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THE EFFECTS OF WINTER FROSTS ON XYLEM EMBOLISM AND THE CONSEQUENCES FOR GROWTH AND PHENOLOGY ACROSS PROVENANCES OF SILVER BIRCH IN SCOTLAND

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A Thesis submitted for the Degree of Master in Philosophy
April 2002

CONTENTS

ABSTRACT

Silver birch has the potential to become an important component of upland forestry throughout Great Britain, However, to realize this potential, more knowledge is necessary on the ecology of growth and reproduction of this species and, especially, about its silvicultural requirements. Particularly, worries have been expressed in the past with regard to the frequent occurrence of phenotypes characterized by poor stem and crown form. Winter damage to young twigs by frost has been suggested as an important potential reason for such occurrence. Silver birch requires protection from low temperatures and drying winds: the death of terminal buds and shoot cambium is often observed in North Scotland (Blackburn. & Brown 1988). Frost damage to the new shoots of birch have also been observed to occur in some years in early spring in Southern Scotland. Environmental differences across sites and annual climatic variations may have profound effects on the regulation of the timing of bud-burst and flowering during spring and the timing of growth cessation and dormancy development during late summer and fall, as well as on the adaptations to resist to frost damage. Frost may therefore be a major factor responsible for reductions in stem growth, and in the quality of the timber of silver birch in Scotland.

This study examined the variations in stem form and phenology of several provenances of silver birch established in three planted trials in Scotland, and investigated the frequency, extent and duration of sap freezing events at one site and the consequent variations in the hydraulic supply capacity of the shoots (i.e. presence of xylem embolism) in winter and early spring.

The results show that the investigated provenances differed significantly in height and in time of bud-flushing in spring. Provenances from the South-East of Scotland tended to be taller and flush earlier.

The first bud on the top leader flushed earlier than the four subtended buds, i.e., it exerted an apical dominance on the other buds. I attempted the construction of a selection index, in order to detect which provenance gave the best overall performance by combining the scores for height, bud-flushing, and stem shape. Observations of shoot dieback during the summer 2000 showed little mortality of the apical shoots due to frost, in agreement with the temperatures recorded in the previous winter and spring, which were seldom below –5°C. Most of the dieback was localised in the upper and thinner part of the leader stems. The provenances showing the highest frequency of damage were also characterised by earlier flushing. Thermocouples were inserted in the xylem of trees to monitor freezing cycles in the field. Exotherms revealing events of sap freezing were detected at temperatures as high as –0.8/-1 °C. All the investigated provenances developed high values of xylem embolism during the winter. The peak of embolism was ~50 % for 3-year-old shoots and ~71 % for one-year-old shoots. Water content of the twigs was also found to decline during winter. During spring (bud-bursting phase), all provenances recovered from winter embolism, with values dropping from the high values of the winter months to the minimum annual values of April, in association with positive xylem pressures measured at 40 cm from the base of the trees. Experimental freeze-thaw cycles in the laboratory on branches of silver birch confirmed that the development of xylem embolism was linked with changes in temperature from below to above the threshold of zero degrees. Younger shoots were found to be more vulnerable to loss of hydraulic conductivity than older shoots, suggesting that the location of greatest damage by frost is the apical twigs. This is consistent with the qualitative observations of shoot mortality in the field. Differences in flushing and in stem height growth across the investigated provenances are likely to be related to the water relations of the shoots during winter.

DECLARATION

This thesis has been composed by myself from results of my own work, except where stated otherwise, and has not been submitted in any other application for a degree.

Sara Strati
March, 2001.

1.INTRODUCTION

1.1. USE OF BIRCH IN SCOTLAND AND EUROPE

Silver birch (*Betula pendula* Roth), together with downy birch (*B.pubescens* Ehrh.) is an important sources of raw material for the mechanical and the chemical forest industry of Finland. Until the 1960s supplies from natural birch forests were sufficient to meet the needs of the industry, then a shortage of raw material threatened the veneer industry and planting of birch started.

Planting of birch increased significantly in the late 1980s reaching its peak in the beginning of the 1990s. In 1997, nurseries were producing 19.3 million birch seedlings, which was about 13% of the total seedling production in Finland (Sevola 1998).

In the United Kingdom, planting of broad-leaved trees has become increasingly important during recent years and broadleaves now constitute about 60% of all forest planting . In particular silver birch is a widely planted species in upland areas, and is recognized as a species with timber production potential (Lorrain-Smith and Worrell, 1991; Cameron et al.1995; Cameron, 1996; Worrell, 1999). In Scotland it occupies about 43% of the area of broad-leaved woodlands over 0.25 ha in size. In recent years the interest in its use has became progressively greater because of its success in Scandinavia and in other northern countries, where birch has become one of the most valuable pulp and timber species, this has indicated that the same potential might be realised in Scottish forestry. The interest has been prompted also by landscape and biodiversity issues (Lorrain-Smith & Worrell, 1991). The government policy encourages multiple purpose forestry across the full range of appropriate sites in Britain through the Woodland Grant Scheme. The planting target under this scheme is 33,000 hectares per annum and the minimum proportion of broadleaves in any scheme is 5% by area. Birch is an essential component of the Native Pinewood Grant Scheme and it is a requirement that broadleaves should be not less than 15%. (Lorrain-Smith and Worrell, 1991).

Silver birch is fast growing for a hardwood and can grow at yield classes in the range of 6 to 10, on a 40-60 year rotation. Its density is about 673 kg/m^3 (one of the strongest timbers commonly grown in Britain), the maximum breaking strength about 123 N/mm^2, the stiffness/elasticity 13.300 N/mm^2, the compression strength about 59.9 N/mm^2. Current markets include flooring, furniture manufacture and industrial turnery. It is highly suitable for the manufacture of paper and board material. It is particularly suitable for some of the low environmental impact pulping processes now being developed.

In terms of ecological value birch is considered to be a 'soil improver', giving rise to deacified soils and so increasing the fertility of some soils, with increased value for silviculture (Dimbleby 1952; Gardiner 1968). Miles & Young (1980) compared the properties of soils under first-generation birch stands with those on adjacent moorland areas. They recorded a change from a mot to a mull humus type under birch stands, increases in pH, exchangeable calcium and total phosphorus, increased rates of cellulose decomposition and nitrogen mineralisation and a decrease in C/N, C/P and C/K quotients from critically high levels present in the moorland soils.

A marked feature of some birch stands in Britain is forking and a relatively poor form. With form I mean particularly stem straightness, but also stem circularity and branching habit, sometimes weakened by grain distortion and knots.

In *Betula,* the sylleptic branching often continuing for many years characteristically produces lateral branches which occupy the middle part of vigorous annual shoots. These often start growing ahead of the terminal bud, and such a lateral may sometimes curve up, compete with and perhaps come to dominate the leading shoot. Vertical cracking of tree trunks due to potential for frost damage to current growth can be quite considerable thereby wasting their value. Such risks are known to exist where birches have been moved too far north in their distribution here in Scotland and for example in Denmark, Sweden and Finland.

1.2. DIEBACK

The potential usefulness of birch as a maincrop with widespread application is dependent on the availability of selected planting stock which will produce good form. Work at Aberdeen (Blackburn & Brown, 1988) has demonstrated high heritability values for resistance to dieback due to exposure, but the most resistant progenies still suffered severe damage on exposed sites and were unlikely to develop good form.

Lorrain-Smith and Worrell (1991) assessed that the form of birch in Scotland is often poor. From an examinations of nine experimental sites in Scotland in 1977, stem form was acceptable in only two sites. Forking was seen to be the result of low apical dominance (negatively correlated to the altitude of the seed-source, Lorrain-Smith and Worrell, 1991): Kozlowski & Clauser (1966), observed that lateral buds are normally more resistant to frost than terminal buds. This situation makes the leading shoot more vulnerable to damage and can enhance the development of a crooked tree form. One of the factors considered responsible for the poor and crooked form of silver birch in Scotland is the dieback of apical and lateral shoots.

For dieback it is meant the desiccation of the youngest apical and lateral shoots which can influence the shape of the crown and the growth of the plant. Widespread mortality of yellow birch (*Betula alleghaniensis* Britt.) caused by crown dieback has been recorded throughout Eastern North America since 1932 (Sinclair 1952; Pomerlau 1953; Walker et al., 1990). The birch decline that occurred during the 1930s in eastern North America resulted in an estimated stem volume loss of 1400 million m^3 of yellow and white birch over an area of 490,000 km^2 (Pomerlau, 1991). Winter thaws have been implicated in this decline (Braathe 1957, Auclair 1987, Braathe 1995). Thaws have also been proposed as the cause of the recent dieback in hardy commercial apple cultivars in Canada (Coleman et al, 1992).

The mechanism inciting shoot dieback in northern hardwood species seems to consist in prolonged winter thaws followed by late frosts in the spring (Pomerleau, 1991; Auclair et al., 1992, 1996, 1997). Soil freezing and winter root thaw-freeze events (Auclair et. al., 1996; Cox and Malcolm, 1997; Zhu et al., 2001) have been suggested as the triggering factors of dieback in yellow (*Betula alleghaniensis* Britt.) and white birch (*Betula papyrifera* Marsh). In Northeast Scotland Lines and Brown (1982) noted that planted non –native trees were more susceptible to early and late frosts and winter dieback of the crown than indigenous seed sources. Frost and chilling temperatures produce ecological boundary that affect large numbers of species in a similar manner. Survival capacity at low temperatures in the field depends on more than just the ability of certain essential organs to withstand freezing injury and the time of phenological events is essential to avoid injury both during the winter and on the resumption of growth in the spring.

1.3. BREEDING MANAGEMENT

Much of the birch woodland in Scotland is of low quality, but limited examples occur which demonstrate that good stem form can be achieved (McRobbie 1991). In Scotland Brodie (1990) suggested that selection against susceptibility to vertical frost cracking was an important criterion for clones selection of *B.pendula* at specific sites, (Good et al., 1985).

Over the past 50 years the Forestry Commission, the Institute of Terrestrial Ecology near Edinburgh, and the Scottish plant breeding stations near Edinburgh have shown active interest in the improvement of birch (utilizing the variations in growth and phenology that can be observed in transplants of different populations when they are transferred to a common habitat).

Seed of *B.pendula* from plus trees or good stands from Scandinavia failed in field trials planted out in 1954 were (Philip, 1978; Wood, 1951; Edwards 1957). Also data from the Forestry Commission trials of *B. pendula* indicated that height growth of the Finnish, Swedish, Norwegian and Bulgarian provenances were 10 to 30% less than that of Scottish or English controls, and that on average the survival of the Scandinavian provenances was less than the survival of the British ones (Worrell, 1999).

Many of the exotic seed sources of *B.pendula* appeared to be more susceptible to both early and late frosts and winter dieback of the crowns than indigenous seed sources (Lines and Brown, 1982).

Despite these finding, these recent decades have been characterized by a widespread planting of continental origin broad-leaved stock. However more recently indigenous sources have started to become more widely available.

Most of the work with birch (Lines and Brown, 1982; Pelham et al., 1984; Blackburn and Brown, 1988) indicated such a large amount of variation in most morphological characteristics examined at both the provenance and individual tree levels that, if heritable, it could give strong impetus for a breeding program. This raises the question of the relative merits of different seed sources, both native and non-native, for the production of planting stock.

In the late 1970s and early 1980s, as part of the birch breeding program, seed origin/progeny trials mainly from the North-East of Scotland but including also some selections from England and Continental Europe, were established from the University of Aberdeen, on several sites in Eastern Scotland, with the aim of identifying the best phenotypes and of investigating on the heritability of form and growth of selected individuals.

Since about 1970, a small number of trials have been established in Scotland to test the performance of different origins of planting stock of silver birch: from Scandinavia, from England, and from Scotland.

In particular, two trials of different origins of planting stock of silver birch from Scotland and England in Dunkeld and in Moray have been subjected from 1998 (one year from planting) to phenological and morphological observations by the University of Edinburgh and the Northern Research Station (Tree Improvement Branch, Forestry Commission). Provenances showed a high level of variability for phenological and morphological features from the very beginning (2 years of age) (Donnell, 1998; Armstrong, 1999; Tansey, 2000). Significant variation in height, diameter and form were found among the progeny of selected individual trees of *B. pendula* and *B. pubescens* Ehrh. (years 2-3) also by Blackburn and Brown (1988).

It became then apparent that new studies were needed to investigate in more detail the variability in phenological (the synchrony between flushing, bud set dates and climate of the growing site, risk of frost damage and risk of not exploiting the full growing season and therefore growing less rapidly) and morphological characteristics across provenances, to understand their heritability as well as to clarify the environmental causes and physiological processes responsible for the observed poor form.

1.4. BUD-BURSTING

In cool and temperate zones, warm summers with a long daylight period are favourable for the growth of plants, but winters are characterised by short days and cold temperatures. During their evolution perennial plants and trees have developed regulatory systems to overcome the alternating cycle of seasons that threatens their survival.

The patterns of adaptive variation will be expected to be more closely linked to environmental conditions (Rehfeldt et al. 1984) if the species has been present in the area for a long period. Birch pollen goes back to Pleistocene (2 millions years ago), in Britain and in Germany. Birches were part of the boreal forest some 10,000 years ago in England, in Germany, in Denmark and in the Netherlands.

The high variability expected for birches due to their long residence in the British Isle. could be advantageous for breeding management. Variation in bud burst would may also permit the selection of provenances adapted to future climatic conditions.

Tree populations possess bud dormancy mechanisms dependent on the selection of cool temperatures in the fall and early winter to provide chilling to break physiological dormancy, and warm temperatures in the spring to cue the resumption of growth. Chilling and degree day requirements interact with local climate to determine the risk of spring frost damage to trees. Thus the variability reflects an ecological balance between adaptation to earlier dates of bud burst, allowing a longer growing season, versus increased risk of spring frost damage occurring because plants resuming shoot growth sooner are more likely to be damaged by frost.

Phenological studies can aid in the clarification of the causes of frost damage in birch and, by extension, can usefully inform provenance choice and selection in Britain.

1.5. WATER RELATIONS

The ability of xylem to transport water from roots to leaves is determined by its hydraulic conductivity. Although the xylem is designed to offer the least resistance to water flow and has hydraulic conductivities millions of times greater than parenchymatous tissues (Pallardi 1989), its contribution to total resistance from soil to leaves can be substantial in tall plants (20-60% in woody species according to Sperry et al. 1988). A strong correlation between foliar phenology and the degree to which a tree was subject to winter embolism was found by Wang et al. (1992) among deciduous hardwoods species. The greater the late winter loss of hydraulic conductivity (i.e. the greater the loss of the capacity to transport water from the soil through the xylem to the leaves), the later a tree was leafing out in the spring, providing a broad comparative support for the postulated dependence of spring budbreak on hydraulic conducting capacity.

The hydraulic conductivity per unit pressure gradient (k_h) is the most commonly measured parameter and equals the ratio between water flux (f, Kg s^{-1}) through an excised stem segment and the pressure gradient (dP/dx, MPa m^{-1}) causing the flow (Tyree and Ewers, 1991).

Studies dealing with the water status of the xylem sap in branches of trees during the winter period show that variation in degree of embolism can occur as a consequence of the frost-thaw alternation (Sperry et al, 1993; Ameglio et al., 2001). Winter xylem embolism, is described as the presence of air-filled tracheids and/or vessels, resulting in a substantial impairment of xylem transport. It seems to occur as a result of the low solubility of gases in ice and to be strictly dependent on the internal pressure and on the size of the xylem conduit: larger xylem vessels are more vulnerable to cavitation by freezing than smaller vessels and tracheids (Hammel, 1967; Sucoff 1969; Ewers 1985; Sperry and Sullivan, 1992; Lo Gullo and Salleo, 1991; Hacke and Sauter, 1996; Langan et al.,1997).

Winter xylem embolism seems to have important potential consequences on vegetation, such as a reduction in tree growth and development of shoot dieback (Sperry et al, 1988).

In more detail, winter embolism may be the factor responsible for shoot dieback because of the phenomenon of frost desiccation: repeated cycles of frost and defrost cause dehydration in the xylem cells due to the spreading of air bubbles in the vessels. Frost desiccation is described as a phenomenon of dehydration, a common feature among several environmental stresses (Tranquillini, 1979). The process of dehydration due to low temperatures can be caused by the freezing of the sap in the xylematic conduits: this dysfunction results from the nucleation of gas bubbles during freezing. When xylem temperature rises, if the ice melts slowly and no tension develops in the xylem, then the bubble of air will dissolve in the sap. But if tensions develop beyond some critical values, then the bubbles will expand to make the conduit fully embolised and dysfunctional. This phenomenon may also have consequences in terms of reduced tree growth, if it impaired water uptake in spring after bud-break and if it reduces the length of the growing season.

Many plants cavitate extensively during freezing weather. These plants tend to be winter deciduous and restore water transport after freezing by growing new conduits or refilling cavitated ones by increasing the xylematic pressure to near or above the atmospheric via root pressure.

Sperry et al. (1993) found that embolism always fell from maximum to minimum annual values in spring within a few weeks prior to leaf flush.

As with other species with diffuse-porous woods, in *Betula pendula* the differentiation of new xylem cells in the main stem does not usually start until one to three weeks or more after flushing of the buds (Sperry et al. 1988) The recovery from xylem cavitation in spring in diffuse-porous species has been attributed in many occasions to root pressure (Sperry et al. 1988; Sperry 1993).

Such positive pressure is thought to help dissolve the gas in the sap and/or push the undissolved gas out of the vessels until cavitated vessels become filled with water.

A positive xylem pressure does not commonly occur in all woody species. In *Betula* spp. the recovery of conductivity was associated with positive xylem pressures ranging from 50 to 60 kPa in March and April (Hacke & Sauter 1996, and Sperry et al., 1994). The positive xylem pressures were found frequently to occur during a 2-month period prior to leaf expansion (Sperry et al. 1994).

1.6. OBJECTIVES AND STRUCTURE OF THE THESIS

The thesis investigates the differences in bud-bursting, stem growth and form, freezing of the sap, winter embolism and refilling in provenances of silver birch. There are 5 chapters in the thesis.

Chapter 1introduces the subject.

Chapter 2 aims to identify the major characters (bud-bursting, stem growth and stem form) distinguishing silver birch provenances from one another and to draw preliminary conclusions over the role that genetic variability plays in birch provenance selection in Britain. This chapter presents the results of systematic investigations of three planted trials (one in Southern, one in Central and one in Northern Scotland) of silver birch provenances to determine their variation in growth rate, stem form dieback and phenology.

Chapter 3 aims to determine whether frost damage and variability in stem growth across provenances are a function of the sensitivities of the different provenances to subsequent cycles of sap freezing/thawing or to the absolute temperatures below zero reached during winter and spring. The susceptibility to cavitation by freezing provides a hypothetical link between xylem structure, phenology, and refilling capacity. In this chapter I document the presence of freezing exotherms due to change of state in the water inside xylematic conduits directly in the field; I assess the existence of a relationships between freezing temperatures and sap freezing in early winter and just before spring in existing plantations of birch provenances, I relate freezing temperature differences across provenances to differences in phenology and, I attempt to predict events of sap freezing using a climatic model of the interested area.

Chapter 4 tests the Hypothesis that winter frost desiccation is responsible for the precocious dieback in young shoots of birch seedlings and for the dysfunction of xylem conductivity. The chapter also discusses the possibility that shoot dieback might be determined by the lack of recovery upon thawing in the spring as a consequence of damage to the living cells either in the roots (where hydraulic pressure for refilling is produced), or in the shoot. In particular, two processes, i.e., winter development and spring recovery from xylem embolisation, were investigated with a preliminary study to explore the significance of these phenomena for the development of a high quality tree stem.
In this chapter the relationships between winter frost and xylem functionality are presented, particularly focusing on the variability in shoot hydraulic supply during winter. Freeze-thaw events were simulated on branches of silver birches to investigate the effective influence of low temperatures on the fluctuations on xylem hydraulic

conductivity. Hydraulic conductivity and vessel diameters of apical and basal shoots were measured to find out whether differences were present between the two types. Hydraulic conductivity and development of root pressure were measured and correlated with bud-flushing, stem form and frost desiccation damages.

Chapter 5: comprises a summary of the main conclusions drawn from all the experiments so as to bring together the entire body of work and highlight the main findings of the study.

2.VARIATION IN VIGOUR, TREE FORM AND PHENOLOGY AMONG SEED-SOURCES OF SILVER BIRCH IN SCOTLAND, AND IMPLICATIONS FOR PROVENANCE CHOICE.

2.1. INTRODUCTION

Success in the establishment and productivity of forest tree plantations is determined largely by the species used. Whitin species the most useful information with regard to choice of planting material relates to seed source. The relevant information is obtained by making a systematic investigation using planting trials of potential species and provenances to determine their growth performance and ecological characteristics.

The degree of habitat specialisation or ecotype development found in natural populations is demonstrated by the great variation in growth and phenology that can be observed in transplants of different populations when they are transferred to a common habitat. The genetic basis of ecotype differentiation was first recognised by the Swedish botanist Turesson (1922) using transplants from many regions and growing them together in the same experimental garden.

The strength of the breeding barrier which causes and reinforces the intra-specific variability in ecotypes is a function of the mode of reproduction and the ecological distinctiveness of their habitats. Such are the forces of selection in plant populations that even within a small geographical area different types may evolve in response to varying ecological pressures. This relatively small-scale variability has important consequences for the planning and layout of experimental tests of provenance and individual variation in the desired characters (i.e., growth, stem form, phenology, etc.).

By far the greatest effort in forest genetics in Britain concentrated on tree breeding of introduced conifers, reflecting forestry priorities during recent decades. The management of genetic diversity of native trees has remained fragmentary and restricted in scope. However it is increasingly accepted that a more comprehensive and consistent approach to genetic management of native species is now needed (e.g. Native Woodland Policy

Forum, 1996). The importance of this has been reinforced by the adoption of the principles of sustainable forestry (Department of the Environment, 1994). These policy statements have the intention of strengthening the importance of native species in British Forestry. They also make it clear that genetic management of trees needs to be aimed at securing all the benefits associated with sustainable forestry, including: economic benefits resulting from appropriate provenance choice, selection and tree breeding, and environmental and cultural benefits associated with genetic conservation (Ennos et al., 1998).

Most of the work with birch in Britain (Lines 1987; Pelham et al, 1988; Blackburne and Brown, 1988) has indicated that a significantly large variation exists in most characteristics examined at both the seed origin and individual tree levels. This variation could be selected for and used in any future birch improvement programme.

In the late 1970s and early 1980s a tree breeding project based at Aberdeen University led to the establishment of progeny trials investigating the heritability of form and growth of selected individual trees from a range of sources of silver birch, mainly from the North East of Scotland, but including also some selections from England and Continental Europe. Since about 1970 a small number of trials have been established in Scotland to test the performance of different origins of planting stock of silver birch: from Scandinavia, from England, and from Scotland.

These initial observations reinforced the perception that genetic factors (possibly acting in conjunction with the occurrence of environmental stresses, such as leader browsing or frost damage) were at least partially responsible for the common observation that many semi-natural stands of silver birch also displayed generally poor stem form. It became then apparent that new studies were needed to investigate in more detail the variability in phenological characteristics across provenances, as well as to clarify the environmental causes and physiological processes responsible for the observed poor form. The few progeny trials of *B. pendula* and *B. pubescens* Ehrh. have demonstrated that there is significant variation in height, diameter and form among the progeny of selected individual trees at years 2-3 (Blackburn and Brown, 1988).

Lack of apical dominance and a shrubby appearance are very characteristic of downy birch (*B. pubescens*) in Britain. In Scandinavian timberline birch forests, a genetically distinct form *B. pubescens var. tortuosa* represents *Betula pubescens.* This type of birch keeps its twisted "krummholz" form even when transplanted to lower and more favourable habitats (Crawford 1989).

Presumably the twisted and slow-growing form of this variety of birch has had a greater survival capability at the timberline and has therefore been preferentially selected. The permanence of these stunted forms even when the birches are transplanted in more favourable habitats suggests that the production of scrub krummholz form is not entirely due to the direct pruning effects of exposure. It is possible that krummholz forms are a genetically controlled growth response regulated by internal growth factors which are selected as a result of poor growing conditions. Poor soil aeration can also alter internal concentrations of growth regulators, which can be related to changes in tree form of the phenotype.

By contrast, silver birch does not adopt the shrub form, but often in Scotland its shape is poor and dieback of apical and lateral shoots can lead to a crooked form.

Prolonged winter thaws followed by late frosts in the spring have been recognised as an important mechanism inciting shoot dieback in northern hardwood species (Pomerleau, 1991; Auclair et al., 1992, 1996, 1997). Soil freezing and winter root thaw-freeze events (Auclair et. al., 1996; Cox and Malcolm, 1997; Zhu et al., 2001) have been suggested as the triggering factors of dieback in yellow (*Betula alleghaniensis* Britt.) and white birch (*Betula papyrifera* Marsh).

Frost and chilling temperatures produce ecological boundaries that affect large numbers of species in a similar manner. The hardening of plants to withstand freezing temperatures is a stepwise process. At temperatures between +5 and 0°C plants attain a first level of frost hardiness which enables them to withstand a moderate frost. The highly developed degree of hardiness is lost when frost becomes less severe but can be re-established rapidly. During bouts of cold winter weather, frost tolerance in trees can increase noticeably in one or two days and the full effect can develop within 10 days. Dehardening is a more rapid process than hardening and can take place within two-four days. Survival capacity at low temperatures in the field depends on more than just the ability of certain essential organs to withstand freezing injury, and the time of phenological events is essential to avoid injury both during the winter and on the resumption of growth in the spring.

The dormant buds of woody plants are the most resistant tissues to freezing injury. However even for buds within the same tree there are differences in tolerance, which varies in relation to the position of the bud on the tree (Quamme, 1973, Calamassi et al., 2001).

Lateral buds are normally more resistant than terminal buds (Kozlowski &Clauser, 1966). A certain number of terminal and lateral buds can be lost in a severe winter but the tree will survive. This situation can enhance the development of a crooked tree form. Phenological studies can aid in the clarification of the causes of frost damage in birch and, by extension, can usefully inform provenance choice and selection in Britain.

The timing of leaf emergence and blossoming in temperate forests is critical in determining the length of the periods of foliation and the probability of spring frost damage to the newly emerging leaves and flowers. One expected effect of global warming on forest trees in boreal and alpines area is that the onset of bud burst will be advanced because of milder winters and warmer springs. In boreal areas, early bud burst will result in the early onset of growth and subsequent prolongation of the short growing season, and this might increase wood production in the way described by Beuker (1994) for Norway spruce and Scots pine origins from Northernmost Finland. Heide (1985) calls this phenomenon “capacity adaption”. Earlier bud burst, however, could result in an increased risk of damage from late spring frosts, leading to a lack of survival adaptation, depending on the flexibility of the system responsible for bud burst (Koski 1985).

2.2. OBJECTIVES OF THIS CHAPTER

This chapter presents the results of systematic investigations of planted trials of silver birch provenances to determine their variation in growth rate, stem form and phenology. The results are based on trials established using several provenances over three sites (one in Southern, one in Central, and one in Northern Scotland). The results will be employed to identify the major characters distinguishing silver birch provenances from one another and to draw preliminary conclusions over the role that genetic variability plays in birch provenance selection in Britain.

2.3. MATERIALS AND METHODS

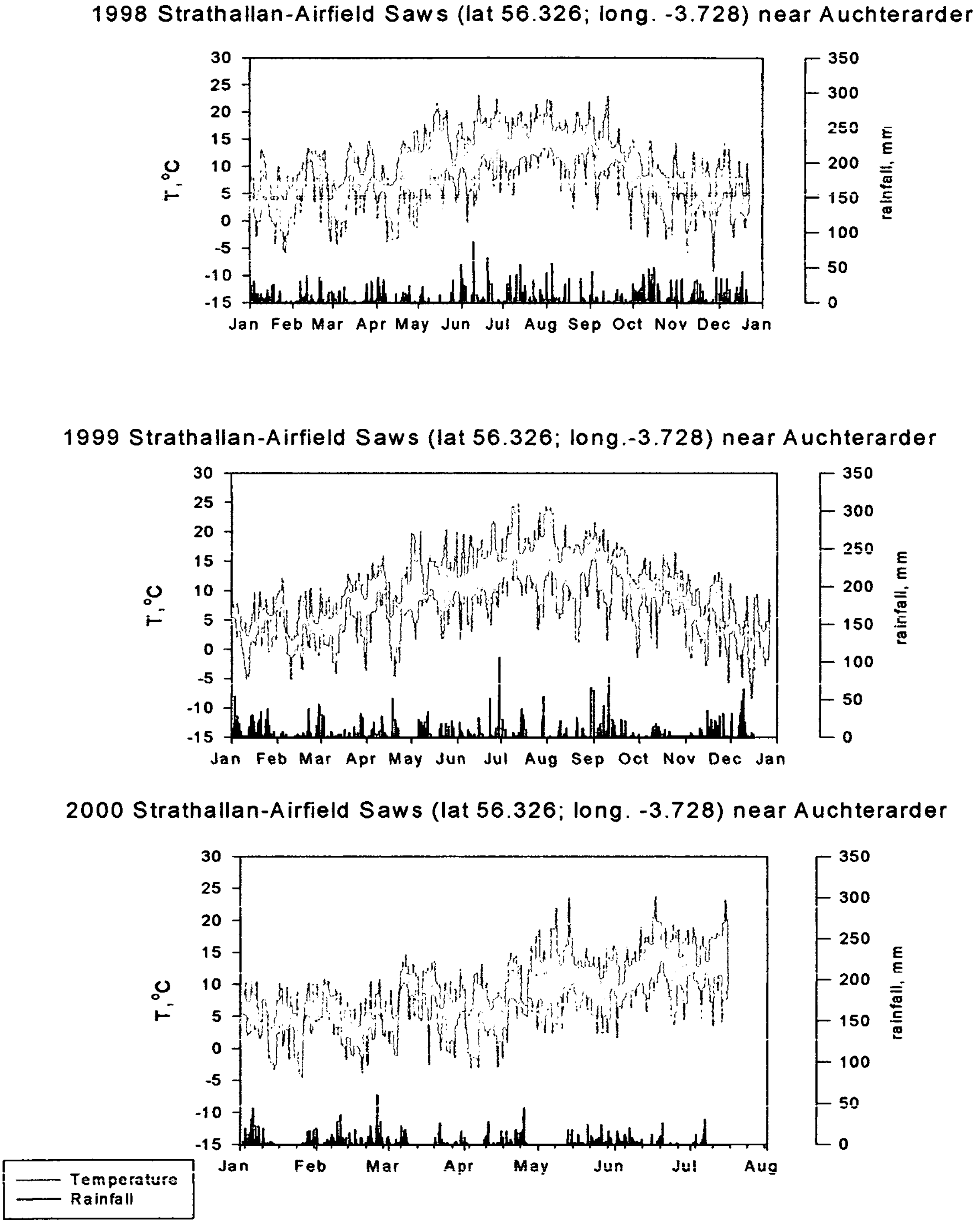
2.3.1 THE RESEARCH SITES

Details on the trials and their locations are given in Table 2.1. Elgin 64, Craigvinean 21, Bush Estate (the numbering follows the system implemented by Forest Research for experimental trials) were chosen to compare the same provenances across sites and to maintain continuity in phenological observations undertaken from the year of the planting.

Hourly temperature and rainfall data obtained from the British Atmospheric Data Centre from 1998 to 2000, are shown in Figs.2.1. 2.2. and 2.3, for the closest available meteorological stations to Craigvinean 21, Elgin 64 and Bush Estate, respectively.

Table 2.1. Details of seed source trials of silver birch in Scotland.(Worrell et al, 2000)

Name of the trial	Elgin 64	Craigvinean 21	Bush Estate
Number of seed lots	37	37	8
Planting year	1998	1997	1996
Age	3	3	5
Location	Elgin	Tayside	Midlothian
Lat. (N)	57° 40’	56° 35’	55° 85’
Long (W)	3° 12’	3° 40’	3° 15’
Site Elevation (m s.l.)	110	280	152
Rainfall (mm a^{-1})	820	1200	720
Soil type	Brown earth	Gleyed upland brown earth	Loamy brown earth



1998 Strathallan-Airfield Saws (lat 56.326; long. -3.728) near Auchterarder

1999 Strathallan-Airfield Saws (lat 56.326; long.-3.728) near Auchterarder

2000 Strathallan-Airfield Saws (lat 56.326; long. -3.728) near Auchterarder

Figure. 2.1.Hourly temperatures and daily rainfall in Strathallan-Airfield Saws (Craigvinean) from 1998 to 2000

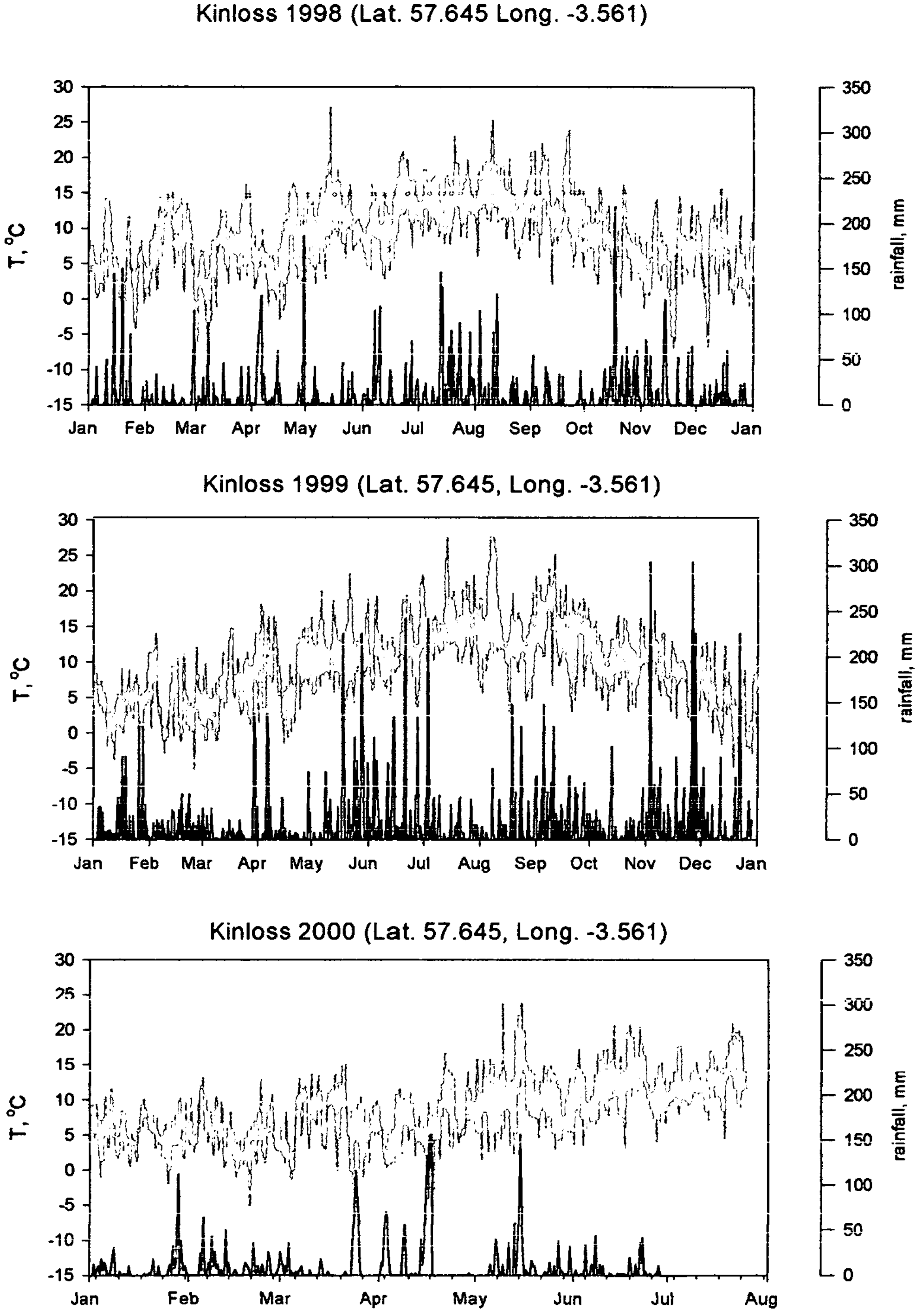
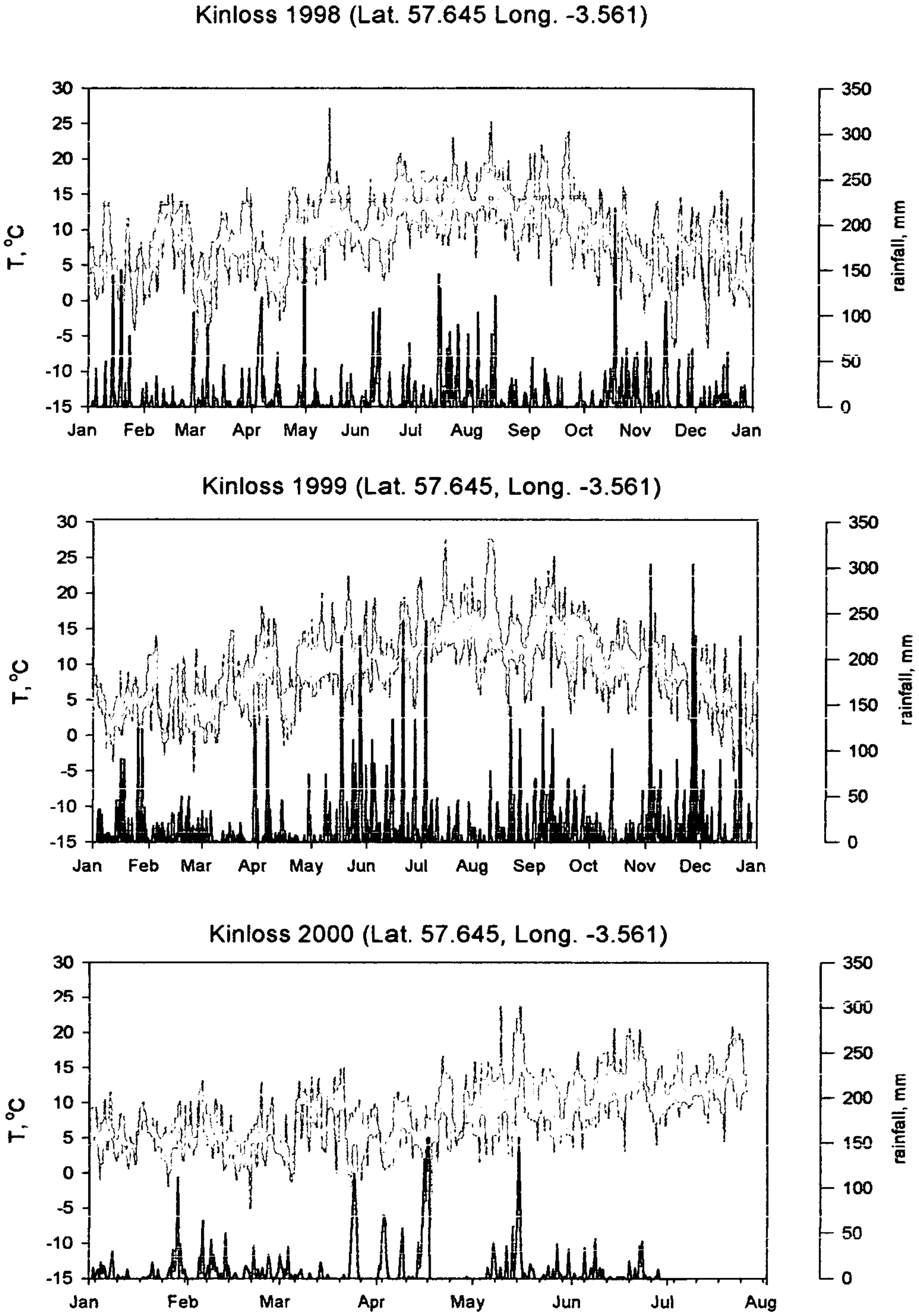


Figure 2.2. Hourly temperature and daily rainfall in Kinloss station (Elgin) from 1998 to 2000.

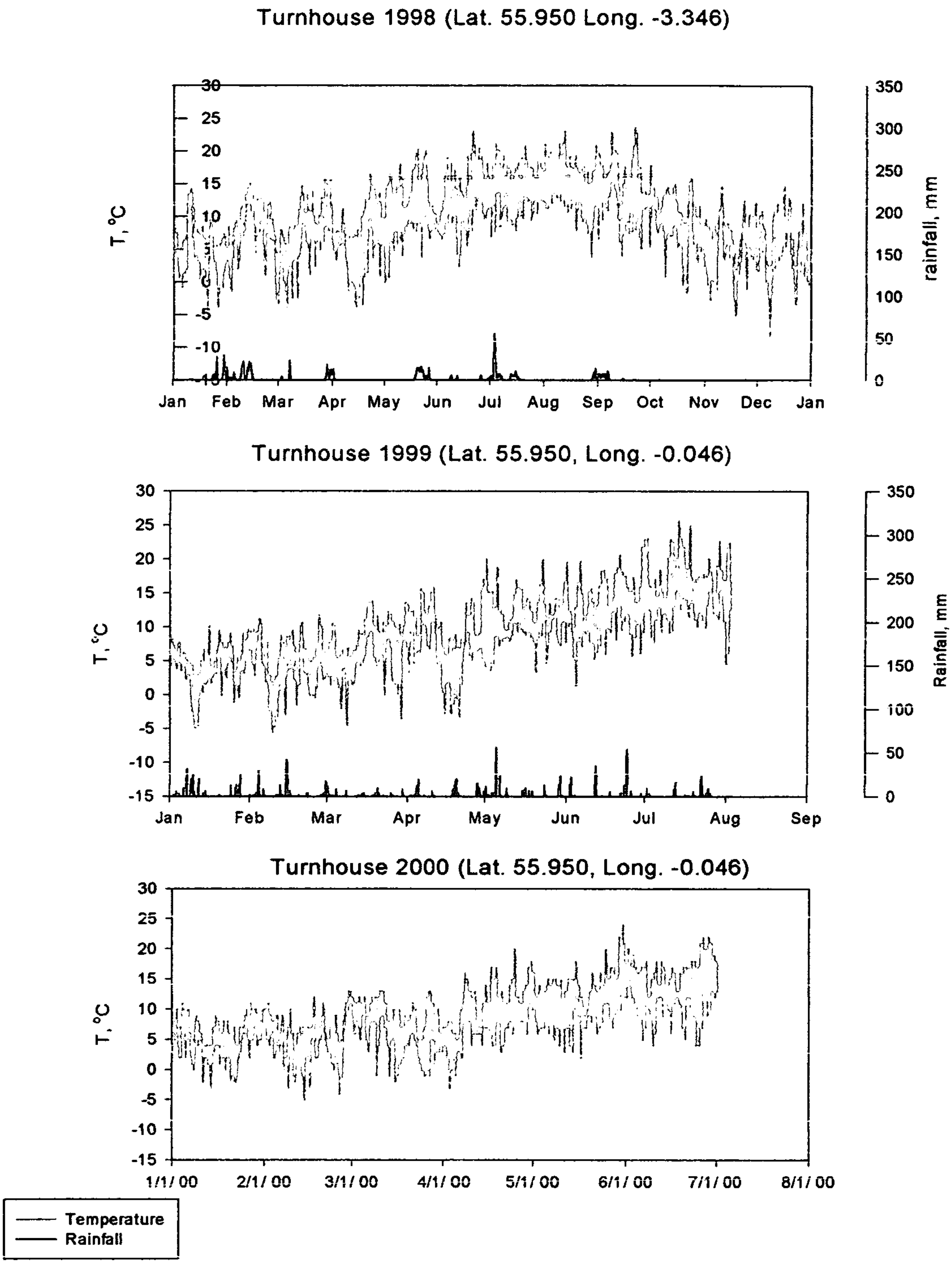


Kinloss 1998 (Lat. 57.645 Long. -3.561)

Kinloss 1999 (Lat. 57.645, Long. -3.561)

Kinloss 2000 (Lat. 57.645, Long. -3.561)

Figure 2.2. Hourly temperature and daily rainfall in Kinloss station (Elgin) from 1998 to 2000.


Turnhouse 1998 (Lat. 55.950 Long. -3.346)

Turnhouse 1999 (Lat. 55.950, Long. -0.046)

Turnhouse 2000 (Lat. 55.950, Long. -0.046)

Figure 2.3. Hourly temperatures and daily rainfall in Turnhouse station (Bush) from 1998 to 2000.

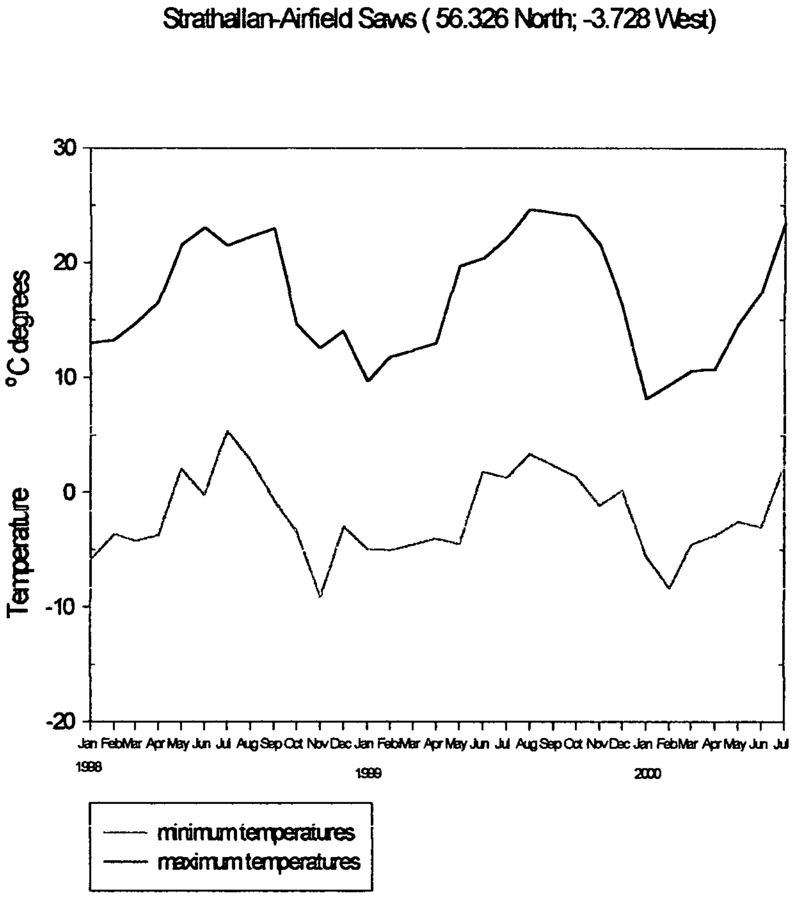


Figure 2.4. Monthly average of maximum and minimum temperatures recorded in Strathallan Airfield Saws (Craigvinean) from 1998 to 2000.

Figure 2.4 shows the trend of average monthly minimum and maximum temperatures from January 1998 to June 2000 at Strathallan Airfield Saws station (to represent Craigvinean 21). The coldest months were November 1998 (-10°C degrees) and February 2000 (-6°C degrees).

Over the period 1999-2000 the minimum temperatures during March and April varied between – 3.7°C and –5°C. The maximum temperatures in March and April varied between +10 °C and + 17 °C, with an excursion between maximum and minimum temperatures of 14-20 °C.

Figure 2.5 shows the trend of the average monthly minimum and maximum temperatures recorded at Kinloss station (representative of Elgin 64) from 1998 to 2000. Minimum temperatures were milder in comparison to Strathallan Airfield Saws station, arriving to –8° C in November-December 1998. During March and April, minimum temperatures are between –1°C and –3°C, although in March 1998 temperatures were particularly cold, decreasing to –6° C. The maximum temperatures vary between +14 °C to +18°C. Thermal excursion ranges were between 21 and 15°C.

Maximum temperatures were in July and August and arrived at 25 °C.

Maximum and minimum temperatures of Turnhouse (the closest station to Bush Estate) are recorded in Figure 2.6. At Turnhouse the maximum temperature has been of +26 ° C in July 1999. The minimum temperatures occurred in November 1999 and February 2000, with the absolute minimum in November 1998 (-8°C.). During March and April, minimum absolute temperatures varied between –3 and –4.5 degrees, with a thermal excursion of 20°C.

The coldest station appears to be Strathallan Airfield Saws where the temperatures in March and April reached –5°C, even if in 1998 the minimum temperature in April in Kinloss was of –6°C. The differences in the extremes are minimal. The thermal excursion during these months is always of around 20°C.

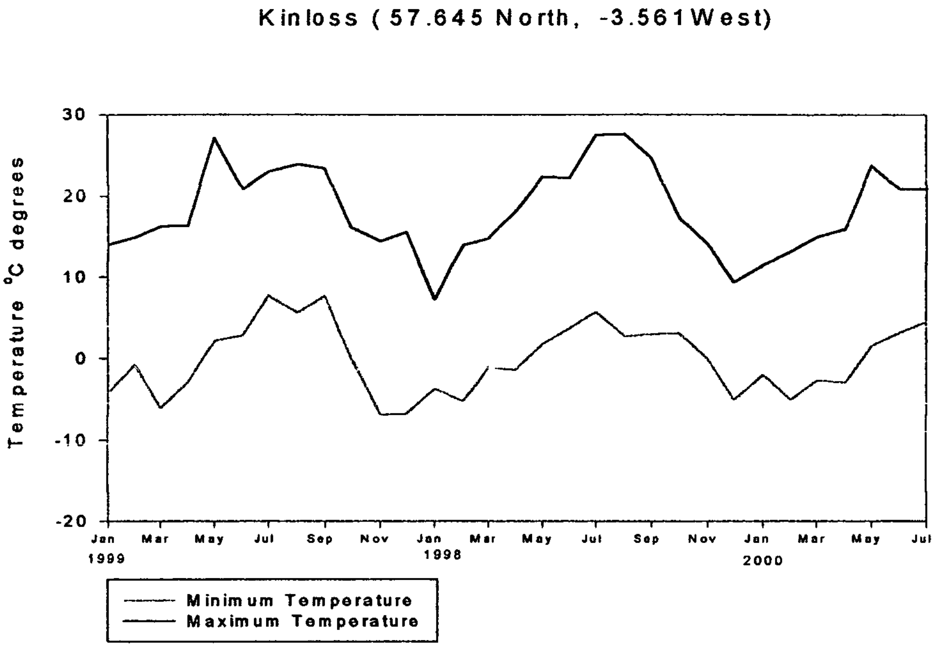


Figure 2.5. Monthly averages of maximum and minimum temperatures recorded in Kinloss (Elgin) from 1998 to 2000

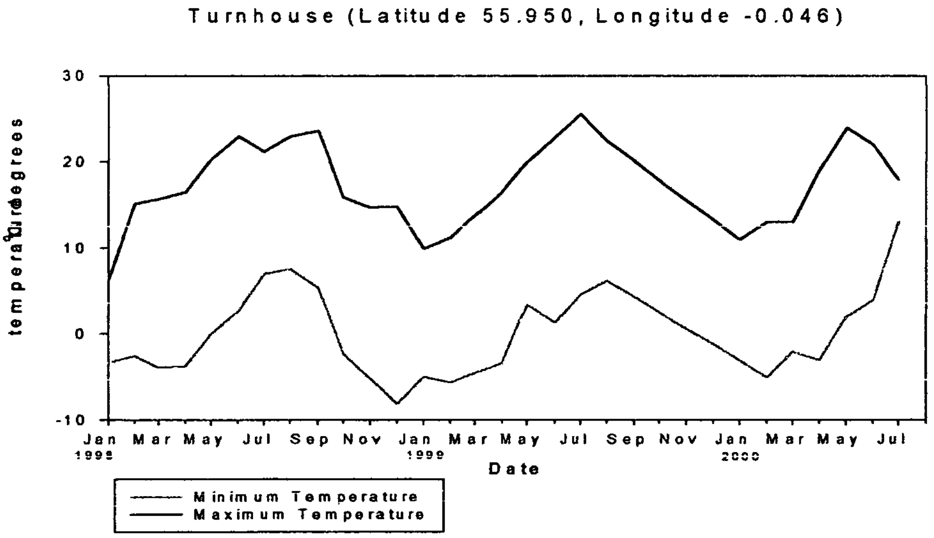


Figure 2.6. Monthly averages of maximum and minimum temperatures recorded in Turnhouse (Bush) from 1998 to 2000

2.3.2. THE PROVENANCES

The provenance trials at Craigvinean 21 and Elgin 64 included 37 seed sources of *B. pendula* from Scotland and Northern England. In both experiments several sources of *B. pubescens* were included, though these are not considered in this study. Several of the *B. pendula* seed sources also included a small proportion of *B. pubescens* seeds as a result of difficulties on the part of the seed collectors in accurately telling the two species apart in the field. The provenance trial in Bush Estate included eight seed sources of *B. pendula,* part of the 37 in Craigvinean/Elgin.

The names, abbreviations and locations of origin (with latitude and longitude) of the 37 provenances employed in Craigvinean 21 and in Elgin 64 are given in Table 2.2. The eight provenances employed at Bush Estate are also given in Table 2. 2.

2.3.3. METHODS

2.3.3.1. MEASUREMENTS OF TREE SIZE

Traits related to size, tree form and timber quality of the stems were either assessed or measured. Stem diameters (mm) were measured with a calliper perpendicularly on two sides of the stem at 20 cm height and the mean value used. Tree height (cm) from the ground to the top of the apical leader was measured with a graduated steel tape. Length and number of lateral branches were recorded from the top of the apical leader to the ground. Six plants for each plot were measured for all the parameters mentioned.

2.2.3.2. ASSESMENT OF STEM STRAIGHTNESS

The scoring of stem straightness was based on a visual assessment whereby five stages of stem form were recognised (Table 2.3). As high scores indicate a loss of stem straightness strictly speaking this index should be referred to as "stem crookedness". However, it will sticks to its denomination of "stem straightness" for consistency with previous studies. Measurements took place from April to May 2000.

2..3.3.3. ASSESMENTOF BUD FLUSHING

The stage of budburst was determined for each plant four times from the 10th of March to the 15th of May 2000. Scoring was based on a visual assessment, where five stages of budburst were recognised (Table 2.4). Six plants were chosen for the estimation of bud flushing. For each plant, the first five buds starting from the top of the apical leader to the bottom were individually assessed.

Table 2.2. Number of the seed lot, location of seed origins NGR (National grid reference), Latitude and Longitude of each of the three trials in Craigvinean, Elgin and Bush Estate.

PROVENANCE In Craigvinean and In Elgin		Provenance In Bush Estate	NGR	LATITUDE		LONGITUDE	
BI95(10)Lot900	LEANACHAN FT. WILLIAM		NN222771	56°51'4.98"	N	4°54'57.70"	W
BI95(10)Lot901	GLEN SPEAN ROY BRIDGE		NN290808	56°53'13.70"	N	4°48'25.73"	W
BI95(10)Lot904	TOMICH AFFRIC	BI95(10)Lot904	NH315283	57°18'51.47"	N	4°47'53.23"	W
BI95(10)Lot905	STRATHGARVE WOOD GARVE		NH408605	65°36'23.75"	N	4°39'53.40"	W
BI95(10)Lot906	BAITLAWS LAMINGTON		NS979308	55°33"36.32"	N	3°37'8.26"	W
BI95(10)Lot911	WAUCHOPE BORDERS		NT587075	55°21'35.07"	N	2°39'5.54"	W
BI95(10)Lot912	LOCHARBRIGGS DUMFRIES	BI95(10)Lot912	NX991810	55°6'47"	N	3°34'55.24"	W
BI95(10)Lot914	LANGBANK RENFREWS	BI95(10)Lot914	NS3972	55°16'11.26"	N	4°31'24.26"	W
BI95(10)Lot915	ACHNATRA INVERARAY		NN1109	56°9'47.84"	N	5°2'38.73"	W
BI95(10)Lot916	CREAGAN LOCH CRERAN	BI95(10)Lot916	NM9744	56°9'11.59"	N	5°15'44.53"	W
BI95(10)Lot917	CRUACH ARDURA MULL	BI95(10)Lot917	NM68295	56°13'17.48"	N	5°44'22.10"	W
BI95(20)Lot900	DUNALASTAIR TUMMEL BRIDGE		NH733614	57°37'29.90"	N	4°7'18.37"	W
BI95(20)Lot901	DALL MILL BLACK WOOD OF RANNOCH		NH589568	57°34'45.87"	N	4°21'36.07"	W
BI95(20)Lot903	GLEN FESHIE KINCRAIG		NO849988	57°4'48.51"	N	2°14'56.86"	W
BI95(20)Lot904	STRAANRUIE ABERNETHY		NH996154	57°13'6.67"	N	3°39'45.89"	W
BI95(20)Lot905	DELNAPOT BLACKSBOAT ELGIN		NJ169370	57°24'57.53"	N	3°23'1"	W
BI95(20)Lot906	SPLINDLE MUIR WESTFIELD ELGIN		NJ153648	57°39'55.26"	N	3°25'11.71"	W
BI95(20)Lot907	WOOD OF ALDBAR MONTREATHMNT		NO569548	56°40'59.11"	N	2°42'12.95"	W
BI95(20)Lot908	SILVIE ALYTH		NO273484	56°37'18.95"	N	3°11'5.68"	W
BI95(20)Lot909	LADY JANE'S PLTN.INGLISMALDIE		NO665713	56°49'55.60"	N	2°32'56.57"	W
BI95(20)Lot910	MUIR OF DINNET ABOYNE		NO433999	57°5'12.41"	N	2°56'8.35"	W
BI95(20)Lot911	BIRKHILL ALFORD	BI95(20)Lot911	NJ595163	57°14'8.45"	N	2°40'15.64"	W
BI95(20)Lot912	PANNANICH WOOD BALLATER		NO390965	57°3'20.48"	N	3°0'20.78"	W
BI95(20)Lot913	INVERMOSSAT STRATHDON		NJ495184	57°15'13.28"	N	2°50'13.57"	W
BI95(20)Lot914	KYLOEAG SPINNINGDALE		NH662910	57°53'19.03"	N	4°15'25.48"	W
BI95(20)Lot915	GLENTRESS PEEBLESSHIRE		NT286406	55°39'13.26"	N	3°8'5.40"	W
BI95(20)Lot916	FLOORS KELSO	BI95(20)Lot916	NT7028	55°18'1.31"	N	2°28'9.89"	W
BI95(20)Lot917	MELLERSTAIN KELSO		NT6538	55°18'0.15"	N	2°32'47.75"	W
BI95(20)Lot918	PETERSMUIR E. LOTHIAN		NT47566	55°21"2.10"	N	2°49'40.95"	W
BI95(20)Lot919	NEWTYLE HILL CRAIGVINEAN		NO03542	56°13'14.30"	N	3°33'22.94"	W
BI95(20)Lot920	RANNOCH PERTHSHIRE		NN5958	56°10'44.95"	N	4°15'49.28"	W
BI95(20)Lot921	KILLIN PERTHSHIRE		NN5631	56°10'18.89"	N	4°18'53.35"	W
BI95(20)Lot922	ELIBANK PEEBLESSHIRE		NT355365	55°37'4.11"	N	3°1'27.20"	W
BI95(20)Lot925	WHITE BRIDGE GLEN GARRY		NN284007	56°10'5.06"	N	4°45'50.76"	W
BI95(30)Lot900	FINSTHWAITE ESTATE		SD363865	54°16'12.08"	N	2°58'41.64"	W
BI95(30)Lot901	WITHERSLACK ESTATE		SD431874	54°16'44.09"	N	2°52'26.37"	W
BI95(40)Lot900	CASTLE HOWARD		SE705700	54°7'15.05"	N	0°55'16.42"	W

Table 2.3. Definition of the scores for stem straightness

SCORE	DEFINITION
1	Absence of sweeping, leader dominant
2	Nearly straight clear leader, no damage
3	Slightly crooked (contortions)
4	Very crooked/no clear leader
5	Stem malformed contorted with no clear leader

Table 2.4. Definition of the scores for bud flushing

SCORE	DEFINITION
1	Bud not swollen and still closed
2	Bud swollen but still closed
3	Bud opening
4	Leaf starting to extend
5	Leaf fully open

2.3.3.4.ASSESMENT OF BUD AND/OR BRANCH DESICCATION

For six plants in each plot the number of desiccated branches was counted. Length of the desiccation, and number of dead buds were also determined.

2.3.4. DATA ANALYSIS

The plots were originally laid out using a statistical design based on an incomplete blocking structure. For experiments with large numbers of seed lots, the advantage of incomplete blocking structures may be to provide a mechanism for better control of site variations. This class of design is useful for treatments which do not have a factorial structure. It is in general more efficient than designs using randomised blocks, especially with the recovery of information between sub-blocks (Cochran and Cox, 1960).

The experimental design of the trials in Craigvinean and Elgin is based on a generalised lattice. A generalised. lattice design can be viewed as a particular case of a randomised blocks design, whereby the blocks provide incomplete replication to test for interaction between provenances and within block position. The design at Craigvinean and Elgin consists of three blocks of 37 plots each (one for each provenance). Each plot comprises 24 seedlings of the same provenance. Plots are grouped in sub-blocks: each block is divided into seven sub-blocks composed of six plots and one sub-blocks of five plots (Fig 2.7).

The model for a generalised lattice design with just one incomplete blocking structure is given as:

$$Y= G\upsilon + R\rho + Z\beta + X\tau + \varepsilon$$

where Y= equals to the dependent variable, $G\upsilon$ equals the parametric mean of the populations, $R\rho + Z\beta + X\tau$ are the treatment effects for blocks, sub-blocks and plots and $\varepsilon$is the error term. G, R, Z, and X are the estimated numeric coefficients. The data analysis was carried out using Minitab (vers. 12.2, 1998), and Statistica (vers.5.1.97.). The results were checked using GENSTAT (Courtesy of Alvin Milner, Forest Research in Bush Estate). Homogeneity of variance was tested with a Kolmogorov-Smirnov test.

The provenance trial in Bush Estate included eight sources of *B. Pendula* from Scotland and the North of England. Seedlings were planted in a randomised complete block design divided into three blocks where each provenance is represented by a plot of 24 trees (six trees times four lines). The provenances were allocated randomly to the plots within the blocks.

Because ages of the plants Bush Estate was different from the other two, we limited our analysis to budbursting.

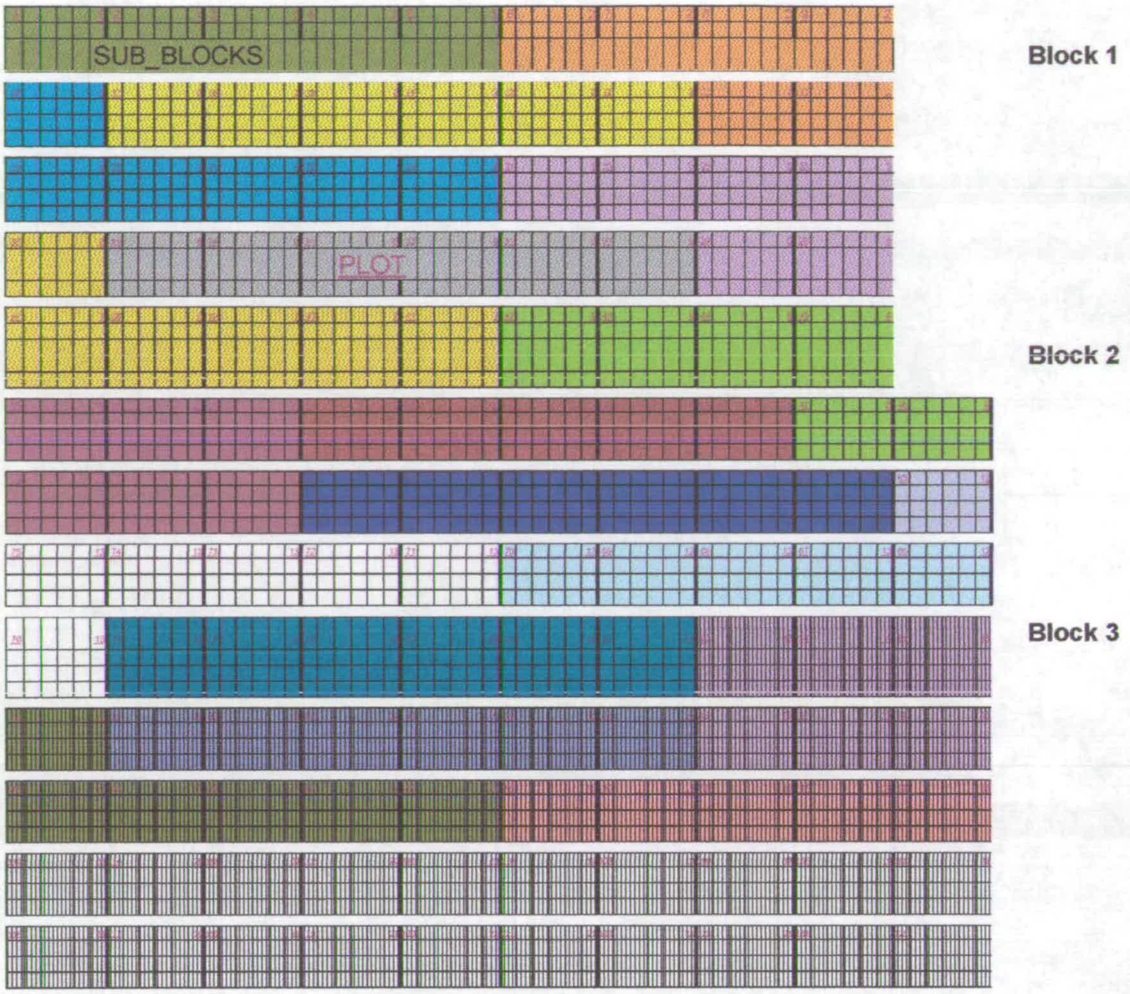


Figure 2.7: Example of generalised lattice design, as it was applied in Craigvinean and Elgine. Each colour identifies a particular sub-blocks within each block.

2.4.RESULTS

2.4.1.CRAIGVINEAN

2.4.1.1. MEASUREMENTS OF TREE SIZE

Significant differences were found both among sub-blocks and among provenances. Provenances differed for height (Table 2.5, $p < 0.05$). The tallest provenances were Witherslack Estate, White Bridge Glen Garry and Killin Pertshire. The shortest provenances were Strathgarve Woodgarve, Dall Mill Black Wood of Rannoch, Leanachan Ft William and Acnatra Inverary. Sub-blocks data of height differed significantly from one another depending on the particular combination of provenance plots (Table 2.5).

Stem diameter Didn't differ across blocks no difference could be detected among provenances (Table 2.7).

2.4.1.2. ASSESMENT OF STEM STRAIGHTNESS

Stem form showed large variation between blocks and sub-blocks: environmental and random combination of were evident factors. However no significant difference was apparent across seed origins (Table 2.8).

2.4.1.3. ASSESMENT OF PHENOLOGY

Provenances differed in their flushing stages from the 20th of March ($p< 0.01$, Tables 9a to 9d); the variation reached its peak of significance in early April ($p< 0.0001$) before declining in mid April. The seed origins to flush earliest were: Lady Jane's pltn. Inglismaldie, Silvie Alith, Castle Howard and Locharbriggs Dumfries, whereas the provenances flushing latest were: Strathgarve Wood Garve and Cruach Ardura Mull (Table 2.10).

2.4.1.4. RELATIONSHIP AMONG PARAMETERS

Stem straightness was significantly correlated with branching habit, with plants characterised by a poor habit (defined by a curved shape) also having fewer ramifications (Table 2.11).

Tree growth parameters were highly correlated to one another. Branchiness, diameter and height were significantly related. Flushing on 7th of April was positively correlated with diameter, with provenances flushing earlier tending to have larger stem diameters. (Table 2.11 a). Height and flushing scores were both negatively correlated with latitude and longitude of the origin of the populations despite the fact that height and flushing state were not significantly related to one another (Table 2.11 a and b). The correlation of both against latitude and longitude suggests that a correlation between these two parameters may arise in the future. Provenances coming from the South-East tended to flush earlier and were of bigger size at three years of age.

Table 2.5. Analysis of variance for height: df, degrees of freedom; MS, Mean Squares; F distribution: regression MS/Residual MS; p, probability level. The data were analysed using a generalised lattice design. Normality of residuals was checked using a Kolmogorov-Smirnov test. Significant differences are highlighted in bold characters in the probability column.

Table 2.5	df	MS	F	p
Blocks	2	711.53		
sub-blocks(adjusted)	18	234.75	2.82	**<0.01****
Provenances	36	164.74	1.98	**<0.05***
Provenances (adjusted)	36	156.16	1.88	**<0.05***
Residual	54	83.03		
Total (plot means)	119	143.32		

Table 2.11c shows the correlation coefficients between the four dates when flushing was recorded. Budbursting scores for the 20 March (79 Jd.) were highly significantly correlated with budbursting scores for the 4 April (94 Jd.) and for the 17 April (107 Jd.). Values for the 4 April were also highly correlated with values for the 17 April. The variation in flushing stages across provenances was largest on the 4 April. Sand Hutton, Silvie Alyth and Inglismaldie were the earliest ones to flush.

Table 2.6. Average height for all 37 provenances in Dunkeld, in order from the tallest to shortest.

Provenances	Latitude °N	Longitude °W	Height
WITHERSLACK ESTATE	54.279	2.874	99.39
WHITE BRIDGE GLEN GARRY	56.168	4.764	90.50
KILLIN PERTHSHIRE	56.172	4.315	89.21
KYLOEAG SPINNINGDALE	57.889	4.257	88.78
SILVIE ALYTH	56.622	3.185	88.44
WAUCHOPE BORDERS	55.360	2.652	88.44
INVERMOSSAT STRATHDON	57.254	2.837	87.78
PETERSMUIR E. LOTHIAN	55.351	2.828	86.56
RANNOCH PERTHSHIRE	56.179	4.264	86.50
BIRKHILL ALFORD	57.236	2.671	86.33
LOCHARBRIGGS DUMFRIES	55.113	3.582	85.58
WOOD OF ALDBAR	56.683	2.704	85.56
PANNANICH WOOD BALLATER	57.056	3.006	85.17
FLOORS KELSO	55.300	2.469	85.00
FINSTHWAITE ESTATE	54.270	2.978	85.00
MELLERSTAIN KELSO	55.300	2.547	84.67
GLENTRESS PEEBLESSHIRE	55.654	3.135	84.38
CREAGAN LOCH CRERAN	56.153	5.262	84.31
ELIBANK PEEBLESSHIRE	55.618	3.024	84.11
GLEN SPEAN ROY BRIDGE	56.887	4.807	83.78
CASTLE HOWARD	54.121	0.921	82.72
GLEN FESHIE KINCRAIG	57.080	2.249	81.83
DUNALASTAIR TUMMEL	57.625	4.122	81.30
CRUACH ARDURA MULL	56.222	5.739	81.22
BAITLAWS LAMINGTON	55.560	3.619	78.56
STRAANRUIE ABERNETHY	57.219	3.663	78.33
LADY JANE'S	56.832	2.549	78.22
TOMICH AFFRIC	57.314	4.798	77.67
LANGBANK RENFREWS	55.270	4.523	77.44
NEWTYLE HILL CRAIGVINEAN	56.221	3.556	77.00
MUIR OF DINNET ABOYNE	57.087	2.936	76.98
DELNAPOT BLACKSBOAT ELGIN	57.416	3.384	76.56
SPLINDLE MUIR WESTFIELD	57.665	3.420	75.56
STRATHGARVE WOOD GARVE	57.607	4.665	70.28
DALL MILL BLACK WOOD	57.579	4.360	68.44
LEANACHAN FT.	56.851	4.916	68.17
ACHNATRA INVERARAY	56.163	5.044	62.22

Table 2.7. Analysis of variance for diameter:

	df	Adj.MS	F	p
Block	2	0.810	2.61	0.082
Sub-blocks	18	0.430	1.39	0.174
Provenances	36	0.268	0.86	0.687
Residual	54	0.310		
Total	*110*			

Table 2.8. Analysis of variance for stem straightness

	df	Adj.MS	F	p
Block	2	5.47	23.2	**0******
Sub-blocks(replies)	18	0.411	1.76	**0.054***
Provenance	36	0.222	0.96	0.555
Error	54	0.235		
Total	*110*			

Table 2.9a. Analysis of variance for flushing

9th of March (59 Julian days)	df	MS	F	p
Blocks	2	0.0019		
Sub-blocks(adjusted)	18	0.002		
Provenances	36	0.0026		
Provenances (adjusted)	36	0.0024	1.33	n
Residual	54	*0.0018*		
Total (plot means)	110	0.0021		

Table 2.9 b. Analysis of variance for flushing

20th of March (79 Julian days)	df	MS	F	p
Blocks	2	*0.0138*		
Sub-blocks(adjusted)	18	0.0036		
Provenances	36	0.0145		
Provenances (adjusted)	36	0.0115	2.45	**<0.01****
Residual	54	0.0047		
Total (plot means)	110	0.0079		

Table 2.9c. Analysis of variance for flushing

4Th of April (94 Julian days)	df	MS	F	p
Blocks	2	0.0022		
Sub-blocks(adjusted)	18	0.0113		
Provenances	36	0.0314		
Provenances (adjusted)	36	0.0304	2.95	<0.0001****
Residual	54	0.0103		
Total (plot means)	110	0.0173		

Table 2.9d.. Analysis of variance for flushing

17th of April (107 Julian days)	df	MS	F	p
Blocks	2	0.0125		
Sub-blocks(adjusted)	18	0.0131		
Provenances	36	0.0166		
Provenances (adjusted)	36	0.0156	1.31	<0.001***
Residual	54	0.0119		
Total (plot means)	110	0.0136		

2.4.1.5. ASSESMENT OF DESSICCATION

The percentage of total plants showing leader or branch desiccation attributable to frost was 4.16%, with a percentage of provenances involved of 36.6%. Figure 2.8 shows the relationship between provenances showing frost damages and their stage of flushing for early March when plants enter in their vegetative period. The provenances showing evidence of frost desiccation were in a slightly more advanced stage of flushing although differences were not significant. The provenances with more evident frost desiccation damage were: Invermossat Strathdon; Rannoch Perthishire; Finsthwaite Estate; Dall Mill Black Wood of Rannoch; Kyloeag Spinningdale; Langbank Renfrews; Birkhill Alford; Delnapots Blacksboat Elgin, Killin Pertshire; Sand Hutton, and Tromie Bridge Kingussi (downy birch).

The earliest and the latest provenances differed by about one week in achieving a certain budbursting stage (stage 3). The earliest provenance (Silvie Alyth) reached stage 3 around 12 April, whereas the latest provenance (Cruach Ardura Mull) reached the same stage around 18 April.

Table. 2.10. Flushing stage of the provenances in Craigvinean forest in early April, in order of precocity.

Provenances	Latitude °N	Longitude °W	Bud-burst score
LADY JANE'S PLTN.INGLISMALDIE	56.832	2.549	2.36
SILVIE ALYTH	54.279	2.874	2.31
CASTLE HOWARD	56.168	4.764	2.19
LOCHARBRIGGS DUMFRIES	56.172	4.315	2.18
MELLERSTAIN KELSO	57.889	4.257	2.10
ELIBANK PEEBLESSHIRE	56.622	3.185	2.10
DUNALASTAIR TUMMEL BRIDGE	55.360	2.652	2.06
BAITLAWS LAMINGTON	57.254	2.837	2.06
FINSTHWAITE ESTATE	55.351	2.828	1.91
BIRKHILL ALFORD	56.179	4.264	1.91
WITHERSLACK ESTATE	57.236	2.671	1.88
KYLOEAG SPINNINGDALE	55.113	3.582	1.87
WOOD OF ALDBAR	56.683	2.704	1.87
FLOORS KELSO	57.056	3.006	1.86
INVERMOSSAT STRATHDON	55.300	2.469	1.83
PETERSMUIR E. LOTHIAN	54.270	2.978	1.82
DELNAPOT BLACKSBOAT ELGIN	55.300	2.547	1.81
RANNOCH PERTHSHIRE	55.654	3.135	1.79
KILLIN PERTHSHIRE	56.153	5.262	1.77
MUIR OF DINNET ABOYNE	55.618	3.024	1.76
LANGBANK RENFREWS	56.887	4.807	1.74
LEANACHAN FT. WILLIAM	54.121	0.921	1.73
GLEN FESHIE KINCRAIG	57.080	2.249	1.71
SPLINDLE MUIR WESTFIELD	57.625	4.122	1.70
GLEN SPEAN ROY BRIDGE	56.222	5.739	1.70
NEWTYLE HILL CRAIGVINEAN	55.560	3.619	1.70
PANNANICH WOOD BALLATER	57.219	3.663	1.64
CREAGAN LOCH CRERAN	56.832	2.549	1.59
ACHNATRA INVERARAY	57.314	4.798	1.58
GLENTRESS PEEBLESSHIRE	55.270	4.523	1.57
WAUCHOPE BORDERS	56.221	3.556	1.52
TOMICH AFFRIC	57.087	2.936	1.49
STRAANRUIE ABERNETHY	57.416	3.384	1.48
DALL MILL BLACK WOOD OF	57.665	3.420	1.47
WHITE BRIDGE GLEN GARRY	57.607	4.665	1.43
STRATHGARVE WOOD GARVE	57.579	4.360	1.26
CRUACH ARDURA MULL	56.851	4.916	1.11

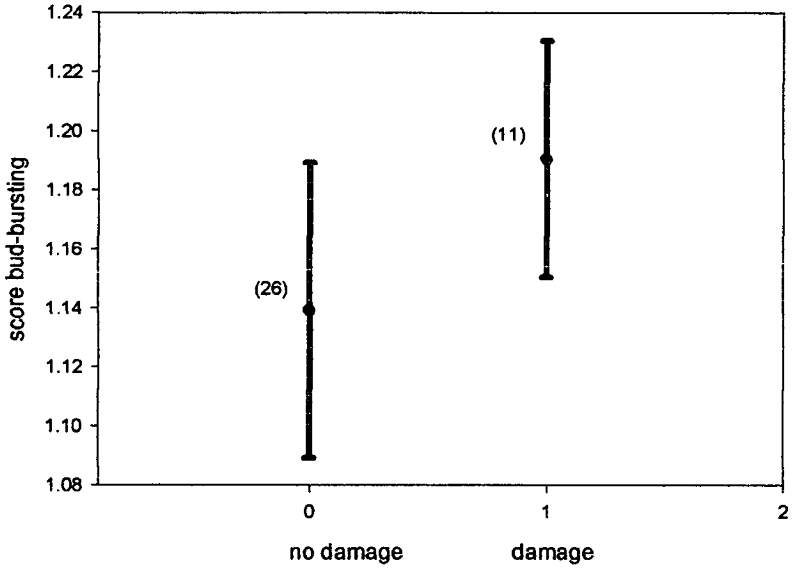


Figure 2.8. Relationship between provenances showing evidence of desiccated branches and stage of budbursting in early March (Numbers in brackets indicate number of provenances for each class of damage). Lines indicate standard errors bars.

Bud-flushing showed a relationship with latitude of the site of origin whose strength was dependent on the assessment date. In particular, the relationship became more clear on assesment dates later in the season (Fig. 2.9 and Table 2.11b-2.11a)

Table 2.11.a) Table of Pearson correlation coefficients between various tree size and form parameters at Craigvinean. **b)** Table of Pearson correlation coefficients between tree size, form and flushing scores against latitude and longitude. **c)**: Table of Pearson correlation coefficients between flushing score dates. Values in bold are significantly different from zero. *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$

(a)

	Branchiness	Diameter	Flushing 94 Jd	Height
Straightness	**-0.34***	-0.15	-0.2	-0.05
Branchiness	_	**0.38***	0.15	**0.41***
Diameter	_	_	**0.36***	**0.64*****
Flushing 94 Jd	_	_	_	0.31

(b)

	Latitude	Longitude
Crookedness	-0.09	-0.06
Branchiness	0.01	-0.18
Diameter	-0.20	-0.38
Height	**-0.38***	**-0.35***
Flushing 59 julian days	-0.18	-0.06
Flushing 79 julian days	**-0.38***	**-0.42***
Flushing 94 julian days	**-0.4***	**-0.49***
Flushing 107 julian days	**-0.39***	**-0.39***

c)

flushing	59 Julian days	79 Julian days	94 Julian days	107julian days
59 Julian days	—	0.10	-0.06	-0.09
79 Julian days		_	**0.68*****	**0.58****
94 Julian days		_	_	**0.76*****
107 Julian days		_	_	_

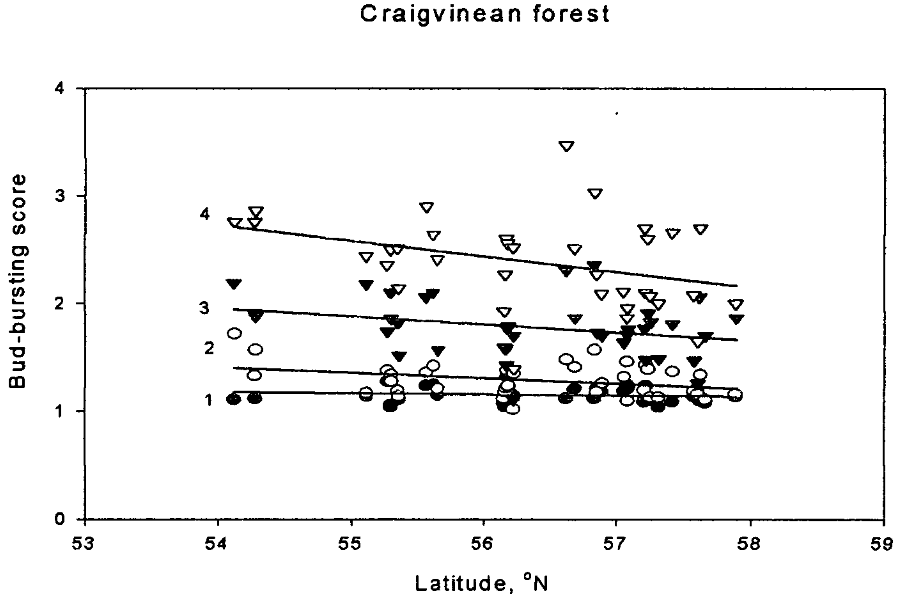


Figure 2.9. Bud-scores for 37 provenances during four assessment dates plotted against latitude of their origin

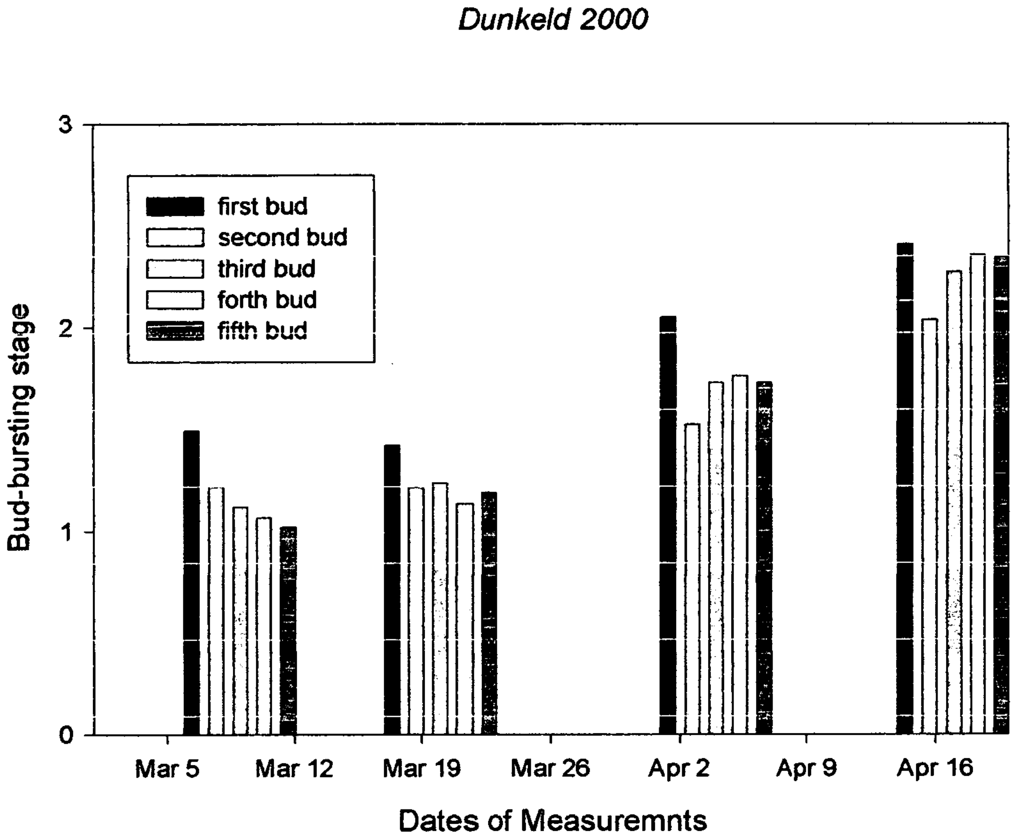


Figure 2.10: Budbursting stages of the top five buds for silver birch at Craigvinean forest. The first bud indicates the top leader whereas the fifth indicates the fifth bud from the top.

The development of flushing for the first five buds from the top, without any distinction between provenances, is shown in Fig. 2.10: the first bud shows a flushing dominance in comparison to the other buds during all stages of flushing. By contrast the fifth bud was the latest to flush until the second part of March, and the earliest to flush in subsequent dates.

From the first to the second date of recording a slight decrease in the average flushing scores were found for the first and the second bud. A possible explanation could be the death of one of the first two buds or alternatively the subjectivity of the visual assessment technique, particularly during the initial phases of bud opening.

2.4.1.6. INDEX SELECTION

Height of the stem, stem straightness and flushing stage on 10 of March, were provisionally considered as the most important characters to assess the risk for frost damage (score point 1-5). Consequently these parameters were combined to select an index for tree breeding. The improvement of 10% in height (eight centimetres of differences calculated on the base of the average of height of all the seedlings measured) was considered as important as the improvement of 60% in straightness (1 score of differences between provenances: 5 very crooked to 1 straight) and as the 60% in flushing delay (1.44 score differences in flushing stage) considering the early March budbursting scores of the provenances, as values predicting the possibility of frost damages in the provenances flushing earlier. For each parameter considered in the building of the index selection, the increase of each single unit was calculated: 1cm increase in height is 1/8 (or 0.12) as important as 1 point decrease in crookedness and 1.5 decrease in flushing score. This assumption was translated into a set of weights, calculated on the mean values of height, stem score and flushing stage: $W_{sh}=0.12$, $W_{ss}=0.9$, $W_{fs}=1.44$.

The weights were used to construct the following simple index:

$$I=0.12P_{sh} - 0.9P_{ss}-1.44P_{fs}$$

Where P_{sh}, P_{ss} and P_{fs} were individual mean provenance measurements for height, stem straightness, and flushing stage adjusted for block effects.

Trees having the highest index value would therefore be preferred for future breeding.

There may be little benefit in including two or more highly positively correlated traits in selection indices. For example, stem height, diameter and total length of branching are highly correlated so height alone has been considered.

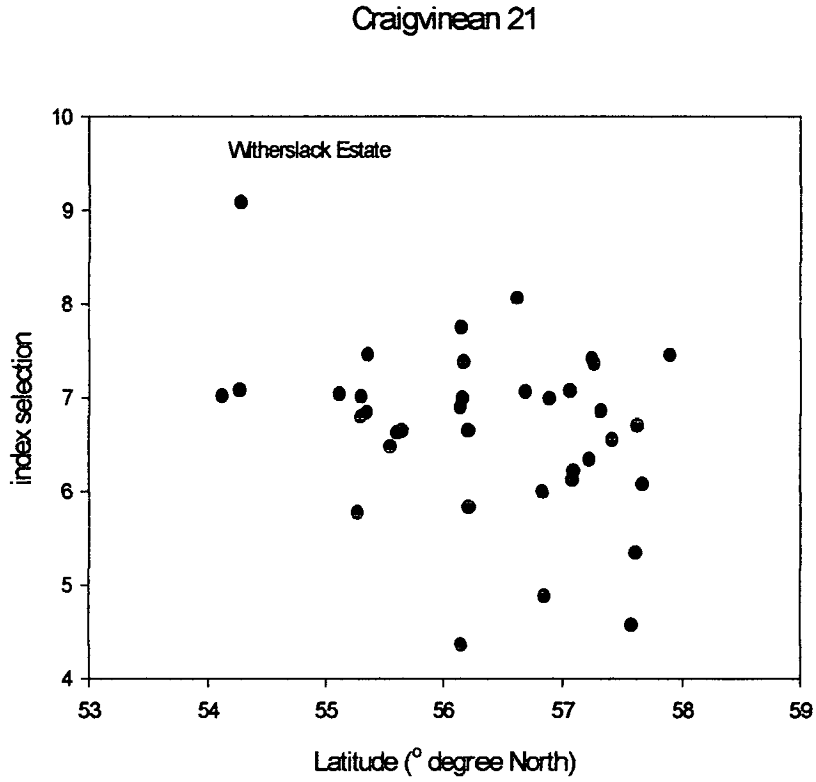


Figure 2.11. Index selection of provenances at Craigvinean 21.

Fig.2.11 shows the selection index for the provenances in Craigvinean ordered following a 45° gradient from South-East to North-West. The provenances with higher values are the ones with the best shape, growth rates in height and minor risk of frost damageand would therefore be preferred for future breeding (Cotterill and Dean1990) The best provenance is Witherlack Estate and the worst one is Acnatahra Invera.

2.4.2. ELGIN

2.4.2.1. MEASUREMENTS OF TREE SIZE

Provenances showed significant variations in their average morphological traits.

Provenances differed for height (Table 2.12, $p<0.05$). The tallest provenances were Castle Howard, Locharbriggs Dumfries, Baitlaws Lamington, Newtyle Hill Craigvinean and Finsthwaite Estate. The shortest provenances were Birkhill Alford, Wauchope Borders, Splindle Muir Westfield Elgin and Straanruie Abernethy (Table 2.13)

There were no differences between blocks and sub-blocks. Provenances differed also for stem diameter ($p<0.05$) (Table 2.14). The provenances with largest stem diameter were Castle Howard, Locharbriggs Dumfries, Finsthwaite Estate, and Witherslak Estate, the provenances with smallest diameter are Straanruie Abernethy, Pannich Wood Ballater, Wauchope Borders, Rannoch Perthshire, Strathgarve Woodgarve (Table 2.15).

2.4.2.2. ASSESMENT OF STEM STRAIGHTNESS

The results of the analysis of variance for stem straightness is shown in Table 2.16. Differences were significant between blocks, indicating that environmental factors were prevalent on differences among seed origins: seedlings in block 2 tended to be more crooked (Table 2.16).

2.3.2.3. ASSESMENT OF PHENOLOGY

The results of the analysis of variance for flushing dates are shown in Table 2.17. Provenances differed in their flushing stages from 8 of March ($p<0.01$). The differences were slightly less significant on 21 March. The provenances which were in an advanced state of flushing on 18th April were: Mellerstain Kelso, Castle Howard, Elibank Peeblesshire, Lady Jane's and Dunalastair Tummel Bridge, whereas the provenances which were slowest to flush were Rannoch Perthshire, Strathgarve WoodGarve, Tomich Affric and Cruach Ardura Mull (Table 2.18).

The largest difference between the earliest and the latest provenances in achieving a certain stage of bud-opening (state 3) was of 2 weeks: the 4th of April for Castle Howard, and the 17th of April for Cruach Ardura Mull.

this dominance progressively disappears with time.

Table 2.13. Average height (cm) for all provenances at Elgin

Provenances	Latitude	Longitude	Height
CASTLE HOWARD	54.12	0.92	111.11
LOCHARBRIGGS DUMFRIES	55.11	3.58	101.10
BAITLAWS LAMINGTON	55.56	3.62	100.00
NEWTYLE HILL CRAIGVINEAN	56.22	3.56	98.67
FINSTHWAITE ESTATE	54.27	2.98	98.56
ELIBANK PEEBLESSHIRE	55.62	3.02	96.22
FLOORS KELSO	55.30	2.47	93.94
DUNALASTAIR TUMMEL BRIDGE	57.62	4.12	93.25
GLEN FESHIE KINCRAIG	57.08	2.25	89.33
WOOD OF ALDBAR MONTREATHMNT	56.68	2.70	88.50
KYLOEAG SPINNINGDALE	57.89	4.26	87.33
WITHERSLACK ESTATE	54.28	2.87	86.00
LANGBANK RENFREWS	55.27	4.52	83.94
INVERMOSSAT STRATHDON	57.25	2.84	83.89
ACHNATRA INVERARAY	56.16	5.04	83.11
KILLIN PERTHSHIRE	56.17	4.31	79.25
DELNAPOT BLACKSBOAT ELGIN	57.42	3.38	78.44
LADY JANE'S PLTN.INGLISMALDIE	56.83	2.55	77.40
CRUACH ARDURA MULL	56.22	5.74	76.11
PETERSMUIR E. LOTHIAN	55.35	2.83	75.50
MUIR OF DINNET ABOYNE	57.09	2.94	75.08
SILVIE ALYTH	56.62	3.18	74.44
DALL MILL BLACK WOOD OF RANNOCH	57.58	4.36	73.06
CREAGAN LOCH CRERAN	56.15	5.26	71.90
RANNOCH PERTHSHIRE	56.18	4.26	71.11
GLEN SPEAN ROY BRIDGE	56.89	4.81	70.89
WHITE BRIDGE GLEN GARRY	56.17	4.76	69.56
LEANACHAN FT. WILLIAM	56.85	4.92	69.10
PANNANICH WOOD BALLATER	57.06	3.01	66.89
MELLERSTAIN KELSO	55.30	2.55	65.83
TOMICH AFFRIC	57.31	4.80	63.35
GLENTRESS PEEBLESSHIRE	55.65	3.13	62.78
STRATHGARVE WOOD GARVE	57.61	4.66	62.33
BIRKHILL ALFORD	57.24	2.67	62.33
WAUCHOPE BORDERS	55.36	2.65	62.08
SPLINDLE MUIR WESTFIELD ELGIN	57.67	3.42	61.50
STRAANRUIE ABERNETHY	57.22	3.66	60.50

Table 2.14. Analysis of variance for diameter: df-degrees of freedom, MS Mean Squares, F-ratio MS/Residual MS; p probability level. The data were analysed using a generalised lattice design. Normality of residuals was checked using a Kolmogorov-Smirnov test. Significant differences are highlighted in bold characters in the probability column. *$p<0.05$; **$p<0.01$; *** $p<0.001$

	df	adj. MS	F	p
Blocks	2	0.02209	0.51	0.603
Sub-blocks	27	0.04856	1.12	0.342
Provenances	45	0.07809	1.8	**0.013***
Error	71	0.04331		
Total	145			

2.4.2.5. INDEX SELECTION

Height, stem straightness and flushing score at the beginning of March were combined to construct an index for tree breeding, following the same procedure as for Craigvinean. The improvement of 10% in height was considered as important as the improvement of 60% in straightness and as 60% delay in flushing. This assumption was translated into a set of weights, calculated on the mean values of height, stem score and flushing stage: $W_{sh}=0.17$, $W_{ss}=-0.88$, $W_{fs}=-1.33$.

The weights were used to construct the following simple index:

$$I=0.17P_{sh} - 0.88P_{ss}-1.33P_{fs}$$

Where P_{sh}, P_{ss} and P_{fs} are the individual mean provenance measurements for height, stem straightness, and flushing stage adjusted for block effects. The coefficients were the same for P_{sh}, and very similar for P_{fs}, changing instead consistently for P_{sc} across provenances. Trees having the highest index value would therefore be preferred for future breeding. Based on this index, the best provenances in Elgin were Castle Howard and Locharbriggs Dumfries. It must be noted that the provenance selected at Craigvinean *was* instead Witherslack Estate. However, the performance of this provenance was also quite high in Elgin

Table 2.15. Average of stem diameter for provenances at Elgin

Provenances	Lat.°N	Long.°W	Stem diameter (cm)
CASTLE HOWARD	54.12	0.92	1.14
LOCHARBRIGGS DUMFRIES	55.11	3.58	1.13
FINSTHWAITE ESTATE	54.27	2.98	1.00
WITHERSLACK ESTATE	54.28	2.87	0.98
NEWTYLE HILL CRAIGVINEAN	56.22	3.56	0.96
DUNALASTAIR TUMMEL	57.62	4.12	0.94
ELIBANK PEEBLESSHIRE	55.62	3.02	0.93
BAITLAWS LAMINGTON	55.56	3.62	0.90
FLOORS KELSO	55.30	2.47	0.87
DELNAPOT BLACKSBOAT	57.42	3.38	0.81
LANGBANK RENFREWS	55.27	4.52	0.80
GLEN SPEAN ROY BRIDGE	56.89	4.81	0.78
GLEN FESHIE KINCRAIG	57.08	2.25	0.77
KILLIN PERTHSHIRE	56.17	4.31	0.76
ACHNATRA INVERARAY	56.16	5.04	0.75
INVERMOSSAT STRATHDON	57.25	2.84	0.75
WOOD OF ALDBAR	56.68	2.70	0.75
WHITE BRIDGE GLEN GARRY	56.17	4.76	0.74
CREAGAN LOCH CRERAN	56.15	5.26	0.72
SILVIE ALYTH	56.62	3.18	0.72
LADY JANE'S	56.83	2.55	0.70
CRUACH ARDURA MULL	56.22	5.74	0.69
TOMICH AFFRIC	57.31	4.80	0.69
SPLINDLE MUIR WESTFIELD	57.67	3.42	0.68
LEANACHAN FT. WILLIAM	56.85	4.92	0.67
MELLERSTAIN KELSO	55.30	2.55	0.64
PETERSMUIR E. LOTHIAN	55.35	2.83	0.63
KYLOEAG SPINNINGDALE	57.89	4.26	0.62
BIRKHILL ALFORD	57.24	2.67	0.60
DALL MILL BLACK WOOD OF	57.58	4.36	0.58
MUIR OF DINNET ABOYNE	57.09	2.94	0.55
GLENTRESS PEEBLESSHIRE	55.65	3.13	0.53
STRAANRUIE ABERNETHY	57.22	3.66	0.52
PANNANICH WOOD	57.06	3.01	0.48
WAUCHOPE BORDERS	55.36	2.65	0.47
RANNOCH PERTHSHIRE	56.18	4.26	0.47
STRATHGARVE WOOD	57.61	4.66	0.39

Table 2.16. Analysis of variance for stem straightness, MS, Mean Squares, F-ratio MS/residuals; p, probability level. The data were analysed using a generalised lattice design. Normality of residuals was checked using a Kolmogorov-Smirnov test. Significant differences are highlighted in bold character in the probability column. $P<0.05$, **$p<0.01$;*** $p<0.001$.

	df	Adj ms	F	p
Blocks	2	0.02209	6.24	**0.003***
Sub-blocks	27	1.7017	1.11	0.349
Provenances	45	0.304	0.42	0.999
Error	71	0.114		
Total	145			

Table 2.17. Analysis of variance for flushing, MS Mean Squares, F-ratio, MS/Residual MS, P probability level. The data were analysed using a generalised lattice design. Normality of residuals was checked using a Kolmogorov-Smirnov test. Significant differences are highlighted in bold character in the probability column. $P<0.05$, **$p<0.01$, ***$p<0.001$

(a) Flushing 60 Julian days (10/03)	df	Ms	f	p
Blocks	2	0.0497		
Sub-blocks (adjusted)	27	0.0037		
Provenances	48	0.0079		
Provenances(adj)	48	0.0067	2.03	**<0.01***
Residual	69	0.0033		
Total (plot means)	146	0.0055		

(b) Flushing 81 Julian days (22/03)	df	MS	F	p
Blocks	2	0.0476		
Sub-blocks (adj)	27	0.016		
Provenances	48	0.0446		
Provenances (adj)	48	0.0405	2.08	**<0.01***
Residual	69	0.0195		
Total (plot means)	146	0.0275		

(c) Flushing 95 Julian days (5/04)	df	MS	F	p
Blocks	2	0.0013		
Sub-blocks (adj)	27	0.0143		
Provenances	48	0.0526		
Provenances (adj)	48	0.0497	3.31	**<0.001***
Residual	69	0.015		
Total (plot means)	146	0.027		

(d) Flushing 109 Julian days (19/04)	df	Ms	F	p
Blocks	2	0.0775		
Sub-Blocks (adj.)	27	0.0138		
Provenances	48	0.0459		
Provenance's(adj.)	48	0.0393	4.79	**<0.001***
Residual	69	0.0082		
Total (plot means)	146	0.0226		

Table 2.18. Mean flushing scores for 37 Provenances in Elgin the 18th of April

Provenances	Latitude	Longitude	Flushing score
MELLERSTAIN KELSO	55.300	2.547	3.67
CASTLE HOWARD	54.121	0.921	3.42
ELIBANK PEEBLESSHIRE	55.618	3.024	3.37
LADY JANE'S	56.832	2.549	3.34
DUNALASTAIR TUMMEL	57.625	4.122	3.22
FLOORS KELSO	55.300	2.469	3.21
GLENTRESS PEEBLESSHIRE	55.654	3.135	3.17
LOCHARBRIGGS DUMFRIES	55.113	3.582	3.16
DELNAPOT BLACKSBOAT	57.416	3.384	3.08
FINSTHWAITE ESTATE	54.270	2.978	3.06
WITHERSLACK ESTATE	54.279	2.874	3.04
LANGBANK RENFREWS	55.270	4.523	3.02
SPLINDLE MUIR WESTFIELD	57.665	3.420	3.00
MUIR OF DINNET ABOYNE	57.087	2.936	2.98
SILVIE ALYTH	56.622	3.185	2.98
KYLOEAG SPINNINGDALE	57.889	4.257	2.91
LEANACHAN FT. WILLIAM	56.851	4.916	2.89
GLEN FESHIE KINCRAIG	57.080	2.249	2.88
PETERSMUIR E. LOTHIAN	55.351	2.828	2.86
BIRKHILL ALFORD	57.236	2.671	2.84
BAITLAWS LAMINGTON	55.560	3.619	2.83
GLEN SPEAN ROY BRIDGE	56.887	4.807	2.78
WHITE BRIDGE GLEN GARRY	56.168	4.764	2.77
KILLIN PERTHSHIRE	56.172	4.315	2.72
NEWTYLE HILL CRAIGVINEAN	56.221	3.556	2.71
PANNANICH WOOD BALLATER	57.056	3.006	2.66
DALL MILL BLACK WOOD OF	57.579	4.360	2.65
WAUCHOPE BORDERS	55.360	2.652	2.61
INVERMOSSAT STRATHDON	57.254	2.837	2.61
ACHNATRA INVERARAY	56.163	5.044	2.57
WOOD OF ALDBAR	56.683	2.704	2.53
CREAGAN LOCH CRERAN	56.153	5.262	2.36
STRAANRUIE ABERNETHY	57.219	3.663	2.32
RANNOCH PERTHSHIRE	56.179	4.264	2.32
STRATHGARVE WOOD GARVE	57.607	4.665	2.19
TOMICH AFFRIC	57.314	4.798	2.18
CRUACH ARDURA MULL	56.222	5.739	2.12

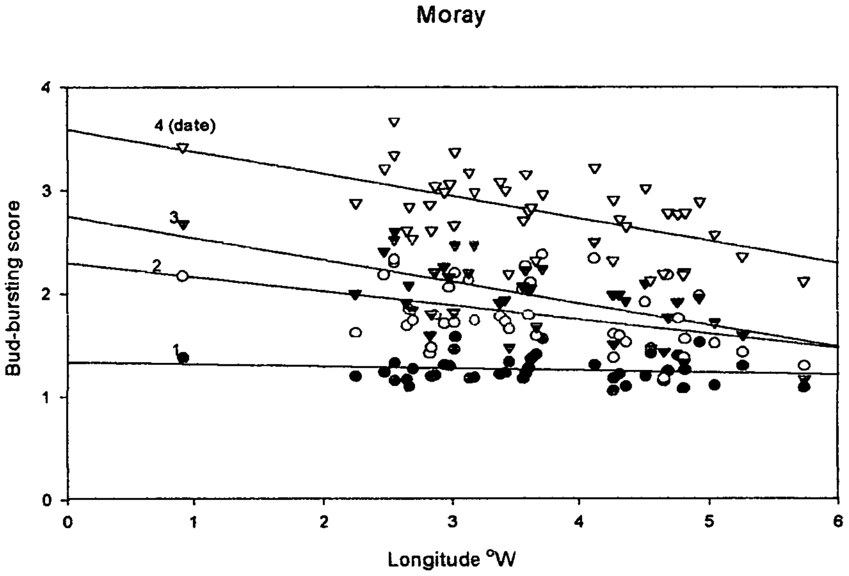


Figure 2.12. Bud-scores for 37 provenances during the four assessment dates plotted against longitude.

Table 2.19.a) Tables of Pearson correlation coefficients between various tree size and form parameters at Elgin; **b)** Table of Pearson correlation coefficients between tree size, form and flushing scores against latitude and longitude. **c)** Table of Pearson correlation coefficients between flushing scores dates. Values in bold are significantly different from zero. *, p<0.05; **, p<0.01; ***, p<0.001

(a)

	Branching	Diameter	Flushing	Height
Straightness	-.20	-0.9	-0.2	-0.35
Branching	–	0.65***	0.20	0.73****
Diameter	–	-	0.36*	0.86****
Flushing	–	-	-	0.34*

(b)

	Latitude	Longitude
Straightnesss	0.15	0.16
Branching	-0.45**	-0.22
Diameter	-0.55****	-0.24
Flushing 1	-0.31*	-0.15
Flushing 2	-0.33*	-0.42**
Flushing 3	-0.24	-0.59*
Flushing 4	-0.24	-0.57****
Height	-0.49**	-0.33*

(c)

	59 Julian days	80 Julian	95 Julian	108julian days
60 Julian days		0.37*	...0.23	.......0.24
80 Julian days	-		0.79****	0.8****
95 Julian days				0.92****
108 Julian days	-	-		

Fig.2.14 shows the selection index for the provenances in Elgin, ordered following a 45° gradient from South-East to North-West. The provenances quoted with the higher values are the ones with best shape performances and least risk of frost damages and would therefore be preferred for future breeding (Cotterill and Dean,1990).

2.4.3 BUSH ESTATE

2.4.3.1.ASSESMENT OF PHENOLOGY

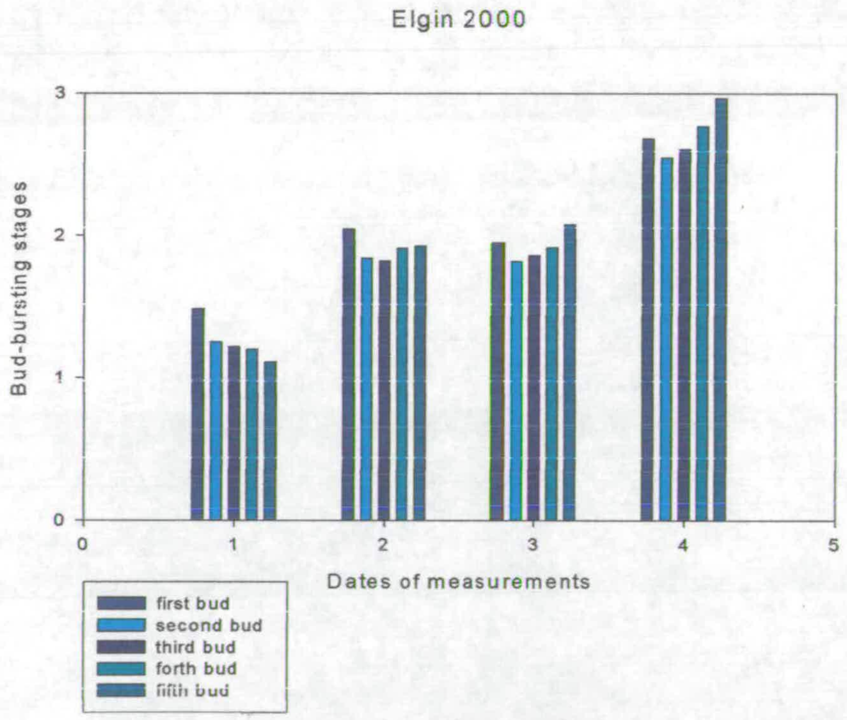


Figure 2.13. Budbursting stages of five buds from the top of the apical leader to the bottom.

The budbursting scores were significantly different across provenances for all the dates recorded. (from 31st March to 14th April) (Table 2.20).

Three provenances coming from South East (Floors Kelso, Birkhill Alford, and Langbank Renfrews) flushed earlier in comparison to the others. Blocks 1 and 4 showed higher flushing scores in comparison to blocks 2 and 3 for all the dates.

No correlation was apparent between flushing-scores, longitude, and latitude of the sites of origin, probably due to the small number of provenances tested (Figure 2.15)

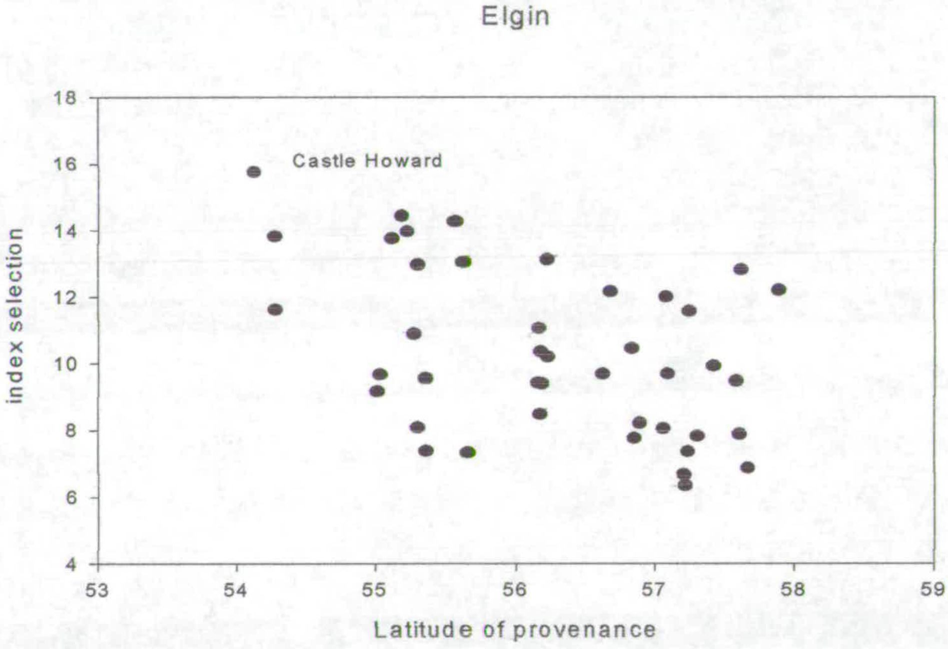


Figure 2.14. Index selection at Elgin 64

The dominance ratio between the five buds from the top of the apical leader for all the

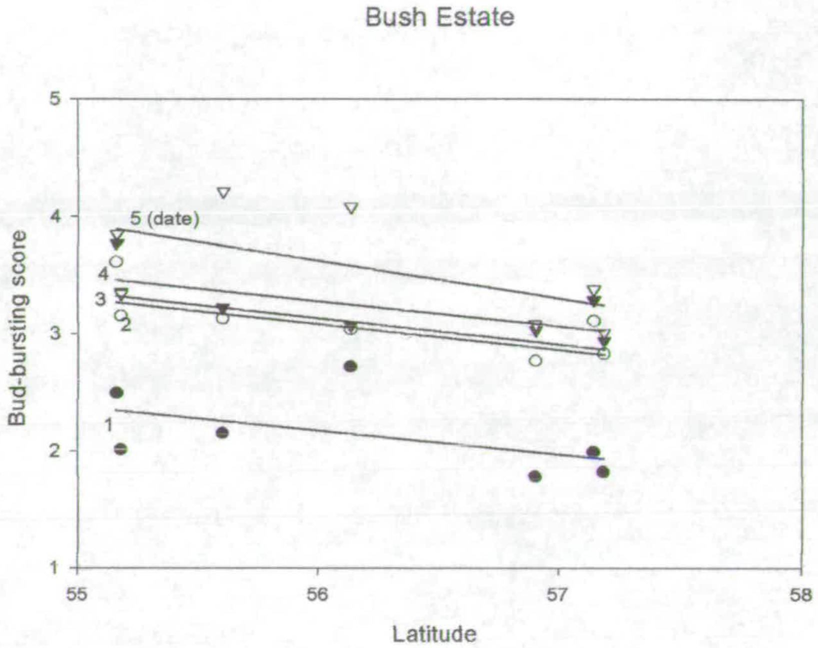


Figure 2.15. Bud flushing at Bush Estate ordered by latitude of the site of origins (seven and not eight provenances are plotted in the graph because “e10” is an improved provenance).

provenances is shown in Fig 2.16. The apical dominance of the first bud was very evident at this site.

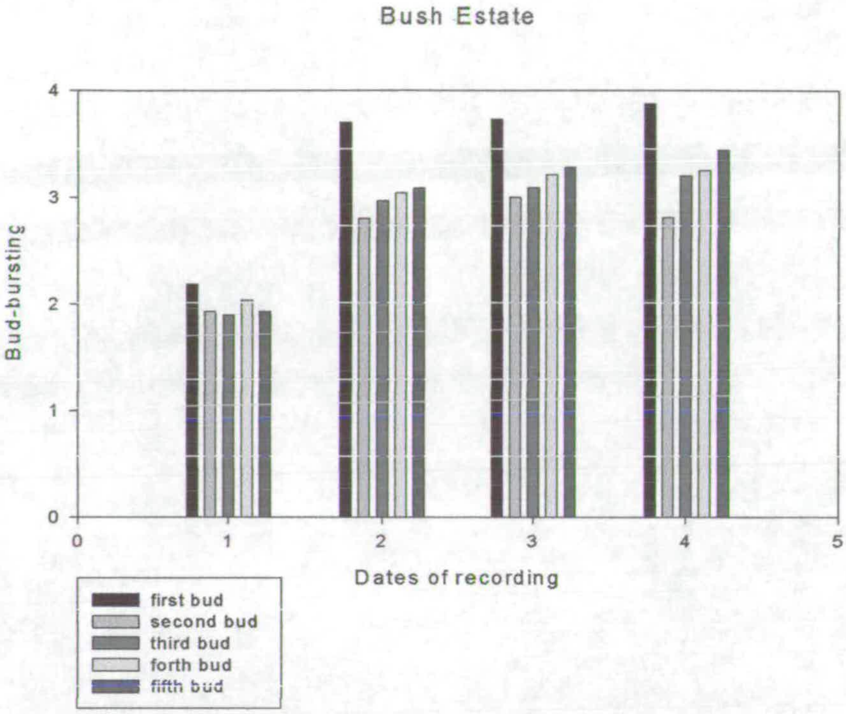


Figure 2. 16. Budbursting stages of the first five buds on the apical leader.

Table 2.20. a).- Analysis of variance for flushing scores in Bush Estate on the 31st of March;**b)** analysis of variance for flushing score on the 5th of April; **c)** analysis of variance for flushing score on the 10th of April; **d)** analysis of variance for flushing scores on the 14th of April.

(a)

31-Mar-00	df	MS	F	p
Blocks	3	1.53	2.70	**0.03**
Provenances	7	7.23	12.75	**<0.001**
Residuals	21	7.60	13.41	

(b)

5-Apr-00	df	MS	F	p
Blocks	3	2.92	3.91	**<0.05***
Provenances	7	8.95	11.99	**<0.001****
Residuals	21	5.41	7.25	

(c.)

10-Apr-00	df	MS	F	p
Blocks	3	2.64	4.08	**0.0068***
Provenances	7	8.12	12.56	**<0.0001*****
Residuals	2	3.81	5.89	

(d)

14-Apr-00	df	MS	F	p
Blocks	3	4.17	1.57	**<0.05***
Provenances	7	6.42	1.38	**<0.0001*****
Residuals	21	3.54	1.18	

2.4.4. COMPARISONS OF THE THREE TRIALS

Table 2.21: Absolute minimum temperatures and minimum temperatures in March at the three field sites in 1998, 1999 and 2000.

	Absol.min.T (1998)	Absol.min.T (1999)	Absol.Min.T (2000)	March Min 1998	March Min. 1999	March Min. 2000
Craigvinean	-9.1°C	-8.0°C	-4.5°C	-4.2°C	-3.5°C	-3.5°C
Elgin	-6.8°C	-5.0°C	-5.0°C	-5.0°C	-1.0	-1.0
Bush Estate	-8.0°C	-5.0°C	-5.0°C	-3.4°C	-4.6°C	-4.1°C

The absolute minimum temperatures and the minimum temperature in March from 1998 to 2000 at the three trial field sites are shown in Table 2.21.

The minimum temperature in March/April varied for Craigvinean and Bush Estate stations around –5 °C, values considered as risky for frost damage to young seedlings of silver birch. (Linkosalo et al., 2000), and for Elgin in 1999 and 2000 were around –1°C.

Table 2.20. a).- Analysis of variance for flushing scores in Bush Estate on the 31st of March;**b)** analysis of variance for flushing score on the 5th of April; **c)** analysis of variance for flushing score on the 10th of April; **d)** analysis of variance for flushing scores on the 14th of April.

(a)

31-Mar-00	df	MS	F	p
Blocks	3	1.53	2.70	**0.03**
Provenances	7	7.23	12.75	**<0.001**
Residuals	21	7.60	13.41	

(b)

5-Apr-00	df	MS	F	p
Blocks	3	2.92	3.91	**<0.05***
Provenances	7	8.95	11.99	**<0.001****
Residuals	21	5.41	7.25	

(c.)

10-Apr-00	df	MS	F	p
Blocks	3	2.64	4.08	**0.0068***
Provenances	7	8.12	12.56	**<0.0001*****
Residuals	2	3.81	5.89	

(d)

14-Apr-00	df	MS	F	p
Blocks	3	4.17	1.57	**<0.05***
Provenances	7	6.42	1.38	**<0.0001*****
Residuals	21	3.54	1.18	

2.4.4. COMPARISONS OF THE THREE TRIALS

Table 2.21: Absolute minimum temperatures and minimum temperatures in March at the three field sites in 1998, 1999 and 2000.

	Absol.min.T (1998)	Absol.min.T (1999)	Absol.Min.T (2000)	March Min 1998	March Min. 1999	March Min. 2000
Craigvinean	-9.1°C	-8.0°C	-4.5°C	-4.2°C	-3.5°C	-3.5°C
Elgin	-6.8°C	-5.0°C	-5.0°C	-5.0°C	-1.0	-1.0
Bush Estate	-8.0°C	-5.0°C	-5.0°C	-3.4°C	-4.6°C	-4.1°C

The absolute minimum temperatures and the minimum temperature in March from 1998 to 2000 at the three trial field sites are shown in Table 2.21.

The minimum temperature in March/April varied for Craigvinean and Bush Estate stations around –5 °C, values considered as risky for frost damage to young seedlings of silver birch. (Linkosalo et al., 2000), and for Elgin in 1999 and 2000 were around –1°C.

Averages of budbursting scores for each of the five buds on the apical leader at the three sites are reported in Fig 2.17 for each date of recording.

Seedlings in Bush Estate were the first to flush, followed by seedlings in Elgin and later on by the seedlings in Craigvinean. The seedlings in Craigvinean remained in the range of "buds swollen" to "buds green half opened" for 34 days. While on the 10th of March (66 Julian days) the average of flushing score was very similar for Craigvinean and Elgin, by the 21st of March (89-90 Julian days) seedlings at Elgin were definitely more advanced. The longitude of the three trials: (Bush Estate 3.150 ° West, Elgin –3.35 ° West and Craigvinean -3.66° West) probably exerted a higher influence than latitude on bud flushing. Craigvinean appears to be the coldest station and the station where the seedlings flush later. This was probably because of its altitude (280m a.s.l.), in comparison to the 110m a.s.l. in Elgin and to the 152 m a.s.l. in Bush Estate.

The first bud on the apical leader appeared to exert its dominance on the other buds more clearly at Bush Estate (the site furthest South) than at Craigvinean and Elgin (further North) (Fig 2.17). This may be related to the presence or absence of a straight form or shrubby form. The characteristic growth patterns of many plant species reflect the influence of apical dominance. Plants that grow tall and unbranched reflect a strong apical dominance influence, while plants that are short and shrubby give evidence of a weak influence of apical dominance. It would be interesting to determine wheter this difference in the apical dominance of the first bud on the others will favour the development of a more branchy habit in the long term.

Stem diameters at Elgin and at Craigvinean were not significantly correlated with one another (Fig 2.18). This result was expected, as provenances did not differ from one another within each trial. Tree heights at the two sites were not correlated across provenances (Fig. 2.19).

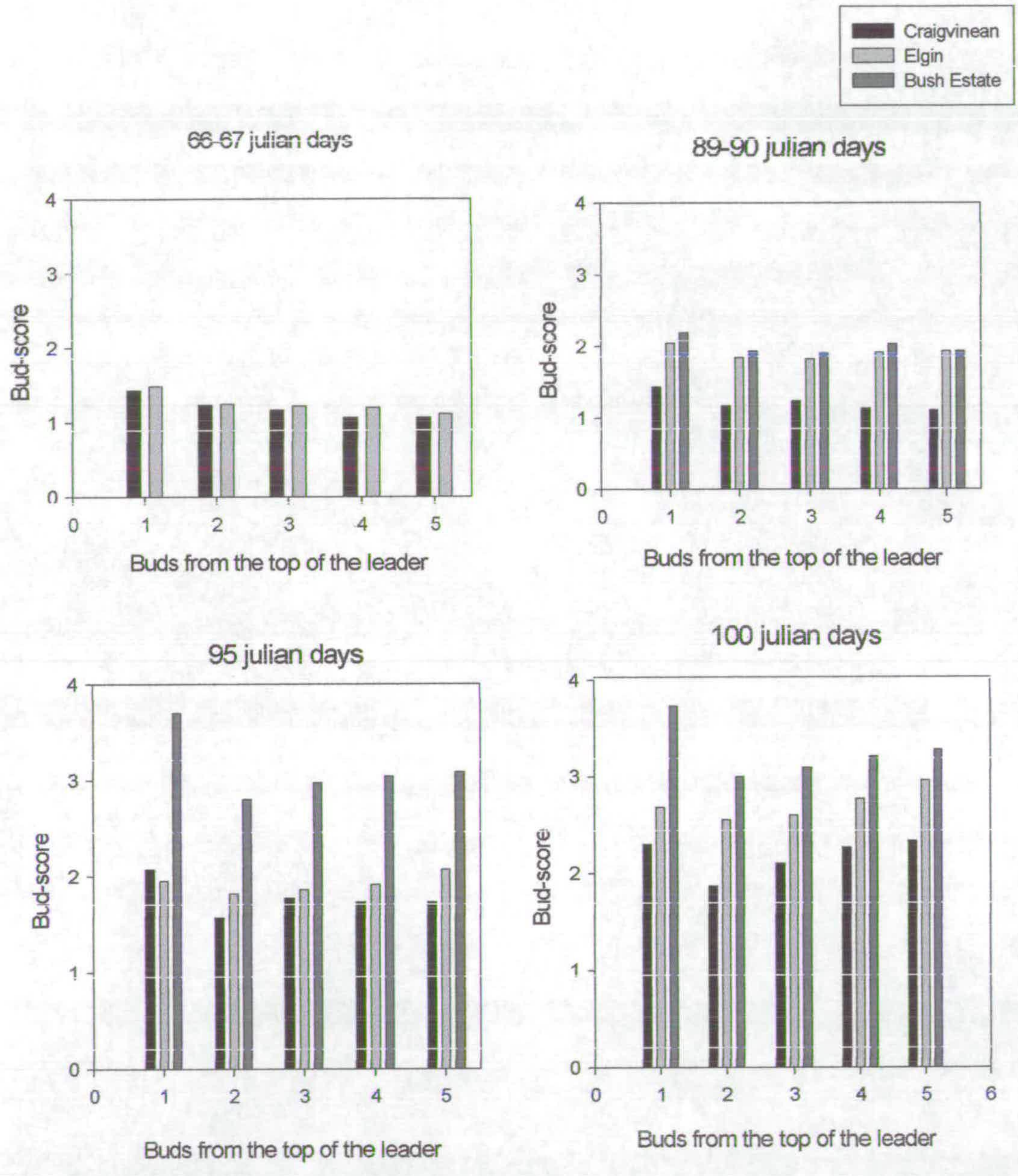


Figure 2.17: Comparison of bud-bursting scores at the three sites. The scores for the five most apical buds from left to right.

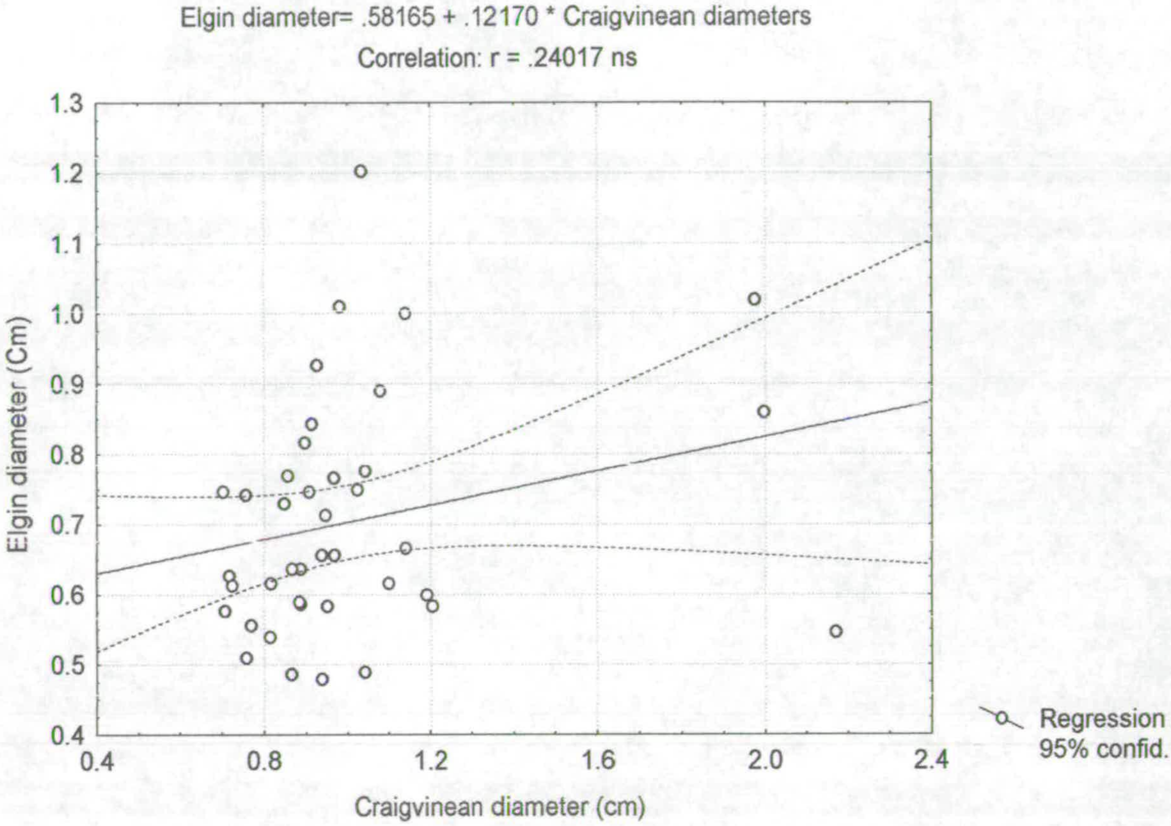


Figure 2. 18 Relation between average diameters for each provenance at Elgin and Craigvinean.

Flushing stages were correlated across provenances at the two sites. The correlation across sites increased from the first date to the fourth one (Fig. 2.20, 2.21, 2.22, 2.23).

There was no correlation between branchiness measured across the two sites. Overall, across provenances, Castle Howard gave a relatively good performance followed by Finsthwaite Estate, Locharbriggs Dumfries, Baitlaws Laming and Witherslack Estate.

Further study on the heritability of stem form and its development are needed.

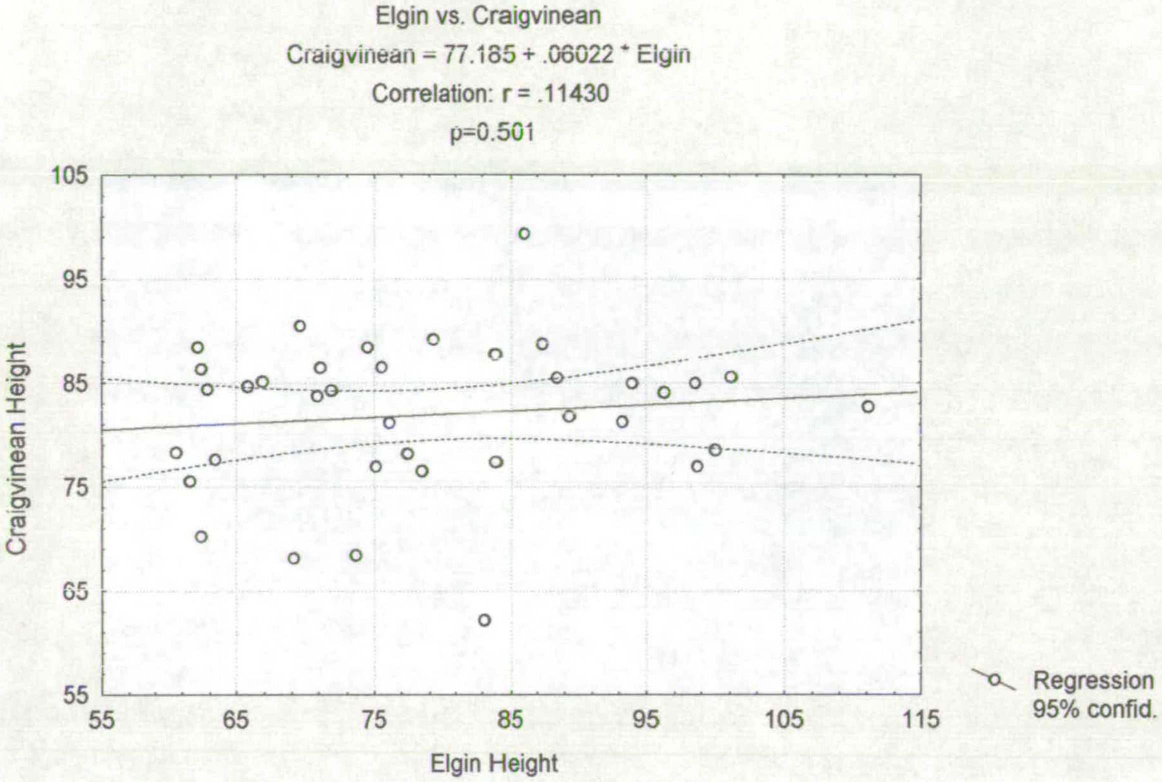


Figure 2.19. Relation between average height for each provenance at Elgin and Craigvinean.

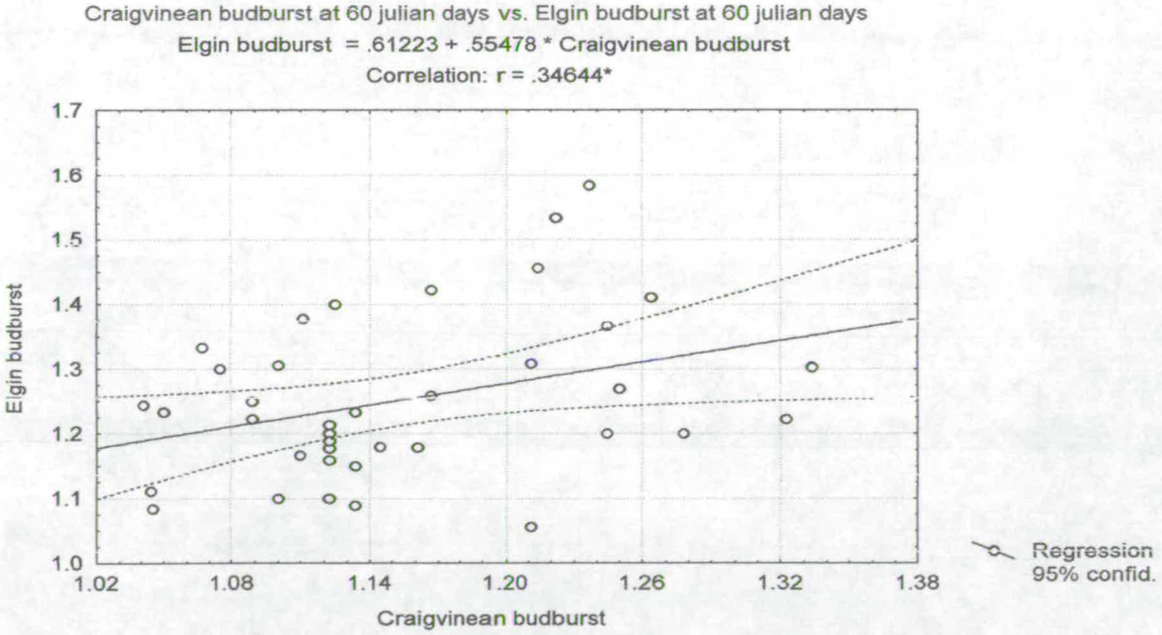


Figure 2.20. Correlation between budbursting scores for each provenance at 60 Julian day at the two trials.

2.5. DISCUSSION AND CONCLUSIONS

The trials at Craigvinean and Elgin have been the object of phenological and morphological observations by the University of Edinburgh and the Northern Research Station, Tree Improvement Branch, since 1998 (Donnelly 1998, Armstrong 1999). The trial in Bush Estate was also studied in 1999 (Bruce and McKay, 2000).

Combining the data from these various studies, it appears that provenances started to differ in height when they were two years old at Craigvinean, and one year old at Elgin.

Budbursting scores were different among provenances both in Craigvinean and in Elgin from the first year since planting. However the degree of variability amongst provenances varied with the site. In Elgin there is particular evidence of geographic patterns among the seed sources, with Southern and Eastern sources appearing to be relatively early flushing.

Conversely, the seedlings planted in Craigvinean flushed later and were slower to differentiate.

After three years, provenances differed for height and flushing stages at both sites.

Branchiness, diameter and height were positively correlated with one another.

Origins from the East showed definitely improved growth characteristics. Longitude seemed to exert a stronger influence then latitude on bud-flushing and height growth, showing significant trends among seed origins and among trials.

The apical dominance of the first bud on the top leader was more accentuated in the South then in the North. This could be associated with the development of the characteristic shrubby form in Northern areas.

In birch the leader is the keystone to the architecture, size and shape of the whole tree (Maillette, 1982). The degree of dominance, development and potentialities of the first bud could be used as an indicator in terms of predicting stem form and understanding when to intervene with appropriate culture regimes (Zhu et al., 2001).

Early selection aims to increase the efficiency and decrease the cost of genetic testing by recommending early indicator traits which could be well correlated with the mature traits. Height of two years old silver birch families in Norway was significantly correlated with the height of the same families at 16 years of age (unpublished data, Tom Skroppa). Since no correlation was apparent for branchiness across trials, a possible evaluation of the provenances with more or less ramifications is still considered precocious. Variability in growth characteristics within populations occurs in young seedlings, but tends to disappear with time (Worrell et. al., 2000). This could be the result of the large micro-site variability encountered by young seedlings. Microenvironment variability may become less important as trees get older.

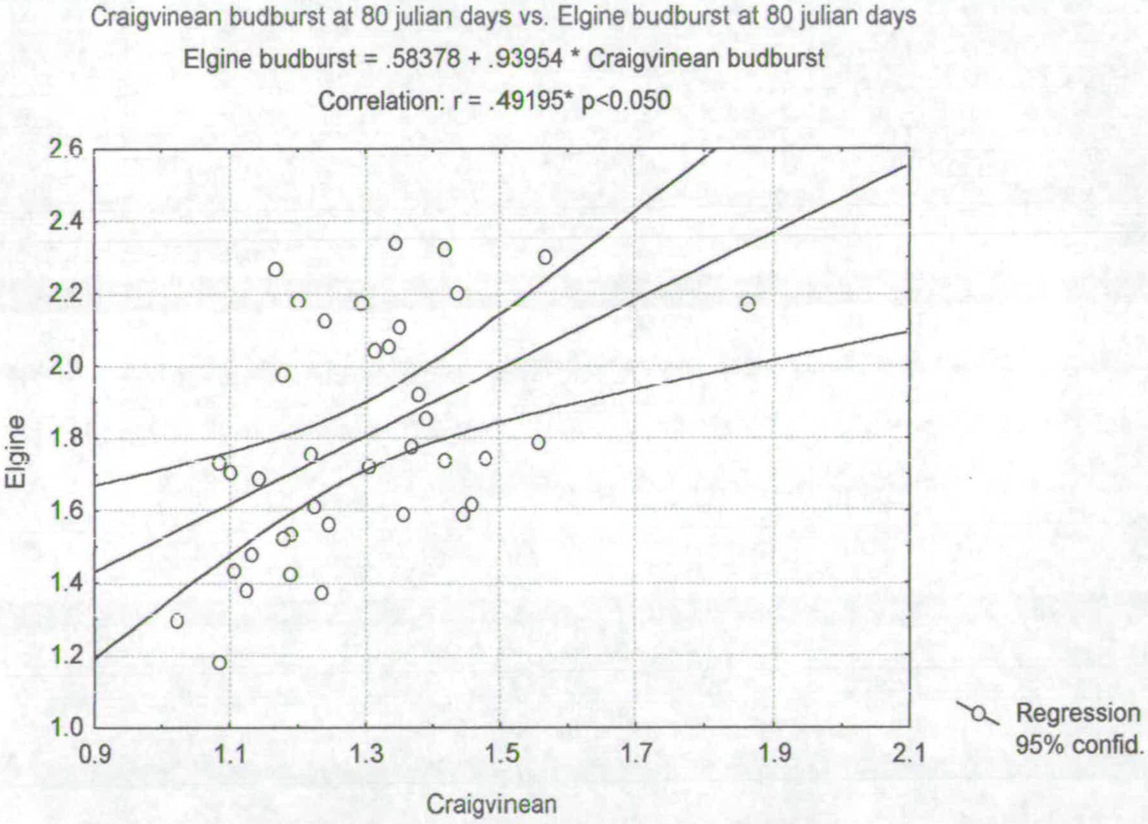


Figure 2.21. Correlation between budbursting scores for each provenance's at 80 Julian days at the two trials.

Attempts to identify and select specific sources most suitable for breeding within the best populations, is complicated by the fact that early growth rate alone is not a good indicator

Consequently, frost damage seem more likely to occur when plants deharden in spring than during winter.

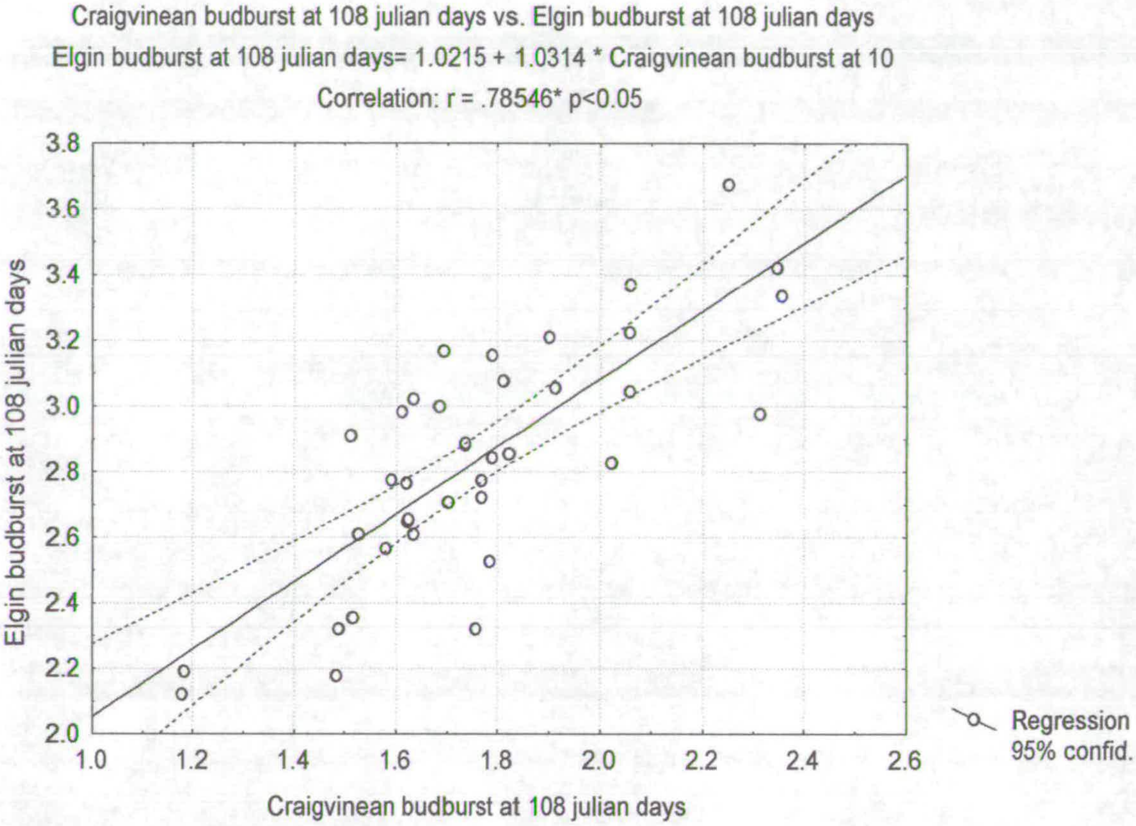


Figure 2.23. Relation between budbursting at 108 Julian days between the two trials.

The risk of damaging frosts occurring in the period between the date of budburst and 30 June (an arbitrary final date) is assumed to be inversely proportional to the minimum screen air temperature < 2 °C in that period (Linkosalo et al., 2000).

The qualitative observations on dieback carried out at Craigvinean showed that the damage appeared to be localised in the upper and thinner part of the leader stem. Provenances showing the highest percentage of damage were also those flushing earlier.

The most desirable response to warm weather in spring is to speed up budburst taking full advantage of the early warming, while minimising the risks of encountering subsequent frosts.

Climate changes, which may lead to a gradual warming, may also increase the frequency of extreme climate events, such as frost, and strong winds, increasing silver birch's predisposition to frost inducing damage. Any decrease in mean temperature on the date of budburst, or an increase of the variance in spring temperatures, is likely to increase the risks of subsequent frost damage. In silver birch, the potential paths of development of a bud through one growth season are complex. Buds, which have survived the winter, may die in springtime, may remain inactive or may open and expand their leaves (Maillete, 1982) Buds that remain dormant in spring and survive through the summer contribute to the bud bank of the next winter.

The risk of frost damage was estimated as the percentage of years having one or more occasions when minimum temperatures were below the threshold of –5°C degree between the occurrence of bud burst and June 30. The threshold temperature for damage in newly unfolded leaves of *Betula* is not well established. In a study of historical frost damage to *Betula alleghaniensis* Britton. in Canada and associated laboratory tests, Calme et al. (1994) inferred a threshold air temperature of around –5° C.

Observations of minimum temperatures after the recorded bud burst dates (i.e., in the period March to April) during the period 1998-2000 indicate that the minimum temperature never fell below –5°C in the period going from March to April. This together with the observation that extensive spring frost damage of birch was seldom observed at the examined sites over three years, offers some support for the –5 °C threshold adopted here.

3. MICROCLIMATOLOGY OF A BIRCH PLANTATION AT CRAIGVINEAN FOREST: FREQUENCY AND EXTENT OF XYLEM SAP FREEZING.

3.1. INTRODUCTION

In the previous chapter the presence of significant differences in bud phenology and tree shape and size were demonstrated across a range of native Scottish and English provenances. The differences were apparent along a geographical gradient of North to South and East to West, suggesting that environmental differences across the UK can have profound effects on the performance and the likelihood of frost damage in silver birch.

Silver birch has been proposed as a native species for afforestation and reforestation in Scotland but it is true that often, in comparison with birches of other northern countries, its shape is quite poor.

Trees don't achieve outstanding height and stem diameter, and often they present damage on apical shoots. This makes them not suitable for timber production. The objective of this study was therefore to focus on the role of frost desiccation in determining the form of silver birch.

The central hypothesis of this study was that frost desiccation is responsible for the precocious dieback in young shoots of birch seedlings and for the dysfunction of xylem conductivity caused by winter embolism. These two phenomena are one of the possible causes of the contorted and poor shape of the trees.

Frost desiccation is described as a phenomenon of dehydration, a common feature among several environmental stresses (Tranquillini, 1979). The process of dehydration due to low temperatures is attributed principally to the freezing of the sap in the xylematic conduits: this dysfunction results from the nucleation of gas bubbles during freezing. When temperature rises, if the ice melts slowly and no tension develops in the tissue, then the air will dissolve. But if tensions develop beyond some critical values, then the bubbles will expand to make the conduit fully embolised and dysfunctional. Apparently, the vulnerability to freezing-thawing cavitation is related to vessel size: embolism was almost complete after a single freeze-thaw event in oak with vessels 100 *u*m in diameter, but only 70% of the conduits embolised in maple with vessels 40*u*m in diameter and only 30% of the conduits embolised in conifers with tracheids 10*u*m in diameter (Davis et al., 1999).

The mechanism of development of xylem embolism by freeze-thaw cycles has been well documented in many broadleaf and conifer species (Sucoff 1969, Sperry et al. 1988, Just & Sauter 1991, Lo Gullo & Salleo 1993, Lemoine et al. 1999). It has been described for the genus *Betula*, i.e. *B. platyphylla var. japonica* in Japan (Utsumi et al. 1988), *Betula occidentalis* in Utah (Sperry & Sullivan 1992), and *Betula papyrifera* in Alaska (Sperry et al. 1994). It has also been described for silver birch in Northern Germany (Hacke & Sauter 1996), but there is no evidence to show that such a phenomenon is present for the same species in the very oceanic Scottish climate.

The potential importance of the phenomenon can be better understood if one considers that in the studies reported above for various birch species, the reported rate of xylem dysfunction (loss of conductive capacity) caused by the presence of air emboli, varied between 20 and 100%.

Another potential cause of frost desiccation is represented by the differences in temperature between the upper warmed parts of the plants, (activated by high level of irradiance in spring), and the possibly still frozen root systems. Under these conditions, plants are unable to obtain soil water due to the low soil hydraulic conductivity. Soil moisture can also influence hardiness and survival because it affects tissue hydration and indirectly soil temperature.

The freezing of water in plant tissues in late spring and early autumn is associated with various types of injury. These include black heart and frost cracking in xylem of trees and shrubs; blossom kill; death of vegetative shoots in late maturing perennial species; death of buds and bark in plants which lose hardiness rapidly during transient warm spells in winter.

A strong correlation between exothermal temperatures and living xylematic cell injuries (measured as electrolyte leakage) was found by Ashworth (1983) studying the profile of temperatures of xylematic conduits in apricot and peach. Living xylem cell injuries were found to occur over a range of temperatures corresponding to the lowest temperature exotherm at several dates. The seasonal changes in exotherm temperature were found to parallel changes in sensitivity to freezing injury.

In many woody species, bark, xylem tissue, buds and other organs of the plants have been found to respond differently to the freezing stress and presumably to have different mechanism of freezing resistance: in many hardy woody species, living xylem cells have been found to be considerably less hardy in midwinter than buds or cells of the living bark (Quamme, 1973). As in the case of xylem ray injury, the killing temperature of buds coincided with a sudden exotherm or release of heat. These exotherms appeared as buds began to acclimate in the autumn and shifted to progressively lower temperatures as acclimation proceeded persisting until flower bud expansion in the spring.

Although quite a few profiles have been studied during the freezing of a number of plants, only in rare instances has it been possible to demonstrate that sudden exothermic changes in xylematic vessels were associated with freezing injury to hardy plants. Nonetheless low temperature exotherms have been related to woody plants distribution (George et al., 1974), and freezing-thawing cycles have been interpreted as a cause of vulnerability to embolism (Sperry et al., 1993).

The disappearance and reappearance of lowest temperatures exotherm with changes in the hydration of stems suggests first, that the exotherm results from the freezing of the water (Quamme, 1971), and second that there is a relation with the plant's water content. Usually in plants which acclimate, water content (degree of hydration) almost invariably decreases with increasing hardiness, and increases as plant deacclimate. So frost hardiness could be considered as a form of drought tolerance because the removal of water from cells to extracellular ice imposes a considerable desiccation stress on the protoplasm.

Frost hardiness in most plants appears to be related to tolerance of extracellular freezing, whose extent and occurrence may vary in relation to the seasonal temperatures experienced in many hardwood species.

The likely increased duration and frequency of mid-winter thaws in light of global climate change can greatly can increase the risks of freezing injury, winter cavitation and dieback in northern birches thereby interfering and altering their biological clocks. Early spring in particular is considered the risky season for frost stem desiccation.

Studies on budburst in *B.pubescens* and *B.pendula* prove that warm periods in early spring considerably reduce the thermal time requirement (accumulated day degrees >0°C) for budburst and thus advance budburst (Heide 1993). Swelling and bursting of buds dramatically increase frost sensitivity and therefore severe freezing after a warm period represents the greatest risk of frost damage.

Freezing resistance changes markedly with season and stage of development. Hardy trees and shrubs which survive –196°C during winter dormancy may be killed at –3°C during active spring growth (George et al., 1974). The frost resistance of silver birch is equated to a threshold of damaging temperature of –32°C in December, and -26°C in February (Bruce & McKay 1999).

In spring, birches progressively lose their frost hardiness and a series of physiological processes responsible for budbursting and for the start of the vegetative growth take place. In this period, the temperature likely to cause possible damage and dysfunction to the living cells and to the xylem water conductivity is of about –5 °C (Bruce & McKay, 1999; Sperry et al., 1994), a quite common temperature in late March and April in Scotland. During the active period of growth, the leaves and new shoots of unacclimated hardy trees and shrubs can be injured by –1 to –3° C temperature (Burke et al., 1976).

Significant differences in shoot frost hardiness across a range of native Scottish provenances have been demonstrated by Bruce and Mackay (1999) and Blackburn & Brown (1988). The differences were apparent along geographical gradients suggesting that environmental differences across Scotland can have profound effects on the adaptations of silver birch to resist stem frost damage and sub-zero temperatures. This intraspecific variability may also determine whether provenances from different regions of the country differ in their vulnerability to freeze-thaw cycle embolism. Bruce and Mackay (1999) tested the Electrolyte Leakage of eleven randomly distributed Scottish provenances in the country. A general tendency for Eastern seed origins to require slightly cooler conditions to cause 50% shoot mortality than Western seed origins was found. These origins also demonstrated an earlier flushing compared to Western ones. In early April most western seed origin suffered 50% damage just below –5°C while all eastern seed origins appear to withstand almost -6°C.

It is possible that the observed damage is a function of the sensitivities of the different provenances to subsequent cycles of sap freezing/thawing or to the absolute temperatures below zero reached during frosty nights. It is also possible that they are determined by the lack of recovery upon thawing in the spring as a consequence of damage to the living cells either in the roots where pressure is produced, or in the shoot. The susceptibility to cavitation by freezing provides a hypothetical link between xylem structure, phenology, and refilling capability.

3.1.1.OBJECTIVES

In order to detect and study episodes of frost desiccation, the seasonal courses of air, soil and xylem temperature were recorded in the forest of Craigvinean from the 14 of February to mid April 2000. The aims were: 1) to document the presence of the exotherms due to changes of state in the xylematic conduits of birches directly in the field; 2) to assess the existence of a relationship between freezing temperatures and sap freezing in early winter and just before spring in existing plantations of birch provenances; 3) To relate freezing temperature differences across provenances to differences in phenology and 4) to predict events of sap freezing using a climatic model of the interested area.

Two provenances of silver birch were chosen for further measurements, because they had proven different in the tests for electrolyte leakage during winter and spring (Bruce &

MacKay, 1999) (*Birkhill Alford* Northeast of Scotland and *Locharbriggs Dumfries* Southwest of Scotland). We predicted that different provenances have evolved mechanisms for coping with a potentially extensive loss of water transport capability caused by freezing events. These mechanisms would include the coupling of vegetative phenology, xylem features and refilling capability.

3.2. MATERIALS AND METHODS

3.2.1. STUDY SITE

Experiments were conducted at the Craigvinean Forest previously described in Chapter 2, and in the laboratory using branches detached from 7 year-old silver birch growing in a provenance trial at the University of Edinburgh.

3.2.2. LABORATORY EXPERIMENTS

HYDRATED BRANCHES AND DEHYDRATED BRANCHES EXPOSED TO RAPID FREEZE-THAW CYCLES

An experiment was conducted by subjecting cut branches to a controlled freezing treatment.

Branches of silver birch were collected in January-February 2000 from a seven years old trial at the University of Edinburgh. Two groups of six branches each were randomly selected from six plants. One of the two groups was used as control whereas the second group was hydrated and kept in plastic bags filled with water for five hours. Branches belonging to both groups were then left in a freezer overnight undergoing a cooling rate of about 0.8°C min^{-1} from room temperature down to –15°C. Treated branches were then removed from the freezer, and allowed to thaw until they returned to room temperature. Cooling and warming rates of stem segments were determined through thermocouples, inserted into holes of 0.5mm diameter drilled by a cordless precision power tool drill into the bark of stems. The thermocouples were held in place with masking tape, for each of the 12 stems. The temperatures were recorded at 1 minute intervals, with a datalogger (Model 21x, Cambell Scientific, Inc.).

3.2.3.CRAIGVINEAN FOREST

Studies were conducted in the field from February to April 2000 on 3-year-old silver birch seedlings. The seedlings were selected to belong to two provenances. The choice of these two provenances was determined based on the results of a previous study (Bruce and Mackay, 1999). They were Birkhill Alford, (57°14'8.45'' Lat, 2°40'15.64 Long) and Locharbriggs Dumfries (55°6'47''Lat, 3°34'55.24 Long.). The two provenances were shown to be respectively the least damaged and the most damaged by the low temperatures predicted to cause 50% of shoot mortality (LT50) (Bruce and McKay, 1999).

Birkhill Alford appeared to have a more advanced flushing at the beginning (21st March) and at the end (17th April) compared to Locharbriggs Dumfries, during the measuring campaign.

Six plants from the two seed sources were chosen to carry out the xylem temperature measurements. For practical reasons we chose the 12 plants, belonging to the two provenances which were closest to the datalogger in central position. Air, stem and soil temperatures, and soil water potential were continuously monitored using two dataloggers (Models 21X , and CR10, Campbell Scientific, UK 1990), placed in on insulated box between the two sources plots. Twenty-five thermocouples were used to measure air temperature, stem temperature and soil temperature, and two tensiometers (Skye Instruments) were used to measure the soil water potential in each plot.

Stem thermocouples were inserted in to a small hole of 0.5mm diameter drilled by a cordless precision power tool drill into the bark and taped into position so that the thermal junction of the thermocouple was adjacent to the outermost xylem ring. The hole was made at 20cm height from the bottom of each seedling. Each thermocouple was inserted to a depth of 2-3 mm. Once inserted, the stem was surrounded by insulating foam of about 10cm length along the stem. Another thermocouple was applied over the foam to record the air temperature. The thermocouple junction diameters varied between 0.3 and 0.4 mm, which means that each junction was probably in contact with several vessels, parenchymatic cells and fibers (the diameter of birch vessels range from 30 to 130μm). One thermocouple was inserted ten centimeters below the soil surface and two tensiometers were inserted at 20cm depth below the soil surface, to measure the water potential and the relative soil temperature at each plot.

Temperatures were measured once every two minutes, averaged every 30-minute interval throughout the day from February to April 2000. The thermocouples were of type T: copper and copper-nickel (also known as Constantan) conductor combinations (tolerance class of ± 30μV (± 0.5 °C) or ± 60μV (± 1 °C); temperature range –40°C to +125°C); each thermocouple had seven strands of 0.2mm diameter. The junction was made by fusion of the two extremities with non corrosive Flux 5 core 60/40 tin/lead BS219 KP.

A program was written to the loggers to record temperatures every 2 minutes in stems if the air temperature was less than 4 °C and every hour if the air temperature was higher then +4°C. Temperatures were recorded and downloaded every 15 days starting from 9th of February.

The Tensiometers (LD1 6DF) were fitted with a low pressure transducer stabilised for temperature and linearity. The measurements were made directly in hPa. The head of the instruments which houses the pressure transducer, is machined from acrylic and is fully sealed for outdoor use. The shaft holding the water is also made of acrylic and again is fully sealed into the porous ceramic bulb which allows the transfer of water for the pressure to be measured.

A hollow length of pipe of similar diameter as the tensiometers shaft (22-25mm/o.75) was used to delicately make a pilot hole, so as to not alter the soil structure. Any bubble present was removed. An insulation foam was placed over the exposed tops to prevent water freezing in the tube.

A recording time of six hours was adopted: four temperature probes, four tensiometers and one soil block were used in total.

Silicone sealant was applied around the cables to prevent moisture entering the box.

3.2.4.THE DTA TECHNIQUE

To determine the freezing points of tissue water, the differential thermal analysis (DTA) technique was used as it is a very sensitive method for detecting exothermic changes. Its advantage consists (Mackenzie, 1970) in the possibility to study the freezing of minute quantities of water in living tissues. This technique has been used in research principally for two reasons: one to detect straightway freezing points directly related to xylem injuries and frost injuries, and the other one to individuate freezing/thawing cycles in xylem and relate them to the ratio of embolised conduits.

When Differential thermal analysis (DTA) is employed, a record is made of the temperature difference between the sample and a reference material, against time or temperature, as the two specimens are subjected to identical temperature regimes in an environment heated or cooled at a controlled rate. The graphical record, the DTA curve, shows sharp increases or decreases in the temperature difference, depending on whether a change in the sample causes absorption or liberation of heat. The method records all changes in enthalpy, whether accompanied by a change in weight, e.g. phase (change of crystalline structure, boiling, sublimation, evaporation, melting), or chemical reactions such a redox reactions, decomposition, dehydration and dissociation. However, DTA indicates nothing about the kind of change taking place in one or several steps. The nature and mechanism of the change can be analysed by other methods (e.f., x-ray technique).

In DTA the temperature conditions are dynamic. The difference between the temperature of the sample and that programmed is the fundamental condition of the method. The introduction of DTA is related to the discovery of the thermocouple. An exploitation of the method, mainly in quantitative analysis, is complicated owing to the number of experimental conditions, which can fundamentally influence the results. Every chemical reaction or physical transformation liberates or absorbs heat, causing a change in temperature. Such as a change may also be accompanied by a change in weight corresponding to the formation of reaction products. DTA is capable of determining changes that are not accompanied by a change in weight, such a change in crystal structure, or melting. Thus DTA can record every enthalpy change, exo- and endothermic, caused by any structural or chemical change.

Generally phase transitions, reductions, dehydration, and some decomposition reactions are endothermic, while oxidation, some other decomposition reactions, and crystallisation are exothermic.

The position of the resultant temperature change on the temperature axis is characteristic of the investigated substance under the given experimental conditions, and may be used for its identification.

The important factor for a given change is not the total amount of heat liberated or absorbed, but the rate at which this heat change, $\Delta Q/\Delta t$ occurs.

Energy changes, which take place on heating or cooling of the sample, may be measured by a direct recording of the heating or cooling curve while the sample is exposed to continuous heating or cooling following a known linear programme.

An exothermic effect causes an increase in the heating rate ($f'(t) > K$) whereas an endothermic effect causes a decrease in the heating rate ($f'(t) < K$, $K > 0$), where $f'(t)$ is the slope of the temperature function $T = f(t)$ representing the rate of temperature changes and being equal to a certain variable $f'(t) = K$. When an exo- or endothermic change takes place over time, the shape of the curve changes and the slope of the curve assumes a different value.

In recent years DTA has been extensively developed and has brought about a tendency to express DTA curves in mathematical terms and to make use of them for quantitative determination of the heat of reaction or of other changes occurring. The quantitative aspect of the method is that a measure of the heat of reaction and hence also of the amount of the active substance in the sample can be made from a consideration of some characteristics of the curve, mainly of the area under the curve, expressed by its integral. However, the majority of the mathematical expressions for the DTA curves are more or less approximate and often based on assumptions, which are not always completely valid.

This does not mean that quantitative applications of DTA are meaningless, but it shows that they have a limited validity and that several factors should be considered carefully from case to case.

3.2.5.WHY EXOTHERMS?

The density of ice is 0.92 g/cm^3, the crystal system is hexagonal and the number of molecules in unit cell are four. Its relatively low density, which accounts for some of the properties of liquid water and of the high-pressure ices, has lead to its structure, open and with empty spaces to accommodate interstitial water molecules. Ice near 0 °C can be melted by the application of pressure.

Ice crystals can grow in two simple distinct ways: by freezing of liquid water or by direct sublimation from the vapor phase. The thermodynamic force driving any crystallization process is an excess of the chemical potential of molecules in the environment relative to its value in a bulk crystal. The total chemical potential excess may be divided into two parts:

- a component which is the driving force for transport of water molecules through the environment to the growing interface,
- A component which is necessary to achieve the incorporation of molecules into the crystal itself (transport of latent heat away from this interface).

At 0.006 bar and 0.01 °C the molal volume of ice is 1.63 cm^3 mole^{-1}, and the latent heat is 1430 cal mole^{-1}. If the system contains another component in addition to water, the situation can be much more complicated because crystal growth depends upon the transport of this component as well and there may also be competing processes occurring at the interface with the growing ice crystal.

Some additional components, such as air growth from the vapor, have a relatively small and simply understandable effect, but more complicated phenomena occur, for example, in the freezing of brine or sugar solutions.

When a small quantity of a liquid is cooled below its equilibrium temperature it does not immediately freeze, but remains for some time in a metastable supercooled state. It is not possible to maintain the supercooled state indefinitely or to achieve more than a limited degree of supercooling before spontaneous crystallisation occurs. It is found experimentally that the maximum supercooling attainable increases with increasing purity of the liquid, particularly as far as foreign particles in suspension are concerned, and that it is easier to supercool small droplets than larger volumes of liquid. When a liquid is supercooled, it is energetically favourable for it to change to the crystalline state. First, a very small volume of liquid must crystallise, and this crystal must then grow until all the liquid has frozen. A small crystal embryo is however in an energetically unfavourable state, because of its very large surface-to-volume ratio and the positive free energy associated with its interface with the liquid (Fletcher, 1970).

3.2.6. FACTORS AFFECTING THE DTA CURVE.

If the DTA curve is used for qualitative purposes, the shape, position, and number of endothermic and exothermic peaks is important. By a simple change of conditions, say cooling rate or external atmosphere, the positions, and the number of curve peaks will be changed. Differential thermal analysis, since it is a dynamic temperature technique, has a large number of factors, which can affect the resulting experimental curves. The DTA curve is dependent upon two general categories of variables, which are summarised in the table below:

INSTRUMENTAL FACTORS	SAMPLE CHARACTERISTIC
Wire and bead size of thermocouple junction	Particle size
Cooling or heating rate	Thermal conductivity
Speed and response of recording instruments	Heat capacity
Thermocouple location in the sample	Amount of sample

3.2.6.1.WIRES

In the measurement of temperature, the thermocouple may be used from near absolute zero to over 2500°C. As it is an electrical generator, it may be used to operate an indicator directly without external power supplies, and the indicator may be at a considerable distance from the temperature being measured. The thermocouple comprises two dissimilar metal wires joined to each other at both ends. Each junction acts as a local generator or Electro motive force measured in volts and of a value, which depends on its temperature. If the temperature of the junctions is not identical, the difference will cause a current to flow in the circuit. If the temperature of one junction called the reference or "cold"junction is known, the temperature of the second junction, called the measuring or "hot" junction, can be found. (Mackenzie, 1972)

3.3.RESULTS

3.3.1.BRANCHES EXPOSED TO RAPID FREEZE-THAW CYCLES IN THE LABORATORY

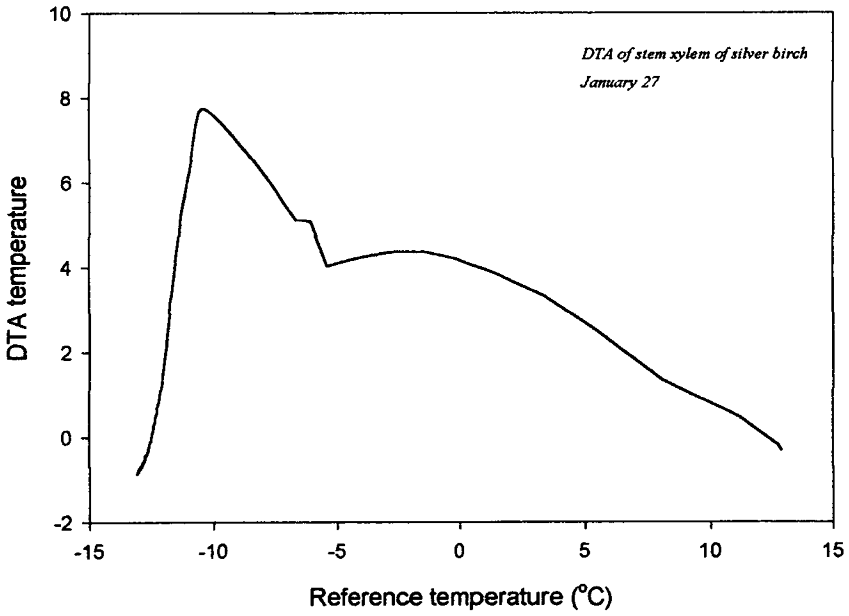


Figure 3.1. DTA xylem temperature versus air temperature

At the beginning of the experiment (extreme right point of the curve in Fig. 3.1.), the reference air temperature was about 12.5°C, with no thermal gradient between air and xylem temperatures (i.e., DTA equated zero). Upon exposure of the sample branch to freezing conditions, the reference air temperature rapidly dropped. The xylem temperature also tended to drop but a lower rate (because of thermal inertia of the tissue), causing the DTA values to increase. A clear exotherm was evidenced when the reference temperature dropped below –5°C, demonstrating that water started to freeze between –5°C and –10°C in January. The exotherms occurred over a narrow temperature range, indicating that once freezing was initiated, ice spread rapidly. The freezing course depicted in Fig. 3.1. was typical of other experiments of the same kind not reported here. Upon rapid freezing, the air-xylem T difference rose to ~8°C suggesting a large release of heat, then xylem temperature changed towards the temperature of the reference air. The water content of the branches in January was 73%. The exotherm was sharp and very well definable. No endothermic events were observed over the temperature range of the exotherm.

3..3.2. FIELD MEASUREMENTS AT CRAIGVINEAN FOREST

3.3.2.1. AIR TEMPERATURE

Figure 3.2 shows the records of hourly air temperatures in Craigvinean Forest, from the first of March to the 4th of April. Air temperature started to increase around the 13th of March.

Minimum hourly air temperatures recorded from the first of March to the 4th of April (beginning of the vegetative season) were grouped into three classes: 90 hours were recorded in the range from 0° C to –1°C; 72 hours were comprised between –1°C to –3°C, and 10 hours were comprised between –3°C and –5°C. Usually the lowest temperatures occurred during the late night and the early mornings. The highest temperatures (during midday) could rise to + 20°C with a temperature excursion between night and day of 20-25 degrees.

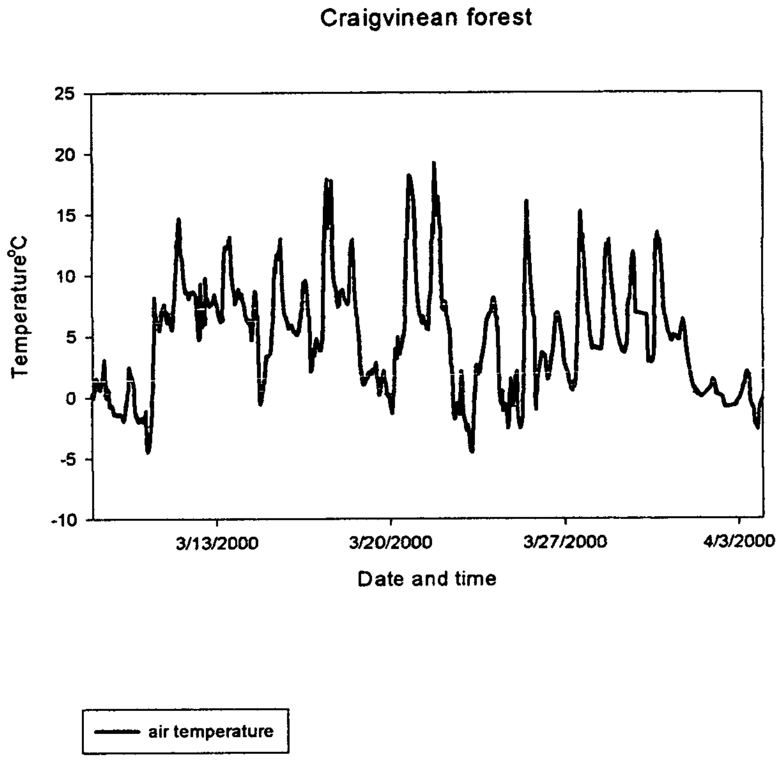


Figure 3.2 Hourly air temperature in Craigvinean forest from the 8 of March to the 4th of April

The hourly data of the temperatures recorded by the logger at the field site were correlated with the hourly temperatures available from the nearest weather station. The nearest station, Strathallan Airfield Saws, is located on the road B8062 near Millean, at Lat 56°326' N and Long -3°728'N. The regression between the two series is significant (($p< 0.05$, Figure 3.3) although the scatter is extremely large. This highlights the importance of local temperature measurements to relate the environmental conditions to the impact of freezing on the plants. Craigvinean also appeared to have much colder temperatures, probably because of its altitude and location in the forest (200 m.s.l.).

The latitude and longitude of Craigvinean, (located on the right of A9 road from Dalguise) are: 56°567' N and -3°640 'W.

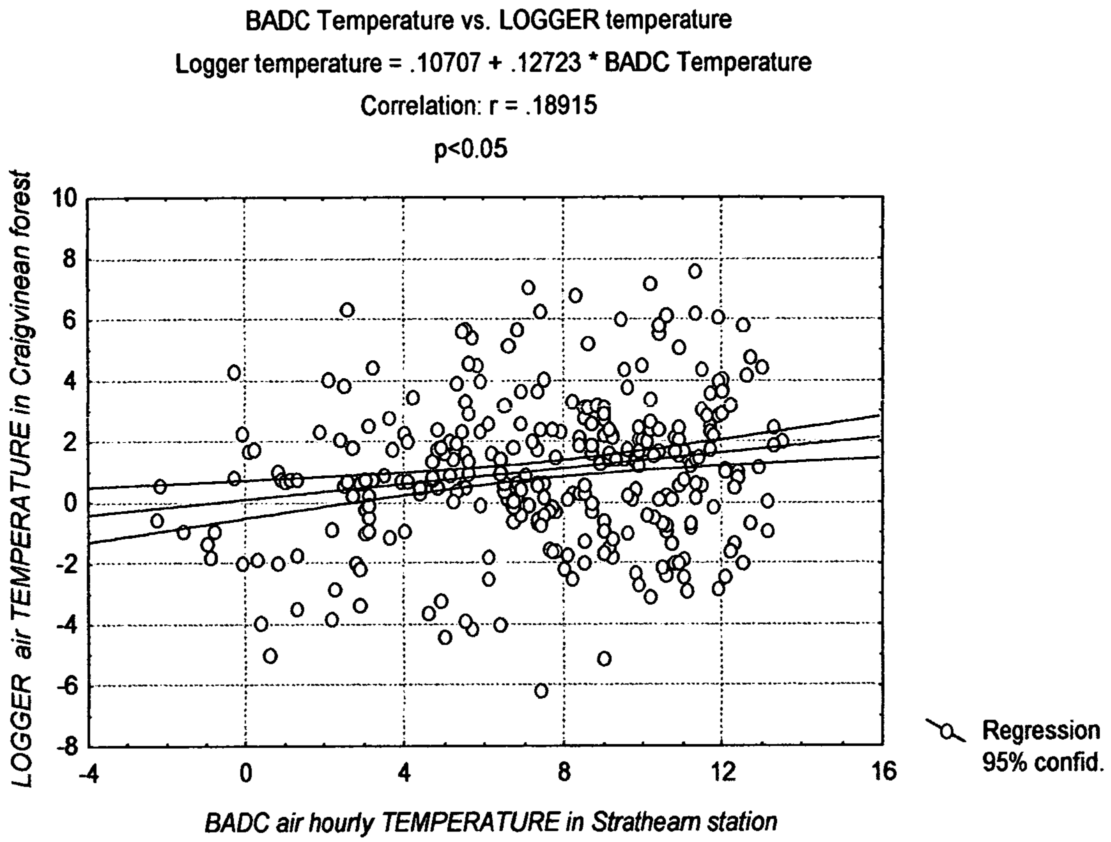


Figure 3.3: Correlation between hourly temperatures at Craigvinean forest measured with thermocouples in situ and hourly temperatures at the Straetharn Saw weather station.

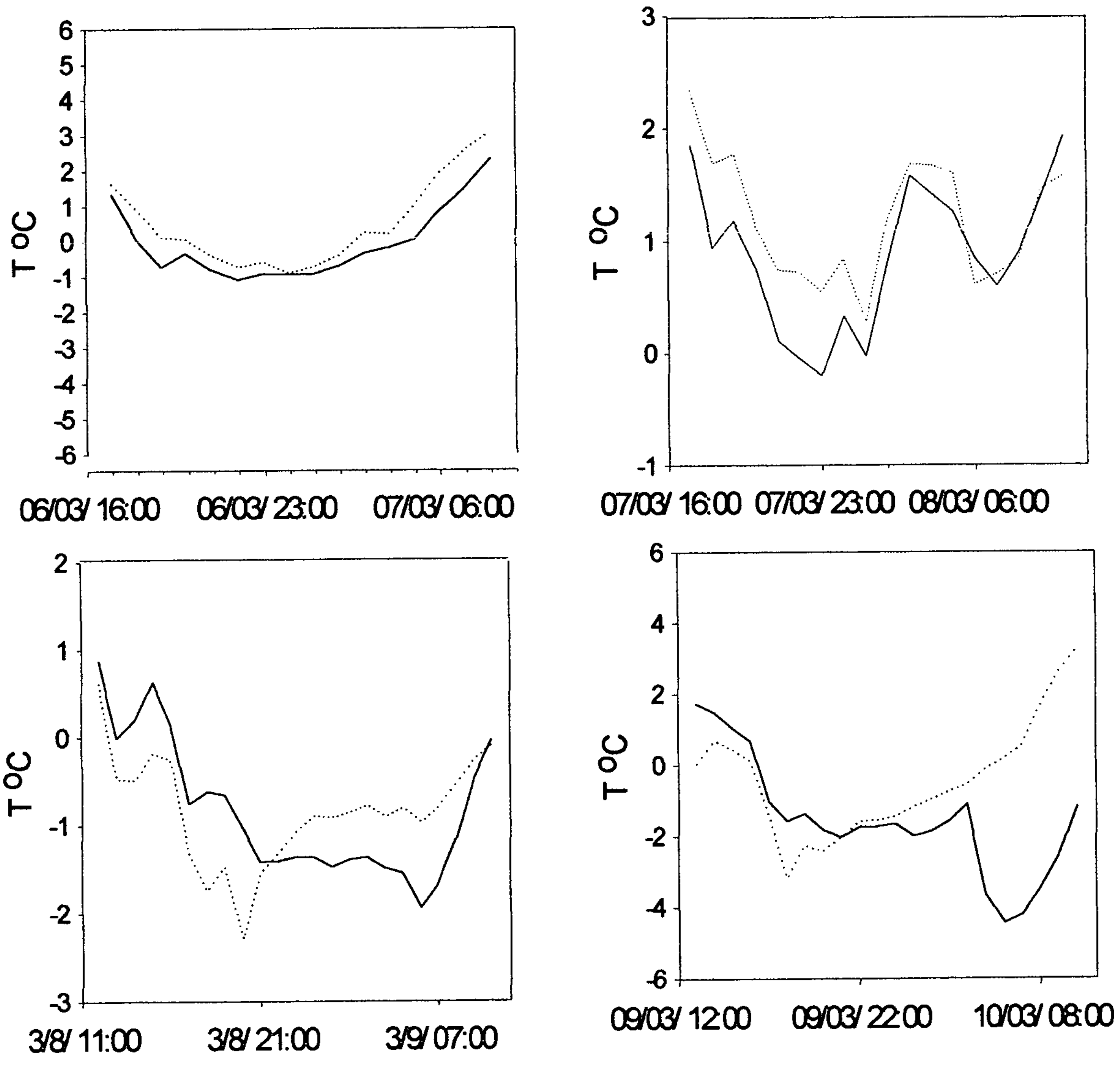


Figure 3.4. Particulars of soil and air temperature from 14 February to 10 March.

3.3.2.2. SOIL TEMPERATURE

Soil temperature data are available from February to the 21st of March (Figure 3.4). The correlation between air temperature and soil temperature was highly significant: ($p<0.0001$, $r=0.81$ Figure 3.5). Soil temperatures followed air temperature, and usually they were higher during the night and early morning. The highest difference in terms of was recorded the on 10th of March in the early morning: air temperatures decreased below –4°C while soil temperature was 2°C.

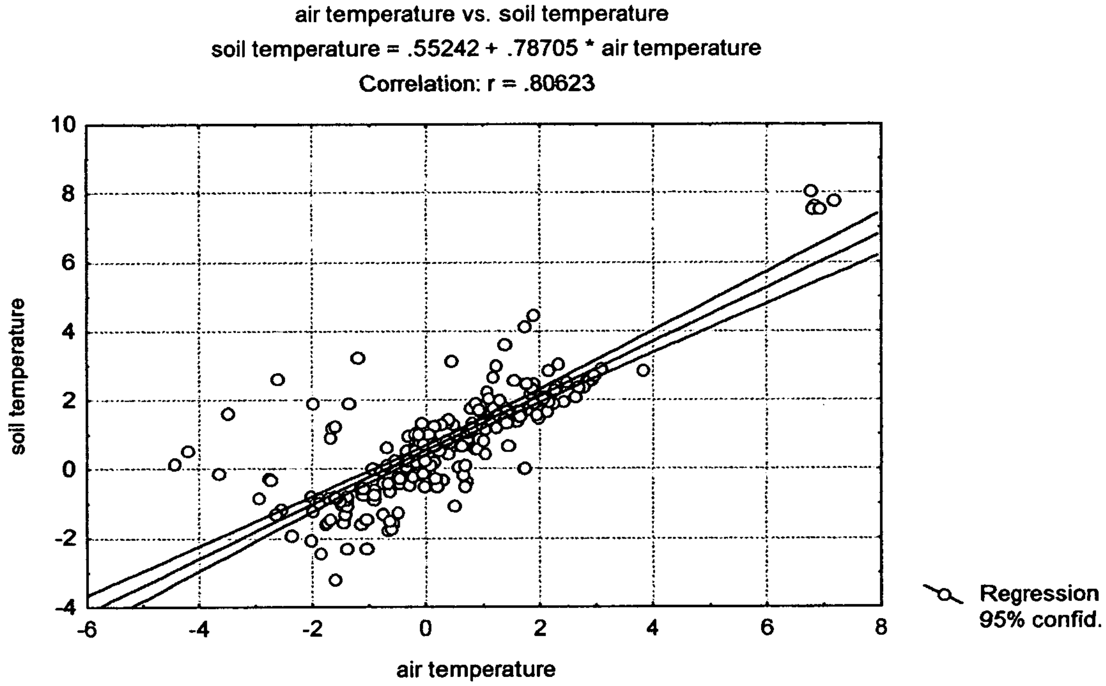


Figure 3.5. correlation between hourly temperature and hourly soil temperature in Craigvinean forest from 14 February to 4 March

3.3.2.3. SOIL WATER POTENTIAL

Soil water potential varied between –2.75 kPa and 0.05 kPa during the whole period of the observations (14 February-4 April) (average –0.17 kPascal). The "driest" month was February (-0.28 kPascal) and the wettest month was March. The figures record some fluctuations following diurnal and nocturnal cycles, but overall the soil remained fairly wet throughout the recording period.

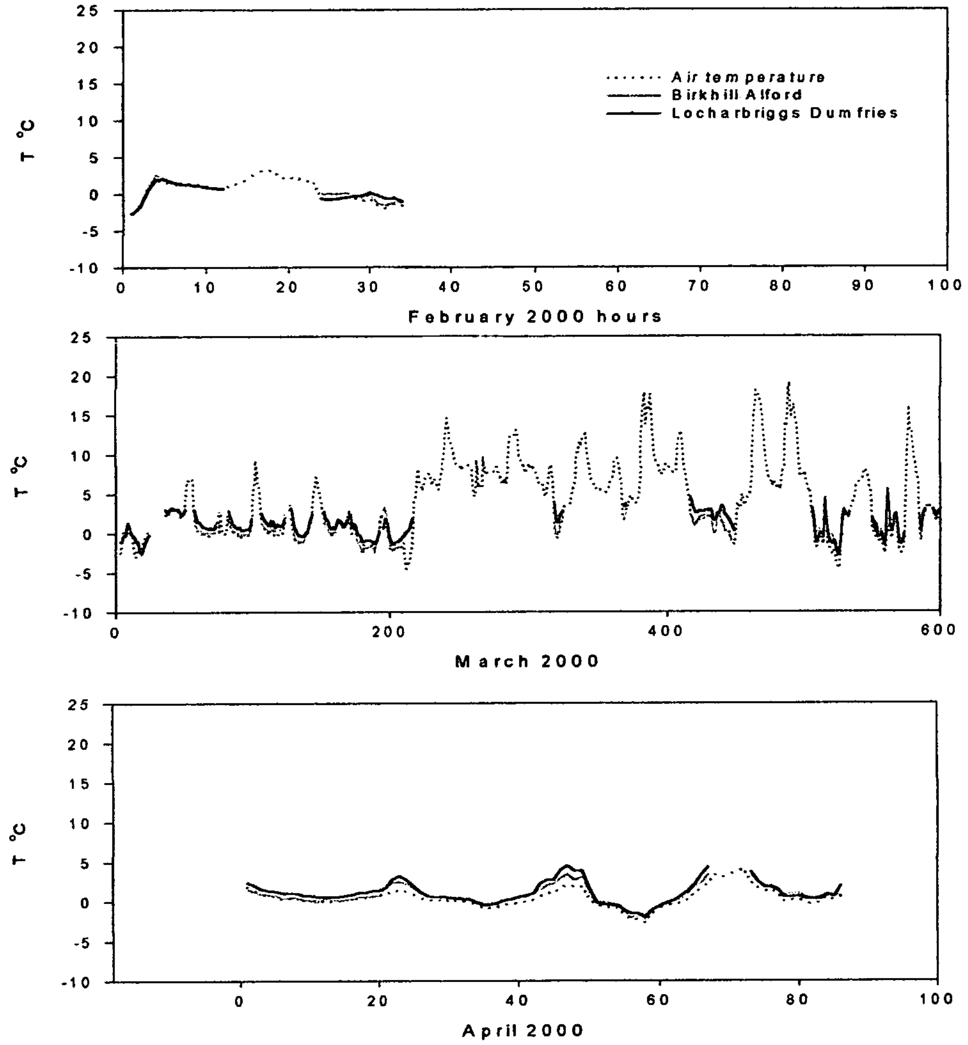


Figure 3.6. Average of xylem temperature of Birkhill Alford and Locharbriggs Dumfries birches from February to the 4th of April.

3.3.2.4. XYLEM TEMPERATURE

The temperatures of the xylem of the two investigated provenances are shown in Figure 3.6. Hourly mean temperatures from the 14th of February to the 3rd of April varied between –3°C and + 6°C.

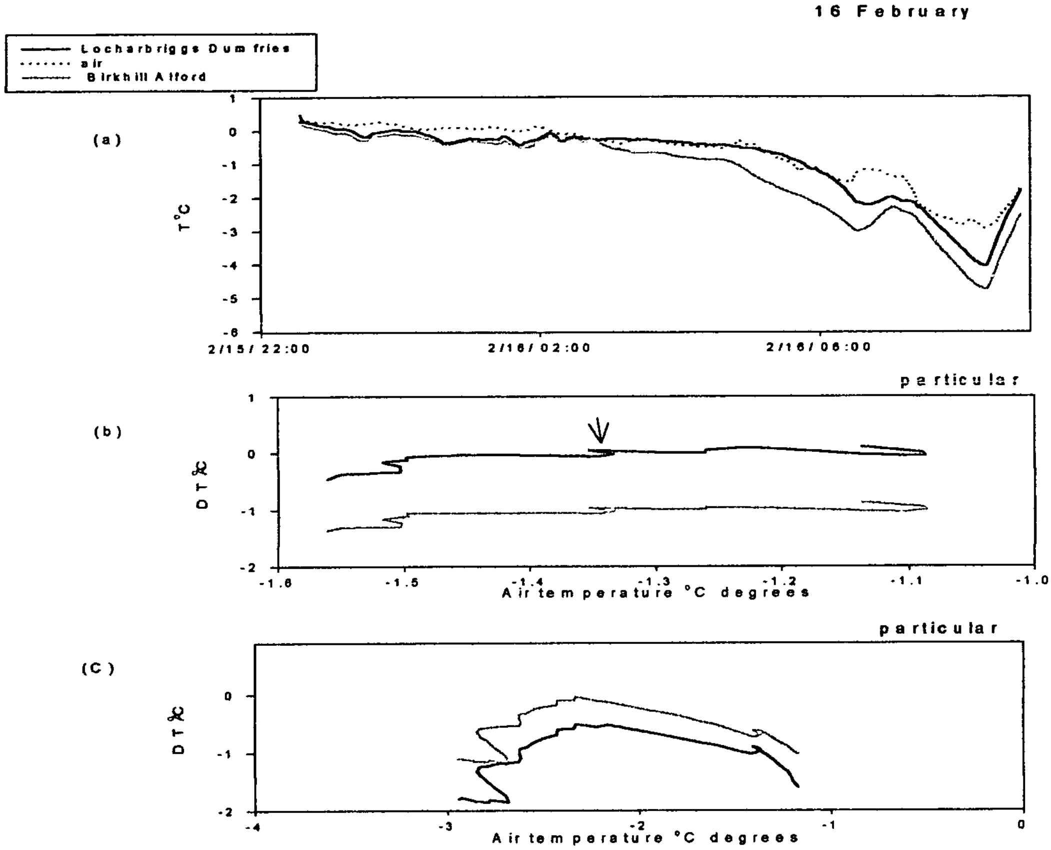


Figure 3.7. Air temperature and xylem average temperatures of the provenances Birkhill Alford and Locharbriggs Dumfries in February.

Birkhill Alford and Locharbriggs Dumfries differed slightly in their range of temperature variations. Birkhill Alford xylem temperature show the widest range, reaching more negative values than Locharbriggs Dumfries in February and until the 20th of March.

The temperature of the two provenances were very highly correlated with air temperature and soil temperature. The correlations were all significant ($p<0.0001$, $r=0.89$ and $r=0.76$ respectively).

3.3.2.5. DETECTION OF EXOTHERMS

The analysis of the exotherms was made twice a month from February to April 2000.

3.3.2.5.1. FEBRUARY

During February 2000 air temperature went below zero twice: on the 16th of February and on the 25th of February. Figure 3.7a. reports the trend of air temperature and the average of the xylematic temperatures of the two provenances during the night and the early morning of the 16th of February. The minimum air temperature was of –3° C degrees. The xylematic temperatures of the two provenances were lower than air temperature and, in

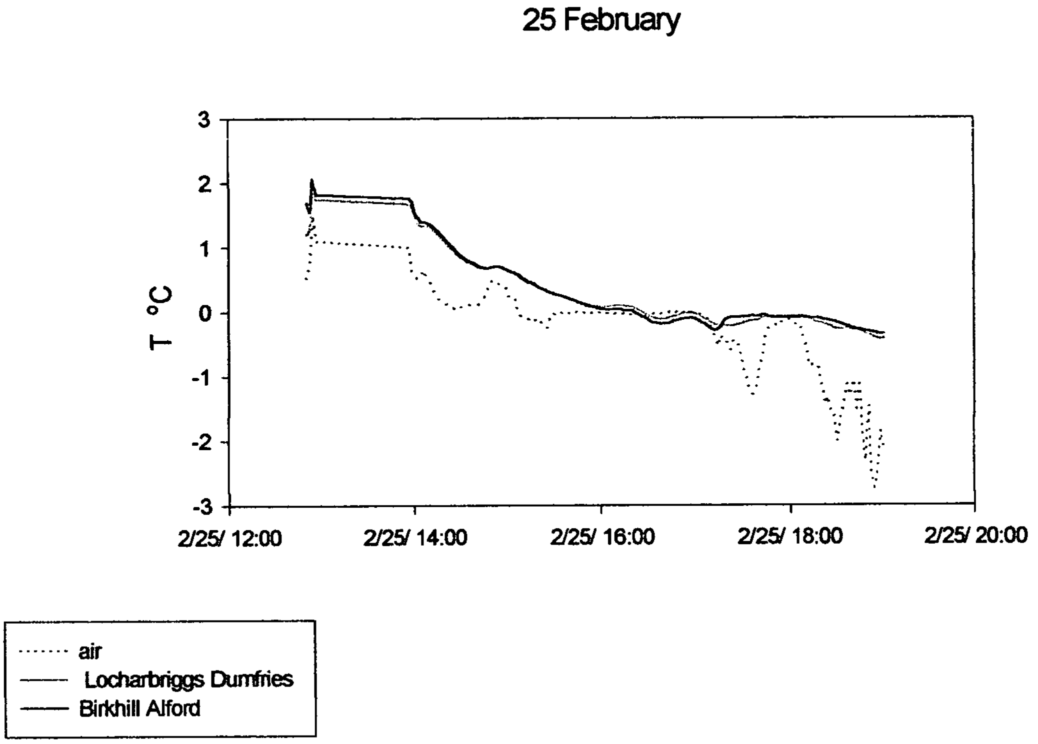


Figure 3.8. air temperature and xylematic average temperature of the provenance Birkhill Alford and Locharbriggs Dumfries in February.

particular for Birkhill Alford, the xylem cooled more than for Locharbriggs Dumfries. The trend of xylematic temperatures for Birkhill Alford was more linear and less subject to variations than for Locharbriggs Dumfries.

Locharbgiggs Dumfries showed a small peak of heat release. From the DTA analysis the exotherm was shown to occur at –1.18°C both for Birkhill Alford and Locharbiriggs Dumfries.

Figure 3.8. reports the trend of air temperature and of the average of the xylematic temperatures of the two provenances during the evening of the 25th of February. The air temperature was cooler than xylem temperatures. The minimum air temperature was – 2.74 °C degrees while the minimum xylem temperatures were –0.4°C degrees. There were no evident peaks of heat release.

The trend of the temperatures was very similar for the two provenances.

3.3.2.5.2. MARCH

Using the first ten days of March 2000, hourly temperature values fell below zero several times, usually during the night and early morning usually, with values between –1°C and –3 °C. There were three hours of continuous temperatures below –3°C on the 10th of March. Temperatures fell below zero again in the period from the 19th of March to the 25th of March, with eleven hours of temperatures between –2°C and –5°C and 25 hours of temperatures below the threshold of –1°C.

Figures 3.9 and 3.10 show the records of the air temperatures and the xylem temperatures of the two provenances in the night of the 8 March and the evening of the 19 March.

In the night of the 8th of March (Figure 3.9), air temperature was less then –1 °C. The Provenances Birkhill Alford and Locharbriggs Dumfries, average xylem temperatures were cooler than air temperature.

For Locharbriggs Dumfries, the average xylem temperatures were more subject to small trend variations and showed a peak of heat release when air temperature was –1 °C. Birkhill Alford trend of temperature was more homogeneous with no evidence of heat release .

During the evening of the 19th of March (Figure 3.10) the minimum temperature decreased to –8.5 °C degrees. The two xylem temperatures dropped more than the air temperature. Locharbriggs Dumfries average xylem temperature dropped more than Birkhill Alford xylem temperature and from the DTA analysis, exotherms were revealed from peaks of temperatures increases at –1°C, -4°C, -6°C and –8 °C indicating a continuous change of state, with a progressive formation of ice in the xylem vessels.

Birkhill Alford trend of temperature was more homogeneous and showed a small heat release when the air temperature was –6°C.

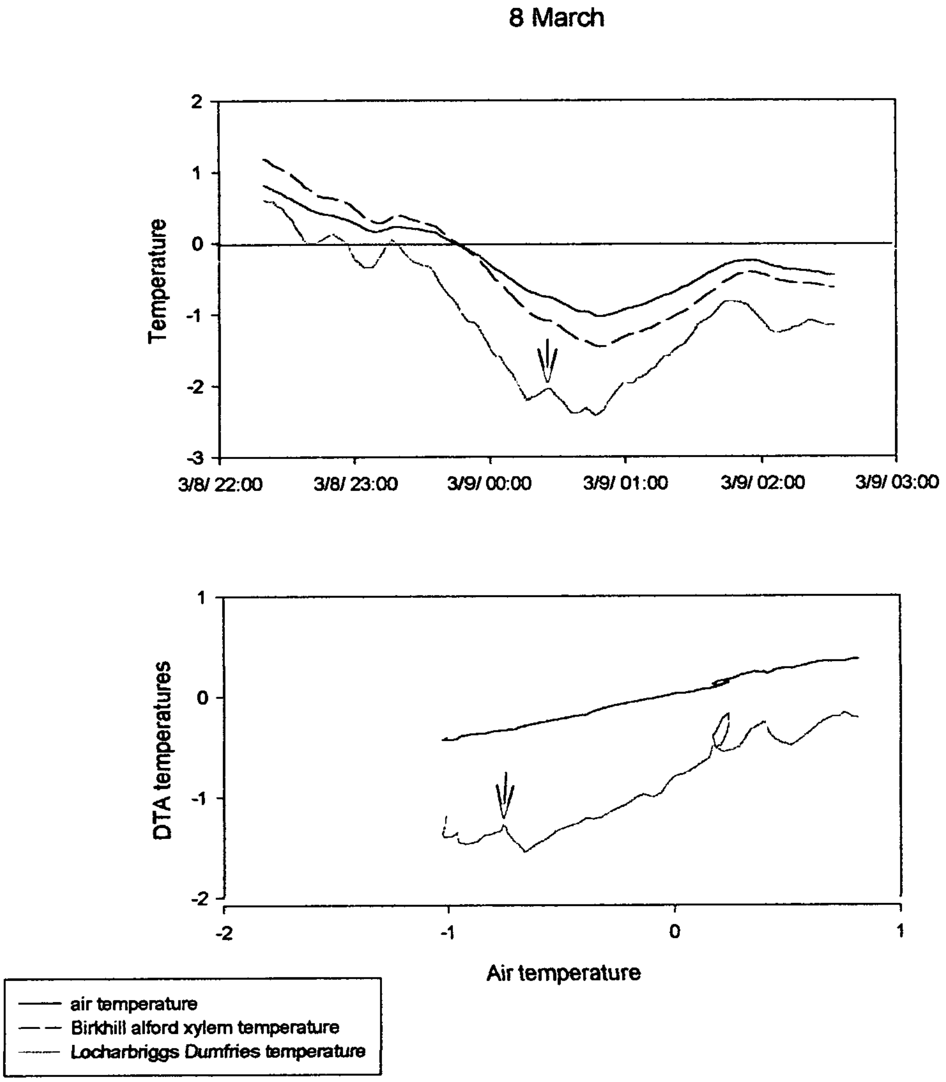


Figure 3.9. Air temperature and xylematic average temperature of Birkhill Alford and Locharbriggs Dumfries during the night of 8th March.

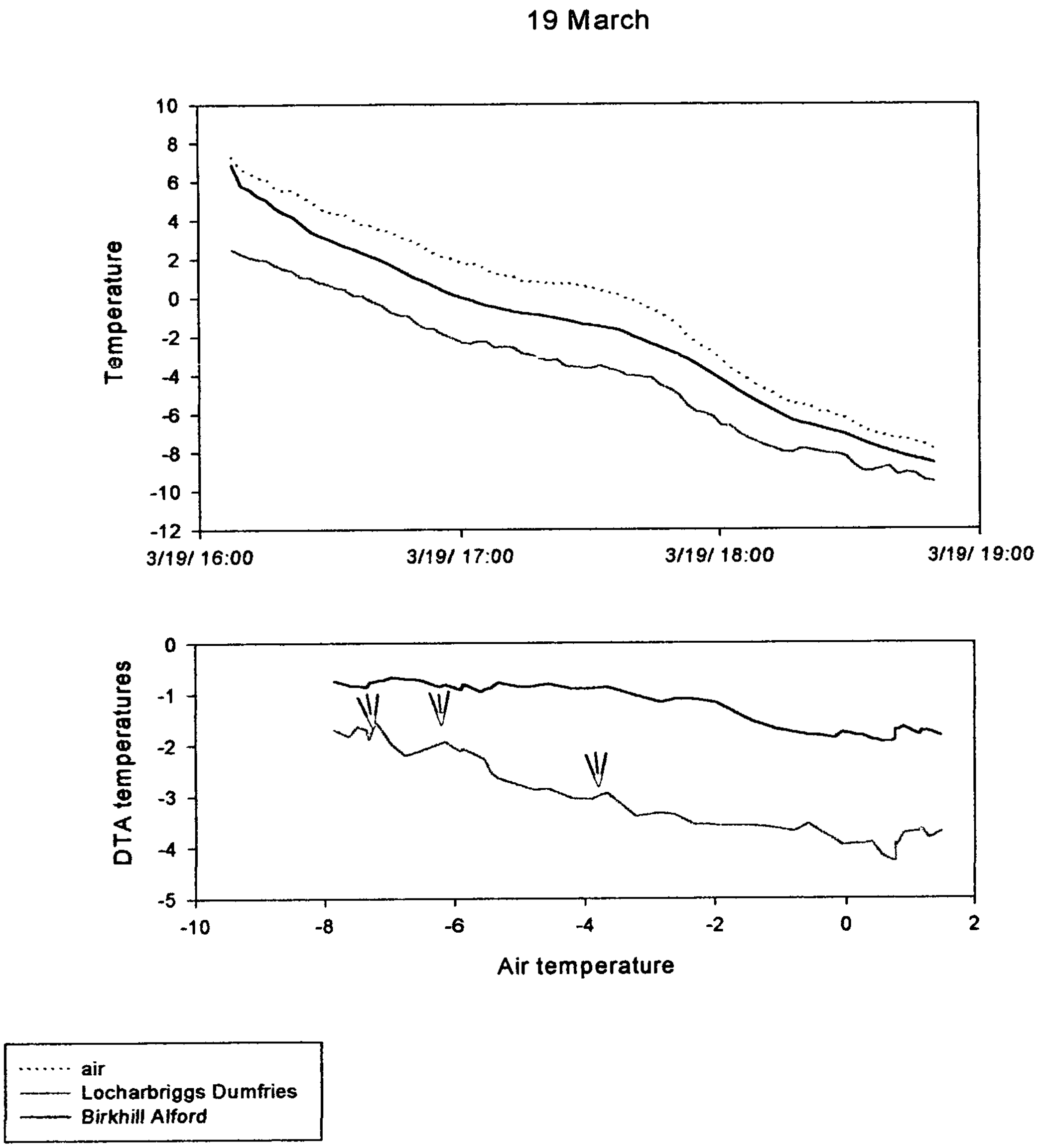


Figure 3.10. air temperature and average xylematic temperature in Birkhill alford and Locharbriggs dumfries provenances during the night of 19th March.

3.2.5.3. APRIL

In April 2000 temperatures were recorded until the 17th. Below zero temperatures were between -2°C and –5°C. They occurred sporadically during the nights and the early mornings of the days assessed. Figure 3.11 shows the trend of air temperature and of xylem temperatures of Birkhill Alford and Locharbriggs Dumfries during the evening of 10th of April. The minimum air temperature was – 4°C.

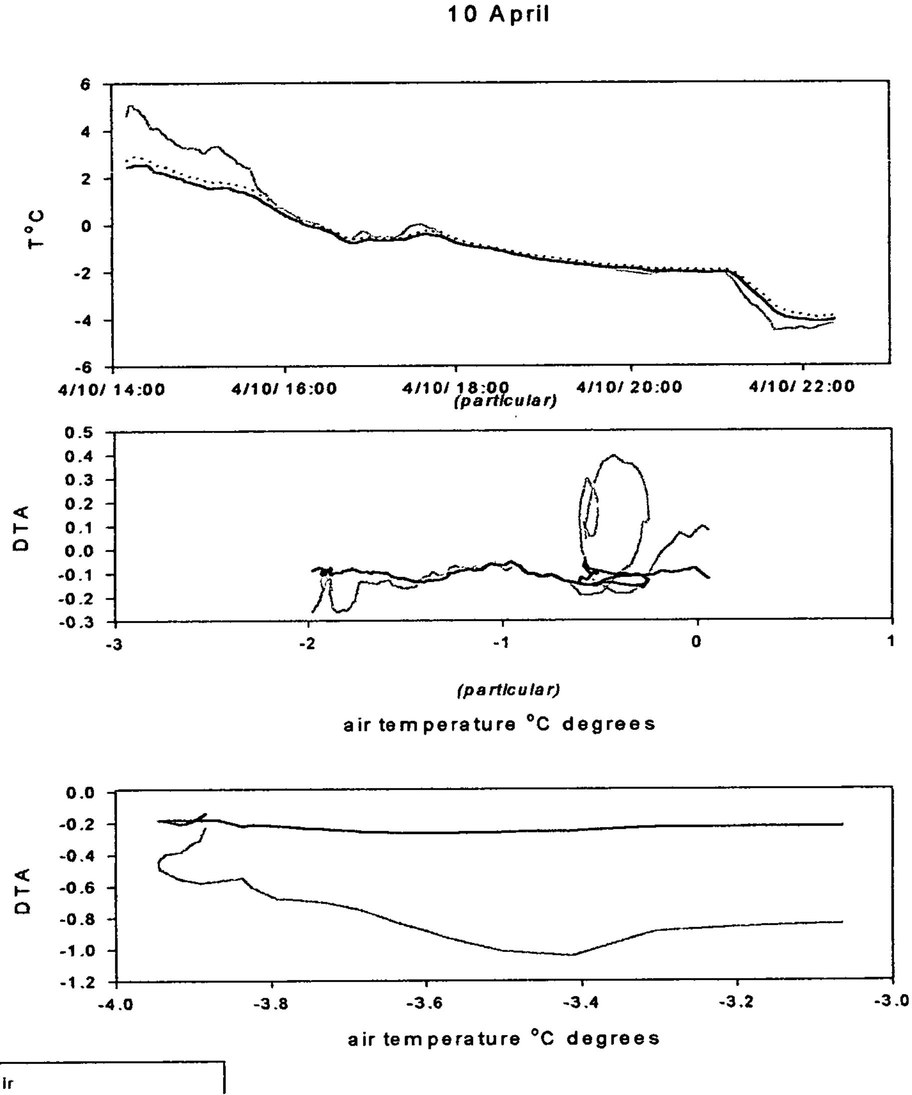


Figure 3.11. Air temperature and average xylematic temperature in Birkhill Alford and Locharbriggs Dumfries during the evening of 10th of April.

Birkhill Alford average xylem temperature was very close to air temperature and

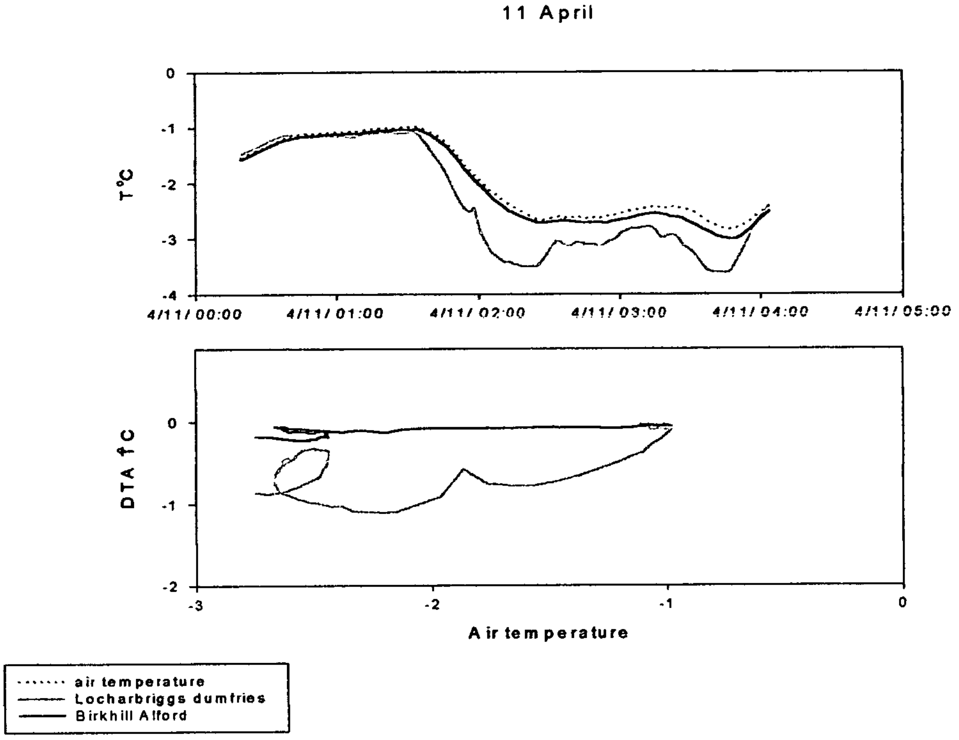


Figure 3.12. air temperature and average xylematic temperature in Birkhill alford and Locharbriggs Dumfries provenances in the early morning of the 11th of April.

no peaks of heat release were evident. The average of the xylem temperature for Locharbriggs Dumfries showed instead two peaks of heat release: when the air temperature was-0.7°C and when the air temperature was –3.8 °C.

Figure 3.12 records the air temperature and the xylematic temperatures of the two provenances in the early morning of the 11th of April. The minimum air temperature was–3.8°C. Birkhill Alford trend of xylematic temperature was homogeneous with no signs of peaks due to heat release. Locharbriggs Dumfries trend of temperature was cooler than the air temperature and showed two peaks of heat release, when the air temperature was –2°C and –3° C.

3.3. DISCUSSION AND CONCLUSIONS

The averaged hourly temperatures below zero recorded in Craigvinean forest are shown for each month in the following table.

	0>T (C°) >-1 hours	-1°C<T<-3°C hours	-3°C<T<-5°C hours	T<-5°C hours
February 2000	12	15	-	-
March 2000	45	61	7	-
April 2000	20	15	3	1

The lowest temperatures occurred during the late nights and the early mornings. The lowest temperature was of –8°C on the 19th of March and it lasted for a fraction of one hour. Hourly temperatures never fell below –4°C/-5°C i.e., the critical temperatures considered at risk for frost injuries, and did not last for more than two or three hours.

Soil temperature was highly correlated with air temperature ($p<0.0001$). The soil temperature was warmer than air temperature during the nights and early mornings and viceversa. The highest thermal excursion between air temperature and soil temperature was recorded the 10th of March in the early morning: air temperature decreased below –4°C and the soil temperature was 2°C. More investigations would be required to ascertain the role of difference in temperatures between upper and underground plant organs in relation to frost damage.

Hourly temperatures in tree stems from the 14th of February to the 10th of April varied between -3°C and + 6°C.

From the observation of the xylem temperatures, Locharbriggs seedlings showed records more subject to sudden variations and to peaks due to heat release at –1°C.

Birkhill Alford temperatures were more homogeneous and followed more strictly air temperature. Their average stem diameters was smaller than for Locharbriggs Dumfries.

Herrington (1969) found that .in spring when the ground was colder than the air the transpiration stream had a cooling effect on the stem, marked particularly during the rising of the sap. He also showed that the cooling effect measured in the region of the cambium was greater in ring porous than in diffuse porous and coniferous trees. The decline in wood temperature has been considered as a mechanism contributing to the water uptake also by Tyree (1983): the mechanism is thought to involve the partial displacement of air spaces (i.e. pockets of air trapped in the lumina of wood fibers or in previously cavitated vessel lumina) with water into the lumina. As the temperature of the stem decreases, the air volume would contract in proportion to the absolute temperature according to the ideal gas law. Also, the solubility of the gases increases with decreasing temperature further, reducing the air volume in the lumina.

Exotherms were detected between 0° and –8°C with the first peak at –0.8/-1 degrees. The exotherms were very visible for Locharbriggs and less visible for Birkhill. Birkhill Alford showed only one exotherm in February during the entire period of assessment. Ice nucleation temperature depends on the composition of the solution as well as on the prevalence of ice nucleators such as dust, ice nucleating active bacteria (*Pseudomonas syringae*), wind and agitation. Nucleation temperature can greatly influence (plant) survival after a frost episode. Ice nucleation at warmer temperatures (-1, -2°C) allows slow ice growth in extracellular space, so that the plant is able to tolerate freezing cycles. However, as the nucleation temperature is lowered, the chance of ice formation in the intracellular spaces increased and the ice growth is relatively rapid.

Usually the temperature of ice formation is lower if less solute is present in the studied solution.

Water content, solutes concentration, and vessels diameters are thought to be related and more investigations would be required to determine provenance differences in these parameters.

Figure 3.13 shows the phenological features of Birkhill Alford and Locharbiggs Dumfries in Roslin, Craigvinean forest and Moray. Locharbriggs Dumfries (South-West) flushed earlier than Birkhill Alford (North-East). In Criagvinean, in early March Birkhill was more advanced in its flushing stage and showed signs of frost damage (see Chapter 2).

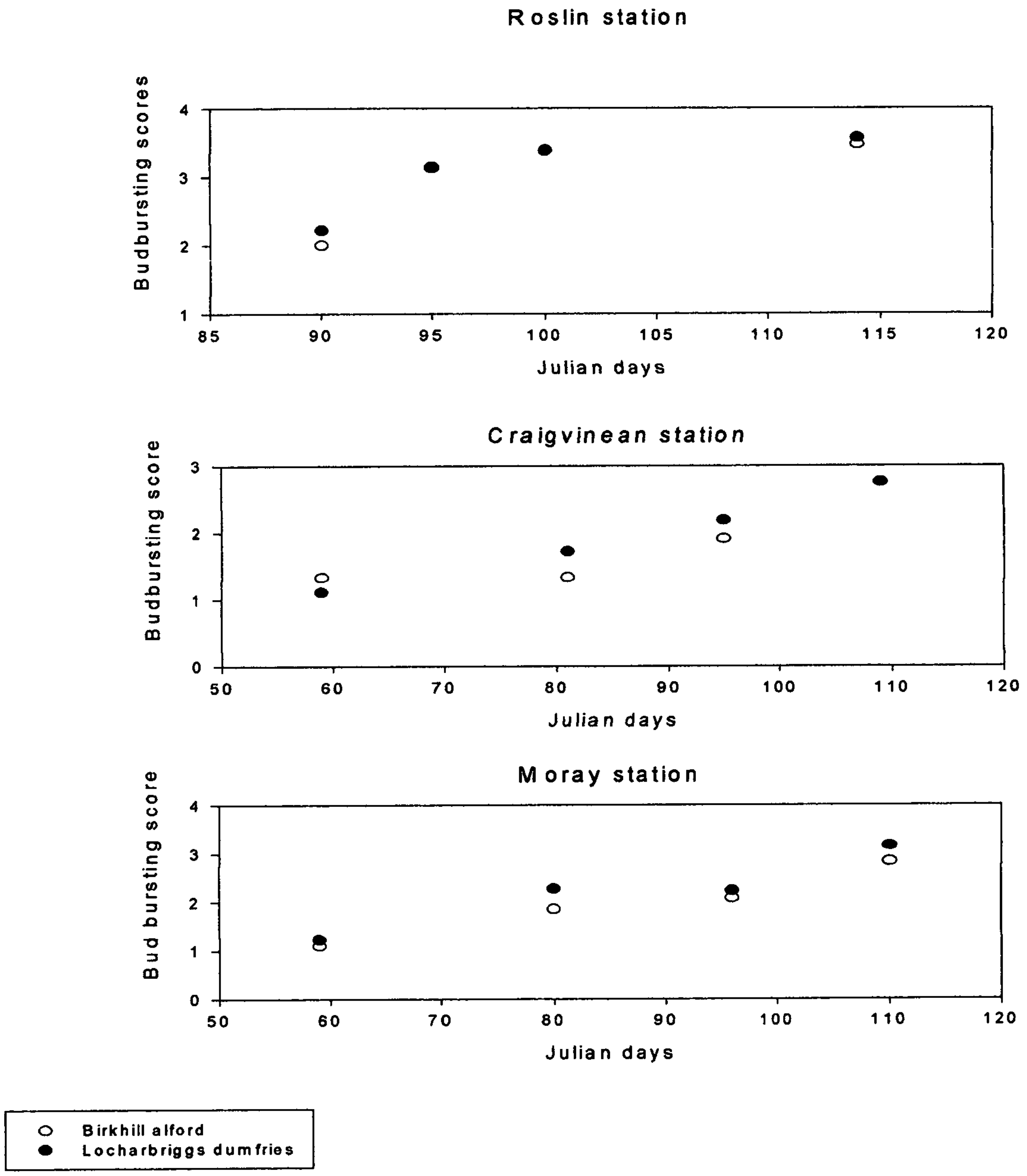


Figure 3.13. Budbursting of Birkhill and Locharbriggs seedlings in the three stations

4. DEVELOPMENT OF WINTER EMBOLISM IN 2000

4.1. INTRODUCTION

The differences in size, crown form as well as the presence of some desiccated branches for some seed origins (see chapter 2) suggested that an investigation of the features of xylem hydraulic conductance, development of embolism and recovery from embolism was required to explore the significance of these phenomena for the production of a high quality tree stem.

In particular two processes, i.e., winter development and spring recovery from xylem embolisation, were investigated with a preliminary study.

Many plants cavitate extensively during freezing weather. These plants tend to be winter deciduous and restore water transport after freezing by growing new conduits or refilling cavitated ones by increasing the xylematic pressure to near or above the atmospheric via root pressure.

Winter xylem embolism seems to have important potential consequences on vegetation, such as a reduction in tree growth and development of shoot dieback (Sperry et al, 1988).

In more detail, winter embolism may be the factor responsible for shoot dieback because of the phenomenon of frost desiccation: repeated cycles of frost and defrost cause dehydration in the xylem cells due to the spread of air bubbles in the vessels. This phenomenon may also have consequences in terms of reduced tree growth, if it impaired water uptake in spring after bud-break and if it reduced the length of the growing season.

A strong correlation between foliar phenology and the degree to which a tree was subject to winter embolism was found by Wang et al. (1992) among deciduous hardwoods species. The greater the late winter loss of hydraulic conductivity, the later a tree was leafing out in the spring, providing a broad comparative support for the postulated dependence of spring budbreak on hydraulic conducting capacity.

The phenomenon of xylem embolisation has been documented in many broadleaf and conifer species (e.g. Sucoff 1969, Sperry et al. 1988, Just & Sauter 1991, Lo Gullo &

Salleo 1993, Lemoine et al. 1999) but there is no evidence to show that such a phenomenon is present also for *Betula pendula* Roth. in the oceanic Scottish climate. Winter xylem embolism is described as the presence of air-filled tracheids and/or vessels, resulting in a substantial impairment of xylem transport. It occurs as a result of the low solubility of gases in ice and is strictly dependent on the internal pressure and on the size of the xylem conduit: larger xylem vessels are more vulnerable to cavitation by freezing than smaller vessels and tracheids (Hammel, 1967; Sucoff 1969; Ewers 1985; Sperry and Sullivan, 1992; Lo Gullo and Salleo,

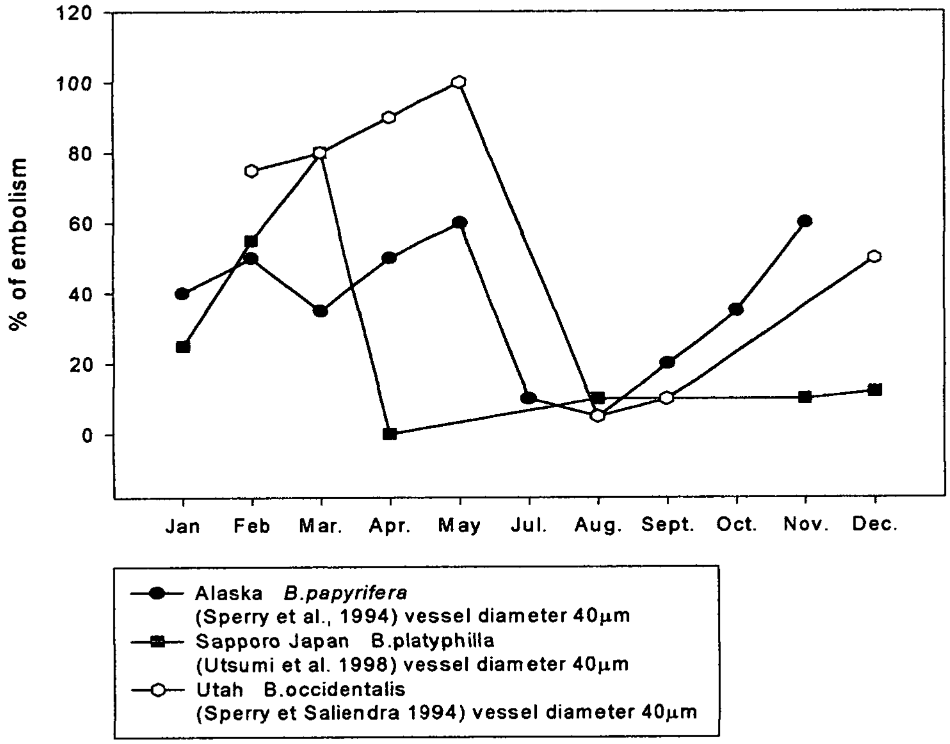


Figure 4.1 Percent of embolism recorded for Betula species in 1994 and in 1998.

1991; Hacke and Sauter, 1996; Langan et al.,1997). The degrees of embolism reported in the literature for various *Betula* species throughout a winter-spring-summer period are given in Figure 4.1.

In all cases, embolism appeared to reach a maximum during the winter months with subsequent recovery during spring. The diameter of the most representative class of vessels was about 40μm for all the reported studies. Because of that, the variation in the degree of embolisation across studies may be attributed to the differences in climate across the locations of all the experiments. Sperry et al. (1993) found that the increase in embolism during winter corresponded with potential freeze-thaw events, although no relationship between embolism and freezing intensity defined as absolute temperature below zero was found for water birch. They also found that embolism always fell from maximum to minimum annual values in spring within a few weeks prior to leaf flush.

The recovery from xylem cavitation in spring in diffuse-porous species has been attributed in many occasions to root pressure (Sperry et al. 1988; Sperry 1993).

Such positive pressure is thought to help dissolve the gas in the sap and/or push the undissolved gas out of the vessels until cavitated vessels become filled with water.

A positive xylem pressure does not commonly occur in all woody species. In *Betula*, the recovery of conductivity was associated with positive xylem pressures ranging from 50 to 60 kPa with higher values in the late afternoons, in March and April (measured 1m above the ground in 10m tall trees) (Hacke & Sauter 1996, Sperry et al., 1994). The positive xylem pressures were found to occur frequently during a 2-month period prior to leaf expansion (Sperry et al. 1994).

The direct observation of xylematic temperatures during winter 1998 and spring 1999 allowed the detection of frequent exotherms in the Locharbriggs provenance at Craigvinean. However, the number of shoots found to be desiccated was very small.

In this chapter we analysed the relationship between winter frost and xylem functionality, looking at the variability in shoot hydraulic supply during winter through the measurement of hydraulic conductivity and wood relative water content in silver birch. Freeze-thaw events were simulated on branches of silver birches to investigate the effective influence of low temperatures on the fluctuations on xylem hydraulic conductivity.

Because the observations recorded in Chapter 2 indicated that dieback occurred almost entirely in the apical and terminal parts of the shoots, hydraulic conductivity and vessel diameters of apical and bottom shoots were measured to find out whether differences were present between the two types.

Root pressure and xylem hydraulic conductivity were also measured in spring. Hydraulic conductivity and development of root pressure were also correlated with bud-flushing, stem form and frost desiccation damages.

4.2. MATERIALS AND METHODS.

4.2.1.STUDY SITES

The experiments were conducted both in the field and in the laboratory. Branches for embolism measurements were collected at the Craigvinean forest trial, Elgin trial and at the University of Edinburgh provenance trial. Stem pressure measurements were conducted at Craigvinean forest and at the University of Edinburgh trial. The provenances chosen were Locharbriggs Dumfries, Birkhill Alford and Castle Howard at the Craigvinean and Elgin trials plus 7 year-old silver birches (of a mixture of unknown provenances) growing at the University of Edinburgh. Castle Howard (Lat. 54°.12' N, Long. 0.°92' W) was chosen because it showed the best performance in terms of index selection at the Moray site, whereas Locharbriggs Dumfries and Birkhill Alford were chosen to maintain the continuity with the previous studies (Chapter 3).

4.2.2. DESCRIPTION OF THE EXPERIMENTAL SET-UPS

4.2.2.1 CRAIGVINEAN AND MORAY TRIAL STATIONS

The following three provenances of *Betula pendula* were selected for embolism measurements: Locharbriggs Dumfries, Birkhill Alford and Castle Howard. Four long branches were collected monthly from each provenance, by randomly selecting one branch from four different individuals.

During April and May, six plants for each provenance were also selected for the measurement of root pressure.

4.2.2.2.EMBOLISM OF BRANCHES EXPOSED TO RAPID FREEZE THAW CYCLES

An experiment was conducted by subjecting cut branches to a controlled freezing treatment.

The measurements were made on two-year-old branches of silver birches collected from the Birkhill provenance growing at Craigvinean forest. Two groups of six branches each were collected from six plants in January 2001. The branches were cut submerged in water, covered by a plastic sheet and brought to the laboratory. One of the two groups was used as a control, whereas the other was kept in a temperature-controlled chamber where branches could be entirely enclosed at –15°C for 2 h (Immersion circulator DC50, Refrigerated Circulator K40 Haake connected to a polystyrene insulated cooling chamber). Treated branches were then removed from the freezer, kept in a vertical position in the air and allowed to thaw until they returned to room temperature.

Treated branches and controls were then subject to embolism measurements.

4.2.2.3. EMBOLISM IN APICAL AND IN BASAL BRANCHES

Measurements were made on branches cut from seven years old birches growing in a provenance trial outside the University of Edinburgh greenhouses. Two groups of twelve branches were collected from the apical part of the crowns (shoots of the new year), and from the basal part of the crown (shoots of second-third year) in January 2001. Embolism was estimated via its effect on hydraulic conductivity as described in 4.2.3.1. Vessels diameters were measured in one-year old shoots and in the two-three year old shoots.

4.2.3.TECHNIQUES

4.2.3.1. HYDRAULIC CONDUCTIVITY

Xylem embolism was measured on branch segments about 15 cm long (usually 12 branches for each provenance) and 0.5 to 1 cm in diameter, cut from larger branches collected from the field. After cutting, the branches were immediately put in water filled pots, and immediately recut under water for about 10 cm, wrapped in plastic bags, transported to the laboratory. There they were cut into smaller segments under water to avoid causing additional embolism. Wood disks of 5-10 mm in diameter were cut into small pieces of measured length for the measurement of water content. After shaving the ends with sharp razor blades and after removing the bark, they were attached to plastic tubing under water to measure hydraulic conductivity. The tubing apparatus was filled with degassed water and algicide (HPFM Refill, 8 drops (0.1ml) per litre (20-25 ppm). The hydraulic conductivity of each segment was measured using a gravity-induced positive pressure gradient (about 70kPa m^{-1}) across the segment.

Four segments were prepared from each tree, giving 12 segments per collection date per provenance.

The perfusing solution was stored in a supply tank made from PVC pipe capped at both ends. The solution was routed via a three-way stopcock into a secondary supply reservoir consisting of a graduated cylinder closed with a vented rubber stopper. Adjusting the stopcock isolated the secondary reservoir from the pressurised solution and allowed flow by gravity from this reservoir through the stem and into a drain reservoir on an electronic balance.

A computer in communication with the balance was programmed to output the conductivity following the Autoconductivity Program by Dr. M. Tyree (Botany Department, University of Vermont, version 2.0 September 1995). The maximum conductivity was achieved in the following manner. Once the conductivity of a segment had been measured, the segment was flushed by applying a regulated pressure of 75 kPa to the supply tank and directing solution to the stem, by passing the secondary supply reservoir. The efflux from the stem was routed away from the balance reservoir to prevent overflowing. After at least 30 min of flushing the pressure was measured as before.

Hydraulic conductivity (k^{init}, kg m s^{-1} MPa^{-1}) is defined as the water flow rate (kg/s^{-1}) in a stem of length L(m), imposed by a pressure drop of ΔP (MPa).

$$K^h = W/(\Delta P/L)$$

The loss of hydraulic conductivity (PLC) was computed as:

$$PLC=100*(1-K^{init}/K^{max}).$$

Therefore, presence of embolism was estimated via its effect on hydraulic conductivity (Sperry et al. 1988).

Stem diameters were measured before the conductivity measurements to compute the saturated xylem area-specific conductivity (k^s, kg m^{-1} $^{s-1}$ MPa^{-1}); which is an estimator of the xylem hydraulic efficiency (mainly controlled by vessel size and density).

4.2.3.2. XYLEM WATER CONTENT

$$W_c = (F_w - D_w) / D_w \times 100$$

Water content per dry mass (WC, %DW) of shoots was determined from where (FW) and (DW) are fresh and dry weights respectively. Wood cores of 5-10 mm in diameter were cut into small pieces of measured length (dL), wrapped in parafilm "M" and subsequently analysed gravimetrically. The dry weight, D_w, was determined after drying for 48h at 80°C.

4.2.3.3. VESSEL DIAMETERS

Twigs with diameter of between 3 and 7 mm were studied from both 1-year-old shoot and 3-years-old shoots. Three transverse sections per twig were prepared for analysis from the branches described in 4.2.2.3. Fifty vessels were measured per section. Vessel diameters were measured from transverse sections at the widest part of the opening while excluding cell wall. Vessel frequencies were calculated as the means of five areas per transverse section. Measurement of vessel elements was made directly from glass microscope slides using a Leitz (Wetzlar, Germany) laborlux K. incident light microscope at a magnification of 25x. For most of the stems used in the experiments, thin (about 30-40μm thick) sections were manually cut, stained in a solution of alcohol, glycerol and safranin red for two days, washed and mounted in Caledonian balsam on microscope slides. Since vessels were elliptical in cross-section, the vessel hydraulic diameter (i.e. the diameter of the capillary of circular cross-section having the same flow rate under the same pressure gradient, Mencuccini & Comstock, 1997) was estimated using the formula for ellipses (Lewis 1992). Weighted averages of hydraulic diameters (d_h, μm) for each section were calculated using the formula $d_h=2\ \Sigma r^5/\Sigma r^4$, where r is the radius of the circle with equivalent area of the ellipse (Mencuccini & Comstock, 1997).

4.2.3.4. ROOT PRESSURE

Bubble manometers were constructed from 1-ml glass pipettes sealed at one end by flame. These were attached in the evening to freshly cut branches with a short piece of a flexible vinyl tube filled with water. The micro-pipette was filled with water in the proximal end and with air at the distal end, at the beginning of the experiment. Special care was taken to get a tight fit on the plant organ (using a hose clamp if necessary) and to eliminate air between the cut plant surface and the pipette. After allowing the system to equilibrate overnight, the bubble length in the manometer was measured at predawn (L_{pd}) (the xylem pressure of bleeding trees compressed the bubble). The three-way stopcock was then regulated to measure the bubble length in the manometer at atmospheric pressure. The xylem pressure was calculated from the volume change of the bubble. Temperature was assumed to be constant during the measurements. Beginning in April 2001, the occurrence of positive xylem pressure was monitored twice a week for a week. Measurements were conducted between 6: 00:00 a.m. and 19:00:00. Most of the measurements were made at 1m above ground level.

Xylem sap pressures were recorded at the base of the shoots. Xylem sap pressure (P_x, kPa) was calculated from a relation derived from the ideal gas law:

$$P_x = 100((L_{atm}/L_{pd})-1)$$

Where L_{atm} and L_{pd} are bubble length at atmospheric pressure and bubble length in the manometer at predawn, respectively.

4.3. RESULTS

4.3.1. WINTER XYLEM EMBOLISM

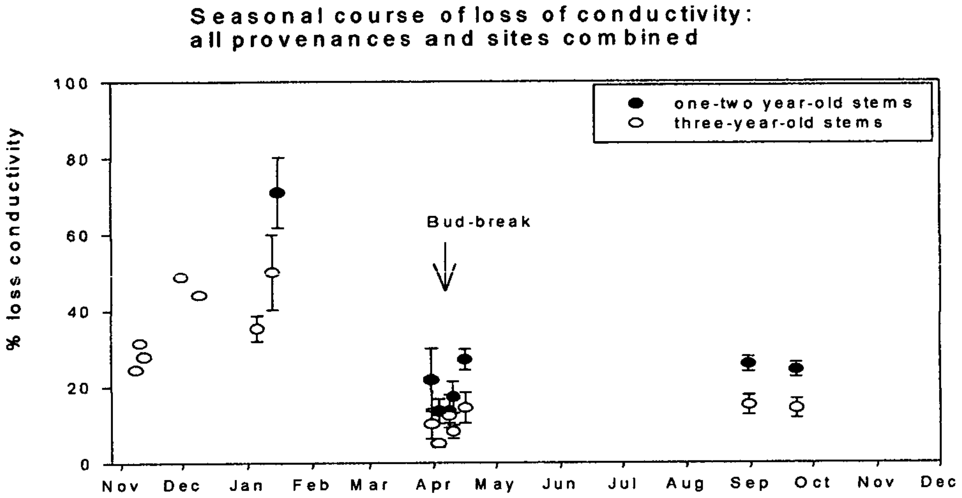


Figure 4.2. Seasonal course of loss of conductivity in silver birch. Vertical bars equal standard errors

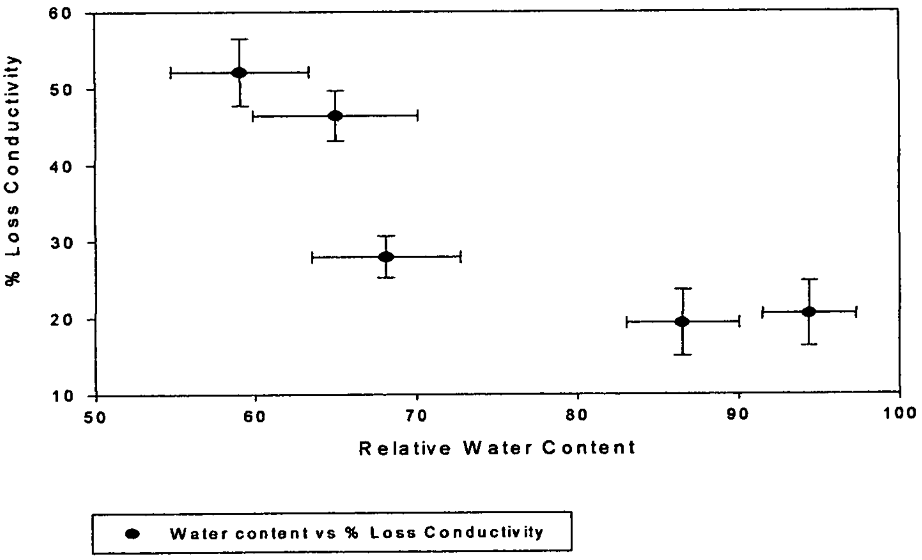


Figure 4.3.. Percentage loss conductivity plotted against the water content in winter. Vertical bars and horizontal bars are standard errors.

Percentage loss of conductivity changed during the period November 2000 to December 2001 (Figure 4.2). The percentage of loss of conductivity did not exceeded 71% for one/two year-old stems and 60% for three-year-old stems. The highest values were found in January (50-70%) and the lowest values in April (0-20%). In April, when the vegetative season had already started, the percentages of embolism were low, around 20% in the younger stems and even less in older stems. Winter embolism generally increased in winter, but a certain reduction was evident in January for the older stems. The younger stems showed a higher percentage loss of conductivity in comparison to the older ones.

The mean loss of hydraulic conductivity for all the shoots was also plotted against the corresponding shoot water content (Figure 4.3). The increased loss of conductivity in winter was associated with a decrease of relative water content in the shoots.

Figure 4.4 shows the percentage of the mean of the results for embolism in spring, summer and autumn for the three provenances at two field stations of Craigvinean and Elgin. All the values of percentage loss of conductivity are less than 30%. Although the differences are not significant, Birkhill Alford shows slightly higher values in April and in September than Locharbriggs Dumfries and Castle Howard. This higher level of embolism could be related to the delay in budbursting and in growth that this provenance shows in comparison to the other two tested, but the data are too limited to draw a firm conclusion.

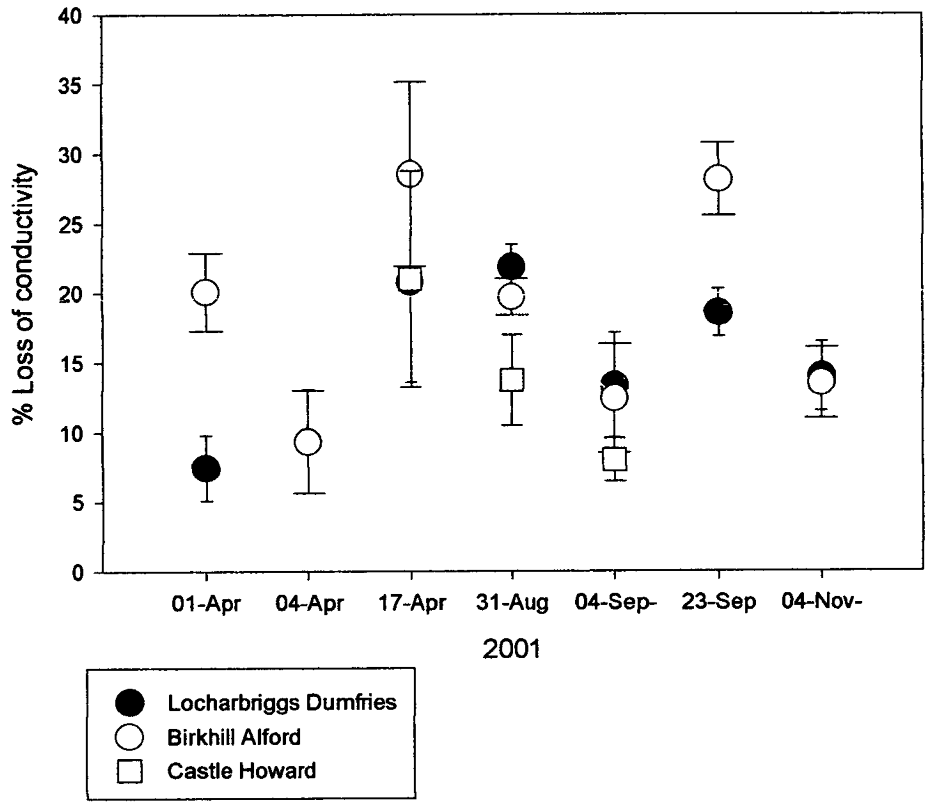


Figure 4. 4. % Percentage loss of conductivity at Craigvinean and Elgin. Vertical bars represent standard errors.

4.3.2.RELATIONSHIP BETWEEN XYLEM EMBOLISM AND TEMPERATURE

To test the hypothesis that the percentage of embolism in silver birch is associated with the number of hours below the threshold of –1.0°C, temperature data were compiled from Strathallan Airfield Saw from November 2000 to November 2001.

Data were obtained from the British Atmospheric Data Center ((BADC website). The values of percentage loss of conductivity measured for the samples collected in Craigvinean Forest and at the Edinburgh University trial were plotted against the number of hours when the temperature fell below –1.0°C between a specific sampling date and the previous one. Despite the small number of observations recorded, the percentage of embolism appears to increase with the number of hours with temperature below –1°C. The highest value of embolism ~(50%) is associated with the highest number of hours (35) when temperature fell below –5.0°C even though the

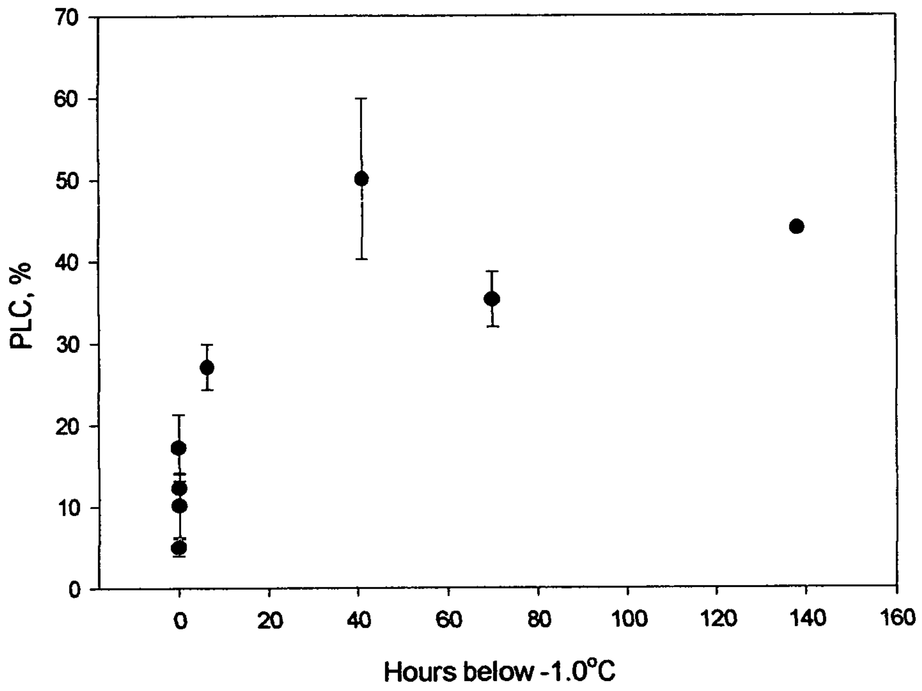


Figure 4.5. Cumulative number of hours below –1°C plotted against percentage loss of conductivity (PLC) for samples taken at Craigvinean Forest. Vertical bars equal standard errors.

sum of the hours below the threshold of –1.0°C was only 43. This may indicate a possible relationship between loss of hydraulic conductivity and absolute negative temperature.

4.3.3.EMBOLISM OF BRANCHES EXPOSED TO RAPID FREEZE THAW CYCLES

The effects of one freeze-thaw cycle on the loss of hydraulic conductivity for the Birkhill Alford provenance are plotted in Figure 4.6a.

A highly significant difference ($p<0.0058$) between control stems and stems subjected to a rapid freeze cycle was found. The treated stems had, on average, a percentage

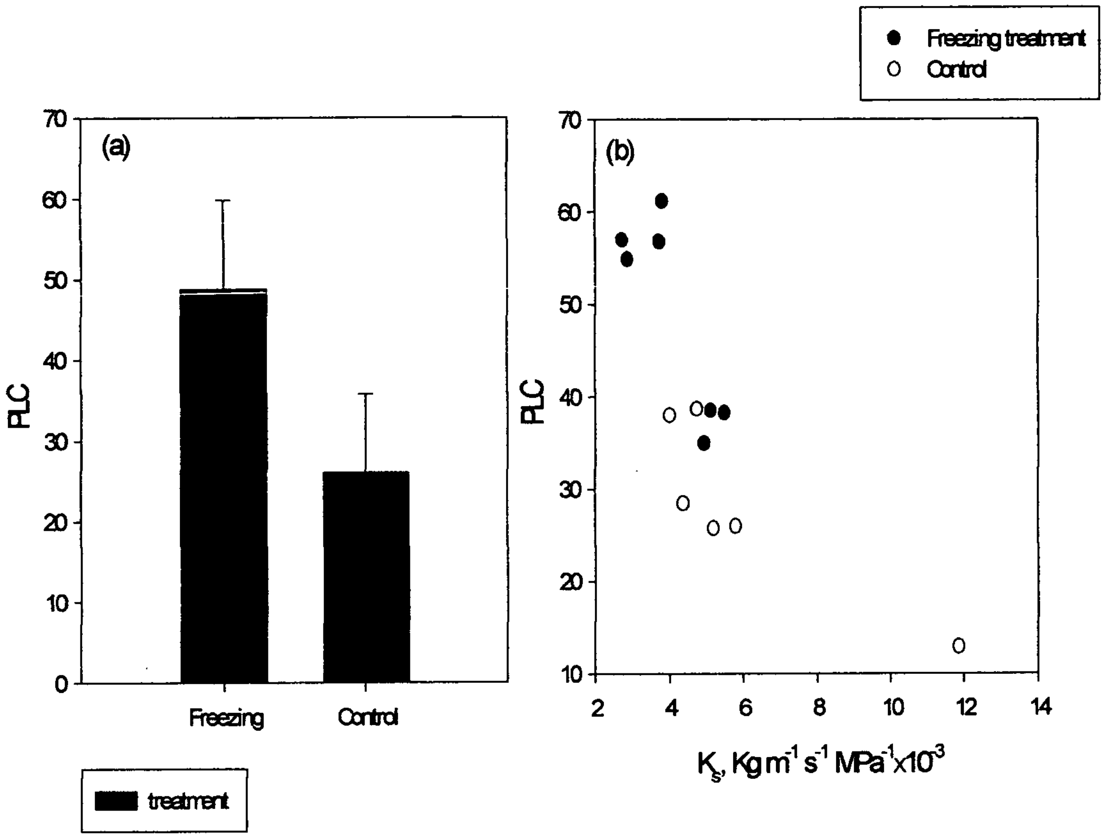


Figure. 4.6. Percent loss of xylem hydraulic conductivity (PLC, %) measured in branches of Birkhill Alford provenance exposed to one freeze-thaw cycle and control branches: a)mean and standard errors for the two treatments; b) values of PLC plotted as a function of the respective specific conductivity, K_s of the segment.

loss of conductivity twice the value of the control stems. Percentage loss of conductivity is plotted against the corresponding value of specific conductivity in Fig. 4.6b. The X axis represents the sample specific conductivity (K_s), which provides information about the hydraulic efficiency of a stem segment on a cross sectional area basis, calculated as $K_s = K_h/A$, where A is the cross sectional area. Apical branches (i.e. branches with low K_s), showed a drastic increase in PLC (60%)

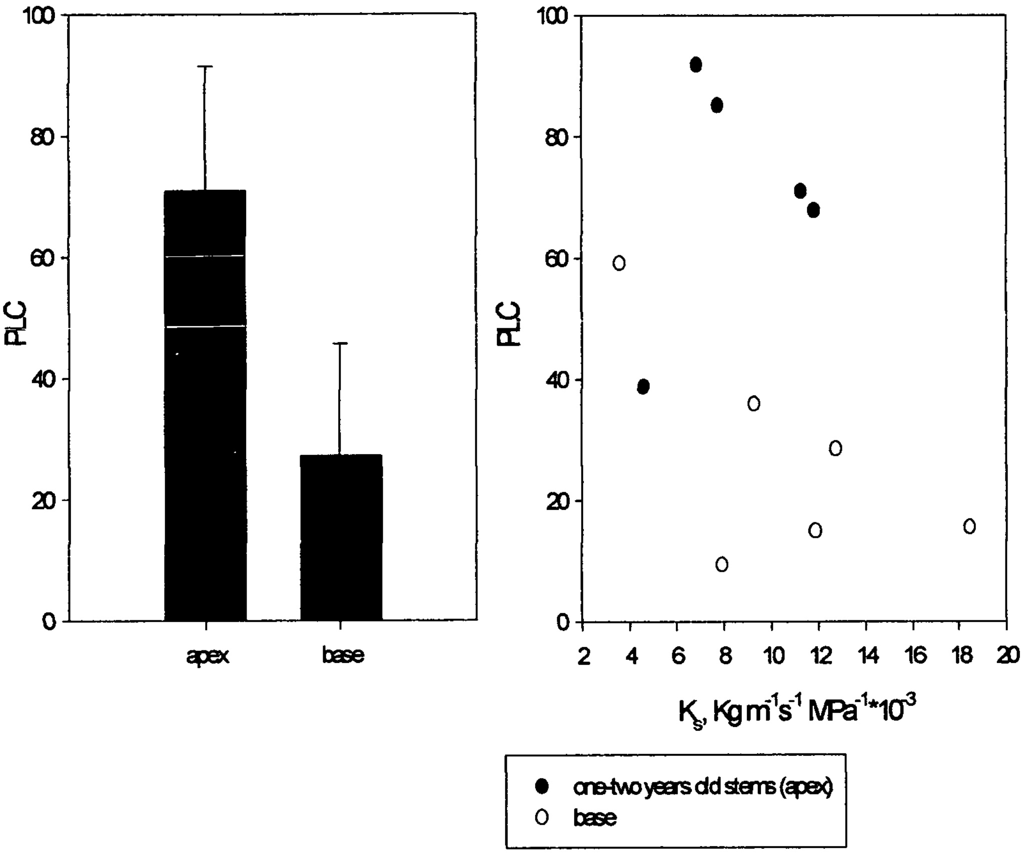


Figure 4.7. Percent loss of xylem hydraulic conductivity (PLC, %) measured in one-two years old stems and in two-three years old stems in seven years old silver birches growing at the Edinburgh University trial. A) Mean and standard errors for the two classes of branches; b) values of PLC plotted as a function of the sample specific conductivity, K_s.

when subject to a rapid freezing cycle. It is clear from Figure 4.8b that there is a negative correlation between sample specific conductivity and PLC, suggesting that size may affect PLC. The Pearson correlation coefficient between K_s and PLC was significant ($p=0.0032$, $r=-0.82$), indicating that, for small values of K_s the percentage of embolism due to the freezing treatment increases.

4.3.4. COMPARISON OF EMBOLISM IN APICAL AND IN BASAL BRANCHES

The degree of embolisation of young shoots (apical stems) versus older shoots (three-year old stems) is presented in Fig. 4.7a. Apical branches showed very large losses of conductivity compared to older stems. On average, apical branches showed PLC values three times the values of the 2-3 year-old stems. Fig. 4.7b again plots PLC against the specific conductivity K_s of the sample.

The frequency distributions of vessel hydraulic diameters d_h for both the apical twigs and the two/three year old branches are shown in Fig. 4.8. Fig. 4.8a shows that the mode for the distribution of vessel diameters is in the range of 30-45µm for 1 year old stems and for three years old stems, whereas Fig. 4.8b highlights the importance of each diameter class with respect to its contribution to the sample hydraulic conductivity (which is proportional to Σd_h^4). The number of conduits with diameter in the 30-45µm class is slightly higher in the younger shoots. Probably a fraction of the xylem vessels in the one-year shoots are still part of the protoxylem developed from procambial strand cells on the inner side of the strand. The first phase of maturation involves elongation and distension movements that usually destroy the primary vessels replaced successively by the secondary metaxylem (Speranza & Calzoni 1998).

4.3.5. ROOT PRESSURE

In all the three provenances tested, xylem pressure at the beginning of April fluctuated from positive values in the morning to negative values in the evenings, with maximum values of 30 kPa on April 1st and lower values from April 4th to April 6th . Birkhill Alford showed the highest values in the morning of April 1st. The differences across provenances seemed consistent over time, but further investigations will be necessary to determine whether these differences are real and if it is existing a correlation between date of bud-break and intensity of pressure (Fig. 4.9).

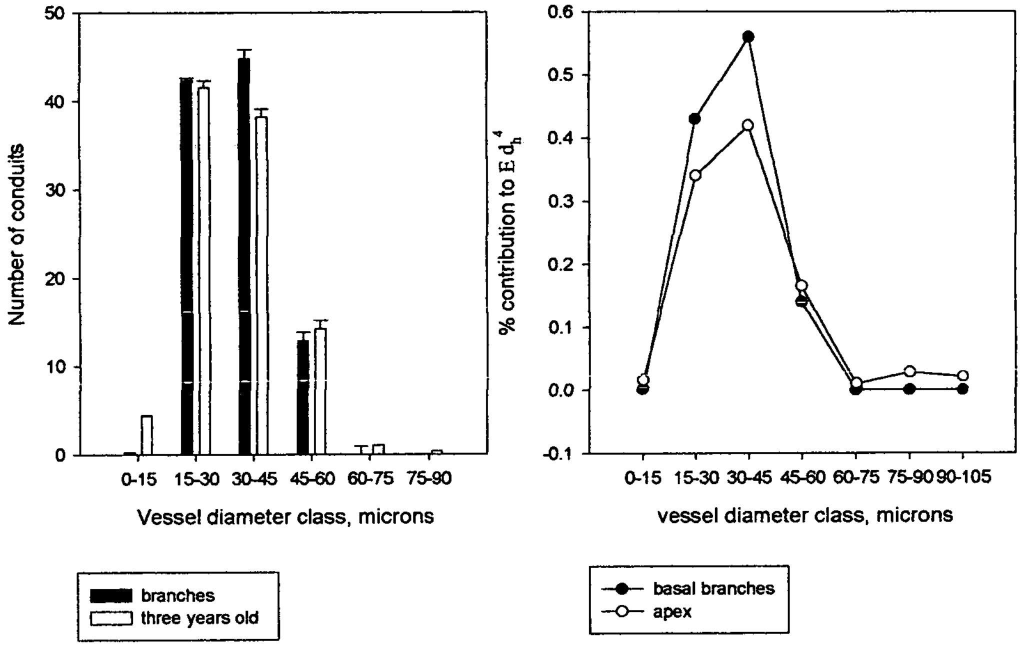


Figure 4.8. Vessel frequency and hydraulic diameter measured in 1 year old stems and three years old stems.

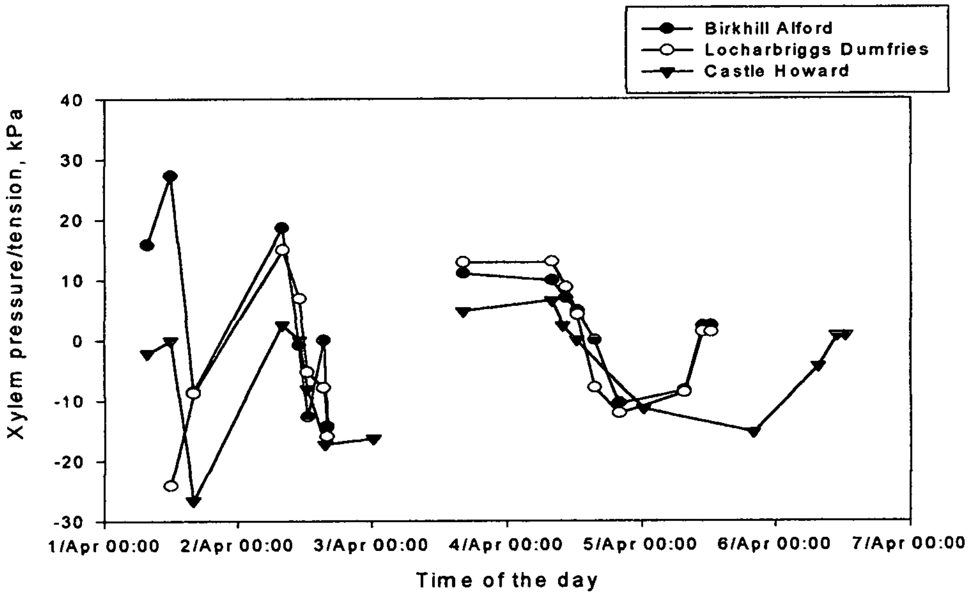


Figure 4.9. Xylem pressures measured in provenances of Birkhill alford, Castle Howard and Locharbriggs Dumfries in April 2001.

4.4. DISCUSSION

In this study, the seasonal occurrence of xylem embolism in *Betula pendula* was investigated. High values of embolism were found during winter. The peak of embolism was around 50% for 3-years-old shoots and 70% for 1-year old shoots. Comparing these values across species, Scottish silver birch developed winter embolism levels similar to the ones for paper birch from Alaska (Sperry et al., 1994). Investigations into the water status of the xylem sap of trees during the winter period show that embolism can occur as a consequence of the frost-thaw alternation (Cochard and Tyree, 1990; Just and Sauter, 1991; Ameglio et al., 1995; Pockam and Sperry, 1997). Our experimental freeze-thaw cycles on branches of silver birch in winter (Figure 4.6) confirmed that the increase in embolism is linked with environmental variations of temperature above and below the freezing point. In the field experiment the percentage of embolism increased with the number of cumulative hours below –1°C. Not many data-sets have been published showing a relationship between cumulative hours with temperatures below a certain thresholds and PLC. In other studies however winter embolism increased gradually for birch species and was correlated with cumulative number of freeze-thaw cycles (Sperry et al; 1994 and Utsumi et al; 1998). With the progressive increase of embolism, the water content of the stems appeared to decrease sigmoidally (Figure 4.3). The mechanism of water-storage in woody species is still not very well defined. Tyree and Yang (1990) proposed that water-storage in plants occurs with three mechanisms corresponding to three different phases of the dehydration curve of the stem: elastic storage, capillary storage, and cavitation release. Elastic water-storage in wood was considered minimal, because woody cells have thick, lignified, inelastic walls. Capillary storage was thought to occur in embolised wood cells (wood fibers, tracheids, vessels) and in intercellular spaces, where water could be held in the tapered ends by capillary forces generated across the menisci at the gas-water interface; cavitation release was thought to occur when the water potential becomes negative enough to cause a cavitation event. This process creates a new capillary storage cell and most of the water in the cell lumen is immediately sucked into the surrounding tissue.

In six evergreen species in a Hawaiian dry forest, Stratton et al. (2000) found that stem water storage consisted, at least in part, of the lumens of the functional xylem conduits themselves. The results of recent studies on woody species suggest that a substantial fraction of the functional xylem conduits may be dynamically emptied and refilled throughout the day (Zwieniecki & Holbrook 1998; Melcher 1999). Stored water has been found in specialised stem parenchyma tissue outside the water transport pathway (Goldstein, et al 1984; Holbrook & Sinclair 1992) as well as in the sapwood.

The literature concerning stem water content and its relationships with xylem conductivity during winter is still scarce. From our findings, the water content in the apical stems decreases with progression of the winter and with increasing percentage loss of conductivity.

Ameglio et al. (2001) found a complex relationship between xylem pressures and temperature. Air temperatures between -3°C and 3°C were often associated with sharp increases in pressure, whereas temperatures below –5°C or above 4°C were more often associated with decreases in pressure. The formation of ice and the consequent formation of air bubbles could be responsible for movement of the water in surrounding vessels. Upon thawing, if no root pressure develops there will be a progressive decline of the water content in the upper parts of the plants. This could explain why apical twigs showed higher rates of embolism than older more basal shoots. The curvilinear relationship shown in Figure 4.5, identified as phase two, by Tyree and Yang (1990) seems to indicate that most of the water loss occurs before the increase in the percentage of embolism of the wood tissue. This same phenomenon was explained by a capacitative effect of the elastic water storage by Tyree and Yang (1990), but it could be also attributed to the water stored in the parenchymatic cells and in the phloem pathway in silver birch.

Refilling of embolism is most active in spring before bud-break. At present only two mechanisms have been proposed to explain a resorption of hydraulic conductivity in spring: sap pressurisation (which leads to refilling) or cambial growth (which leads to the production of new functional vessels). During spring (during the period of bud-flushing), birch recovered with PLC values falling from maximum to minimum annual values (around 15% for 3 years old stems and 5% for 1 year old stem), in association with positive xylem pressure measured at 40 cm from the base of the trees. The Pressure measurements were conducted relatively late in the season (flushing had already started) and therefore values were lower than expected from the literature, as root pressure was likely already dropping.

Birkhill Alford showed a peak pressure in the early morning of early April, during the stage of bud swelling. By that stage, Locharbriggs Dumfries and Castle Howard were more advanced in their stage of bud-flushing and their mean of stem pressure was equal to zero. The peak of pressure recorded for Birkhill Alford was of 30kPa, and pressure ceased on the 5th-6th of April, when the buds were in the phase of opening. A clear positive correlation between air temperature and xylem pressure has been found by Ameglio et al. (2000) in walnut trees in spring. Further analysis are required to better document the cycles of the stem pressure and its relationships with temperature and the freezing-thawing cycles in silver birch. Xylem water status is likely to be strongly related to the dynamics of the carbon reserves retrieved for growth of buds and vascular cambium. From the data presented in the study, the three provenances investigated at Craigvinean forest showed only a small difference in their percentage of embolism in spring and summer (Fig.4.4). Birkhill, the latest provenance to flush and the less developed in height, also showed the highest values in percentage of embolism in April.

The data shown in Fig. 4.7 suggest that younger shoots are more vulnerable to loss of hydraulic conductivity than older shoots. Maruta (1996) explained the development of winter desiccation and injury in current-year shoots of deciduous larch by the inadequate cuticle development during a short cool growing season. The thin cuticle would then fail to protect against water loss during the winter due to high winds; this would then lead to extensive xylem embolism.

Lemoine et al.(1999) explained why, in apparent contradiction to the theory of larger conduits being more vulnerable, apical shoots with smaller vessels were the most vulnerable to freeze-thaw events: during freezing, water was expelled downward from the basis of apical shoots of *Fagus sylvatica*. When water was allowed to freely enter the shoot from the base upon thawing, little embolism developed. However, when water was not freely available from the base, high levels of embolism developed in the apical shoots. Although bubbles were likely to be smaller in these terminal shoot, the capillary pressure they developed was not high enough to compensate for the decrease in xylem pressure. Terminal shoots also tend to be more vulnerable in the field because they are more exposed to the sun and exhibit a higher surface-to-volume ratio.

Utsumi et al. (1999) found that, in contrast to earlywood vessels, many of the current year's latewood vessels retained water in their lumina in *Fraxinus mandshurica* var. *japonica*. He found that latewood vessels were less vulnerable than earlywood vessels to cavitation due to freezing (Ewers, 1985; Sperry and Sullivan, 1992; Tyree et al., 1994, Tyree and Cochard, 1996).When cavitation occurs in earlywood vessels of ring-porous trees, latewood vessels, which have relatively smaller diameters than earlywood vessels, should contribute to the water transport system. Latewood vessels formed during the previous year might play a major role in water transport at the onset of the growth season in early spring, when newly formed earlywood vessels are not yet functional. If the shoots are newly formed, the lack of this secondary transport system can make them more vulnerable to freezing-thawing events.

The final differentiation of the vascular system in the shoot consists of the conversion of procambium blocked out behind the apical meristem into mature elements of the xylem and phloem. In a number of seed plants, xylem maturation has been found to be considerably more complex than phloem differentiation. In *Linum* spp., xylem maturation is delayed until after the start of phloem maturation. Xylem maturation proceeds both acropetally and basipetally ultimately establishing a connection with the mature system. Thus, the primary xylem system, although continuous when mature, is discontinuous during its development making it more vulnerable to freezing-thawing cycles in spring. Taylor and Sussex (1989) reported that the interconnection of vascular strands was regulated by the flow of auxin in specific pathways. Sachs (1981) had proposed that the development of the vascular system throughout a plant results from initial local differences in the flow of auxin through cells, which leads to the establishment of preferred channels of auxin transport. These channels become progressively improved pathways of auxin movements and drain the surrounding regions at the same time that their cells are induced to undergo differentiation as vascular elements. Connections are established with pre-existing channels that are highly preferred pathways but whose auxin supply has been depleted. In this way Sachs visualises the building up of the integrated conducting system of the plant body. In the apical regions differentiation is predominantly acropetal: therefore embolism can be a very important factor in causing shoot desiccation during the phases of organ differentiation. The mechanism of cavitation release described above and the unlignified nature of the cell walls of young shoots, could be the responsible factor of the high permeability to water, pushed by the positive pressure in spring (Pickard, 1981; Yang and Tyree, 1992), through the walls provoking desiccation and death of the terminal apex.

The limited mortality observed in the plot of Craigvinean is in agreement with the fact that in the year of the assessment of dieback, temperatures fell below –1° C for only 13 hours and 28 hours in March and April (Table 4.1) and never fell below –5°C (temperature considered as risk for frost damages in spring). In the year of the conductivity measurements, March had 73 hours with temperatures below –1°C and 29 hours with temperature below –5°C. However, a clear recovery from embolism occurred in April (when the temperature fell below –1°C only for seven hours, Table 4.1.) indicating that the refilling of the vessels occurred in a period without frost damage risks. It cannot be excluded that an anticipated budbursting in correspondence with a late frost may cause extensive embolism and mortality in successive years. It has to be remembered though, that this analysis has been conducted using the BADC dataset, whose temperature records are not very closely linked to the actual measurements carried out in situ.

Table 4.1. Number of hours with temperature below –1°C and –5°C monthly for the 2000 and 2001 (data from BADC for Strathallan-Airfield Saw)

	-1°C≤T≤-5°C	T ≤-5°C		-1°C≤T≤ -5°C	T≤-5°C
January 2000	51	-	January	101	32
February 2000	28	-	February 2001	64	30
March 2000	13	-	March 2001	73	29
April 2000	28	-	April 2001	7	-
May 2000	-	-	May 2001	-	-
October 2000	-	-	October 2001	-	-
November 2000	2	-	November 2001	10	-
December 2000	101	32	December 2001	133	9

5. CONCLUSIONS

5.1. ANALYSIS OF PROVENANCE DIFFERENCES ACROSS SITES

My results showed that seedling of silver birches of different provenances maintain their characters for phenology across sites, in agreement with the finding of Blackburn and Brown (1988). Species such as pine, birch, juniper, alder, which have been present in Scotland for relatively long periods may display patterns of adaptive variation more closely linked to environmental conditions than more recent arrivals such as ash, present for only a few generations (Rehfeldt et al. 1984, Ennos et al. 1998). For this reason probably silver birch shows a high level of character inheritance since the juvenile phases. However, being the correlation coefficient for height across the two trials not significant (chapter 2), may indicate that bud-bursting has a stronger heritability than height and stem form, these last two being more dependent on the immediate influences of the surrounding environment. According to the data of chapter 2, East-sea-level sites favour the growth of birch in Scotland, in agreement with the finding of Forbes and Kenworthy (1973). An explanation for the higher growth rates of Southern-provenances is that photoperiod has a pronounced effect. Longman (1976) found that *B. pubescens* plants, grown in a phythotron, showed highly significant increase in height growth with the increasing of day length. (Habjorg 1972), found that the critical day-length necessary for terminal buds to become active varied considerably among provenances. While more southerly seed sources of *B.pubescens* and *B. papyrifera* needed only 14h day-length, some northern provenances required up to 20-24h. The complexity of the interactions between seed source, site climate, and the long-lived nature of trees makes the selection of an appropriate management option to reduce the risk of spring freezing damage difficult. Forest managers frequently reduce the likelihood of frost damage by selectively planting provenances with high requirement of accumulate degree days, calculated for each year at each weather station as the sum of the daily average temperatures in excess of 5°C after January 1 (Beuker 1994). Colder average temperatures at time of bud-burst were correlated with higher probability of freezing damage after bud-burst. Temperature at bud burst was proposed as an indicator of risk for freezing damage by Cannell and Smith (1986). These selection criteria may however reduce productivity as a result of the under-utilization of the growing season (Nienstaedt 1985). However, although relative productivity (i.e., provenance to provenance differences) may be affected by selection for later budburst, absolute differences in productivity may be less drastically affected, due to increased summer temperatures and elevated atmospheric CO_2 favouring growth (Pastor and Post 1988, Wang et al., 1994, Colombo 1990.). A basic requirement is that under a range of Scottish conditions, with exposure from maritime climate and normal levels of damages, acceptable form must be achieved under field conditions. Having considered the relative risks and benefits of the options above mentioned, and given the importance of an early selection (to decrease the cost of genetic testing by recommending early indicator traits) (Lee, 1997), the height of the stem, stem straightness and flushing stage at the beginning of the vegetative season, were combined in a provisional index to assess the best provenances. In agreement with this, we built an index based on the assignament of distinct weights to height, stem form and risk of frost damage (assumed to increase by early flushing).

The provenances achieving the highest values were the ones with best shape performances and minor risk of frost damages and would therefore be recommended for future breeding. (Cotterill and Dean,1990).

5.2.SEASONAL VARIATIONS IN XYLEM WATER TRANSPORT

Bud break and shoot growth activity in woody plants consists of several intra-space and extra-meristematic sub-processes where environmental factors, hormones, nutrients and water availability interact. Normal formation of leafy shoot results from the co-ordination of these sub-processes (Crabbe' and Barnola, 1996). For instance the xylem water status is strongly related to the dynamics of the carbon reserves retrieved for growth of buds and vascular cambium.

Nevertheless, to this day very few studies have been devoted to determine the water availability to buds and apical shoots in a tree during the winter period (Ameglio et al, 2001, Young and Houser, 1980; Astegiano et al., 1988; Cottignies, 1990); moreover the physiological mechanisms which regulate the phenomenon of embolism in winter and the process of refilling of vessels in spring are not yet clearly understood.

Across species, Scottish silver birch developed winter embolism levels similar to the ones for paper birch from Alaska (Sperry et al., 1994). The maximum values obtained: (50% embolism for 3-years old shoots and 70% embolism for 1 year old shoots in January), are in the range of other values found for birches in other countries

(Utsumi et al 1998, Sperry et al., 1994) and indicate that younger apical shoots are more subject to water loss and cavitation in winter than the older laterals.

In relation to the development of the winter embolism, the water content of birch stems (both for one year old and three years old stems) appeared to decrease sigmoidally.

The curvilinear relationship between relative water content and percentage loss of conductivity indicates that the water loss precedes the development of embolism of the wood tissue. It has been explained by a capacitative effect of the elastic water storage by Tyree and Yang (1990), but more probably due to the considerable decline in stem water content, it could be attributed to the water stored in the parenchymatic cells and in the phloem pathway: stored water has been found in specialised stem parenchyma tissue outside the water transport pathway and in the sapwood by Meinzer &Monasterio (1984). The progressive decline of water content could be explained by formation of ice and its melting in winter. Ice formation could first cause the movement of water in the surrounding vessels and, secondly the progressive water movements towards the lower parts of the plants, with consequent cavitation.

Ameglio and Cruiziat, (1992), found the variation of the water status to be temperature dependent and linked to water and sugar fluxes between the different compartments of the xylem, More recently (Ameglio & Cruiziat ,2001) a complex relationship between xylem pressures and temperature was reported. Air temperatures between –3°C and 3°C were often associated with sharp increases in pressure, whereas temperatures below –5°C or above 4°C were more often associated with decreases in pressure.

From our results the increase in embolism in silver birch during the winter period could be related to occurrence of temperatures below –1 °C (temperature of occurrence of wood exotherms): hydraulic conductivity declined curvilinearly with the number of hours when temperature was below –1°C (temperature of exotherms, Chapter three) and the percentage of embolism resulted to be higher when temperatures felt below –5°C, indicating a possible relationship between vulnerability to cavitation by freeze-thaw cycles and the intensity of frost, in agreement with the finding of Pockman and Sperry (1997), Tyree et al., (1994), Ewers et al., (1997), Pockmann et al., (1997), Hammel, (1967); Sucoff (1969); Ewers (1985); Sperry and Sullivan, (1992); Lo Gullo and Salleo, (1991); Hacke and Sauter, (1996); Langan et al.,(1997).

The pattern of embolism was correlated between the time of flushing for a broad range of temperate deciduous tree species, with the diffuse-porous hardwoods which incurred in less loss of hydraulic conductivity and leafing out significantly earlier than the ring and semi-ring porous species (Wang 1992). From our data the provenances of silver birch in Craigvinean forest showed no significant differences in their percentage of embolism in spring and summer. Birkhill Alford, the latest provenance to flush and the less developed in height, showed the highest values in percentage of embolism in the early spring (Chapter Four). The lack of significant adaptive change in degree of embolism avoidance could reflect their greater reliance on refilling and tolerance mechanism (Wang et al., 1992).

PLC values in spring (April) fell from maximum to minimum annual values (around 15% for 3 years old stems and 5. % for 1 year old birch stem). In this period the plants were already in a vegetative phase.

The recovery from xylem cavitation in spring in diffuse-porous species has been attributed in many occasions to root pressure (Ameglio et al 2001, Sperry et al. 1988; Sperry 1993, O'Malley and Milburn, 1983; Steudle, 1994; Hacke and Sauter, 1996). Such positive pressure is thought to help dissolve the gas in the sap and/or push the undissolved gas out of the vessels until cavitated vessels become filled with water. Sperry et al (1994) and Hacke & Sauter (1996), found a positive xylem pressure occurring during a 2-month period prior to leaf expansion in birches.

In April, in correspondence with the recovering of the hydraulic conductance, the birches were already in the vegetative phase and the xylem pressure measured was positive, in particular Birkhill Alford showed higher positive pressure during the stage of bud-swelling. By that stage, Locharbriggs Dumfries and Castle Howard were more advanced in their stage of bud-flushing and their mean of stem pressure was equal to zero. The peak of pressure recorded for Birkhill Alford was of 30kPa, and pressure ceased the 5th-6th of April, when the buds were swelled but still closed, indicating that probably Birkhill Alford seedlings had already achieved the full peak of root pressure by the time this survey was done.

The rising of the sap, and consequentially positive pressure inside the stem were found to be positively correlated again to temperature by Herrington (1969): the decline of temperature was associated with positive pressure inside the stems . The decline in wood temperature has been considered as a mechanism contributing to water uptake also by Tyree (1983).

Our measurements of wood temperature (through the DTA analysis) easily detected exotherms for Locharbriggs seedlings but less easily visible for Birkhill seedlings: Locharbriggs seedlings showed more discontinuous records subjected to variations and to peaks due to heat release at –1°C in comparison to Birkhill Alford. Some careful measurements of changes of water content status and sap pressure during winter and spring in several provenances are desirable to establish the magnitude of the change in relation to the total xylem water content.

5.3.ANALYSIS OF DIEBACK AND RISK OF FROST DAMAGE

Crown anomalies including tufting of leaves, mortality of leaves, buds, twigs and branches are characteristics of dieback. Symptoms commonly occur concurrently with one or several diseases and insect infestations. For example trunk and branch canker and root infections of *Armillaria* spp. are often observed on trees showing dieback, and these infections can progressively result in the death of whole trees, and extending over much of a forest region.

Massive episodes of dieback have been manifested in Eastern Northern America since the 1930s where the birch decline resulted in an estimated stem volume loss of 1,400 million m^3 of yellow and white birch over an area of 490,000km^2 (Pomerlau, 1991). Episodes of dieback have also been recorded on the most important commercial species in Europe. Auclair (1987) report that most stands of white-barked birches in the maritime region show some dieback symptoms, but datasets in Scotland on birch-forest dieback episodes are not available.

In 1980 a monitoring system of standardised regional and international decline/dieback (Alexander and Barnard, 1992 has been implemented by the Canadian Forest Service and Acid rain National Early Warning System (Arnews) (Hall, 1993, Millers et al., 1989). A similar system would also be desirable in the UK and Northern Europe.

Standard numeric codes were developed to measure annually the degree of severity of dieback from observations of external crown condition, and from an estimate of the areal extent of reported symptoms. From a combination of these codes, a numeric index of crown dieback was developed and used to identify major patterns in timing and geographic incidence of episodes over the interval from 1910 to 1990 (Auclair et al., 1995).

The dieback in the trial of Craigvinean (Chapter Two) was assessed through the detection of desiccation of lateral and apical branches and death of buds. The provenances affected by the dieback were only a few. At the beginning of the vegetative season (March) their flushing tended to be more advanced in comparison to the provenances not showing desiccation.

The limited mortality observed in the plot of Craigvinean is in agreement with the fact that in the year of the assessment of dieback the number of hours when temperatures fell below –1°C were 13 and 28 in March and April (2000) respectively with no hours with temperatures below –5°C (temperature considered as risk for frost damages in spring).

Freezing temperatures, and in particular winter thaws followed by sudden, severe freezing, were found to be correlated (under the form of a combined index of freezing and drought stress) to the numeric index of dieback recorded in North America and North Europe (Auclair et al., 1995). Solomon (1986) showed a high sensitivity of Northern hardwoods to dieback under continued climatic warming.

Related studies have emphasised the need to consider seriously the possibility that global warming may lead to dieback of some of the dominant tree species (King and Neilson, 1992). From our data, the provenances flushing earlier might be considered to be at higher risk to be damaged from dieback in case of a long thawing followed by freezing stress in late winter-spring.

A database on dieback assessment in relation to temperature would be useful to understand the magnitude of the phenomenon in relation to temperatures in Scotland to investigate further the physiological dys-functionality, and to assess the timing and the level of susceptibility of forest populations to dieback. If consistent over time these systems will provide invaluable quantitative measurements on forest health. (Braathe 1957, Auclair 1987, Braathe 1995).

In Scotland, birches occupied 58,000 ha in 1991, of which only the 29 % was considered high forest. Much of this was also considered of poor quality (Lorrain-Smith & Worrell, 1991).

Dieback in a juvenile phase can influence the form and the use of mature birch for industry. The form of woody plants is determined in fact by the differential elongation of buds and branches, and the expression of a particular growth habit is commonly associated with the phenomenon of apical dominance (Lyndon, 1998). The shoot apex, tiny and enclosed in the apical bud, forms the whole of the shoot system of plants as well as having a key role in producing leaves and flower. The rate at which the shoot meristem grows determines the rate at which cellular material is available for further growth of the apical system, and so it is one of the major determinants of the rates of shoot growth and leaf initiation, and may indeed be the major factor in limiting plant growth rate in extreme habitat (Korner and Menendez-Riedl 1989).

As the shoot apex is more prone to suffer dehydration damage (Chapter two) and, (Chapter Four) and is more vulnerable to loss of hydraulic conductivity than older shoots, it is clear how its desiccation or inadequate water content can be of primary importance for the growth and stem form of the seedling.

In agreement with our findings there is strong evidence supporting the fact that dieback is caused by freezing-thawing events in spring, during the period of refilling and differentiation of a new cambium (Ewers, 1985; Sperry and Sullivan, 1992; Tyree et al., 1994, Tyree and Cochard, 1996).

The final differentiation of the vascular system in the shoot apex consists of the conversion of procambium blocked out behind the apical meristem into mature elements of the xylem and phloem. In a number of seed plants, xylem maturation has been found to be considerably more complex than phloem differentiation. Thus, the primary xylem system, although continuous when mature, is discontinuous during its development making it more vulnerable to freezing-thawing cycles in spring. This might be why embolism formation can be a very important factor in causing shoot desiccation during the differentiation of the organs. The mechanism of cavitation release described above, and the unlignified nature of the young shoots walls (Maruta, 1996) unable to protect against water loss during the winter, could be responsible for the high permeability to water, pushed by the positive pressure in spring (Pickard, 1981; Yang and Tyree, 1994), through the walls provoking the desiccation and death of the terminal apex.

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ACKNOWLEDGEMENTS

This thesis has been possible thanks:

Dr. Maurizio Mencuccini, ,my supervisor, Lectures in Physiological Ecology at the IERM Department of Edinburgh University.
Dr. Ned Cundall, Project Leader, Broadleaf Improvement, Forest Research of the Forestry Commission in Roslin, Edinburgh.
Professor John Grace Head of the IERM Department at the Edinburgh University, and Professor of Environmental Biology.
Paul Jarvis, Professor of Forestry and Natural Resources at the University of Edinburgh..
Johanna Pully Technician of the trees physiological lab and organiser of the workshop on Field techniques in Canaries Islands.
Maddalena Scarlino student of Forestry from the University of Florence.
Nathalie D'Andrea, friend.
Sandra Patino, expert in water relations and now researcher in Colombia.
Mathew William, lecturer in Ecology at the IERM Department at Edinburgh University.
Allistair Kydd expert in PC.
To my parents, living in Italy.