

Temperature – Bud-Burst Relationships in Amabilis and Subalpine fir Provenance Tests Replicated at Different Elevations

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Summary

Within each of four plantations ranging from 430 m to 1400 m in elevation, high elevation provenances of two *Abies* L. species flushed early, with the acceleration due to 1000 m difference in provenance elevation being approximately seven days. Between and within species differences in dates of bud-burst were due to both heat-sum and threshold temperature differences. In subalpine fir (*A. lasiocarpa* (Hook.) Nutt.) these are both low, this species flushing very early. In the amabilis fir (*A. amabilis* (Dougl.) Forbes), threshold temperatures are significantly lower in high elevation provenances, suggesting an adaptation to a short growing season. Terminal buds flushed about a week later than laterals, except in the occasional case where the chilling requirement of the former was apparently not fully met, delaying their bud-burst and causing the difference to be nearer to two weeks. Among plantations, bud-burst was delayed one day per approximately 20 m rise in plantation elevation.

Key words: *Abies amabilis*, bud-burst phenology, altitudinal provenances, heat-sum, threshold temperature.

Zusammenfassung

In jeder von vier Pflanzungen in Höhenlagen zwischen 430 m und 1400 m trieben die Hochlagenprovenienzen von zwei *Abies* L. Arten, mit einem Vorsprung von ungefähr 7 Tagen aus, was auf 1000 m Höhenunterschied in ihrer Herkunft zurückzuführen ist. Unterschiede im Zeitpunkt des Austreibens zwischen und innerhalb der Arten waren auf Differenzen in der Wärmesumme und der Schwellenwert-Temperatur zurückzuführen. Für *Abies lasiocarpa* (Hook.) Nutt. sind diese beiden Werte gering, sodaß diese Art sehr früh austreibt. Für *A. amabilis* (Dougl.) Forbes ist die Schwellenwert-Temperatur der Hochlagenprovenienzen deutlich niedriger. Dies läßt auf eine Anpassung an die kurze Vegetationsperiode schließen. Die Endknospen brauchen etwa eine Woche später als die Seitenknospen auf, mit Ausnahme der seltenen Fälle, in denen der Kältebedarf der Endknospen scheinbar noch nicht gedeckt war, was deren Aufbrechen verspätete und die Zeitdifferenz auf nahezu zwei Wochen vergrößerte. Zwischen den Pflanzungen war das Austreiben der Knospen um etwa einen Tag pro 20 m Höhenunterschied verzögert.

Introduction

Pacific silver fir or amabilis fir [*Abies amabilis* (Dougl.) Forbes] has a wide latitudinal range in western North America, from the southern panhandle of Alaska to the Klamath mountains of northern California, occurring in a band rarely extending much further than 300 km from the coast. In British Columbia (see Figure 1) it grows from sea level to approximately 800 m in the north, and from 300–400 m to 1500 m in the south, often being a component of the forests at timberline. Neither amabilis fir, nor the other two B. C. fir species, subalpine [*A. lasiocarpa* (Hook.) Nutt.] and grand [*A. grandis* (Dougl.) Lindl.] have been

used in the B. C. reforestation programme, partially because of real or imagined problems with balsam woolly aphid (*Adelges piceae* Ratzeburg), and partially because of the somewhat limited uses of fir wood. The exotic noble fir (*A. procera* Rehd.), which occurs about 125 km south of the B. C. border in Washington State, is in fact our most widely planted fir species, and according to Franklin (1964) may be "pre-adapted" to growth in B.C., its large seed size having delayed its northward re-invasion after the last glacial period. The importance of grand fir to western European forestry has led to various provenance trials being established (e.g. Kleinschmit, 1978), but I know of no provenance work in subalpine and amabilis firs. The latter, however, despite its rather low specific gravity, is becoming an important timber species, particularly at higher elevations (where it is quite pro-

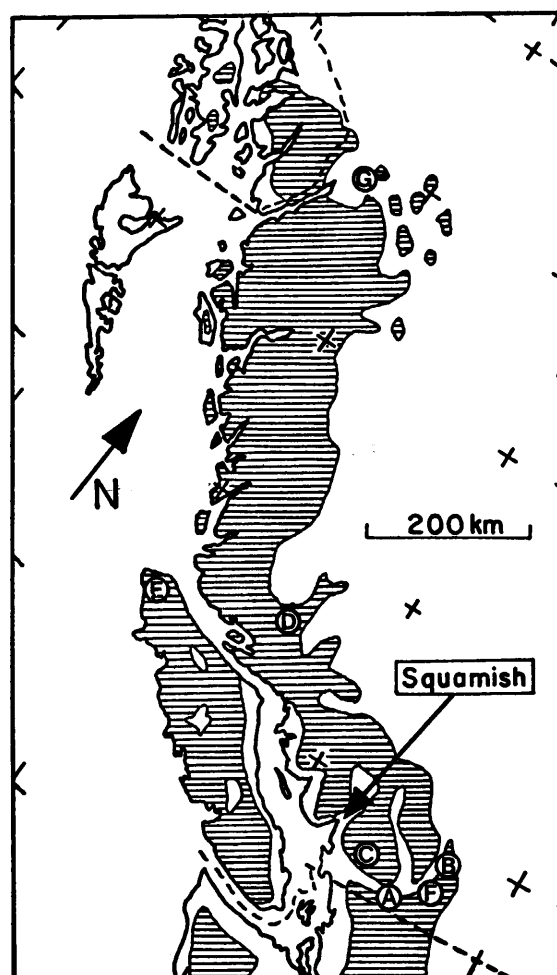


Figure 1. — The northern part of the range of amabilis fir (after Krajina et al. 1982 & Little 1971) showing the origins of provenances of both species.

ductive), the major part of easily accessible stands of low elevation species having been logged. The species shows some interesting variations within an altitudinal transect, in physiology and morphology. For example, at low elevations its needle retention is about eight years, but at timberline it is perhaps twenty years. This could be due to genetic or environmental factors, such as slower cycling of nutrients in the soil of the cooler subalpine forests. My own interest is in the genetic adaptations required for growth where the growing season is short, and with its large altitudinal range, amabilis fir has good potential for studies of these. Consequently, the B. C. Forest Service, J. P. KIMMINS, the forest ecologist of this faculty, and myself have set up provenance tests of this species to test growth performance, and ecological and genetic adaptations of plants grown from seed taken from stands at various elevations. In this paper I consider variation in the physiology of bud burst.

Review

Numerous studies, particularly in Europe, and elsewhere with European species, have shown that when provenances from different elevations and latitudes are grown in a common environment, buds of those from high elevations and latitudes flush first. This has been consistently demonstrated in the 1938 IUFRO Norway spruce [*Picea abies* (L.) KARST] provenance tests, such as in the New Hampshire replications (WORRALL, 1975). There are exceptions, but many of these can be explained if dormancy phenomena are considered as a comprehensive whole, such as described by VEGIS (1964). Thus KRIEBEL and WANG (1962) showed that in northern plantations, northern provenances of sugar maple (*Acer saccharum* L.) flush early, but the reverse is true in southern plantations. Evidently the chilling requirement of northern provenances is high, as shown by PERRY and WANG (1960) for red maple (*Acer rubrum* L.), and this requirement is not completely met in a mild southern winter, so that bud-burst is delayed. The situation with western North American species is less clear, for instance in Douglas-fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] (e.g. WHITE *et al.* 1979, SWEET, 1965) and California white fir (*A. concolor* LINDL.) LIBBY *et al.* 1980). This is probably because many other factors are certainly involved, particularly water availability. It has been suggested (BOUVAREL, 1961 for Norway spruce; WHITE *et al.* 1979 for Douglas-fir) that provenances from areas with early dry seasons have early bud-burst. Since early bud-burst results in early bud set, at least in determinate species, the high rates of water loss from incompletely cuticularised leaves are over before the critical dry spell. My own experience with two B. C. *Populus* L. species tends to confirm the general picture of early bud-burst in plants from cooler and/or more continental climates. *Populus tremuloides* var. *vancouveriana* (TREL.) SARG, the Vancouver Island form of trembling aspen, flushes its buds a month later than the interior *P. tremuloides* MICH. when both are grown in Vancouver. Similarly, *Populus balsamifera* L., balsam poplar, of Yukon origin, burst their buds so early in Vancouver that they immediately set buds, presumably in response to the short days of February and March, relative to the very long or continuous days at bud-burst time in their native environment. The local black cottonwood, *P. balsamifera* var. *trichocarpa* (TORR. et GRAY) BRAYSHAW, flushes buds about two months later. Early bud-burst is useful, in that the plant can fully utilize what

little growing season there is available. At least in continental climates this does not also require a greater retention of some degree of cold hardiness in full flush, because such climates are not so subject to late frosts as are more maritime ones (VEEN, 1954). These topics are reviewed by HESLOP-HARRISON (1964) in his "Forty Years of Genecology", and TRANQUILLINI (1979) has thoroughly summarized his own ideas, and those of others, in his "Physiological Ecology of the Alpine Timberline".

The general early response to the rising temperatures of spring by cool climate provenances is a result of their ability to metabolise or respire at lower temperatures, as shown by PISEK and WINKLER (1958) for Norway spruce provenances, and perhaps these provenances have also a steeper respiration rate/temperature curve. RÉAUMUR (1735) tried to explain "the velocity of biological processes" in terms of temperature, and in the field of agriculture, differences in temperature-dependent phenological patterns are neatly summarized by heat-sum and threshold temperature values (ARNOLD, 1959), though some authors consider this to be an over-simplification. The method requires that the respiration rate/temperature curves be straight lines, crossing the abscissa at the threshold temperature. Clearly this is only very approximately the case, as shown by the data of PISEK and WINKLER, *op. cit.* Timing of developmental stages is determined by the heat sum accumulated above a certain threshold temperature, below which there is "no" respiration. For instance, if the threshold temperature were the often cited 5°C, and bud-burst required 100 degree days, then the plants would flush, at 7°C, in $100/(7-5) = 50$ days, or in $100/(9-5) = 25$ days at 9°C. If plants are grown in two temperature regimes, the two times of bud-burst allow the calculation of both threshold temperatures and heat sum values. CAMPBELL and SUGANO (1975) have used the technique in their very detailed nursery-bed studies of bud-burst phenology of Douglas-fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] provenances. The method works sufficiently well for producers of seed to be able to state when their products will produce a harvestable crop, with heat sums quoted usually on a 5°C threshold temperature basis. MERRIAM'S (1920) characterisation of "life zones", summed heat above a 6°C threshold. Curiously, foresters have not adopted the idea more fully. I think it would be particularly useful in seed orchard work and in other aspects of seed production. If heat sums are known, fairly accurate predictions of the dates of bud-burst, anthesis, etc. can be made. Presumably the same method could be used to estimate the date of seed maturity, though other environmental factors such as low moisture availability might cause delay. Orchardists estimate degree of fruit maturity in such a way.

In the present study I attempt to show that high altitude provenances of amabilis fir have low heat sums and low threshold temperatures for bud-burst.

Materials

The provenance tests consist of five provenances of amabilis fir and two of subalpine fir. The latter species grows widely at higher elevations in northwestern North America, basically to the west of the Rocky Mountains. The origins of these provenances are shown in Table 1 and in Figure 1. The elevation of origin is adjusted to the latitude of provenance A by 65 m per degree, since the lapse rate is about .6°C per 100 m of elevation rise, and the temperature is reduced about .4°C per degree of north

Table 1. — Origin of Provenances.

Species	Provenance	Lat.	Long.	Alt. (m)	Alt. Adj. (m)
<i>A. amabilis</i>	Mt. Thureton (A)	49°05'	121°50'	1430	1430
"	Anderson River (B)	49°40'	121°20'	1200	1240
"	Pitt River (C)	49°28'	122°50'	1000	1025
"	Klinaklini (D)	51°10'	125°45'	300	435
"	San Josef River (E)	50°43'	128°10'	100	205
<i>A. lasiocarpa</i>	Coquihalla River (F)	49°20'	121°25'	1100	1115
"	Terrace (G)	55°30'	128°50'	183	600

latitude, on the Pacific coast. The tests are replicated at 430 m (I), 780 m (II), 1100 m (III), and 1400 m (IV) in the Mamquam Valley about 15 km east of Squamish, at 49° 45' north, 123° 00' west. In this valley, the natural range of *amabilis* fir extends down to about 350 m. The experiment thus resembles the provenance trials of CLAUSEN, KECK and HIESER (1948) with yarrow (*Achillea* L. spp.) on a transect of the California Sierra, except that they used clonal materials. Plants were raised from seed of general B. C. Forest Service collections (often squirrel caches) and were raised at Chilliwack nursery, either as bareroot stock or in styroblock containers. They were planted out, as 2—0 stock, in the spring of 1978, except at the top plantation, where snow precluded planting. By the time planting was possible, the woods were closed because of extreme fire danger! This plantation was made in July of 1979, the stock overwintering in pots at UBC. Thus there is here a confounding of planting date and stock type with plantation site. This will have to be taken into account when growth is assessed (probably in 1985), but I think is of little or no consequence to phenology of bud-burst, this trait being under very strong genetic control. The plantations are on sites logged in the mid-1970's and are on relatively gentle slopes, each with a generally northwest aspect. There the similarities end, because in each plantation there is truly prodigious site variability—rocks, swampy patches, large stumps and herbaceous and shrub competition. This precluded equal spacing distances between plants. These sites are production environments and I feel will yield data of more practical utility than do those tests, in artificial environments, designed to detect genetic differences that may or may not be of significance to forest management. The plantations are also difficult to reach, since the logging roads that allow access now have minimal or no

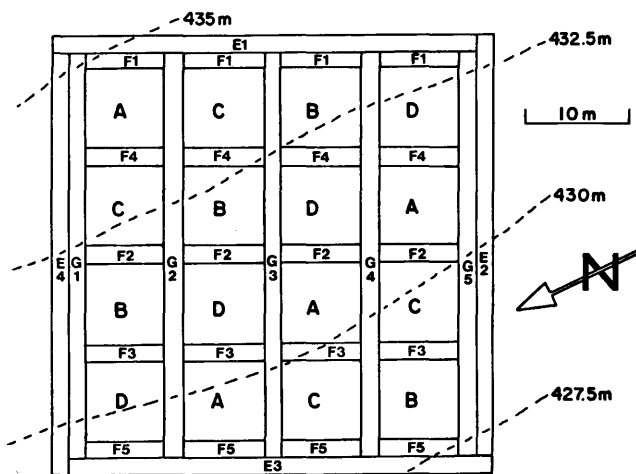


Figure 2. — The layout of Plantation II. Provenances A B C & D are in the Latin square, E F & G are in single rows with their replication number following.

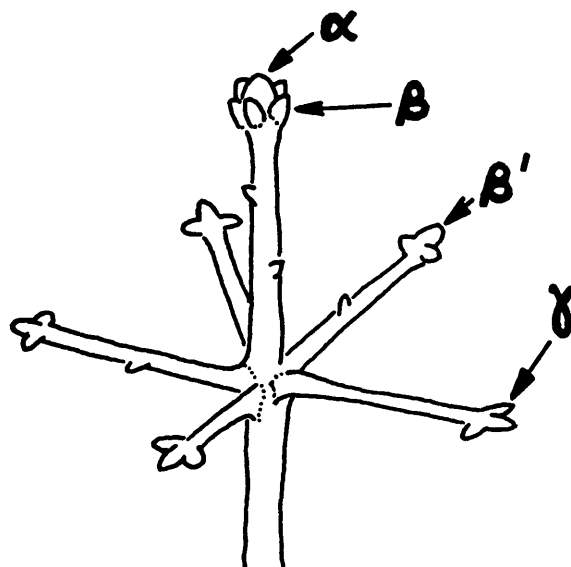


Figure 3. — A diagrammatic representation of the top of a fir plant to show the bud types on which observations were made.

maintenance. The top plantation is 25 km from a paved road.

To counteract the within plantation variability (including the minor elevation variation), a 4 × 4 Latin square design was chosen, using provenances A, B, C and D, with 25 trees per cell at approximately 1 m spacing. Between cells (columns) were planted single rows of subalpine fir G and between rows, subalpine fir provenance F (about 20 plants) as buffer strips. The columns are arranged at approximately right angles to the contour lines. Then, unexpectedly, provenance E of *amabilis* fir became available and was added as a single row around the entire perimeter. This is shown in Figure 2, which is the layout of the lowest elevation plantation. In fact there are five replications for the subalpine fir provenances, but one at random was omitted from all of the analyses.

Methods

(a) Bud-Burst

Bud-burst dates were assessed by observation at 2 or 3 day intervals, when the number of plants with green leaves showing through parted bud scales was counted in each cell. Buds observed were the leading one, α , and the lateral to it, β , the terminal of a lateral branch at the previous years node, β' , and a lateral to it, γ (see Fig. 3). Since there are usually four or five buds of type β there is a slight bias in the estimate of bud-burst date in the early direction, since a plant's buds were considered burst if one bud of the particular type was burst. The same is of course true for bud β , and there is worse bias for bud γ since there are generally two of these per shoot, therefore eight or so per plant. Observations were of the dates for the first bud of the particular type to burst. Numbers of plants with burst buds were plotted versus date, a hand fitted sigmoid curve drawn through the points, and the date when 50% of the plants had burst buds was read off (few cells still retained their initial 25 plants). Each cell therefore yielded one value only. In 1980, data for bud α only were collected, and in 1982 a small amount of data was collected where the main 1981 body of data indicated areas of particular interest. Thus the analysis, for each bud type, can be a Latin square for the *amabilis* fir

provenances A, B, C and D, or a randomized complete block design with four replications if the fifth provenance is added, in addition to the two subalpine fir provenances. In fact the latter alternative was chosen, though use of the Latin square analysis reduces the error of estimate considerably (e.g. see Table 2).

(b) Temperature Observations

In the two upper plantations, "degree day accumulators", or biophenometers (Omnidata Corp., Logan, Utah) had been buried in the snow in the early summer of 1981. These record the heat sum accumulated above five previously chosen threshold temperature values, 3, 4, 5, 6 and 7° C in this case. Heat sums were then plotted *versus* date, so that five values of *apparent* heat sum for bud-burst could be read from these graphs at the data for 50 % flush, in the different temperature regimes of the two upper plantations. These apparent heat sums were converted to real heat sums by a method similar to that described by ARNOLD (1959). Consider an example: In a plant where the heat sum for bud-burst is 100 degree C days, and the threshold temperature is 5° C, bud-burst, if the plant were grown at 8° C, will occur in $100/(8-5) = 33\frac{1}{3}$ days. At 10° C, the buds would burst in $100/(10-5) = 20$ days. If the threshold temperature were not known and heat sum was calculated on the bases of 3, 4, 6 and 7° C (which are the values I programmed into the biophenometers except for the 5° value), the *apparent* heat sums would be $(8-3) \times 33\frac{1}{3}$, $(8-4) \times 33\frac{1}{3}$, $(8-6) \times 33\frac{1}{3}$ and $(8-7) \times 33\frac{1}{3}$ degree days in the 8° C temperature = 167, 133, 67 and 33 degree days. At 10° C the *apparent* heat sums would be $(10-3) \times 20$, $(10-4) \times 20$, $(10-6) \times 20$ and $(10-7) \times 20 = 140, 120, 80$ and 60 degree days. But the heat sum must be the same in the two environments. If the base temperature is 3, the difference in apparent heat sum between the 8 and 10° C environments is $167-140 = 27$ degree days; if 4, it is 13; if 6 it is -13; and if 7 its is -27. Clearly, if these differences are plotted versus the assumed threshold, a difference of zero occurs at the correct threshold of 5° C, which is interpolated from the linear regression line. The value of 5° C then allows the heat sum of $33\frac{1}{3}(8-5) = 100$ ° C days to be computed. This is how heat sum and threshold temperature values were obtained in the present study, from dates of bud-burst in the two upper plantations, with assumed thresholds of 3, 4, 5, 6 and 7° C. Four estimates were made for each provenance, by pairing the cells that occur in equivalent "geographical" positions in the two plantations.

For the analyses of these data, and the bud-burst data the methods described by BLISS (1967, 1970) are heavily relied upon.

Results and Discussion

1. Dates of bud burst

(i) Year to year differences

In Figure 4, the dates of bud-burst (α) in 1980 in plantation II are plotted against the 1981 dates, with each point being the mean of four values for each of the seven provenances. The correlation between the dates is clearly very high ($r = .96$ within the *amabilis* fir, $r = .97$ if both species are included). Similarly high correlations were observed for the other three plantations. The Figure indicates a high degree of genetic control over bud-burst, which has long been known. Also there are large year to year differences. The early provenances (the subalpine fir)

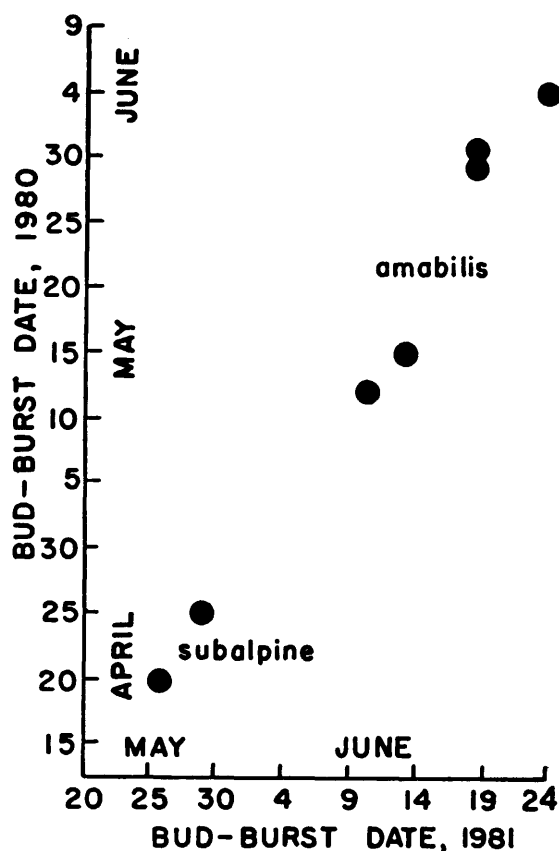


Figure 4. — The dates of bud burst α in successive years in Plantation II. Each point is the mean of four estimates.

lagged about five weeks between 1981 and 1980, and the late provenances by about three weeks. In 1982, in this plantation, bud-burst was a further roughly two weeks late, giving a six week spread over the three years of observation. Such results have been widely reported, and clearly indicate that the attractive idea that day length is involved in growth cessation and in growth initiation is erroneous. A six weeks time span in April-May encom-

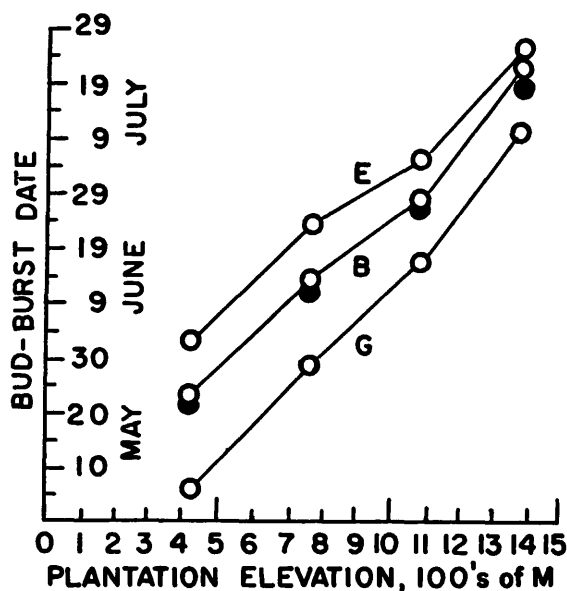


Figure 5. — Bud burst dates α in the four plantations in 1981. The open circles are for provenances E, B & C and are the means of the four replications; the solid points are the overall means for all provenances.

Table 2. — ANOVA for date of bud-burst in Plantation I, 1981.

	Source	d.f.	S.S.	M.S.	F	F ₀₅
a	Provenance	6	14281.1	2380.2	775	2.20
b	Buds	3	1185.5	395.2	129	2.71
b1	α v β , β , γ	1	1108.6	1108.6	361	3.94
b2	β v β , γ	1	71.5	71.5	23	3.94
b3	other contrasts	1	4.4	4.4	1.4	3.94
c	Buds x provenances	18	276.4	15.4	5.0	1.75
c1	Buds x provenance F	3	210.1	70	22.8	3.94
c2	Buds x other provenances	15	66.3	4.4	1.4	1.77
d	Error	84	237.2	2.82		
e	Pooled error, d + c2	99	304.5	3.07		

Table 3. — ANOVA for bud-burst α , 1981, Plantation II, as a Latin square (in parentheses) or as a randomised complete block; provenances A—D only.

	Source	d.f.	S.S.	M.S.	F	F ₀₅
	Provenance	3	114.24	38.08	16.7 (39.8)	3.49 (4.76)
	Error	12	27.37	2.28		
	(Columns)	3	7.96	2.65	2.70	4.76
	(Rows)	3	13.53	4.51	4.61	4.76
	(Error)	6	5.88	.98		

passes about a 2½ hour difference in daylength. Only in the *very unusual* event of insufficient winter chilling does daylength play any role in bud-burst. Probably such a situation can not ever occur in nature, but is not infrequent in provenance tests [see below, section 1 (iv)(c)].

(ii) Plantation differences

The overall average dates of bud-burst for bud α , in 1981, in the four plantations, were May 7.2, May 26.3, June 14.5 and July 8.1 (solid points in Figure 5). Shown in the Figure are the dates for the earliest (B) and latest (E) amabilis fir provenances, and the later of the two subalpine fir provenances G [F, the earlier one was irregular, as described below, section 1 (iv)(c)]. The spread between early and late provenances diminishes slowly passing from plantation I through II to III, but is markedly diminished in IV (see also Figure 6). In the latter plantation "spring" comes very rapidly, temperatures rising from around 0° C in the snow, to mid-summer values of perhaps 35° C as the last ½ m of snow melts within the span of a week. The average slope of the lines indicates a delay in bud-burst of about 1 day per 20 m rise in elevation within a provenance. This may be compared with 1 day per 31 m for several species grown in Austria (BENECKE, 1972) and 1 day in 7 to 15 m in New Zealand (BENECKE *et al.* 1978), or with one day in about 30 m in accordance with HOPKIN's "Law" (1920). Also in Austria, OBERARZBACHER (1977) showed a 1 day delay per 17.2 m rise in elevation for a clone of Norway spruce, and 1 in 15.2 m for a provenance of European larch (*Larix decidua* L.). Such results again show the overwhelming effect of temperature on bud-burst.

(iii) Bud type differences

The lag in date of bud-burst between types α and β is of interest, VEEN (1954) having suggested that a large lag occurs in provenances from maritime climates, so as to protect the "important" bud α . In plantations I, II and III bud β preceded α by 6 to 7 days, buds β' and γ preceded β by 2 to 3 days, these differences being statistically significant (see Table 2). In plantation IV these differences were still significant, but were almost halved. This is because of the very rapid temperature rise at the time of bud-burst at the highest elevation. The only exceptional result was in Plantation I, in 1981, but not in 1982, where in subalpine fir provenance F the α — β lag was 12 days. This situation is discussed more fully in Section 1 (iv) c.

(iv) Genetic differences

(a) Provenance and species

Figures 4 and 5 suggest that there are differences within and between species and this is verified by the analysis of variance in Table 3 for data of bud-burst in Plantation II for the four amabilis fir provenances that are in the Latin square design. These four provenances are significantly different; the analysis also shows the "improvement" in the standard error over the analysis if performed as a randomised complete block. This shrinks from 1.51 days to .99 days. When the fifth provenance is added of course the Latin square analysis can not be used. Also of interest in this analysis is the near-significance of the "Rows" term. Of the four plantations, this one is on the most steep terrain; since the Columns are at approximately right angles to the contour lines, Row 1 is about 8 m above Row 4, which should result in a difference in bud-burst date of nearly half a day if the relationship of Section I (ii) holds.

(b) Provenance variation as related to altitude of provenance origin

Table 4 is the analysis of variance for date of bud-burst α in plantation I in 1981, for all seven provenances, treated as a randomised complete block with four replications. The significant provenance variation is split into between and within species terms, and the within amabilis fir variation is split into a linear term regressing date of bud-burst against elevation of provenance origin, and "error" terms. Noteworthy are the lack of variation within subalpine fir [discussed below, section 1 (iv) (c)] and the significant linear regression term. High elevation provenances flush early. The date of bud-burst α in plantation is given by the equation $y = 33.48 - .0071 x$ where y is the May date of bud-burst and x is the elevation of provenance origin, in metres. That is, a thousand metre rise in provenance elevation results in buds bursting a week earlier. In the other plantations the regressions are all statistically significant with $y = \text{June } 24.17 - .0079 x$ in plantation II, $y = \text{June } 35.82 - .0057 x$ in plantation III and $y = \text{July } 26.58 - .0047 x$ in plantation IV. These relationships are shown in Figure 6. Similar ones hold for the other bud types. They suggest that high elevation provenances are adapted to a short growing season by having early bud burst. In several cases the term in line g of the analysis, the scatter of the means about the regression line, approached statistical significance. Certainly other ecological factors than elevation are important in bud burst. However the analysis of section 2 (below) confirms a suspicion that provenance C is not yet very well established, and its date of bud-burst is slightly delayed by its lack of vigour, thus contributing to the scatter of the means about the line.

(c) Bud type and provenance interactions

Table 4. — ANOVA for the regression of bud-burst date on provenance elevation, in Plantation I, 1981.

	Source	d.f.	S.S.	M.S.	F	F ₀₅
	Provenances	6	2479.2	413.2	107.3	2.57
	Between species	1	2232.3	2232.3	579.8	4.32
	Within species	5	246.9	49.4	12.8	2.68
	Within subalpine fir	1	.1	.1	.0	4.32
	Within amabilis fir	4	246.8	61.7	15.82	2.84
	Linear	1	222.2	222.2	56.97	4.32
	Scatter of means	3	24.6	8.2	2.1	3.07
	Error	21	80.9	3.85		

Table 5. — Threshold temperatures and heat sums.

Provenance	Altitude	Threshold °C	Heat sum, °C-days
A	1430	3.8	172
B	1240	3.6	185
C	1025	4.2	180
D	435	4.8	173
E	205	5.3	168
F	1115	2.4	115
G	600	2.8	122

Table 2, previously referred to in section 1 (iii) is the analysis of variance of bud burst date for provenance and bud type in 1981 in plantation I. This is a 7×4 randomized complete block with four replications: it shows bud and provenance differences, and a significant provenance \times bud type interaction. This interaction occurred in this plantation only, and in 1981 and not in 1982. Inspection of the data suggests that Provenance F of the subalpine fir is the cause of this interaction, and line cl of the analysis confirms this. When its effect is separated out, the interaction term becomes non-significant. This is of course a contrast chosen *a posteriori*, but the F value of 22.8 is significant well beyond the .1 % level ($F_{.001} = 5.84$). Hence lines d and e could be combined into a pooled error term.

The difference in bud-burst date of bud β between the subalpine fir provenances was about five days, which is similar to the difference expected from the elevation difference of the provenances, and similar to the difference in all the amabilis fir provenances. The difference for bud α should be about the same. In fact it is zero (see line 4 in Table 4). I think this is because terminal buds need more chilling for rest breakage than do laterals, and I suggest that the higher elevation provenance F did not receive complete chilling of its terminal buds (α) in the extraordinarily mild winter of 1980–81. At the level of plantation I there was no snow cover until early March and the temperature hovered around 15° C in late December. Thus bud-burst was somewhat delayed, and the interaction created. This is why data for provenance G, not F, were used in Figure 5.

2. Heat sum and threshold values

From the bud-burst dates in each cell and buffer strip in the top two plantations, and from the 'biophenometer' records, four estimates of the threshold temperature for bud-burst were derived for each provenance, and from these the heat sums were then also derived. The means of these estimates are shown in Table 5. In the case of the subalpine fir, whose thresholds appear to be somewhat less than the minimum of 3° C for which the biophenometers were programmed, extrapolation rather than interpolation was required, so these values may be less reliable.

The heat sums are evidently different between the two species, the subalpine fir flushing early because of this. Within species the heat sums are barely significantly different, and there is no apparent trend with elevation of provenance origin.

In the case of threshold temperatures however, there are large differences between and within species. Subalpine fir flush early because of their low threshold temperature, and high elevation provenances likewise. This was confirmed by analysis of variance and is illustrated in Figure 7. The analysis showed a linear trend within the amabilis fir with the slope equal to $-.00123^{\circ}$ C per m. For the subalpine fir (two points only) it is $-.00077^{\circ}$ C per m.

Since the ANOVA showed no species \times slope interaction a common slope for parallel lines was computed (and hence a line fitted for two points). This is $-.00122^{\circ}$ C per m. For amabilis fir, y , the threshold temperature °C is given by $y = 5.38 - .00122x$ where x is the elevation of provenance origin. For subalpine fir the threshold is $y = 3.56 - .00122x$.

In this regression the previously delinquent provenance C of amabilis fir is much more close to the line than it was in Figure 6. Its lack of vigour delays its bud-burst but does not interfere with the threshold temperature calculation. Its heat sum in Table 5 is probably too high.

The strong inference that must be taken from these results is that provenances from higher elevations are adapted to the shorter growing seasons of their native habitat

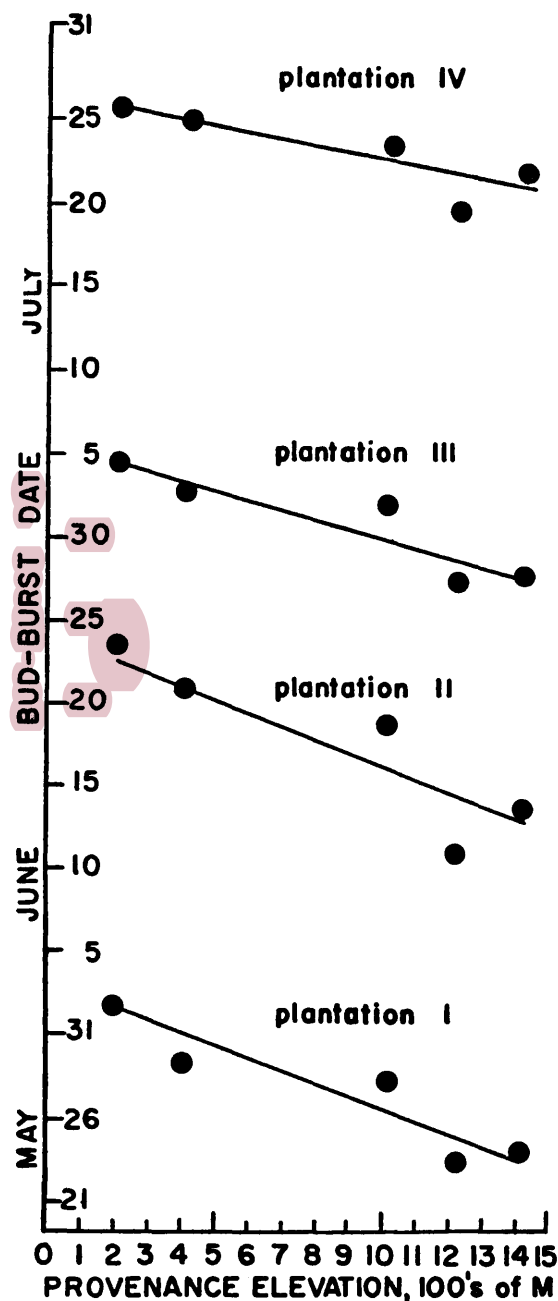


Figure 6. — Regressions for date of bud burst α , 1981, versus elevation of provenance origin, in each plantation. Each point is the mean of four replications. The relationships are significant at the 5 % level.

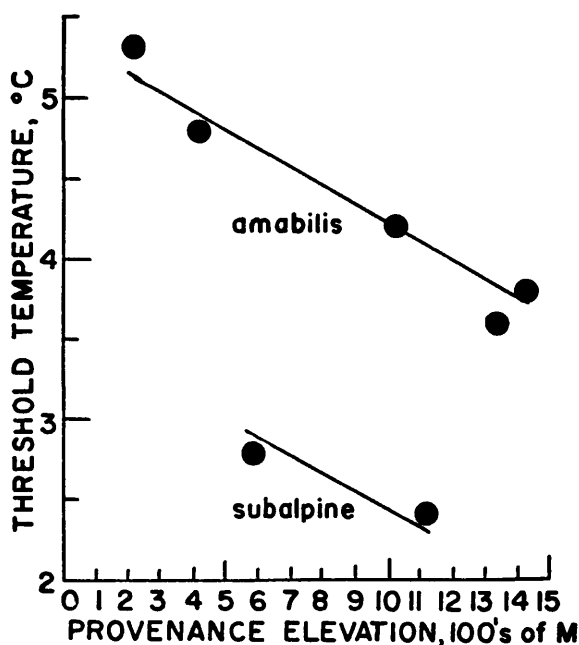


Figure 7. — Regressions of threshold temperature versus elevation of provenance origin, means of four estimates. Parallel lines are fitted: the slope is significant at the 5 % level.

by early bud-burst, caused either by a low heat sum requirement or a low threshold temperature, or both.

CAMPBELL and SUGANO (1975) showed differences in heat sums and thresholds between populations of Douglas-fir seedlings raised in controlled environments. Unfortunately these values varied widely depending on the particular environments used. Likewise, HOLZER *et al.* (1979) showed low heat sums for early flushing clones of Norway spruce, but these values differed up to 50 % depending on which environment (6°C, 12°C or 18°C) the plants were grown in. Are such results an artifact due to controlled and very unnatural temperature regimes? The latter authors curiously assumed a threshold of 0°C for all clones. Reworking their data *via* ARNOLD's (1959) methods to yield calculated thresholds rather than assumed ones, drastically reduces the variation in heat sum between environments. Heat sums remain low for the early flushers, but all the threshold values are in the 2–2½°C range. Considerable reworking of data presented by OBERARZBACHER (1977), with Norway spruce clones, I think shows results similar to mine, with an early flushing clone having a threshold of 2.6°C, and a late flusher a threshold of 5.7°C. Perhaps there is as much variation in threshold temperature within populations as between population means, as is the case with many other traits.

The 1.22°C change in threshold temperature per 1000 m difference in provenance elevation may be compared with that for related variables. PISEK and WINKLER (1958), working with Norway spruce, showed a displacement between respiration rate-temperature curves of about 1°C in winter, and 3–6°C in summer, per 1000 m difference in provenance elevation. FRYER and LEDIG (1972), using greenhouse grown balsam (*Abies balsamea* L.) showed a 9°C (!) difference in the optimum temperature for photosynthesis per 1000 m difference in provenance elevation. These re-

sults all show there are adaptations to cool temperatures; only their magnitude is in question.

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