Frost hardiness of 16 European provenances of sessile oak growing in Scotland

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Summary

The frost hardiness of 16 European provenances of sessile oak *Quercus petraea* (Matt.) Liebl. originating from six European countries was examined from autumn until budburst in spring using the method of relative conductivity.

There were significant differences of frost hardiness between provenances and a strong relationship between phenology and frost hardiness. In spring, provenances that burst bud early dehardened earlier than provenances that burst bud later. In autumn, provenances that stopped growing early were more frost hardy than provenances that continued to grow.

The interprovenance ranges of frost hardiness were greatest in spring and autumn and least in midwinter. Consequently, it was not possible to demonstrate significant differences of frost hardiness between provenances in December and January.

Overall, German, Polish and Danish provenances were more frost hardy than French, Austrian and British provenances. French provenances were least hardy at all times.

Introduction

Within Europe, oaks comprise 27 per cent of all broadleaved forest (Flies, 1993) and demand for oak planting stock is great. However, good seed crops do not occur every year (Penistan, 1984), and therefore to maintain planting programmes, both interprovenance and international transfers of seed and planting stock are common practice. In the 10 years to 1982, more than half of the oak seed used in the countries of the European Economic Community originated in the Netherlands (Gordon and Fraser, 1982), and amounts of non-indigenous seed of broadleaved species in commerce in Britain, greatly exceed those from native sources. However, international oak seed transfers are not a recent phenomenon. In the late seventeenth to early eighteenth century, oak stands were established in Sweden using seed of Polish origin (Krahl–Urban, 1959), and up to 4000 tonnes of acorns, largely from south-eastern Europe, were imported annually into Germany in the nineteenth century (Lüdemann, 1962). Trees established from such imported seed sources have hybridized with local populations, and in consequence, at least some of the variation currently observed in stands/provenances has an anthropogenic component (Kleinschmit, 1993).

Whereas for conifers grown in Europe, a substantial literature exists which provides detailed information on the suitability of species and provenances for specific sites and areas, the information available to guide provenance selection for broadleaves is much poorer. Kleinschmit (1993) reviewed intraspecific variation in European oak species and found substantial between and within provenance differences for leaf morphology, phenology, growth, wood and bark characteristics, roots, seed and flower production.

Although some information on frost damage to oak provenances is available, detailed information on frost hardiness is meagre. Frost damage can be sustained by oaks at any time between autumn and spring and deaths of winter dormant seedlings up to 3 or 4 years old is not uncommon (Jones, 1959). Although aritifical stands are most likely to be damaged, partly because maintenance removes the shelter of weeds (Junack, 1954), and because unsuitable provenances have been deployed, there are instances of death of naturally regenerating stands as far west as Bellême in Normandy (Dengler, 1944). Day and Pearce (1946) reported an exceptional instance of damage in the UK where 68 per cent of trees were killed in the year of planting. They also found that leading shoots of young oak trees were more prone to damage by spring frosts than other shoots, and that oak seemed less tolerant of spring frost than beech or ash. Although oak trees of all sizes sustained frost damage, large trees tended to recover reasonably well.

Spring frost damage is commoner in oak than winter damage (Jones, 1959) and predictably, Verchenko (1975) found that in spring, late flushing oaks were less severely damaged by frost than early flushing provenances. Liepe (1993) reported that provenances from the south and south-east of Europe flushed early, and were more prone to spring frost damage. Although Deans and Harvey (1995) found significant between-provenance differences of frost damage to leaves in late spring, because all plants were at the same phenological stage (growing rapidly), they found no significant relationship with flushing date.

In autumn, southern provenances of oak set bud later than northern provenances and are therefore more prone to being damaged by frost (Kienitz, 1879; Cieslar, 1923), however, in winter, Oppermann (1932) and Krahl-Urban (1959) found that provenances from central France and the UK seemed less tolerant of cold than other provenances.

More recently, in a detailed study conducted in controlled conditions, Liepe (1993) found that the frost hardiness of various plant organs declined as flushing progressed. In general, terminal buds were less hardy than lammas shoots or secondary buds irrespective of flushing stage, but frost hardiness rankings between provenances were not consistent. Liepe's data suggested that a frost of –8°C would be cold enough to kill all lammas shoots and terminal buds once plants were fully flushed, and overall, French and Turkish provenances seemed less hardy than the others tested.

While most studies have simply reported damage, or examined the relationship between frost hardiness and flushing, the objective of this study was to compare frost hardiness of European provenances of sessile oak from autumn until budburst in spring.

Methods and materials

Plant material

Young plants from 16 European provenances of sessile oak *Quercus petraea* (Matt) Liebl. were grown in a fenced plot in a field near Edinburgh, Scotland (55° 52′ N, 3° 13′ W) which had previously been agricultural grassland. Eleven of the provenances were planted as 1-year-old undercut transplants in December 1990, the remaining five provenances were planted as 2-year-old undercut transplants in December 1991. Details of the provenances, i.e. countries of origin, latitude, longitude and year of planting, are listed in Table 1.

Frost hardiness testing

At intervals of 2–3 weeks from mid September 1992 until mid April 1993, 60 current year leafless lammas shoots 2–5 cm thick and 7–10 cm in length were detached from randomly selected plants in each provenance. These unwashed

Table 1: Names, location details, year of planting and mean temperature (°C) damaging 50 per cent of shoots between September and April and November and February, for 16 provenances of *Quercus petraea* growing in Scotland. Frost hardiness assessments were calculated by probit analysis using either relative conductivity in excess of the upper 95 per cent confidence limit of unfrozen control shoots (statistics), or relative conductivity greater than 20 per cent to discriminate undamaged from damaged shoots

Provenance name	Country of origin	Latitude	Longitude	Elevation m.a.s.l.	Year of planting	Sept to April Statistics (°C)	Nov to Feb Statistics (°C)	Nov to Feb Relative conductivity >20 per cent (°C)
Horbylunde	Denmark	56°08′N	9°25′E	78	1990	−16.7	−18.9	−23.4
Dymock	England	51°57′N	2°27′W	80	1990	−14.2	−16.0	−20.6
St Aubin du Cormiere	France	48°17′N	1°29′W	90	1990	−14.5	−16.9	−21.8
Berce	France	47°47′N	0°27′E	155	1990	−12.9	−14.6	−20.0
Longchamp	France	47°16′N	5°18′E	230	1990	−12.7	−14.7	−19.8
Troncais	France	46°40′N	2°47′E	250	1990	−14.1	−14.9	−21.2
Belleme	France	48°24′N	0°32′E	205	1990	−13.7	−15.4	−19.9
Gelnhausen	Germany	50°15′N	9°32′E	200	1990	−15.9	−17.8	−22.9
Hainback	Austria	48°14′N	16°13′E	330	1990	−15.2	−17.5	−22.3
Farchau	Germany	53°40′N	10°46′E	43	1990	−17.5	−20.0	−23.5
Molln	Germany	53°37′N	10°45′E	36	1990	−16.4	−18.6	−22.3
Ebrach	Germany	49°51′N	10°30′E	390	1991	−17.5	−19.4	−23.3
Lappwald	Germany	52°20′N	10°09′E	180	1991	−16.5	−19.2	−22.9
Cochem	Germany	50°05′N	7°03′E	400	1991	−15.9	−18.7	−22.3
Klostermarienberg	Austria	47°25′N	16°34′E	310	1991	−14.0	−17.0	−21.7
Sycow	Poland	51°11′N	17°56′E	210	1991	−17.9	−19.5	−24.0
l.s.d. P=0.05	–	–	–	–	–	1.2	3.9	2.8

shoots were sprayed with deionized water before being placed into a programmable freezing chamber and subjected to a series of cold temperatures (10 shoots from each provenance at each temperature). Because frost hardiness differed at each test date, freezing temperatures were varied in the range 0 to –30°C among tests. For each test, temperatures were selected such that the warmest temperature should not damage the shoots and the coldest should kill all tested materials. Additionally, an unfrozen 'control' series was kept in the dark at +4°C. Freezing was achieved by cooling the programmable freezing chamber at 10°C h^{-1} to 2°C and subsequently at 5°C h^{-1} until the selected temperature was reached. The test temperature was maintained for 3 h, then the cabinet was warmed at 10°C h^{-1} to 2°C. The latter temperature was maintained until the chamber doors were opened several hours later, thus ensuring that rapid increases in subzero tissue temperature did not occur.

Conductivity measurements

For both frozen and control shoots, a piece of stem 2 cm long was cut from the centre, the ends of this small piece were then trimmed to leave the central 1 cm, which was placed in a small polypropylene scintillation vial to which 15 ml of deionized water of known conductivity were added. All samples were then stored for 7 days at 4°C in an unlit refrigerator to permit electrolyte leakage from damaged tissues into bathing solutions while minimizing microbial activity. On removal from the refrigerator and allowing the solutions to come to room temperature, conductivities of the bathing solutions were measured with a temperature compensated platinum electrode. The vials containing the shoots and bathing solutions were then autoclaved at 121°C for 120 min (Deans *et al.* 1995). Lids were slackened slightly on the vials during autoclaving to prevent bursting, while minimizing evaporation. Total conductivity (conductivity produced by the release of all diffusible electrolytes), was measured 24 h after autoclaving. Because the contents of the vials were sterile, interim storage between removal from the autoclave and recording total conductivity, was at room temperature.

Data and analyses

Relative conductivity, i.e. conductivity after freezing, divided by conductivity after autoclaving, and then expressed as a percentage, was taken as the measure of freezing injury (Deans and Harvey, 1995). In assessing whether plants had sustained damage, it was assumed that relative conductivities within the 95 per cent confidence limit of the unfrozen (control) shoots, did not differ significantly from controls. Where relative conductivities exceeded the upper 95 per cent confidence interval, the interpretation was that shoots had been significantly injured by the freezing treatments. Subsequent to allocating plants to injured and healthy categories, for each provenance, at each time of freezing, the numbers of damaged and undamaged plants in each treatment were subjected to probit analysis. The temperature estimated as damaging 50 per cent of shoots (Lt50, Deans *et al.* 1992) in each provenance at each time of testing was then calculated. Comparisons of Lt50 between provenances were subsequently made by analysis of variance.

Although this method of damage assessment avoids any subjective decision-making on the part of operators, and is therefore acceptable to statisticians and quality assurance auditors, it cannot be used to define the temperature of tissue death. Instead, it discriminates between treatments by identifying the warmest temperature at which significant differences of electrolyte leakage can be detected between frozen and control shoots. In order to provide some indication of likely killing temperatures, probit analyses using relative conductivity in excess of 20 per cent to discriminate live from dead tissues, were performed in parallel with the main study. Deans *et al.* (1995) found that relative conductivities of about 24 per cent discriminated live from dead tissues in summer, but cautioned on the dangers of using a single value of relative conductivity for damage assessments made at different times during the year. There was a significant positive relationship between the probit estimates of Lt50 from the statistical and relative conductivity >20 per cent methods (P=<0.001), which is described by the equation:

$$Y = -4.8 + 0.887\,X$$

where Y is the calculated lethal temperature (°C) for 50 per cent of shoots as estimated from relative conductivity >20 per cent, and X is the damaging temperature for 50 per cent of shoots estimated from statistical procedures, (R^2 = 95 per cent).

Results

As assessed either by relative conductivity in excess of the 95 per cent confidence limit of control shoots, or by relative conductivity greater than 20 per cent, there were significant differences of frost hardiness between provenances. Mean frost hardiness (means calculated from Lt50s estimated from 95 per cent confidence limits for all dates of freezing), is presented for all provenances in Table 1. Whereas the French provenances, Longchamp and Berce in particular, and the Austrian provenance Klostermarienberg, were least frost hardy, provenances from Denmark, Germany and Poland were generally more tolerant of low temperatures.

Interprovenance ranges of Lt 50 estimated by relative conductivity >20 per cent, and the autumn to spring pattern of development and loss of frost hardiness, is presented for all provenances in Figure 1. Mean Lt 50 declined rapidly from about −10°C in late September to about −24°C in December before increasing in a slower less regular pattern to about −10°C by mid April. Although there was an interprovenance range of about 7°C for frost hardiness in autumn and spring, in midwinter, the range of frost hardiness was much smaller, (about 3°C in December.)

It was surprising that some dehardening occurred between early December and the

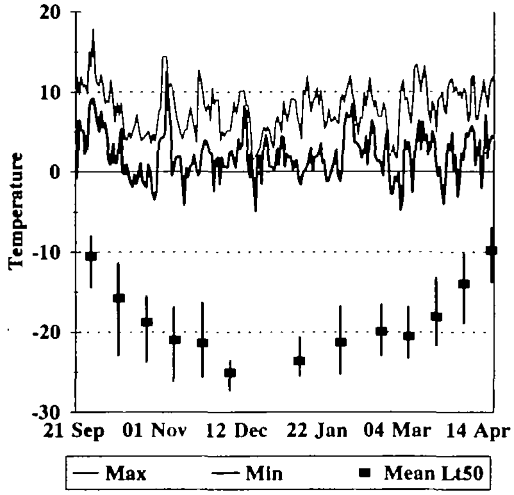

Figure 1. Maximum and minimum daily air temperatures (°C) and mean lethal temperatures (Lt50) for 50 per cent of shoots of *Quercus petraea* (■), near Edinburgh in Scotland from September 1992 until mid April 1993. Vertical bars indicate the interprovenance range of Lt50 at each date of testing

beginning of March, however the dehardening took place against a background of increasing maximum daily temperatures and relative absence of frost, (Figure 1). This relatively warm period was followed by a period of colder weather (9 days) centred on 1 March, which included frost on six successive nights, and subsequently, there was a slight increase in frost hardiness. Thereafter, the plants dehardened smoothly as temperatures and photoperiod increased.

During winter (mid November until late February), there were significant differences in Lt50s between provenances, those from Poland, Germany and Denmark were hardier than some of the others (Table 1). Conversely, the French and British provenances were among the least hardy. The average lethal temperatures as estimated by relative conductivity greater than 20 per cent suggest that during this period, the hardiest provenances could survive temperatures of about –24°C and the least hardy about –20°C.

In midwinter (December/January) frost hardiness was maximal, however the interprovenance range of Lt50s was smaller than at other times, and thus it was not possible to identify statistically significant differences of frost hardiness between the provenances using statistical methods to discriminate damaged from undamaged shoots.

Interprovenance ranges of frost hardiness were larger in spring and autumn and it was possible to demonstrate differences between provenances during these seasons. In spring and autumn the extent of frost hardiness reflected the phenologies of the provenances. Deans and Harvey (1995) concurrently examined phenological details of the provenances utilized in this study, Figure 2 illustrates the relationship between spring frost hardiness (assessed on April 19 1993) and dates of budburst in 1993. Budburst was assumed to have taken place when 50 per cent of buds possessed protruding leaf edges, the condition defined as budburst stage 3 by Kleinschmit and Svolba (1979).

There was a significant positive relationship between budburst date and spring frost hardiness ($P = <0.001$, $R^2 = 57$ per cent. Provenances that were closest to budburst were less frost hardy than those that burst bud later. Conversely, in autumn, provenances that continued to grow late in the season were less frost hardy at that time than provenances that had stopped growing earlier (Figure 3, $P = <0.001$, $R^2 = 71$ per cent).

There were no significant differences of frost hardiness between provenances for tissues

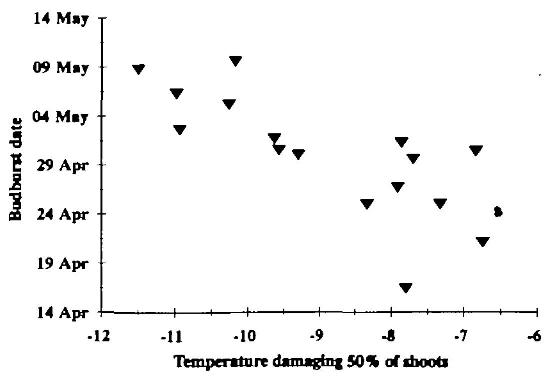

Figure 2. Relationship between dates of budburst and frost hardiness (temperature (°C) damaging 50 per cent of plants as assessed on 19 April) for 16 European provenances of *Quercus petraea* growing in Scotland

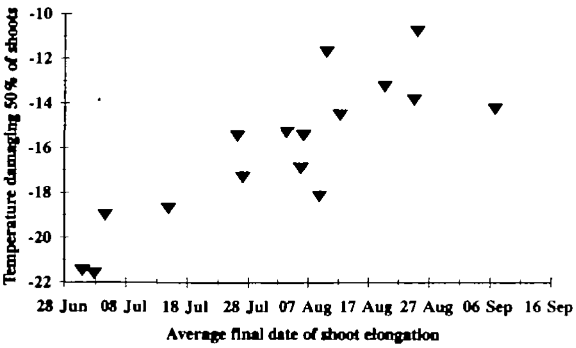

Figure 3. Relationship between the lethal temperature for 50 per cent of shoots (°C assessed at the end of September) and the average date on which growth cessation (shoot elongation) occurred (n=25) for 16 European provenances of *Quercus petraea* in Scotland

which were actively growing. Such tissues were damaged by temperatures of about −5 to −7°C irrespective of season (data not presented).

Discussion

Although Liepe and Konig (1994) found that during flushing in sessile oak, frost hardiness was influenced more by phenology than by provenance, this study revealed significant differences of frost hardiness between provenances of sessile oak during the seasons spring, autumn and winter. Nevertheless, the results of the present study confirm the earlier observation that phenology is of major importance for frost hardiness in spring and autumn, and highlights the risk of planting (1) early flushing provenances in areas that are prone to late spring frost and (2) provenances that grow late in autumn where autumnal frosts are early. Since the French provenances used in this study were generally less hardy than the others, were prone to flush early, and grew late in the autumn, they would seem a poor choice both for very cold districts and where either late or early frosts are frequent. Similarly, the British provenance Dymock, and the Austrian provenances seemed less frost hardy from November until February than the German and Polish provenances, confirming the views of Oppermann (1932) and Krahl-Urban (1959) that at least some British and French provenances are less tolerant of cold in midwinter than other provenances.

Using the non-subjective techniques applied in this study, it was not possible to demonstrate significant differences of frost hardiness between provenances in midwinter (December and January). However, there were only two freezing tests during this period of maximal frost hardiness and plant physiological status differed between the dates of frost hardiness testing, thus reducing the chances of finding significant differences between provenances. Thereafter, the extent of frost hardiness declined during the relatively warm period which occurred between mid December and the beginning of March. Given a longer period at maximum frost hardiness, and a greater number of observations, it seems likely that significant differences could have been found. Using visual scoring of cambial damage (Deans *et al.*, 1992), it was possible to detect significant differences of frost hardiness between provenances in midwinter. However, because the interprovenance range of frost hardiness was smallest in midwinter, such differences were smaller than those prevailing in spring and autumn.

This study has revealed significant differences of frost hardiness between provenances of sessile oak which may be of value in guiding provenance selection where failure of local supplies renders seed or plant transfers necessary. Although frost hardiness was strongly associated with phenology, there were differences between provenances during the winter period when physiological activity was least. That the plants reacted to relatively warm weather in winter by dehardening, as previously reported for *Nothofagus procera* (Deans *et al.*, 1992), suggests that if the winter climate of Europe becomes warmer as predicted, there may be an increased risk of winter frost damage to oaks. Because the risks from radiation frosts will be greatest for young plants (their susceptible tissues are closer to the ground surface than those of taller plants) there may be some merit in adopting planting systems that provide local shelter for young oaks.

Acknowledgements

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