Frost Hardiness of Red Alder (*Alnus rubra*) Provenances in Britain

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SUMMARY

The phenology and frost hardiness of shoots of 15 provenances of *Alnus rubra* growing in Scotland were measured over one autumn, winter and spring. Dates of budset (in September) and the onset of rapid frost hardening (in October-November) occurred about 2 days earlier for each degree latitude of origin northwards, except for an Idaho provenance. However, all provenances dehardened at about the same time in March and burst their buds between 8 and 14 April. Assuming that rapid frost hardening in the autumn was triggered primarily by shortening daylengths, Alaskan provenances of *A. rubra* seemed better adapted to British conditions than southern British Columbian provenances, which have been most commonly planted. However, even Alaskan provenances are prone to spring frost damage. Scottish *A. glutinosa* and Alaskan *A. sinuata* set buds and frost hardened 1–2 weeks before even the Alaskan *A. rubra*, and burst their buds 2–3 weeks later in April-May. All three species were hardy to below −30° C from December to mid-March.

INTRODUCTION

In Britain, *Alnus rubra* Bong. (red alder) has been planted in over 30 forest trials since the 1930s in order to explore its potential as an 'amenity' tree and as a source of fibre, comminuted wood, saw timber and biologically fixed nitrogen. In many instances the species has exhibited the two attributes that have attracted much attention in the Pacific Northwest (e.g. Trappe *et al.*, 1968; Briggs *et al.*, 1978; Atkinson *et al.*, 1979; Gordon *et al.*, 1979), namely (i) rapid juvenile growth compared, in Britain, with *Alnus glutinosa* (L.) Gaertn. and *Picea sitchensis* (Bong.) Carr., and (ii) an ability to improve soil conditions and to supply nitrogen to associated species (Malcolm *et al.*, 1985).

However, in almost all the British trials *A. rubra* has suffered 'dieback' (possibly exacerbated by wind damage) by ages 12–15 (Peace, 1962; Lines and Brown, 1982). One hypothesis to explain dieback is that the trees become deficient in nutrients with age, in a similar but more acute manner to that described in *A. rubra* by DeBell and Radwan (1984). Most of the British trials were planted on peaty soils, which may inhibit nodulation, and which are low in available P (phosphorus), although dieback has occurred even on mineral soils and when high levels of P and K (potassium) were added, plus molybdenum and cobalt, which are needed for effective N_2-fixation.

An alternative hypothesis, or contributory factor, is that *A. rubra* in Britain has been repeatedly damaged by frost, often followed by the formation of cankers by weakly parasitic fungi (which invade wind-induced cracks and wounds). Most trials were planted with *A. rubra* originating from less than 100 m altitude at 48–50 °N in Washington and southern British Columbia, and have been planted in Britain at up to 250 m at 52–58 °N. Much of the seed used in British trials was collected at Lennox Forest near Glasgow, from belts of trees originally planted on the edges of compartments of Sitka spruce. The seed origin of these trees was Vancouver (from what is now the Port Coquitlam and New Westminster suburbs). More northerly seed sources were rarely planted in Britain until the mid-1970s, and severe spring and/or autumn frost damage was reported in many of the early plantings.

Tarrant (1961) reported that *A. rubra* originating at 15 m in Washington was severely frosted when planted at over 750 m in the Wind River Experimental Forest near Carson, Washington. DeBell and Wilson (1978) found that Juneau (Alaska) and Sandpoint (Idaho) provenances suffered much less frost damage than provenances from coastal Oregon, Washington or southern Vancouver Island when planted near Olympia, Washington and at Cascade Head, Oregon. *A. rubra* breeding was abandoned in Japan because of its susceptibility to frost damage (Hall and Maynard, 1979).

In 1982, a study began to examine the performance of northerly provenances of *A. rubra* in Britain. This paper reports the results of experimental determinations of their frost hardiness compared with southerly provenances and native *A. glutinosa* in Scotland.

MATERIALS AND METHODS

Plant material

During the autumn of 1982 seeds of *Alnus rubra* were collected at 15 locations between Washington and Alaska, and from one high altitude location in Idaho (Fig. 1, Table 1). In addition, one seedlot of *Alnus sinuata* (Regel) Rydb. (Sitka alder) was collected near Juneau, Alaska, and seeds of *Alnus glutinosa* were collected from both a mild site in western Scotland (Loch Fyne) and a colder site in southeastern Scotland (Cribbs Hole, near Bonchester Bridge, Table 1).

The seeds were stratified at 3° C for five weeks, and were sown in a glasshouse at the Bush Estate, Penicuik, Scotland on 6 April 1983. The seedlings were grown outside in 9 cm diameter pots from June 1983 until April/May 1984, when they were planted in two trials in loam soil at the Bush Estate (55° 51′ N, 185 m altitude). In trial 1, eleven trees of each provenance were planted in each of four randomized blocks at 0.8 × 1.0 m spacing. In trial 2, seven trees of each provenance were planted in each of four randomized blocks at 1.25 × 2.50 m spacing.

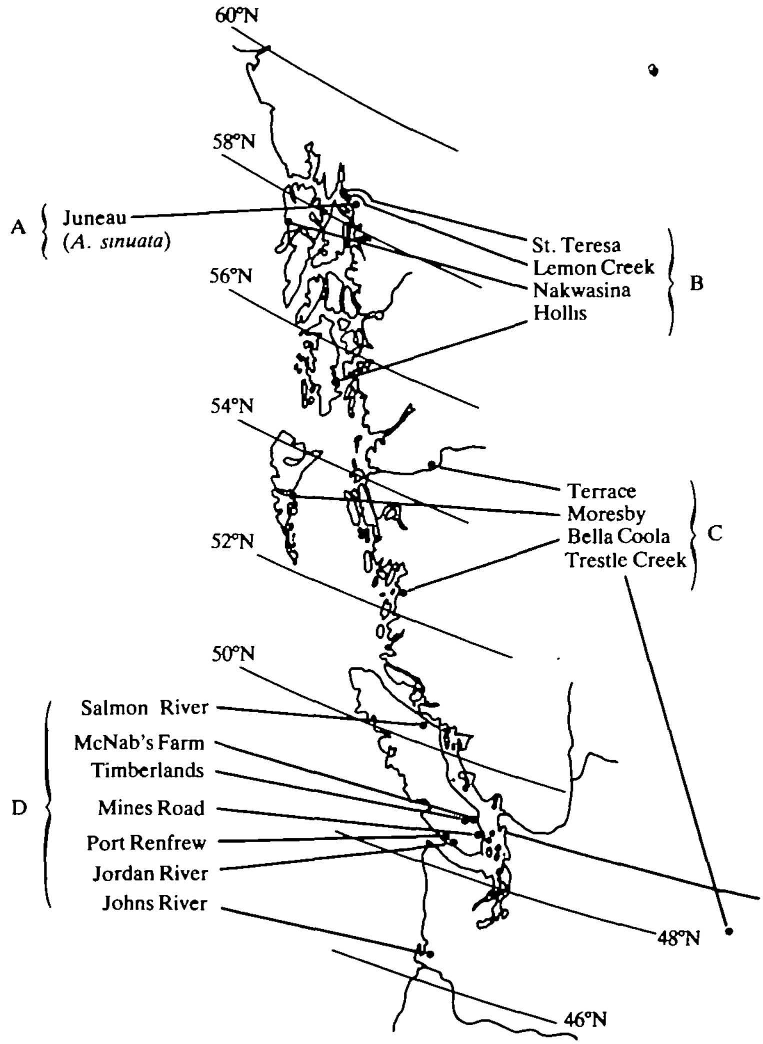

Figure 1. Origins of 15 provenances of *Alnus rubra* and one provenance of *Alnus sinuata* along the coast of western North America from Alaska to Washington State. A, B, C and D refer to their groupings in Tables 1 and 2.

During 1984 the trees in both trials grew to between 0.5 and 2.0 m tall. The presence or absence of terminal buds (budset) was recorded in trial 1 every 3–4 days during September-October 1984. Shoots were then cut from this trial for assessments of frost hardiness (see below). The presence or absence of emerging leaves (budburst) was recorded in trial 2 every week during March-April 1985. The mean date when 80 per cent of the trees of each provenance had achieved budset and budburst was estimated for each block.

TABLE 1. *Origins of seedlots of* Alnus rubra, Alnus glutinosa *and* Alnus sinuata

Notation in Figs. 1 & 3	Species	Location of origin	Region & Country	Latitude °N	Longitude °W	Altitude (m)	Age of Trees (years)
A	*A.glutinosa*	Bonchester Br. (Cribbs Hole)	Roxburgh, Scotland	55°22′	2°39′	229	40
A	*A.glutinosa*	Loch Fyne	Argyll, Scotland	56°14′	4°58′	135	40
A	*A.sinuata*	Juneau	Alaska, USA	58°20′	134°20′	60	–
B	*A.rubra*	St Teresa	Alaska, USA	58°25′	134°50′	30	19–52
B	*A.rubra*	Lemon Creek	Alaska, USA	58°25′	134°40′	30–60	29–89
B	*A.rubra*	Nakwasina	Alaska, USA	57°30′	135°50′	30	17–18
B	*A.rubra*	Hollis	Alaska, USA	55°25′	132°50′	60–100	17–19
C	*A.rubra*	Terrace	B.C., Canada	54°31′	128°32′	–	–
C	*A.rubra*	Moresby	B.C., Canada	53°10′	131°57′	–	–
C	*A.rubra*	Bella Coola	B.C., Canada	52°23′	126°46′	–	–
C	*A.rubra*	Trestle Creek	Idaho, USA	48°20′	116°05′	740	*ca.*25
D	*A.rubra*	Salmon River	B.C., Canada	50°19′	125°56′	55	*ca.*60
D	*A.rubra*	McNab's Farm	B.C., Canada	50°03′	123°52′	15	*ca.*60
D	*A.rubra*	Timberlands Lake	B.C., Canada	49°03′	123°56′	168	*ca.*45
D	*A.rubra*	Mines Road	B.C., Canada	48°42′	123°41′	521	*ca.*22
D	*A.rubra*	Port Renfrew	B.C., Canada	48°30′	124°20′	182	*ca.*30
D	*A.rubra*	Jordan River	B.C., Canada	48°22′	124°01′	90	*ca.*60
D	*A.rubra*	John's River	Wash., USA	46°25′	123°46′	75	*ca.*30

Measurement of frost hardiness

The frost hardiness of detached shoots (from the 1984 growth) was determined by subjecting shoots to simulated night frosts in a programmable freezing chamber. Only one freezing treatment was given per night. Samples of 15 detached shoots, each 5–10 cm long, of each seedlot were freeze-tested at between −3 °C and −39 °C on between 80 and 128 occasions between 5 September 1984 and 15 May 1985 (the smaller provenances were tested at less frequent intervals). The purpose-built freezing chamber and temperature controller used were modified versions of those described by Cannell and Sheppard (1982). The chamber (50 × 50 × 140 cm) was unlit, and the shoots were held horizontally about 5 cm from the floor in air which slowly circulated over cooling coils contained in an insulated compartment. The air temperature was controlled by a system built around a Tiny Basic Controller (Essex Electronics Centre, England) linked to two platinum resistance temperature sensors. An algorithm was developed so that the cooling and warming ramps were smooth and the preset freezing temperature was held to within ± 0.5 °C.

The shoots were sprayed with a fine mist of water before freezing. They were then cooled at 5 °C per hour, beginning no more than 2 hours after being detached from the trees. The preset freezing temperature was held for 3 hours, and the shoots were thawed at 10 °C per hour and then held at 9 °C.

After freeze-testing overnight the shoots were placed on a mist bench in a glasshouse at 15–20 °C. After 2 weeks each shoot was scored as alive or dead, based on the degree of brown coloration of the cambium; undamaged shoots remained green.

The percentage of the 15 shoots that were killed on each occasion was plotted as shown in Fig. 2, and the temperature giving 50 per cent kill (LT_{50}) was delineated by eye. The lines giving LT_{50} may be regarded as accurate to about ± 1 °C.

RESULTS

Seasonal pattern

The seasonal pattern of frost hardening and dehardening in relation to temperatures, daylengths, and dates of budset and budburst, is illustrated in Fig. 2, which presents data for the Jordan River provenance of *A. rubra*. The shoots were hardy to about −5 °C (LT_{50}) at the time of 80 per cent budset on 22 September. During the following five weeks the shoots hardened slowly to about −8 °C (*ca.* 0.6 °C/wk). From the beginning of November to mid-December there was a period of rapid hardening to an LT_{50} of about −35 °C (*ca.* 4.5 °C/wk). In the case of Jordan River provenance, the onset of accelerated hardening coincided with a −4.5 °C frost on 6 November, but in other provenances accelerated hardening occurred before this frost, and so was probably triggered by shortening daylengths and/or the cool spell in early

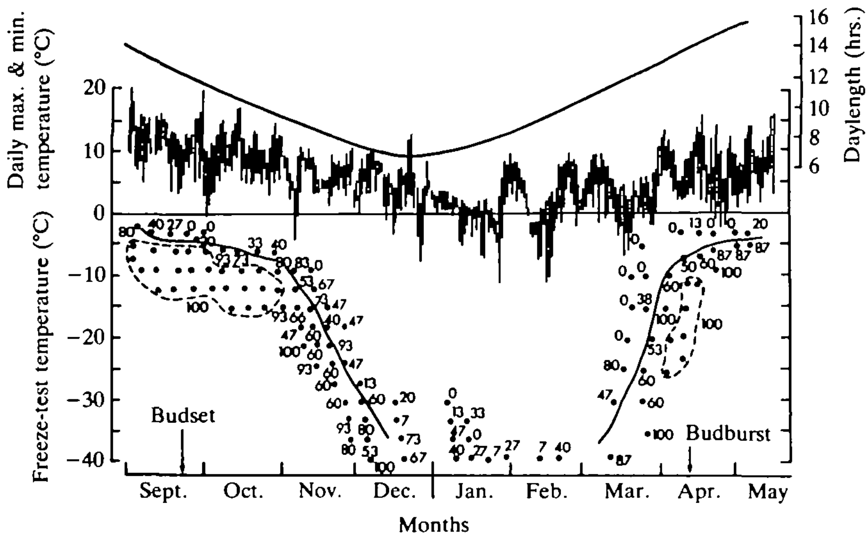

Figure 2. Percentage of 15 shoots of *Alnus rubra* (from Jordan River, Vancouver Island) that were killed when freeze-tested at different temperatures on 110 occasions during the winter of 1984/85. The dashed lines encircle values of 100 per cent kill. The line drawn through the points marks the temperatures giving 50% kill (LT_{50}). The dates of 80 per cent budset and 80 per cent budburst are indicated. The trees were growing outside in Scotland in the temperature and daylength regimes shown. Similar data were used to delineate the LT_{50} lines for all the provenances listed in Table 1 (see Fig. 3).

October. From mid-December to early March all trees were hardy to below −30 °C (LT_{50}). During March, the shoots of Jordan River provenance dehardened to about −15 °C, even before the onset of warm weather about 1 April. Budburst occurred around 11 April, following a 'heat sum' (thermal time) of 49 day °C>5 °C since 1 January (306 day °C>0 °C). At budburst the shoots were hardy to no more than −7 °C but were damaged to some extent at temperatures below −3 °C.

Species and provenance differences

The species and provenances were divided in to groups A, B, C and D, depending upon their seasonal patterns of frost hardening and their dates of budset and budburst.

Group A consisted of *A. glutinosa* from Scotland and *A. sinuata* from Juneau. These species set buds on or before 1–2 September and began rapid hardening about 20 September—before there was any cooling trend—presumably in response to daylengths below 12.0 hours (Fig. 3). Rapid dehardening occurred during the month of April and budburst occurred about 30 April (Table 2). *A. glutinosa* from the mild location in western Scotland (Loch Fyne) was slightly less hardy than *A. glutinosa* from the colder

TABLE 2. *Dates of 80 per cent budset and 80 per cent budburst on provenances of* Alnus rubra, Alnus glutinosa *and* Alnus sinuata *growing at the Bush Estate, Penicuik, Scotland. The trees were measured at the end of their second growing season. Budburst was defined as the first appearance of green leaves.*

Group	Species	Origin	Date of budset	Date of budburst
A	*A.glutinosa*	Bonchester Br.	2 Sept	30 April
	A.glutinosa	Loch Fyne	<1 Sept.+	28 April
	A.sinuata	Juneau	<1 Sept.+	2 May
B	*A.rubra*	St. Teresa	1 Sept.	11 April
	A.rubra	Lemon Creek	1 Sept.	9 April
	A.rubra	Nakwasina	1 Sept.	8 April
	A.rubra	Hollis	1 Sept.	8 April
C	*A.rubra*	Terrace	18 Sept.	8 April
	A.rubra	Moresby	15 Sept.	8 April
	A.rubra	Bella Coola	17 Sept.	8 April
	A.rubra	Trestle Creek	17 Sept.	10 April
D	*A.rubra*	Salmon River	8 Sept.	10 April
	A.rubra	McNab's Farm	14 Sept.	12 April
	A.rubra	Timberlands Lake	20 Sept.	14 April
	A.rubra	Mines Road	16 Sept.	11 April
	A.rubra	Port Renfrew	18 Sept.	11 April
	A.rubra	Jordan River	22 Sept.	11 April
	A.rubra	John's River	22 Sept.	12 April
	L.S.D. P = 0.05 (days)		4.6	2.6

+ Budset had already occurred before these trees were observed on 1 Sept.

location in southeastern Scotland (Bonchester Bridge) both in the autumn and during late April.

Group B consisted of the Alaskan provenances of *A. rubra*, which also set buds about 1 September, but which did not begin rapid hardening until mid-October, at a daylength of about 10.5 hours. Rapid dehardening occurred in late March, and budburst occurred on 8–11 April, about three weeks before budburst on *A. glutinosa* and *A. sinuata* (Fig. 3, Table 2).

Group C consisted of provenances of *A. rubra* from the Skeena River (Terrace), Queen Charlotte Islands (Moresby), mid-latitude British Columbia (Bella Coola) and Idaho (Trestle Creek). These provenances did not set buds until 15–18 September, and they did not begin hardening until the last week in October, at a daylength of about 9.5 hours. However, they

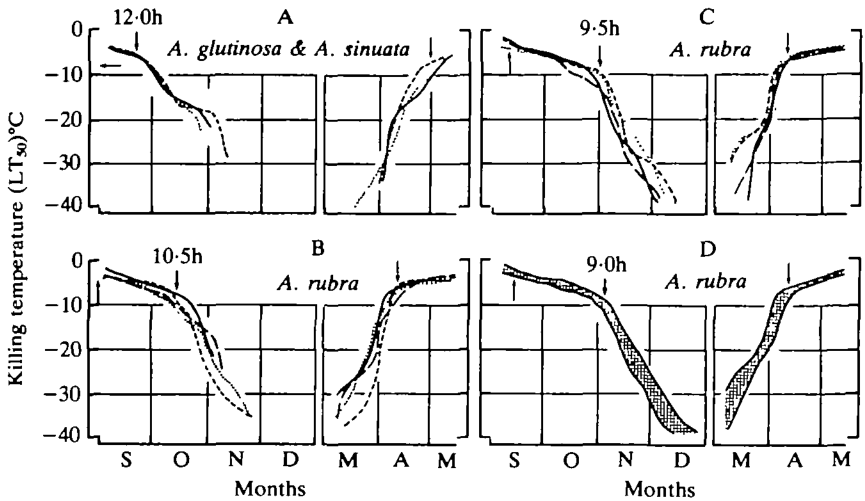

Figure 3. Temperatures that killed 50 per cent of the shoots (LT_{50}) of different species and provenances of *Alnus*, grouped as in Figure 1 and Table 1. Arrows indicate the daylength (hours) at the onset of accelerated hardening in the autumn, and the mean dates of 80 per cent budset (in September) and 80 per cent budburst (in April).

A ———— Bonchester Bridge (*A. glutinosa*)
---------- Loch Fyne (*A. glutinosa*)
- - - - Juneau (*A. sinuata*)

B ———— Lemon Creek
---------- Nakwasina
- - - - - - - St Teresa
..... Hollis

C ———— Trestle Creek
---------- Terrace
- - - - - - - Bella Coola
· - Moresby

D Range of values for seven southerly provenances listed in Table 1 and Figure 1.

dehardened and burst their buds at about the same time in March-April as the Alaskan provenances of Group B.

Group D consisted of *A. rubra* provenances from a range of altitudes on Vancouver Island, and one provenance from Washington (John's River). They set buds between 8 and 22 September: the most northerly provenance, Salmon River, set buds first, and the most southerly provenance, John's River, set buds last, but there was no systematic difference between provenances from different altitudes (Table 2). Group D provenances began rapid hardening about one week later than those in Group C, at a daylength of about 9.0 hours. They also dehardened and burst their buds a few days later than the provenances in Group C.

DISCUSSION

There was a clear trend from north to south in both the date of budset (Table 2) and in the onset of rapid frost hardening (Fig. 3) among coastal *A. rubra* provenances grown in Scotland. Among the coastal provenances, the altitude of origin, over the range 15–521 m, had little apparent effect; however, the Trestle Creek, Idaho lot from 740 m (close to the upper limit of this species) behaved like the provenances from about 5° further north. Latitude accounted for 70 per cent of the variation in dates of budset; both budset and the onset of rapid hardening occurred about two days earlier for each degree latitude north—excluding the Idaho provenance. There was no such marked north-south trend in the dates of dehardening in spring or in the dates of budburst: all provenances of *A. rubra* dehardened rapidly at the end of March, and the average date of budburst of the southerly provenances (Group D) was only three days later than the date of budburst of the Alaskan provenances (Group B).

Thus, some increase in autumn frost hardiness could be obtained by planting Alaskan rather than southerly sources of *A. rubra* in Britain, but there would be no improvement in frost hardiness in the spring.

All provenances of *A. rubra* were much more susceptible to frost damage than native Scottish *A. glutinosa* during early April; the buds burst on all the *A. rubra* trees 2–3 weeks before they did on *A. glutinosa* (Table 2, Fig. 3). Furthermore, even the Alaskan *A. rubra* provenances set buds and began rapid autumn frost hardening at least 1–2 weeks later than *A. sinuata* from the same region of Alaska (Fig. 1 and 3). The rapid growth of *A. rubra* in Britain, compared with *A. glutinosa*, may be partly attributed to its prolonged period of growth or of active photosynthesis before leaf-fall in autumn, and to its early foliation and light interception in spring.

All *A. rubra* provenances, like *A. glutinosa*, were hardy to below −30 °C from December to mid-March. This level of hardiness is more than adequate to avoid winter frost damage in Britain, where absolute minimum temperatures below −20 °C occur rarely, except at high altitudes (Anon, 1975; Murray *et al.*, 1986). Interestingly, −30 °C is also well below the absolute minimum temperatures experienced in much of the natural range of *A. rubra*.

In an earlier paper (Cannell *et al.*, 1985), we reviewed some of the literature on autumn frost hardening of trees in natural conditions in the temperate zone, and concluded that daylength is often the principal trigger for the onset of what we have called 'rapid' autumn hardening. Assuming that this was the case in this study, then the critical daylengths for the onset of rapid hardening of *A. glutinosa*, Alaskan *A. rubra*, northern British Columbian *A. rubra*, and southern British Columbian *A. rubra* (corresponding to our groups A, B, C and D) were about 12.0, 10.5, 9.5 and 9.0 hours, respectively. These values may be compared with corresponding values for young trees of *Picea sitchensis* from Alaska (Cordova), the Queen

Charlotte Islands, and Oregon (Denmark) of 13, 10–11, and 9 hours, respectively (Cannell *et al.*, 1985). This comparison suggests that Alaskan *A. rubra* (Group B) growing in Britain will often harden off in the autumn at about the same time (15 October at 56° N) as young trees of *P. sitchensis* of Queen Charlotte Islands (Q.C.I.) provenance. *P. sitchensis* from Q.C.I. is well-adapted to the British uplands climate, where young trees suffer mild autumn frost damage no more than one year in ten (Cannell *et al.*, 1985). By contrast, *A. rubra* from southern British Columbia (including Vancouver Island) may harden off as late as young *P. sitchensis* trees from Oregon, which are much more prone to autumn frost damage in Britain.

In conclusion, there may be a considerable advantage in collecting seed of *A. rubra* from Alaska rather than from southern British Columbia for planting in Britain, especially in upland areas where *A. rubra* might be of value in mixtures. However, even Alaskan *A. rubra* may be prone to spring frost damage owing to early dehardening and budburst and, before recommendations are made on the choice of provenance, more needs to be known about growth rates, form and the occurrence of dieback.

A. glutinosa, even from mild areas of Britain, is hardy in late autumn and early spring, but it has a correspondingly short growing season and a slow rate of growth.

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REFERENCES

Anon. 1975 Maps of mean and extreme temperature over the United Kingdom 1941–1970. Climatological Memorandum No. 73. Meteorological Office (Met. 0.3), Bracknell, Berkshire, England.

Atkinson, W. A., Bormann, B. T. and DeBell, D. S. 1979 Crop rotation of Douglas-fir and red alder: a preliminary biological and economic assessment. *Bot. Gaz.* (Chicago), **140** (Suppl.): S102–S107.

Briggs, D. G., DeBell, D. S., and Atkinson, W. A. (*Editors) 1978 Utilization and management of alder*. USDA Forest Service, Gen. Tech. Report PNW-70.

Cannell, M. G. R. and Sheppard, L. J. 1982 Seasonal changes in the frost hardiness of provenances of *Picea sitchensis* in Scotland. *Forestry* **55**, 137–153.

Cannell, M. G. R., Sheppard, L. J., Smith, R. I. and Murray, M. B. 1985 Autumn frost damage on young *Picea sitchensis*. 2. Shoot frost hardening, and the probability of frost damage in Scotland. *Forestry* **58**, 147–168.

DeBell, D. S. and Wilson, B. C. 1978 Natural variation in red alder. In *Utilization and management of alder*. Edited by D. G. Briggs, D. S. DeBell and W. A. Atkinson. USDA Forest Service, Gen. Tech. Report, PNW-70. 193–208.

DeBell, D. S. and Radwan, M. A. 1984 Foliar chemical concentrations in red alder stands of various ages. *Plant and Soil* **77**, 395–399.

Gordon, J. C., Wheeler, C. T. and Perry, D. A. (*Editors*) 1979 *Symbiotic nitrogen fixation in the management of temperate forests*. Oregon State University, Corvallis, Oregon.
Hall, R. B. and Maynard, C. A. 1979 Considerations in the genetic improvement of alder. In *Symbiotic nitrogen fixation in the management of temperate forests*. Edited by J. C. Gordon, C. T. Wheeler and D. A. Perry. Oregon State University, Corvallis, Oregon. 322–344.
Lines, R. and Brown, J. 1982 Broadleaves for the uplands. In *Broadleaves in Britain*. Edited by D. C. Malcolm, J. Evans and P. N. Edwards. Institute of Chartered Foresters, Edinburgh. 141–149.
Malcolm, D. C., Hooker, J. E. and Wheeler, C. T. 1985. *Frankia* symbiosis as a source of nitrogen in forestry: a case study of symbiotic nitrogen-fixation in a mixed *Alnus-Picea* plantation in Scotland. *Proc. Royal Soc. Edinburgh* **85B**, 263–282.
Murray, M. B., Cannell, M. G. R. and Sheppard, L. J. 1986 Frost hardiness of *Nothofagus procera* and *Nothofagus obliqua* in Britain. *Forestry* **59**, 209–222.
Peace, T. R. 1962 *Pathology of trees and shrubs*. Oxford University Press.
Tarrant, R. F. 1961 Stand development and soil fertility in a Douglas fir-red alder plantation. *Forest Sci.* **7**, 238–246.
Trappe, J. M., Franklin, J. F., Tarrant, R. F., and Hansen, G. H. (*Editors*) 1968 *Biology of alder*. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.