbh reductions or possible large increases were not adjusted for, but otherwise past-sizes were reconstructed by assuming reasonable change based on the performance of like stems. All assumed changes were omitted from stem growth analyses.

Separate species of birch, oak and willow stems were grouped together for analysis. Stems identified as <5cm gbh in 1986 were scored as 3cm gbh for basal area calculations. The basal area of rhododendron was calculated by assuming each $2m^2$ covered accounted for a single 20cm gbh stem. Annual rates of change were based on 10 growing seasons. Standing dead wood volumes were calculated by assuming stems were cylindrical in shape.

The estimated volume and length of fallen dead wood recorded on the line transects were calculated using the formulae provided by Warren and Olson (1964):

$L = [(\pi \times N)/(2 \times l)] \times 10000$
$V = [(\pi^2/8l) \times \sum(n \times d^2)] \times 10000$
where:-
L = estimated fallen dead wood length ($m\ ha^{-1}$)
N = total number of recorded stems
l = total transect length (m)
V = estimated fallen dead wood volume ($m^3\ ha^{-1}$)
n = number of stems in each diameter class *
d = mid-class diameter (cm) *
* using seven 5cm classes from 5-9.9cm to >60cm

Time and costs

The 1996 field work took 32 person-days with two recorders working together. A further 36 person-days were required to prepare the Excel spreadsheet, carry out analyses, and write and produce the report. Additional costs were for travel, subsistence and measuring equipment.

5. General changes in stand structure and composition

Canopy gaps

In 1996 canopy gaps covered about 12% of the whole transect area (Table 1). Along transect 1 they were infrequent, and only 3 sections attained 10-15% gaps. On transect 2 they were more common; 2 sections attained 10-20% gaps, two attained 20-30%, and two attained 30-40%. Gaps were especially caused by the fall and windblow of birches (see also Table 8) and the loss of oak boughs. Birch windblow was associated with all sections that had >20% gaps. In most instances gaps were filled below by understorey growth and no canopy gaps permitted an extensive influx of light to reach the woodland floor.

Change in basal area of stems alive >1.3m height

The basal area of the transects increased from 32.5 to 36.2m^2 per hectare between 1986-96, giving an average annual increase of about 0.4 m^2 per hectare (Table 2). Oak accounted for over half the total basal area at both dates and had the greatest annual increment rate. Birch and lime were also important, each accounting for about 20% of the total, but birch had a low annual increment rate while lime increased rapidly. The other 15 species each accounted for <5% of the total and only hazel had a notable increment rate.

Change in density of stems alive >1.3m height

Between 1986-96 the density of living stems >1.3m height declined by 14% from about 2765 to 2380 stems per hectare (Table 3). Hazel was the most numerous species, and, although the total number of hazel stems changed little, it increased its dominance from 44 to 52% of all stems. Lime, birch and ash were respectively the most numerous of the other species and all three declined between 1986-96; ash by nearly half, birch by about one-third, and lime by 20%. Oak, although dominating the basal area (Table 2), accounted for only about 2.5% of all stems. Many of the minor species remained at the same density in 1986 and 1996, apart from blackthorn and rhododendron that increased greatly, rose that died out, and holly that recruited its first stem into the stand. Rhododendron areal coverage increased from 42m^2 to 70m^2.

Change in relationship between stem density and gbh

In 1986 and 1996 the size class distribution of all stems standing alive >1.3m height conformed broadly to the negative exponential; i.e. as stem size increased, stem density declined rapidly (Figure 3). However after a smooth decline in numbers to 120cm gbh, the remaining population formed an extended and uneven distribution of trees to >300cm gbh.

Between 1986-96 the change in the relationship between stem density and mean stem gbh for stems alive >1.3m height was examined. Eighteen 600m^2 transect sections were available (transect 1, sections 3-12; transect 2, sections 1-6 and 8-9). Only stems attaining 5cm gbh were included because stems below this threshold were under-recorded in 1986. The changes were compared with those predicted by the -1.5 slope self-thinning rule that relates declining plant density (p) to the mean biomass (w) of surviving plants by the power equation $w = Kp^{-1.5}$ (Yoda *et. al.* 1963; White 1981). Comparison using stem gbh measurements was justified as $w \alpha$ gbh (White 1981).

Table 1: Percentage canopy gaps in each 30m-long (600m^2) transect section in 1996

Transect: section	Gaps %	Transect: section	Gaps %
1.1	8.9	1.12	13.3
1.2	12.0	2.1	17.0
1.3	15.4	2.2	36.3
1.4	5.6	2.3	37.0
1.5	2.2	2.4	4.6
1.6	4.9	2.5	11.4
1.7	1.6	2.6	21.4
1.8	8.2	2.7	21.1
1.9	1.4	2.8	9.3
1.10	7.1	2.9	3.3
1.11	5.8	All	11.8

Table 2: Basal area of all stems alive >1.3m height in 1986 and 1996

Species	1986	1996	Change rate
Major canopy species	**(m^2 ha^{-1})**	**(m^2 ha^{-1})**	**(m^2 ha^{-1} a^{-1})**
Oak	18.24	19.57	0.13
Birch	6.82	6.94	minimal
Lime	5.35	6.54	0.12
Ash	0.27	0.45	minimal
Major underwood species			
Hazel	0.69	1.34	0.07
Hawthorn	0.58	0.56	minimal
Minor species			
Yew	0.12	0.15	minimal
Field maple	0.08	0.10	minimal
Alder	0.07	0.09	minimal
Beech	0.06	0.11	minimal
Rhododendron	0.06	0.10	minimal
Sweet chestnut	0.05	0.16	minimal
Willow	0.05	0.07	minimal
Crab apple	0.05	0.06	minimal
Sycamore	0.01	0.02	minimal
Blackthorn	<0.01	<0.01	minimal
Rose	<0.01	<0.01	minimal
Holly	-	<0.01	minimal
Total	32.51	36.24	0.37

(calculated using all recorded stems standing and fallen alive >1.3m and based on study area of 1.12ha)

Table 3: Density of all stems alive >1.3m height in 1986 and 1996

Species	**1986**	**1996**	**Change rate**	**Change**
Major canopy species	**(n ha^{-1} a^{-1})**	**(n ha^{-1} a^{-1})**	**(n ha^{-1} a^{-1})**	**%**
Lime	504.5	401.8	-10.3	-20
Birch	396.4	263.4	-13.3	-34
Ash	370.5	198.2	-17.2	-47
Oak	67.9	62.5	-0.5	-8
Major underwood species				
Hazel	1229.5	1238.4	0.9	1
Hawthorn	133	141.1	0.8	6
Minor species				
Rhododendron	18.8	31.3	1.3	67
Beech	14.3	10.7	-0.4	-25
Blackthorn	6.3	12.5	0.6	100
Field maple	6.3	6.3	0.0	none
Sweet chestnut	3.6	3.6	0.0	none
Crab apple	2.7	2.7	0.0	none
Sycamore	2.7	2.7	0.0	none
Yew	2.7	2.7	0.0	none
Willow	2.7	1.8	-0.1	-33
Alder	0.9	0.9	0.0	none
Rose	0.9	0.0	-0.1	lost
Holly	0	0.9	0.1	new
Total	2763.4	2381.3	-38.2	-13.8

(calculated using all recorded stems standing and fallen alive >1.3m and based on study area of 1.12ha)

Sections with a high mean stem gbh in 1986 all showed a similar trend; stem density declined logarithmically as mean gbh increased logarithmically and the change slopes fell within the range -0.7 to -1.5 (Figure 4). One section with a low mean gbh value that lay close to the maximum limit set by the -1.5 population slope, showed a similar self-thinning trend. However several sections with low mean gbh values changed differently. Two thinned similarly but their change slopes were -2.4 and -2.6, indicating that thinning had been minimal while the mean basal area increased. In four other sections change was quite different; the slopes ranged from -0.3 to +0.6 and stem density increased between 1986-96. These sections all lay along transect 2 and change was strongly influenced by the recruitment of many small girth hazel and hawthorn stems (Table 5).

Overall the changes compared favourably with those predicted by the -1.5 slope self-thinning rule; approximate -1.5 slope thinning occurs in stands close to the maximum threshold defined by the -1.5 population slope, and in stands below this threshold thinning is reduced and recruitment possible.

Table 4: Number, fate and recruitment of stems alive >1.3m height between 1986-96

	1986		Fate of 1986 stems by 1996				Recruitment 1986-96				
Species	Stems standing alive >1.3m	Stems <20cm gbh in 1996, assumed omitted in 1986	Stems standing alive >1.3m	Stems fallen alive >1.3m	Stems standing alive <1.3m	Stems died	All new stems standing alive >1.3m	New stems standing alive	New stems fallen alive	New trunk shoots or forks	New individuals
Major canopy species											
Lime	564	9	442	6	-	116	-	-	-	-	-
Birch	441	5	292	3	1	145	-	-	-	-	-
Ash	412	7	221	-	24	167	1	1	-	1	-
Oak	76	-	70	-	-	6	-	-	-	-	-
Major underwood species											
Hazel	1365	52	1037	15	15	298	333	329	4	14	58
Hawthorn	146	14	108	2	8	28	45	45	-	-	43
Minor species											
Beech	16	-	12	-	1	3	-	-	-	-	-
Field maple	7	-	7	-	-	-	-	-	-	-	-
Blackthorn	7	-	2	1	-	4	11	10	1	-	11
Sweet chestnut	4	-	4	-	-	-	-	-	-	-	-
Sycamore	3	-	3	-	-	-	-	-	-	-	-
Yew	3	-	3	-	-	-	-	-	-	-	-
Willow	3	-	2	-	-	1	-	-	-	-	-
Crab apple	2	-	2	-	-	-	-	-	-	-	-
Alder	1	-	1	-	-	-	-	-	-	-	-
Rose	1	-	-	-	-	1	-	-	-	-	-
Holly	-	-	-	-	-	-	1	-	1	-	1
Total	**3051**	**87**	**2206**	**27**	**49**	**769**	**391**	**385**	**6**	**15**	**113**

(calculated using all recorded stems and based on study area of 1.12ha; excluding rhododendron)

6. Mortality and recruitment

Fate and recruitment of stems alive >1.3m height

3051 stems were recorded as standing alive >1.3m height in 1986 (Table 4). These included 105 stems, mostly on complex hazel stools, assumed to have been omitted in the 1986 survey (see section 1.7), although only 87 were small enough (<20cm gbh in 1996) to have been possible period recruits. By 1996 one-quarter of the 1986 population had died. Most of the remainder survived standing alive, but a few had fallen alive or had been reduced to alive <1.3m height.

Recruitment from 1986-96 amounted to 391 new stems, a few of which were classified as fallen alive. Only a few recruits were trunk shoots or forks that might have been omitted in 1986. Many new stems were on individuals in existence in 1986, but 113 new individuals established over the decade. Recruiting stems and individuals had similar distribution patterns (Table 5); at the scale of the 30m transect section numbers were significantly rank-correlated ($r_s = 0.934$, $n = 18$, $r_{critical} = 0.728$, $p = 0.0005$). They occurred in only some parts of transect 1, but in all sections of transect 2. Their exclusion from sections 4, 5, 8, 9 & 12 of transect 1 coincided with areas of lime dominance (Figure 6), and their exclusion from sections 10 and 11, with dense bracken-dominated ground vegetation below an oak/ birch canopy (Figures 8 and 12). Recruits tended to be more numerous where more canopy gaps existed; abundance of stem recruits ($r_s = 0.438$, $n = 18$, $r_{critical} = 0.401$, $p = 0.05$) and individual recruits ($r_s = 0.564$, $n = 18$, $r_{critical} = 0.550$, $p = 0.01$) was significantly rank-correlated with number of gaps present in each transect section (Table 1).

Table 5: Number of recruiting stems and individuals (in brackets) between 1986-96 in each 30m-long transect section

Transect: section	Area (m^2)	Hawthorn	Hazel	Holly	Blackthorn	Ash	New stems	New individuals
1.1	300	3 (3)	8 (3)	-	-	-	11	6
1.3	600	-	21 (2)	-	-	-	21	2
1.4	600	-	-	-	-	-	-	-
1.5	600	1 (1)	-	-	-	-	1	1
1.6	600	1 (1)	18 (1)	-	-	-	19	2
1.7	600	-	13 (0)	-	-	-	13	-
1.8	600	-	1 (1)	-	-	-	1	1
1.9	600	-	-	-	-	-	-	-
1.10	600	-	-	-	-	-	-	-
1.11	600	-	-	-	-	-	-	-
1.12	700	-	-	-	-	-	-	-
2.1	600	3 (3)	16 (2)	1 (1)	-	-	20	6
2.2	600	5 (5)	34 (5)	-	9 (9)	1 (0)	49	19
2.3	600	20 (19)	67 (19)	-	2 (2)	-	89	40
2.4	600	2 (1)	29 (7)	-	-	-	31	8
2.5	600	2 (2)	30 (7)	-	-	-	32	9
2.6	600	2 (2)	27 (3)	-	-	-	27	5
2.8	600	2 (2)	27 (3)	-	-	-	29	5
2.9	600	4 (4)	42 (5)	-	-	-	46	9
Totals	12760	45 (43)	333 (58)	1 (1)	11 (11)	1 (0)	391	116

(calculated using all recorded stems and based on study area of 1.12ha; excluding rhododendron)

Turnover and recruitment differed considerably amongst the major canopy species. Over 90% of oak stems survived, while only 78% of lime and 66% of birch remained standing alive. However none of these species made any stem recruitment. Ash had the lowest survival rate at just 54%, and a further 6% were reduced to alive only below 1.3m height. A single ash trunk fork recruited during the decade and a further 7 stems, that were probably omitted in 1986, could have been additional recruits.

The two most numerous underwood species, hazel and hawthorn, had similar living stem survival rates (74-76%). However an additional 5% hawthorn to 1% hazel were reduced to alive below 1.3m height. Recruitment of hazel stems and new individuals was considerable, accounting for 85% of all new stems and 58% of all new individuals. Indeed recruitment could have been greater as 52 stems <20cm gbh in 1996 were counted as probable omissions in 1986. Although hawthorn had less new stems, most were seedling recruits and consequently accounted for nearly 40% of all newly established individuals. Hazel and hawthorn had moderate to high recruitment along transect 2, but were much more patchy on transect 1. Their distributions mimicked that of the whole recruiting population.

Many minor species changed little. However, beech declined by a quarter as 3 of the original 16 stems died and a further was reduced to alive only below 1.3m height. Blackthorn turnover was very high; 4 out the 7 stems present in 1986 died, but 11 new suckers established themselves in sections 2 and 3 of transect 2. The single holly recruit was grazed by deer and pinned to the ground by fallen oak crown debris.

Fate and recruitment of individuals alive <1.3m height

Table 6: Number of individuals alive <1.3m height in 1996 and those alive >1.3m height in 1986

Species	Individuals alive <1.3m in 1996*	Of which alive >1.3m in 1986 **
Hawthorn	720	9
Hazel	248	15
Holly	194	0
Blackthorn	91	0
Ash	72	24
Hornbeam	21	0
Rose	13	0
Beech	6	3
Field maple	1	0
Sycamore	1	0
Yew	1	0
Total	1368	51

(based on transect area of 1.276ha and 1.12ha **)*

Established seedlings and individuals reduced (i.e. alive >1.3m height in 1986) to alive <1.3m height were recorded in 1996 (Table 6). However, because the 1996 survey included an additional 0.156ha not mapped in 1986, it was not possible to identify all individuals that had been reduced from alive >1.3m height. Nevertheless this probably did not significantly effect the results; in the 1.12ha recorded at both dates only 51 of the 889 individuals had been reduced in this way.

Of the individuals recorded in 1996, only about 3% had been reduced from individuals alive >1.3m height in 1986; these were mainly ashes, hazels and hawthorns. The balance were recently established seedlings, apart from 2 hazels that had formed by layering, and they occurred at an average density of 1031 ha^{-1}. Although 11 species were represented, hawthorn was by far the most abundant, whilst hazel, holly, blackthorn and ash were moderately abundant. Hornbeam, which was not represented as an established tree, did occur as a seedling recruit. Many seedlings were deer browsed, although this was not quantified.

Seedlings were not evenly distributed along the transects (Table 7); high densities occurred at the start of transect 1, moderate densities along much of transect 2, and low densities along the rest of transect 1. The latter coincided with the areas where either lime dominated (Figure 6) or where dense bracken stands dominated below a canopy of oak and birch (Figures 8 and 12). The number of seedlings in each section was strongly rank-correlated with the number of recruiting stems ($r_s = 0.759$, $n = 19$, $r_{critical} = 0.712$, $p = 0.0005$) and individuals ($r_s = 0.924$, $n = 19$, $r_{critical} = 0.712$, $p = 0.0005$) (Table 5). In addition seedlings tended to be more numerous in those areas with most canopy gaps ($r_s = 0.446$, $n = 21$, $r_{critical} = 0.435$, $p = 0.025$). Where seedling densities were high or moderate the typical composition included many hawthorns, some hazels, some hollies, and sometimes a few ash or a dense patch of blackthorn. Where densities were low, holly was most abundant, whilst hawthorn and hazel were occasional. Hornbeam was numerous only at the start of transect 1.

Table 7: Number of established seedlings in 1996 in each transect section

Transect: section	Area (m^2)	Hawthorn	Hazel	Holly	Blackthorn	Ash	Hornbeam	Other	Total
1.1	600	89	53	6	-	17	6	12	183
1.2	600	83	20	36	43	5	13	-	200
1.3	600	12	5	19	-	-	1	-	37
1.4	600	-	-	34	-	-	-	-	34
1.5	600	3	3	11	-	-	-	-	17
1.6	600	4	-	1	-	2	-	-	7
1.7	600	1	3	2	-	-	-	-	6
1.8	600	1	-	4	-	-	-	1	6
1.9	600	-	-	1	-	-	-	-	1
1.1	600	-	-	1	-	-	-	-	1
1.11	600	-	-	3	-	-	-	-	3
1.12	700	-	-	2	-	-	-	-	2
2.1	600	48	10	6	-	11	-	-	75
2.2	600	34	10	4	19	2	1	-	70
2.3	600	54	14	5	28	-	-	-	101
2.4	600	62	19	13	-	2	-	-	96
2.5	600	33	12	5	1	2	-	1	54
2.6	600	43	7	6	-	4	-	-	60
2.7	600	116	25	12	-	1	-	2	156
2.8	600	69	26	13	-	-	-	1	109
2.9	600	59	26	10	-	1	-	2	98
2.10	60	1	2	-	-	1	-	-	4
Totals	**12760**	**711**	**233**	**194**	**91**	**48**	**21**	**119**	**1317**

Distribution patterns and fate of stems for major canopy species

Lime

In 1986 a large number of lime stems standing alive >1.3m height were recorded. They were sized up to 100cm gbh and conformed to a right-skewed normal distribution (Figure 5). Lime stems occurred only along transect 1 and on only 89 separate individuals (Figure 6); 66 were multi-stemmed coppice stools, 25 of which had at least 10 living stems present, and one had 29 living stems. In several cases the coppice stools were so closely aggregated that it was difficult to identify just how many separate individuals existed; close coppice individuals were perhaps fragments of very old individuals. 18 of the individuals were single- or twin-stemmed probable seedling recruits. These mostly located on the margins of the existing distribution. Within the areas where lime stools predominated only canopy oaks co-existed (Figure 12) and there was no hazel underwood (Figure 14).

Lime mortality between 1986-96 was moderate (Table 4), restricted to stems <50cm gbh, and as stem size decreased, proportional mortality rose rapidly (Figure 6). Stem loss mainly thinned out multi-stemmed individuals; although 117 living stems died only 4 individuals were lost, and the percentage of single-stemmed individuals rose by 8% to 34%. Virtually all of the mortality was accredited to competitive exclusion, but a few stems may have been blown over. Most (69%) stems that died had fallen over by 1996, and proportionally more of the larger stems remained standing.

Birch

In 1986 birch was represented by a large stem population spread across almost all size-classes up to 170cm gbh (Figure 7). Very few stems were below 10cm gbh or above 140cm gbh and collectively they formed a right-skewed normal distribution. 92% were single-stemmed trees, the remainder being multi-stemmed individuals with up to three stems present.

Birches were not equally distributed along the transects (Figure 8). They occurred most abundantly along parts of transect 1, mainly in the form of dense, aggregated, mixed-sized groups. Exclusion from substantial parts of the transect coincided with the dominance of large lime stools (Figure 6), but elsewhere mainly coincided with large canopy oaks (Figure 12). Along transect 2 birch was only abundant from 10-50m and 70-80m, where it formed two fairly dense, mixed-sized groups; elsewhere it was very local. Exclusion from much of this transect coincided with a profusion of canopy oaks and underwood hazels.

Birch mortality between 1986-96 was high (Table 4), concentrated in the smaller size-classes, and proportional loss increased greatly as stem size decreased (Figure 7). Loss was more-or-less equally divided amongst single- and multi-stemmed individuals. The general effect on the ground was a thinning of existing dense birch groups. Most (72%) of the stems that died had fallen over by 1996, but proportionally more of the larger stems that died remained standing.

Table 8: Individual records of windblow damage to birch between 1986-96

Stem sizes (gbh cm in 1986)	Fate
102, 72, 72, 68, 67, 66, 59, 54, 49, 44, 42, 39, 38	Died 1986-96; recorded as windblown, fallen or snapped off and dead in 1996
40, 40	Died 1986-96; recorded as windblown, hung-up and dead in 1996
59, 59, 25	Died 1986-96; recorded as windblown, leaning and root plate lifted in 1986
64, 31	Died before 1986; recorded windblown, dead and fallen in 1986
60, 38, 35	Alive in 1996; recorded as windblown, fallen and alive in 1996
137, 73	Alive in 1996; recorded as windblown, leaning and root plate lifted in 1996
89, 86, 62, 59, 53	Alive in 1996; recorded as having major crown loss due to windblow

Most mortality, especially amongst the smaller stems, was accredited to competitive exclusion. However windblow, especially of larger stems, was important (Table 8); 18 of the stems that died between 1986-96 were windblown, and these accounted for half of all stems >40cm gbh that died. In addition, most of the stems in 1996 that had fallen but remained alive were windblown, and four medium-large stems that remained alive had major portions of their crowns blown out. Windblow also damaged the birch population before 1986; a few of the fallen birch, including some that remained alive, were mapped as windblown, and three of the windblown stems that died between 1986-96 had their root plates lifted by windblow before 1986. Windblow especially effected birches from 265-280m and 325-340m along transect 1, and 20-50m, 70-80m and 170-180m along transect 2.

Ash

Nearly all recorded ash stems standing alive >1.3m height in 1986 were <30cm gbh, and 78% were smaller than 10cm gbh (Figure 9). Only 19 of the 400 individuals were twin-stemmed, and virtually all appeared to be of seedling origin.

Ash formed a very dense group at the start of transect 2 (Figure 10). This area differed greatly from the rest of the transects; it was a wet headwater swamp with much canopy birch, some oak, and little understorey hazel and willow (Figures 8, 12, and 14). Several birches here were toppled or suffered crown damage by windblow before 1986 or through to 1996. The ashes were mainly small seedling stems, interspersed with a few rapidly developing poles, but a larger ash sized 51cm gbh also occurred. Few ashes existed elsewhere along the transects; many were small, suppressed, understorey saplings, but some, especially a group at the start of transect 1, included some rapidly developing poles.

Ash mortality was relatively high between 1986-96 (Table 4). No trees larger than 20cm gbh died and 96% of deaths were stems below 10cm gbh (Figure 9). All of the stems reduced to alive only below 1.3m in 1996 were failing saplings. Mortality and reduction of stems was accredited to competitive exclusion, although a few stems were knocked over by falling trees or canopy debris. Nearly all (95%) stems that died had fallen over by 1996.

Oak

The 1986 oak population had far fewer stems than the other main species, but ranged from 40-344cm gbh with most stems sized 140-240cm gbh (Figure 11). Oaks were generally scattered along both transects and all were single stemmed trees. They were especially abundant from 30m onwards on transect 2, where they occurred as a scatter of mixed-sized trees (Figure 12). Although there were fewer oaks on the second half of transect 1, these were all >200cm gbh. Oak was consequently interspersed within the distributions of all the main species (Figures 6, 8, 10, 14 and 16). They appeared to be mostly retained standards at the last coppicing, but undoubtedly represented a wide range of ages. Some of the smaller oaks <100cm gbh could have been recruits since the last coppicing. The cluster at 65-70m along transect 1, which occurred with several large birches, may represent an even-aged cohort.

Oak mortality between 1986-96 was restricted to 6 smaller-sized trees; all were <140cm gbh and most were between 60-79cm gbh (Figure 11). The deaths were accredited to competitive exclusion, apart from one of the larger trees located at the start of transect 2 that failed standing in full sunlight. Half of the trees that died remained standing in 1996.

Hazel

Hazel stems standing alive >1.3m height were very abundant in 1986. However the largest stem was only 26cm gbh and 60% were <7.5cm gbh; the population generally conformed to a negative exponential distribution (Figure 13). 73% of the 357 individuals were multi-stemmed and one very large stool had 31 living stems present. However this was the exception; only 4% of individuals had 10 or more living stems, and 10% had only a single living stem <10cm gbh. Hazels were especially numerous along most of transect 2 (Figure 14), but were patchily distributed on transect 1. Their exclusion on the latter was mostly coincident with areas where lime stools predominated (Figure 6), although from 280-340m the canopy was mixed oak and birch and the ground vegetation was dominated by dense bracken (Figures 8 and 12).

Between 1986-96 hazel mortality was moderate (Table 4), but stems died in virtually every size class and proportional mortality was greatest in the very largest and very smallest size-classes (Figure 13). Nevertheless most stems that died were <7.5cm gbh. A few remained alive on the ground or only at the stem base; the later were nearly all <5cm gbh. Stem loss mainly resulted in the thinning of multi-stemmed individuals; although 824 living stems failed only 37 individuals were lost. Most mortality was accredited to competitive exclusion, but some was caused by strikes from falling canopy debris and windblown trees. Just over three-quarters of stems that died had fallen over by 1996, and proportional collapse was particularly high for stems <5cm gbh.

Hawthorn

In 1986 hawthorn stems standing alive >1.3m height were far less numerous than hazel (Table 4). 101 individuals were recorded and most (74%) were single-stemmed. No very large stools existed and 6 was the maximum number of living stems on any individual. Very few stems were >50cm gbh and most of the remainder were sub-equally divided amongst the smallest three 10cm gbh classes (Figure 15). Hawthorns were not abundant on transect 1; there was a single large-stemmed group from 60-70m along and a scatter of small suppressed stems from 150-225m (Figure 16). Along transect 2 it was quite numerous, with stems of all sizes interspersed with understorey hazels, but it was absent from the headwater swamp near the transect start.

Stem mortality was limited (Table 4) and included stems of all sizes, although most were <30cm gbh (Figure 15). Many (60%) stem failures resulted in the complete loss of an individual. A few stems remained alive on the ground and some very small stems were reduced to alive <1.3m height. Mortality was accredited mainly to competitive exclusion, but some stems were knocked over by falling trees or boughs. 69% of stems that died had fallen over by 1996, and only stems <30cm gbh remained standing.

7. Growth

Growth of major canopy species

Table 9: Statistics showing the most significant regressions of stem gbh change rate (cm a^{-1}) on initial gbh size (cm) and the mean gbh change rate between 1986-96 for major canopy species

Species	Regression equation	n	F	p	r^2	mean
Lime	$y = 0.0224x - 0.3743$	445	352.4	<0.0001	0.443	0.433
Birch	$y = -0.0001x^2 + 0.0208x - 0.2475$	290	63.6	<0.0001	0.307	0.431
Ash*	$y = 0.0730x - 0.2271$	210	155.0	<0.0001	0.427	0.437
Oak	$y = 0.0018x + 0.5408$	76	2.3	0.13	0.030	0.857

*(calculated using all available stems standing alive >1.3m in 1986 and 1996; *excludes the two largest girth stems)*

For the four major canopy species, growth of stems between 1986-96 standing alive >1.3m height was examined. For each the most significant (p_{min} 0.05) linear or quadratic regression of gbh change rate per annum (cm a^{-1}) on initial size (cm), and the mean gbh change rates were determined (Table 9).

Lime

Highest lime growth rates were attained by larger girth stems, and although there was some variation, progressively smaller stems tended to grow more slowly (Figure 17). This was confirmed by the regression analysis; the most significant regression was the linear relationship that accounted for 44% of the total variation (Table 9). There was a clear influence of canopy position and crown size on stem growth (Figure 17; Table 10); typically the most rapidly growing stems were in the uppermost canopy layer with medium or small crowns, whilst stems in progressively lower strata and with smaller crown sizes tended to grow more slowly. However there was considerable variation between stems of similar status, and overlap between the smallest crowns in the upper strata and largest crown sizes in the lower strata when comparing adjacent layers. The mean growth rates of lime stems in various canopy and crown size categories were compared using ANOVA (Table 11). The results supported the apparent patterns.

Birch

The fastest growing birches were medium girth stems (50-105cm gbh); progressively smaller and the largest sized stems grew much more slowly (Figure 18). Regression analysis confirmed the relationship; the most significant regression was the quadratic relationship, accounting for 31% of the total variation ($r^2 = 0.31$) (Table 9). For stems of up to 50cm gbh the position of this line was similar to the lime regression line, but thereafter the birch line tailed off. Nevertheless, both species had similar mean increment rates (ANOVA F <0.1, p = 0.96). Birch stem growth appeared to be partly related to canopy position and crown size (Figure 18; Table 12). The most rapidly growing stems were in the uppermost canopy layer and growth rates decreased progressively down through the strata. Within strata layers crown size and growth were generally positively related, except for in the canopy layer where the largest girth stems with large crowns grew little. Within these patterns there was much variation between similar status stems, and considerable overlap between the smallest crowns above and largest crowns below when comparing adjacent strata. The mean growth rates of stems in various canopy and crown size categories were compared using ANOVA (Table 13) and the results supported the apparent trends.

Ash

The two larger girth ash canopy stems grew quite slowly. The remaining small-girth cohort ranged from rapid to very slow growing according to their girth, canopy position and crown size (Figure 19; Table 14). The fastest growing stems included most of the larger girth sub-canopy poles, and the regression analyses (which excluded the two extra-ordinarily large stems) found the linear regression was most significant and accounted for 43% of the total variation (Table 9). Declining growth rates coincided with progressive movement down through the strata and decreasing crown size. ANOVA testing showed that the differences between the mean growth rates of the various canopy and crown size categories were all significantly different (Table 15). The average growth of ash was not significantly different from that of lime and birch (ANOVA $F_{lime}<0.1$, $p = 0.93$, $F_{birch}<0.1$, $p = 0.89$).

Oak

Oak growth was very variable and only partly related to stem girth, crown size and canopy position (Figure 20; Table 16). Within the mid-size range (120-250cm gbh) growth rates were extremely variable and many trees in the canopy layer with medium to very large crowns grew slowly. However the fastest growing oaks were medium to very large crowned, canopy trees, sized 175-240cm gbh, and the slowest included the smallest girth trees, the very largest girth tree, most of the sub-canopy, understorey, and small crowned canopy trees. Neither the linear or quadratic regressions were significant (Table 9), and ANOVA testing found no significance difference ($p<0.05$) between various crown size and canopy position categories (Table 17). Although oak growth rates were extremely variable, unlike lime, birch and ash, very few stems grew at extremely low rates and the mean growth of oak was significantly greater than all of these species (ANOVA $F_{lime} = 34.6$, $F_{birch} = 43.0$, $F_{ash} = 50.0$, $p<0.001$).

Table 10: Mean gbh change rate (cm a^{-1}) for lime stems between 1986-96 shown according to various canopy and crown size categories in 1996

Stem canopy position; crown size	Number of stems	Mean change rate (cm a^{-1})
Canopy; medium	15	1.783
Canopy; small	67	1.248
Sub-canopy; medium	16	0.784
Canopy; very small	23	0.633
Sub-canopy; small	49	0.407
Understorey; medium or greater	50	0.406
Sub-canopy; very small	26	0.077
Understorey; small	131	0.072
Understorey; very small	36	0.064
Ground; all	32	0.042

(calculated using all recorded stems standing alive >1.3m in 1986 and 1996)

Table 11: Significance of ANOVA comparisons between mean gbh change rates (cm a^{-1}) from 1986-96 for lime stems in various canopy and crown size categories in 1996

Canopy position		**Ground**	**Understorey**	**Understorey**	**Sub-canopy**	**Understorey**	**Sub-canopy**	**Canopy**	**Sub-canopy**	**Canopy**
	Crown size	**All**	**Very small**	**Small**	**Very small**	**Medium or greater**	**Small**	**Very small**	**Medium**	**Small**
Canopy	Medium	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
Canopy	Small	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*0.001*	-
Sub-canopy	Medium	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*0.005*	*0.004*	0.203	-	-
Canopy	Very small	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*0.034*	*0.031*	-	-	-
Sub-canopy	Small	*<0.001*	*<0.001*	*<0.001*	*<0.001*	0.990	-	-	-	-
Understorey	Medium or greater	*<0.001*	*<0.001*	*<0.001*	*<0.001*	-	-	-	-	-
Sub-canopy	Very small	0.186	0.600	0.894	-	-	-	-	-	-
Understorey	Small	0.352	0.786	-	-	-	-	-	-	-
Understorey	Very small	0.324	-	-	-	-	-	-	-	-

(numbers are probability values for significance of difference between categories; those in italics are significant at $p<0.05$)

Table 12: Mean gbh change rate (cm a^{-1}) for birch stems between 1986-96 shown according to various canopy and crown size categories in 1996

Stem canopy position; crown size	Number of stems	Mean change rate (cm a^{-1})
Canopy; medium or large	24	1.094
Canopy; small	74	0.808
Canopy; very small	31	0.350
Understorey; medium or large	20	0.318
Sub-canopy; small or medium	45	0.247
Sub-canopy; very small	8	0.194
Understorey; small	73	0.109
Understorey; very small	11	0.091

(calculated using all recorded stems standing alive >1.3m in 1986 and 1996)

Table 13: Significance of ANOVA comparisons between mean gbh change rates (cm a^{-1}) from 1986-96 for birch stems in various canopy and crown size categories in 1996

Canopy position		**Under-storey**	**Under-storey**	**Sub-canopy**	**Sub-canopy**	**Under-storey**	**Canopy**	**Canopy**
	Crown size	**Very small**	**Small**	**Very small**	**Medium or small**	**Medium or large**	**Very small**	**Small**
Canopy	Medium or large	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*0.027*
Canopy	Small	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	-
Canopy	Very small	*0.002*	*<0.001*	0.120	0.126	0.635	-	-
Understorey	Medium or large	*0.002*	*<0.001*	0.165	0.349	-	-	-
Sub-canopy	Medium or small	0.102	*0.001*	0.641	-	-		-
Sub-canopy	Very small	0.165	0.143	-	-	-	-	-
Understorey	Small	0.695	-	-	-	-	-	-

(numbers are probability values for significance of difference between categories; those in italics are significant at $p<0.05$)

Table 14: Mean gbh change rate (cm a^{-1}) for ash stems between 1986-96 shown according to various canopy and crown size categories in 1996

Stem canopy position; crown size	Number of stems	Mean change rate (cm a^{-1})
Sub-canopy; small	11	1.377
Sub-canopy; very small	12	0.875
Understorey; small	118	0.462
Understorey; very small	54	0.151
Ground; all	12	0.05

(calculated using all recorded stems standing alive >1.3m in 1986 and 1996)

Table 15: Significance of ANOVA comparisons between mean gbh change rates (cm a^{-1}) from 1986-96 for ash stems in various canopy and crown size categories in 1996

Canopy position		Ground	Under-storey	Under-storey	Sub-canopy
	Crown size	All	Very small	Small	Very small
Sub-canopy	Small	*<0.001*	*<0.001*	*<0.001*	*0.011*
Sub-canopy	Very small	*<0.001*	*<0.001*	*<0.001*	-
Understorey	Small	*<0.001*	*<0.001*	-	-
Understorey	Very small	*0.002*	-	-	-

(numbers are probability values for significance of difference between categories; those in italics are significant at p<0.05)

Table 16: Mean gbh change rate (cm a^{-1}) for oak stems between 1986-96 shown according to various canopy and crown size categories in 1996

Stem canopy position; crown size	Number of stems	Mean change rate (cm a^{-1})
Canopy; very large	9	1.172
Canopy; large	28	0.923
Canopy; medium	29	0.803
Sub-canopy or understorey; all	5	0.590
Canopy; small	5	0.5

(calculated using all recorded stems standing alive >1.3m in 1986 and 1996)

Table 17: Significance of ANOVA comparisons between mean gbh change rates (cm a^{-1}) from 1986-96 for oak stems in various canopy and crown size categories in 1996

Canopy position		Sub-canopy or under-storey	Canopy	Canopy	Canopy
	Crown size	All	Small	Medium	Large
Canopy	Very large	0.127	0.062	0.104	0.260
Canopy	Large	0.189	0.084	0.395	-
Canopy	Medium	0.409	0.223	-	-
Canopy	Small	0.691	-	-	-

(numbers are probability values for significance of difference between categories)

Growth of major underwood species

Table 18: Statistics showing the most significant regressions of stem gbh change rate (cm a^{-1}) on initial gbh size (cm) and the mean gbh change rate between 1986-96 for hazel and hawthorn

Species	Hazel	Hawthorn
regression equation	$y = -0.0098x + 0.4965$	$y = -0.0033x + 0.3139$
number of stems	770	75
F statistic	12.7	3.0
probability	0.0004	0.090
r^2 statistic	0.016	0.040
mean	0.406	0.231

(calculated using all available stems standing alive >1.3m in 1986 and 1996)

Hazel and hawthorn growth between 1986-96 was examined. For stems standing alive >1.3m height in 1986 and 1996, the most significant (p_{min} 0.05) linear or quadratic regression of gbh change rate per annum (cm a^{-1}) on initial size (cm) and the mean gbh change rates were determined (Table 18).

Hazel

Hazel stem growth was not strongly related to girth; the linear regression was significant, but accounted for very little of the variation and the line slope was not significantly different from zero ($p = 0.05$). Canopy position did not appear to influence growth as much as crown size (Table 19). ANOVA testing of the mean stem growth rates in various canopy and crown size categories (Table 20) confirmed this; highest mean rates were recorded in large crowned ground layer stems and medium crowned understorey stems, while lowest rates were recorded in very small crowned ground and understorey stems. Average growth of hazel was not significantly different from that of lime, birch and ash (ANOVA $F = 0.6$, $p = 0.63$), but was significantly greater than hawthorn (ANOVA $F = 24.4$, $p < 0.0001$).

Hawthorn

Hawthorn stem growth was not strongly related to girth, crown size or canopy position. The linear regression was significant, but accounted for very little of the variation, and the line slope did not significantly differ from zero ($p = 0.05$) (Table 18). No significant differences were found between the mean growth rates of stems in various canopy and crown size categories (Tables 21 and 22).

Table 19: Mean gbh change rate (cm a^{-1}) for hazel stems between 1986-96 shown according to various canopy and crown size categories in 1996

Stem canopy position; crown size	Number of stems	Mean change rate (cm a^{-1})
Ground; large	15	0.683
Understorey; medium	98	0.659
Understorey; small	443	0.403
Ground; medium	41	0.361
Ground; small	66	0.250
Ground; very small	21	0.145
Understorey; very small	20	0.12

(calculated using all recorded stems standing alive >1.3m in 1986 and 1996)

Table 20: Significance of ANOVA comparisons between mean gbh change rates (cm a^{-1}) from 1986-96 for hazel stems in various canopy and crown size categories in 1996

Canopy position		Under-storey	Ground	Ground	Ground	Under-storey	Under-storey
	Crown size	Very small	Very small	Small	Medium	Small	Medium
Ground	Large	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	0.818
Understorey	Medium	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	-
Understorey	Small	*<0.001*	*<0.001*	*<0.001*	0.324	-	-
Ground	Medium	*<0.001*	*<0.001*	*0.013*	-	-	-
Ground	Small	*0.009*	*0.035*	-	-	-	-
Ground	Very small	0.579	-	-	-	-	-

(numbers are probability values for significance of difference between categories; those in italics are significant at p<0.05)

Table 21: Mean gbh change rate (cm a^{-1}) for hawthorn stems between 1986-96 shown according to various canopy and crown size categories in 1996

Stem canopy position; crown size	Number of stems	Mean change rate (cm a^{-1})
Ground; small or medium	13	0.277
Understorey; medium	21	0.257
Understorey; small or very small	34	0.222

(calculated using all recorded stems standing alive >1.3m in 1986 and 1996)

Table 22: Significance of ANOVA comparisons between mean gbh change rates (cm a^{-1}) from 1986-96 for hawthorn stems in various canopy and crown size categories in 1996

Canopy position		**Understorey**	**Understorey**
	Crown size	**Small or very small**	**Medium**
Ground	Medium or small	0.455	0.767
Understorey	Medium	0.530	-

(numbers are probability values for significance of difference between categories; those in italics are significant at $p<0.05$)

8. Stratification

Canopy position, crown size, stature, and dieback of major species.

The status of stems alive >1.3m height in 1996 was qualified by recording their canopy position, crown size, stature, and the extent of visible dieback.

Table 23: Crown position of stems alive >1.3m height for all major species in 1996

Species	Canopy	Sub-canopy	Understorey	Ground
Birch	154	63	142	7
Lime	109	94	240	43
Oak	83	5	1	-
Ash	3	24	187	14
Hazel	-	-	1104	492
Hawthorn	-	1	89	90
Others	3	10	32	14
Total	**352**	**197**	**1795**	**660**

(calculated using all available stems alive)

Lime

Lime was a major canopy species accounting for 31% of all stems (Table 23). Most canopy limes were erect, many appeared vigorous, and crown dieback was very limited, although the modal crown size was small (Tables 24 and 25). They included most of the stems >50cm gbh, and as gbh increased so did crown size (Figure 21).

Most lime stems (78%) were in lower strata. They were especially abundant in the sub-canopy, accounting for 48% of all stems. These stems were mainly erect, small-crowned, over-topped stems, few of which remained vigorous. Girth range was smaller and crown dieback more widespread than in the canopy layer, the latter mostly effecting the smallest girth stems that had the smallest crowns.

Nearly 60% of lime stems existed in the understorey and ground layers, collectively ranking second to hazel. These lower strata stems included most of the smallest limes <40cm gbh. Only a moderate number of erect stems persisted in the understorey, some having medium-sized crowns with little dieback. Most were arched, leaning, or spreading, and all the lateral, fallen, pinned, and snapped stems were found in these layers. Crown dieback was relatively widespread, especially in the ground layer, and again stems with smaller girths and crown stems were effected most.

Birch

Birch was the most numerous canopy species accounting for 44% of all stems in this layer (Table 18). Most of these were erect, small crowned stems, sized 40-130cm gbh, with little dieback; some appeared to be quite vigorous (Tables 26 and 27; Figure 22). Crown size was generally positively correlated with increasing girth, but some larger trees still had quite small crowns. Dieback mainly effected those stems with smaller crowns, which correspondingly had small girths.

Many birches (58%) occurred in lower strata. In the sub-canopy they accounted for 32% of all stems. They were mostly far smaller in girth and proportionally suffered more dieback than canopy stems. Only about half were erect over-topped stems, very few of which remained vigorous. The rest were arched, leaning, or spreading stems, except two that had had their tops snapped out.

Nearly 40% of birches were in the understorey. Most were 10-30cm gbh, somewhat smaller than sub-canopy stems. Just over half were classed as erect and most of the others were arched, leaning, spreading, or squat. A few had their tops snapped out and a single large crowned tree, with a largely dead crown, had fallen into this layer. Crown dieback was relatively widespread; 35% of stems had at least moderate dieback, some were clearly failing, and progressively smaller crowned stems suffered more dieback. Only seven birches survived in the ground layer. Four were <20cm gbh and the three larger girth were all fallen windblown trees. Virtually all stems had at least moderate dieback.

Ash

Only the three largest girth ash stems reached into the canopy layer, and only the very largest had a sizeable crown (Table 28; Figure 23). The sub-canopy layer also contained few ashes. These were sized between 10-40cm gbh and included many of the 20-40cm gbh ashes. Most were healthy (Table 29), erect, small or very small crowned stems, and some were vigorously extending poles.

Over 80% of ashes were in the understorey layer and nearly all fell into the 0-20cm gbh classes. The smallest girth stems were mainly a mixture of erect, arched, leaning and spreading stems, mostly with very small crowns, several of which were visibly dying back. The larger girth stems were mostly erect stems with healthy small crowns. The few ground layer ashes were nearly all <10cm gbh and most had very small crowns. Half were arched, leaning, or spreading, and most were dying back.

Oak

Most oaks were in the canopy layer and, although they only accounted for only 24% of all canopy stems, many had very large or large healthy crowns (Tables 18, 30 and 31; Figure 24). There was a clear relationship between crown size, dieback, and girth; smaller girth trees tended to have smaller crowns with more dieback than larger girth ones. Only a few oaks persisted in the sub-canopy and understorey. Most were small girth trees with medium or small crowns, a couple of which had notable dieback.

Hazel

Hazel dominated the understorey and ground layers; 62% of all understorey and 75% of all ground layer stems were hazel (Table 23). Those in the understorey tended to be larger; nearly all >20cm gbh stems were in the understorey and the modal classes were 10-15cm gbh in the understorey and 5-10cm gbh in the ground layer (Figure 25). In both layers, as girth decreased crown size tended to become smaller, and progressively smaller crowns had more dieback (Tables 32 and 33). In addition the overall incidence of dieback was much higher in the ground layer.

About half the understorey stems were classed as erect, and 73% of these were considered to be vigorous. Most others were classed as arched, leaning, spreading or squat, but only 26% of these were considered to be vigorous. As crown size increased, proportionally less stems were classified as erect, and proportionally less as vigorous. In the ground layer far less (25%) stems were erect, and most (60%) were arched, leaning, spreading or squat. Again larger crowned stems tended to be non-erect and less vigorous. Most of the lateral, fallen, and pinned stems were in the ground layer.

Hawthorn

Apart from a single large girth sub-canopy stem, hawthorn stems were nearly equally divided between the understorey and ground layers (Table 18; Figure 26). Here they respectively accounted for only 5% and 14% of all stems.

Stems from all size classes were represented in the understorey, but most larger girth stems were here. Many were erect, small or medium crowned stems with limited dieback (Tables 34 and 35), and crown size and girth were generally positively correlated. Moderate dieback mainly effected smaller crowned stems and several very small crowned stems had severe dieback.

Nearly all ground layer stems were <30cm and most of these were <10cm gbh. The latter included most of the recruiting seedlings between 1986-96 and the few sized 40-50cm gbh which had fallen over. Many stems were erect with small or very small crowns, and nearly all the lateral, fallen, or pinned stems remained in this layer. Girth and crown size were quite strongly correlated here, but dieback to medium crowned stems was greatest.

Table 24: Canopy position, crown size, and stature of lime stems alive >1.3m height in 1996

		Stature						
Canopy position	**Crown size**	**Erect & vigorous**	**Erect**	**Arched, leaning, spreading, & vigorous**	**Arched, leaning, spreading**	**Snapped**	**Lateral, fallen, pinned**	**Totals**
Canopy	Medium	12	2	2	-	-	-	16
	Small	43	11	6	9	-	-	69
	Very small	5	11	1	7	-	-	24
						-		
Sub-canopy	Medium	4	6	-	6	-	-	16
	Small	7	37	-	7	-	-	51
	Very small	-	21	-	6	-	-	27
Understorey	Large	-	-	1	1	-	1	3
	Medium	-	11	-	36	1	2	50
	Small	-	51	-	89	2	6	148
	Very small	-	14	-	20	5	-	39
Ground	Medium	-	-	-	3	-	3	6
	Small	-	1	-	17	-	5	23
	Very small	-	-	-	6	4	4	14
Totals		71	165	10	207	12	21	486

(calculated using all available stems)

Table 25: Canopy position, crown size, and dieback of lime stems alive >1.3m height in 1996

Canopy position	Crown size	None/part dieback	Moderate dieback	Severe dieback	Very severe dieback	Totals
Canopy	Medium	16	-	-	-	16
	Small	69	-	-	-	69
	Very small	22	2	-	-	24
Sub-canopy	Medium	16	-	-	-	16
	Small	47	4	-	-	51
	Very small	15	9	2	1	27
Understorey	Large	2	-	-	-	2
	Medium	48	2	-	-	50
	Small	109	33	6	-	148
	Very small	2	16	5	16	39
Ground	Medium	4	2	-	-	6
	Small	13	8	2	-	23
	Very small	3	1	1	9	14
Totals		366	77	16	26	485

(calculated using all available stems)

Table 26: Canopy position, crown size, and stature of birch stems alive >1.3m height in 1996

Canopy position	Crown size	Stature							Totals
		Erect & vigorous	Erect	Arched, leaning, spreading, & vigorous	Arched, leaning, spreading	Squat	Snapped	Lateral, fallen, pinned	
Canopy	Large	-	1	-	-	-	-	-	1
	Medium	8	13	1	2	-	-	-	24
	Small	27	43	4	17	-	-	-	91
	Very small	3	23	-	12	-	-	-	38
							-		
Sub-canopy	Medium	-	3	-	2	-	-	-	5
	Small	2	24	-	21	-	1	-	48
	Very small	-	4	-	5	-	1	-	10
Under-storey	Large	-	-	-	-	-	-	1	1
	Medium	-	11	-	10	1	1	-	23
	Small	-	57	-	41	3	4	-	105
	Very small	-	8	-	5	-	-	-	13
Ground	Large	-	-	-	-	-	-	1	1
	Medium	-	-	-	-	-	-	1	1
	Small	-	-	-	3	-	-	-	3
	Very small	-	-	-	1	-	-	1	2
Totals		40	187	5	119	4	7	4	366

(calculated using all available stems)

Table 27: Canopy position, crown size, and dieback of birch stems alive >1.3m height in 1996

Canopy position	Crown size	None/part dieback	Moderate dieback	Severe dieback	Very severe dieback	Totals
Canopy	Large	1	-	-	-	1
	Medium	24	-	-	-	24
	Small	85	5	1	-	91
	Very small	32	2	2	2	38
Sub-canopy	Medium	4	1	-	-	5
	Small	41	6	1	-	48
	Very small	6	1	3	-	10
Under-storey	Large	-	-	1	-	1
	Medium	21	1	1	-	23
	Small	69	30	5	1	105
	Very small	3	-	1	9	13
Ground	Large	-	1	-	-	1
	Medium	-	1	-	-	1
	Small	1	2	-	-	3
	Very small	-	1	-	1	2
Totals		287	51	15	13	366

(calculated using all available stems)

Table 28: Canopy position, crown size, and stature of ash stems alive >1.3m height in 1996

Canopy position	Crown size	Stature					Totals
		Erect & vigorous	Erect	Arched, leaning, spreading, & vigorous	Arched, leaning, spreading	Lateral, fallen, pinned	
Canopy	Medium	-	-	-	1	-	1
	Very small	1	1	-	-	-	2
Sub-canopy	Small	4	5	1	2	-	12
	Very small	2	10	-	-	-	12
Understorey	Small	3	99	2	23	1	128
	Very small	-	37	-	22	-	59
Ground	Small	-	-	-	3	-	3
	Very small	-	8	-	3	-	11
Totals		10	160	3	54	1	228

(calculated using all available stems)

Table 29: Canopy position, crown size, and dieback of ash stems alive >1.3m height in 1996

Canopy position	Crown size	None/part dieback	Moderate dieback	Severe dieback	Very severe dieback	Totals
Canopy	Medium	1	-	-	-	1
	Very small	2	-	-	-	2
Sub-canopy	Small	12	-	-	-	12
	Very small	12	-	-	-	12
Understorey	Small	118	10	-	-	128
	Very small	49	8	2	-	59
Ground	Small	2	1	-	-	3
	Very small	-	8	2	1	11
Totals		196	27	4	1	228

(calculated using all available stems)

Table 30: Canopy position, crown size, and stature of oak stems alive >1.3m height in 1996

Canopy position	Crown size	Stature			Totals
		Erect	Arched, leaning, spreading	Pollard	
Canopy	Very large	11	-	-	11
	Large	34	-	-	34
	Medium	31	1	-	32
	Small	6	-	-	6
Sub-canopy	Medium	1	-	-	1
	Small	3	-	1	4
Understorey	Medium	-	1	-	1
Totals		86	2	1	89

(calculated using all available stems)

Table 31: Canopy position, crown size, and dieback of oak stems alive >1.3m height in 1996

Canopy position	Crown size	None/part dieback	Moderate dieback	Severe dieback	Very severe dieback	Totals
Canopy	Very large	11	-	-	-	11
	Large	31	3	-	-	34
	Medium	25	6	1	-	32
	Small	3	2	-	1	6
Sub-canopy	Medium	1	-	-	-	1
	Small	2	1	1	-	4
Understorey	Medium	1	-	-	-	1
Totals		74	12	2	1	89

(calculated using all available stems)

Table 32: Canopy position, crown size, and stature of hazel stems alive >1.3m height in 1996

Canopy position	Crown size	Stature							Totals
		Erect & vigorous	Erect	Arched, leaning, spreading, & vigorous	Arched, leaning, spreading	Squat	Snapped	Lateral, fallen, pinned	
Under-storey	Medium	35	27	13	48	1	-	2	124
	Small	315	105	111	291	10	6	5	843
	Very small	76	25	8	22	1	2	-	134
Ground	Large	-	1	1	12	-	-	2	16
	Medium	3	1	1	42	10	-	12	69
	Small	2	35	8	110	40	3	34	232
	Very small	12	67	4	48	19	3	22	175
Totals		**443**	**261**	**146**	**573**	**81**	**14**	**77**	**1595**

(calculated using all available stems)

Table 33: Canopy position, crown size, and dieback of hazel stems alive >1.3m height in 1996

Canopy position	Crown size	None/part dieback	Moderate dieback	Severe dieback	Very severe dieback	Totals
Understorey	Medium	124	2	-	-	126
	Small	761	78	5	-	844
	Very small	120	8	4	2	134
Ground	Large	16	-	-	-	16
	Medium	52	17	-	-	69
	Small	146	75	11	-	232
	Very small	82	57	14	22	175
Totals		1301	237	34	24	1596

(calculated using all available stems)

Table 34: Canopy position, crown size, and stature of hawthorn stems alive >1.3m height in 1996

Canopy position	Crown size	Stature					Totals
		Erect	Arched, leaning, spreading	Squat	Snapped	Lateral, fallen, pinned	
Sub-canopy	Medium	1	-	-	-	-	1
Understorey	Medium	18	8		1	-	27
	Small	35	15	1	1	2	54
	Very small	6	1	-	1	-	8
Ground	Medium	1	4	-	1	5	11
	Small	24	4	-	-	3	31
	Very small	36	7	1	-	4	48
Totals		121	39	2	4	14	180

(calculated using all available stems)

Table 35: Canopy position, crown size, and dieback of hawthorn stems alive >1.3m height in 1996

Canopy position	Crown size	None/part dieback	Moderate dieback	Severe dieback	Very severe dieback	Totals
Sub-canopy	Medium	1	-	-	-	1
Understorey	Medium	25	2	-	-	27
	Small	38	14	2	-	54
	Very small	5	-	3	-	8
Ground	Medium	3	6	2	-	11
	Small	25	4	2	-	31
	Very small	45	1	1	1	48
Totals		142	27	10	1	180

(calculated using all available stems)

9. Debarking

Bark-stripping by grey squirrels

Grey squirrel bark-stripping was recorded in 1996. Two of the three sycamore stems appeared to have been damaged; the largest 46cm gbh had lost its leader at 2m up the trunk probably due to squirrel stripping, and the 20.5cm gbh stem had some basal damage.

Table 36: Condition, growth and scale of squirrel bark stripping to living beech stems in 1996

Status: 1 = standing alive >1.3m; 2 = standing alive <1.3m	Gbh (cm)	Increment rate 1986-96 (cm a^{-1})	Canopy position	Crown size	Crown dieback	Stripping damage score
1	24	na	Understorey	Very small	Very severe	4/4
2	22	1.2	Ground	Very small	Very severe	4/4
1	45	0.5	Understorey	Medium	Very severe	3/4
1	56	1.7	Sub-canopy	Medium	Part-dieback	3/3
1	49.5	1.7	Sub-canopy	Small	Part-dieback	3/3
1	25	1.3	Understorey	Medium	Part-dieback	3/3
1	25.5	1.5	Understorey	Medium	Part-dieback	3/2
1	38.5	na	Sub-canopy	Very small	Part-dieback	2/3
1	42	2.0	Understorey	Medium	Part-dieback	3/1
1	24	na	Understorey	Medium	Part-dieback	3/1
1	29	na	Understorey	Medium	Dieback	1/3
1	65	na	Canopy	Small	Part-dieback	2/2
1	44	na	Sub-canopy	Medium	Part-dieback	2/2
1	29	na	Understorey	Medium	Part-dieback	2/2
1	42	1.9	Understorey	Large	Part-dieback	2/1
1	35	na	Understorey	Medium	Part-dieback	2/1
1	36	na	Understorey	Medium	Part-dieback	1/1
1	16	0.7	Ground	Very small	Dieback	1/1
1	26	1.4	Understorey	Small	Part-dieback	1/0
1	26	1.3	Understorey	Medium	Part-dieback	1/0
1	9	na	Understorey	Small	Part-dieback	1/0

(calculated using all available stems; na = not available)

Otherwise all beech stems suffered damage (Table 36). Most damage scores below 2m and above 2m were quite similar, and 21 trees had been at least partly damaged, 11 had been severely damaged, and 3 were ring-barked. Size-class damage was not significantly rank-correlated with stem gbh ($r_s = 0.116$, $n = 21$, $r_{critical} = 0.370$, $p = 0.05$), but was greatest amongst the size-classes >40cm and 22-29cm gbh stems; 5 out of 7 stems >40cm gbh, and 6 out of 9 22-29cm gbh stems were at least severely damaged. Nor was increment rate between 1986-96 significantly rank-correlated with damage ($r_s = -0.086$, $n = 10$, $r_{critical} = 0.648$, $p = 0.05$), but, based on the limited available data, 5 out of 8 faster growing stems were severely damaged. Severe damage to sub-canopy stems was notably high; 3 out of the 4 sub-canopy stems were at least severely damaged, while only half of the 14 understorey stems were damaged similarly. On several trees loss of bark appeared to be causing early crown yellowing, and the only two larger beeches (sized 29 and 34cm gbh) that died between 1986-96 had both been badly debarked by squirrels.

Bark-stripping by deer

Table 37: Bark-stripping by deer to all living and dead standing stems <20cm gbh in 1996

Species	No damage	Limited damage	Moderate damage	Severe damage	Standing killed by debarking
Hazel	1146	5	17	4	2
Ash	186	2	1	1	2
Hawthorn	95	3	-	-	-
Lime	60	-	2	1	-
Birch	46	-	1	-	-
Crab apple	-	-	-	1	-
Sycamore	1	-	-	-	-
Holly	1	-	-	-	-
Blackthorn	13	-	-	-	-
Total	1548	10	21	7	4

(calculated using all available stems)

Basal bark-stripping to all living and dead standing stems was recorded in 1996. Apart from damage attributed to grey squirrels and some cases caused by falling trunks and canopy debris, stripping was attributed to deer (Table 37). This debarking was restricted to stems <20cm gbh, 63% of which were <10cm gbh, and only 2.4% of all living stems <20cm gbh were damaged and <1% were severely damaged.

Hazel had the most damaged stems, and these represented 2.2% of all living hazels stems below 20cm gbh. A couple of dead standing hazels had been killed by deer bark-stripping, as had a couple of ash. Otherwise a few living ash, hawthorn, lime, birch and crab apple stems were damaged. Damage to lime represented 5% of all living lime stems below 20cm gbh, and the single severely damaged crab apple was the only one below 20cm gbh in the population. The few sycamore, holly and blackthorn stems below 20cm gbh were not damaged. Other species had no stems below 20cm gbh and had no damage recorded.

10. Dead wood

Change in basal area of dead standing stems >1.3m height

Table 38: Basal area ($m^2 ha^{-1}$) of all dead standing stems >1.3m height 1986 and 1996

Species	1986	1996	Change
Major species			
Oak	0.27	0.27	minimal
Birch	0.22	0.37	+0.15
Lime	0.11	0.11	minimal
Hazel	0.09	0.06	-0.03
Ash	0.01	<0.01	minimal
Minor species			
Hawthorn	0.04	0.04	minimal
Beech	<0.01	0.01	minimal
Blackthorn	<0.01	<0.01	minimal
Rose	0	<0.01	minimal
Total	0.75	0.86	+0.11

(calculated using all recorded stems standing dead >1.3m and based on study area of 1.12ha)

The basal area of dead standing stems >1.3m height increased slightly from 0.75 to 0.86m² per hectare between 1986-96 (Table 38). However this still only represented 2.3% of the total standing basal area. In 1986 oak was the most abundant species and birch was fairly abundant. By 1996 birch had increased greatly and become the most abundant species. Other species changed little in abundance.

Change in density of dead standing stems >1.3m height

Table 39: Density ($n ha^{-1}$) of all dead standing stems >1.3m height 1986 and 1996

Species	1986	1996	Change
Major species			
Hazel	97.3	81.3	-16
Lime	46.4	33.0	-13.4
Birch	43.8	39.3	-4.5
Ash	32.1	8.9	-21.2
Oak	1.8	3.6	minimal
Minor species			
Hawthorn	11.6	9.8	minimal
Beech	0.9	2.7	minimal
Blackthorn	0.9	0.9	minimal
Rose	0	0.9	minimal
Total	234.8	180.4	-56.4

(calculated using all recorded stems standing dead >1.3m and based on study area of 1.12ha)

The density of dead standing stems >1.3m height decreased from about 235 to 180 stems per hectare between 1986-96 (Table 39). This represented a decline from about 8% to 7% of all (living and dead) stems standing >1.3m height. Hazel was the most abundant species in 1986 and 1996, and lime and birch remained prominent. Ash was also prominent in 1986, but by 1996 it had declined sharply. There were several minor species which changed little in abundance.

Fate and recruitment of dead standing stems >1.3m height

Table 40: Number, fate, recruitment and throughput of dead standing stems >1.3m height 1986-96

	1986	1996	Fate of 1986 stems by 1996		Recruitment 1986-19		Throughout 1986-96	
Species	Stems dead standing >1.3m	Stems dead standing >1.3m	Still dead standing >1.3m	Dead fallen /<1.3m	Alive >1.3m in 1986	Not present in 1985	Standing alive>1.3m in 1986	Not present in 1986
Hazel	113	88	9	104	66	13	233	1
Lime	53	37	1	52	36	-	81	-
Birch	49	44	3	46	41	-	105	-
Ash	36	10	1	35	9	-	158	-
Hawthorn	13	11	-	13	10	1	22	-
Oak	2	4	1	1	3	-	3	-
Blackthorn	1	1	-	1	1	-	3	-
Beech	-	1	-	-	1	-	2	-
Rose	-	1	-	-	1	-	-	-
Sallow	-	0	-	-	-	-	1	-
Total	267	197	15	252	168	14	608	1

(calculated using all recorded dead standing stems >1.3m height in 1986 and 1996)

In 1986 there were 267 dead standing stems >1.3m height (Table 40). Only 15 of these remained in the same state in 1996. Recruitment of new stems between 1986-96 amounted to 182 stems, a small number of which recruited and died during the period. Therefore by 1996 the total number of dead standing stems had fallen by 26% to 197 stems. The size-class distribution of all stems at both dates approximated to the negative exponential; stem number fell rapidly as stem girth increased (Figure 27). In addition there was a very high throughput of 609 stems, virtually all of which were standing alive >1.3m in 1986.

All of the main species displayed similar patterns of change; low survival, high recruitment, and high throughput. Hazel had the most dead standing stems at both dates, but these were mostly small girth and their total abundance declined somewhat (Figure 27). Birch and lime remained quite numerous, and although most stems were <30cm gbh, several larger birch existed in 1986 and by 1996 these had increased further. Ash was moderately abundant in 1986, represented by numerous dead standing saplings, but by 1996 it had declined to the low numbers maintained by hawthorn and oak. This was mainly caused by the exceptionally high throughput of ash (439% of 1986 population) and its relatively low recruitment (25% of 1986 population). Although there only a few dead standing oaks, these alone included trunks over 100cm gbh, including one tree at 118cm gbh that remained dead standing; the only other relatively large survivors were two birches at 25cm and 27cm gbh and a hazel at 24cm gbh. A slight increase in dead standing oaks, combined with the rise in larger birches, meant that by 1996 the number stems >60cm had increased somewhat.

Volume and condition of dead standing stems >1.3m height

Table 41: Quantity and status of dead standing stems >1.3m height in 1996

	Oak	Birch	Lime	Hazel	Hawthorn	Ash	Beech	Blackthorn	Rose	All
Abundance										
Volume (m^3 ha^{-1})	4.8	3.0	0.7	0.2	0.2	<0.1	<0.1	<0.1	<0.1	9.0
Number of stems	4	43	37	87	11	10	1	1	1	195
Height										
0-2.9m	-	6	10	55	3	1	-	-	1	76
3-9.9m	-	28	23	31	8	9	1	1	-	101
10m+	4	9	4	1	-	-	-	-	-	18
Degree of rot										
Solid	4	21	16	34	6	6	-	-	-	87
Part-rotten	-	17	15	35	4	3	-	-	-	74
Rotten	-	3	4	3	-	-	-	1	-	11
Very rotten	-	1	-	-	-	-	-	-	-	1
Not available	-	1	2	15	1	1	1	-	1	22
Bark %										
0-24	-	1	10	1	-	-	-	-	-	12
25-49	1	-	-	-	-	-	-	-	-	1
50-74	-	-	5	-	-	-	-	-	-	5
75-100	3	38	20	43	9	4	-	-	-	117
Not available	-	4	2	43	2	6	1	1	1	60

(calculated using all recorded stems standing dead >1.3m and based on study area of 1.12ha)

There 195 dead standing stems record in 1996 that amounted to an estimated volume of 9.0m^3 ha^{-1} (Table 41). Most snags were either short (<3m) or medium (3-10m) height, with little decay, and most bark remaining.

Oak accounted for the most volume of any species, but had only four trees recorded. These were all solid, taller than 10m, and three had most bark intact. Otherwise only birch accounted for a substantial portion of the total volume. Most birches were taller than 3m and nine were taller than 10m. Lime and hazel had many recorded stems, but most were quite short and amounted to little volume. Several birch, lime and hazel stems were well decayed, and a large number of limes had lost most of their bark.

Quantity, distribution and condition of dead fallen stems

The quantity, condition and origin of fallen dead wood was estimated using the line transect method (Table 42). The total estimated length and volume were 1683m per hectare and 15.1m^3 per hectare respectively. Most fallen stems were small (<10cm diameter) and had little decay, many had lost considerable amounts of bark, and most had originated due to competitive exclusion.

Five species were recorded. Oak was the most abundant, accounting for half of the total volume and 58% of the total length. Most oak stems appeared to be old, were small, quite solid, had little bark, and originated from shaded-out lower canopy boughs. Birch was also abundant, accounting for 44% of the volume and 31% of the length. Most birches were small diameter, with most bark intact, but they ranged from solid to well decayed. Although most stems had been recently excluded, several had been windblown, including the two stems that were larger than 20cm diameter. Otherwise a few, small diameter, competitively excluded, lime, hawthorn and hazel stems were recorded.

Table 42: Quantity, condition and origin of fallen dead stems from line transect survey in 1996

	Oak	Birch	Lime	Hawthorn	Hazel	All species
Abundance						
Estimated volume (m^{3}ha^{-1})	7.7	6.6	0.5	0.2	0.2	15.1
Estimated length (m ha^{-1})	972	524	112	37	37	1683
Number of stems recorded	26	14	3	1	1	45
Stem diameter						
5-9.9cm	19	10	3	1	1	34
10-19.9cm	7	2	0	0	0	9
20-29.9cm	0	2	0	0	0	2
Stem age						
Recent	12	14	2	1	1	30
Old	14	0	1	0	0	15
Decay state						
Solid	12	4	2	0	0	18
Part-rotten	7	4	1	0	0	12
Rotten	5	5	0	1	1	12
Very rotten	2	1	0	0	0	3
% remaining bark						
0-24	13	1	1	0	0	15
25-49	3	0	0	0	0	3
50-74	4	1	1	0	1	7
75-100	6	12	1	1	0	20
Stem origin						
Competitive exclusion	24	10	1	1	1	37
Windblow/snow weighting	2	4	0	0	0	6
Knocked over by falling debris	0	0	2	0	0	2

(calculated using all recorded fallen stems attaining 5cm diameter)

11. Discussion

A decade of studying stand change at Langley Wood provides only a glimpse of the potential successional and disturbance patterns. Certainly during this time disturbance has been limited and growth relatively predictable. Further, the two study transects provided only a very limited sample from a selected area of the wood; in order of rank abundance, hazel-birch-oak, lime-oak, birch-oak, and wet birch-ash stands are crossed. This record of actual change and the interpretation of current stand characteristics provides an opportunity to quantify current trends and outline historical patterns. These provide a benchmark against which future rates of change and trajectory can then be compared. Nevertheless, any quantitative extrapolation to change in the rest of the wood must be done with care because of the selectivity in the area recorded.

General stand changes

The study stands were probably last coppiced between 1920-1940, and have since been left to naturally develop, apart from the removal of dead trees and fallen timber, some hazel and ash rods, and, perhaps, the occasional good oak (pers. comm. Nigel Anderson). Regeneration after coppicing usually results in the establishment of a quasi-even aged cohort below any retained standard trees. This regeneration can arise from stump regrowth, seedling recruitment and the development of retained advanced regeneration. After several decades of relatively undisturbed growth, such stands produce a characteristic size-class distribution, which can be recognised in the stands at Langley (Figure 3). The number of surviving stems forms a smooth negative exponential decline against increasing stem girth, except in the largest size-classes where an uneven and extended distribution is observed. The first group represent the survivors from the cohort that established soon after the last coppicing, and the latter represent most of the retained standards. These stands typically amount to basal areas in the range of 32 to 36m^2 ha^{-1} as recorded at Langley (Table 2) (Peterken and Jones 1987, 1989; Mountford 1994; Mountford and Peterken 1998).

Between 1986-96 three general features of stand change were recognised; (i) the canopy remained more-or-less closed; (ii) the basal area increased; and (iii) the density of living stems decreased (Tables 1, 2 and 3). These patterns combine with the observed size-class distributions to infer that since the last major coppicing patterns of stand change have broadly conformed to those described in the *stem exclusion stage* of stand development (Oliver and Larsen 1996). Further evidence is given in the detailed analyses of the major species (see below).

The stem exclusion stage is typical of unmanaged, relatively undisturbed, young-middle aged, temperate broadleaved stands that establish as even-aged cohorts after catastrophic disturbance (Oliver and Larsen 1996). After disturbance a *stand initiation stage* occurs when a wave of regeneration reforms a closed canopy. Then regeneration ceases as the stands pass into the stem exclusion stage. As individual stems grow and compete for the limited available resources, inevitably the less-competitive stems are progressively excluded, grow more slowly, and eventually die. These leave increasingly larger-sized survivors that accumulate more above-ground biomass than is lost through exclusion. Over time a negative exponential size-class distribution is produced, with a few rapidly growing 'winners' and many suppressed slow-growing 'losers'. Although stems die, the canopy remains more-or-less closed during this stage, because the exclusion process is gradual and surviving crowns rapidly expand to infill any gaps that are produced. Although some larger openings at Langley did arise because of wind-damage to birch, these were relatively small-scale and probably only accelerated changes that would be expected in due course through exclusion. The stem exclusion process has been statistically quantified by the *self-thinning rule* (Yoda *et. al.* 1963; White 1981), and many transect sections at Langley demonstrated the density-dependent thinning patterns that are expected by this rule (Figure 4).

A further trend observed during the stem exclusion stage is that recruitment remains restricted. This is because of the intense competition for resources and heavy canopy shading at the woodland floor. Between 1986-96 this pattern was observed in the lime-oak and birch-oak transect sections (Tables 5 and 7; Figures 6, 8 and 12). Historically it is probable that most stands at Langley have followed a similar pattern for at least several decades. However in the hazel-birch-oak transect sections recruitment of stems, individuals and seedlings was significant (Tables 5 and 7; Figures 8, 12, and 14). In the wet birch-ash stand advanced regeneration ash seedlings had developed *en masse* in the recent past (Figure 10). Such recruitment is indicative of progression into *understorey re-initiation stage* of stand development, when, after several decades of stem exclusion, a low stratum of herbs, shrubs, and advanced regeneration invades the woodland floor (Oliver and Larsen 1996).

The understorey re-initiation stage arises because more permanent growing space is released in the canopy. As canopy trees mature they occupy growing space less aggressively, including that released by on-going exclusion and minor disturbances. In turn this provides more light, nutrients, carbon dioxide, and a less extreme micro-climate at the ground. Certainly recruitment of new stems, individuals and seedlings between 1986-96 occurred in areas where most light was available (i.e. where canopy gaps were greatest) (Tables 1, 5 and 7) and where stands were well below the predicted self-thinning threshold slope (Figure 4). The same conditions apparently facilitated the ash seedling cohort in the wet birch-ash stand, which have developed following the death of a large canopy tree in about 1960 (pers. comm. Nigel Anderson). Recruitment has been inhibited elsewhere apparently by the heavy shade of canopy limes or the competitive-effect of dense bracken ground vegetation.

The main species recruiting new individuals are inevitably fairly shade-tolerant and included only a selection of existing species (Table 6). Most were hazel and hawthorn, and in the hazel-birch-oak stands these will simply replenish the existing underwood layer. However, if holly and hornbeam seedlings develop further they will recruit new species into the stand, at least locally. Most significant would be hornbeam, a potentially long-lived shade-bearing tree that could alter the composition of the stand significantly. The divergence in the natural transitions in the lime-oak/birch-oak and the hazel-birch-oak/wet birch-ash stands relates to the endurance of particular conditions that established when the stands were first initiated.

Patterns amongst the major species

Lime

Lime was a major canopy species that remained numerous between 1986-96 (Tables 2, 3 and 23). Its basal area remained moderate but increased greatly (Tables 2). No new stems or seedlings established (Tables 4 and 6).

Lime distribution was intensely conservative (Figure 6), formed by aggregated, large coppice stools, and a few marginal saplings, which all appeared to be survivors from a quasi-even-aged post-coppicing cohort (Figure 5). This localised distribution pattern is also evident at the landscape scale. Lime currently only exists in a few patches in the west of the Langley Wood and in two other outlying groups. Lime would have been the potential dominant in this area before human management (Bennet 1989), and its present relic distribution probably reflects two main factors:

- The landscape distribution of past management types. Lime is highly selected by browsing animals and probably became extinct in areas treated as wood pasture. In areas where it was treated as coppice it probably persisted, due protection from excessive livestock browsing and its ability to respond vigorously, and almost perpetually, to repeated regular cutting (Pigott 1989).

- The limited reproductive and colonisation abilities of lime. Lime is unable to produce fertile seed in cool British summers (Pigott and Huntley 1981) and in warm summers requires unshaded boughs on stems over 25 years old (Pigott 1975). In a traditional coppice regime the cycle perhaps extended to 25 years (Peterken 1993a). Fruits, although winged, are not widely distributed, and recruitment from either seedlings or branch end layering tends to occur at or slightly beyond the margins of mature trees (Pigott 1975; Peterken and Jones 1989).

Where lime survives, its superior competitive ability was clearly demonstrated. Apart from a few nearby standard oaks, lime had locally excluded most other stems and inhibited recent recruitment (Tables 5 and 7; Figures 6, 8, 10, 12, 14 and 16). Stem survival rates between 1986-96 were fairly high. Losses were small-sized and mainly resulted in the thinning of multi-stemmed stools (Table 4; Figure 5). All large stems survived and many grew very rapidly (Figures 5 and 17). Consequently the basal area increased substantially and lime singly amassed over 30% of the total basal area increase (Table 2).

Nevertheless, mortality and growth of lime were strongly influenced by stem exclusion processes. Only a small portion of lime stems grew very rapidly; these tended to be the largest girth stems, which were erect and vigorous, with medium-sized crowns, positioned in the uppermost canopy layer, and had limited dieback (Tables 9-11, and 24-25; Figure 17). Thereafter performance deteriorated correspondent with a decline in photosynthetic potential; progressively down through the strata girths declined, stems grew more slowly, dieback was more widespread, stature tended to be arched, leaning, or lateral, and mortality increased. Even within each strata similar evidence of exclusion was apparent. The shade-bearing capacity of lime resulted in the persistence of many lower strata stems (Table 23), which potentially could endure a very protracted phase of demise requiring both canopy exclusion and major crown-size reduction. Evidence that the exclusion process had predominated for many decades was revealed in the recent size distributions (Figure 5 and 21); the smallest <10cm gbh stems represent the least competitive and the largest *c.*100cm gbh stems the most competitive survivors from the quasi-even-aged cohort.

The pattern of lime stool distribution, sapling recruitment, and competitive ability observed in Langley, are closely parallelled in similar stands recorded over a half century at Lady Park Wood (Peterken and Jones 1987, 1989; Mountford 1994). Lime appears to be a potentially long-lived dominant tree, but with a naturally-confined distribution.

Birch

Birch was also a major canopy species, whose stem density and basal area remained at second rank between 1986-96 (Tables 2, 3 and 23). No new stems or seedlings established (Table 4 and 6).

The size-class distributions suggested that most of the population was from an even-aged cohort that had undergone stem exclusion processes for many decades (Figure 7 and 22). They were mainly seedling survivors, a few being from multi-stemmed possible coppice stools. Some of the largest stems were probably retained standard trees. Along many parts of the transects birch was quite abundant, mainly interspersed in groups amongst canopy oaks with or without a hazel understorey, and also as an overstorey above sapling ashes in the wet headwater swamp area (Figures 8, 10, 12 and 14). Mixed birch stands occupy much of Langley Wood; birch-oak stands are Peterken type 6Db, birch-oak-hazel stands are Peterken type 6Dc, and wet birch-ash stands are Peterken type 3A. Therefore change in these stands accounts for much of the local landscape. Birch typically occurs on acid free-draining soils (Peterken 1993a) and, as a light-demanding colonist (Grime *et al* 1990), its abundance suggests that the last fellings consisted of fairly large coupes, with the few retained standard birches providing a large seed rain. Birch was generally excluded from areas with dense lime (Figures 6 and 8), and some areas where canopy oaks and a dense hazel understorey prevailed (Figures 8, 12 and 14). The first undoubtedly reflects the competitive nature of lime, the latter perhaps because gaps between the standard oaks were small and hazel aggressively out-competed any birch seedlings.

Birch was generally less competitive than lime and its basal area increased only minimally between 1986-96 (Table 2). Although stem survival rates were lower than lime, most losses were still small girth stems and these amounted only to a general thinning of existing birch groups (Table 4; Figure 7). Most medium girth trees survived and generally matched the growth of lime; it was only the very largest birches that grew much more slowly (Figures 7 and 18). The latter was a clear sign of natural maturity, which arises at different times in different species, but for birch a longevity of about 60-70 years is typical in lowland Britain (Grime *et al* 1990).

The post-coppice cohort was strongly influenced by stem exclusion processes. Only a few stems grew rapidly; these tended to be the erect, larger girth, medium- or large-crowned, canopy stems with little dieback (Tables 12-13, and 26-27; Figure 18). As photosynthetic potential declined, stem performance followed suit; progressively down through the strata girth-sizes declined, stems tended to grow more slowly, dieback was more widespread, stature tended to be arched, leaning, or lateral, and mortality increased. Similar patterns were evident within each strata. Fewer birch than lime existed in the lower strata (Table 23), as expected for a shade-intolerant species, but mortality still appeared to be a gradual process combining canopy exclusion and crown reduction.

Change in birch was also effected by windblow (Table 8). Both before and between 1986-96, numerous medium and large girth trees were blown over, snapped off, tipped over, or suffered major crown loss. Like most damage caused by natural disturbances in woodland (Peterken 1996), the effect was notably patchy, selectively damaging larger girth birch trees in only some areas of the stands. Overall canopy loss was quite small-scale and probably only accelerated changes that would be expected in due course through exclusion and natural senescence

These patterns of change in birch have been recorded in similar stands at Lady Park Wood (Peterken and Jones 1987, 1989; Mountford 1994), and account for its classification as a short-lived pioneer species in British lowland woodland (Peterken 1996). In the next few decades, it can be expected that birch will begin to decline as it reaches its natural longevity. Unless some catastrophic disturbance occurs, no effective recruitment can be expected.

Ash

Only two large ash were present within the transects (Figure 9), individuals that presumably established soon after the last coppicing. However most of the population were in the form of small girth maiden saplings and poles that were concentrated in the wet headwater birch-oak stand and thinly scattered through the birch-oak-hazel stands (Figures 8, 9, 10, 12 and 14). These saplings appeared to be of more recent origin and their distribution corresponded with the areas where established seedlings were recorded in 1996 (Table 7). However it may be possible that at least some saplings are long suppressed individuals that established at the last coppicing. Those in the wet birch-ash stand developed following the death of a large canopy tree in about 1960 (pers. comm. Nigel Anderson). This left a light canopy of birch and a nearby ash tree to act as a seed source (Figures 8 and 10). By 1986 a mass of suppressed seedlings had ensued (Figure 9), and by 1996 a few had been released into vigorous sub-canopy poles (Table 23; Figure 19), presumably facilitated by canopy openings caused by windblow of birch (Table 8).

The restricted distribution of ash, especially older trees, reflects the fact that many areas of the wood are too acid or too dry, represented instead by birch-oak (Peterken type 6Db) or birch-oak-hazel stands (Peterken type 6Dc). There might also in the past have been selection against ash in favour of oak. Recent colonisation of ash into the birch-oak-hazel stands may relate to moderating soil conditions combined with an improving light regime. Continued monitoring will show if the established ash seedlings here are capable of further development. The same must be true in the wet birch-ash stands, probably because the canopy birch have reduced water-logging to facilitate the entry and development of ash saplings once enough light became available.

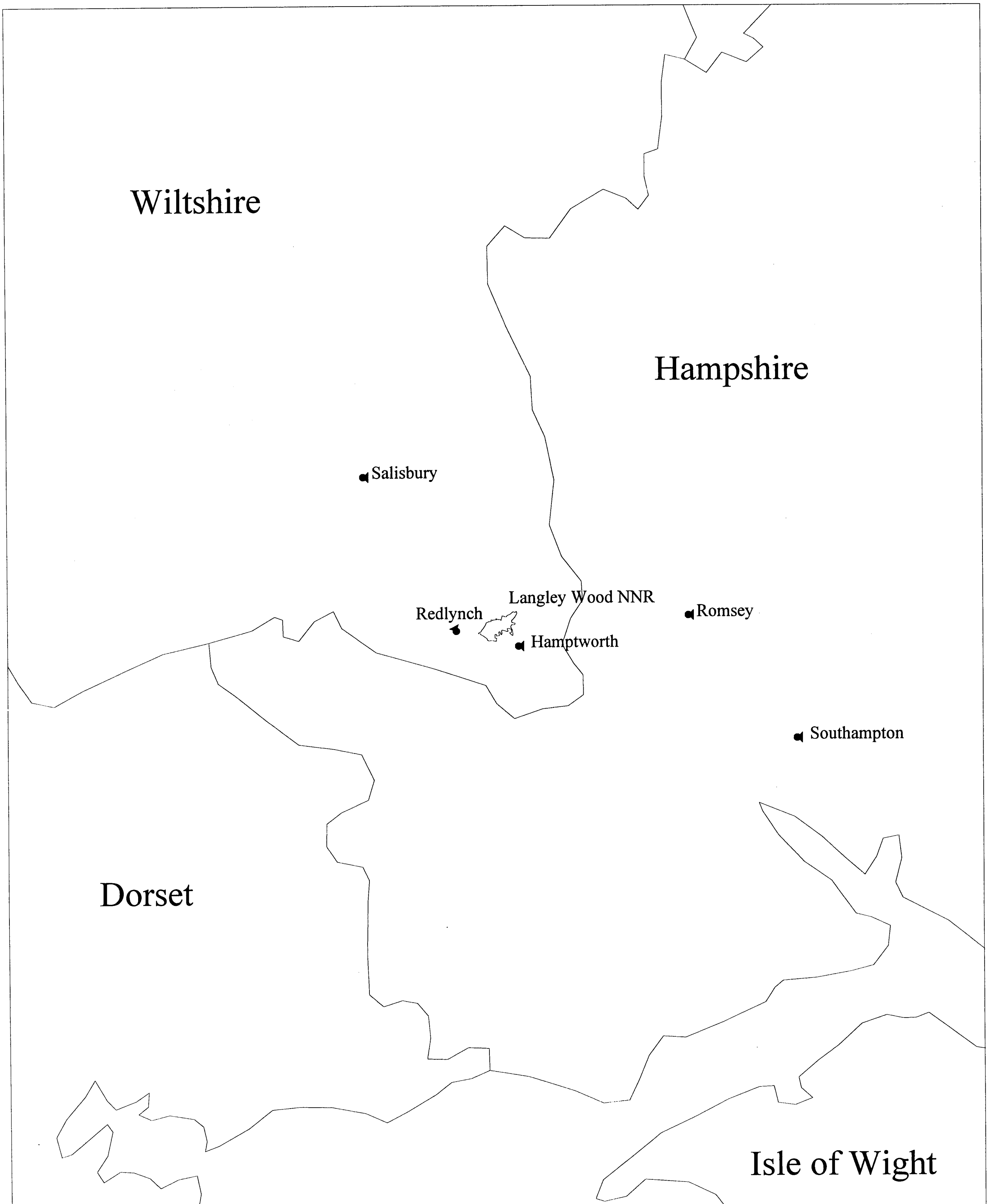
Performance of the sapling cohort was strongly influenced by exclusion processes. A huge number of saplings failed or were reduced to a few remaining basal leaves between 1986-96; these were amongst the smallest girth stems in 1986, and those that were crushed and pinned by falling canopy debris were amongst the weakest and most excluded saplings (Tables 4; Figure 9). The slowest growing survivors were in the ground layer, where stems tended to be small girth, mostly arched over, and with considerable dieback (Tables 14-15 and 28-29; Figures 19 and 23). Growth increased progressively as stems climbed upward through the strata and as crown size increased, coincident with increasing girth size, improved stature, decreasing crown dieback, and increasing survival. The fastest growing released poles were amongst the largest in the cohort in 1986, and accessed most photosynthate by growing upward into the sub-canopy.

In the foreseeable future, and in the absence of catastrophic disturbance, only a small minority of the ash sapling cohort will be released to assert themselves in the canopy. In the birch-ash stand it is likely that the birch canopy will eventually be replaced by ash. In the birch-oak-hazel woodland sapling development will be far more restricted amongst the long-lived oaks, but some poles look capable of forming canopy trees, especially if canopy space becomes available.

Oak

Oak was the third major canopy species, dominating the stand basal area between 1986-96 (Tables 2 and 23). It was represented by relatively few, mostly large girth, healthy, large-crowned, canopy trees, most of which survived and grew well (Tables 3, 23, 30 and 31; Figures 11 and 24). No recruitment or seedlings established (Tables 4 and 6). Oak standards were remarkably evenly scattered, both along the transects (Figure 12), and throughout much of the wood. They appear to represent a wide range of ages, from the largest and oldest at perhaps 300

Figure 1. Location of Langley Wood NNR



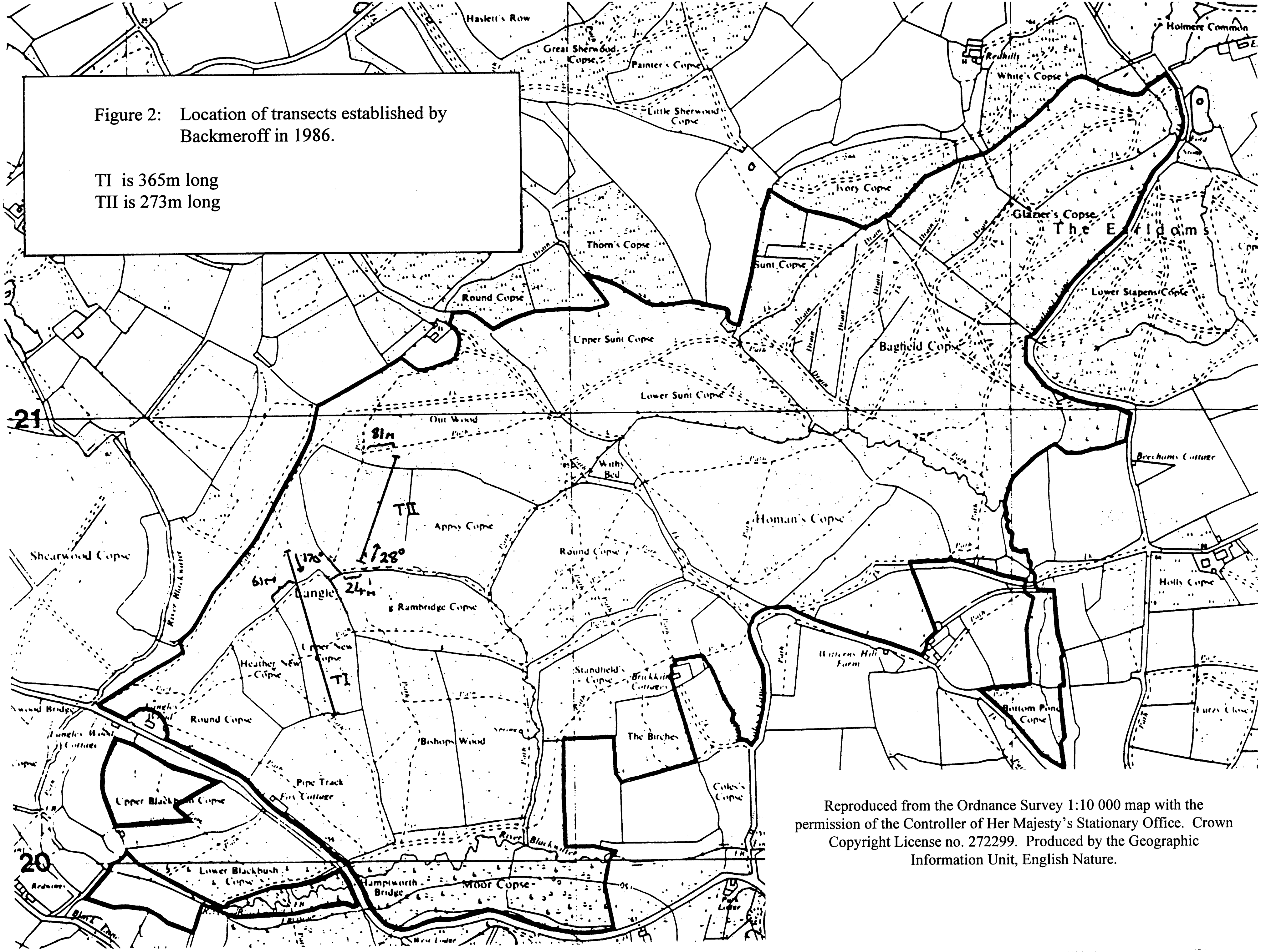


Figure 2: Location of transects established by Backmeroff in 1986.

TI is 365m long
TII is 273m long

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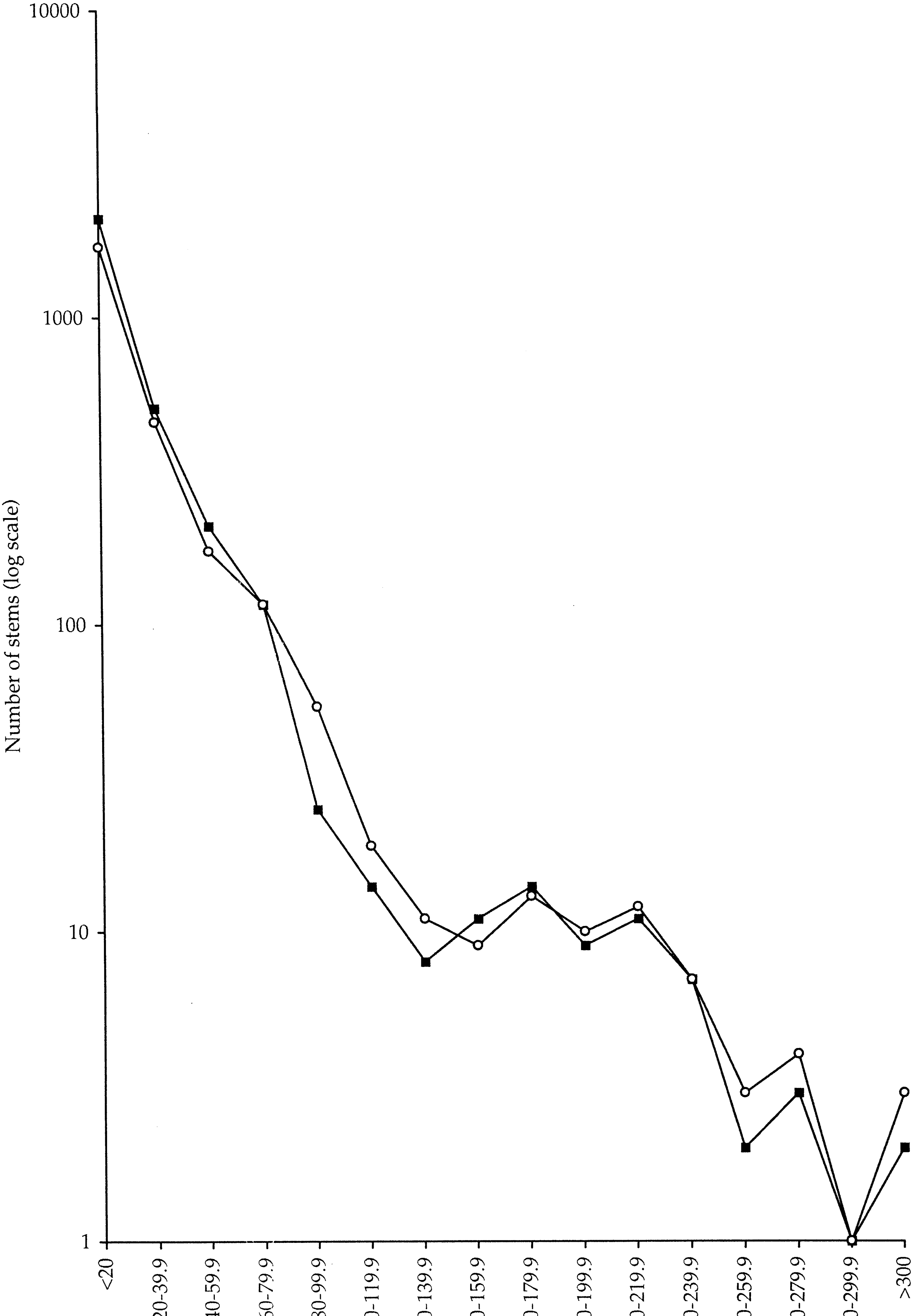

Figure 3: Size-class distribution of all stems alive >1.3m in 1986 (■) and 1996 (○).

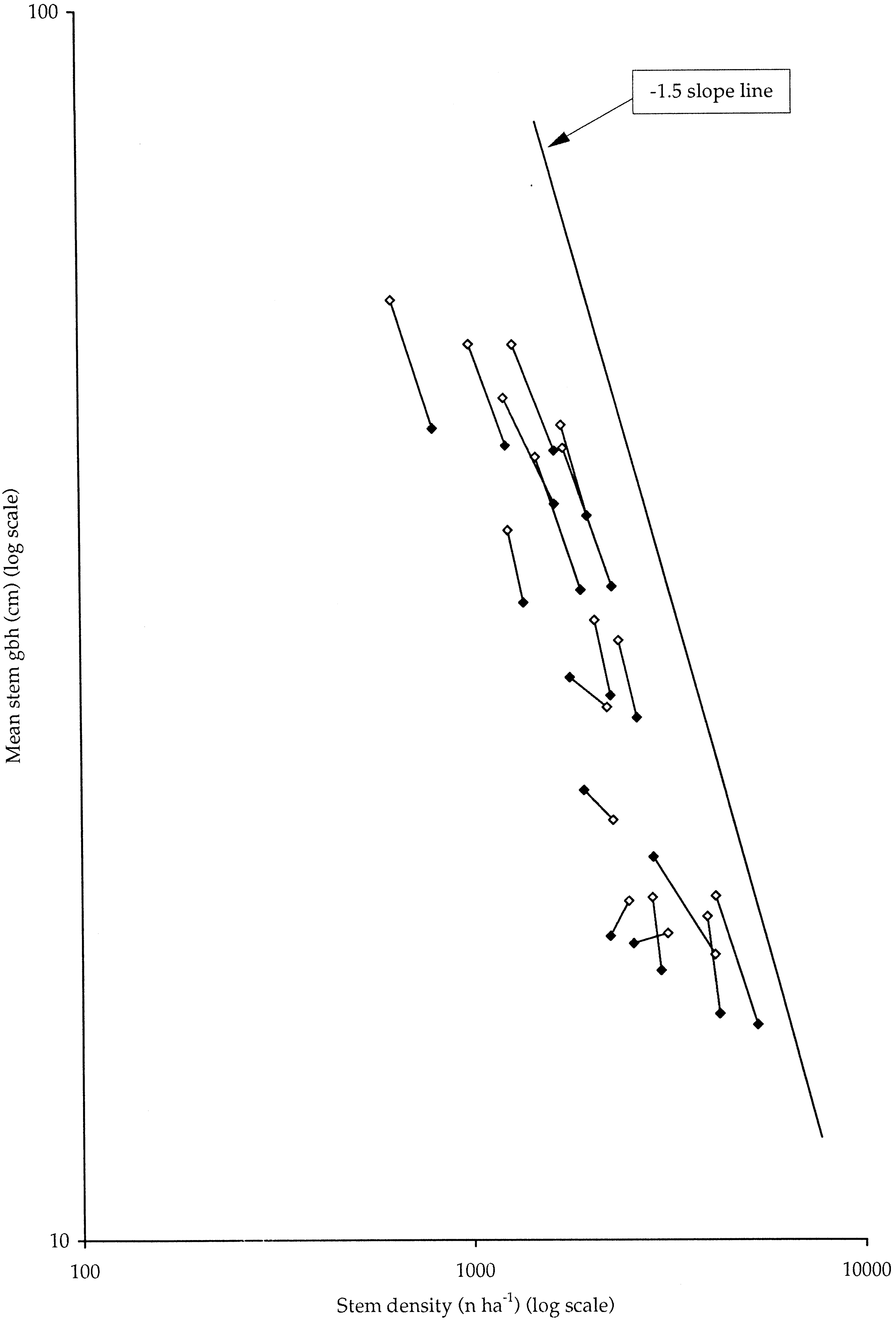

Figure 4: Change in the relationship between stem density and mean gbh from 1986 (◆) to 1996 (◇) for eighteen 600m^2 transect sections.

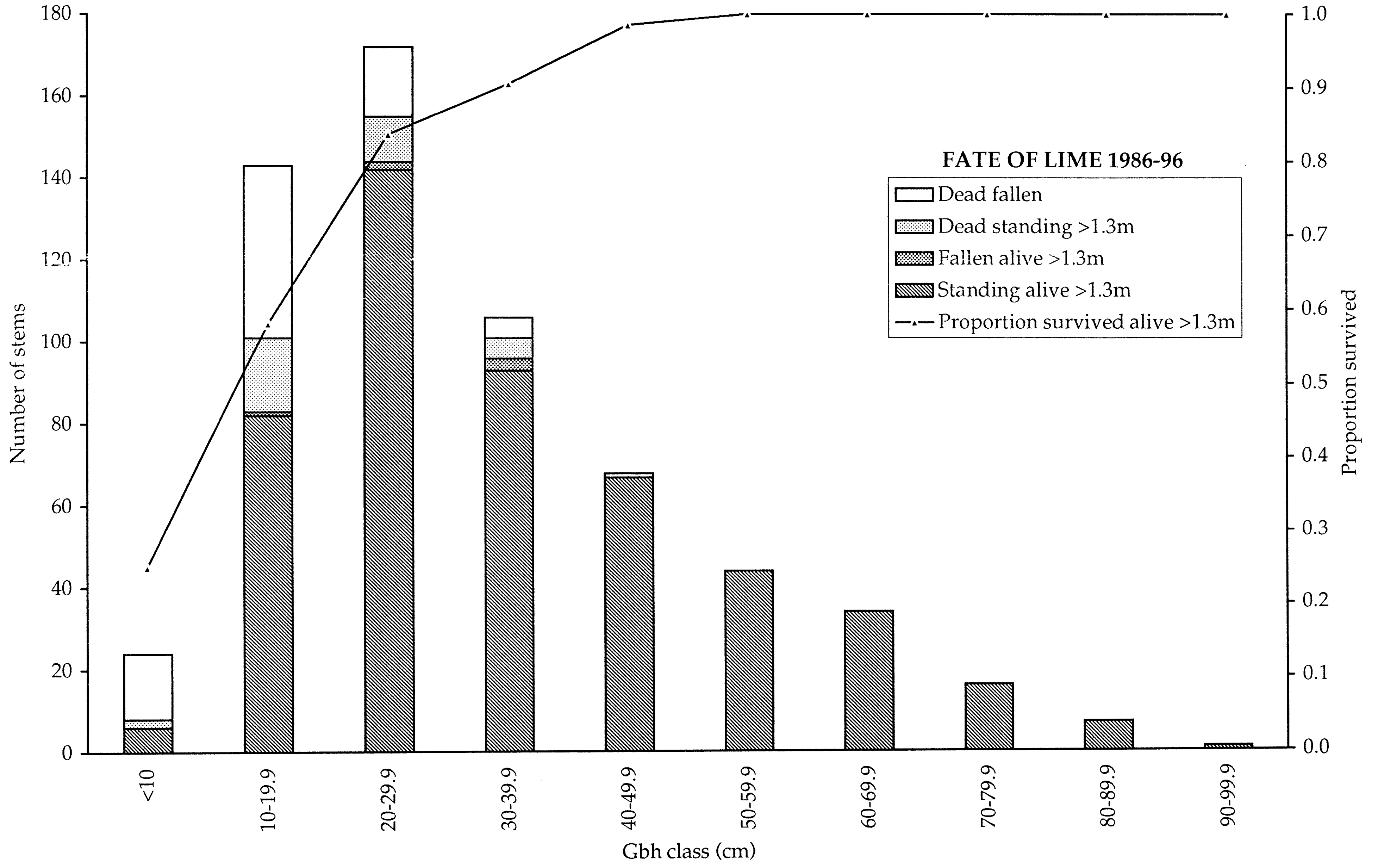

Figure 5: Size class fate and proportional survival of lime stems standing alive >1.3m height in 1986 by 1996.

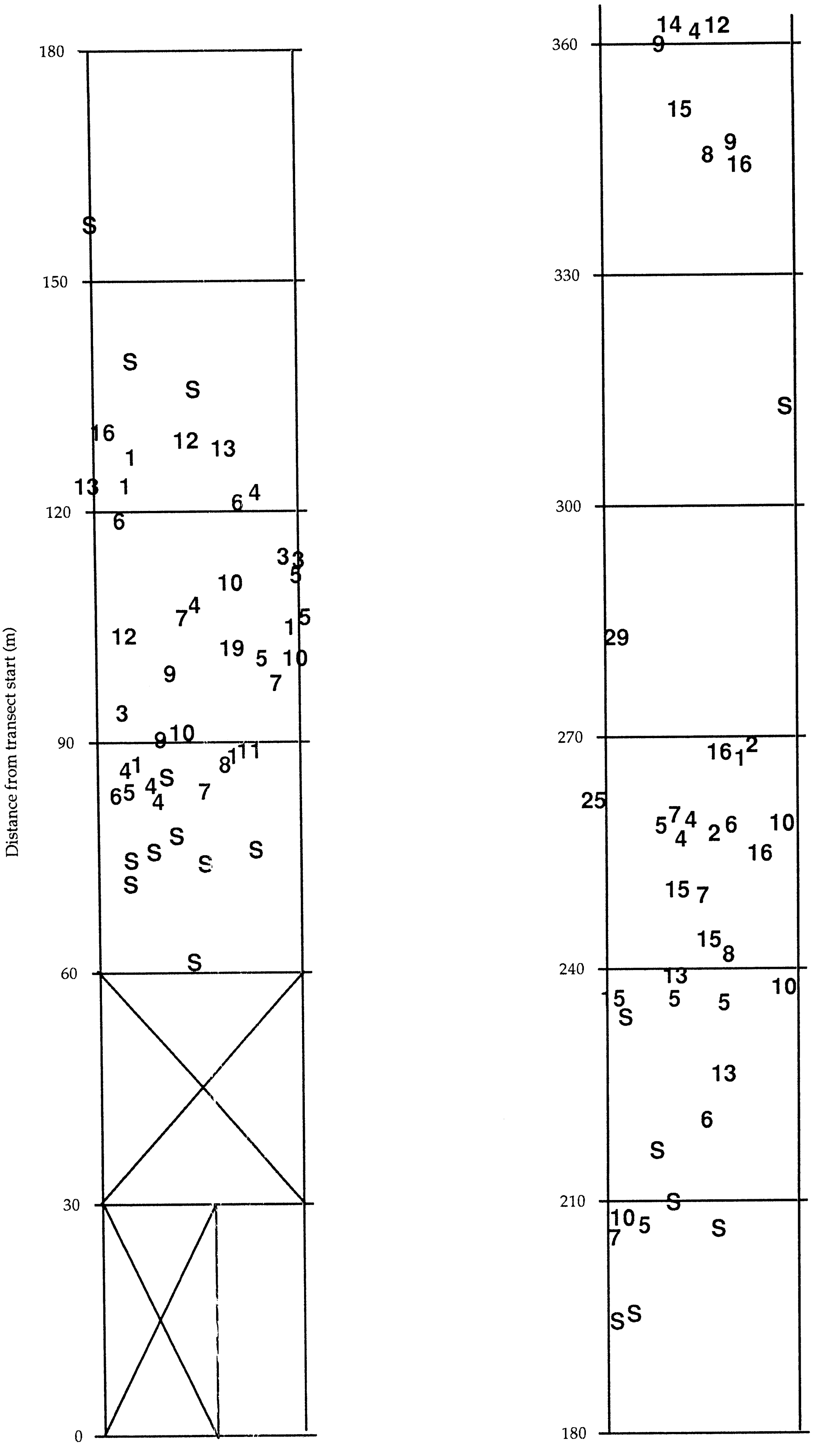

Figure 6: Distribution of limes along transect 1 in 1986. Each point represents an individual. Values = number of stems standing alive on stool. S = seedling recruit . Sections marked X were not recorded.

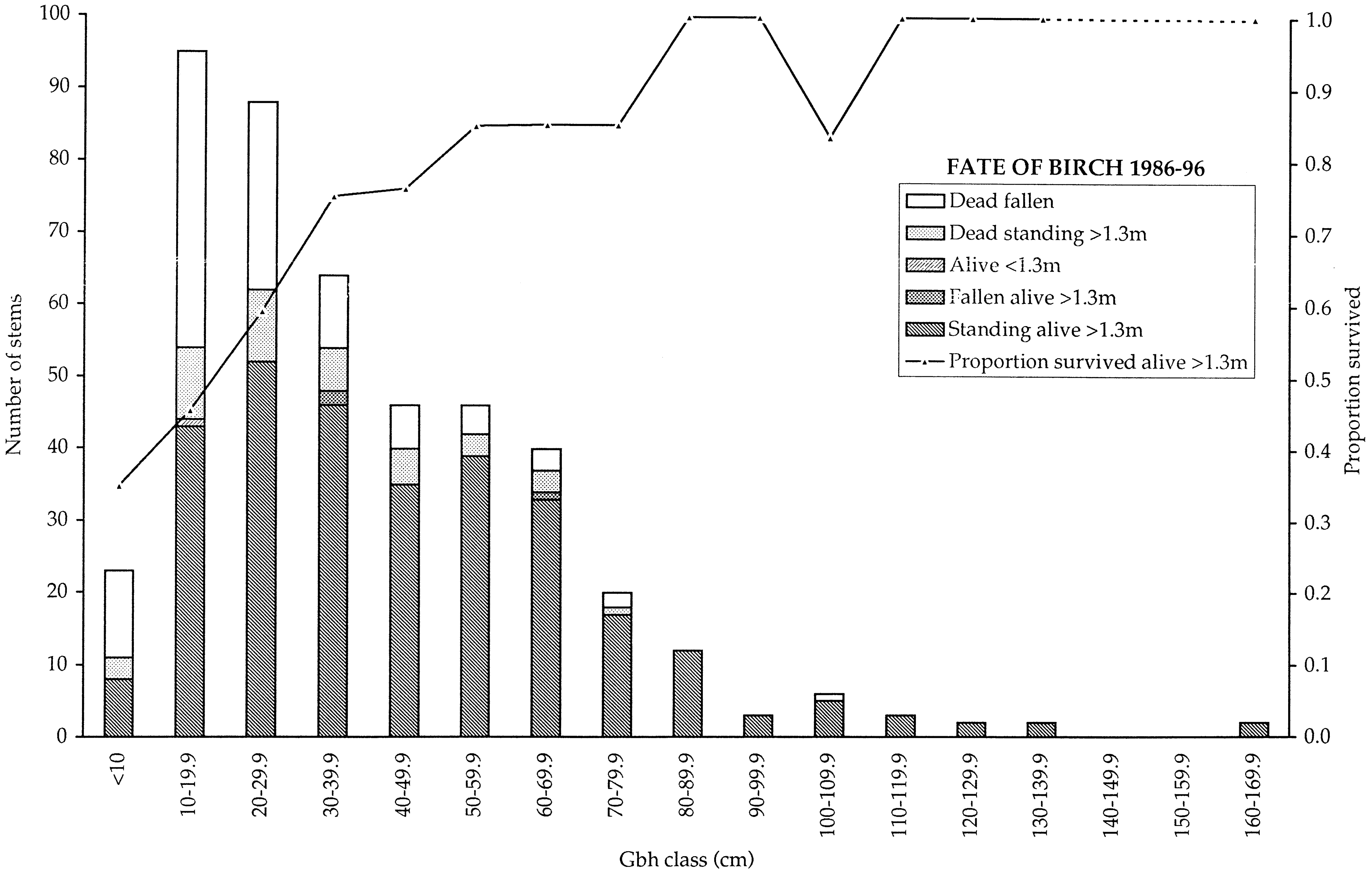

Figure 7: Size class fate and proportional survival of birch stems standing alive >1.3m height in 1986 by 1996.

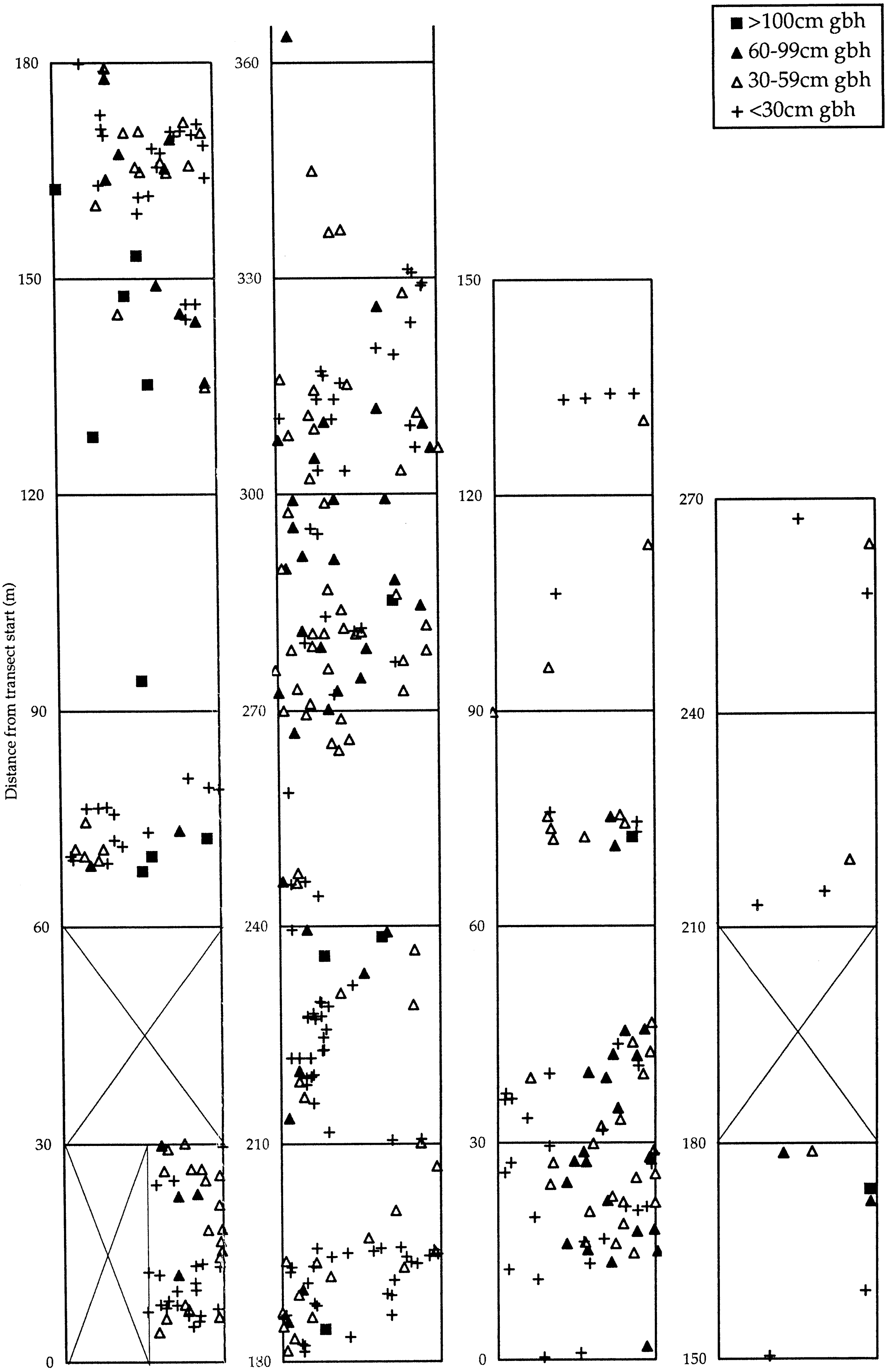

Figure 8: Distribution of live standing birches along transects in 1986. Symbols show location and size of stems. Multi-stemmed individuals are based on size of largest stem. Sections marked X were not recorded.

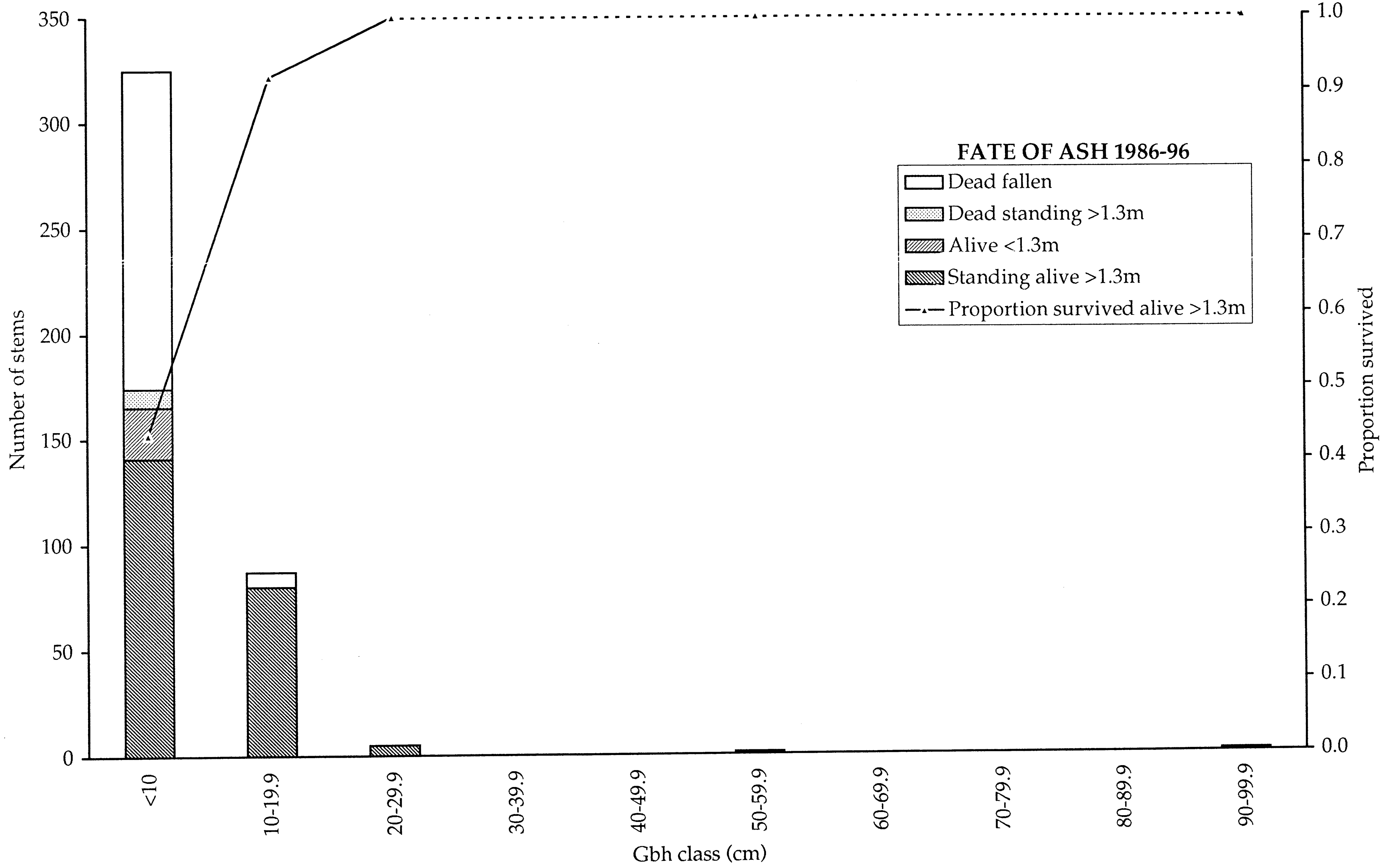

Figure 9: Size class fate and proportional survival of ash stems standing alive >1.3m height in 1986 by 1996.

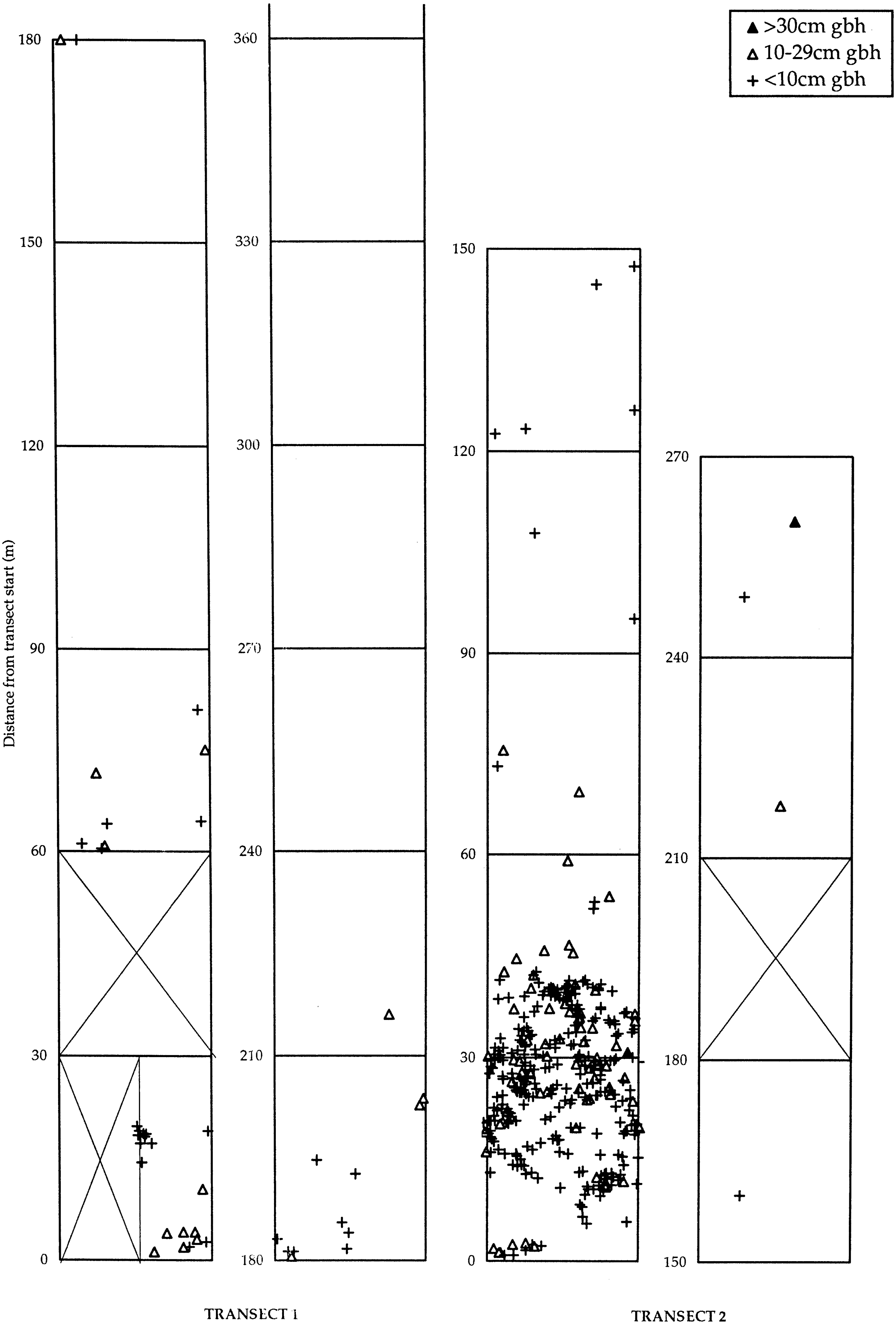

Figure 10: Distribution of live standing ashes along transects in 1986. Symbols show location and size of stems. Multi-stemmed individuals are based on size of largest stem. Sections marked X were not recorded.

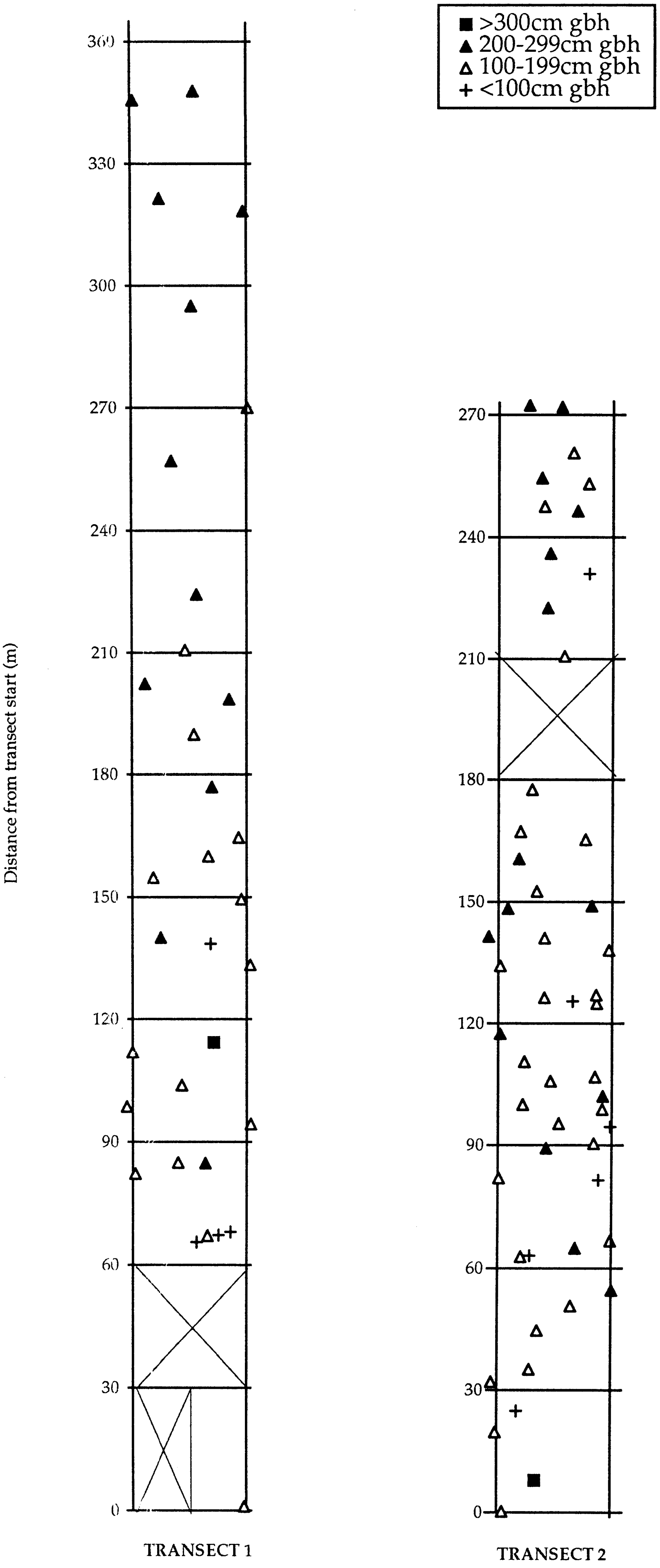

Figure 12: Distribution of live standing oaks along transects in 1986. Symbols show location and size of stems. Multi-stemmed individuals are based on size of largest stem. Sections marked X were not recorded.

years, to the smallest and youngest, which may have been recruited at the last coppicing, but the majority area probably around 200 years old. Their distribution and abundance is mostly a product of promotion under past coppice and wood pasture management regimes.

Performance of oak between 1986-96 revealed minimal stem exclusion. Mortality was restricted to smaller-sized trees, but one tree failed standing in full sunlight (Figure 11). There was the expected exclusion relationship between stem girth, crown size and dieback (Tables 30 and 31; Figure 24), and, as expected for this shade-intolerant species, only a few small girth trees persisted in the sub-canopy and understorey (Table 23). However only some of the growth patterns could be explained by exclusion. The fastest growing trees were medium-large crowned canopy trees, whilst the slowest included many of the small crowned canopy trees and most of the lower strata trees (Tables 15-16; Figure 20). Nevertheless the very largest girth and large crowned canopy trees grew quite slowly, and many mid-size canopy trees grew at very different rates. Natural senescence probably explains the slowing growth of the largest trees, but the poor performance of many mid-size trees probably relates to their past retention on sub-optimal sites.

This pattern of low mortality and variable growth has been observed in other populations of oak in former coppices (Peterken and Jones 1987, 1989; Backmeroff and Peterken 1989; Mountford 1994, 1997b; Mountford and Peterken 1998). Some individuals appear to have the potential to live for many centuries. Recruitment is typically minimal and regeneration appears to require a major canopy disturbance.

Hazel

Hazel stems were more abundant than any other species, dominating the understorey and ground layers (Tables 3 and 23). However most were small girth and amounted to a small percentage of the stand basal area (Table 2; Figure 13). Hazel stems mostly occurred on multi-stemmed stools, but few had very many stems. The size-class distribution suggested that many stems were survivors from a quasi-even-aged post-coppicing cohort, but at least some small girth stems were of more recent origin; between 1986-96 hazel demonstrated the ability to replace itself on multi-stemmed stools, a form of natural coppicing, and some new individuals and numerous seedlings had established by 1996 (Tables 4 and 6).

Only in the birch-oak-hazel transect sections (Peterken type 6Dc), which are very widespread in Langley Wood, did hazel form a dense underwood (Figures 8, 10, 12 and 14). Hazel is typical in such former coppice stands on light acid soils (Peterken 1993a), having being promoted by the past management; it sprouts vigorously when cut regularly and thrives in the high-light coppice-environment. Hazel was excluded from areas with dense lime (Figures 6 and 14), shaded out by this competitive species, and it was also absent from some birch-oak areas (Peterken type 6Dc) (Figures 8, 12 and 14), perhaps because the soils were too sandy.

Hazel generally performed well (Table 2, 4, 6, 9, and 18-20; Figure 13). Percentage mortality was quite low, average stem growth was similar to lime, birch and ash, stems losses were mainly small-sized and mostly resulted in the thinning of existing multi-stemmed stools. The basal area increased substantially and many new stems, individuals and seedlings established.

Exclusion processes appeared to explain some of the growth and mortality patterns between 1986-96 (Tables 32-33; Figure 13 and 25). Mortality was mainly of small girth stems, survivors in the ground layer tended to have smaller girths and more dieback, and smaller girth survivors within each strata tended to have smaller crowns and more dieback. However there was a poor relationship between stem girth and growth, although larger crowned stems did tend to grow faster than smaller ones, and a proportion of stems in nearly all size classes failed, the greatest being in the largest size-classes (Tables 18-20; Figure 13). This was partly explained by strikes from falling canopy debris, but exclusion due to crown weighting appeared important; very many hazels were arched, leaning, or spreading and the proportion of such stems that appeared non-vigorous rose as crown size increased (Tables 32-33). Indeed stems that appeared vigorous were mainly erect and small crowned.

Similar patterns of mortality and growth have been recorded for hazel in other near-natural stands, and certainly individual stems have the potential to attain far greater maximum sizes (Mountford 1994; Mountford and Peterken 1998). However this is the first time that hazel has been recorded in the regeneration associated with understorey reinitiation. Combined with the other patterns of change, it is probable that, at least for the next few decades, hazel will continue to provide a dense self-regenerating underwood in the birch-oak-hazel stands at Langley. However, hazel tends to die out below heavily shading trees (Peterken and Jones 1987), and future oak crown expansion may facilitate this. In contrast, any canopy disturbance will serve to perpetuate hazel.

Hawthorn

Hawthorn was the other common underwood species, but it was far less abundant than hazel and accounted for a very small percentage of the stand basal area (Table 2 and 3). Hawthorn individuals were mostly single-stemmed, no very large stools existed, and the size-class distribution suggested that the population contained many larger girth survivors from a quasi-even-aged post-coppicing cohort (Figure 15). However at least some smaller stems were of recent origin; between 1986-96 some new stems arose and very many seedlings <1.3m height had established by 1996 (Tables 4 and 6). The distribution of hawthorn and the newly established seedlings paralleled that of hazel; they were abundant only in the birch-oak-hazel transect sections (Peterken type 6Dc) (Figures 8, 10, 12, 14 and 16). Exclusion from the other stands presumably occurring for similar reasons.

Performance of hawthorn between 1986-96 was indifferent (Tables 4; Figures 17 and 20-21); stem survival was fairly high, but average growth of survivors was much poorer than its counterpart hazel. Consequently and the basal area remained virtually static. Turnover of individuals was high (Tables 4 and 6); most failures resulted in the loss of entire individuals, but recruitment exceeded losses and was mainly from new seedlings. Overall the density of stems slightly increased (Table 3).

Exclusion processes only partly explained performance patterns. Deaths occurred in all size-classes, although most were of smaller girth stems, and growth bore little relation to girth, crown size or canopy position (Tables 18, and 21-22; Figure 15 and 26). Some mortality was accredited to damage and pinning by falling trees and canopy debris.

Hawthorn has shown similar patterns of growth and mortality in other near-natural stands, and typically exists as an intermediate-lived, moderately shade-tolerant, underwood species (Peterken and Jones 1987, 1989; Mountford 1994; Mountford and Peterken 1998). This is the first time that hawthorn has been recorded regenerating during understorey reinitiation, and combined with the fact that individual stems can attain sizes up to almost 100cm gbh (Mountford and Peterken 1998), it is most probable that it will maintain itself in the underwood of the birch-oak-hazel stands at Langley.

Exotics

The current management plan provides for the control of exotic trees and shrubs. Three exotic species were recorded on the transects (Tables 2 and 3). Rhododendron remained as a single patch but spread rapidly at the rate of 10cm per year. Four sweet chestnuts were present in 1986, all of which survived, and the largest canopy tree increased, remarkably, from 64cm to 120cm. Three sycamores were present in 1986, all of which survived in the understorey, and the largest tree increased from 36cm to 46cm. None of the three species recruited new stems, and only sycamore had established a single seedling <1.3m high by 1996 (Table 6). Regeneration of exotics, at least in the vicinity of the transects, appears to be virtually absent, but some existing individuals are developing vigorously, and could provide potential seed sources for gap-phase regeneration: immediate control is accordingly recommended.

Impacts of grey squirrel and deer bark-stripping

In 1996 grey squirrel bark-stripping was widespread amongst beech (Table 36) and had badly damage the largest of three sycamore stems. This was despite a cull of about 300 squirrels in 1995 (pers. comm. Nigel Anderson). Most beeches were debarked and often severely so, with the greatest amounts of debarking on stems 22-29cm and >40cm gbh. There was some evidence to show that fast growing sub-canopy stems were especially vulnerable to attack. Severe debarking was causing early crown yellowing in some trees and resulted in the only two medium-girth beech deaths between 1986-96.

Quite similar patterns of grey squirrel bark-stripping were recorded in Lady Park Wood between 1983-93 (Mountford 1997a): over the decade squirrels had badly debarked over 50% of beech individuals, attacking mainly intermediate 30-80cm gbh stems, especially fast-growing ones which they repeatedly debarked, and some trees that were potential canopy dominants died. Beech is renowned as a potential long-lived, shade-bearing, and dominant tree (Peterken 1996), and has apparently been limited within Langley Wood by past management practices. The establishment of several vigorous young trees suggested that it may increase in the wood, but it is clear that its potential is being seriously compromised by squirrel debarking. However, badly damaged trees can persist and even continue to grow rapidly (Mountford 1997a).

Basal bark-stripping accredited to deer was very small-scale, mainly effected small stems <10cm gbh, most of which were hazel, although lime had the greatest percentage damage (Table 37). This was despite the fact that the total number of deer in Langley have apparently increased in recent years and colonisation by muntjac has occurred (pers. comm. Nigel Anderson). In Monks Wood, the latter have increased substantially since the mid-1980s and have destroyed and badly stripped advance regeneration and small girth stems in c.75 year old mixed broadleaved stands (Mountford and Peterken 1998).

Changes in the dead wood component

The basal area of dead standing wood between 1986-96 remained very low and represented a small percentage of the total stand basal area (Table 38). However most stems were small girth, so the number of standing stems was considerable (Table 39; Figure 27). The survey of snags in 196 found that, apart from being mainly small girth, they were mainly short-medium height (<10m), had little decay, and most bark remaining (Table 41). Compared to other similar aged near-natural stands the basal area was much lower (Mountford and Peterken 1998) and slight compared to the levels approaching 10 m^2 ha^{-1} that can amass (Mountford 1997b). The low standing accumulations were related to the enormous turnover of stems (Table 40). Only 6% of dead standing stems in 1986 remained standing in 1996, throughput of stems standing alive in 1986 and dead fallen by 1996 amounted to 2.3 times the total number of standing stems in 1986, and a small number of stems recruited, died, and fell over between 1986-96. Despite the turnover basal area levels changed little and were mostly of oak and birch. Oak and birch also accounted for most of the snag volume, with decay in oak appearing slow and decay in birch, lime and hazel appearing more rapid. The total number of stems fell by only about a quarter and small girth hazels predominated throughout (Tables 38 and 39; Figures 28). Larger dead standing material remained extremely scarce, the only stability coming from one oak trunk >100cm gbh. However larger standing birches did increase, and large girth snags tended to remain upright for longer than small girth ones (Figures 5 and 7).

The estimated 15m^3 ha^{-1} fallen material volume and 1683m ha^{-1} dead wood length (Table 42) were at the lower end of the ranges given for derelict coppice sites in Britain (Kirby *et al.* 1998), and were far lower than the 50-150m^3 per hectare typical of old-growth temperate forests (Peterken 1996; Kirby *et. al.* 1998). Fallen dead wood composition was similar to standing; most stems were small <10cm diameter and fairly solid, most volume was of oak or birch, and decay of oak appeared slow, whilst decay in birch appeared rapid (Table 42). The low accumulations must be related to rapid decay of most material, although most recently inputted stems were mainly small girth which contribute little to the fallen volume. Removal of fallen dead wood for firewood in the recent past will also have reduced accumulations.

The total dead wood volume (standing and fallen), estimated at about 24m^3 ha^{-1} (Tables 41 and 42), was far lower than the 46-132m^3 ha^{-1} reported from various natural old-growth temperate broadleaved forests (Peterken 1996).

References

Backmeroff, C.E. 1987. Langley Wood SSSI: Long-term monitoring programme summer 1986. *Unpublished Report, NCC.*

Backmeroff, C.E. and Peterken, G.F. 1989. Long-term changes in the woodlands of Clairinsh. *Transactions of the Botanical Society of Edinburgh* 45, 253-97.

Bennet, K.D. 1989. A provisional map of forest types for the British Isles 5000 years ago. *Journal of Quaternary Science* 4, 141-44.

Grime, J.P., Hodgson, J.G. and Hunt, R. 1990. *The Abridged Comparative Plant Ecology.* Chapman and Hall, London.

Kenward, R.E. and Dutton, J.C.F. 1996. Damage by grey squirrels. II. The value of prediction. *Quarterly Journal of Forestry* 90, 211-218.

Kirby, K. and Reid, C. 1997. *Preliminary nature conservation objectives for Natural Areas: woodland and forestry.* English Nature Research Report No. 239. English Nature, Peterborough.

Kirby, K.J., Reid, C.M., Thomas, R.C. and Goldsmith, F.B. 1998. Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. *Journal of Applied Ecology* 35, 148-155.

Mountford, E.P. 1994. Sixteen years of change in a near-natural mixed deciduous woodland: Lady Park Wood young-growth stands. *Unpublished B.Sc. (Hons) Thesis, Edge Hill University College.*

Mountford, E.P. 1997a. A decade of grey squirrel bark-stripping damage to beech in Lady Park Wood, UK. *Forestry* 70, 17-29.

Mountford, E.P. 1997b. Stand change along the Denny Inclosure transect 1956-96. *Unpublished Report, Ecoscope Applied Ecologists.*

Mountford, E.P. and Peterken, G.F. 1998. *Monitoring natural stand change in Monks Wood National Nature Reserve.* English Nature Research Report No. 270. English Nature, Peterborough.

Oliver, C.D. and Larsen, B.C. 1996. *Forest Stand Dynamics.* Wiley, New York.

Peterken, G.F. 1993a. *Woodland Conservation and Management.* 2nd Edition. Chapman and Hall, London.

Peterken, G.F. 1993b. Management Issues. *Unpublished Consultation Paper, English Nature.*

Peterken, G.F. 1996. *Natural Woodland: Ecology and Conservation in Northern Temperate Regions.* Cambridge University Press, Cambridge.

Peterken, G.F. and Backmeroff, C.E. 1988. *Long-term monitoring in unmanaged woodland nature reserves.* Research & Survey in Nature Conservation No. 9. Nature Conservancy Council, Peterborough.

Peterken, G.F. and Jones, E.W. 1987. Forty years of change in Lady Park Wood: the old-growth stands. *Journal of Ecology* 75, 477-512.

Peterken, G.F. & Jones, E.W. 1989. Forty years of change in Lady Park Wood: the young-growth stands. *Journal of Ecology* 77, 401-429.

Pigott, C.D. 1975. Natural regeneration of *Tilia cordata* in relation to forest-structure in the forest of Bialowieza, Poland. *Philosophical Transactions of The Royal Society of London B* 270, 151-179.

Pigott, C.D. 1989. Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. IV. Estimates of ages of the trees. *New Phytologist* 112, 117-21.

Pigott, C.D. and Huntley, J.P. 1981. Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. III. Nature and causes of seed sterility. *New Phytologist* 87, 817-39.

Sheppard, D.A. 1989. A preliminary account of the insect fauna of Langley Wood NNR. *Unpublished Report, Nature Conservancy Council.*

White, J. 1981. The allometric interpretation of the self-thinning rule. *Journal of Theoretical Biology* 89, 475-500.

Yoda, K.T., Kira, H., Ogawa, H. and Hozumi, K. 1963. Self thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology Osaka City University* 14, 107-29.

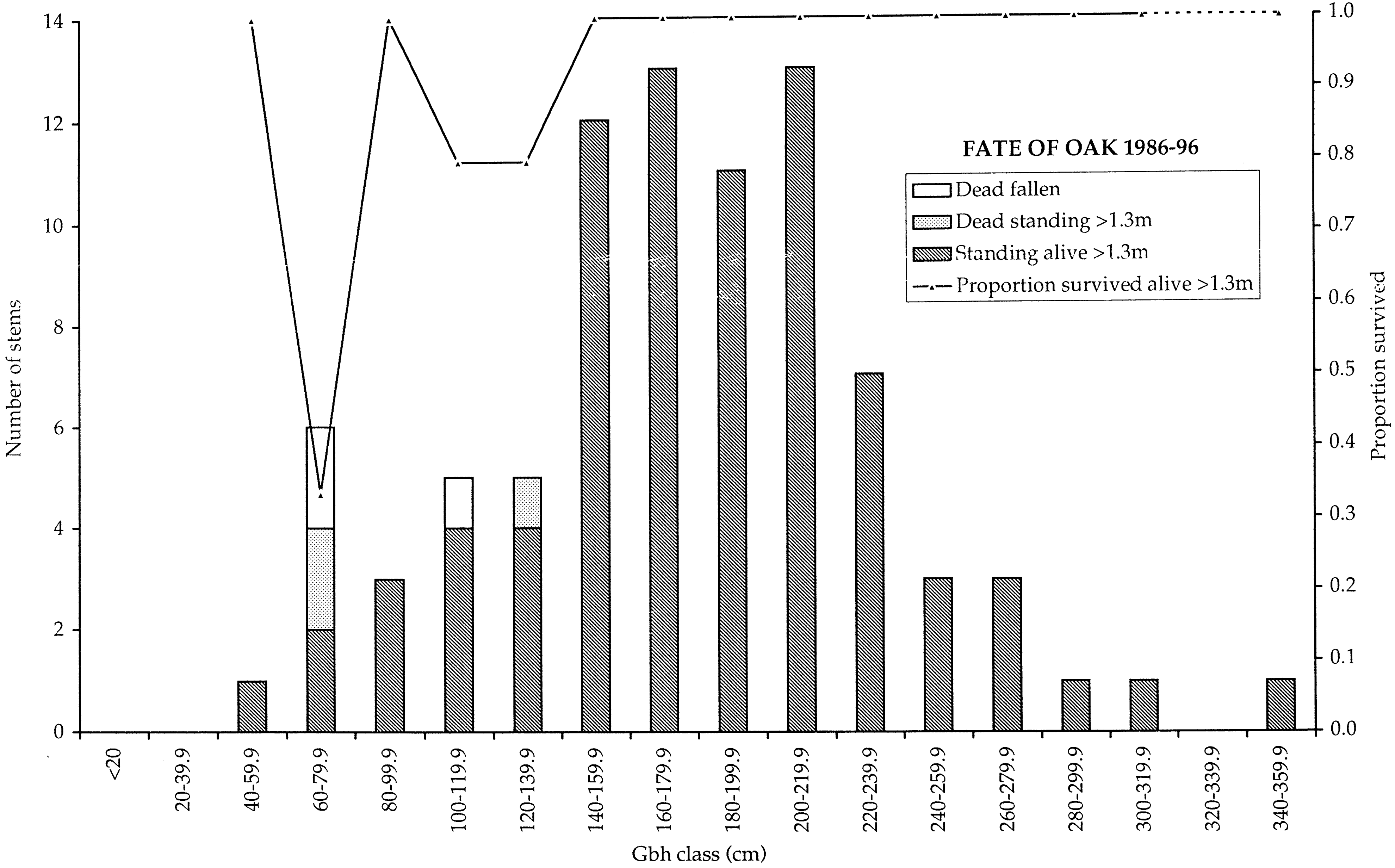

Figure 11: Size class fate and proportional survival of oak stems standing alive >1.3m height in 1986 by 1996.

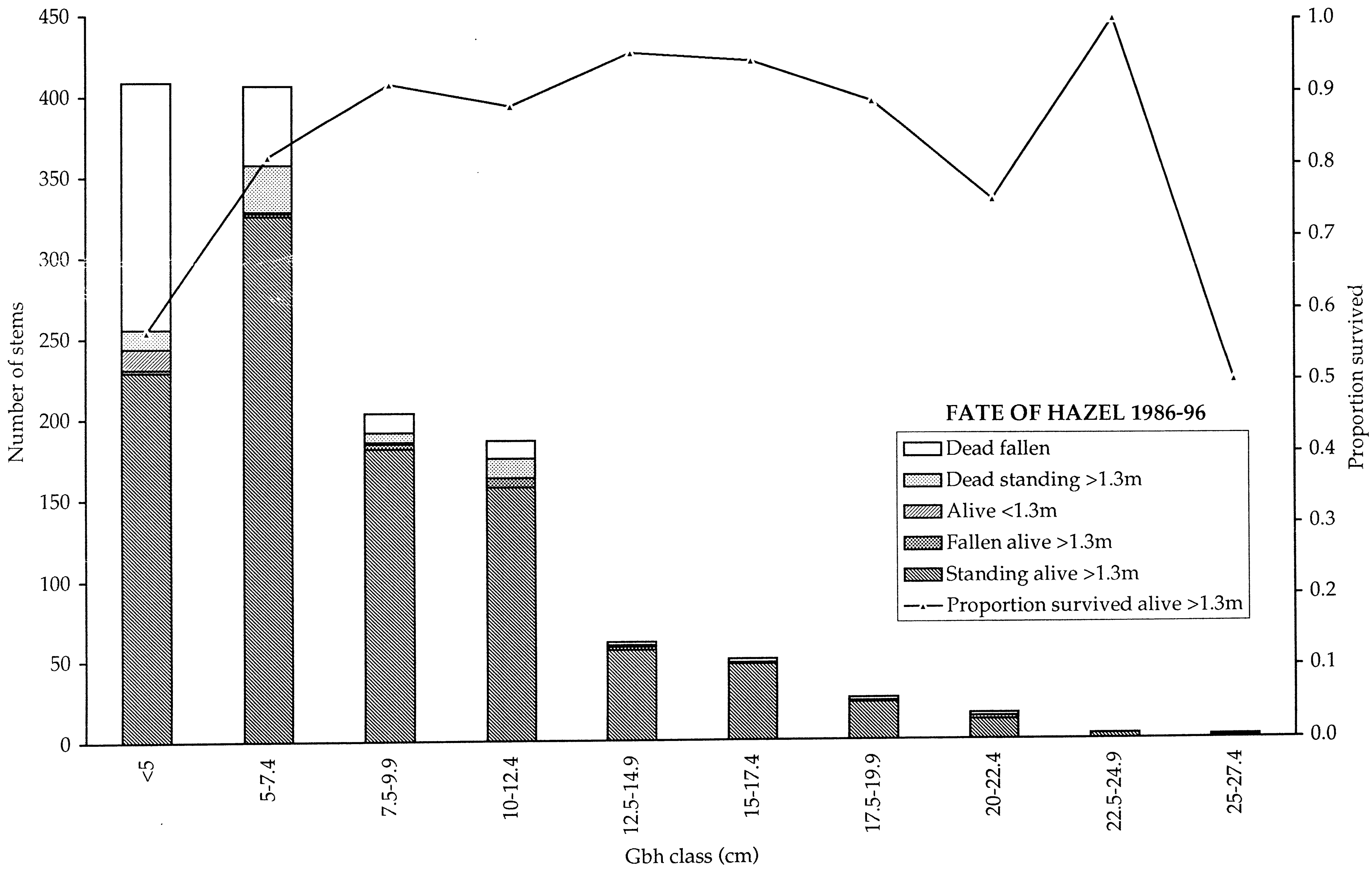

Figure 13: Size class fate and proportional survival of hazel stems standing alive >1.3m height in 1986 by 1996.

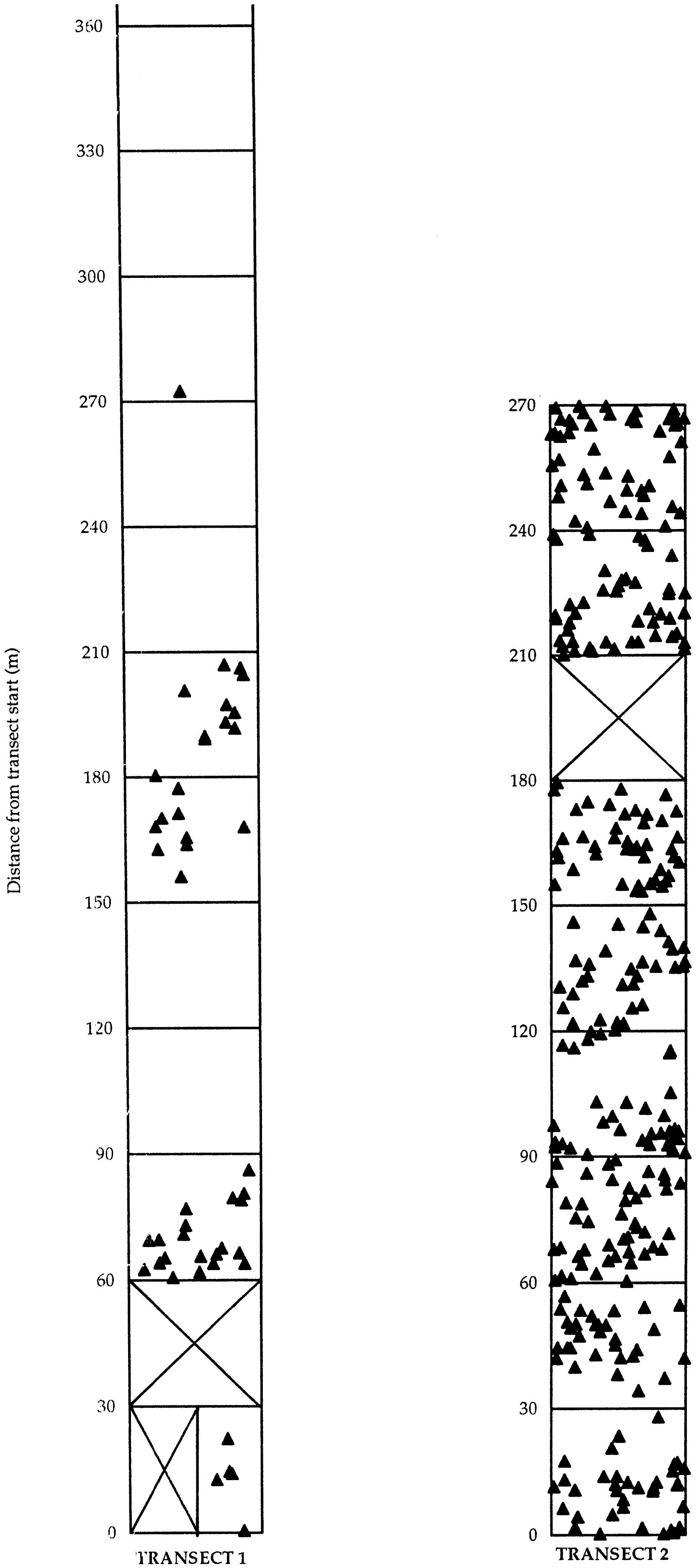

Figure 14: Distribution of live hazel individuals along transects in 1986. Symbols show location of each individual. Multi-stemmed individuals are based on size of largest stem. Sections marked X were not recorded.

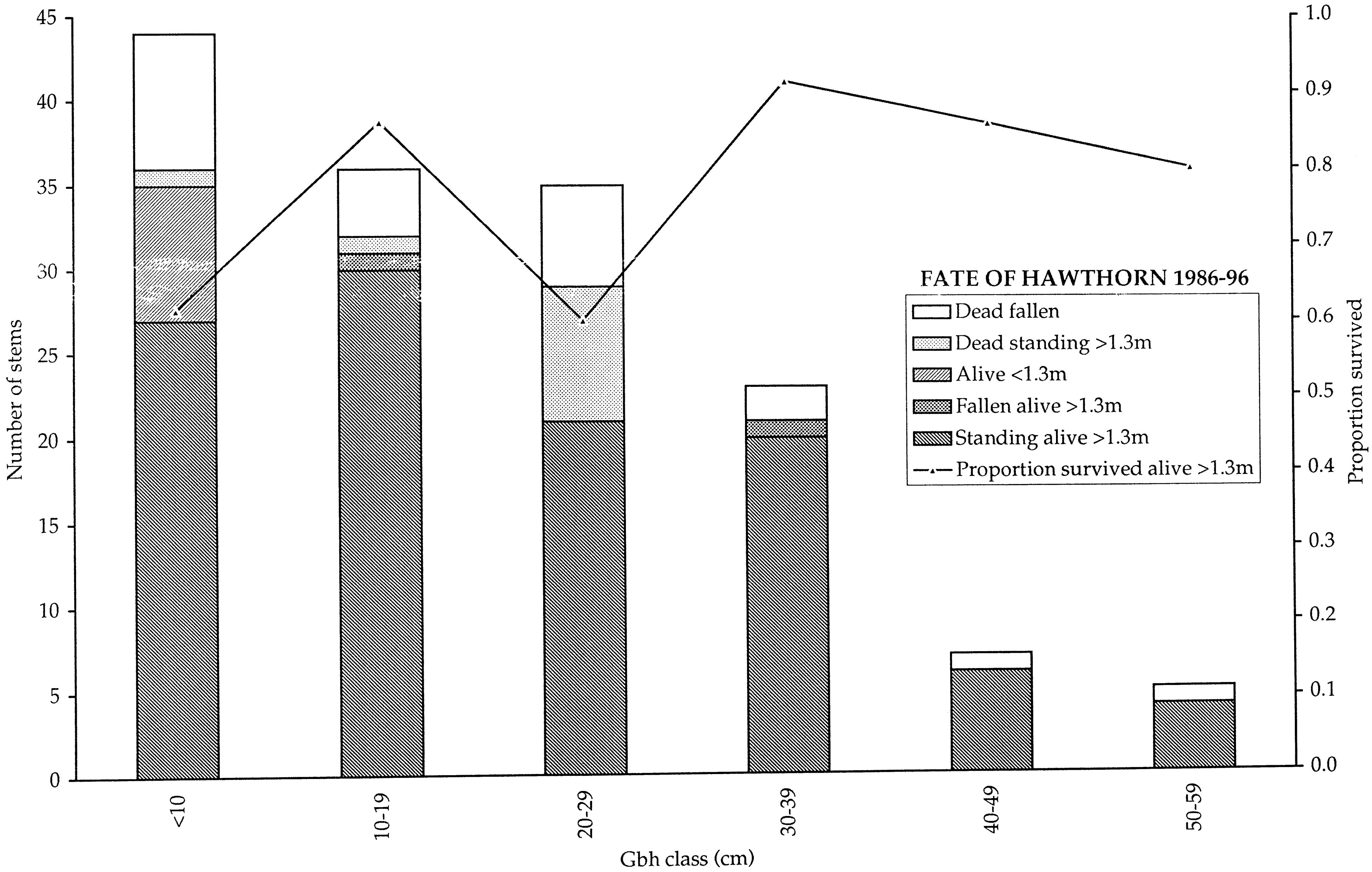

Figure 15: Size class fate and proportional survival of hawthorn stems standing alive >1.3m height in 1986 by 1996.

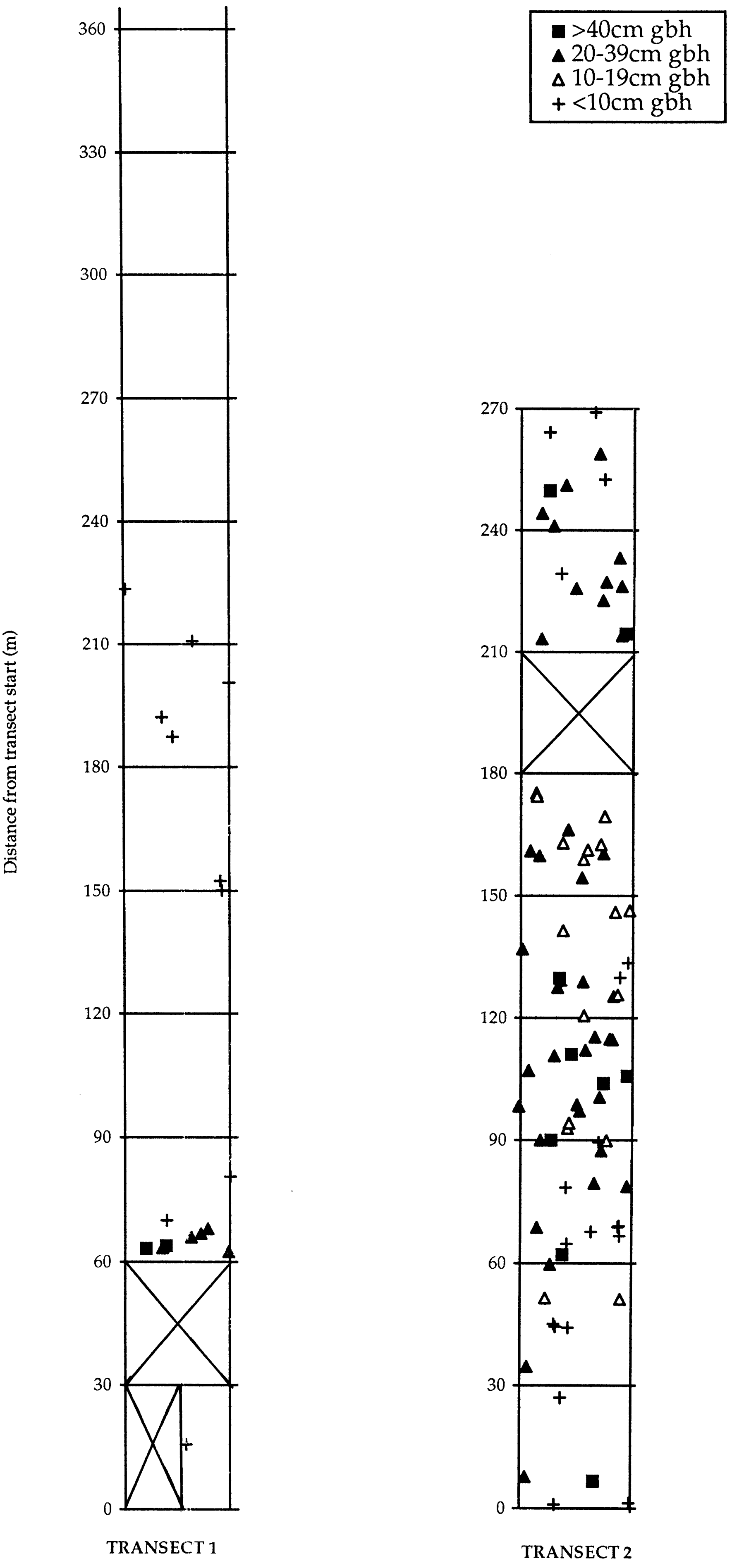

Figure 16: Distribution of live hawthorn individuals along transects in 1986. Symbols show location and size of each individual. Multi-stemmed individuals are based on size of largest stem. Sections marked X were not recorded.

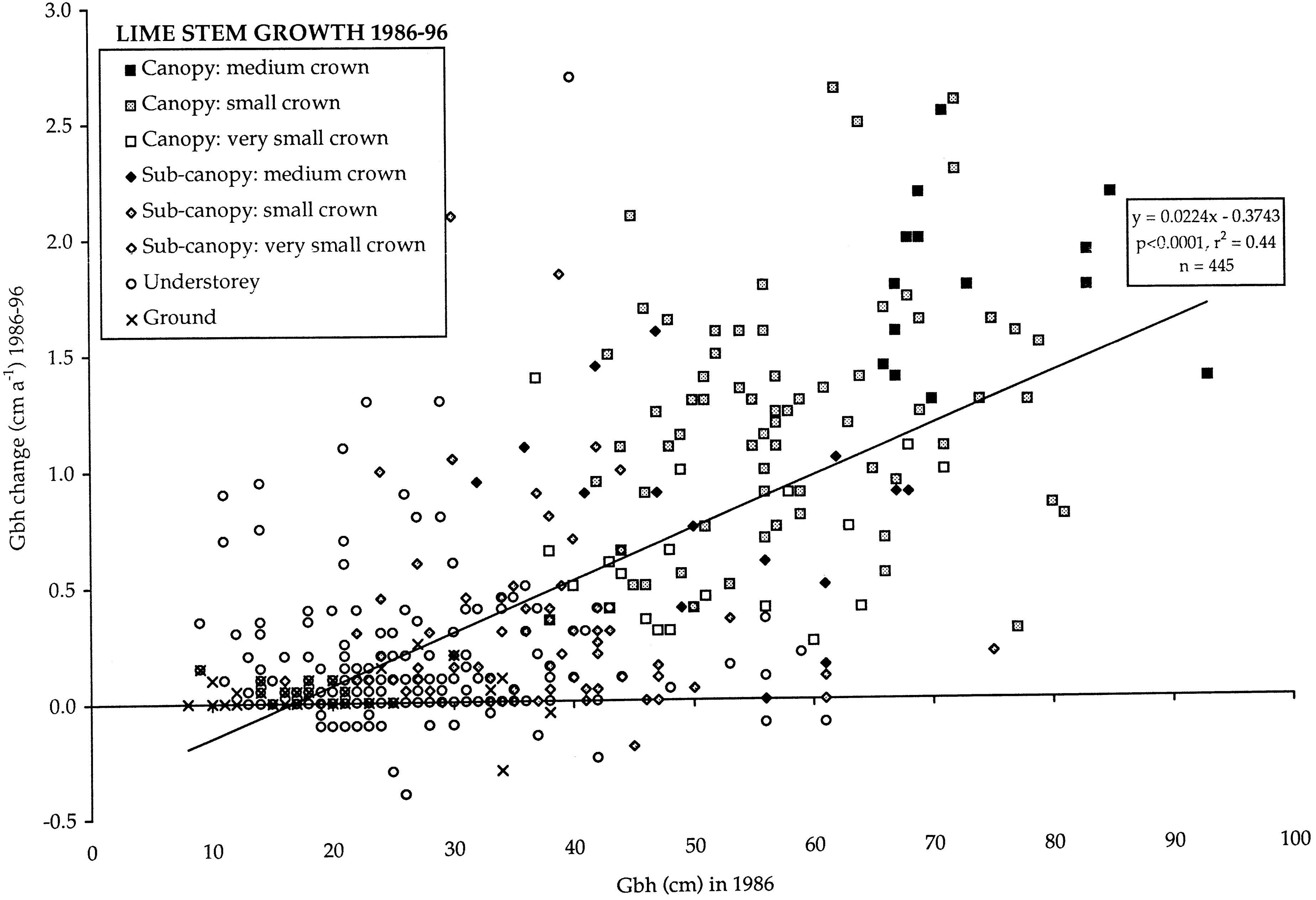

Figure 17: Relationship between stem gbh change and initial size for lime between 1986-96. The linear regression line and equation, and stem canopy position and crown size in 1996 are shown.

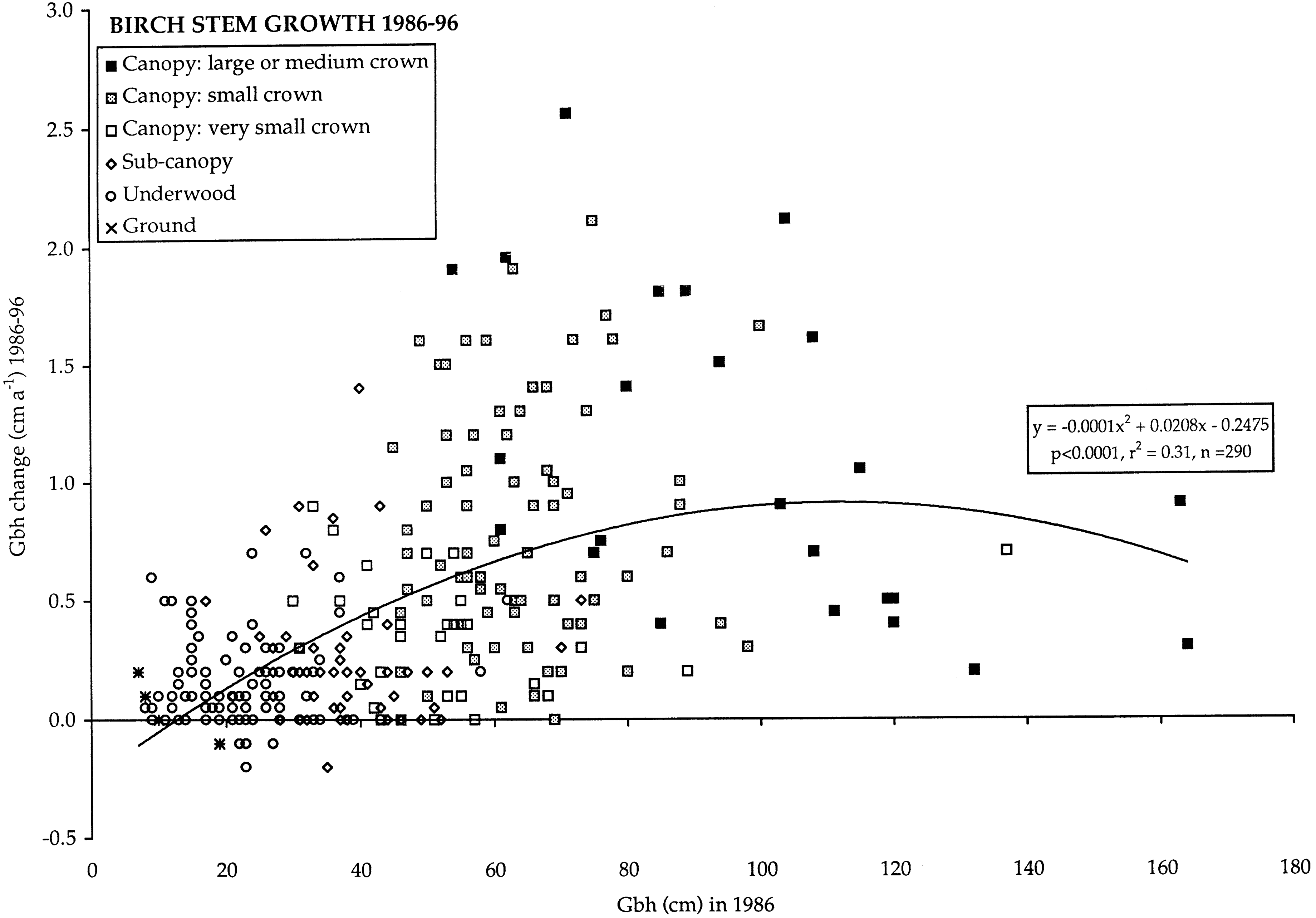

Figure 18: Relationship between stem gbh change and initial size for birch between 1986-96. The quadratic regression line and equation, and stem canopy position and crown size in 1996 are shown.

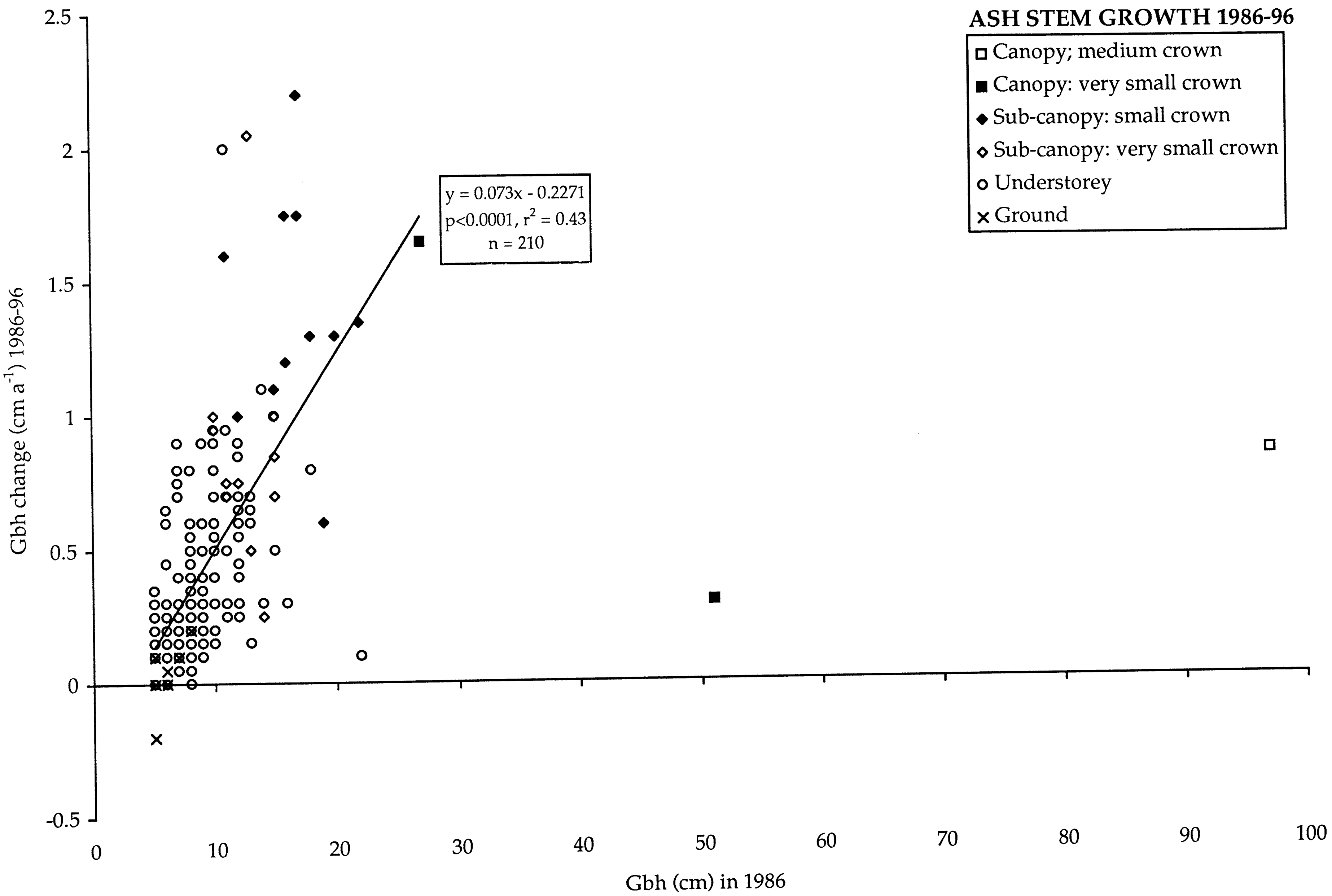

Figure 19: Relationship between stem gbh change and initial size for ash between 1986-96. The linear regression line and equation, and stem canopy position and crown size in 1996 are shown.

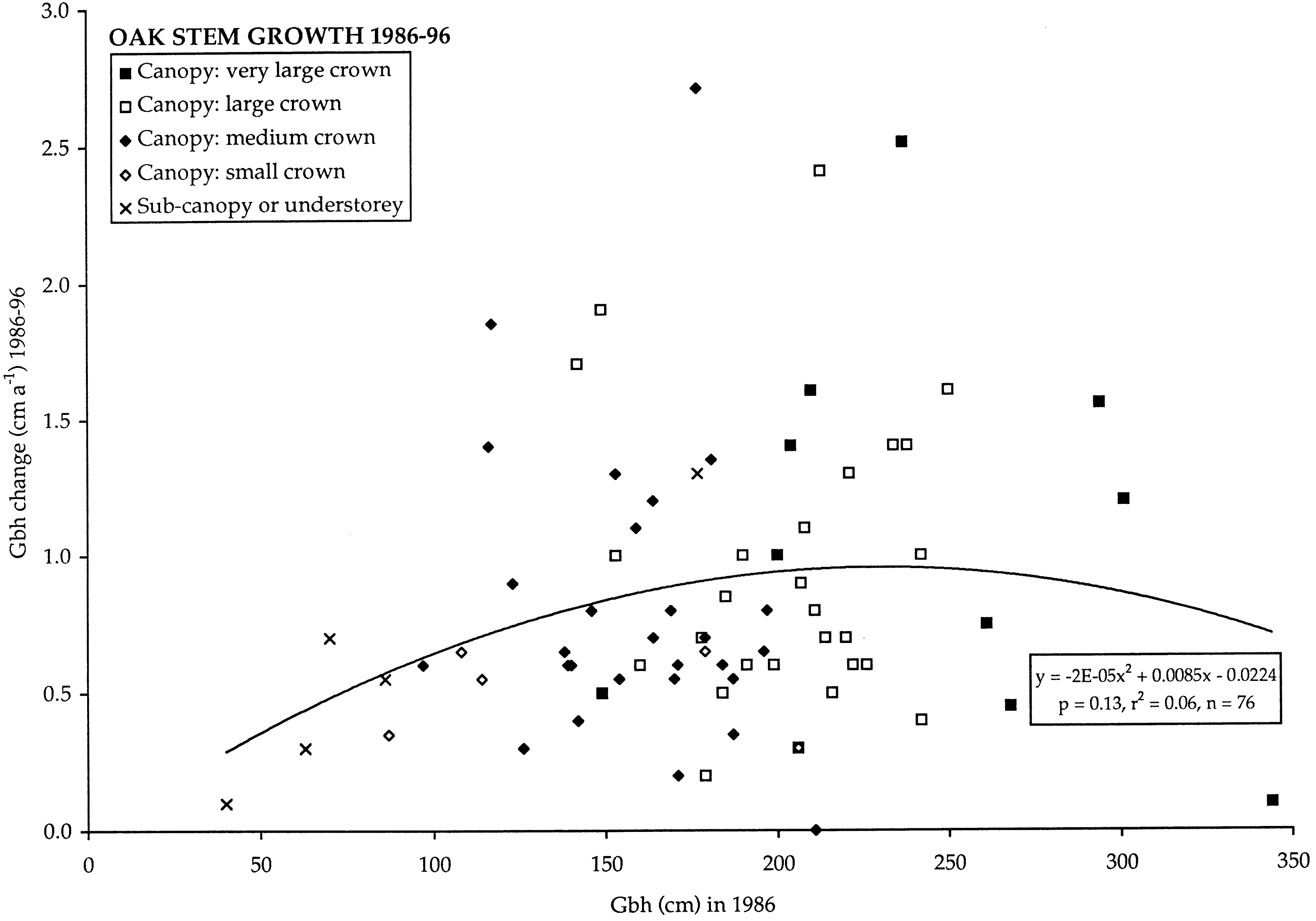

Figure 20: Relationship between stem gbh change and initial size for oak between 1986-96. The quadratic regression line and equation, and stem canopy position and crown size in 1996 are shown.

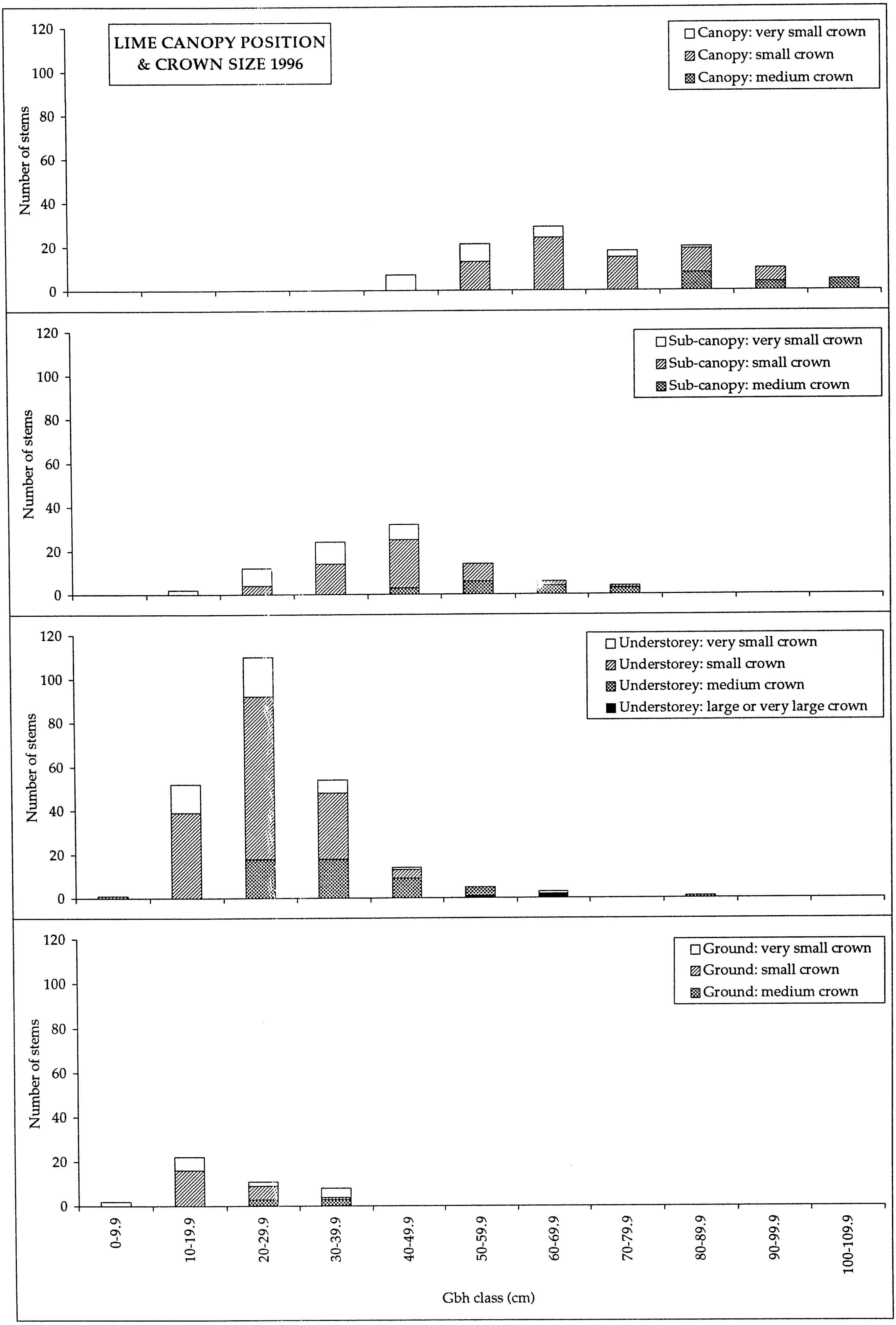

Figure 21: Size-class distribution of living lime stems in 1996 shown in relation to their canopy position and crown size.

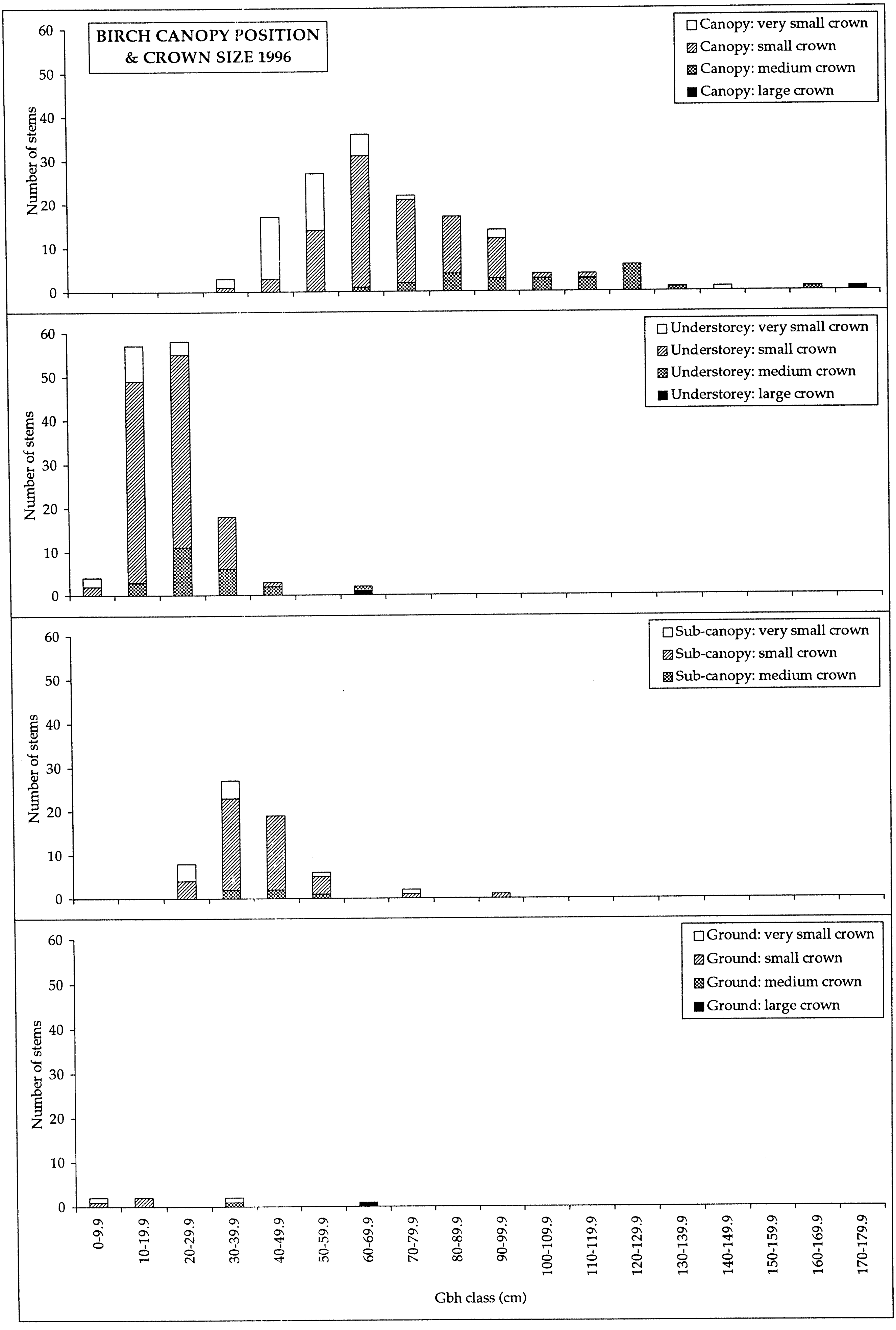

Figure 22: Size-class distribution of living birch stems in 1996 shown in relation to their canopy position and crown size.

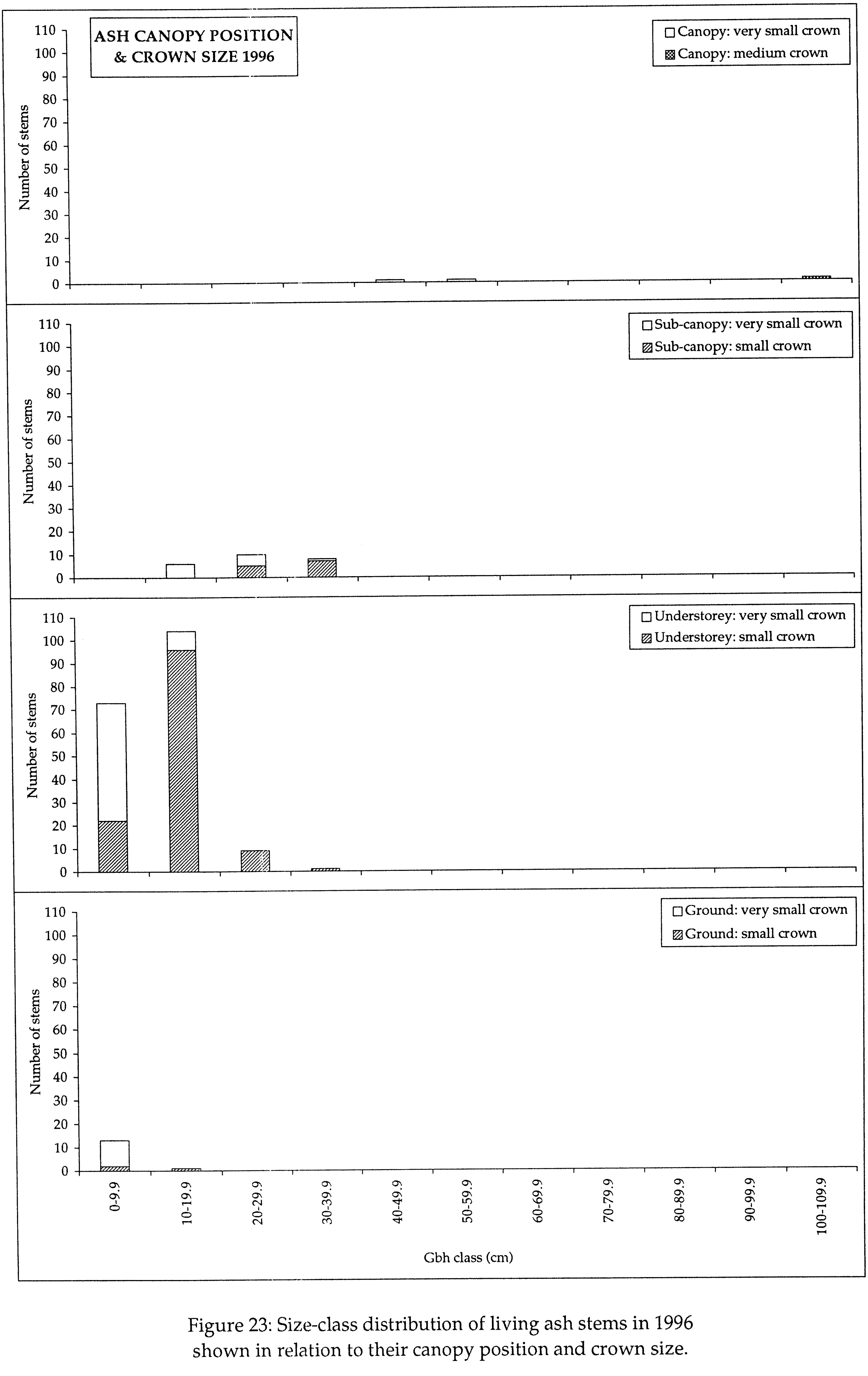

Figure 23: Size-class distribution of living ash stems in 1996 shown in relation to their canopy position and crown size.

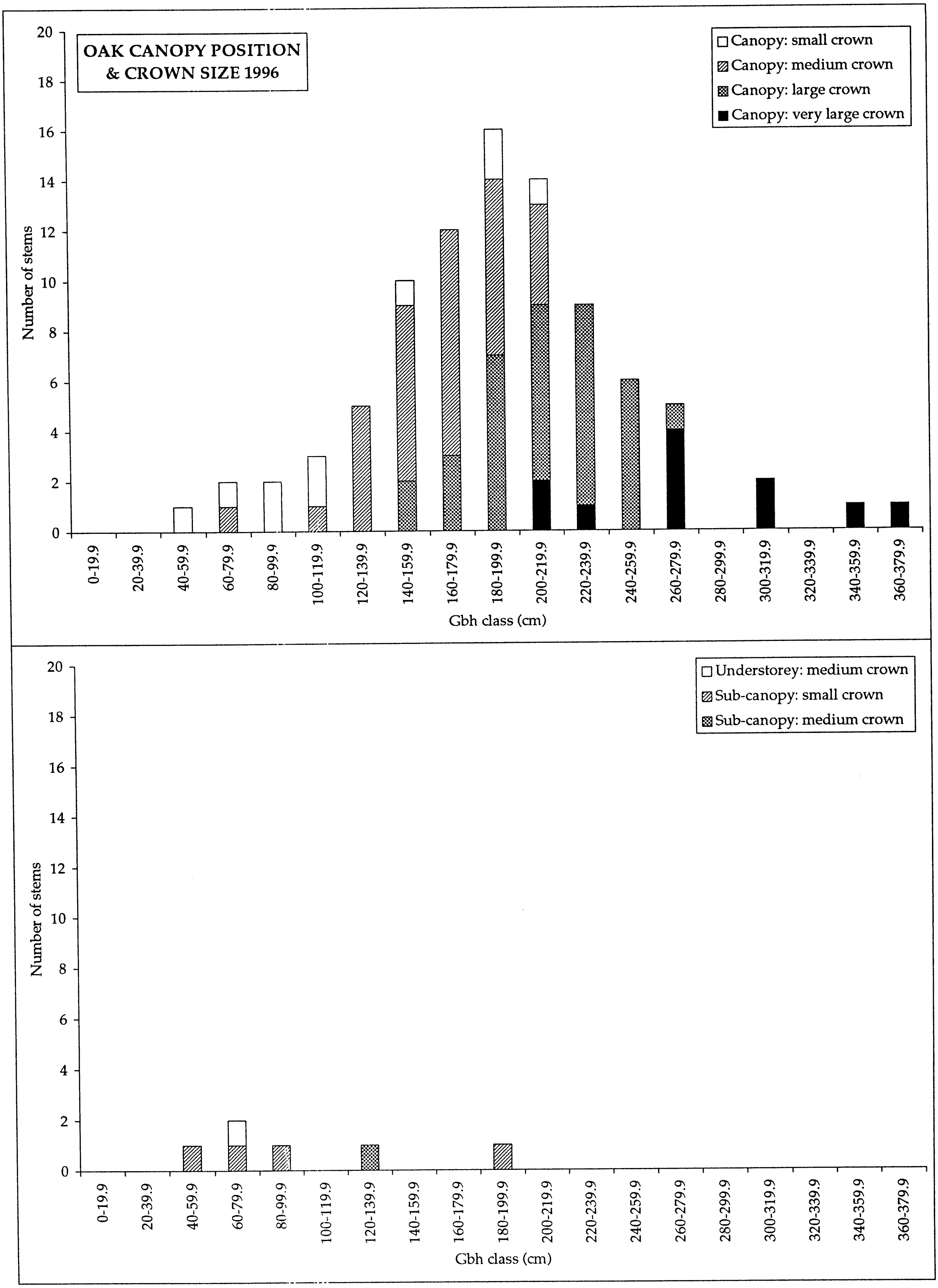

Figure 24: Size-class distribution of living oak stems in 1996 shown in relation to canopy position and crown size.

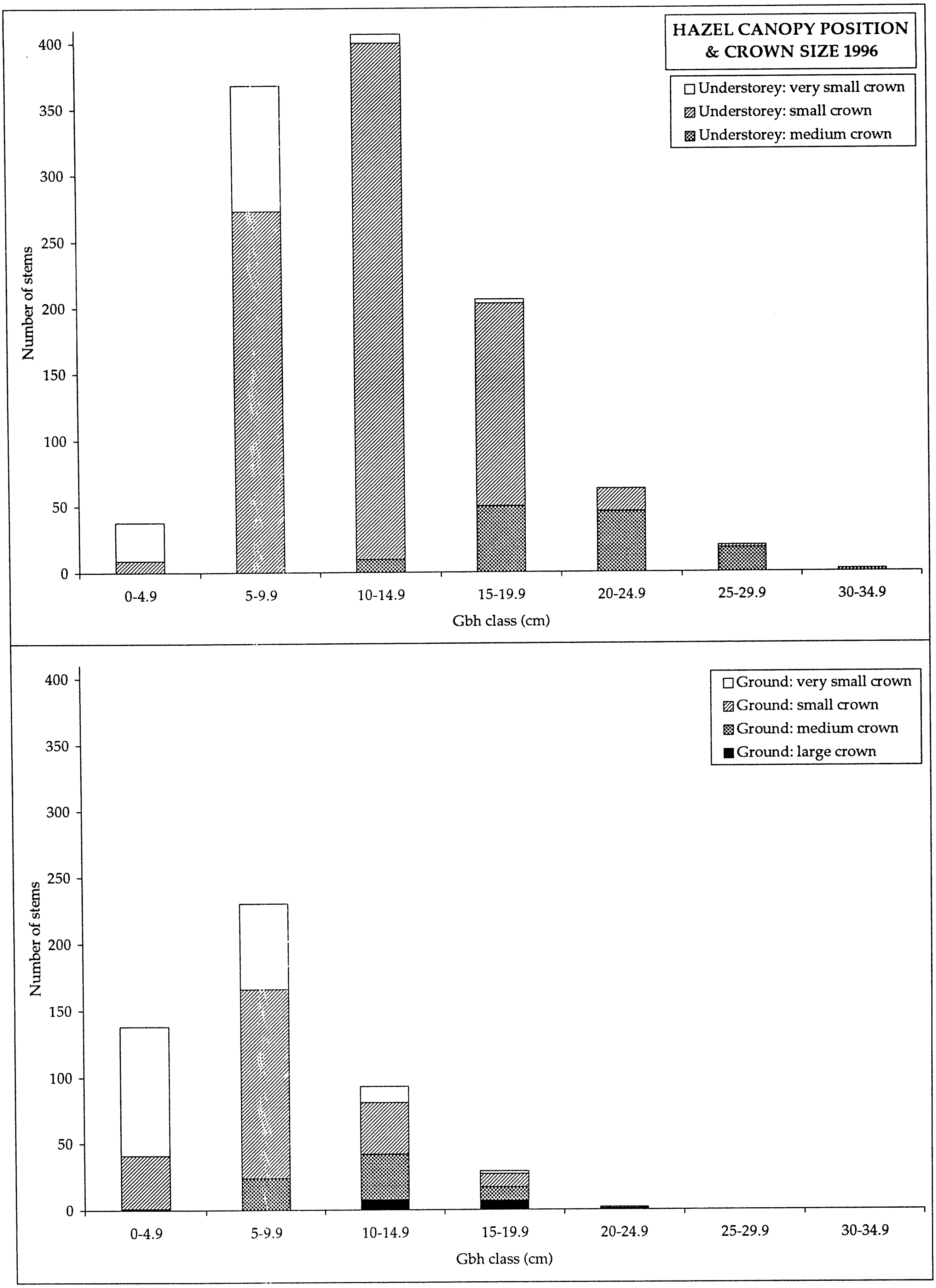

Figure 25: Size-class distribution of living hazel stems in 1996 shown in relation to canopy position and crown size.

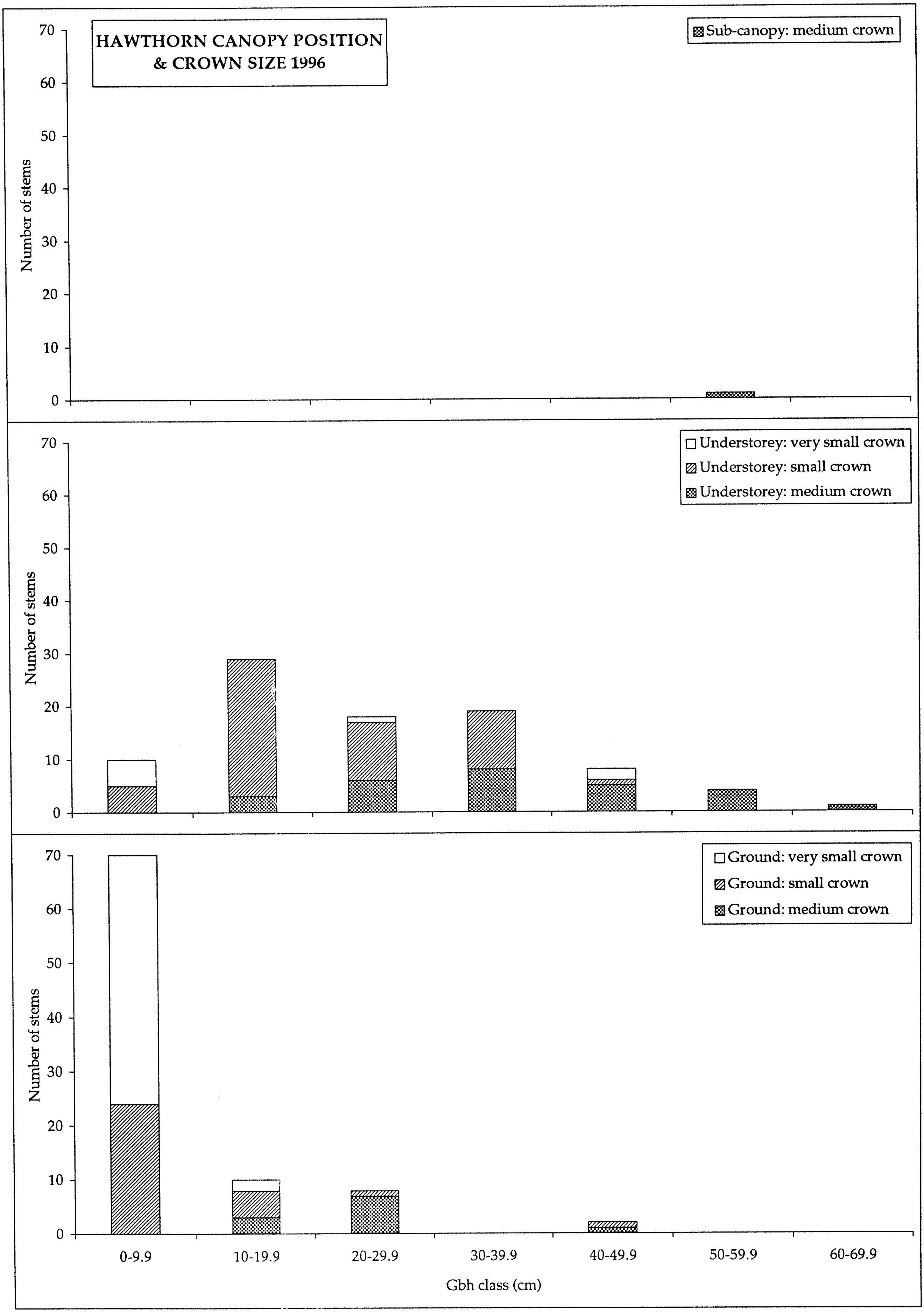

Figure 26: Size-class distribution of living hawthorn stems in 1996 shown in relation to canopy position and crown size.

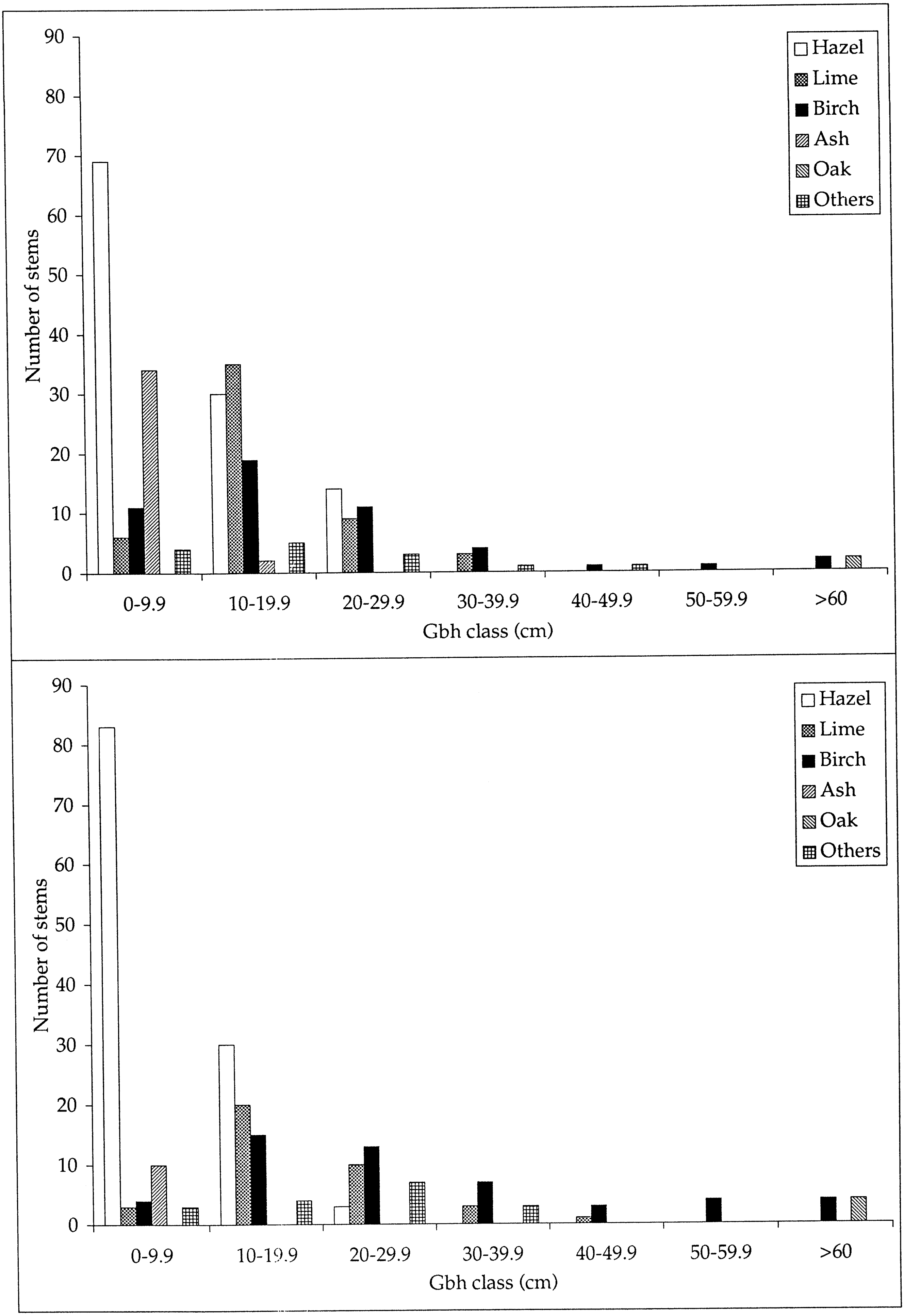

Figure 27: Size-class distribution of dead standing stems
for each species in 1986 (above) and 1996 (below).