USE OF PHENOLOGY FOR EXAMINING PROVENANCE TRANSFERS IN REFORESTATION OF DOUGLAS-FIR

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INTRODUCTION

"Seed transfer" in reforestation is the process of moving seed, or seedlings, from place of origin to alternative planting sites. Strong support for the theory of optimality of local populations has been presented by Langlet (1936) and Clausen, Keck & Hiesey (1948). Consequently, use of non-local seed is avoided if possible to minimize losses of vigour or fitness; but in cases where local seed is not available, transfer guides are necessary. For Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) in western Washington and Oregon, present guides are rules of thumb taken from Swedish models. Therefore, a method for early examination of effects of moving seed would be helpful. This report presents a simple predictive model which uses timing of vegetative bud burst for examining responses of seedlings to transfer.

The main assumptions included in the model were: (1) genetic differentiation in timing of bud burst is in response to adaptive selection; (2) the timing of bud burst in an adapted phenotype is a function of the physiological response of that provenance to temperature; (3) chilling requirements of all provenances will be satisfied by normal winter temperatures, regardless of the part of the region to which they are moved. Only the first assumption is examined in this report, by the method of provenance-habitat correlations. The other two assumptions are supported in the literature; for example, timing of bud burst appears to be almost exclusively temperature mediated if chilling requirements are met (Wommack 1964; Lavender & Hermann 1970). Also the chilling requirement of Douglas-fir is less than 80 days of temperatures lower than 10° C (Wommack 1964), whilst in any winter most of the region under consideration will have more than 100 days in which maximum temperatures will not rise above 12° C (Wakefield 1969). The exceptions are in south-coastal Oregon and California, a negligible part of the Douglas-fir region.

The model required two sets of equations. The first, based on an experiment using forty-four provenances, describes timing of bud burst as a function of average daily temperature. The second describes pattern of average daily temperature at stations where provenances were collected. Together, the equations provided functions for predicting bud-burst dates. Predicted dates were then used to examine hypothetical effects of transferring seed along elevational and latitudinal gradients.

MATERIALS AND METHODS

Provenance collections were made from the nearest cone-bearing stand at forty-four weather stations of the U.S. Weather Bureau (Table 1). Most collections were within...
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<th>Latitude (degrees)</th>
<th>Longitude (degrees)</th>
<th>Elevation (m)</th>
<th>Distance from Pacific (km)</th>
<th>Bud burst function intercept (log, DARD)</th>
<th>Station temperature intercept (°C)</th>
<th>Station temperature rate (°C/day)</th>
<th>Predicted date of bud burst (days after 22 Dec.)</th>
<th>Date last spring frost (days after 22 Dec.)</th>
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<td><strong>Range</strong></td>
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<td>39·42</td>
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<td>0·057</td>
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<td></td>
<td>48·25</td>
<td>124·37</td>
<td>1·60</td>
<td>210</td>
<td>-0·612</td>
<td>3·60</td>
<td>0·135</td>
<td>182</td>
<td>186</td>
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<tr>
<td><strong>Mean</strong></td>
<td>44·80</td>
<td>122·46</td>
<td>512</td>
<td>113</td>
<td>-0·802</td>
<td>-2·64</td>
<td>0·097</td>
<td>128</td>
<td>145</td>
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<td><strong>Standard deviation</strong></td>
<td>2·4</td>
<td>0·97</td>
<td>423</td>
<td>62</td>
<td>0·11</td>
<td>4·2</td>
<td>0·018</td>
<td>27</td>
<td>19</td>
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0·75 km of stations, and only four beyond 1·5 km. Wind-pollinated seed from four trees in each stand was stratified for 4 weeks, germinated in early May 1969, and transplanted into pots in late May. Eighteen pots were made up per provenance. Provenances were represented by seventy-two seedlings each, eighteen per parent. Four seedlings, one from each parent within a provenance, were assigned to each pot; and these pots were grown in a coldframe until October, then in a lathhouse until entering temperature treatment.

Temperature treatments were applied in a glasshouse room. Average temperatures were increased by incremental weekly thermostat advances of approximately 2·5° C from 12·5° C to 25° C in 6 weeks. Temperature was recorded continuously at 15 cm above mean plant height and averaged somewhat below the thermostat settings. At lower temperatures used in the experiment, day versus night fluctuated from 3° to 6° C; at higher temperatures, from 8° to 12° C.

Three pots of seedlings from each source were brought into the glasshouse at weekly intervals, starting 13 January and ending 17 February. By 13 January, chilling requirements had almost certainly been satisfied by lathhouse temperatures, at least to a condition where additional chilling days had negligible effect on bud-burst date. Further, temperatures between 13 January and 17 February were sufficiently cool that promotive effects on bud burst of warm temperatures during this period were also probably negligible. Coincident with placing pots in the glasshouse, the thermostat was advanced gradually from week to week, as previously noted, so that bud expansion of succeeding weekly lots occurred under higher average temperatures.

In the glasshouse, the bench design was completely randomized for source, time of treatment, and replication. Fluorescent lamps added morning and evening light to extend natural day length to 16 hours, a photoperiod chosen to exceed maximum day length at any of the forty-four stations. Seedlings were examined every 3·5 days, i.e., Monday a.m. and Thursday p.m. Bursting was recorded when the first green needles appeared between the scales of terminal buds. Observations used in analysis were: (1) the number of days to bud burst from entry of the pot into the glasshouse until the mean date of bud burst of its four seedlings, and (2) a mean temperature per pot which was calculated by averaging temperatures taken from 2-h points on a continuously recording (day and night) strip chart. Temperatures were averaged from the time the pot entered the glasshouse until the mean date of bud burst of its four seedlings.

Prediction of bud-burst timing for a provenance required estimates of regression constants in an equation to describe the bud-burst response of the provenance to temperature. Of the models tested for fit to bud-burst response, the one accepted was Azzi's (1956) 'index of sprouting', as later modified by Arnold (1959). In Arnold's version, the mean temperatures appropriate to a series of plantings made in the spring were regressed against 'developmental units'. This model can be formulated as:

$$100 \left( w_i^{-1} \right) = a + bX_i$$

where $w_i = $ days to reach the given developmental event in the $i$th planting, and $X_i = $ temperature averaged over $w_i$ in the $i$th planting.

The constant (100) transforms the reciprocal into Arnold's 'developmental unit' which then can be read as daily average rate of development (DARD), i.e. if 25 days are required for a bud to come to breaking, the rate of development is $100/25 = 4\%$ per day = 4 DARD. With estimates of $a$ and $b$ that are appropriate to a specified developmental event, the above equation predicts the event. Daily temperatures are inserted
Prediction in seed transfer reforestation

in the equation and daily DARDs are calculated. When DARDs sum to 100, the event, in this case a predicted date of bud burst, is reached.

To analyse the glasshouse experiment, days to bud burst were first changed to DARDs. Then, to provide a satisfactory linear fit to results, and to reduce heterogeneity of variance, DARDs were transformed to logarithms and analysed in the following covariance model:

$$\log_e \text{DARD} = s_i + b (X_{ij} - \bar{X}) + f_{ij}$$

where $s_i$ = effect of the $i$th source, $X_{ij}$ = average temperature of the $j$th observation in the $i$th source, and $f_{ij}$ = residuals.

Based on the model, days to mean bud burst ($W$) at a constant daily temperature ($X$) is given by:

$$W = \frac{100}{e^{a+bX}}$$

and the bud-burst function by: $\text{DARD} = e^{a+bX}$ where $a$ and $b$ are constants specific to each provenance. In the following pages the bud-burst function intercept $a$ will be condensed to 'bud-burst intercept' or referred to as FI in tables and figures.

Prediction of bud-burst timing also required an equation to describe average daily temperature at a station as a function of date. For the two or three early spring months in which development toward bud burst is occurring, average daily temperatures are rising at an almost constant rate and thus can be fitted to linear equations. The sine function is perhaps more appropriate (Vittum, Dethier & Lesser 1965); but in using the linear form, loss of information is negligible and all subsequent arithmetic operations are less complex. Therefore, the generalized station temperature equation was $X = d + cT$ where $X$ is average daily temperature and $T$ is time in days after 22 December, the winter solstice.

The predicted date of bud burst at a station for an average year was calculated by integrating a station temperature equation with respect to the provenance bud-burst function to determine the day at which DARDs accumulated to 100%. An average year is defined as one in which the spring course of daily temperature at a station follows averages established over a 21-year period of record. An observation for a climatic variable for stations was based on data from 1948 through 1969, with four exceptions—two stations having only 8 years of record, two only 16.

RESULTS

Provenance temperature responses

On the average, in the covariance analysis of $\log_e$ DARDs of provenances, individual regression lines explained about 80% of the variation in DARDs. Means were highly significantly different ($F = 9\cdot06^{**}$), regression coefficients were not ($F = 0\cdot91$ N.S.). Therefore, the forty-four regression lines generated by the analysis are non-coincident but parallel, and, by projection, intercepts $(a)$ are also non-coincident. Consequently, the function to describe temperature response was taken to have the same rate coefficient $(b)$ for all provenances. From the common line of the co-variance analysis, this is $b = 0\cdot125$ ($\log_e$ DARD per $^\circ C$ per day). Since the rate change coefficient is constant, it follows that the bud-burst process has the same temperature coefficient ($Q_{10} \sim 3\cdot5$) for all provenances.

As indicated by statistically different intercepts $(a)$, genetic differentiation has occurred among provenances in temperature requirements for bud burst. Variation is not large
(Table 1, \( a = -0.8015, \) S.D. = 0.11, C.V. = 14\%); but its effects are magnified considerably in calculation of DARDs or days to bud burst. The effect on the calculated time to bud burst of differences in intercepts depends on the average temperature in which bud burst occurs. This is illustrated in Fig. 1, in which two surfaces relate days-to-bud-

\[ X = d + cT \]

where \( X \) is the average daily temperature and \( T \) is time in days after 22 December. For examining the relation of bud burst to climate, five collection stations were omitted as being non-representative of the region of major interest by virtue of their location in the Cascade Mountains’ rain shadow. Intercepts \((d)\) for the remaining thirty-nine stations ranged from approximately \(-11^\circ C\) to \(4^\circ C\), and regression coefficients \((c)\) ranged from 0.057° C per day to 0.135° C per day (Table 1). Intercepts mainly reflected differences in mean annual temperature and were closely related to mean minimum temperatures in January \((d = 0.30 + 1.125X - 0.101(X)^2); d = \) intercepts, \( X = \)
average daily minimum, $R^2 = 0.94$). Regression coefficients measure the rate of spring increase in temperature. Colder locations usually have higher rates of increase. For the thirty-nine stations, there was a negative correlation between intercepts $(d)$ and coefficients $(c)$ of $r = -0.90$.

**Relation of station climate to genetic differentiation**

In Douglas-fir, timing of bud burst has been assumed to be primarily an adaptation to temperature climate; a case in point is the common hypothesis that bud burst is synchronized with date of last spring frost in response to selection by frost (Irgens-Moller 1957; Sweet 1965; Sorensen 1967). A second variable of potential significance is early summer moisture stress, which may act to shorten the latter half of the growing season and create compensatory pressures for an early bud burst. Another is latitude, which has been emphasized by Swedish genecologists (Langlet 1936; Hagner 1970). Climatic variation is often strongly associated with latitude, and population adaptations are often achieved by a modification of photoperiodic reaction.

Habitat–provenance correlations were examined with respect to eight climatic variables, which were: (1) LSF (last spring frost) which was the average date of the last spring minimum of 0°C at a station, measured in number of days after 22 December; (2) LSF at -2.22°C; (3) LSF at -4.44°C; (4) length of frost-free season (0°C–0°C); (5) standard deviation of year-to-year differences in LSF at 0°C; (6) mean daily temperature at LSF used as an index of the magnitude of fluctuation in daily temperatures; (7) precipitation index which was the sum of the mean precipitations at a station for the months of May, June and July; (8) latitude. Descriptive statistics for 1 and 8 are given in Table 1.

Correlations between climatic variables and bud-burst intercepts $(FI)$ were statistically significant for six of eight variables (Table 2). In addition, intercorrelations among climatic variables were obvious. When analysed by stepwise multiple regression, six variables were dropped from the model on the basis that their inclusion did not significantly reduce the sum of squares in bud-burst intercepts $(FI)$. The resulting equation was:

$$FI = 0.7742 - 0.0292 \text{ (latitude)} - 0.0024 \text{ (LSF(-2.22°C))}$$

with $R^2 = 0.60$ and standard error from regression = 0.0068.

Thus, of the habitat factors considered, the two that contributed significantly (at $P < 0.01$) to explanation of variation (after intercorrelations with other variables were discounted) were latitude and date of last spring frost of intensity -2.22°C. It should be noted that precipitation was significantly correlated with bud burst intercepts and would have entered the model had it not been correlated also with latitude, which was, in turn, even more closely associated with intercepts.

Correlations of climatic factors with predicted dates of bud burst (EDB—Table 2) are generally stronger than with bud-burst intercepts and differences are greater for frost variables. Correlations of frost dates with EDB were obviously enhanced by climatic elements that are common to frost variables as well as to the temperature estimates used in predicting bud burst. However, the same common elements are likely in nature. If so, this is an illustration that phenotypes may be more closely correlated with selecting agents in nature than is indicated by provenance–habitat correlations based on provenance performance in a 'common garden'.

**Seed-transfer effects**

To illustrate effects of seed movement in terms of geographic parameters, thirty-six hypothetical plantation sites were selected representing twelve locations in each of three
Table 2. Simple correlation coefficients based on data from thirty-nine stations and respective provenances (variables are defined in text)

<table>
<thead>
<tr>
<th></th>
<th>EDB</th>
<th>LSF (0° C)</th>
<th>LSF (−2.22° C)</th>
<th>LSF (−4.44° C)</th>
<th>Frost-free season</th>
<th>Standard deviation in LSF (0° C)</th>
<th>Mean temp. at LSF (0° C)</th>
<th>Precipitation</th>
<th>Latitude</th>
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<tbody>
<tr>
<td>FI</td>
<td>−0.67*</td>
<td>−0.37</td>
<td>−0.43</td>
<td>−0.42</td>
<td>0.37</td>
<td>0.02</td>
<td>0.21</td>
<td>−0.40</td>
<td>−0.55</td>
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<tr>
<td>LSF (0° C)</td>
<td>0.70</td>
<td>0.95</td>
<td>0.89</td>
<td>−0.97</td>
<td>−0.44</td>
<td>0.30</td>
<td>−0.06</td>
<td>−0.27</td>
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<tr>
<td>LSF (−2.22° C)</td>
<td>0.77</td>
<td>0.94</td>
<td>0.88</td>
<td>−0.94</td>
<td>−0.33</td>
<td>0.22</td>
<td>−0.39</td>
<td>−0.19</td>
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<td>LSF (−4.44° C)</td>
<td>0.80</td>
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<tr>
<td>Frost-free season</td>
<td>−0.70</td>
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<td>Standard deviation in LSF (0° C)</td>
<td>−0.16</td>
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<td>Mean temp. at LSF (0° C)</td>
<td>−0.38</td>
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<td>Precipitation</td>
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<td>Latitude</td>
<td>0.35</td>
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* Values exceeding ±0.32 significant at P<0.05; values exceeding ±0.41 significant at P<0.01.
vertical transects. At the 45th parallel, one transect extended in a plane reaching from 300 to 1200 m in elevation and from 50 to 150 km east of the Pacific Ocean. The other two transects were identical in make-up but were located along the 44° N and 46° N parallels. Three hypothetical provenances were chosen to move to these plantations. Provenances came from three spots in the central transect (45th parallel) at 600 m elevation at points 50, 100, and 150 km from the ocean.

To evaluate seed-transfer, expected dates of bud burst were calculated. Two preliminary steps were required. First, it was necessary to describe station temperature intercepts \( d \) and coefficients \( c \), and bud-burst intercepts \( F_l \), as functions of latitude, elevation, and distance from the ocean. The functions required for this step were provided by three stepwise multiple regression analyses of \( F_l \), \( ds \) and \( cs \), and geographic parameters, for the provenance collection stations. The three analyses successively fitted the three dependent variables to geographic parameters. Resulting equations were:

\[
\begin{align*}
F_l &= 0.27 - 0.0005 \text{ latitude}^2 - 0.0036 \text{ elevation} + 0.0000015 \text{ (elevation} \times \text{ distance),} \\
& \quad R^2 = 0.55; \\
\hat{d} &= 2.71 - 0.018 \text{ distance} - 0.000076 \text{ (latitude} \times \text{ elevation}) - 0.000023 \text{ (elevation} \times \text{ distance),} \\
& \quad R^2 = 0.88; \\
\hat{c} &= 0.061 + 0.00042 \text{ distance} - 0.0000014 \text{ distance}^2 + 0.00000053 \text{ (latitude} \times \text{ elevation),} \\
& \quad R^2 = 0.70.
\end{align*}
\]

Latitude is in degrees, elevation is in metres above sea level, and distance from the ocean is in kilometres.

In the second step, the above equations were used to calculate constants for station temperature functions for the thirty-six hypothetical plantation sites and expected flushing intercepts for provenances indigenous to the sites. In the final step, two bud-burst dates were calculated for each plantation location for each of the three provenances. The predicted dates (local) and (introduced) were, respectively, the expected mean dates of bud burst for an indigenous, local provenance growing in a plantation at its point of origin, and for one of the hypothetical provenances after its movement to the plantation (Table 3). The difference between predicted dates (local) and (introduced) provided an index of the effect of transfer.

Hypothetical effects of movement are illustrated in Fig. 2. In each diagram, two surfaces can be compared. The zero surface, slightly above the base of the block and in the same plane, represents the expected performance of the indigenous population planted at each of the plantation sites, i.e. predicted dates (local) minus (local) = 0. The boldline top surface is the response of the introduced provenance compared to the local as predicted dates (local) — (introduced). Fig. 2(a) gives effects of moving seed from a provenance whose station is on the 45° parallel, 150 km from the ocean, and 600 m in elevation to other plantations on the same parallel. For example, seedlings would be expected to break buds about 5 days earlier than the local provenance in an average year if moved to a plantation at the same elevation (600 m) but 100 km nearer the coast. When the line connecting the four plantations which are 150 km from the coast is compared to the line for plantations 50 km from the coast, it can be seen that effects of movement along an elevational transect are greater the closer one approaches the coast. This reflects the influence of the lower bud-burst intercepts of coastal provenances operating in combination with the lower rates of increase in spring temperature common to the coastal region. Surfaces in Fig. 2 (a, b, c) are in parallel planes, but differences in predicted dates move toward the negative by 2–3 days for every 50 km the provenance is
FIG. 2. The bold broken line surface in each subfigure represents the performance of one hypothetical provenance at twelve hypothetical plantation sites including the point of origin of the provenance (circle). Performance is measured as the number of days that the introduced provenance is expected to be earlier (above the 0 surface) or later (below the 0 surface) than the local provenance.
Table 3. Predicted dates of mean bud burst at twelve hypothetical plantation sites along latitude 45° N (dates in column 3 are for provenances indigenous to sites; dates in columns 4, 5 and 6 are for three provenances hypothetically transferred to the twelve sites; the three provenances are all from stations at 600 m elevation, but 50, 100, and 150 km from the ocean)

<table>
<thead>
<tr>
<th>Hypothetical plantation sites</th>
<th>Expected date of bud burst (days after 22 Dec.)</th>
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<tr>
<td></td>
<td>Provenance origin</td>
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<tr>
<td>Distance from ocean (km)</td>
<td>Elevation (km)</td>
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<td>50</td>
<td>300</td>
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<td>1200</td>
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nearer the ocean. Transfers directly to the north, or to the south, by 1° of latitude created a set of surfaces parallel to, but, respectively, 3-4 days above or below those in Fig. 2.

DISCUSSION

A short-term field test of the model does not appear to be feasible. A predicted date of bud burst is an estimated average date resulting from a station temperature pattern based on 21 years of record. It is unlikely that a 2- or 3-year trial would adequately sample the average temperature pattern of a station.

Some subjective evidence, however, leads one to accept the model as a first approximation. Experimental results support an assumption that timing of bud burst is in response to adaptive selection. Genetic differentiation in bud-burst intercepts among populations was correlated with hypothesized selection agents, evidence that the temperature response is not random. Also, predicted dates of bud burst are generally in accord with Hopkin's (1918) empirically derived 'law' which states that in temperate North America a given phenological event will vary by 4 days for each 1° of latitude or 400 ft of elevation. From Table 3, it can be calculated that predicted dates of bud burst of local populations were later, on the average, by 5.5 days for every increase in elevation of 400 ft at a distance of 150 km from the ocean, and later by 4.9 days for every 400 ft at a distance 50 km from the ocean. Also, from a regression equation relating predicted dates (EDB) to latitude (EDB = -50.86 + 4.0 latitude), dates were later by 4.0 days per degree of latitude. Similar rates of change with elevation and latitude have been reported for phenological events in Britain (Smith 1938; Jeffree 1960) and Japan (Sekiguchi 1951).

Additional evidence is supplied by Silen's (1963) study of phenology of pollen shedding in Douglas-fir. Four elevational transects were sampled, two each in Coast and Cascade Ranges of western Washington and Oregon. Averaged over transects, dates of shedding of pollen were later by 5.2 days per 400 ft. This corresponds exactly to the average rate calculated from predicted bud burst dates in the present experiment. Silen (1963) reported
some variations in observed rates among transects, but did not detect significant differences between Coastal and Cascade populations.

Before the present model can be used to prescribe seed transfer rules, several refinements are in order. In this experiment, photoperiod during temperature treatment was longer than for any day of the year in the region, and presumably did not differentially affect bud burst. Evidence from previous work (Wommack 1964) indicated that Douglas-fir lacks a bud-burst reaction to photoperiod once chilling requirements are met. However, in view of the relation of bud-burst intercepts to latitude, chilling requirements may not have been completely satisfied or there may have been other residual effects of photoperiod. At any rate, it may be necessary to include either chilling or photoperiod effects in subsequent models. This question is now in the first phases of investigation.

SUMMARY

This report explores the use of prediction of timing of vegetative bud burst to examine response of seedlings to seed transfer in reforestation. Two sets of simple equations provide the model. The first set was derived from a glasshouse experiment using forty-four provenance collections made at weather stations in western Washington, Oregon, and northern California. It had the form $\hat{W} = \frac{100}{e^{a+bX}}$ where $W =$ mean number of days to bud burst of terminal buds and $X =$ average daily temperature. Provenances had the same coefficient $b$, but differed in intercepts $a$, which, in turn, were correlated ($R^2 = 0.60$) with latitude and date of last spring frost at collection stations. The second set had the form $\hat{X} = d + cT$ where $X$ is as above and $T$ is time in days after 22 December. Dates of bud burst were predicted for hypothetical populations along elevational and latitudinal transects. Although it was not possible to objectively test predictions, they were generally in accord with Hopkin's bioclimatic 'law' and other available evidence. Results of a hypothetical transfer indicated that moving seed in east-west directions is likely to be more maladaptive than moving seed an equivalent north-south distance.

REFERENCES


Prediction in seed transfer reforestation


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