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Early Performance of Interior Douglas-fir
(*Pseudotsuga menziesii* var. *glauca*)
Seed Sources on Five Ecologically Diverse Sites
in Southwestern Alberta

by

Leonard K. Barnhardt ©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF FOREST SCIENCE

EDMONTON, ALBERTA

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled EARLY PERFORMANCE OF INTERIOR DOUGLAS-FIR (*PSEUDOTSUGA MENZIESII* VAR. *GLAUCA*) SEED SOURCES ON FIVE ECOLOGICALLY DIVERSE SITES IN SOUTHWESTERN ALBERTA submitted by Leonard Keith Barnhardt in partial fulfillment of the requirements for the degree of Master of Science.

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Date December 22/95

ABSTRACT

Eight Alberta seed sources of interior Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca*) were selected to study the geographic variation in height, survival and several phenological traits. Field trials were established with one year old container grown seedlings on five ecologically diverse sites in southwestern Alberta. Seedlings were assessed at the end of the third growing season after out planting for percent survival, total height, and plant health and vigour, and during the third growing season for bud-burst and bud-set timing.

Significant differences among sources were found for all five traits studied and contrasts of northern versus southern sites showed that northern sites had significantly better survival, plant health and growth. Trait expression for seed sources was geographically complex with survival, height and plant health showing marked differences with elevation and latitude while bud-burst and bud-set timing seemed more influenced by distance of seed source origin from the continental divide. Survival and height growth were strongly and inversely correlated.

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Early Performance of Interior Douglas-fir
(*Pseudotsuga menziesii* var. *glauca*)
Seed Sources Planted on Five Ecologically Diverse
Sites in Southwestern Alberta

I. INTRODUCTION

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) has the greatest latitudinal range of any commercial North American conifer and dominates the most productive forest lands of western North America (Silen, 1978). It is a spectacular tree attaining ages up to 1,400 years, heights to 117 metres and diameters to 4.7 metres (Issac and Dimock 1965; Hermann and Lavender 1990). This capacity for growth and longevity has led to the development of old, high volume and commercially valuable stands which are increasingly at the centre of the conflict between commodity and ecological values and the controversy over what should be harvested and what should be retained in managed forests (Thomas 1991; Brooks and Grant 1992).

As a commercial timber species, Douglas-fir is valued for its rapid growth, wood quality and relative freedom from pests and disease. It is primarily used for dimension lumber but is also used to produce specialty products such as plywood, high grade finish boards, veneers, railroad ties, mining timbers, structural beams and Christmas trees (Silen 1978; Corrao 1990).

Although it does not have an extensive native range in Alberta, Rocky Mountain Douglas-fir (*P. menziesii* var. *glauca* (Beissn.) Franco), commonly referred to as interior Douglas-fir, is an important component of southwestern foothills and mountain corridor forests. These forests are highly prized primarily for their recreational and scenic value, but also, on a limited basis, as a source of timber for local residents and mills. The volume of Douglas-fir harvested is small on a provincial scale, and as a species it only accounts for about 0.14 percent of the provincial merchantable conifer volume, 22 percent of which falls outside public lands managed for timber production (Alberta Forest Service 1992).

Despite its limited utilization as a timber species in Alberta, there has been some interest in Douglas-fir as an optional reforestation species for selected sites in the southwest. This is largely due to its ability to tolerate drought and its relative freedom from pests and disease. This interest was heightened in the mid to late eighties when serious mountain pine beetle (*Dendroctonus ponderosae*) attacks occurred in extensive stands of mature lodgepole pine (*Pinus contorta* Dougl. ex. Loud) and localized drought problems were encountered in establishment of white spruce (*Picea glauca* (Moench) Voss) plantations, these being the two major commercial timber species in the region. Although a modest operational seeding and planting program for Douglas-fir was started in the late nineteen eighties and early nineties, none of the nearly 80 million seedlings produced for the provincial reforestation program in 1994 were Douglas-fir, indicating a recent decline in interest.

Douglas-fir is one of the most extensively studied forest species and more genetics research is being done on it than on any of its associates (Silen 1978), however, there is limited knowledge or research on the genetics of Alberta populations. The present study is part of a larger project initiated by the Land and Forest Service in the mid to late eighties to address this deficiency through the study of variation in seed source and family performance of interior Douglas-fir tested on a variety of forest sites in southwestern Alberta (Figure 1). This study's specific objective, as part of the wider investigation, was to develop a better understanding of variation in the early growth and development of native populations of interior Douglas-fir and their relationship to geographical variables of seed source origin. This knowledge is important for guiding seed transfer, assessing the impact of environmental change on the adaptedness of populations, guiding gene resource management and accounting for patterns of phenotypic variation (Rehfeldt 1991).

The specific research objectives were achieved by investigating differences in third-year field survival, height, and plant health as well as bud-burst and bud-set timing of traits for eight native seed sources. The specific null hypotheses to be tested were:

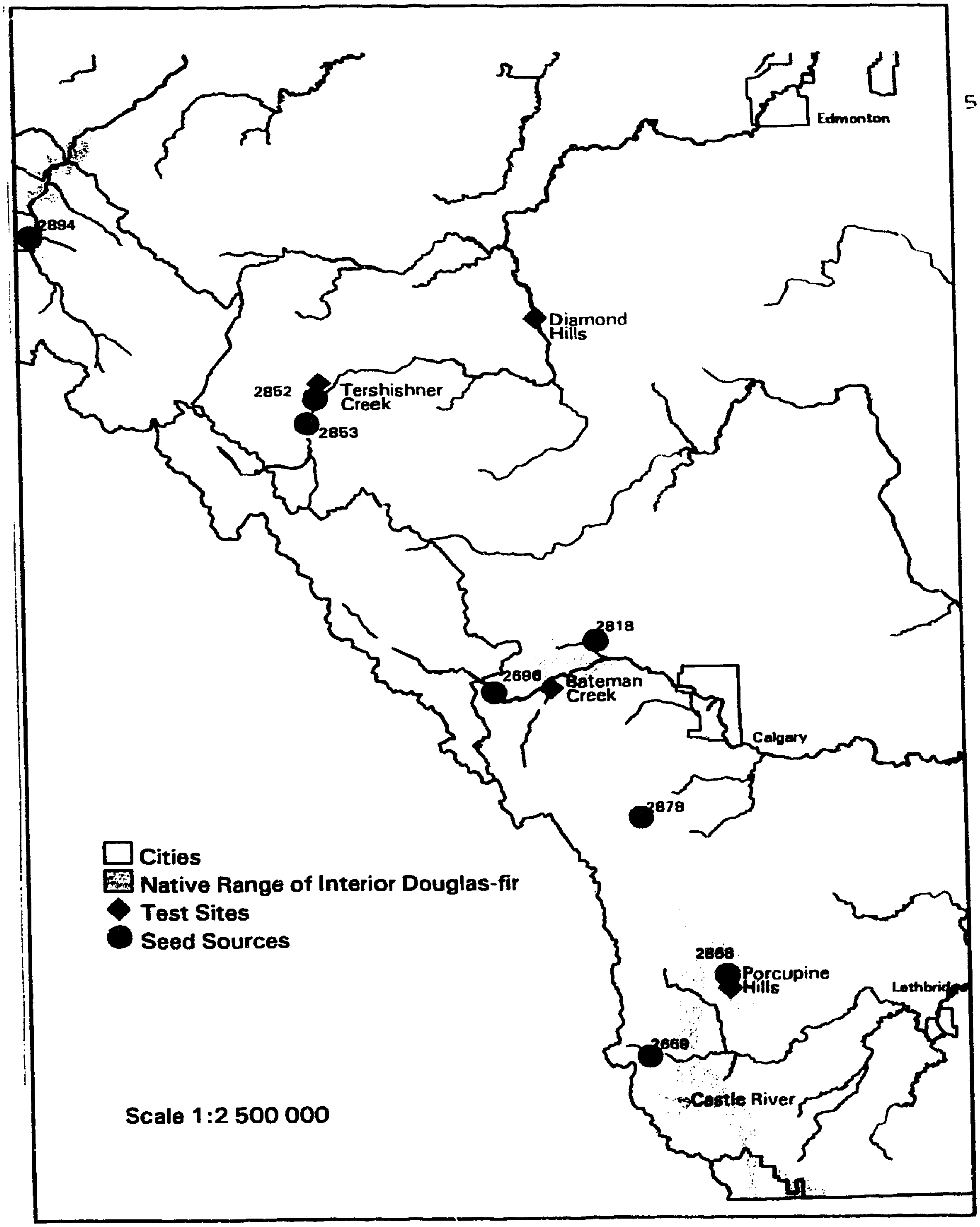


Figure 1. Native range, test sites and seed source locations for Douglas-fir in Alberta

Note: seed source reference numbers contained in Table 1

1. there are no seed source differences for the traits studied;

2. there are no clinal relationships between mean trait performance for sites and seed sources and geographic or climactic variables describing test sites or seed source origins.

II. LITERATURE REVIEW

A. Nomenclature

Douglas-fir was discovered by Archibald Menzies, a naturalist and ship's surgeon aboard Captain Vancouver's ship the Discovery on the west coast of Vancouver Island, British Columbia around 1792 (Hermann 1982). Its nomenclatural history has been convoluted with it being assigned at various times to five genera (*Pinus*, *Abies*, *Picea*, *Tsuga*, and *Pseudotsuga*) and seventeen species. Partial resolution of this impasse occurred in 1950 when a Portuguese botanist Franco, proposed *Pseudotsuga menziesii* (Mirb.) Franco as a replacement for the most common but controversial name, *Abies taxifolia* Poir. and the more obscure but valid name *Abies menziesii* Mirb. (Hermann 1982).

Problems associated with identifying and naming the species have also led to difficulty in agreement on naming varieties, which are still not resolved (Hermann 1982), although segregation into a few varieties has been accepted (Zavarin and Snajberk 1973). The coastal variety (*P. menziesii* (Mirb.) Franco var. *menziesii)* and interior or Rocky Mountain variety (*P. menziesii* var. *glauca* (Beissn.) Franco) are broadly recognized. However, in continental Europe, coastal Douglas-fir is known as var. *viridis* Aschers. and Graebn., the northern interior as var. *caesia* Aschers. and Graebn. and the southern interior as var. *glauca* Schneider (Zavarin and Snajberk 1973; Hermann 1982).

B. Taxonomy

Douglas-fir has all the morphological traits characteristic of the genus *Pseudotsuga,* which is distinguished by woody cones with persistent scales and protruding, trident like bracts. It has spindle shaped, pointed buds, soft narrow leaves, larch-like winged seed and resin blisters on smooth bark that becomes corky and furrowed with age (Hosie 1973; Silen 1978).

Distinguishing between the coastal and interior varieties is more difficult as no single morphological trait is reliable for identifying them. Generally, the interior variety differs visually from the coastal variety by having more bluish-coloured leaves, smaller cones, and a shorter more tapered form (Hermann and Lavender 1990). In addition to differences in morphological traits, the two varieties are also reported to differ in longevity, patterns and rates of growth (Orr-Ewing 1966; Irgens-Moller 1968), frost resistance and cold hardiness (Rehfeldt 1977) drought resistance, (Ferrell and Woodard 1966; Pharis and Ferrell 1966; Larsen 1979), cone producing age, fungus and insect resistance, wood and bark properties, length of time they retain needles, and odour of foliage and cortex (Zavarin and Snajberk 1973; Gower et. al. 1992).

C. Natural Range

Coastal Douglas-fir extends south from the north end of Vancouver Island along the Pacific coast for 2200 kilometres to central California. Interior Douglas-fir begins just north of Prince George in central British Columbia and extends south for 4500 kilometres to Mexico (Hermann and Lavender 1990). Over most of this distance the ranges of the varieties are parallel but independent (Figure 2) except for an extensive area of hybridization in central British Columbia and a lesser zone of intermediacy in north eastern and north central Washington, Northern Idaho and eastern Oregon (Little 1971; Zavarin and Snajberk 1973; Li and Adams 1989).

At the northern extreme of its range, coastal Douglas-fir stands occur from sea level to 760 metres in elevation , while in the south, they extend from sea level to 1670 metres. Elevations for the interior variety begin around 630 metres and range up to 2,600 metres over its continuous range from central British Columbia to southern Idaho and up to 3550 metres over its discontinuous range from Utah to Mexico (Hermann and Lavender 1990).

D. Ancestral History

Few clues to the evolutionary history of *Pseudotsuga* or its centre of origin are available, and whether the genus originated in North America or Asia is not known (Hermann 1985). It is generally accepted that Douglas-fir and bigcone Douglas-fir (*Pseudotsuga macrocarpa* (Vasey) Mayr) are the only North American species, but considerable controversy exists

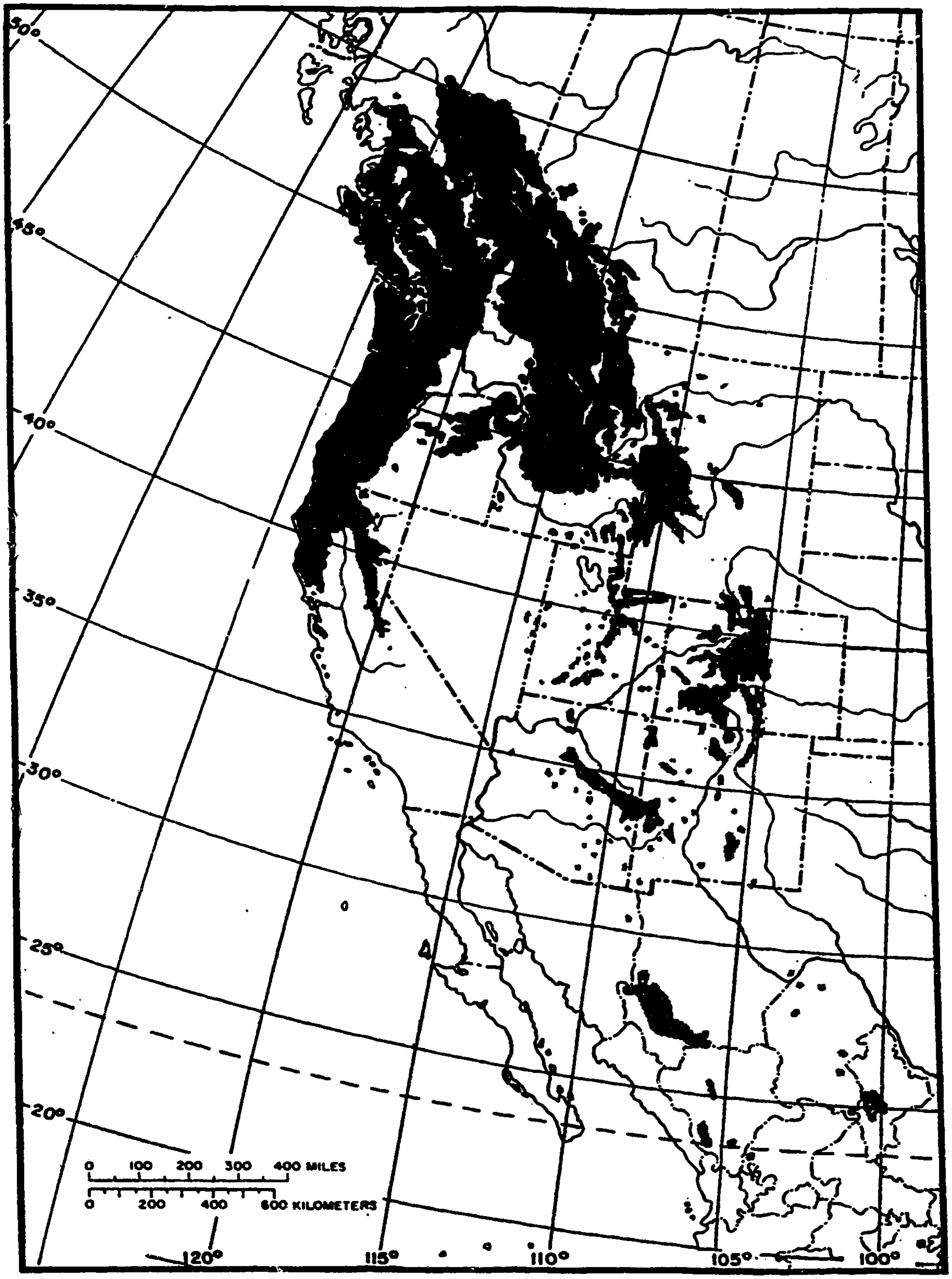


Figure 2. Native Range of Douglas-fir (after Little 1971).

regarding the number of Asian species (Doerksen and Ching 1972; Hermann 1982).

The first megafossils for the genus occur in the Tertiary period (approximately 64 million years before present), and the morphological characteristics of cones, seeds, and needles have changed little since then. Although it bears many morphological similarities to the larches, it is not known whether *Pseudotsuga* descended directly from the larches or branched from a common lineage to Pinus (Hermann 1985).

Throughout the Tertiary, and early Quaternary in North America, ancestral members of the genus *Pseudotsuga* including *Pseudotsuga sonomensis* Dorf., predecessor of *P. menziesii,* were distributed over much of the present day range of Douglas-fir except at higher latitudes where they extended considerably farther north (Hermann 1985). The main difference in the distribution of these ancestors and that of present day Douglas-fir is that they appear to have been a minor component in stands until the sudden dominance of *Pseudotsuga* in the Pleistocene (Hermann 1985).

The differentiation of Douglas-fir into coastal and interior varieties is an event whose time of occurrence is uncertain (Hermann 1985) but on the basis of a neutral gene model (Nei 1975) and allozyme variation, estimations suggest that the two varieties have been in existence for at least half a million years with divergence occurring in the middle Pleistocene (Li and Adams 1989).

E. Life Cycle

Flowering in Douglas-fir commonly begins at twelve to fifteen years and maximum cone production occurs between 200 and 300 years (Hermann and Lavender 1990). By September, in the year prior to seed production, egg shaped pollen cone buds can be distinguished from the larger seed cone buds and darker vegetative buds. Pollen cone primordia are usually clustered around the base of the extending shoot, with cone and vegetative primordia borne singly toward the end. All types are possible in intermediate positions (Allen and Owens 1972; Hermann and Lavender 1990).

Anthesis and pollination occur between March and June, and seed matures from mid-August to mid-September for the coastal variety, depending on latitude and elevation. Flowering in the interior variety occurs in mid-April to late June with cone ripening varying from late July to mid-August (Hermann and Lavender 1990).

Seed crops are cyclic with good cone crops occurring about every five years but with cycles varying between two and seven years. Variation in cone crops is more dependent on abortion and destruction of reproductive buds than on the numbers of reproductive primordia formed from year to year (Allen and Owens 1972; Hermann and Lavender 1990). Weather conditions during development, particularly precipitation, temperature and light appear to be important factors in determining cone crops (Allen and Owens 1972).

Germination of Douglas-fir is epigeal and occurs in mid-March to early April in warmer portions of its range and as late as mid-May in cooler portions. Seedling growth is slow and indeterminate in the first year and moisture stress often induces dormancy by midsummer (Hermann and Lavender 1990).

Seedling growth after the first year is determinate but usually slow except on good sites and in areas where lammas growth occurs. Once a seedling is well-established growth rates can reach up to one metre annually on good sites (Hermann and Lavender 1990), and rates of 61 centimetres per year can be sustained for a century with vigourous growth continuing up to 200 years (Silen 1978).

The longevity of the species and its phenomenal capacity for growth can lead to very high standing volumes of timber in pure, well-stocked stands. For the coastal variety, volumes in old growth stands have reached 5456 m^3/ha. The interior variety does not produce the same volumes and the upper limit is around 840 m^3/ha (Silen 1978).

F. Ecology

Douglas-fir is a montane species of mid latitudes and elevations. Within the heterogenous environments of the montane it is widely distributed but generally occurs in a mild and humid region with dry summers. Annual mean temperatures within its range generally vary from 7.2°C to 12.8°C with absolute maximum temperatures reaching 43°C and minimums -36°C (Issac and Dimock 1965).

It occupies both sedimentary and igneous parent materials of various textures and a range of site conditions (Issac and Dimock 1965), but best development occurs on well-aerated, moist, deep soils having a pH range of five to six (Silen 1978; Hermann and Lavender 1990). It does not thrive on poorly drained soils or soils with an impervious layer near the surface (Issac and Dimock 1965).

At lower elevations and in the southern portion of its range it is usually bounded by drought tolerant forests of ponderosa pine (*Pinus ponderosa* Laws) or mixed ponderosa pine and oaks (Brayshaw 1970; Bolsinger 1988). In these environments it prefers north aspects where moisture is more available and high temperatures are not as lethal to seedlings (Brayshaw 1970; Whitney 1985).

At higher elevations Douglas-fir gives way to more frost tolerant Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forests. At the northern extent of its range it is an associate of lodgepole pine (*Pinus contorta* Dougl.), white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill)

B.S.P.). In these environments it is generally limited by cold winter temperatures (Brayshaw 1970; Whitney 1985).

Being a fire adapted species, Douglas-fir's distribution is also strongly controlled by stand history. In the absence of fire, it is slowly replaced over several centuries by more shade-tolerant species (Hermann and Lavender 1990). However, due to its longevity over much of its range, Douglas-fir is often able to persist as a major component in stands much longer than average fire return intervals (Agee 1991).

Both varieties of Douglas-fir may function as either a seral or climax species in natural stands (Whitney 1985) and it is somewhat ironic that the greatest development and dominance occurs where it functions as a seral component and that climax status is generally achieved in mixed stands and peripheral environments.

G. Genetics

Douglas-fir is recognized as one of the most genetically diverse of forest tree species (National Council on Gene Resources 1982). This variation is substantial at all levels and appears to be in response to intense selection pressures of both a temporal and spatial nature (Campbell 1979; Rehfeldt 1983).

Speciation

The number of species comprising the genus *Pseudotsuga* is not yet established and varies from six (Orr-Ewing 1966; Thomas and Ching 1968) to in excess of ten (Martinez 1963). Douglas-fir and bigcone Douglas-fir are generally well accepted as the only two North American species and are distinguishable by the former having yellow-green rather than bluish-grey leaves, smaller cones, bracts which extend further beyond the bud scale, and less stalky form. Confusion is further made unlikely due to allopatric ranges with bigcone Douglas-fir being limited to a small area in southern California (Elias 1980). As a result of allopatric ranges, natural hybrids of these two North American species are unknown and although artificial hybrids have been successfully produced, crossability is rather low (Ching 1959).

The five generally recognized Asian species include Japanese Douglas-fir (*Pseudotsuga japonica* (Shirasawa) Beissner discovered between Kii and Yamato Province in Japan, Formosan Douglas-fir (*P. wilsoniana* Hayata) discovered on Mt. Morrison, Tiawan, Chinese Douglas-fir (*P. sinensis* Dode) first discovered in the Yunnan Province of southwestern China, Forrest's or long-budscale Douglas-fir (*P. forrestii* Craib) collected in 1914 by Forrest in the Mekong Valley at latitude 27°40'N and Eastern China yellow fir or dogstail tree (*P. gausseni* Flous) from Anhwei Province, China.

Information on these Asian populations is very incomplete as they are relatively rare and grow in terrain difficult to access (Hermann 1982). So far, attempts at crossing Douglas-fir with these Asian species have been unsuccessful (Silen 1978).

This difficulty in crossing may in part be due to Douglas-fir's unique karyotype which differs from that of all the other members of *Pseudotsuga* by having five metacentric, six subterminal, and two telocentric chromosomes in place of the six metacentric and six subterminal chromosomes typical for the family Pinaceae (Livingston 1971; Doerksen and Ching 1972; De-Vescovi and Sziklai 1975). This difference in karyotype would suggest chromosome breakage and that Douglas-fir is not only unique but the youngest member of the genus (Livingston 1971).

Varietal and regional variation

Several attempts have been made to aid the taxonomic classification of varieties through terpene and allozyme analysis. Rudloff (1972) stated that the two varieties can be reliably distinguished on the basis of volatile leaf terpenes. Zavarin and Snajberk (1973) using cortical monoterpene analysis and Li and Adams (1989) using allozyme analysis were both able to demonstrate differences between the coastal and interior varieties as well as between the northern interior variety *caesia* and southern interior variety *glauca*.

In Li and Adam's (1989) study, 51 percent of the genetic variation accounted for by populations was due to the two commonly recognized varieties, while 75 percent of population variation could be accounted for by classifying populations into coastal, southern interior and northern interior races. It also showed that the coastal and northern interior varieties had higher levels of expected heterozygosity than the southern interior variety but that the southern interior variety was characterized by greater population differentiation.

Population variation

Based on allozyme studies, Douglas-fir shows great genetic variability as expressed by the number of polymorphic loci and occurrence of rare alleles. Most of this variation (commonly greater than 90%) is reported to occur within populations (Yeh and O'Malley 1980; Merkle and Adams 1987; Li and Adams 1989; Westfall and Conkle 1992). In these studies, only weak clinal correlations with geographical variables are reported, unlike those for physiological traits (Merkle and Adams 1987; Li and Adams 1989), although Yeh and O'Malley (1980) using single loci and, more recently, Westfall and Conkle (1992) using multi locus analysis have described significant correlations with geographic variables.

In their range wide allozyme analysis of seed collected from 104 locations throughout the native range of Douglas-fir, Li and Adams (1989) found populations to be polymorphic at 37 percent of loci with a range of five to 65 percent and mean expected heterozygosity to be 0.137 with a range of 0.021 to 0.239. Generally, genetic diversity tended to decline toward the periphery of the species range. Differentiation among populations accounted for 24 percent of total genetic variation, which is higher than that reported by other studies, although these usually represented smaller geographic ranges. Based on genetic distance, one unique population collected from General Cepeda, Coahuila, Mexico (elevation 2500 m) and classified as *Psuedotsuga flahaulti* Flous by Martinez (1963) may warrant consideration as a separate species.

Micro evolution is also important in Douglas-fir. Performance is strongly controlled by the relationship between geographic variables and seed source and accounts for a high proportion of the total variability observed for adaptive and performance traits (Rehfeldt 1989). Statistical analysis of these strong geographic clines has provided evidence for latitude, elevation, location, and aspect races for both varieties of Douglas-fir (Hermann and Lavender 1968; Campbell 1979; Sorensen 1979; Rehfeldt 1979a; Rehfeldt 1982; Sorensen 1983). These clines can be so steep that seed transfer guidelines are critical to regeneration success (White *et al* 1981), and in some areas the risk of maladaption is sufficient to warrant encouragement of natural regeneration (Sorensen 1979).

Mating system

Douglas-fir is a monoecious, wind pollinated species and the proportion of outcrossed progeny is generally high (Shaw and Allard 1982; Omi and Adams 1986). Flowering is strongly influenced by spring temperatures with cooler temperatures generally being associated with a later and shortened breeding season (Copes and Sniezko 1991). The receptive period for female flowers of a given clone is six to eight days and pollen release is generally three to five days with most dispersal being complete after four days (Barner and Christiansen 1962; Ebell and Schmidt 1964; Owens *et al.* 1981; Copes and Sniezko 1991). Substantial differences occur in the timing of flowering between clones, and in a wind pollinated orchard of twenty clones in Oregon, Copes and Sniezko (1991) found that the breeding season varied from sixteen to twenty-seven days depending on spring weather conditions.

Twenty-five percent to 75 percent of all pollen catch is composed of a tree's own pollen but this leads to only about 7 percent selfed seed in an average seedlot (Orr-Ewing 1954). Individual trees may vary in the amount of filled seed they produce through selfing from 2 percent to more than 20 percent (Sorensen 1973; Sorensen and Miles 1974). This selfing in Douglas-fir has been found to lead to inbreeding depression and in one study by Sorensen and Miles (1982) led to an inbreeding depression of 15.6 percent for second year survival and 29.0 percent for ten year height.

III. MATERIALS AND METHODS

A. Seed Collections

Open-pollinated bulk seed collections were made from eight naturally occurring merchantable stands of interior Douglas-fir from along its continuous range in the southwestern foothills and from its discontinuous range in isolated mountain corridors to the north (Figure 1). These collections represented the full range of latitudinal and elevational distribution for Douglas-fir in Alberta (Table 1) with the exception of non-merchantable Douglas-fir forest types occurring on steep rocky outcrops and high elevation southerly aspects in the subalpine. Four of the collections were made from ten or more trees, one from five trees, one from a single tree and two from hand picked cones taken from several squirrel caches in larger stands (Appendix A).

Table 1. Geographic origin of seed sources

	Location			
Seed source *Accession #*	Latitude (°N)	Longitude (°W)	DECD* (km)	Elevation (m)
Crowsnest Pass *(2669)*	49°31'	114°26'	11.0	1370
Porcupine Hills *(2868)*	49°52'	114°02'	46.8	1600
Marston Creek *(2878)*	50°25'	114°30'	25.9	1615
Canmore Corridor *(2696)*	51°05'	115°20'	33.4	1340
Ghost River *(2818)*	51°17'	114°44'	99.4	1465
Alstone Creek *(2852)*	52°17'	116°22'	60.6	1280
Cline River *(2853)*	52°11'	116°26'	99.8	1400
Edith Lake *(2894)*	52°55'	118°05'	36.1	1065

* Distance east from the Continental Divide

Seeds were sown in Hillson containers (175 cc) in January of 1990 and grown in the greenhouses at the Genetics and Tree Improvement Centre at Smoky Lake. A standard growing regime was used with a day temperature of 25° C, a night temperature of 16° C and a photoperiod of eighteen hours. In mid June the stock was moved out of the greenhouse to shade frames to harden-off and was then shipped to the Elbow Ranger Station and placed in heel-in beds to overwinter. In mid May of 1991, the stock was pulled from the heel-in beds at the Elbow Ranger Station, sorted and out-planted within a week at five ecologically diverse test sites in and adjacent to the Montane Natural Subregion (Alberta Environmental Protection 1994).

B. Field Test Sites

The five test sites selected for establishing the trials reflected a wide range of environments found within and adjacent to the natural range of interior Douglas-fir in the province (Figure 1) (Tables 2 and 3). All test sites had naturally occurring stands of pure or mixed Douglas-fir in the vicinity except Diamond Hills which is located approximately 85 kilometres east of the nearest identified area of occasional occurrence. A more complete description of individual field test sites is provided in Appendix B.

The field layout design for trials included establishment of five identical trials on the five sites. Field layout design for each site was randomized complete block with six blocks per site. Each of the eight seed sources within a block was established as a square and contiguous 25-tree plot with trees planted at 2.5 metre tree spacing.

Table 2. Geographic location of test sites

	Location		
Test Site	Latitude	Longitude	Elevation
Castle River	49°23'	114°20'	1350
Porcupine Hills	49°53'	114°01'	1670
Bateman Creek	51°03'	114°49'	1450
Tershishner Creek	52°19'	116°23'	1400
Diamond Hills	52°37'	115°05'	990

Due to stock shortages at the time of out-planting, several modifications to the layout design were made. The Ghost River source was only included in the Castle River and Bateman Creek trials and the Canmore source was not planted in the Diamond Hills trial and only established in two of six blocks at the Tershishner Creek site. The Cline River and Alstone Creek seed sources were established on all sites but only in five of six blocks in the Porcupine trial. The remaining four seed sources were established in all blocks at all sites.

Table 3. Natural Subregion classification and selected climatic characteristics of field test sites

Test site	Region	MAT (°C)	MST (°C)	MAP (mm)	MSP (mm)	GDD	FFP
Castle River	Montane	3.0	12.9	852.0	181.1	1087	39
Porcupine Hills	Montane	N/A	13.2	N/A	183.3	N/A	72
Bateman Creek	Lower Foothills	1.4	11.4	610.7	249.4	822	17
Tershishner Creek	Montane	2.2	13.1	486.2	183.6	1036	72
Diamond Hills	Lower Foothills	2.6	14.1	556.1	274.6	1245	100

MAT mean annual temperature
MAP mean annual precip.
GDD growing degree days >5°C
MST mean summer temperature (June-July-August)
MSP mean summer precip. (June-July-August)
FFP frost free period in days.

Trials were established within existing genetics experimental areas, which are fenced for protection from animal damage. Vegetative competition was controlled initially by double discing, and subsequent to planting, by hand weeding in late June or early July.

C. Measurements

Measurements for the main variables of interest were taken in the third field growing season (1993). Bud-burst data were collected in early May through June and bud-set scores were taken from mid July to early September. Survival, plant-health scores and three-year field height measurements were made in late September through early October.

Survival was assessed by examining all trees in each plot and scoring them as dead or alive. Trees were scored as alive if any living needles were visible on the main stem or any basal shoots. Trees were scored as dead where there was no sign of living needles or buds. Survival was expressed as the percent of living trees per 25-tree plot.

Third- year field height of each living seedling was measured as stem length in mm from the ground surface to the tallest living tip. Height to the terminal bud could not be used due to extensive frost damage and dieback in several of the plantations.

As height performance is not always a valid measure of adaptiveness (Rehfeldt 1983), a subjective plant health scoring system based on ocular assessment and six classes was developed. The objective was to determine if this scoring system could be used to distinguish differences in general plant health and fitness between seed sources and trial sites independent of height performance. The plant- health score was based on observation of the following characteristics for each tree:

1. signs of climatic damage to needles, buds or shoots;
2. foliage colour;
3. needle length;
4. living biomass;
5. shoot diameter;
6. bud size.

Based on these characteristics, an aggregate score was assigned to each experimental tree according to the scoring system outlined in Appendix C, Table C1, with the healthiest trees receiving a score of six and the unhealthiest a score of one.

For assessing bud-burst day, a subset of five trees per 25-tree plot for each block, seed source and trial were selected on which to assess the date of bud burst. Trees were selected systematically starting at the beginning of each block. The first five living trees having five or more healthy buds were selected and marked. As with three-year height, terminal buds could not be used for assessment due to extensive die-back and frost damage on several test sites.

Bud-burst commencement was scored on each of the five trees per plot as the number of days after April thirtieth when bud scale separation and needle protrusion first occurred on one or more buds in the upper two thirds of the crown. Trees were observed and scored every third day with allowance for interpretation of bud burst initiation and completion date one day forward or one day back from the observation date.

Bud-set timing was scored on the same subset of trees as bud burst. As bud development and bud set are a slow process, observations for each trial were made sequentially on a weekly basis from July fourteenth through September tenth. An average bud development score from zero (no sign of bud development) to three (majority of buds completely set) based on buds in the upper two thirds of the crown of each selected tree was used to trace bud development during each weekly assessment. A more detailed description of the scoring system for bud set is provided in Appendix C, Table C2.

During bud-set monitoring, it was determined that many seedlings experienced a second flush. As a result, the bud-set scoring system was modified and trees with a flushing terminal or several flushing laterals were given a score of four followed by a second score of one through three to reflect bud development after the second flush. For analysis, trees experiencing a second flush were assigned a score of 2.5 until the reflushing buds were set whereupon they were again assigned a score of three. This was done to reflect the renewed growth activity which implies a lack of complete bud set and dormancy, and is similar to methods used by Sorensen (1983).

D. Testing of Assumptions

The SAS univariate procedure (SAS Institute Inc. 1988) was used to check for outliers and proper frequencies of observations for both the original data set and compiled plot mean files. The Shapiro-Wilk statistic generated by the SAS univariate procedure (SAS Institute Inc. 1988) was used for checking the assumption of normality. As an additional test, residuals output from the General Linear Model procedure (SAS Institute Inc. 1988) for traits were plotted against predicted values and rank for residuals as a visual check that residuals appeared randomly distributed, to have constant variance and were independent of predicted values.

E. Analysis of Variance and Comparison of Means

In order to test the hypothesis that there were no differences in seed sources for the five traits of interest, analyses of variance (ANOVA) was performed on plot means for both individual test sites as well as the across-site analyses. The SAS Type IV General Linear Model (GLM) procedure (SAS Institute Inc. 1988) was used as the data were not balanced and there were missing cell values. F-test probabilities produced by these runs were then used to determine if at least one of the seed sources was significantly different ($P<0.05$) for any of the traits. The model used was:

$$Y_{ijkl} = \mu + S_i + B(S)_{j(i)} + A_k + AS_{ik} + \varepsilon_{ijk}$$

where:

Y = an observed value for the dependent variable
μ = the overall mean for the dependent variable
S = a deviation due to the mean for site i
$B(S)$ = a deviation due to the mean for block j within site i
A = a deviation due to the mean for seed source k
AS = an interaction deviation due to source k on site i
ε = an interaction deviation ($A * B(S)_{kj(i)}$)

The analysis of variance format and expectation of the mean sums of squares (Table 4) assuming equal numbers was based on a multi-way, completely randomized, model (Steel and Torrie 1960).

SAS GLM Type IV expected mean squares were generated for use in calculating variance components due to the imbalance and missing observations. Variance components were calculated following Model II, Method 2 (Henderson 1953).

Table 4. Theoretical analysis of variance format and expectation for the mean sums of square for the across-site analyses

Source of Variation	d.f.	Expected Mean Squares
Site	3	$1\sigma^2_\varepsilon + 6\sigma^2_{AS} + 8\sigma^2_{B/S} + 48\sigma^2_S$
Block/Site	20	$1\sigma^2_\varepsilon + 8\sigma^2_{B/S}$
Seed source	7	$1\sigma^2_\varepsilon + 6\sigma^2_{AS} + 24\sigma^2_A$
Seed source *Site	21	$1\sigma^2_\varepsilon + 6\sigma^2_{AS}$
Source*Block/Site	140	$1\sigma^2_\varepsilon$
Total	191	
N	192	

Where the F-test was significant for the main effect seed source, the null hypothesis was rejected and multiple comparison of least square means (LSM) was performed on the data using the Pdiff option under the least square means statement of the SAS GLM procedure (SAS Institute Inc. 1988). This method was used as it is suitable for use on data having missing cell values and unbalanced cell sample sizes. It is a multiple t-test which tests all possible probability values for the hypothesis:

Ho: that least square mean_i equals least square mean_j
Ha: that least square mean_i does not equal least square mean_j

Individual site ANOVA'a were run using the following model:

$$Y_{ij} = \mu + B_i + A_j + \varepsilon_{ij}$$

where:

Y = an observed value for the dependent variable
μ = the overall mean for the dependent variable
B = a deviation due to the mean for block i
A = a deviation due to the mean for seed source j
ε = a deviation due to the interaction of $A_j * B_i$.

The analysis of variance format and expectation of the mean sums of squares assuming a completely randomized model for these analyses is given in Table five.

Table 5. Theoretical analysis of variance format and expectation of the mean sums of squares for individual trial analyses

Source of variation	d.f.	Expected mean squares
Block	5	$1\sigma^2_\varepsilon + 8\sigma^2_B$
Seed Source	7	$1\sigma^2_\varepsilon + 6\sigma^2_A$
Seed source*Block	35	$1\sigma^2_\varepsilon$
Total	47	
N	48	

F. Correlations and Regressions

The second research objective was to test if trait expression for sites and seed sources was clinally related to geographic or climatic variables associated with seed source origin or test site. The first step was to explore site relationships. The SAS correlation procedure (SAS Institute Inc. 1988) was used to compute all possible combinations of trait means for sites with climatic and geographic variables describing test sites (Table 2 and 3). This procedure provided simple Pearson product-moment correlations and significance probabilities for linear relationships.

The second step taken was to explore relationships between mean trait values of seed sources and geographic variables of seed source origin. Only geographic variables (Table 1) were used as adequate climatic data representative of seed source origins were not available. All possible simple correlations between the least square means for sources (generated from the across site analysis of variance) and the geographic variables describing seed source origin were tested.

Once this was completed, linear and multiple linear regressions for seed source means were run to further explore the nature of relationships between variables. The form of the linear models was:

$$Y = b_o+b_1X_1,$$

and

$$Y = b_o+b_1X_1+b_2X_2,$$

where:

Y = a predicted value
bo= the intercept
X1= the first predictor variable
b1= a slope coefficient for predictor variable X1
X2= the second predictor variable
b2= a slope coefficient for predictor variable X2

As adaptive clines are commonly non-linear (Rehfeldt 1989), polynomial regressions were also run with geographic variables of origin to determine if any significant relationships could be detected. The model used was:

$$Y = bo+b_1X_1+b_2X_1^2$$

where:

Y = a predicted value
bo = the intercept
b_1 = a coefficient for geographic predictor X_1
X_1 = a geographic predictor variable

b_2 = a coefficient for the square of geographic predictor X_1

X_1^2 = the square of geographic predictor variable X_1

G. Principle Component Analysis

As a last step, principle component analysis was applied to across site adjusted least square means for traits to investigate and summarize polynomial relationships between performance, phenological and geographic variables. The SAS principle component procedure (SAS Institute Inc. 1988) was used for the analysis according to the following model:

$$Y=XB+\varepsilon$$

where:

Y = an *nxp* matrix of the centred observed variables

X = the *nxj* matrix of scores on the first *j* principle components

B = is the *jxp* matrix of eigenvectors

ε = an *nxp* matrix of residuals

IV. RESULTS

A. Site and Seed Source Trait Relationships

Survival on the Bateman Creek site was so poor (3.9%) that it could not be assessed for bud-burst and bud-set timing and only provided 14 reliable plot means out of a potential 48 for other traits. As a result, this test site was dropped from the across site analyses for all traits except percent survival.

Both performance and phenological traits were greatly influenced by test sites. Calculation of variance components showed that site accounted for a minimum of 77.5 percent and maximum of 92.1 percent of total variation for the five traits studied (Tables 6,10,14,18,and 22). Block replications within sites indicated much greater environmental homogeneity explaining only 0.0 percent to 1.0 percent of total variation.

Contrasts of performance traits between the northern test sites (Tershishner Creek and Diamond Hills) and the southern ones (Castle River and Porcupine Hills, and in the case of percent survival, Bateman Creek) were consistently significant with the northern sites demonstrating better mean survival (97.6 vs. 37.3 percent), three-year height growth (33.5 vs. 19.7 cm) and plant-health score (5.3 vs. 3.0). These contrasts were included in the analysis after observations during field assessment which showed dramatic differences in survival, plant health and growth between northern and southern sites.

In the analyses of variance, significant F-tests ($P < 0.05$) for the main effect seed source were found for all traits in the across site analyses and significant seed source by site interactions were recorded for percent survival and bud-burst day (Tables 6,10,14,18 and 22). F-tests for seed sources on individual test sites were significant for four of five sites for percent survival, all sites for three-year height and bud-burst day, three of four for plant-health score, and two of four for bud-burst week (Appendix E).

Survival

The W statistic test for normalcy of plot means for percent survival ranged from 0.740 to 0.982 for individual test sites and was 0.825 for the across-site analysis. The value recorded for the across-site analysis appears to have been lower than for three of the individual test sites, due to the extreme difference in survival rates for northern and southern sites (Appendix D, Figure D1). Plots of residuals against predicted percent survival and residuals by rank did not indicate any pattern or trend that would indicate serious violation of the assumption of constant variance or independence of observations (Appendix D, Figures D1 and D2).

All effects tested in the across-site analysis had significant ($P< 0.05$) F-test values (Table 6). Calculation of variance components indicated that sites explained the greatest proportion of total variation (86.8%) followed by interaction between seed sources and sites (5.6%), seed sources (2.8%) and replications within sites (1.0%).

Table 6. Mean squares, F-test probabilities and variance components for analysis of variance of percent survival

Source of variation	d.f.	Mean Square	F-test prob.	Variance component
Sites	4	53605.7	0.0001	86.8%
Reps/sites	25	188.9	0.0001	1.0%
Sources	7	2288.7	0.0065	2.8%
Sources*sites	24	613.2	0.0001	5.6%
Error	149	65.4		3.8%
Corrected total	209			

Although the F-test showed significant seed source by site interaction, rank correlation coefficients for seed sources among test sites (Table 7) generally showed significant positive correlation coefficients for seed source performance among sites. This would seem to indicate that, although there was interaction, it did not lead to a significant change in rank of sources among most sites.

Table 7. Rank correlation coefficients for seed sources among test sites for percent survival

Test site	Porcupine Hills	Bateman Creek	Tershishner Creek	Diamond Hills
Castle River	0.58*	0.48*	0.44*	0.33*
Porcupine Hills		0.47*	0.52*	0.24
Bateman Creek			0.13	0.13
Tershishner Creek				0.43*

* Significant at $P< 0.05$

Notably, the coefficients between the Castle test site and all others were significant (Table 7), which along with the results of the comparison of means tests (Table 9), indicates the effectiveness of this site in testing for differences in survival performance between sources.

Mean survival (Table 8) varied dramatically among test sites (3.9% to 97.8%), and the contrast of means between northern sites (Tershishner Creek and Diamond Hills) versus southern sites was also significant ($p<0.05$) with an average survival of 97.6 percent versus 37.3 percent.

Table 8. Least square means and standard errors for percent survival, and performance of test sites as a percent of the across-site (overall) mean

Test site	Survival (%)	s.e. (%)	Percent of overall mean
Castle River	61.6	1.7	100
Porcupine Hills	46.4	2.0	76
Bateman Creek	3.9	1.7	6
Tershishner Creek	97.8	2.0	159
Diamond Hills	97.5	2.1	159
Across sites	61.4	2.6	

Variation in mean percent survival was also quite dramatic for seed sources in the across-site analysis (Table 9) and ranged from 77.4 percent (26% above the overall mean) for the Ghost River source to 44.9 percent (27% below the overall mean) for the Lake Edith source.

Although the Ghost provenance had the highest survival rate in the across-site analysis, it was not significantly better than that for the Marston Creek source (Table 9). This may in part be due to the larger standard error for the Ghost source, which was only established on two of the five test sites. These two seed sources also consistently ranked first or second on the individual test sites (Appendix F, Table F1).

Table 9. Least square means and standard errors for percent survival and performance of seed sources as a percent of the across site (overall) mean

Seed source	Survival (%)	s.e. (%)	Percent of overall mean
Crowsnest Pass	64.5_b	2.2	105
Porcupine Hills	66.9_b	2.2	109
Marston Creek	69.9_{ab}	2.2	114
Canmore Corridor	56.0_c	2.7	91
Ghost River	77.4_a	3.6	126
Cline River	57.5_c	2.2	94
Alstone Creek	54.3_c	2.2	88
Lake Edith	44.9_d	2.2	73

Least square means having the same subscript letter are not significantly different at $P<0.05$

The Lake Edith source, which showed significantly poorer survival in the across-site analysis (Table 9), also consistently ranked last in the individual test site analyses (Appendix F, Table F1). This source is unique in its poor survival overall as well as on individual test sites, where at times it was the only significantly different source.

The mean comparison test for the across-site analysis (Table 9) also clearly demonstrates that southern sources survived significantly better than northern sources. This pattern is consistent with rankings produced by the individual test sites as well (Appendix F, Table F1).

Height

The W statistic test for normalcy of plot means for three-year height on individual test sites ranged from 0.973 to 0.985 and was 0.958 for the across-site analysis. Plots of residuals against predicted values and residuals by rank showed no trend or pattern that indicated violation of the assumption of constant variance or independence of observations (Appendix D, Figures D3 and D4).

Only site and seed source effects had significant F-test values in the across-site analysis for three-year height. Calculation of variance components indicated that 77.5 percent of total variation was explained by site effects and 8.4 percent by source effects (Table 10).

Table 10. Mean squares, F-test probabilities and variance components for analysis of variance of 3-year height

Source of variation	d.f.	Mean Square	F-test prob.	Variance component
Sites	3	228324.2	0.0001	77.5%
Reps/sites	20	752.7	0.7949	0.0%
Sources	7	15505.6	0.0001	8.4%
Sources*sites	17	1768.1	0.0526	1.5%
Error	114	1040.4		12.6%
Corrected total	161			

Rank correlations performed on seed sources among sites (Table 11) showed significant coefficients for sources between most sites. This along with F-test results would indicate small differential changes generally with most rank changes occurring between the Castle test site and others.

Table 11. Rank correlation coefficients of seed sources among test sites for 3-year height

Test site	Porcupine Hills	Bateman Creek	Tershishner Creek	Diamond Hills
Castle River	0.29	-	0.25	0.55*
Porcupine Hills		-	0.32*	0.44*
Bateman Creek			-	-
Tershishner Creek				0.45*

* Significant at $P< 0.05$

The range of least-square mean values for three-year height for individual test sites was 19.7 centimetres to 35.2 centimetres (Table 12), with the two southern sites showing

Table 12. Least square means and standard errors for 3-year height and performance of test sites as a percent of the across site (overall) mean

Test site	Height (cm)	s.e. (cm)	Percent of overall mean
Castle River	19.7	4.8	74
Porcupine Hills	19.7	5.7	74
Tershishner Creek	31.8	5.8	120
Diamond Hills	35.2	6.1	132
Across sites	26.6	6.4	

identical mean growth performance. As with percent survival, average performance for mean three-year height as determined by performing a contrast was significantly better on northern test sites (33.5 cm) than southern sites (19.7 cm). Notably, the best mean height growth was achieved on the test site furthest from Douglas-fir's native range (Diamond Hills) while the worst performance was recorded for the two sites within an area of its widest natural distribution.

Least square means for seed sources ranged from a maximum of 31.7 centimetres (19% above the overall mean) for the Lake Edith source to a minimum of 22.9 centimetres (14% below the overall mean) for the Marston source (Table 13).

Mean comparison tests showed the Lake Edith seed source to be taller and different from all other sources in the across-site analysis (Table 13) as well as on two of the four individual test sites (Appendix F, Table F2). In terms of rank, it was first on all but the Tershishner Creek site, where the mean for the Canmore source was higher but not significantly so.

The Marston Creek source was found to be significantly shorter in the across-site analysis (Table 13) and ranked last or second last in four of the five individual trial analyses (Appendix F, Table F2). In rank it was followed closely by the Ghost River source which was only slightly taller (23.5 cm vs. 22.9 cm). The remaining four sources (Crowsnest, Porcupine, Cline and Alstone) were very similar in performance and not significantly different with means ranging between 26.1 centimetres and 26.8 centimetres.

Table 13. Least square means and standard errors for 3-year height and performance of seed sources as a percent of the across site (overall) mean

Seed source	Height (cm)	s.e. (cm)	Percent of overall mean
Crowsnest Pass	26.1_{cd}	0.7	98
Porcupine Hills	26.4_{cd}	0.7	99
Marston Creek	22.9_{e}	0.7	86
Canmore	29.1_{b}	0.9	111
Ghost River	23.5_{d}	1.4	88
Cline River	26.8_{bc}	0.7	101
Alstone Creek	26.2_{cd}	0.7	99
Lake Edith	31.7_{a}	0.7	119

Least square means having the same subscript letter are not significantly different at P<0.05

Simple correlations performed on seed source means showed a strong and significant negative relationship (r= -0.88) between percent survival and three-year height indicating a strong tendency for faster growing sources to have poorer survival.

Plant health

The W statistic test for normalcy of plot means for plant-health score on individual test sites ranged from 0.928 to 0.982 while for the across site analysis it was 0.856. As with survival, the separation in the plot of residuals against predicted values (Appendix D, Figure D5) indicates that the lower across-site value is likely due to the higher health scores recorded for northern versus southern sites. This plot also indicates a slight trend toward greater variance for residuals at higher predicted values. The plot of residuals by rank (Appendix D, Figure D6) and the distribution of error deviations in the residuals by predicted values plot show no trend or pattern that would indicate serious violation of the assumption of independence of observations.

Both sites and seed sources had significant F-test values

(Table 14). From variance component calculations, site accounted for 92.1 percent of total variation while seed sources accounted for 1.2 percent. Seed source by site interactions were not found to be significant.

Table 14. Mean squares, F-test probabilities and variance components for analysis of variance of plant-health score

Source of variation	d.f.	Mean Square	F-test prob.	Variance component
Sites	3	66.02111	0.0001	92.1%
Reps/sites	20	0.13926	0.3454	0.1%
Sources	7	0.67281	0.0109	1.2%
Sources*sites	17	0.17729	0.1406	0.4%
Error	114	0.12450		6.2%
Corrected total	161			

Although seed source by site interactions were not significant as determined by the F-test, low rank correlation coefficients (Table 15) imply frequent changes in rank among sites. This can be readily confirmed by observation of changes in ranking among sites for seed sources in the individual test site analyses (Appendix F, Table F3) and would tend to imply that small amounts of variation were causing frequent changes in rank.

Table 15. Rank correlation coefficients for seed sources among test sites for plant-health score

Test site	Porcupine Hills	Bateman Creek	Tershishner Creek	Diamond Hills
Castle River	0.10	-	0.23	0.33
Porcupine Hills		-	0.02	0.13
Bateman Creek			-	-
Tershishner Creek				0.41*

* Significant at $P < 0.05$

Mean plant-health scores for individual test sites ranged from 2.74 for the Castle River site to 5.45 for the Diamond Hills site (Table 16). As with survival and three-year height, the contrast between the two northern and southern sites showed northern sites to have significantly higher plant health scores. In terms of the plant health, scoring system, (Appendix C, Table C1), mean plant-health scores for sites indicate that all sources of Douglas-fir were better adapted to northern than southern test sites. In general, all sources were performing well on northern sites while on the two soutnern sites health and vigour were poor and seedlings have experienced significant set back and are showing only weak recovery.

Table 16. Least square means and standard errors for plant-health score and performance of test sites as a percent of the across site (overall) mean

Test site	Plant-health score	s.e.	% overall mean
Castle River	2.74	0.05	66
Porcupine Hills	3.17	0.06	78
Tershishner Creek	5.13	0.06	124
Diamond Hills	5.45	0.06	132
Across sites	4.12	0.10	

Adjusted least square means for seed sources tested across sites ranged from 3.89 (4 percent below the overall mean)for the Alstone Creek seed source to 4.33 (7 percent above the overall mean) for the Crowsnest Pass source (Table 17).

Mean comparison tests did not distinguish a single seed source with a significantly better or poorer mean plant-health score in individual or across-site analyses (Table 17; Appendix F,

Table F3). However, there is a trend in both the across-site and individual-site analyses for southern sources to have better (higher) plant-health scores and in the across site analysis, for southern corridor sources to have significantly higher scores than northern corridor sources, with southern foothills sources being intermediate (Table 17).

Table 17. Least square means and standard errors for plant-health score and performance of seed sources as a percent of the across site (overall) mean

Seed source	Plant-health score	s.e.	% overall mean
Crowsnest Pass	4.33_{a}	0.07	107
Porcupine Hills	4.28_{a}	0.07	106
Marston Creek	4.13_{ab}	0.07	102
Canmore	4.30_{a}	0.10	106
Ghost River	4.20_{ab}	0.16	104
Cline River	3.94_{bc}	0.08	98
Alstone Creek	3.89_{c}	0.08	96
Lake Edith	3.94_{bc}	0.07	98

Least square means having the same subscript letter are not significantly different at $P<0.05$

Bud burst

The W statistic test for normalcy of plot means for bud-burst day on individual test sites ranged from 0.880 to 0.946, while the W statistic for the across-site analysis was 0.954. The plot of residuals against predicted values indicates a definite trend for error deviations to increase with later bud burst (Appendix D, Figure D7). Otherwise, the plots of residuals by predicted values and residuals by rank show no trend or pattern that indicates serious violation of the assumption of constant variance or independence of observations (Appendix D, Figures D7 and D8).

Site, seed source and seed source by site interactions all had significant F-test values for bud-burst timing (Table 18).

Table 18 Mean squares, F-test probabilities and variance components for analysis of variance of bud-burst day

Source of variation	d.f.	Mean Square	F-test prob.	Variance component
Sites	3	594.47	0.0001	79.7%
Reps/sites	20	2.59	0.0877	0.6%
Sources	7	44.55	0.0001	10.0%
Sources*sites	17	3.51	0.0133	1.5%
Error	114	1.70		8.2%
Corrected total	161			

Calculation of variance components indicated that sites explained the greatest proportion of total variation (79.7%), followed by sources (10.0%) and seed source by site interactions at (1.5%).

Although the F-test indicated significant seed source by site interactions, these would appear to be largely due to differential changes in bud-burst timing of sources which did not lead to changes in rank, as correlation coefficients for seed source ranks among sites were all significant ranging from 0.34 to 0.99 (Table 19).

Table 19. Rank correlation coefficients for seed source means among test sites for bud burst day

Test site	Porcupine Hills	Bateman Creek	Tershishner Creek	Diamond Hills
Castle River	0.54*	-	0.35*	0.34*
Porcupine Hills		-	0.80*	0.99*
Bateman Creek			-	-
Tershishner Creek				0.70*

* Significant at $P< 0.05$

The coefficient between the Porcupine and Diamond Hills sites at 0.99 is particularly interesting as the mean number of days after April thirtieth to bud-burst is quite different for these two sites.

The mean number of days after April thirtieth when bud burst occurred on sites varied substantially from 12.5 days on the Diamond Hills site to 21.5 days on the Tershishner Creek site (Table 20), a range of nine days. Unlike the pattern for performance traits where northern sites differed from southern sites for bud-burst timing, the Porcupine Hills and Tershishner Creek sites appear most similar.

Table 20. Least square means and standard errors for bud-burst day and performance of test sites as a percent of the across-site (overall) mean

Test site	Bud burst (day)	s.e. (day)	% overall mean
Castle River	16.2	0.2	92
Porcupine Hills	20.3	0.2	115
Tershishner Creek	21.5	0.2	122
Diamond Hills	12.5	0.2	71
Across sites	17.6	0.3	

Adjusted least square means for days to bud burst for seed sources in the across site analysis ranged from 15.8 days (10% below the overall mean) for the Cline River source to 20.1 days (14% above the overall mean) for the Crowsnest source (Table 21).

Table 21. Least square means and standard errors for bud-burst day and performance of seed sources as a percent of the across-site (overall) mean

Seed source	Bud burst (day)	s.e. (day)	% overall mean
Crowsnest Pass	20.1_{a}	0.3	114
Porcupine Hills	17.7_{c}	0.3	100
Marston Creek	16.9_{de}	0.3	96
Canmore	17.9_{bc}	0.4	102
Ghost River	17.8_{bcd}	0.6	101
Cline River	15.8_{f}	0.3	90
Alstone Creek	16.4_{ef}	0.3	93
Lake Edith	18.7_{b}	0.3	106

Least square means having the same subscript letter are not significantly different at $P<0.05$

In the across-site analysis, the Cline River and Alstone Creek sources were significantly earlier as a group than all other sources except the Marston Creek source, while the Crowsnest Pass seed source was significantly slower (Table 21).

The consistent ranking of sources across sites as indicated by the rank correlations is also apparent from observation of rankings of sources for individual test sites (Appendix F, Table F4). In these analyses, the Crowsnest source is consistently last and significantly later for all but the Tershishner test site, while the Lake Edith source is always the second last source to burst bud. Consistent with the across site analysis, the Alstone Creek and Cline River sources were consistently first or second to burst bud.

Bud-burst day was found to be significantly correlated with bud-set week (r= 0.73) indicating that sources which burst bud early also tended to set bud early and vice versa. This would indicate that growth duration for sources was similar (early flushing sources also tended to set bud early) but that growth occurred at different periods within the growing season.

Bud set

The W statistic test for normalcy of plot means for bud-set week on individual test sites ranged from 0.632 to 0.924 while for the across site analysis it was 0.869. The plot of residuals against predicted values and plot of residuals by rank shows no trend or pattern that indicates violation of the assumptions of constant variance or independence of observations (Appendix D, Figure D9 and D10).

Sites, seed sources, and replications within sites all had significant F-test values for bud-set timing. Seed source by site interactions were not significant (Table 22). Calculation of variance components showed that site effects explained the largest portion of total variation (79.8%) followed by seed sources (3.9%) and replications within sites (1.7%).

Table 22. Mean squares, F-test probabilities and variance components for analysis of variance of bud-set week

Source of variation	d.f.	Mean Square	F-test prob.	Variance component
Sites	3	149.66	0.0001	79.8%
Reps/sites	20	1.37	0.0356	1.7%
Sources	7	4.53	0.0002	3.9%
Sources*sites	17	0.54	0.8085	0.0%
Error	113	0.78		14.6%
Corrected total	160			

According to these calculations, seed source by site interaction effects did not account for significant variation but simple rank correlation coefficients (Table 23) indicate that there were rank changes and therefore some seed source by site interaction must have been present.

Table 23. Rank correlation coefficients for seed source means among test sites for bud-set week

Test site	Porcupine Hills	Bateman Creek	Tershishner Creek	Diamond Hills
Castle River	0.24	-	0.06	0.07
Porcupine Hills		-	0.14	0.29
Bateman Creek			-	-
Tershishner Creek				0.24

* Significant at $P< 0.05$

The mean number of weeks after July fourteenth at which bud set was determined to be complete for sites varied from 1.67 to 6.30, a range of 4.63 weeks (Table 24) and, on average, bud set was considered complete by mid August, 4.5 weeks after monitoring was started. The earliness of bud set on the Diamond Hills site, as well as lateness on the Porcupine site, is striking and indicates a strong influence of environmental factors on bud-set timing.

Table 24. Least square means and standard errors for bud-set week and performance of test sites as a percent of the across-site (overall) mean

Test site	Bud set (week)	s.e. (week)	% overall mean
Castle River	4.31	0.12	96
Porcupine Hills	6.30	0.15	140
Tershishner Creek	5.70	0.15	127
Diamond Hills	1.67	0.16	37
Across sites	4.50	0.16	

The adjusted least square means for bud-set week of seed sources across sites ranged from 3.72 weeks (17% below the overall mean) for the Alstone Creek source to 4.92 weeks (9% above the overall mean) for the Lake Edith source (Table 25).

In terms of ranking, The Alstone Creek and Cline River sources were consistently the first to set bud for all test sites (Appendix F, Table F5) and except for the Ghost source were significantly earlier than other sources in the across site analysis. In the across-site and for all but the Diamond

Hills site analyses, the Lake Edith source ranked last.

Table 25. Least square means and standard errors for bud-set week and performance of seed sources as a percent of the across-site (overall)mean

Seed source	Bud set (week)	s.e. (week)	% overall mean
Crowsnest Pass	4.75_a	0.18	106
Porcupine Hills	4.83_a	0.18	107
Marston Creek	4.71_a	0.18	105
Canmore	4.67_a	0.24	104
Ghost River	4.52_{ab}	0.37	100
Cline River	3.84_b	0.18	85
Alstone Creek	3.72_b	0.19	83
Lake Edith	4.92_a	0.18	109

Least square means having the same subscript letter are not significantly different at $P<0.05$

B. Geographic and Clinal Trait Relationships

The damage symptoms exhibited by seedlings on test sites as well as simple Pearson correlation coefficients would indicate that climatic factors were the primary cause of dramatic differences in the expression of traits between sites. Die-back of stems and frost cankers were frequent on the three southern test sites, and extensive frost damage due to a late spring frost occurring during bud burst was directly observed on the Castle site. When climatic and geographic variables for sites (Tables 2 and 3) were correlated with site means for traits, it was found that the highest coefficients were with variables associated with growing season length and heat units during the growing season.

Three-year height was found to be significantly correlated with mean summer temperature (r= 0.89) and frost free period (r= 0.90). Plant-health score was significantly correlated with frost free period (r= 0.89). Although survival was not significantly correlated with any of these variables, it showed the highest coefficients with mean summer temperature (r=0.86), growing degree days (r=0.85) and frost free period (r=0.81). Survival was also positively and significantly correlated with three-year height and plant-health score.

Bud-set week had significant coefficients with elevation of site (r=0.96) and growing degree days (r= -0.99). Although bud-burst day was not significantly correlated with any of the climatic or geographic variables (Table 2 and 3), like bud set, it had the highest coefficients with elevation (r= 0.85) and growing degree days (r= -0.93). This would suggest that both bud-burst and bud-set timing on test sites was highly dependent on heat units during the growing season with warmer sites both bursting and setting bud earlier. Correlations also showed that for sites, bud burst and bud set were not significantly correlated with other traits but were significantly correlated with each other.

Investigations for possible clinal relationships between traits and variables of seed source origin (Table 1) using simple pairwise correlation, multiple regression and polynomial regression was complicated by the fact that, within the native range of Douglas-fir in Alberta, latitude, longitude and elevation are highly inter-correlated (Table 26).

In order to determine their true pairwise correlations, calculation of partial correlations (Fisher 1967) for these three variates was employed. Coefficients remained high for longitude with latitude(r= 0.87) and longitude with elevation

Table 26. Simple pairwise correlations for location variables of seed source origin

	Latitude	Longitude	DECD
Elevation	-0.71*	-0.87*	-0.04
Latitude		0.92*	0.48
Longitude			0.17

* significant at $P<0.05$
Note: DECD = distance in km east of the continental divide

(r= -0.78) but for latitude with elevation was much lower (r= 0.47). As a result, longitude of source was dropped as a predictor variable in subsequent analyses while latitude, elevation, and distance in kilometres east from the continental divide were retained.

Simple pairwise correlations with location variables of source revealed a number of significant and interesting clinal trends (Table 27). Plant-health score was demonstrated to have a significant negative correlation (r= -0.87) with latitude of seed source origin indicating that more northerly sources were less healthy and vigourous than southern sources regardless of site. Although not significant, there was a moderate positive correlation with elevation and negative correlation with distance from the continental divide.

Elevation of source showed a strong positive correlation (r= 0.83) with percent survival and a strong negative correlation with three-year height (r= -0.81) indicating that higher elevation sources were more hardy but grew more slowly, a finding which is consistent with the strong inverse correlation found for survival and growth potential. This inverse pattern for growth and survival is also present for

Table 27. Simple pairwise correlations of traits with locational variables of seed source origin

	Seed source origin		
Trait	latitude	elevation	DECD
Survival (%)	-0.66	0.83*	0.16
Total height (cm)	0.49	-0.81*	-0.26
Plant health score	-0.87*	0.50	-0.46
Bud burst (day)	-0.44	-0.24	-0.54
Bud set (week)	-0.47	0.08	-0.66

* significant at P<0.05
Note: DECD = distance in km east from the continental divide

latitude where moderate correlations were demonstrated and for distance from the continental divide where coefficients were low.

Distance of source east from the continental divide was not found to be significantly correlated with any of the traits studied, but the highest coefficients were with bud-burst and bud-set timing. In terms of bud phenology, correlations indicate there is a trend for eastern and northern sources to burst and set bud earlier.

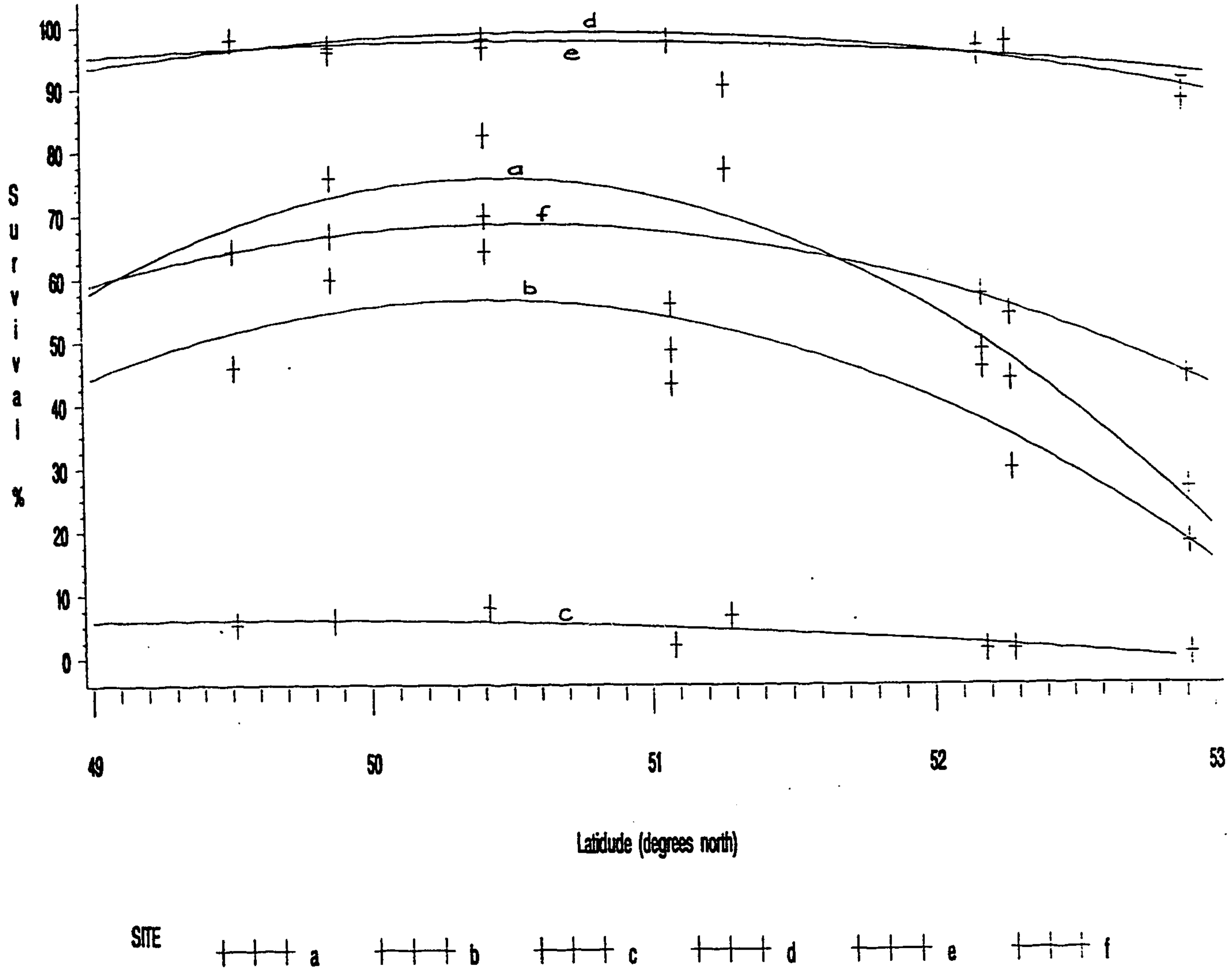
Following simple correlation analysis, stepwise multiple linear regressions of seed source means for traits were run on geographic variables of seed source origin for both the individual test site and across-site analyses. These regressions failed in all cases to enter more than one geographic variable as a significant predictor. As a consequence of this failure, and because adaptive clines are commonly nonlinear (Rehfeldt 1989), further investigations of adaptive geographic clines were conducted using simple linear and quadratic regression.

Clinal relationships for survival

Figure 3 demonstrates clearly that Douglas-fir, regardless of source, was maladapted to conditions during early establishment on the Bateman Creek test site. In contrast to this, overall survival was so high for the Tershishner Creek and Diamond Hills test sites that these sites have questionable value for demonstrating clines or differentiating between seed sources in terms of early survival.

Although the across site regressions failed to be significant, evidence for latitudinal clines for survival were produced by the Porcupine Hills and Bateman Creek test sites (Figure 3; Appendix G, Table G1). The clines demonstrated by all site regressions were non-linear but in the case of the Bateman Creek site the response was quite flat and only the linear fit was significant ($y=97.19-1.82x$; $r^2=0.59$; $p=0.026$). The trend indicated by the clines was for seed sources midway in the latitudinal range to have the best survival.

Strong evidence for elevational clines was demonstrated for survival as significant regressions were produced by the



a = Castle River test site regression (y=-21640.00+860.770789x-8.529665xsquare; rsquare=0.68; p=0.060)
b = Porcupine Hills test site regression (y=-15660.00+623.415316x-6.182250xsquare; rsquare=0.79 p=0.045)
c = Bateman Creek test site regression (y=-1436.531019+58.134199x-0.585662xsquare; rsquare=0.64 p=0.076
d = Tershishner Creek test site regression (y=-4879.066830+196.188344x-1.932867xsquare; rsquare=0.74; p=0.068)
e = Diamond Hills test site regression (y=-2451.315334+100.670367x-0.993929xsquare; rsquare=0.60; p=0.595)
f = Across test site regression (y=-10622.00+423.184370x-4.187783xsquare; rsquare=0.65 p=0.072)

Figure 3. Regression of mean seed source survival on latitude of seed source origin

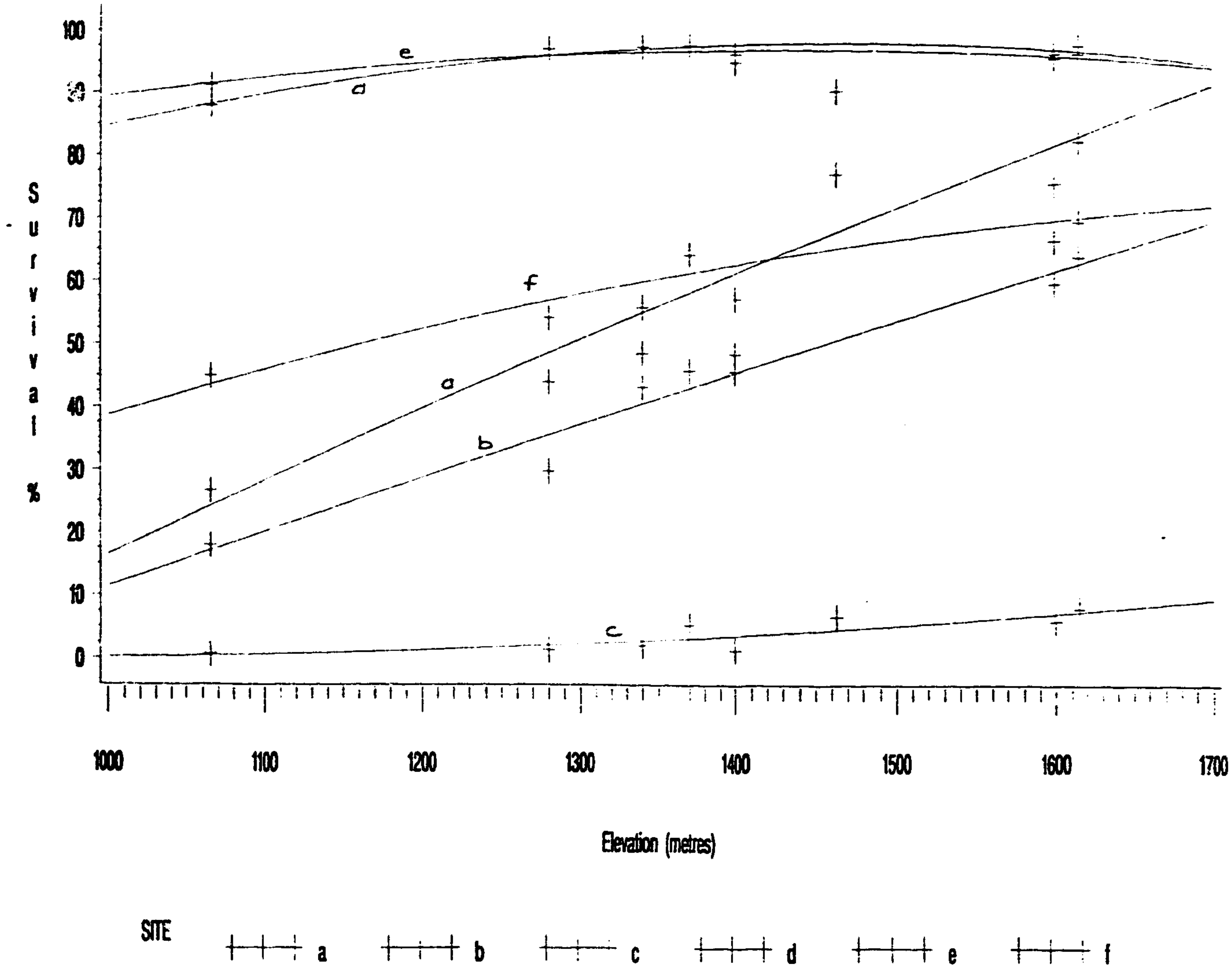
across-site as well as four of the five individual test site analyses (Figure 4; Appendix G, Table G1). The across-site cline demonstrated clearly that high elevation sources survived best and that survival declined nearly linearly at the rate of 5.2% for every 100 metre drop in elevation of seed source origin. This cline also appears somewhat steeper at lower elevations.

Individual test site regressions demonstrated that the two steepest clines were produced by the two most southern test sites (Castle and Porcupine) which were linear (Figure 4), while those produced by the Bateman Creek and two northern sites were non-linear.

Results produced from regression of percent survival on distance of sources from the continental divide (Appendix G, Table G1) would suggest little evidence for a clinal relationship.

Clinal relationships for three-year height

Only the Castle River test site generated a significant regression indicating weak evidence for a latitudinal cline

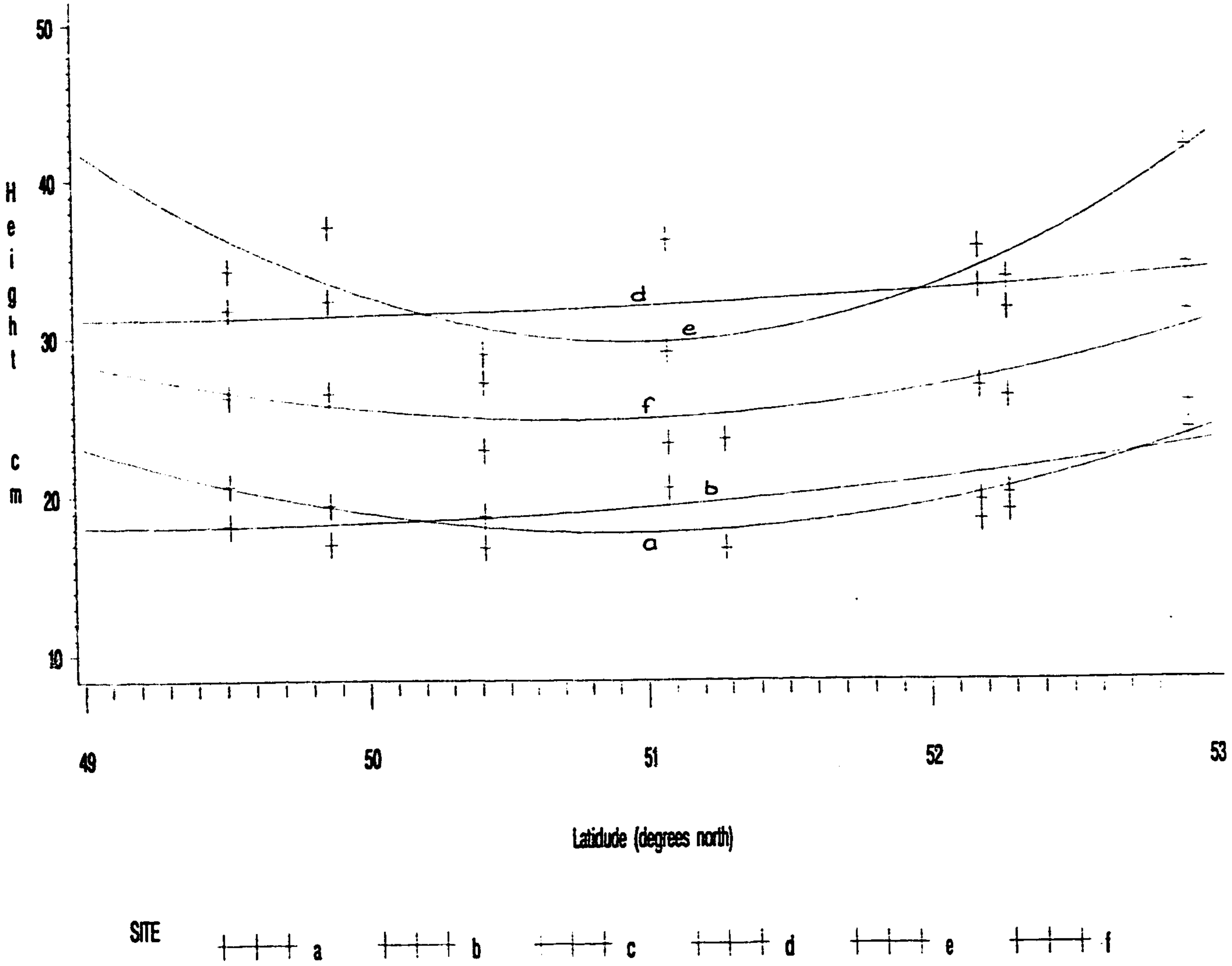


a = Castle River test site regression (y=-88.862787+0.107138x; rsquare=0.76; p=0.005)
b = Porcupine Hills test site regression (y=-71.441956+0.083502x; rsquare=0.96 p=0.0001)
c = Bateman Creek test site regression (y=13.492159-0.028805+0.000015533xsquare; rsquare=0.71 p=0.046)
d = Tershishner Creek test site regression (y=-36.869889+0.184453x-0.000062853xsquare; rsquare=0.94; p=0.004)
e = Diamond Hills test site regression (y=13.165602+0.116828x-0.000040543xsquare; rsquare=0.78; p=0.100)
f = Across test site regression (y=-80.473749+0.160831x-0.000041698xsquare; rsquare=0.71 p=0.046)

Figure 4. Regression of mean seed source survival on elevation of seed source origin

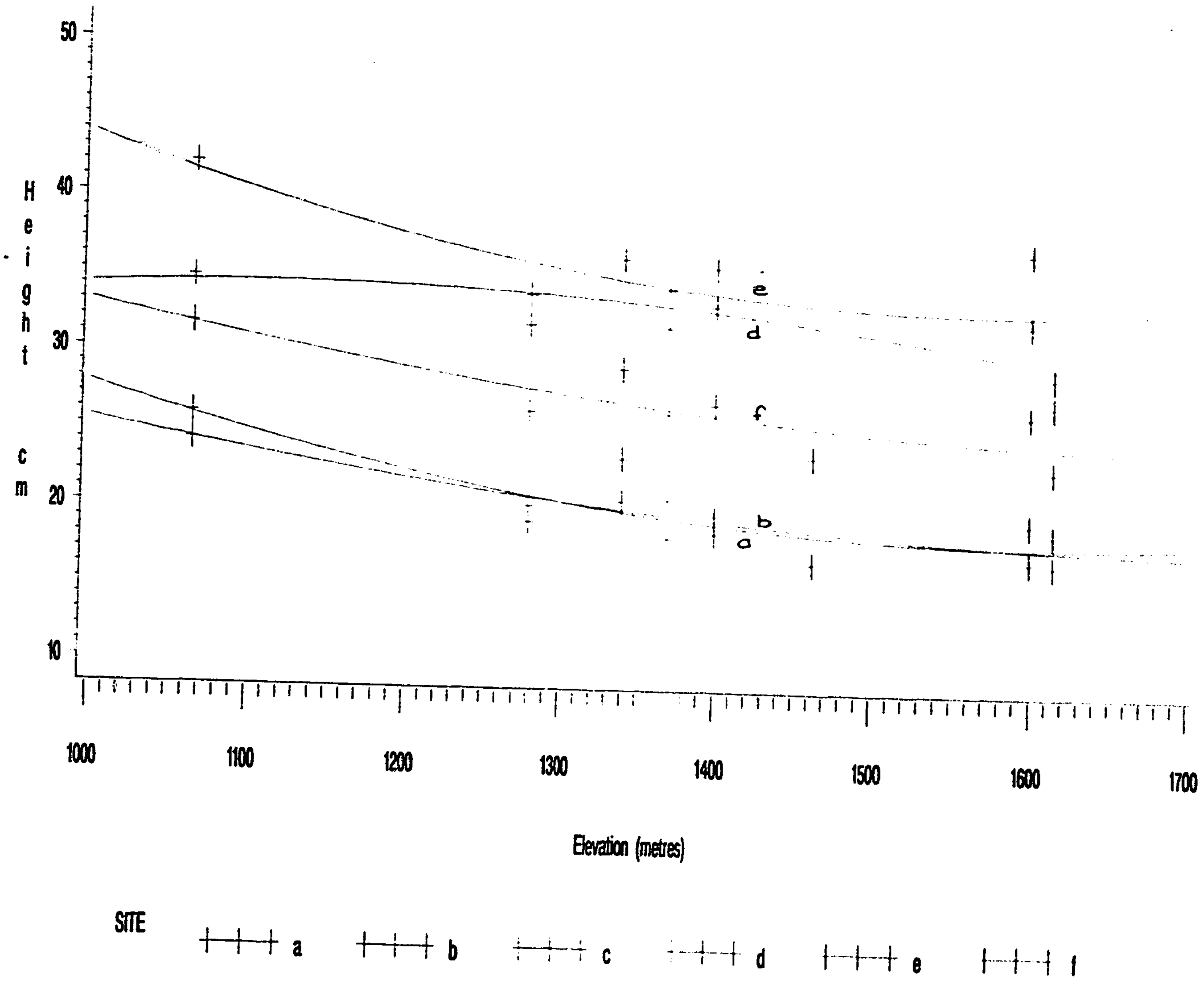
for three-year height (Appendix G, Table G2). This cline was non-linear and demonstrated a trend for central seed sources to be shortest with height of sources increasing to the north and south (Figure 5). The Diamond Hills site regression, although not significant, showed the same trend which, interestingly, is the inverse of the latitudinal cline for survival (Figure 3). This would not be inconsistent with the strong inverse correlation demonstrated for percent survival with three-year height. The other striking feature of this plot is its symmetry, with the southern sites showing poorer height growth but a nearly parallel response between the Porcupine and Tershishner, and Castle and Diamond Hills sites.

Strong evidence for an elevational cline was demonstrated for height growth potential of sources, as the across-site analysis, as well as the two southern tests sites produced significant regressions (Figure 6; Appendix G, Table G2). The general clinal trend was for an inverse relationship with lower elevation sources being taller and height performance declining with increased elevation of source. The best fit for all regressions was non-linear and steeper at lower elevations; however, for the Porcupine and across-site



a = Castle River test site regression (y=38717.00-1514.386175x+14.876357xsquare; rsquare=0.71; p=0.044)
b = Porcupine Hills test site regression (y=9219.443918-367.415823x+3.73369xsquare; rsquare=0.38 p=0.382)
c = Bateman Creek test site (not analyzed)
d = Tershishner Creek test site regression (y=4564.454064-174.440558x+1.788618xsquare; rsquare=0.16; p=0.698)
e = Diamond Hills test site regression (y=82029.00-3207.885640x+31.476392xsquare; rsquare=0.75; p=0.127)
f = Across test site regression (y=31668.00-1239.007104x+12.214579xsquare; rsquare=0.49 p=0.183)

Figure 5. Regression of mean seed source 3-year height on latitude of seed source origin



a = Castle River test site regression (y=599.891378−0.480663x+0.000136xsquare; rsquare=0.76; p=0.028)
b = Porcupine Hills test site regression (y=865.794303−0.853447x+0.000265xsquare; rsquare=0.70 p=0.086)
c = Bateman Creek test site (not analyzed)
d = Tershishner Creek test site regression (y=90.948402+0.450983x−0.000201xsquare; rsquare=0.47; p=0.284)
e = Diamond Hills test site regression (y=1139.981055−1.027631x+0.000326xsquare; rsquare=0.56; p=0.289)
f = Across test site regression (y=711.684485−0.529408x+0.000148xsquare; rsquare=0.68 p=0.056)

Figure 6. Regression of mean seed source 3-year total height on elevation of seed source origin

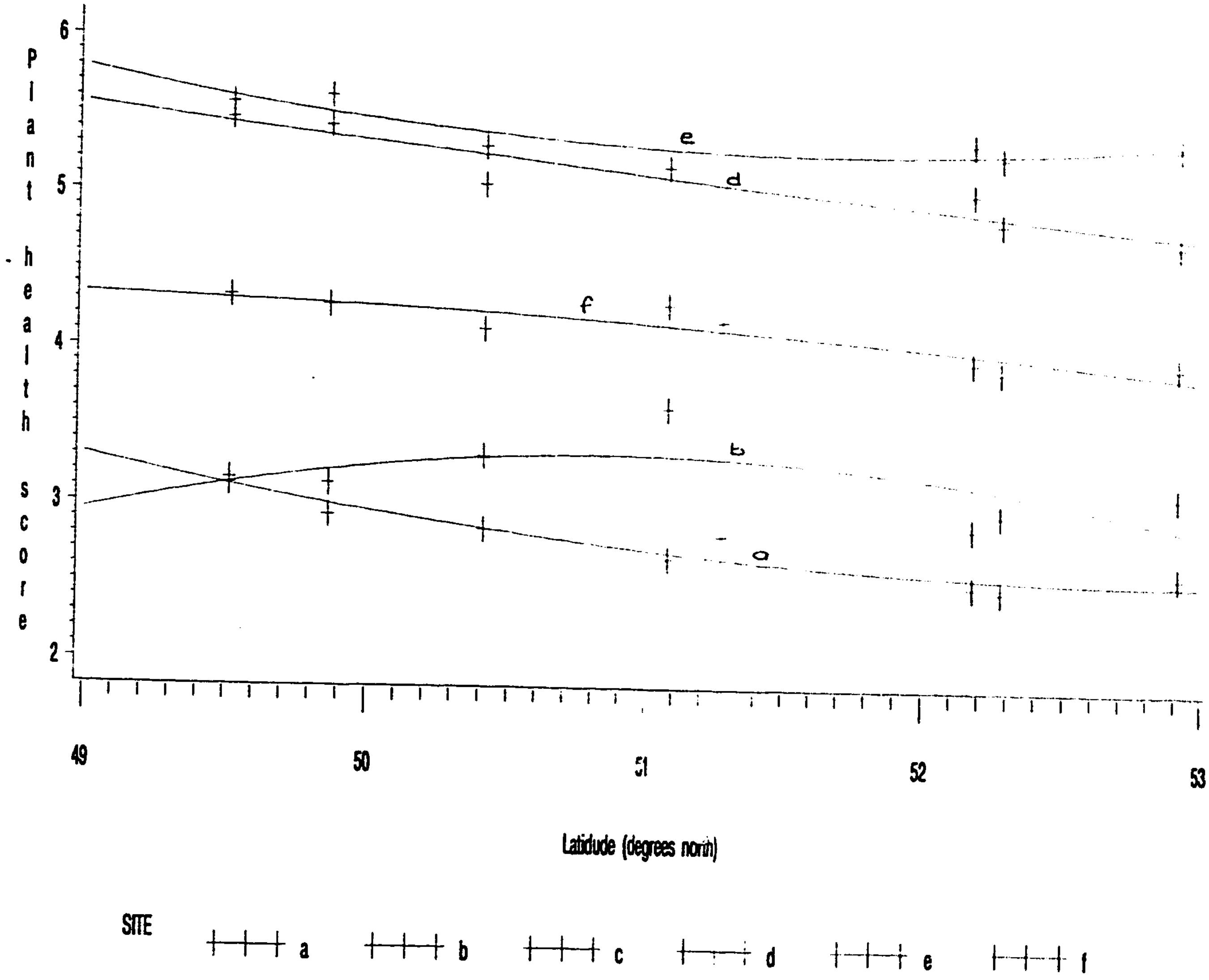
regressions, only the linear fit was significant ($y=384.613-0.133x$ and $y=443.590-0.128x$ respectively) and using the linear equation for the across site regression there would appear to be an approximate 4 percent loss in growth potential for every increase of 100 metres in elevation of source.

No significant clinal relationship was demonstrated for height performance and distance from the continental divide, and r^2 values were consistently low (Appendix G, Table G2).

Clinal relationships for plant-health score

The significant ($p<0.05$) regressions for the Castle River, Tershishner Creek and across-site analyses provided strong evidence for a latitudinal cline for plant-health score, which indicated that plant health declines with increased latitude of source (Figure 7). The clines were generally non-linear but the overall response was quite flat suggesting that differences in performance with latitude are of little practical importance and far outweighed by differences in test site environment.

No evidence was found for a significant clinal relationship



a = Castle River test site regression (y=144.242328-5.354411x+0.050575xsquare; rsquare=0.89; p=0.004)
b = Porcupine Hills test site regression (y=-271.341347+10.797410x-0.106114xsquare; rsquare=0.35 p=0.428)
c = Bateman Creek test site (not analyzed)
d = Tershishner Creek test site regression (y=11.796240-0.176835x; rsquare=0.83; p=0.002)
e = Diamond Hills test site regression (y=189.127602-7.105583x+0.068654xsquare; rsquare=0.76; p=0.120)
f = Across test site regression (y=-39.729419+1.843788x-0.019273xsquare; rsquare=0.78 p=0.024)

Figure 7. Regression of mean seed source plant-health score on latitude of seed source origin

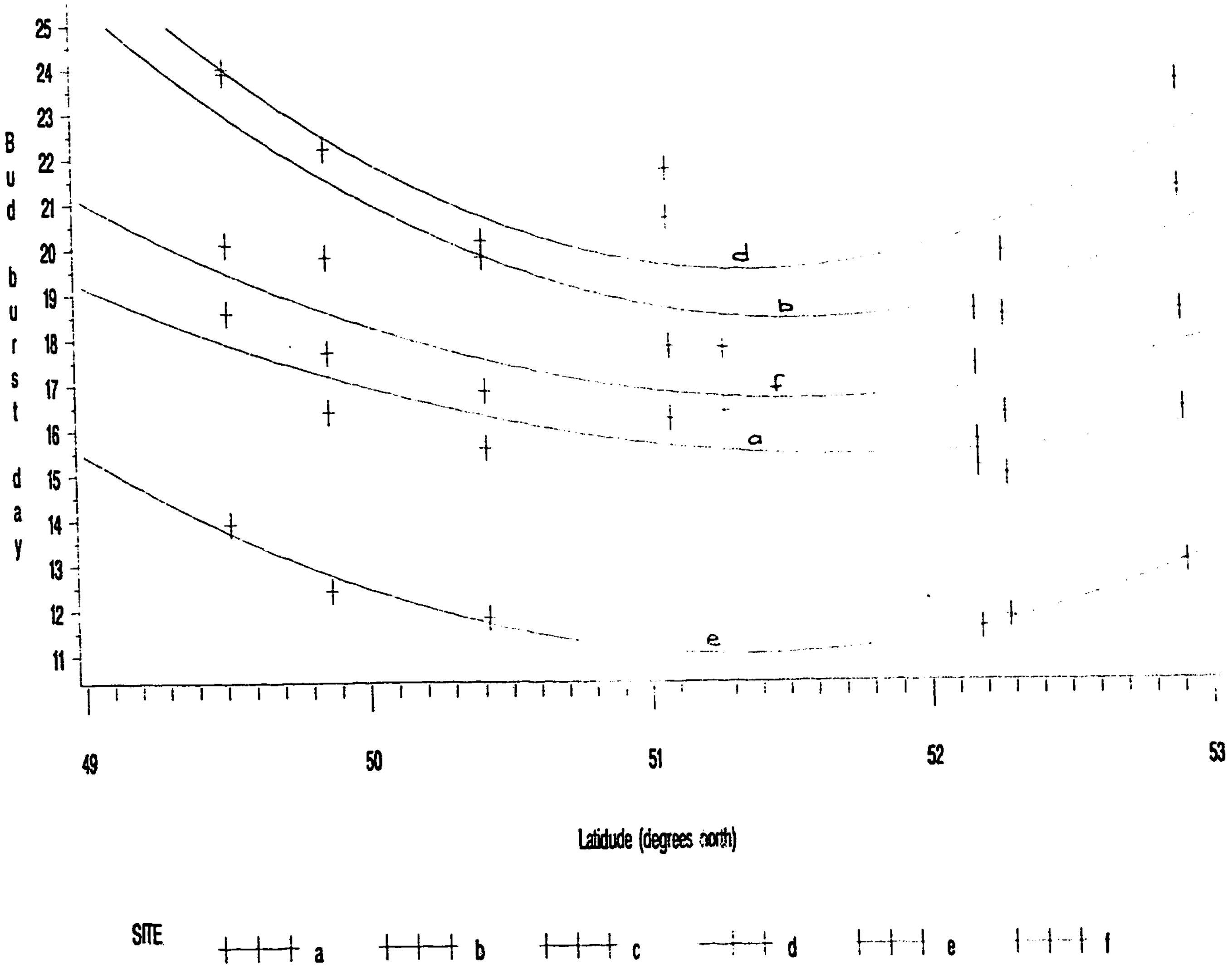
between plant health and elevation or distance east from the continental divide for seed sources (Appendix G; Table G3).

Clinal relationships for bud-burst timing

Evidence for geographic clines for bud-burst timing of sources was weak, particularly for elevation, and no across-site regressions were significant for any of the geographic variables (Appendix G, Table G4). One significant test site regression was recorded for both latitude and distance east of the continental divide.

The significant latitudinal regression was recorded for the Diamond Hills test site (Figure 8). This regression indicated a non-linear cline for earlier bud burst of central sources. Although other site regressions were not significant, they showed consistent quadratic r^2 values (0.58 to 0.62) and were strikingly symmetric with the cline indicated by the Diamond hills test site.

The significant cline for bud-burst day and distance of source east of the continental divide occurred for the Porcupine test site(Figure 9). The trend indicated by this cline is for



a = Castle River test site regression (y=1355.677265-51.810647x+0.500726xsquare; rsquare=0.62; p=0.091)

b = Porcupine Hills test site regression (y=2939.570653-113.342875x+1.099469xsquare; rsquare=0.58 p=0.180)

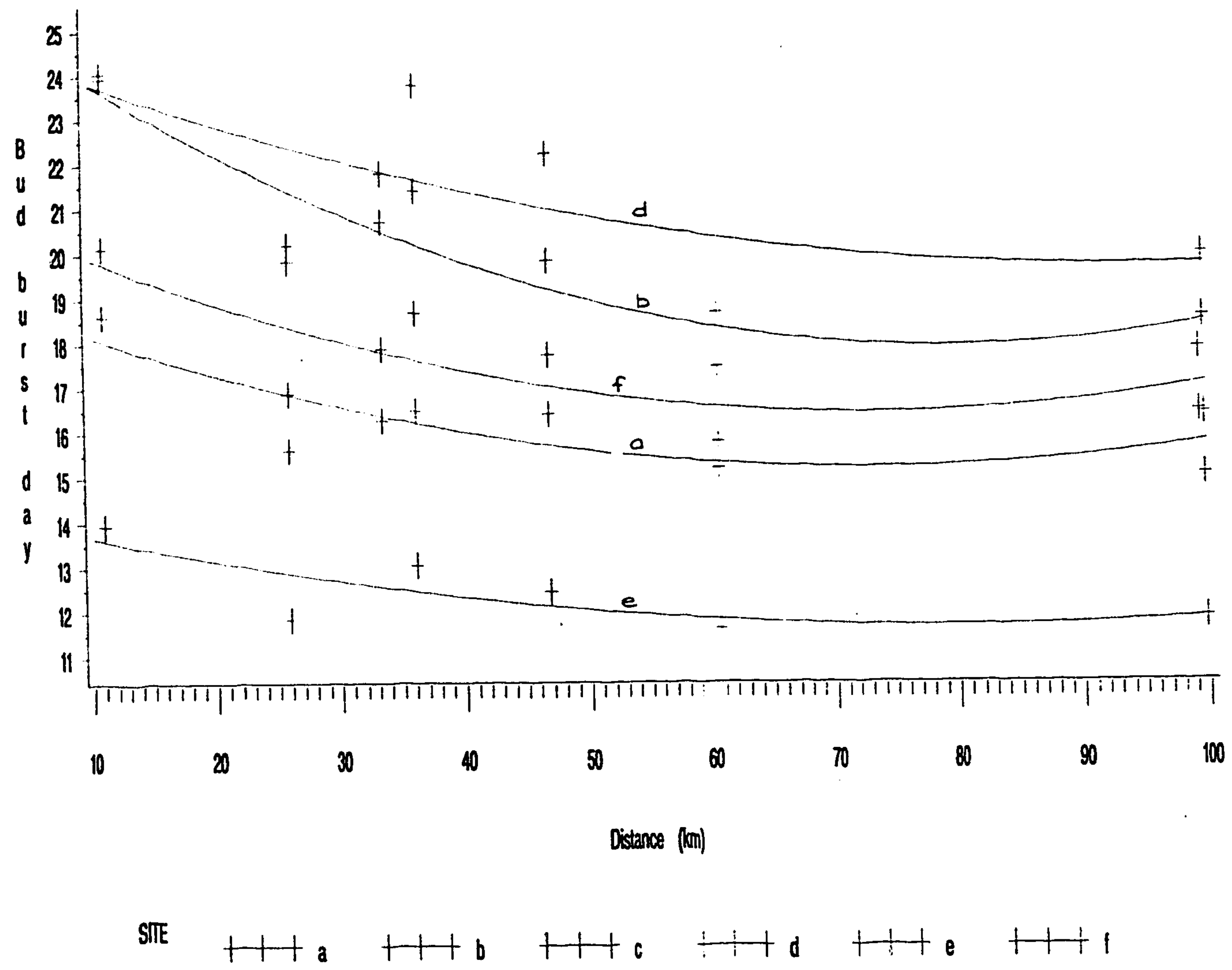
c = Bateman Creek test site (not analyzed)

d = Tershishner Creek test site regression (y=3449.344518-133.526840x+1.299601xsquare; rsquare=0.60; p=0.158)

e = Diamond Hills test site regression (y=2166.480893-83.979814x+0.817994xsquare; rsquare=0.95; p=0.010)

f = Across test site regression (y=1796.913827-69.055577x+0.669677xsquare; rsquare=0.51 p=0.164)

Figure 8. Regression of mean seed source bud-burst day on latitude of seed source origin



a = Castle River test site regression (y=19.162518-0.108871x+0.000748xsquare; rsquare=0.60; p=0.601)
b = Porcupine Hills test site regression (y=25.622490-0.194768x+0.001231xsquare; rsquare=0.80 p=0.040)
c = Bateman Creek test site (not analyzed)
d = Tershishner Creek test site regression (y=24.833361-0.109490x+0.000587xsquare; rsquare=0.43; p=0.326)
e = Diamond Hills test site regression (y=14.268451-0.065252x+0.000410xsquare; rsquare=0.59; p=0.262)
f = Across test site regression (y=21.071840-0.127376x+0.000873xsquare; rsquare=0.56 p=0.127)

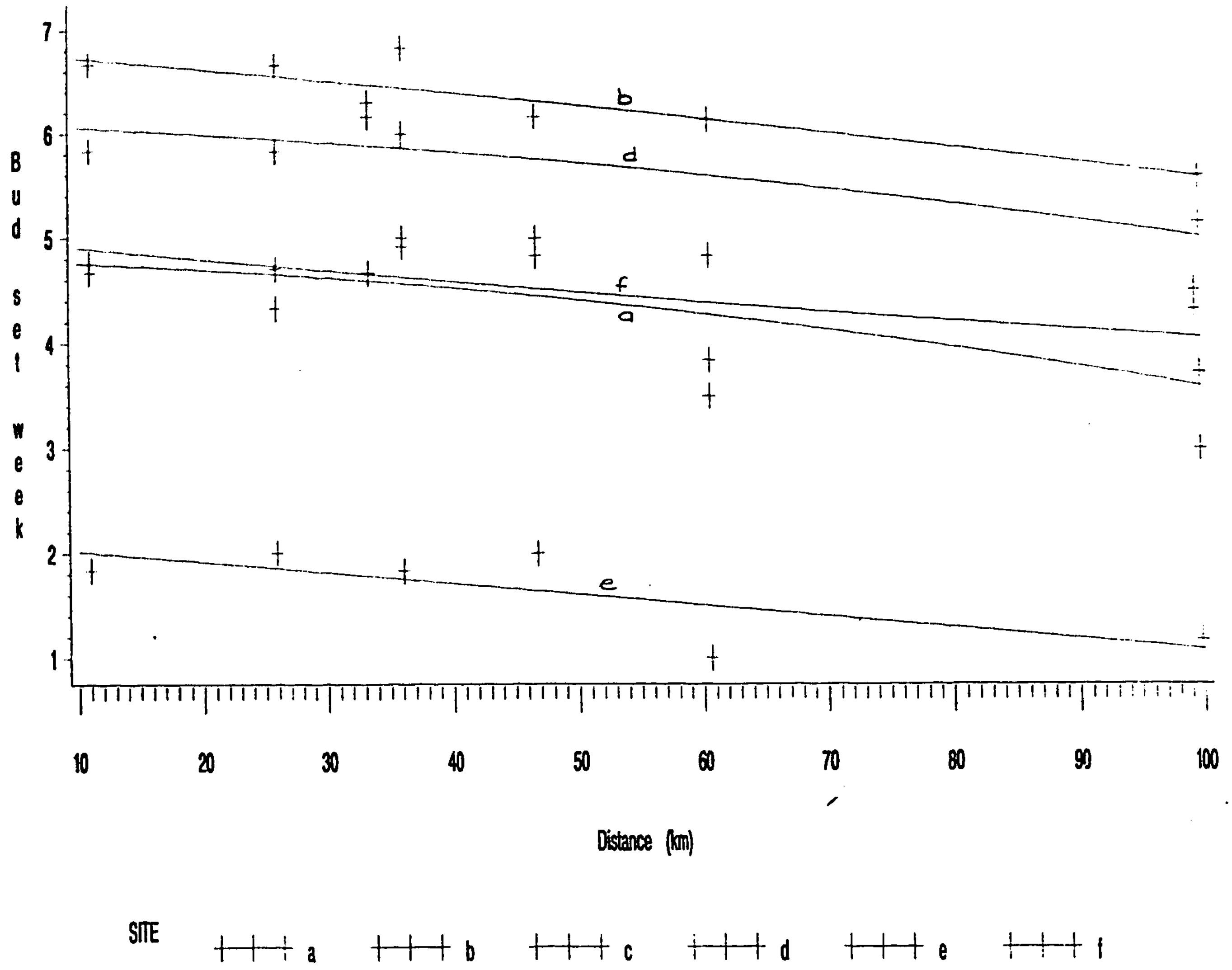
Figure 9. Regression of mean seed source bud-burst day on distance of seed source origin east from the continental divide

bud burst to occur earlier with increased distance east of the continental divide. The overall pattern is similar to that for latitude, with other sites showing moderate quadratic r^2 values (0.43 to 0.60) and notable symmetry with the Porcupine site cline.

Bud set

As with bud-burst timing, there was only weak evidence of geographic clines for bud-set timing of seed sources, particularly for latitude and elevation (Appendix G, Table G5). The only significant regression recorded was for the Porcupine site where a linear cline was demonstrated between week of bud set and distance of seed source origin east of the continental divide (Figure 10).

This cline indicates that bud-set timing follows the same pattern as bud burst with sources nearest the continental divide setting bud latest and sources furthest from the divide setting bud earliest. Although not significant at $p< 0.05$, the moderate r^2 values of other site regressions and common parallel linear response lend credence to this clinal trend.



a = Castle River test site regression (y=4.798516-0.003252x-0.000088xsquare; rsquare=0.41; p=0.262)
b = Porcupine Hills test site regression (y=6.890775-0.012715x; rsquare=0.74 p=0.013)
c = Bateman Creek test site (not analyzed)
d = Tershishner Creek test site regression (y=6.260955-0.011759x; rsquare=0.40; p=0.130)
e = Diamond Hills test site regression (y=2.125906-0.010430x; rsquare=0.54; p=0.094)
f = Across test site regression (y=5.020320-0.011665x+0.000021xsquare; rsquare=0.44 p=0.240)

Figure 10 Regression of mean seed source bud-set week on distance of seed source origin east of the continental divide

C. Principle Component Analysis

Principle component analysis applied to across-site, least square means for the five traits being studied and location information for seed source origins was used to detect linear relationships, summarize trait and geographic information and group seed sources. The analysis demonstrated that 85 percent of standardized variance could be explained by the first two principle components (53.7% for the first and 31.6% for the second) (Table 28).

Table 28. Eigenvalues for the correlation matrix and proportion and cumulative proportion of variation explained by principle components

Principle component	Eigenvalue	Proportion	Cumulative
PRIN1	4.82974	0.536638	0.53664
PRIN2	2.84152	0.315724	0.85236
PRIN3	0.61873	0.068748	0.92111
PRIN4	0.35403	0.039336	0.96045
PRIN5	0.26337	0.029264	0.98971
PRIN6	0.06890	0.007655	0.99737
PRIN7	0.02371	0.002635	1.00000
PRIN8	0.00000	0.000000	1.00000
PRIN9	0.00000	0.000000	1.00000

Loadings for individual eigenvectors for the first principle component, which accounted for the majority of standardized variance, were positive and high for plant-health score, percent survival and elevation of source with large negative loadings on latitude and longitude (Table 29). As a result, sources with positive values on the vertical axis (Figure 11) represent higher elevation, southern sources with higher survival rates and better health and vigour while sources with negative values represent lower elevation northern sources with poorer survival rates and poorer health and vigour.

Table 29. Eigenvectors of the first four principle components for variables describing seed source trait performance and seed source origin

Variable	PRIN1	PRIN2	PRIN3	PRIN4
Latitude	-.431794	-.097860	0.139802	0.337678
Longitude	-.441415	0.100582	0.009745	0.238001
Elevation	0.373952	-.272524	-.359316	0.190601
DECD	-.147455	-.447191	0.666446	-.048443
Survival	0.382810	-.252414	0.320032	0.285126
Height	-.298108	0.403105	-.073116	-.185676
Health	0.391358	0.220959	0.136679	-.323093
Bud burst	0.153392	0.483096	0.521758	-.148332
Bud set	0.212184	0.444575	0.091778	0.740601

For principle component two, eigenvectors for bud-burst day, bud-set week and three-year height had large positive loadings, while distance of seed source origin east of the continental divide had a large negative loading. On the horizontal axis (Figure 11), this places sources which tend to be closer to the continental divide, have greater growth potential and experience later bud-burst and bud-set timing on the positive end of the axis while sources being further from the continental divide with lower growth potential, earlier bud-burst and earlier bud-set timing have negative axis values.

In terms of groupings (Figure 11), the Lake Edith source appears to represent a unique northern mountain corridor population with significantly poorer survival (Table 9) and significantly greater growth potential (Table 13) than any other source. Interestingly, it is also significantly different from its closest geographic neighbours (Alstone Creek and Cline River), in terms of bud-burst and bud-set timing (Table 21 and 25).

The close proximity of the Cline River and Alstone Creek seed sources in Figure eleven confirms their similarity as they

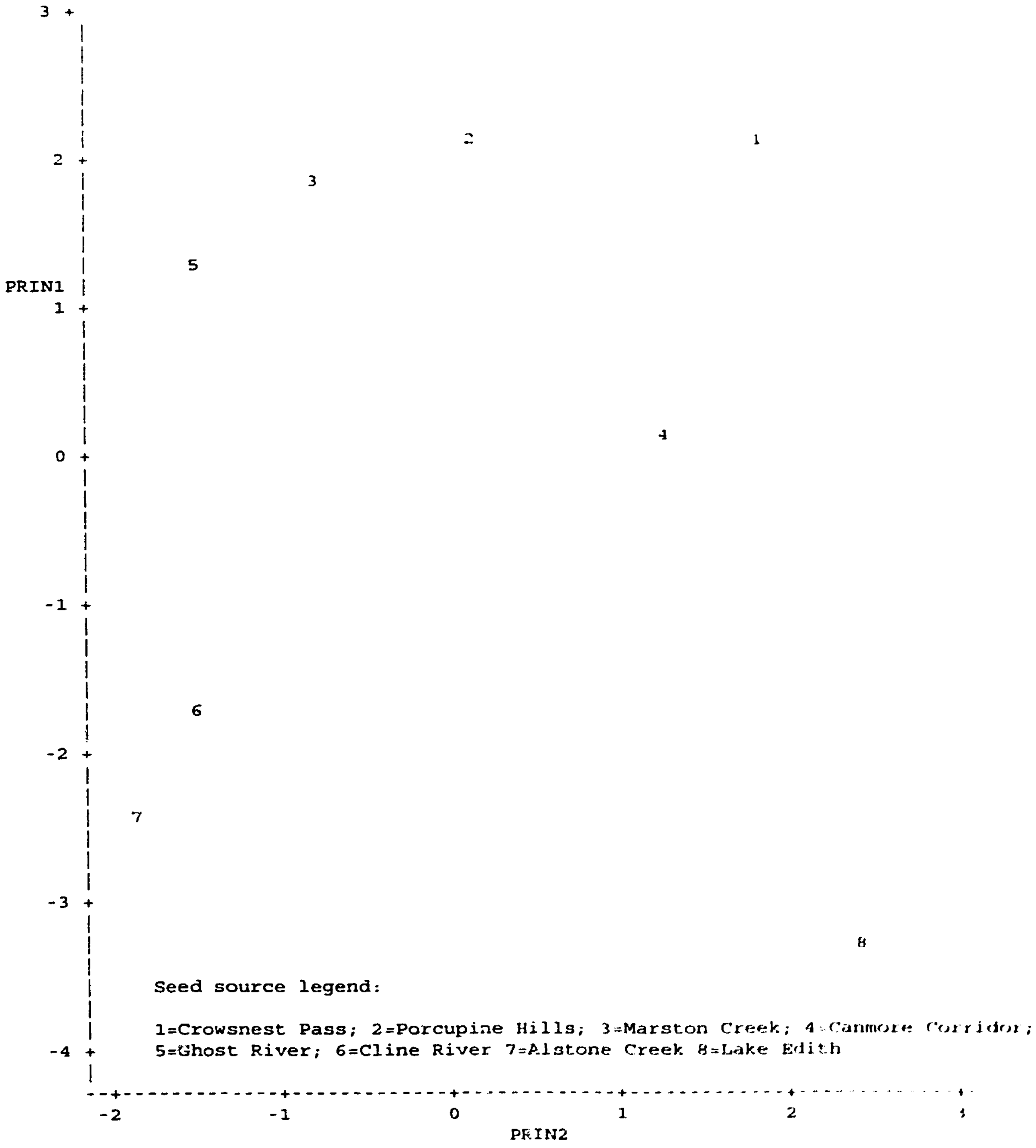


Figure 11. Plot of trait expression and geographic origin information for seed sources in terms of principle components one and two

were not found to be significantly different for any of the traits studied. Their distinct separation from other sources in the plot is due in part to their isolated geographic location in the Kootenay plains corridor, but also due to significantly poorer survival (second worst) (Table 9), significantly earlier bud-burst timing than other sources except Marston Creek (Table 21), and earlier bud set than all sources except Ghost River (Table 25).

The Canmore Corridor and Crowsnest Pass sources, although closest plotted neighbours (Figure 11), are also isolated in terms of plot distance and appear to represent distinct populations. The Canmore source differs from the Crowsnest source in having significantly poorer survival (Table 9), significantly greater early height growth (Table 13) and significantly earlier bud-burst (Table 21). It differs from all other sources except Cline River in having significantly different growth potential (second best) (Table 13). Of particular interest is the fact that it is intermediate in terms of trait expression as well as geography (latitude and elevation) with growth and survival characteristics similar to more northerly sources but overall vigour and plant health more like southern sources.

The Crowsnest source in terms of trait performance is only different for bud-burst timing (Table 21) which is the latest of any source. Although, not significantly healthier, it also had the highest plant-health score and second latest date of bud set.

The remaining three seed sources (Porcupine Hills, Marston Creek, and Ghost River), in terms of plotted distance (Figure 11), appear to form a group of unique southern, high-elevation east-slope populations, which differ from the previous mountain corridor sources by having better survival but poorer growth potential. The trait pattern is complex and these three sources appear to form something of a continuum with a link through the Porcupine Hills source to the Crowsnest Pass source. In terms of survival, the Ghost source had significantly better survival than the Porcupine source, while the Marston source was intermediate and not significantly different from the Porcupine or Crowsnest sources (Table 9). For growth, the pattern changes with the Marston source having significantly lower growth potential than all other sources but the Ghost source not being different from the Porcupine, Crowsnest or Alstone sources, although this may in part be due to the large standard error for the Ghost source which had a comparatively low mean height performance (Table 13).

No significant differences between these three sources or the Crowsnest source occurred for plant-health score (Table 17) as they appear to be intermediate between the healthier southwestern sources and less healthy northern sources. This trend is also apparent for bud burst (Table 21), where this group is only significantly different from the Crowsnest and Cline River sources. The pattern for bud-set is less clear as the intermediate nature of the Ghost source may once again be due to a larger standard error which would otherwise separate the Cline and Alstone sources from all others.

Overall, the principle component analysis in conjunction with the analysis of variance and comparison of means tests appears to demonstrate that corridor populations are unique from each other and different from the three high elevation east slope populations, although there appears to be something of a complex relationship for traits within the foothills group and a partial continuum with the Crowsnest source. Poor discrimination for this group in terms of trait performance appears, in part, to be due to the large standard error for the Ghost source.

V. DISCUSSION

Although there is a wealth of information on the ecological genetics of coastal Douglas-fir, adequate information for gaining an understanding of the genetic composition of the interior variety is more recent (Rehfeldt 1978; Rehfeldt 1991) and for some areas still scant.

Structural genetic information for Alberta populations is of particular interest as they occur at the northeastern limit of the species range and often exist as isolated or marginal populations. These populations frequently border on prairie grassland or boreal forest environments where intense selection pressures and genetic drift effects would be expected. As a result, a knowledge of population genetic structure may be very important to successful reforestation attempts in the montane and adjacent boreal areas of Alberta.

A. Validity of Hypotheses

The results from analytical testing of the data for this study clearly show that seed source effects were significant for all traits of interest. Comparison of means tests also demonstrated that there were unique seed sources in terms of survival, growth and bud burst-timing as well as unique regional groupings for all traits.

Simple correlations and regressions of seed source trait means with geographical variables describing seed source origin also demonstrated significant clinal relationships for all traits. As well, a significant negative correlation was found between height growth and survival of sources and a positive correlation between bud-burst and bud-set timing.

The high proportion of total variation accounted for by sites (77.5% to 92.1%), as well as the substantial range in mean values for traits reported for sites, also underscores the importance of site and environmental influences on trait expression for this study. A twenty-five fold difference in survival between the Bateman Creek and two northern test sites is particularly dramatic but a near two fold difference in three-year height growth, plant-health score and number of days to bud burst and four fold difference in number of weeks to bud set between sites is also noteworthy. Significant contrasts between the northern and southern test sites for survival, growth and plant health also indicate dramatic regional differences.

B. Survival

In summary, survival results for this study showed that:

1. heavy mortality occurred early in the establishment phase of plantations;
2. survival on sites was significantly and positively correlated with plant health and height;
3. survival was better on northern than southern sites;
4. survival was high on sites peripheral to or outside the native montane range for the species;
5. so called 'local' sources seldom survived best on a site;
6. southern sources survived better than northern sources regardless of site;
7. survival of sources followed a strong elevational and weaker latitudinal cline;

8. there were superior sources for survival regardless of plantation location.

Environmental variation

Within the native range of Douglas-fir, there are numerous factors which have been found to adversely affect the survival of both natural and planted seedlings. It is common for mortality to be as high as 75% within the first two years (Isaac and Dimock 1965), and various authors report that the highest mortality occurs in the first year after establishment (Hermann and Chilcote 1965; Wright *et al* 1971; Seidel and Beebe 1983; Waters *et al* 1991). Much of this mortality is attributable to the heterogenous nature of montane environments which exert intense selection pressures during the seedling stage (Campbell 1979). Common reported causes of this mortality are heat injury, drought, plant competition, frost, insects, disease and animals, particularly rodents (Isaac and Dimock 1965; Hermann and Chilcote 1965; Ryker 1975; Seidel and Beebe 1983).

The distribution and survival of Douglas-fir has been found to be strongly influenced by climatic factors (Silen 1978; Ryker and Losensky 1983). Drought and lethally high temperatures are the most commonly cited cause of poor survival for Douglas-fir seedlings of both varieties. Exposed sites at southern latitudes, and south aspects and low elevations throughout its native range are most susceptible (Hermann and Chilcote 1965; Brayshaw 1970; Ryker 1975; Ryker and Losensky 1983; White 1987; Hermann and Lavender 1990).

In the northern and northeastern portion of its range, cold winter temperatures are limiting (Tsukada 1982; Whitney 1985), as cold hardiness for both varieties is not great (Krajina *et al* 1982). At higher elevations, minimum heat requirements during the growing season and short frost free periods are reported to be the major limiting factors to establishment and survival (Brayshaw 1970; Rehfeldt 1979b). Frost during the growing season, particularly the spring, has also been found to be limiting to the interior variety in areas of cold air drainage and frost pockets (Larsen 1981; Reich and van der Kamp 1993).

Consistent with the literature, this study indicated that mortality is high for Douglas-fir in the early establishment phase. A post planting survey conducted at the beginning of the second field growing season (1992) showed that mortality on sites ranged from 93.5 percent (6.5% survival) to 1.8 percent (98.2% survival) for an average of 27.9 percent. By the end of the third growing season an additional 10.7 percent mortality had occurred and mean survival was 61.4 percent (range of 3.9% to 97.3%).

Although drought is commonly cited as a major cause of early mortality in Douglas-fir, it did not appear to be a critical causal agent in this study. Weak inverse correlations were demonstrated between mean survival for sites and mean annual precipitation (r= -0.30) and summer precipitation (r= -0.15) indicating that precipitation was not limiting. As well, the site which would be expected to experience the most frequent growing season water deficits (lowest elevation with the highest mean summer temperature and number of growing degree days) had the second best survival (97.5%).

Results of correlation analysis did indicate that the most probable cause of mortality for Douglas-fir in southwestern Alberta is a short, cool growing season. Although correlation coefficients with survival were not significant, they were consistently high for mean summer temperature (r= 0.86), growing degree days (r= 0.85) and frost free period (r= 0.81). This relationship is supported by the finding that survival, three-year height and plant health for sites were significantly and positively intercorrelated and, in turn, that three-year height and plant-health score had positive and significant correlations with frost free period and mean summer temperature.

Although results from site correlations suggest that short and cool growing seasons are the main limiting factor to survival, differences in damage symptoms and timing of mortality between sites would indicate that other factors may also be causal. Among these, frost-drought due to Chinooks (Sakai 1973; Larsen 1981) and summer droughts would seem the most likely (Ferrel and Woodard 1966; Pharis and Ferrel 1966).

Results also showed that survival on northern test sites was significantly better than on southern sites (97.6 % vs. 37.3%) and that survival was quite variable among southern sites (3.9% to 61.6%). This would suggest that northern sites were environmentally less harsh and that, consistent with the findings of other authors, southern environments within core areas of Douglas-fir distribution were quite heterogenous. This would tend to be confirmed by observation of climate variables for sites (Table 3).

It is particularly noteworthy that the second best survival for northern test sites (97.5% vs. 97.8%) occurred on the Diamond Hills site which is the site furthest outside the natural range of Douglas-fir. The most likely explanation for this appears to be that this site had the longest and warmest growing season (Table 3).

Seed source variation

Variation in adaptive traits important for survival such as freezing and drought resistance appear to show both broad geographic as well as clinal patterns for both varieties of Douglas-fir (Pharis and Ferrell 1966; Campbell and Sorensen 1973; Larsen 1981; Rehfeldt 1986). Clinal patterns are often steep and generally nonlinear (Rehfeldt 1989). Evidence also exists for distinct aspect races that appear to be an adaptation to available moisture differences between north and south aspects (Ferrell and Woodard 1968; Herman and Lavender

1968), and the genotypic composition in adjacent stands has been found to vary, apparently as a response to variable selection pressures in both time and space (Linhart and Davis 1991).

In a wide-ranging study of interior Douglas-fir which included two Alberta provenances, Wright *et al* (1971) reported that early survival of southern interior sources from Colorado, Arizona and New Mexico planted in Michigan and Nebraska was higher than for northern interior sources. Although early survival was better, and winter and frost damage was less for the southern sources initially, frost and winter damage resistance increased with time for northern sources and decreased for southern sources. In the dry Nebraskan plantation, the higher survival of southern sources was attributed to greater drought resistance.

Population differences for drought hardiness in interior Douglas-fir have also been reported by Pharis and Ferrel (1966), with seedlings from a northeast Washington source being hardier than those from Montana and Utah sources. Seedlings tested from an interior B.C. source were also found to be more hardier than those from the Montana source. In his wider ranging study, Larsen (1981) found that drought resistance of Arizona, Colorado, and New Mexico sources was greater than that of British Columbia and Utah sources.

Differences have also been reported for freezing tolerance. Rehfeldt (1986) studying Washington, Idaho, and Montana populations reported finding both geographic and elevational clines. Geographically, north-central Idaho populations had the lowest tolerance with freezing tolerance increasing to the north, south, and southeast following a trend of declining frost free periods. The elevational clines showed the same pattern with frost tolerance increasing with elevation as frost free periods became shorter.

The current study is generally consistent with the literature in that there appears to be both broadly geographic and clinal patterns for survival of seed sources. Mean comparison tests and principle component analysis showed that northern corridor sources had significantly poorer survival than southern corridor and east slope sources regardless of test site. The Canmore and Ghost sources, which are geographically adjacent, strikingly illustrate this geographic pattern.

There is also evidence for a weak latitudinal and strong elevational cline for seed source survival. The latitudinal cline (Figure 3) appears to be non-linear with mid latitude (also higher elevation) sources surviving better than southern or particularly northern sources. The elevational cline (Figure 4) is near linear with low elevation sources showing poorer survival. This elevational cline is quite steep and indicates that, for the sources studied, every increase of 100 metres in the elevation of source will lead to an approximately 5 percent increase in survival.

This clinal trend for increased hardiness of higher elevation sources is consistent with that reported by Rehfeldt (1991) for freezing tolerance and frost free periods. As in his study, site correlation results would indicate that this is likely an adaptive response to shorter and cooler growing seasons at higher elevations.

Although seed source by site interaction was significant for percent survival in the analysis of variance, simple rank correlations indicated that this interaction did not lead to significant changes in rank. In general, so called 'local' sources seldom had the best survival on test sites, and southern sources consistently had better survival than northern sources regardless of site. The easiest explanation for this is that genetic adaptation to site may be so great in Douglas-fir that even movement over short geographic distances may dramatically impact fitness.

Results also showed that hardiness as indicated by survival was greatest on all sites for the Ghost and Marston sources. This can be explained both in terms of ecotypic and clinal variation, as these two sources are both from higher elevations in the southern east slopes. In contrast, the poorest survivor across sites was the Lake Edith corridor source which predictably was the most northerly corridor source and came from the lowest elevation.

The implications of these results indicate there is opportunity to establish Douglas-fir both within and outside its native range, but substantial risk in seed transfer even over short geographic distances within core areas of its distribution. Risks of increased mortality appear to be particularly high for movement of sources south or to higher elevations. Transfers to lower elevations and north appear to be the least risky. Regardless of source, careful selection of plantation sites appears to be critical for adequate survival and results indicate that in particular, frost pockets, areas of cold air drainage, and sites with cool or short growing seasons should be avoided especially for establishment of low elevation sources.

C. Growth

In summary, results of three-year height in this study showed:

1. that growth was better on northern than southern test sites;
2. height growth was positively correlated with mean summer temperatures on sites and negatively correlated with frost free period;
3. the best growth occurred on the test site furthest outside the native range for Douglas-fir;
4. a strong inverse relationship between growth and survival;
5. more easterly, mid latitude and higher elevation sources tended to have lower growth potential while lower elevation, northern and corridor sources tended to have greater growth potential;
6. strong evidence for an elevational cline and weak

evidence for a latitudinal cline;

7. sources with superior height growth potential regardless of test site.

Environmental variation

Initial seedling growth in Douglas-fir is slow (Hermann and Lavender 1990) but this is likely due to environmental constraints as seedlings have been grown to 60 centimetres in two seasons under optimal nursery conditions (Silen 1978). Short growing seasons due to drought or frost are most commonly reported as the limiting factor to the growth of seedlings (Isaac and Dimock 1965; Rehfeldt 1989), but vegetative competition is also a common problem as it can cause shading, smothering and competition for moisture (Hermann and Lavender 1990).

Results of this study show that height growth on northern sites was significantly better than on southern sites, while variation within the two groupings was small. Vegetative competition was not a probable cause as all sites were disced before planting and received annual weeding. Drought also does not appear likely to have limited growth on southern sites as no significant correlations occurred with summer precipitation for stations in the vicinity of sites. As well, height was significantly and positively correlated with higher mean summer temperatures (r= 0.89), which suggests that the warmer (and likely drier sites for at least part of the growing season)had better growth.

Results did indicate that short cool growing seasons were limiting to height growth of interior Douglas-fir in southwestern Alberta. Significant correlations were recorded between site mean height and mean summer temperature (r= 0.89) and frost free period (r= 0.90). This may explain why the best height growth was achieved on the Diamond Hills test site outside the native range for Douglas-fir as this site had the highest mean summer temperature and longest frost free period (Table 3).

Seed source variation

Genetic variation studies for both varieties of Douglas-fir indicate that there is considerable total genetic variability in early growth traits for populations and families within populations (Campbell 1972; Rehfeldt 1974; White *et al* 1981). Sib analysis generally demonstrates that a substantial portion of this variance is additive (Campbell, 1972; Rehfeldt, 1981), although reported heritabilities are generally low to medium (Campbell 1972; Christophe and Birot 1983). The degree and structure of this variability indicate that there is opportunity for gains in growth through breeding (Rehfeldt 1983) as well as careful provenance movement (Wright *et al* 1971).

The present study demonstrated that a significant proportion of total variation in three-year height (8.4%) was due to seed source effects, which is substantial but in the low end of the range reported for interior Douglas-fir (Rehfeldt 1978; Rehfeldt 1981). This variation in height attributable to seed source effects and the analysis of variance results indicating that seed source by site interactions were not significant tends to confirm that there is an opportunity for gains in growth (at least early growth) through careful provenance selection and movement. From examination of mean heights for seed sources, it appears that this early gain could be as great as 38 percent, which is considerable but risky as correlation analysis also indicated that there was a significant and negative relationship (r= - 0.88) between height growth potential and survival.

Early growth in both varieties, like other adaptive traits, has been found to be strongly related to geographic variables (Hermann and Lavender, 1968; Sorensen, 1983), and the relation is often strongly clinal and related to environmental gradients (Campbell, 1979; Rehfeldt 1989). For the interior variety, Rehfeldt (1974) assessed second year height growth in half-sib families from 24 populations originating in Washington, Idaho, and Montana, and reported that Montana populations were shorter than those from Idaho and Washington. He also found differences in height growth between habitat types, with high elevation and frost pocket habitat types being the shortest.

In a later synthesis (Rehfeldt 1989) investigating third-year height for 228 populations of interior Douglas-fir from northeastern Washington, Idaho and western Montana found height performance was greatest for northern Idaho populations in the vicinity of the Washington - Oregon border. From this point, a general trend of declining height performance occurred to the northeast, east and southeast. He also reported that the mean height of seedlings decreased as the elevation of source increased and that clines were non-linear with greater rates of genetic change at lower elevations. He concluded from this study and an earlier study (Rehfeldt 1986) that clinal differentiation in this region was interpretable as an adaptation to a variable frost-free period related to elevation or geography which achieves a balance between selection for high cold-hardiness in severe environments and for high growth potential in mild environments. He also stated (Rehfeldt 1991), that for steeper portions of this cline (elevations below 1524 metres), populations in the same drainage separated by approximately 200 metres in elevation were genetically different (80% probability level) in growth potential. This corresponded to a climatic change of approximately 16 days in frost free period.

Although only eight seed sources were included in the present study, and most of these were not represented by climatic stations that would allow meaningful investigation of clinal relationships between climatic variables and seed source origins, the similarities in broad geographic patterns of variation as well as clinal trends are strikingly similar to those reported by Rehfeldt (1989). As with populations in Idaho and Montana, regional variation indicated that faster growing sources in the present study tended to occur at lower elevations in mountain valley corridors to the west, while slower growing populations were found at higher elevations to the east. Because these slower growing, eastern, and high elevation sources were at intermediate latitudes for the sources studied, a weak nonlinear latitudinal cline was produced showing growth to be lower for sources midway in the latitudinal range. Also, similar to the variation pattern reported by Rehfeldt (1989) there was strong evidence for an elevational cline showing the same nonlinear trend for lower growth potential of high elevation sources but greater rates of genetic change for fast growing sources from lower elevations.

Although this cline could not be directly correlated to freezing tolerance and frost free periods as was the case for Idaho and Montana populations (Rehfeldt 1986; Rehfeldt 1989; Rehfeldt 1991), the high inverse correlation coefficient for survival and height and opposite clines with elevation of source strongly suggest that slower growth at higher elevations is adaptive. Results of site correlations for traits with climatic variables would also suggest that this lower growth potential at higher elevations is a response to short and cool growing seasons.

In terms of individual sources, the Lake Edith source was clearly superior in height growth potential across test sites but predictably had much poorer survival. In contrast, the Marston source representing high elevation eastern slopes was significantly slower growing than other sources but, along with the Ghost source, consistently had the best survival.

The main practical implication of these results is that there appears to be genetically and distinctly superior seed sources for early growth potential. Although there was evidence for change of rank in height growth performance across sites, there is also evidence that differential changes leading to rank changes were small and generally occurred for seed sources of intermediate growth potential. The risk of utilizing these apparently broadly superior sources for growth potential is that they appear to be the least hardy and gains in yield are likely to be offset by higher mortality. This relationship is particularly grave for breeding programs, as selection for growth potential is almost certain to lead to reduced hardiness as determined by survival.

As with survival, it appears that careful selection of site is critical for adequate growth to be realized. This is particularly important for lower elevation, mountain corridor sources, which are generally faster growing but appear to be adapted to milder environments.

D. Plant health

In summary, study results for plant health score show:

1. plant health score was effective in detecting adaptive differences between sites and seed sources;

2. plant health on northern test sites was better than on southern sites, was highly correlated to site survival and growth and to frost free period;

3. that good early adaptive performance can be achieved on sites outside the species range;

4. southwestern sources were better adapted regardless of site than northern sources while mid latitude, high elevation, east slope sources were intermediate;

5. a near linear, inverse cline of gentle gradient exists for latitude and adaptiveness of source.

Environmental variation

It is common for experimental plantations of interior Douglas-fir established in Alberta to exhibit symptoms of climatic damage and physiological stress. Examples include the interior Douglas-fir seed source from McKale River, British Columbia (53° 40'N; 120° 12'W; 823 m), established in 1980 in the Tree Improvement Centre species trial (G118 series) at Pine Ridge Forest Nursery. This trial has surviving trees but, after fifteen years all exist as low shrubs, which exhibit shoot die-back and in most cases a failure to grow beyond average winter snow depth. Similarly, Douglas-fir seedlings established in various other trials in southwestern Alberta including the Douglas-fir drought prone site trials (G149 series), progeny trials (G153 series) and trials in this study (G152 series) continue to exhibit a range of damage symptoms, which appear to be due to varying degrees and kinds of environmental maladaption. These symptoms commonly include shoot die-back, cankers, and discolouration, malformation and loss of needles and buds.

The exact cause of these various types of damage is not known and scoring for all of them would be a daunting task. In response to this problem, the plant health scoring system used in this study was developed to provide a quick method of visually assessing seedling health by assigning a comprehensive score which could be used as an adaptive index. It was developed with the recognition that adaptiveness may be independent of superior height and shoot growth and that disease symptoms often are indicative of environmental stress (Reich and Van der Kamp 1993).

The use of this index appears to have been successful. In general, it followed a pattern similar to that for height in terms of both site and seed source response but, in the case of seed sources seems to have retained the capability of providing an adaptive index independent of height performance.

Results from analysis of plant-health scores for the eight seed sources tested across sites indicated that site effects were much more important in explaining variation than seed sources (92.1% vs. 1.2%). As with survival and height, much of this variation was due to large and signficant differences in the performance scores of seedlings on northern and southern sites (5.3 vs. 3.0).

As expected, mean plant-health scores for sites were highly and positively correlated with site survival (r= 0.98) and three-year height (r=0.98). High plant-health scores in conjunction with these high positive correlations show that Douglas-fir was well adapted on the northern sites including the one furthest outside its natural range. On the other hand, serious setback leading to mortality occurred on southern sites within and adjacent to Douglas-fir's native range.

The exact causes of damage leading to low plant-health scores are not clear but, as with 3-year height, and to a lesser extent survival, a short growing season appears to be implicated. Frost-free period for sites was found to be significantly correlated with mean plant-health scores (r= 0.89), and this is consistent with field observations made during bud flush monitoring on the Castle site, where on May 15 a late spring frost caused extensive damage to opening buds. The die-back and frost cankers observed on the few living trees remaining in the Bateman Creek site are also consistent with damage symptoms typical for frost (Reich and Van der Kamp 1993).

Frost does not seem to be as likely a cause of low plant-health scores for the Porcupine trial site for several reasons. First, bud-burst assessments done on the day after the frost damage was observed on the Castle site did not indicate any damage, and over the subsequent season bud damage was much less on the Porcupine site. Second, although mortality was higher on the Porcupine than Castle site, plant health as indicated by mean site score was better, indicating that seedlings on the Porcupine site may have been recovering from whatever agent had caused the high mortality on this plantation in the second year. Third, although the correlation between plant-health score and frost-free period was significant, the Porcupine site has a frost free period and climatic profile (Table 3) almost identical to that of Tershishner Creek where plant health was significantly better. It may be that a particularly dry summer period or winter desiccation with frozen soils was responsible for this different pattern in plant health and mortality.

Seed source variation

Although seed source effects only explained a small proportion of total variation (1.2%), it was still significant. Rank changes of seed sources among sites were frequent, but changes leading to rank switches were small. Mean comparison tests indicated the existence of distinct groups in terms of adaptive fitness, but these groups overlapped and no unique seed source in terms of plant health was found.

In terms of broad geographical trends, southwestern seed sources had significantly better health scores than northern seed sources, while high elevation eastern slope sources (Marston and Ghost) were intermediate. It is noteworthy that the southwestern group (Canmore, Crowsnest and Porcupine), which ranked highest for plant-health score, tended to be intermediate for growth potential and hardiness as determined by survival.

It is also noteworthy that plant-health scores did not appear to be clinally related to the elevation of source as was the case for survival and height. Instead, there was strong evidence for a latitudinal cline which is consistent with the geographic groupings indicated by mean comparison tests and principle component analysis. This cline shows a near linear response but a gradual gradient (change of approximately 0.1 in mean plant-health score per degree of latitude).

That a group of southwestern seed sources which were neither the fastest growing nor best surviving should be healthiest and best adapted across sites is difficult to interpret. This pattern would suggest that some damaging agent or agents were operating on test sites in a way that was injuring sources which represented the extremes for growth potential and hardiness as well as elevation. One possible explanation that would fit the geographic and clinal pattern is that greater hardiness conferred by higher elevation of origin for eastern sources was being offset by some factor which increased fitness on test sites for less hardy sources originating at similar latitude but from lower elevations closer to the continental divide.

It appears, as with survival and height growth, that site is critical to the adaptiveness of Douglas-fir within its native range. Results also suggest that, with careful selection of seed source and plantation site, Douglas-fir may provide good reforestation performance when established outside its traditional range. Great care must be taken in site selection as factors impacting health and adaptiveness appear complex and sites which from a cursory examination appear quite similar may actually be quite different (Tershishner and Porcupine sites; Table 3).

Results show that both early survival and height growth on sites were highly correlated with plant-health score despite the fact that for sources, the best plant health was achieved by intermediate performers for height and survival. This would suggest that for successful reforestation on most sites selection of the most appropriate seed source would be best served by optimizing for survival and height growth performance. It would also suggest that best overall early performance (survival, growth and adaptiveness) can be expected when southwestern sources are transferred lower in elevation northward and further away from the continental divide.

E. Bud burst

Results for bud-burst timing in this study show that:

1. bud-burst timing was quite variable for sites;
2. bud-burst timing was not correlated strongly with any variables describing test site environment;
3. there was no significant contrast in performance between northern and southern test sites as was the case for survival, growth and plant health;
4. seed source by site interaction was present but rank between sites was very stable;
5. there was evidence for a weak latitudinal and displacement east from the divide cline for sources;
6. broad regional geographic groupings of sources were not apparent, but there were unique small groups and individual sources.

Environmental variation

Variability in bud-burst date and flushing rate in Douglas-fir is considered a response to both genetic and environmental factors, which reduce risks associated with frost, drought, and cold which limit the growing season (Campbell and Sugano 1979; Rehfeldt 1979; White 1987). Bud development and bud-burst are strongly influenced by spring air temperatures as well as photoperiod, soil temperatures and chilling-period (Campbell and Sugano 1975; Campbell and Sorensen 1978;

Campbell and Sugano 1979). The rate of bud development is reportedly increased and bud-burst date moved forward by longer chilling periods and higher spring temperatures (Campbell and Sugano 1979).

Results of the investigation of site effects on bud flushing for this study appear in general to be consistent with the literature. Bud-burst timing was strongly dependent on sites which explained by far the greatest proportion of total variation (79.7%) but seed source effects were also significant. As well, the strong influence of environmental conditions on bud flush in interior Douglas-fir demonstrated by Rehfeldt (1979a), who found up to seven weeks difference in bud-burst date between the same populations planted in different environments, although less dramatic, is confirmed by the range of nine days difference in mean bud flush timing between the Diamond Hills and Tershishner Creek sites.

Somewhat inconsistent with the results reported by others was the failure to find significant simple correlations between location or climatic variables for site and bud-burst date. This was likely in part due to the low number of degrees of freedom but also the use of climatic data which did not adequately characterize mean spring conditions on sites. Reasonably, the highest coefficient recorded was with growing degree days (r= -0.93; p=0.24), which would indicate that bud burst tended to occur first on sites with warmer growing seasons. Also, it can be observed (Table 3 and 19) that there was an orderly progression for earlier bud burst as growing degree days for sites increased.

The general pattern of trait response to site environment, which produced significant contrasts between northern and southern sites for survival, height and plant health, appears to be different for bud-burst. A contrast between northern and southern sites failed to be significant and for bud burst, the Tershishner and Porcupine sites appear most similar (Table 20).

Although the F-test indicated significant site by seed source interaction, rank correlations among sites showed that rankings for bud-burst day across sites were very stable. This would tend to confirm that all sources were responding consistently to sites and that different site environments were the main determining factor in flushing date. This appears to be somewhat unusual for Douglas-fir, where strong genotype by environment interaction due to varied test environments is common for bud development and flushing (Campbell and Sorensen 1978; Steiner 1979).

Seed source variation

Despite the findings that bud development and bud-burst timing are strongly influenced by environmental conditions, particularly spring temperatures, population variation in both rates of bud development and date of bud burst for coastal Douglas-fir have been found (Campbell and Sorensen 1978; Campbell and Sugano 1979). Both studies found bud-burst of populations to be clinally related to latitude, elevation, and distance from the ocean, but responses were non-linear and complex.

Similar geographic and clinal patterns of population variation in bud burst are also reported for interior Douglas-fir (Steiner 1979, Rehfeldt 1979); however, discrepancies between reports are common and relationships, like those for the coastal variety, are often complex. Steiner (1979) investigating bud burst in eleven year old plantations of interior Douglas-fir reported that southern provenances tended to burst bud first, with the slowest flushing populations being from north central Idaho and western Montana and intermediate flushing provenances being from the eastern Rocky Mountains of Alberta and Montana.

Rehfeldt (1979a), studying the ecological adaptations of 50 populations of three-year-old interior Douglas-fir planted in twelve test environments, reported that higher elevation sources burst bud later than lower elevation sources. In another study involving 50 populations from western Montana, Rehfeldt (1982) found eastern populations bursting bud later than western populations, higher elevation populations bursting bud later than lower elevation sources and more northerly populations bursting bud later than more southerly sources.

Broad geographic patterns in bud burst timing for the present study are somewhat contradictory to those reported by others for interior Douglas-fir but consistent in their complexity. Seed source means show that, in terms of rank, the three slowest flushing sources tended to be closer to the continental divide. This is in keeping with the trend indicated by regressions and principle component analysis for bud burst to be delayed as source location approaches the continental divide. This cline appears to be non-linear and steeper as the divide is approached. These results showing more western sources to be later flushing appears to be opposite in trend to those reported by Rehfeldt (1982). This may in part be explained by the close proximity of western sources to more mountainous terrain, as there is a reported tendency for sources closer to mountains to burst bud later in order to avoid the risk of late spring frosts (Larsen 1981).

Weak evidence was also found for a latitudinal cline which was non-linear and indicated that sources midway in the latitudinal range flushed earlier. This is hard to interpret except that these central sources also tended to be further from the continental divide which may have influenced the cline. Unlike the elevational clines reported by Rehfeldt (1979a; 1982), no significant or observable relationship between bud-burst timing and elevation was discernable.

In terms of unique sources, the Crowsnest source was found to be significantly later to flush than others. In contrast, the Cline and Alstone sources from west of Nordegg appear to form a unique early flushing group which was found to be different from all but the Marston source. It would appear, that bud-burst timing variation for the sources in this study is less regional and clinal in nature and shows a greater tendency toward localized ecotypic variation.

In general, results would appear to suggest that bud-burst timing of sources is controlled more by local selection pressures than broadly regional or strongly clinal influences. This is supported by the weak evidence for geographic clines, but significant differences in seed source bud-burst timing were demonstrated by mean comparison tests. The main geographic relationship appears to be for delayed bud burst of sources from closer to the continental divide and interestingly, as indicated by principle component analysis, a tendency for these sources to have greater growth potential.

F. Bud set

In summary, results for bud-set timing in this study show that:

1. there were large differences in bud-set timing for sites with bud-set occurring from late July to late August;
2. as for bud-burst timing, there was not a significant contrast between bud-set timing on northern and southern sites;
3. bud-set was delayed on higher elevation test sites and sites with cooler growing seasons;
4. bud-set timing was only found to be different for the Cline River and Alstone sources;
5. despite small differences in bud-set timing of sources, there was a significant correlation between bud-burst and bud-set timing;
6. there appears to be a weak clinal relationship with distance east from the continental divide with bud-set being delayed as the continental divide is approached;
7. late bud set sources tend to be more westerly, less hardy and of greater growth potential.

Environmental variation

Environmental influences on bud set are generally reported not to be as great as for bud burst (Campbell and Sorensen 1978). Environmental factors which do influence bud set and are reported to significantly hasten its onset and dormancy are shortened photoperiods, cool night temperatures and drought stress (Lavender *et al* 1968).

Over much of its southern and interior range, the majority of shoot elongation in Douglas-fir is reported to be complete by mid July except where unseasonal midsummer precipitation may initiate a short period of secondary flushing (Lavender *et al* 1968). This early bud set is considered to be a response to mid summer drought in drier portions of its range (White 1987) and is known to be a frequent cause of early bud set in first-year seedlings (Hermann and Lavender 1990), where terminal buds may set within three weeks of germination despite indeterminate growth potential (Rehfeldt 1983).

In the present study, environmental variation as determined by variance components for site effects (79.8%) was very similar to that found for bud burst (79.7%). Bud set varied 4.6 weeks between the earliest (Diamond Hill) and latest (Porcupine Hills) sites, and was determined to be complete by the beginning of the last week of July on the Diamond Hills site, but not until the last week in August for the Porcupine Hills test site. As for bud-burst timing, there was no difference in bud-set timing between southern and northern sites, and the Terhsishner and Porcupine sites were most similar.

Simple correlations indicated high coefficients between bud-set week of sites and elevation (r= 0.96) and growing degree days (r= -0.99). This indicates that sites with cooler growing seasons had delayed bud-set while sites with warmer summers substantially hastened bud-set. Bud-set timing on sites was also found to be significantly correlated with bud-burst timing (r= 0.95) but the duration of growth was substantially different for sites. By observing Tables 20 and 22, it can be calculated that the mean growth period on the Diamond Hills site was almost 24 days shorter than that for the Porcupine Hills site. If short growing seasons are limiting to growth, as appears to be the case in this study, this compression of growth period on warmer sites may be an important factor in explaining the exceptional performance for survival, growth and plant health for all sources on the Diamond Hills test site.

Only timing on the Diamond Hills site would indicate the possibility that early bud-set occurred due to drought. However, given the annual and summer precipitation (Table 3), the sites latitude (Table 2) and the exceptional survival and growth on this site drought seems an unlikely cause.

Seed source variation

Typical of many North American trees, growth duration in Douglas-fir is substantially shorter than the frost-free period of its place of origin. Timing of bud-set is frequently reported to be related to the risk of injury by late summer and fall frosts for both varieties and appears to be under strong genetic control(Campbell and Sorensen 1973; Rehfeldt 1991).

Significant variety, provenance and population differences in bud-set timing are reported. Rehfeldt (1977), studying coastal, interior, and hybrid populations, found that interior populations, on average, set bud two weeks earlier than coastal populations. In general, low elevation, southern and more maritime populations are reported to set bud later (Campbell and Sorensen 1973; Campbell and Sorensen 1978 Sorensen 1979), but geographic patterns are complex and at times reversed (Campbell and Sorensen 1978; Sorensen 1979; Rehfeldt 1979a).

Wright *et al* (1971), studying ten provenance groupings from 128 stands collected throughout the natural range of Douglas-fir, found that Alberta and central Montana sources planted in Michigan set bud almost two months earlier than Arizona and New Mexico sources. They also reported a good correspondence between early bud set and winter hardiness.

Substantial differences in bud-set timing for seedlings has also been reported for interior Douglas-fir from four physiographic provinces in the northern United States (Rehfeldt 1979a, 1982, 1983 and 1988). In a synthesis of the 228 populations, Rehfeldt (1989), states that "correlations were so strong (r>0.75) for the traits such as bud set, height, and injury from fall, winter, or spring freezing that the entire suite can be indexed by single traits." From this it can be inferred that bud set roughly follows the same pattern of geographic variation as height and freezing injury. Populations at a common elevation from north eastern Washington and north western Idaho were found to set bud latest with bud-set occurring progressively earlier for populations to the northeast and southeast as the frost free period declines (Rehfeldt 1991).

Although seed source effects for bud-set timing in the present study accounted for a significant proportion of total variation (3.9%), sources never varied more than two weeks in timing on a given site and only varied by 1.2 weeks on average. Mean comparison tests failed to identify any unique source in terms of bud set, but the Cline and Alstone sources were significantly earlier to set bud than all but the Ghost source, which may be a function of the large standard error for this source (Table 25). Interaction was not significant and rank changes were quite stable for the earliest and latest sources but changed frequently for sources of intermediate bud-set timing.

As reliable climatic data were not available for most seed source origins, correlations between bud-set timing and sources were restricted to geographic variables. These correlations failed to produce any significant results and the only significant coefficient occurred with bud-burst (r= 0.73). This along with analysis of variance results for both bud burst and bud set indicates that growth duration for sources is similar but distributed differently over the growing season.

As reported in other work, broad geographic patterns in the present study appear complex and difficult to interpret. This is complicated by the fact that mean comparison tests only detected two significant groupings. The Cline and Alstone source appear to be different from all others except the Ghost source by having earlier bud-set (and because of the correlation apparently earlier bud-burst as well). These two sources are in the Kootenay plains area west of Nordegg and may be unique in terms of bud phenology due to geographic isolation from other Alberta sources.

Bud-set timing has also been found to be clinally related to geographic variables of seed source origin within provinces. Generally, more interior, higher elevation and higher latitude sources have been found to set bud earlier (Hermann and Lavender 1968; White 1987; Sorensen and Campbell 1978; Sorensen 1979; Rehfeldt 1979a; Rehfeldt 1982).

Strong non-linear elevational clines and weak geographic clines are also reported for bud-set date and the intercorrelated traits of freezing resistance, growth and secondary flushing in Idaho, Montana, and eastern Washington

(Rehfeldt 1979a, 1982, 1983, 1988). These strong climatically driven environmental clines are also strongly correlated to the frost-free periods for seed source origins (Rehfeldt 1991).

Unlike results reported by other authors, no evidence was found for elevational clines in this study. The only significant cline detected for bud-set timing of sources was with distance east from the continental divide on the Porcupine Hills site. This cline was linear and indicated that source bud-set timing occurred earlier with increased easterly displacement of sources from the continental divide. This trend was reinforced by principle component analysis, which also demonstrated earlier bud set as easterly displacement from the divide increased. It is also consistent with the reported patterns for broad geographical variation, as it follows a trend for earlier bud set as continentality of climate increases and is likely a response to the increased risk of early fall frost (Larsen 1981).

Although no significant correlations were produced between bud-set and traits other than bud-burst, principle component analysis demonstrated that sources which had later bud-burst (later growth period) tended, for a given latitude, to be more westerly, have greater growth potential, be less hardy and be associated with lower elevation mountain corridors. This would suggest that these sources are adapted to milder environments associated with mountain corridors, where there is a greater risk of late spring but lesser risk of early fall frosts. These sources may be suitable for more eastern sites provided they are warm enough to prevent lengthening of the growth period and are not susceptible to early fall frosts. As these sources are adapted to milder environments, movement to higher elevations or any area with a shorter cooler growing season is likely to increase the risk of maladaption.

Conversely, it appears that seed sources with earlier bud set, and therefore, growth period, are, for a given latitude, more easterly, from higher elevations, hardier and have lower growth potential. These sources can likely be moved substantially lower in elevation and southern latitude members moved northward successfully, but movement westward into areas with increased risk of late spring frosts may adversely affect growth, health and long term survival. This tendency to grow early in the season and be at risk to late spring frosts may in fact explain why the generally hardier, easterly and high elevation sources in this study tended to have poorer plant-health scores than southwestern sources.

Principle component analysis in this study suggests that bud-set timing for Alberta interior Douglas-fir has similar relationships with other traits as was found by Rehfeldt (1991) for interior Douglas-fir from the interior northwestern United States. In this region, bud-set timing was found to be intercorrelated with several other traits, which formed an adaptive complex selecting for high growth potential in mild environments and high freezing tolerance in severe environments (Rehfeldt 1989; Rehfeldt 1991). Because of this, it can be expected that, in southwestern Alberta as well, strong selection for height growth potential in interior Douglas-fir may delay bud set and increase the risk of fall freezing damage.

VI SUMMARY

Test Sites

The dramatic impact of test sites on mean trait performance confirms that, as elsewhere, interior Douglas-fir from southwestern Alberta is native and adapted to areas that are highly heterogenous in terms of environmental conditions. It also underscores the need for careful site selection and care in seed movement if reforestation efforts are to be successful both within or outside its native range.

From test site performance results it appears that short cool growing seasons (as defined by mean summer temperature, growing degree days and particularly frost free period) are the major limiting factor to early survival, growth and health of Douglas-fir in southwestern Albtera. The difference in performance for northern and southern test sites for these traits appears in part to be due to their milder climate, although it does not explain why performance was so different between the Porcupine Hills and Tershisner Creek test sites, which appear climatically quite similar. Although not directly correlated with survival, growth and plant health, the duration of growth for sources, as defined by bud-burst and bud-set timing, appears to have been substantially compressed on sites with longer and warmer growing seasons. This compression likely provided an indirect benefit to survival and performance through frost avoidance.

In conclusion, Results would indicate site differences are more important than broader regional differences in the successful early establishment of Douglas-fir and that there is both an opportunity for movement outside its native range and risk in establishment within its range if plantation sites are not carefully screened for suitability.

Seed sources

Study results showed that there were both superior individual sources and differences among groups of sources in survival and growth performance across sites. These differences appear to be both broadly geographic and clinal. Regional differences indicate more western and mountain corridor sources have greater early growth potential while southeastern foothills sources are slower growing. There is strong evidence for an elevational cline and weaker evidence for a latitudinal cline for growth potential with lower elevation and northern sources showing the best growth. Unfortunately, there appears to be a strong inverse correlation (r= -0.88) between growth potential and hardiness. As a result, hardiness as determined by survival in this study and the broad geographic and clinal patterns for survival are the reverse of those for growth. These results are not unique but are also reported for interior Douglas-fir from Idaho, Montana and northeastern Washington (Rehfeldt 1989; Rehfeldt 1991). This strong inverse relationship between early growth and hardiness is likely to present a substantial barrier to breeding programs attempting to increase growth and yield while maintaining adaptedness for a reasonable range of plantation environments.

Unlike the results for sites, where plant health was intercorrelated with survival and growth, plant health for sources was not significantly correlated with any of the other traits studied. Although not significant, coefficients were higher with bud-burst (r= 0.60) and bud-set (r= 0.63) than with growth (r= -0.23) and survival (r= 0.56). The weak relationship with these later two traits appears to be due to the better adaptive performance (higher mean health score) of southwestern sources, whose performance for growth and survival was intermediate. Strong evidence for a gradual latitudinal cline showing better health scores for more southern sources, and this regional pattern for better adaptive performance of southwestern sources indicates that, over the long term, southern and particularly southwestern sources can be expected to perform best over a range of sites.

Bud-burst and bud-set timing for sources and groups of sources differed significantly from each other but also were significantly correlated (r= 0.73), indicating that early bursting sources were also early to set bud. Analysis of variance of the growth period calculated as the number of days between the mean bud-burst date and midpoint date of mean bud-set week indicated that the duration of growth for sources did not differ. Regional patterns for these two traits indicated that bud-burst timing of sources was strongly influenced by local environments, while bud set showed a broad regional trend for western corridor sources to set bud later. For both these traits there was a weak clinal trend for western sources nearer to the continental divide to have both delayed bud burst and bud set and therefore a tendency to grow later in the season, although the duration of growth appeared no different from more eastern sources. This pattern is not unusual and has been described as an adaptation of cordilleran populations to avoid late spring frosts and for more continental populations to avoid early fall frosts (Larsen 1981).

Although no significant correlations were recorded between the two bud phenology traits and other performance traits, principle component analysis indicates a trend for western sources with a later growth period to be from lower elevations, be from mountain corridor valleys, and for a given latitude to have greater growth potential but be less hardy.

Suggestions for further research

The experimental design of the present study is best suited to analysis of variance for detection of differences in trait performance between seed sources across a range of test site environments It has limited capability for defining clinal relationships, as the number of sources is small and information on the environmental parameters defining the source origins is not readily available. As there is strong evidence for clinal relationships for important performance traits with elevation and latitude and weaker evidence for trends related to distance from the continental divide, a similar study involving an expanded number of sources and better source information would be very valuable in a more definitive description of these clines.

This study is based on trait measurements made after only three years of field-testing of four-year old stock. As a result, despite detection of interesting early seed source differences and clinal trends, results are only tentative for the long term. Relationships once seedlings are established may change dramatically. As an example, it would be interesting to see if the southwestern sources which appeared to be best adapted across sites (i.e., had the best mean plant-health scores) in time outperform the sources which initially seemed more hardy (best survival) or were faster growing. This will require additional measurements and analysis of this trial series.

From analysis of variance and principle component analysis it would appear that in addition to broad regional and clinal trends there are also ecotypic patterns of variation for traits. This is most readily observed in the large differences in trait expression among mountain corridor sources and between these sources and the eastern foothills group. This would suggest that genetic population differentiation may be due to both local and regional selection pressures as well as the possibility of a different migration path for corridor and east slope sources. Additional population studies and the application of biochemical and molecular genetics techniques would likely prove very useful in gaining insights into the obscure origins and evolutionary processes shaping the genetic composition of native Alberta populations.

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APPENDICES

APPENDIX A. Seed source location, collection and population information

a. Crowsnest Pass seed source

The Crowsnest Pass seed source was represented by cones and seed hand collected from several squirrel caches in the vicinity of the Blairmore town site. As a mountain corridor seed source it was likely subject to pollen dispersal from isolated trees and stands in the pass to the west and therefore in terms of gene flow to populations across the divide in British Columbia. These populations are also connected by frequent stands to the east which extend south toward Waterton National Park and north to the Porcupine Hills, although prevailing winds in the corridor do not favour gene flow from these sources.

b. Porcupine Hills seed source

The Porcupine Hills provenance was represented by a single tree collection made from a mature tree in a stand just below and adjacent to the Porcupine Hills test site in the Sharples Creek drainage. As a result, the experimental trees representing this provenance are primarily half-sibs and as such, probably do not fully represent the array of genotypes and variation for traits being investigated for this area.

There is likely unrestricted gene flow for Douglas-fir in the Porcupine Hills due to its abundance. As well, there is reasonable opportunity for gene flow from populations to the west and south along the base of the Livingston Range which are connected to the Porcupine Hills through smaller populations in the Whale Back Ridge and parallel hills.

c. Marston Creek seed source

The Marston Creek seed source was represented by a ten-tree collection made from one of two small adjacent stands of uneven aged Douglas-fir occurring just inside the Green Zone boundary west of Longview. The only potential for gene flow from outside these two stands is from scattered trees existing along the Highwood River where it flows through the front range. This seed source is unique as it appears to represent an isolated remanent with no apparent migration path.

d. Canmore Corridor seed source

Seed used to compose the Canmore provenance was collected from ten Douglas-fir trees in a mixed Douglas-fir, white spruce and lodgepole pine stand in the Canmore corridor between the town of Canmore and the Banff National Park gates. In this area, Douglas-fir occurs in both pure and mixed stands and is fairly common at low to mid elevations.

Gene flow from populations to the east is possible but likely restricted due to the prevailing westerly winds in the corridor. Gene flow from populations to the west in Banff National Park and adjacent areas of British Columbia is likely and would present a possible historic migration path for the species into the foothills area east of the corridor.

e. Ghost River seed source

The Ghost seed source was collected from ten trees in a dominantly Douglas-fir stand located in the MacDonald Hills just inside the Green Zone west of Calgary. The stand was unevenly aged and has a high proportion of merchantable trees (typed as C3Fd in the phase III inventory). Douglas-fir is generally a minor stand component in this area but occasional pure stands occur especially in drier locations. There is potential for gene flow with populations to the west in the Canmore Corridor but the scattered nature of trees and stands in the area may restrict gene flow. There is no apparent opportunity for north or south gene migration along the foothills.

f. Cline River seed source

The Cline seed source was composed from seed hand picked from several squirrel caches in a large stand occupying a glacial fluvial bench below Cline Lookout along the east bank of Abraham Lake. It is representative of Douglas-fir in the Kootenay Plains region of the North Saskatchewan River corridor. The stand is uneven aged and composed of various proportions of lodgepole pine, Douglas-fir, white spruce and poplars. Although Douglas-fir is not abundant in the area, scattered individuals and stands can be found along the full length of Abraham Lake. Gene flow from the east is likely restricted due to the scattered nature of trees and stands and strong westerly winds in the corridor. Gene flow from the west is also likely impeded by the discontinuous distribution of Douglas-fir but would be aided by prevailing winds and the existence of scattered Douglas-fir stands upstream along the North Saskatchewan River into British Columbia.

g. Alstone Creek seed source

The Alstone Creek seed source represents seed collected from five Douglas-fir trees along the west side of Abraham Lake in the vicinity of Alstone Creek. The distribution of Douglas-fir is quite sparse in this area and this collection represents the near eastern limit for the occurrence of Douglas-fir along the North Saskatchewan River corridor. Gene flow from intermittent stands and isolated trees to the west is possible.

h. Edith Lake seed source

The Edith Lake seed source was composed from more than 50 Douglas-fir trees from the access to Edith Lake just north of the Jasper town site. This source represents interior Douglas-fir from the montane section of the Athabasca River corridor and the northern extent for known populations of the species in the province. Gene flow from the east would be restricted by prevailing winds in the corridor and the limited range for Douglas-fir to the east. Gene flow from the west is less restricted due to prevailing winds and greater prevalence. The existence of Douglas-fir along the Miette River toward the British Columbia border indicates a possible historic migration path for the species.

APPENDIX B. Location and ecological description of field test sites

a. Castle River field test site

The Castle River site is located on a glacial fluvial terrace along the Castle River adjacent to the Castle River Ranger Station. The site represents a toe slope position and was formerly occupied by a mixed lodgepole pine and aspen poplar stand with a minor component of white spruce. The site was logged in 1981 and developed as a genetics experimental area. The parent material on the Castle site is a deep, medium to coarse textured, fluvial loam with a low content of fine gravel. The soil as determined by a single pit dug on the edge of the site and field classified according to the criteria established by the Canada Soil Survey Committee (1978) was a well drained Eluviated Dystric Brunisol.

A climate station is situated within 500 metres of the site at the Ranger Station. Thirty year climatic normals (Atmospheric Environment Service 1982a, 1982b and 1982c) for this station were used to characterize the climate for the Castle trial site (Table 3).

Although the Castle River test site is located within the Montane Natural Subregion (Table 3) and falls within the mapped native range for Douglas-fir (Fig. 1) there is only one Douglas-fir in the immediate vicinity of the site. Scattered Douglas-fir occurs along the lower slope in the general vicinity but is more prevalent in mid to upper slope positions and on the opposite side of the valley.

b. Porcupine Hills field test site

The Porcupine Hills test site is located on a high elevation plateau on the west side of Heath Creek below Porcupine fire tower. The original stand was primarily lodgepole pine, with lesser amounts of white spruce, Douglas-fir and subalpine fir. The presence of subalpine fir and occasional hybrids between white and Engelmann spruce in the vicinity indicate that this site represents upper elevations of the Montane Subregion (Alberta Environmental Protection 1994). Both mixed and pure Douglas-fir stands are common in the vicinity. The site was logged in 1981 due to bark beetle attack of the lodgepole pine and developed as a genetics experimental area in 1986.

Parent material on the Porcupine site is a cobbly, medium textured till veneer of approximately 50 cm over bedrock. The soil as determined by a single pit dug adjacent to the site and field classified according to criteria established by the Canada Soil Survey Committee (1978) is a well drained very acid Eluviated Dystric Brunisol.Porcupine fire tower is within two kilometres of the trial site and is the nearest weather station. As it only collects seasonal data, mean annual temperature, precipitation and growing degree days information are not available; the frost free period value used in Table 3 to characterize the trial site is taken from thirty-year climatic normals (Atmospheric Environment Service 1982c) for this station.

c. Bateman Creek field test site

The Bateman Creek test site is located within the Jumping Pound Demonstration Forest approximately 50 km west of Calgary. It is classified as part of the Lower Foothills Subregion of the Boreal Foothills Natural Region but borders on the Subalpine Subregion (Alberta Environmental Protection 1994). The original stand was mixed lodgepole pine, aspen poplar and white spruce. The site was logged in the 1970's and in 1986 a genetics experimental area was developed.

The topography of this trial site is rolling to undulating foothills and the parent material is clay loam till. Soils on the trial site are mapped as well drained, moderately stony to very stony, Orthic Gray Luvisols (Leskiw 1986). There is one known Douglas-fir growing in the vicinity and a small uneven aged stand of Douglas-fir is located just to the east of the Demonstration Forest.

The most representative climate station for the trial site which collects complete data is the Elbow Ranger Station located approximately fifteen km south. Although it is at some distance, elevations and slope position are nearly identical. Thirty year climatic normals (Atmospheric Environment Service 1982a, 1982b and 1982c) for this station are used to represent the trial site in Table 3.

d. Tershishner Creek field test site

The Tershishner Creek test site is located west of Nordegg along Tershishner Creek just above the Bighorn Dam on Abraham Lake. This site is located on the boundary between the Upper Foothills Natural Subregion and the Montane Natural Subregion (Alberta Environmental Protection 1994) which is associated with the North Saskatchewan River Valley.

The original stand on the site was composed of lodgepole pine, white spruce and aspen poplar. It was logged in the late 1960's and planted with lodgepole pine. In 1986, a small area was chosen for development as a genetics experimental area. No Douglas-fir occur on the site but scattered trees can be found along the creek upstream from the site.

The general area is mountainous and the site is located on a glacial fluvial upper terrace along the west side of the North Saskatchewan River. The parent material is a relatively stone free medium textured glacial fluvial blanket or veneer over a gravelly till. The soil as determined by a single pit adjacent to the site is field classified as a moderately well drained Orthic Gray Luvisol.

The nearest climate station is located just below the site at the Bighorn Dam and thirty year normals (Atmospheric Environment Service 1982a, 1982b and 1982c) for this station were used to represent the trial site (Table 3).

e. Diamond Hills field test site

The Diamond Hills test site is located 25 kilometres north of Rocky Mountain House on the top of the west bank of the

North Saskatchewan River. The area is classified as belonging to the Lower Foothills Subregion of the Boreal Foothills Natural Region (Alberta Environmental Protection 1994) and is well outside the natural range of Douglas-fir. The original site was primarily aspen poplar with a small component of lodgepole pine and white spruce. During the period 1960 to 1962 the area was strip scarified and hand seeded to white spruce. Development of the site as a genetics experimental area was started in 1985.

The area in the vicinity of the site is gently rolling. The site itself is inclined and the parent material is a stone free silt loam to loam textured glacial fluvial veneer or blanket over till. The soils on the inclined portion of the site where the trial is planted are moderately well to well drained Eluviated Eutric Brunisols to Orthic and Brunisolic Gray Luvisols which are acid in the upper solum but have carbonates beginning at 50 to 90 cm.

Although the nearest climatic station is at Rocky Mountain House which is 25 kilometres to the south, the climatic data are likely representative for the trial site as it is of similar elevation and proximity to the North Saskatchewan River. Climatic normals (Atmospheric Environment Service 1982a, 1982b and 1982c) for the Rocky station are used to represent the site in Table 3.

APPENDIX C.

Table C1. Plant Health Scoring System

Score	
6	Seedling shows no visible sign of damage and is vigorous with good colour
5	Seedling shows slight damage to foliage or buds, or slight foliage discolouration
4	Seedling shows signs of climatic damage and setback including slight shoot dieback, defoliation or discolouring but still good biomass, buds, and signs of continuing growth
3	Seedling suffering from significant needle, bud or shoot damage, or quite chlorotic and showing signs of poor vigour in the form of spindly shoots, short needles and small buds
2	Seedling suffering from severe dieback of shoots, weak growth, low biomass, small buds and spindly shoots but still showing signs of weak growth
1	Seedling severely damaged and spindly with green foliage but very few and small buds and little sign of growth or potential for recovery

Table C2. Bud-Set Scoring System

Score	
0	no sign of terminal or lateral bud development on any shoots
1	terminal bud visible but no laterals visible or visible but not showing any swelling
2	terminals and laterals visible on shoots with swelling noticeable; lateral buds showing purplish tips but no bud scales; terminal shoot buds showing purplish tip with some mottling indicating bud scale development
3	terminals and laterals on shoots well developed, purplish and showing visible scales
4	some or numerous buds flushing a second time with use of a modifier of 0,1,2 or 3 to monitor bud set of reflushing buds

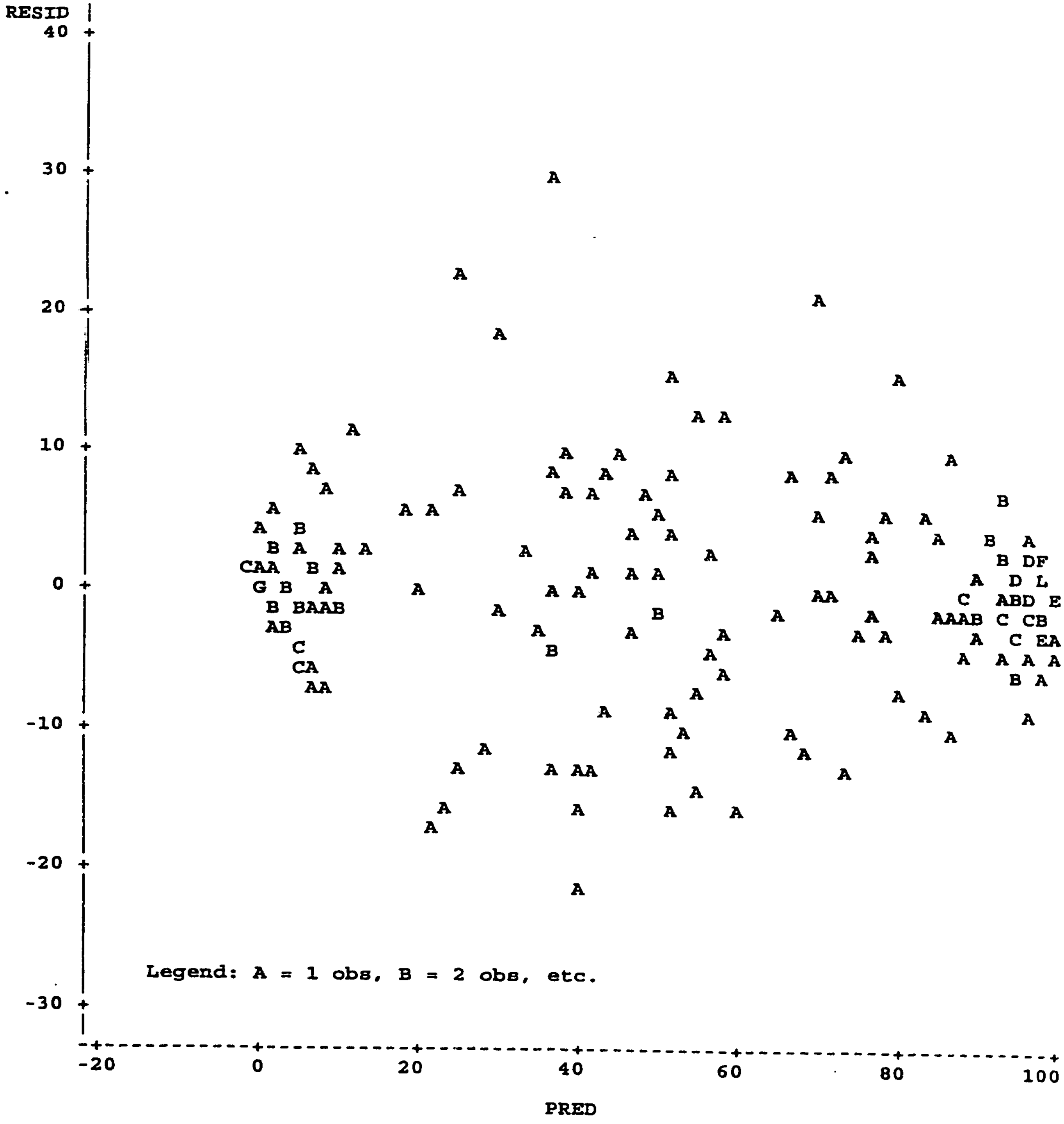

Figure D1. Plot of residuals against predicted values for variable percent survival

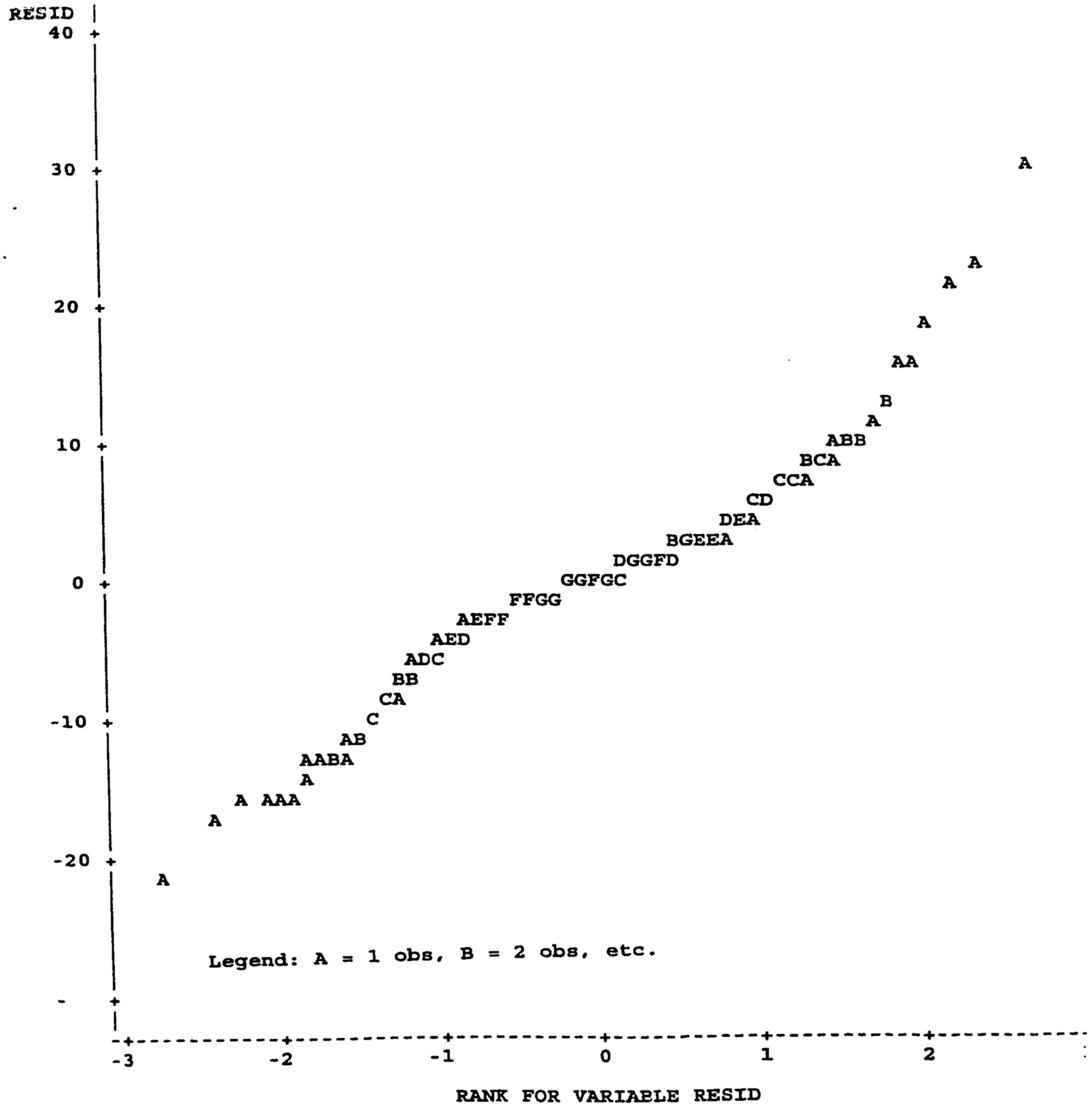

Figure D2. Plot of residuals against residual ranks for variable percent survival

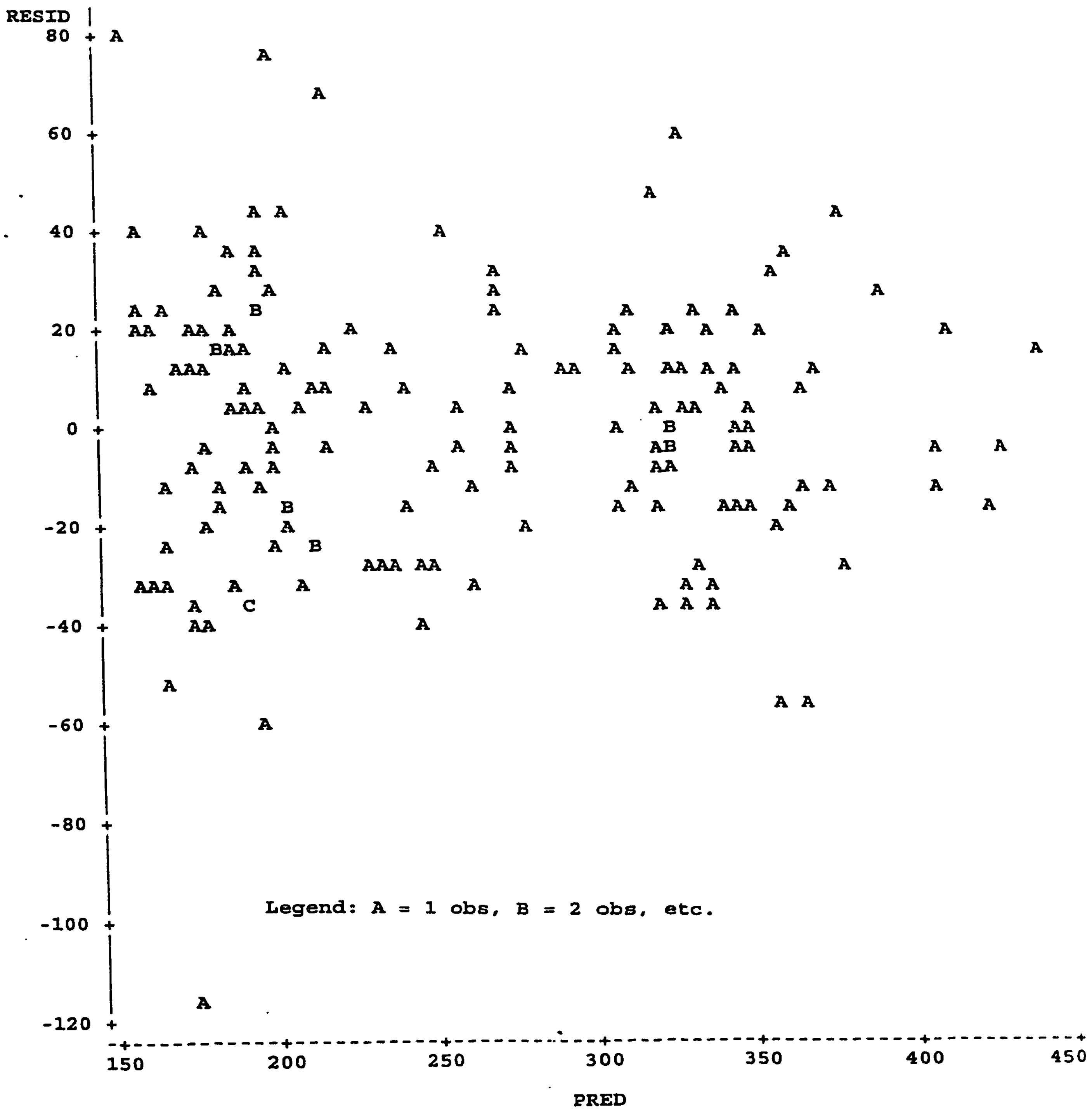

Figure D3. Plot of residuals against predicted values for variable total height

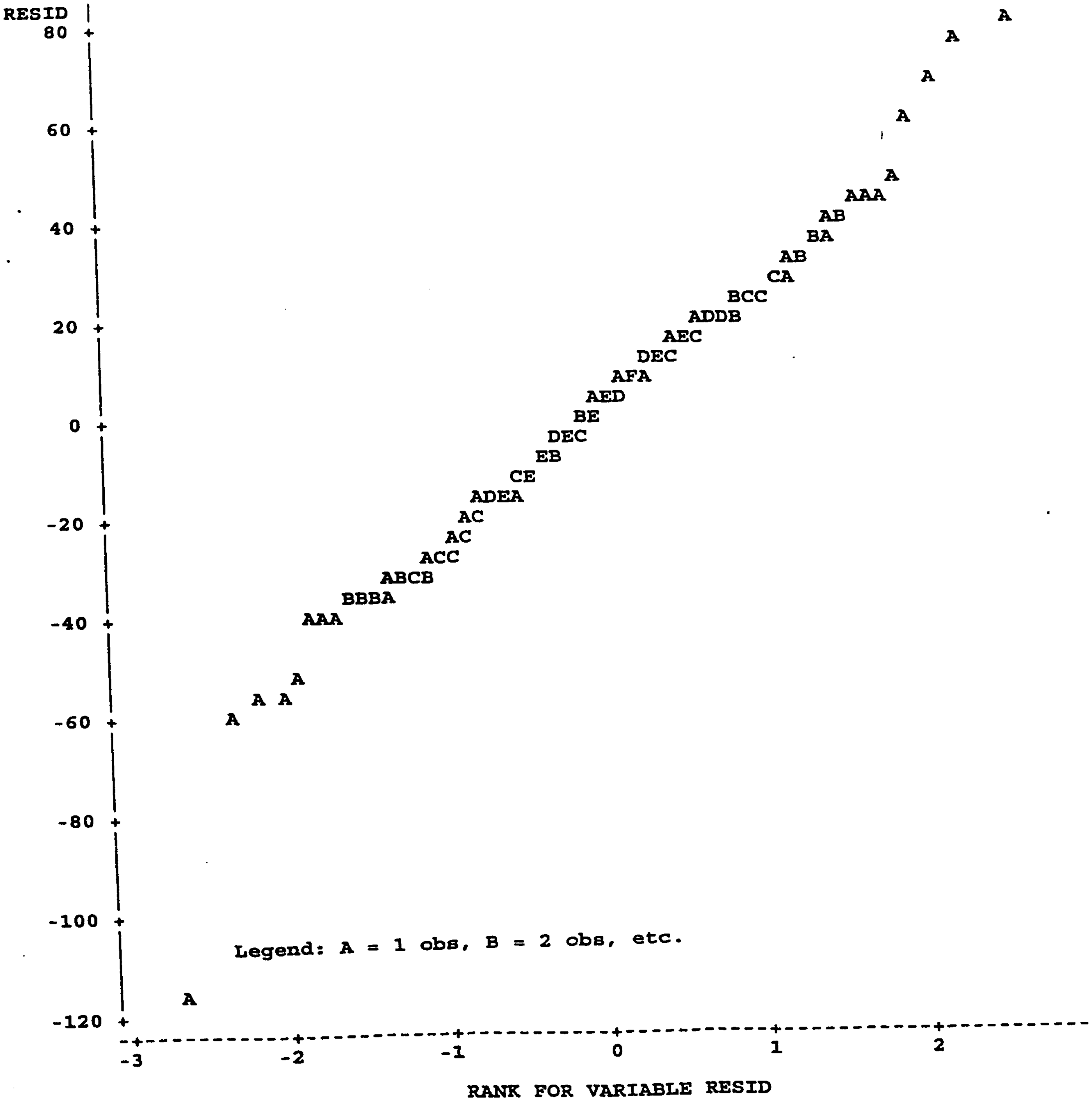

Figure D4. Plot of residuals against residual ranks for variable total height

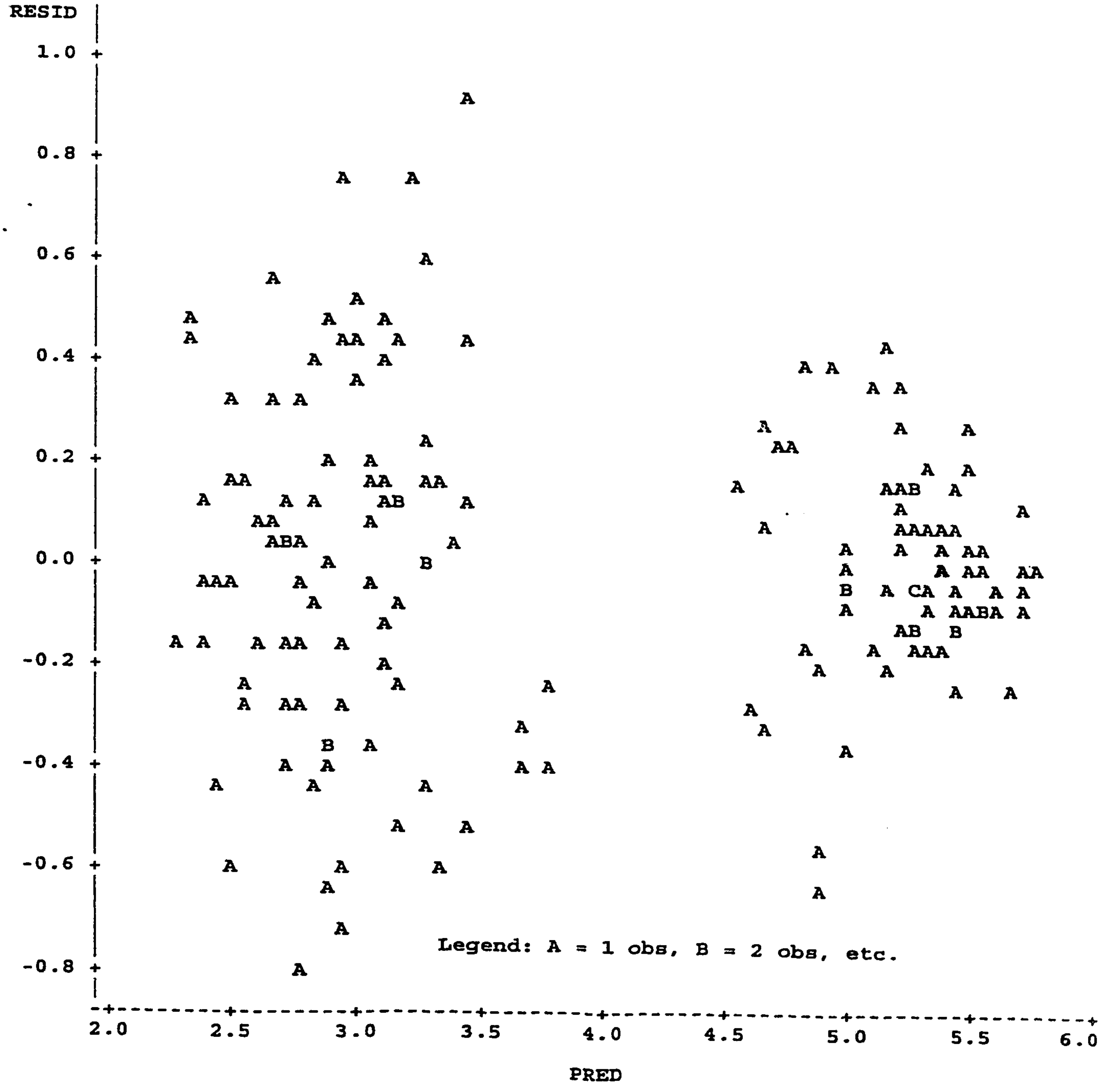

Figure D5. Plot of residuals against predicted values for variable plant health score

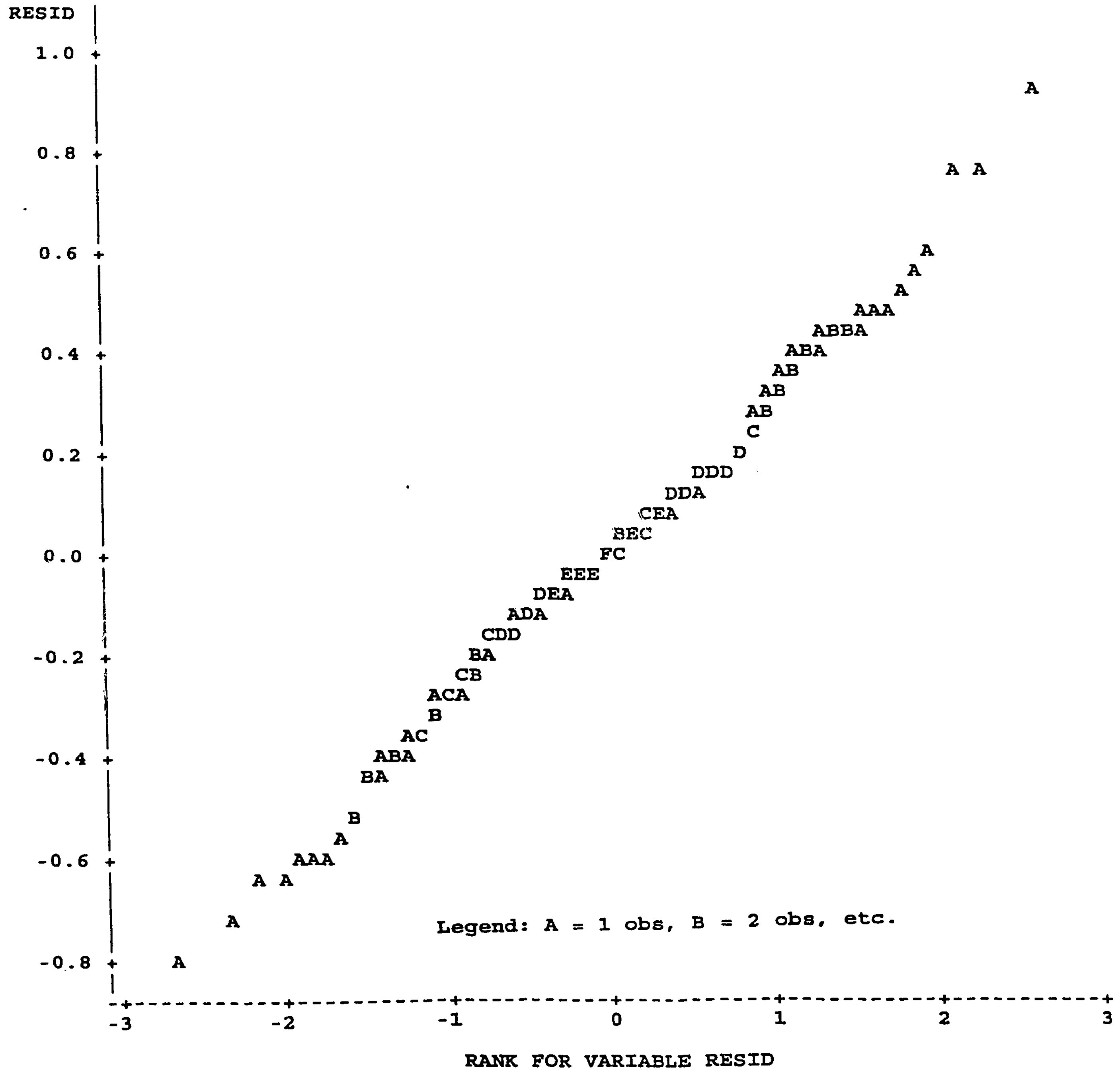

Figure D6. Plot of residuals against residual ranks for variable plant health score

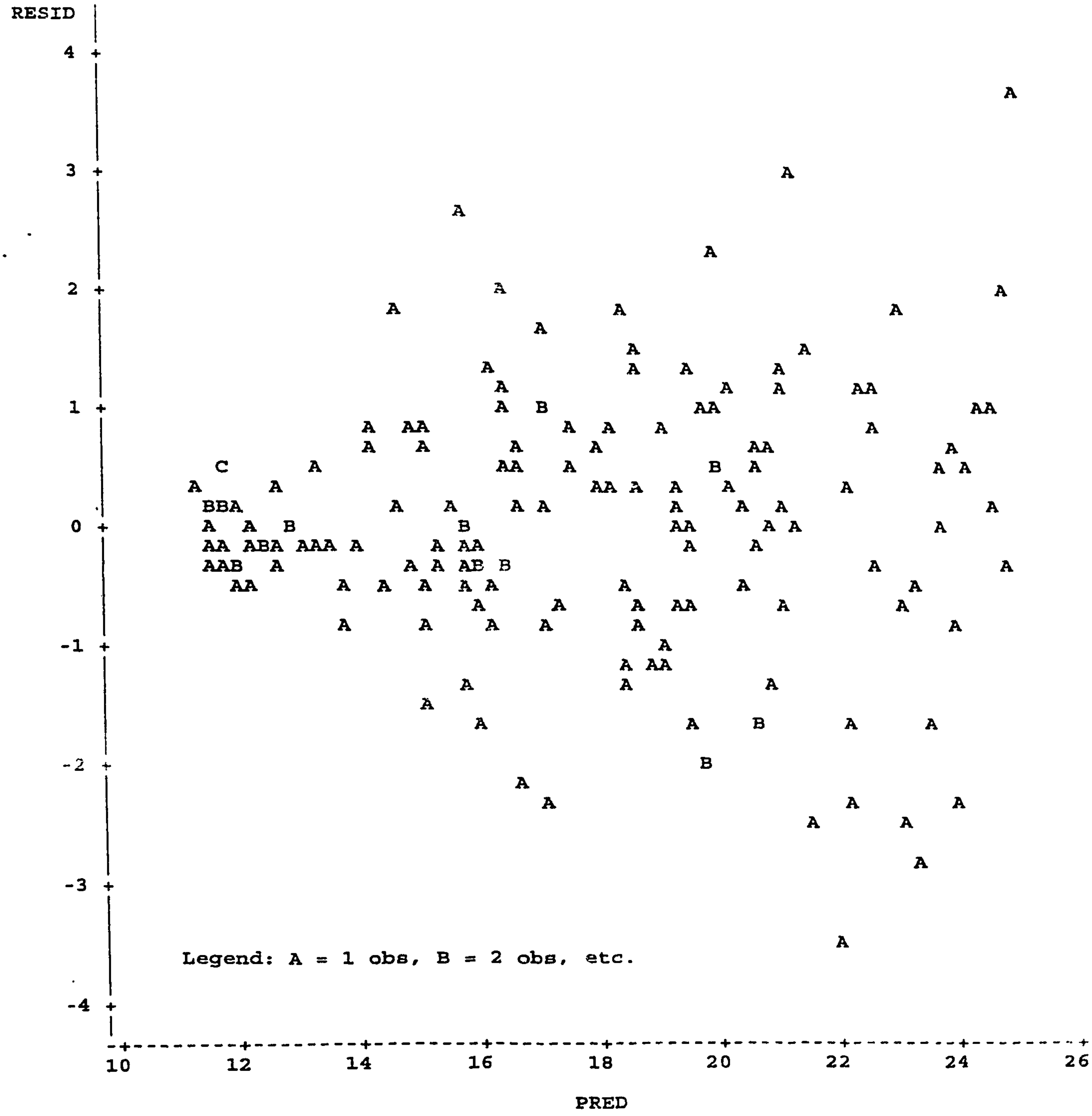

Figure D7. Plot of residuals against predicted values for variable bud burst day

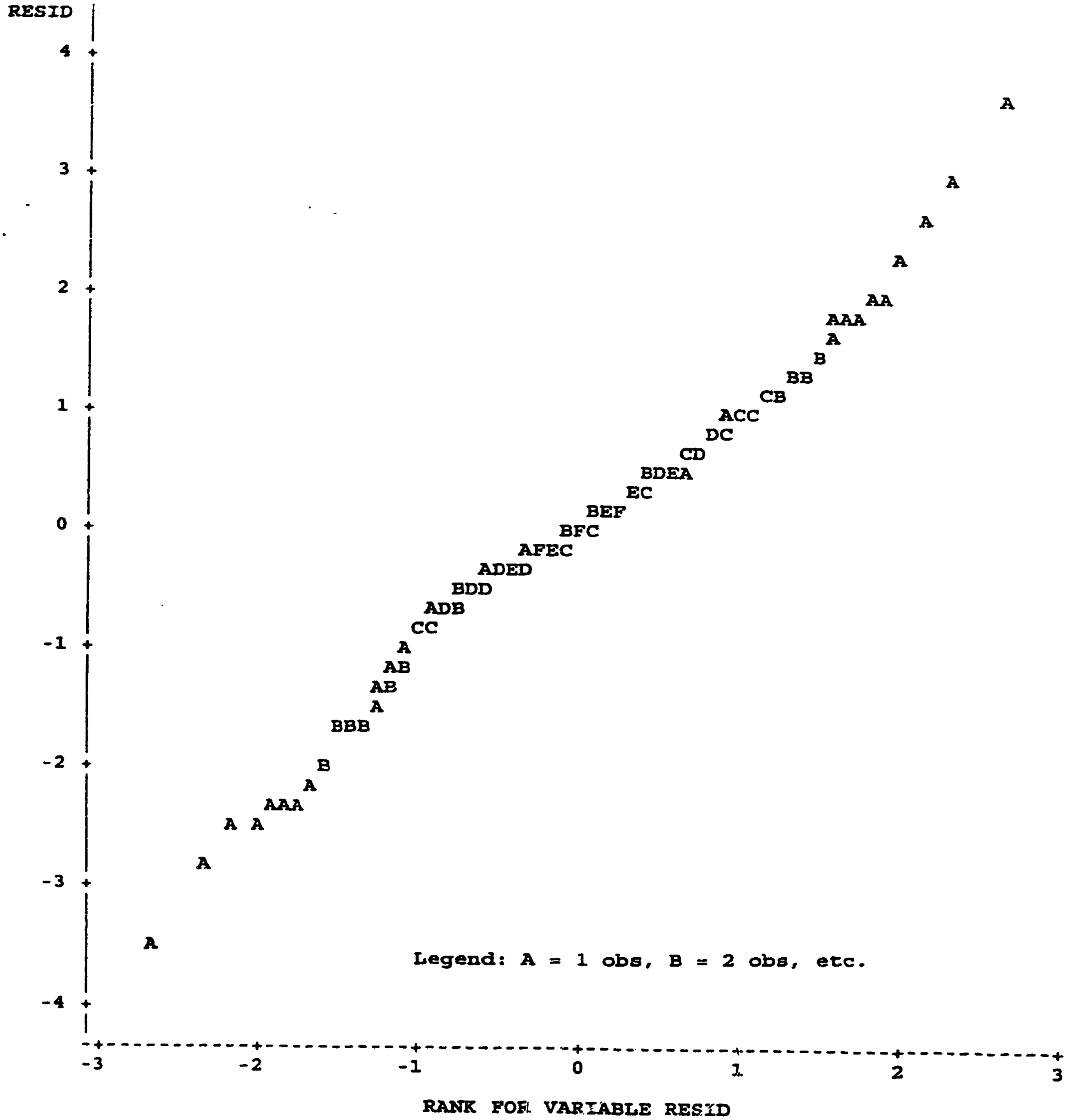

Figure D8. Plot of residuals against residual ranks for variable bud burst day

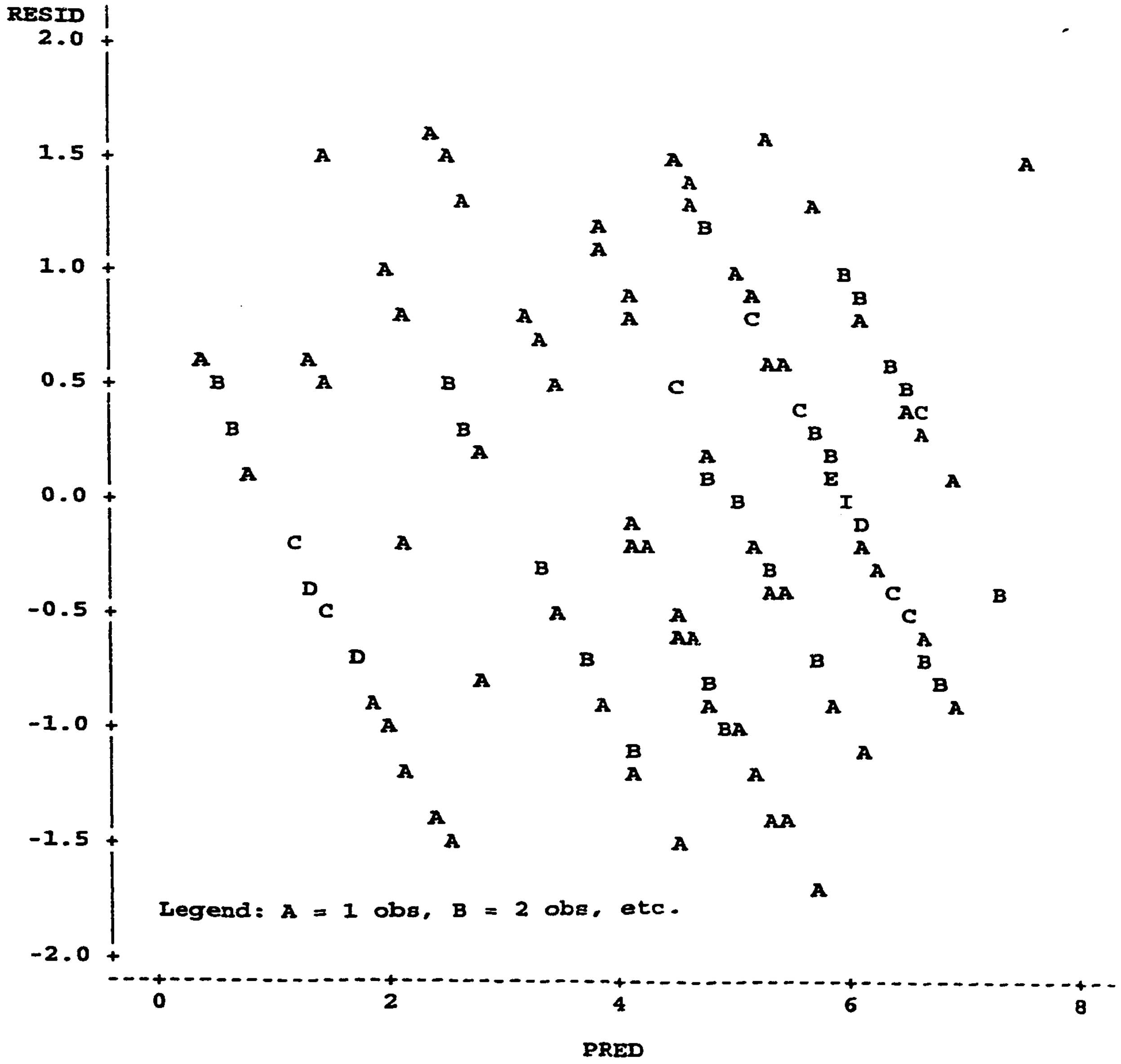

Figure D9. Plot of residuals against predicted values for variable bud set week

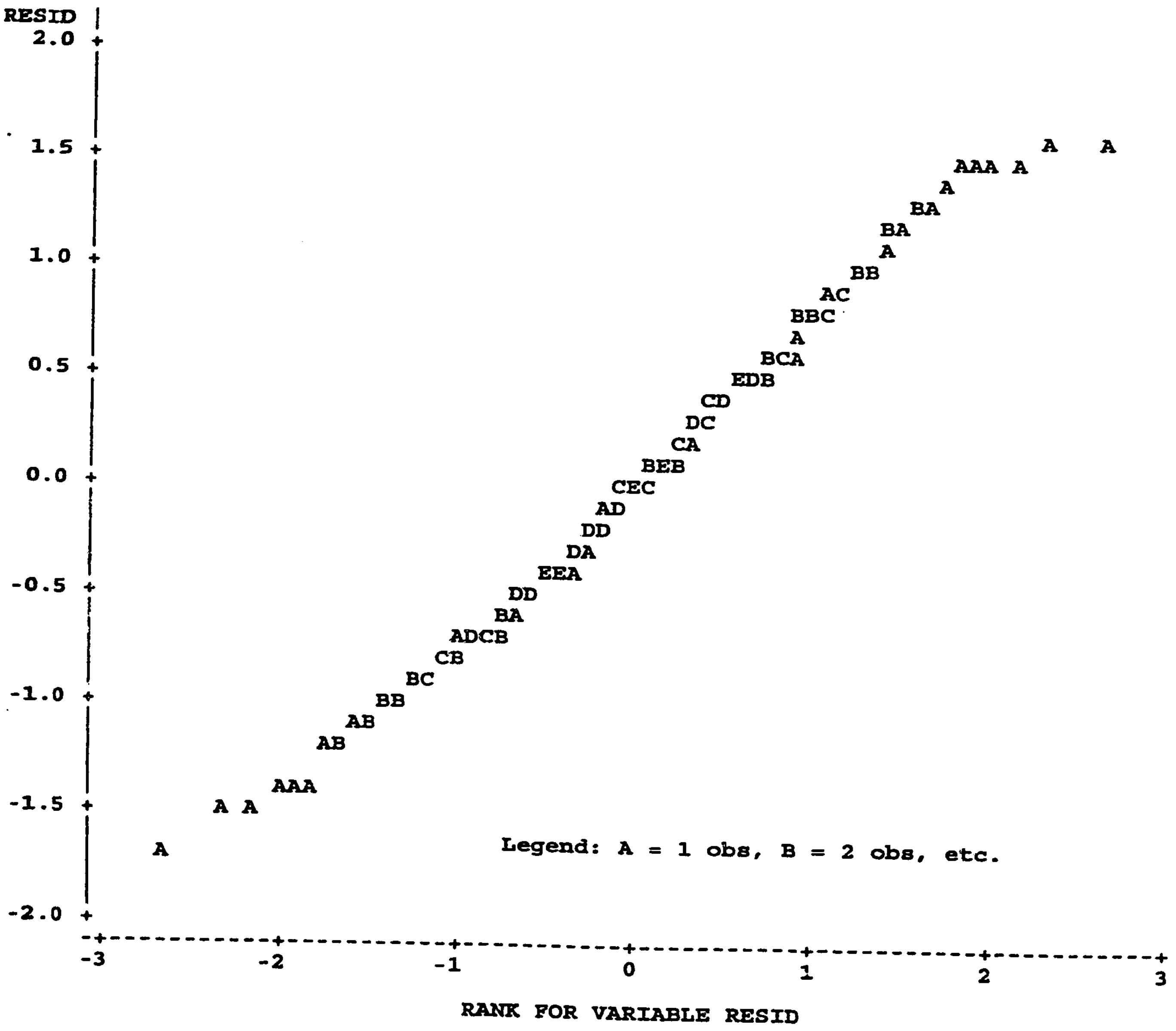

Figure D10. Plot of residuals against residual ranks for variable bud set week

APPENDIX E. F-test probabilities for seed source effect by trait for individual site analyses

Test site	Surv. (%)	Total ht (cm)	Plant health score	Bud burst day	Bud set week
Castle River	0.0001	0.0025	0.0058	0.0004	0.0195
Porcupine Hills	0.0001	0.0152	0.3340	0.0001	0.1909
Bateman Creek	0.0593	-	-	-	-
Tershishner Creek	0.0027	0.0003	0.0012	0.0001	0.0162
Diamond Hills	0.0041	0.0001	0.0013	0.0001	0.3192

APPENDIX F

Table F1. Least square mean percent survival for seed sources by test site

Seed source	Castle River site	Porcupine Hills site	Bateman Creek site	Tershishner Creek site	Diamond Hills site
Crowsnest Pass	75.3_{b}	46.0_{bc}	5.3_{a}	98.0_{a}	98.0_{a}
Porcupine Hills	76.0_{b}	60.0_{ab}	6.0_{a}	96.7_{a}	96.0_{a}
Marston Creek	82.7_{ab}	64.3_{a}	8.0_{a}	98.0_{a}	96.7_{a}
Canmore Corridor	48.7_{c}	43.3_{c}	2.0_{a}	97.8_{a}	-
Ghost River	90.7_{a}	-	6.7_{a}	-	-
Cline River	48.7_{c}	45.8_{bc}	1.3_{a}	96.7_{a}	95.3_{a}
Alstone Creek	44.0_{c}	29.8_{cd}	1.3_{a}	97.3_{a}	97.3_{a}
Lake Edith	26.7_{d}	18.0_{d}	0.7_{a}	88.0_{b}	91.3_{b}

Least square means having the same subscript letter are not significantly different at $P<0.05$

Table F2. Least square mean three-year height (cm) for seed sources by test site

Seed source	Castle River site	Porcupine Hills site	Tershishner Creek site	Diamond Hills site
Crowsnest Pass	20.6_{b}	18.1_{bc}	31.8_{c}	34.2_{b}
Porcupine Hills	19.4_{bc}	17.0_{c}	32.3_{abc}	37.0_{b}
Marston Creek	16.8_{c}	18.7_{bc}	27.1_{d}	28.9_{c}
Canmore Corridor	20.5_{b}	23.3_{ab}	36.2_{a}	-
Ghost River	16.7_{c}	-	-	-
Cline River	19.7_{bc}	18.5_{bc}	33.2_{abc}	35.7_{b}
Alstone Creek	20.1_{bc}	19.1_{bc}	31.8_{bc}	33.8_{b}
Lake Edith	24.1_{a}	25.8_{a}	34.6_{ab}	42.0_{a}

Note: means with the same subscript letter are not significantly different at $P<0.05$

Table F3. Least square mean plant-health score for seed sources by test site

Seed source	Castle River site	Porcupine Hills site	Tershishner Creek site	Diamond Hills Site
Crowsnest Pass	3.16_{a}	3.12_{a}	5.48_{a}	5.58_{a}
Porcupine Hills	2.93_{ab}	3.13_{a}	5.43_{a}	5.63_{a}
Marston Creek	2.84_{abc}	3.31_{a}	5.06_{b}	5.30_{b}
Canmore Corridor	2.66_{bcd}	3.63_{a}	5.19_{ab}	-
Ghost River	2.81_{abcd}	-	-	-
Cline River	2.50_{cd}	2.87_{a}	5.03_{b}	5.35_{b}
Alstone Creek	2.47_{d}	2.96_{a}	4.85_{b}	5.27_{b}
Lake Edith	2.58_{bcd}	3.09_{a}	4.73_{b}	5.35_{b}

Note: means with the same subscript letter are not significantly different at $P<0.05$

Table F4. Least square mean bud-burst day for seed sources by test site

Seed source	Castle River site	Porcupine Hills site	Tershishner Creek site	Diamond Hills site
Crowsnest Pass	18.61_{a}	23.92_{a}	24.03_{a}	13.93_{a}
Porcupine Hills	16.40_{bc}	19.83_{bc}	22.23_{b}	12.43_{c}
Marston Creek	15.60_{bc}	19.83_{bc}	20.[illegible]	11.83_{d}
Canmore Corridor	16.26_{bc}	20.71_{b}	21.79_{bc}	—
Ghost River	16.43_{b}	-	-	-
Cline River	15.18_{bc}	17.45_{d}	18.67_{d}	11.60_{d}
Alstone Creek	15.00_{c}	18.55_{cd}	19.97_{cd}	11.83_{d}
Lake Edith	16.47_{b}	21.40_{b}	23.77_{ab}	13.03_{b}

Note: means with the same subscript letter are not significantly different at $P<0.05$

Table F5. Least square mean bud-set week for seed sources by test site

Seed source	Castle River site	Porcupine Hills site	Tershishner Creek site	Diamond Hills site
Crowsnest Pass	4.67_{bc}	6.67_{a}	5.83_{bc}	1.83_{a}
Porcupine Hills	5.00_{c}	6.17_{a}	6.17_{c}	2.00_{a}
Marston Creek	4.33_{bc}	6.67_{a}	5.83_{bc}	2.00_{a}
Canmore Corridor	4.67_{bc}	6.17_{a}	6.31_{bc}	-
Ghost River	4.33_{bc}	-	-	-
Cline River	3.50_{ab}	6.14_{a}	4.83_{a}	1.00_{a}
Alstone Creek	3.00_{a}	5.61_{a}	5.17_{ab}	1.17_{a}
Lake Edith	5.00_{c}	6.83_{a}	6.00_{c}	1.83_{a}

Note: means with the same subscript letter are not significantly different at $P<0.05$

APPENDIX G

Table G1. Simple linear and quadratic regression r^2 values for percent survival and geographic variables of seed source origin

Test site	Seed source origin latitude	 elevation	 DECD
Castle River	0.48 *(0.68)*	0.76* *(0.76)**	0.01 *(0.08)*
Porcupine Hills	0.61* *(0.79)**	0.96* *(0.96)**	0.11 *(0.13)*
Bateman Creek	0.59* *(0.64)*	0.67* *(0.71)**	0.02 *(0.14)*
Tershishner Creek	0.39 *(0.74)*	0.51 *(0.94)**	0.00 *(0.11)*
Diamond Hills	0.42 *(0.60)*	0.36 *(0.78)*	0.00 *(0.38)*
Across Sites	0.43 *(0.65)*	0.69* *(0.71)**	0.02 *(0.12)*

* significant at $P<0.05$

Note: DECD = distance in km east of the continental divide

Normal values are linear; values in parenthesis are quadratic

Table G2. Simple linear and quadratic regression r^2 values for three-year height (cm) and geographic variables of seed source origin

Test site	Seed source origin		
	latitude	elevation	DECD
Castle River	0.19 *(0.71)**	0.72* *(0.76)**	0.09 *(0.13)*
Porcupine Hills	0.36 *(0.38)*	0.61* *(0.70)*	0.02 *(0.06)*
Tershishner Creek	0.16 *(0.16)*	0.40 *(0.47)*	0.01 *(0.11)*
Diamond Hills	0.22 *(0.75)*	0.48 *(0.56)*	0.00 *(0.17)*
Across Sites	0.24 *(0.49)*	0.65* *(0.68)*	0.07 *(0.21)*

* significant at $P<0.05$

Note: DECD = distance in km east of the continental divide

Normal values are linear; values in parenthesis are quadratic

Table G3. Simple linear and quadratic regression r^2 values for plant health score and geographic variables of seed source origin

Test site	Seed source origin latitude	 elevation	 DECD
Castle River	0.83* *(0.89)**	0.24 *(0.24)*	0.27 *(0.52)*
Porcupine Hills	0.12 *(0.35)*	0.03 *(0.03)*	0.26 *(0.26)*
Tershishner Creek	0.86* *(0.86)**	0.39 *(0.48)*	0.25 *(0.26)*
Diamond Hills	0.55 *(0.76)*	0.12 *(0.12)*	0.23 *(0.24)*
Across Sites	0.76 *(0.78)**	0.25 *(0.28)*	0.22 *(0.29)*

* significant at $P<0.05$

Note: DECD = distance in km east of the continental divide

Normal values are linear; values in parenthesis are quadratic

Table G4. Simple linear and quadratic regression r^2 values for bud-burst day and geographic variables of seed source origin

	Seed source origin		
Test site	latitude	elevation	DECD
Castle River	0.35 *(0.62)*	0.00 *(0.01)*	0.31 *(0.60)*
Porcupine Hills	0.24 *(0.58)*	0.04 *(0.05)*	0.56 *(0.80)**
Tershishner Creek	0.09 *(0.60)*	0.12 *(0.21)*	0.37 *(0.43)*
Diamond Hills	0.15 *(0.95)**	0.11 *(0.11)*	0.42 *(0.59)*
Across Sites	0.20 *(0.51)*	0.06 *(0.07)*	0.29 *(0.56)*

* significant at $P<0.05$

Note: DECD = distance in km east of the continental divide

Normal values are linear; values in parenthesis are quadratic

Table G5. Simple linear and quadratic regression r^2 values for bud-set week and geographic variables of seed source origin

	Seed source origin		
Test site	latitude	elevation	DECD
Castle River	0.18 *(0.29)*	0.00 *(0.27)*	0.40 *(0.41)*
Porcupine Hills	0.04 *(0.29)*	0.01 *(0.32)*	0.74* *(0.74)*
Tershishner Creek	0.21 *(0.22)*	0.01 *(0.18)*	0.40 *(0.40)*
Diamond Hills	0.36 *(0.48)*	0.09 *(0.58)*	0.54 *(0.54)*
Across Sites	0.22 *(0.31)*	0.01 *(0.34)*	0.43 *(0.44)*

* significant at $P<0.05$

Note: DECD = distance in km east of the continental divide
Normal values are linear; values in parenthesis are quadratic