Shoot Growth Phenology, Dry Matter Distribution and Root: Shoot Ratios of Provenances of Populus trichocarpa, Picea sitchensis and Pinus contorta growing in Scotland

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Introduction

Inherent differences in root : shoot weight ratios of trees are of interest as factors that may influence wind stability, and because they may reflect differences in the relative growth rates of the roots and shoots.

Windthrow, basal stem bending and wind-loosening are serious problems in Britain (Edwards et al., 1963; Lines and Booth, 1972) and any genetic gain in wind stability would be valuable. It is assumed in this paper that genotypes which have relatively heavy root systems (and hence proportionately smaller shoots and sail area) will often be better anchored than those with light root systems, although there will, of course, be differences in root morphology and responses to soil conditions. In the case of Pinus contorta there is good evidence that southerly, fast-growing provenances, which are often not wind-firm in Britain, have particularly small root : shoot weight ratios both as nursery seedlings and 8-year-old forest trees (Lines, 1971 and pers. comm.).

The relative growth rates of roots and shoots are important parameters of dry matter producion. They reflect, for instance, the proportion of total dry matter gain that is reinvested in photosynthetic tissue. The functional, hormone-mediated equilibrium that governs the partition of assimilates between shoots and roots is at the core of most models of plant growth (e.g. Brouwer, 1962; Ledig, 1969; de Wit et al., 1971; Promnitz, 1975). The ratio of the relative growth rates of shoots and roots in young plants with exponential growth is given approximately by the 'allometric coefficient' k in the equation:

$$\log \text{ shoot dry weight} = a + k \log \text{ root dry weight.}$$

If k is greater than 1.0 the root : shoot ratio will decrease with increase in plant weight, and if it is less than 1.0 the root : shoot ratio will increase with increase in plant weight (Ledig et al., 1970; Wareing and Patrick, 1975). The value of k is governed by the relative 'activity' of the root and shoot masses, such that root weight X rate (absorption) $\sim$ leaf weight X rate (photosynthesis). Most herbaceous plants will respond to a change in root or shoot 'activity' by a compensating change in root and shoot masses (Thornley, 1972; Hunt, 1975; also Thornley, 1975).

Maggs (1961) working with young apple rootstocks and Ledig et al. (1970), reviewing work on conifer seedlings, agreed that k could differ between tree genotypes, but stressed that k was unusually stable in trees and only altered by drastic environmental treatments or changes in physiology. Such physiological changes undoubtedly include the temperature and photoperiodically induced changes in the activity of the shoot apices, since k can only remain constant as long as both the shoots and roots are competing dry matter sinks. Thus, Wareing (1950) showed that k decreased in Pinus sylvestris seedlings that had stopped

elongating in short days for several weeks; that is, their roots then grew relatively faster than their shoots. The same phenomenon is evident in Heide's (1974) data on dry weight changes in Picea abies seedlings in different photoperiodic regimes. Also, Sweet and Wareing (1968) working on Pinus contorta seedlings, and Schultz and Gatherum (1971) on Pinus sylvestris, showed that provenances which were photoperiodically induced to stop elongating their shoots early in their first growing season subsequently developed relatively large root : shoot dry weight ratios compared with provenances which continued elongating late into the autumn.

This paper describes observations extending those already made by Sweet and Wareing, and Schultz and Gatherum. Do provenances of contrasting species with similar natural ranges show similar geographic trends in root : shoot ratios? Are provenance differences in root : shoot ratio linked with differences in seasonal periods of shoot growth? And do differences in shoot growth phenology alter the values of k as suggested by Wareing (1950) and Heide (1974), and, if so, are the resulting differences in root : shoot ratio compounded over successive seasons?

The three species analysed, Populus trichocarpa, Picea sitchensis and Pinus contorta, all have natural ranges along the western seaboard of North America and are shown to have comparable photoperiodic ecotypes. They are all grown commercially in Britain, where some provenances are clearly ill-adapted to the mild, maritime climate with northern daylength regimes and strong winds.

Populus trichocarpa Torr. and Gray

Periods of shoot elongation

Populus trichocarpa ranges from Alaska to California and inland to the Rocky Mountains and Montana. The dates when clones from throughout this range stopped growing in height between June and October 1951 at Weston, Mass., U.S.A. (42^0 22' N) were inversely correlated with their latitudes of origin (r = —0.82) and the dates for clones from latitudes 45 to 47^0 N (where climatic data were available) were positively correlated with the lengths of the growing seasons at their places of origin (90—220 days, r = 0.79; Pauley and Perry, 1954).

A collection of 98 clones of Populus trichocarpa from 62 locations throughout its range were established in unreplicated rows in a nursery at the Bush Estate, Midlothian, Scotland, in 1972 (55^0 50' N). Some cuttings had been taken from Pauley's surviving collection at Weston with generous help from the Maria Moors Cabot Foundation, and others had been kindly sent by workers in western North America. By taking weekly height measurements on 5 plants during 1973, the date was estimated when each clone completed 95% of its total height growth. Pauley and Perry's findings were confinned, and using Smithsonian tables of global

daylength, *Figure 1* was constructed, relating the latitude and elevation of origin of the clones to the daylength at the time of height growth cessation. In this way Pauley and Perry's data could be compared directly with ours. Multiple regressions relating the daylength when height growth ceased to latitude and elevation of clone origins accounted for over 80% of the variation, and the regression coefficients were not significantly different for the two sets of data. Both at Weston, Mass., and Bush, Scotland, a move north of about 100 miles (1⁰ latitude = 69 miles) or an increase in altitude of origin of about 880 ft (268 m) increased the daylength when height growth had approximately ceased by about 16 minutes. More limited data for *Populus trichocarpa* clones grown at Ås-N.L.H., Norway (59⁰ 40' N) fell within the expected range *(Figure 1)*. In all cases the amounts of height growth made were not closely correlated with the times of height growth cessation (at both Weston and Bush, r = 0.55).

clone) at 21 weekly intervals between June and October 1973. Shoot lengths were measured, and stems, leaves and roots were dried and weighed. The roots reached the base of most pots by mid-August.

All clones distributed their dry matter similarly up to the times when they stopped growing in height. From then on proportionately more dry matter was diverted to their roots and their leaves senesced *(Figure 2)*. Because the Alaskan clones stopped elongating first (*c.* 15 August) they developed a proportionately large weight of roots (over 60% of the total), whereas the Washington clones, which did not stop elongating until after there had been ground frosts (3 October), developed a relatively small root weights (33% of total).

Root : shoot weight ratios

The mean root : shoot dry weight ratios after leaf fall were 1.7, 1.1, 0.7 and 0.5 for the Alaskan, Skeena River,
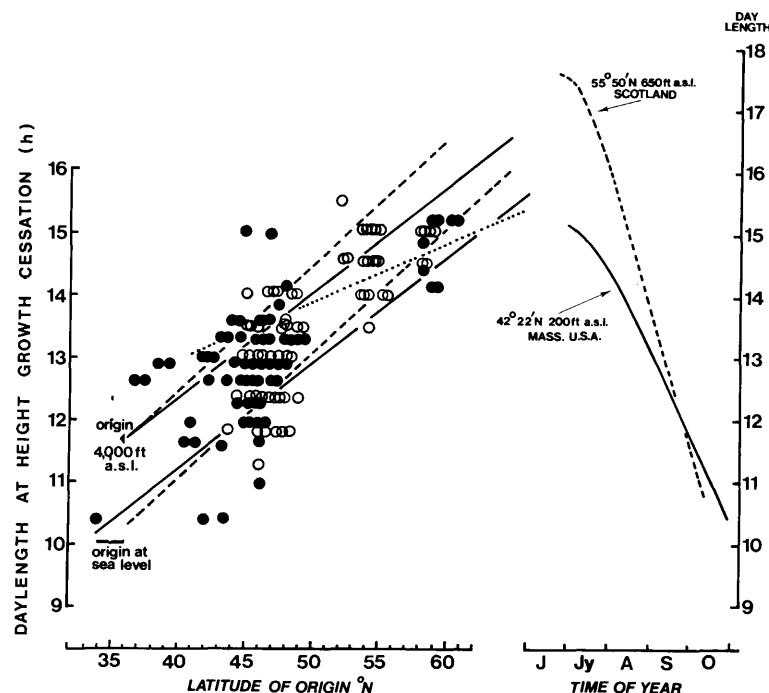

Figure 1. — Relationships between daylengths when clones of *Populus tricho-carpa* stopped growing in height and their latitudes and elevations of origin. Data for Mass., U.S.A. are after Pauley and Perry (1954) by courtesy of the Maria Moors Cabot Foundation. The dotted line was fitted through data for 19 clones grown at Ås-N.L.H., Norway, supplied by Dr. A. Langhammer. Daylengths are defined by the times when the sun's disk is 50' below the horizon. The multiple regressions, where z = daylength in minutes, x = latitude in minutes, and y = elevation in feet, are z = 174 + 0.20x + 0.022y for Scotland, and z = 262 + 0.17x + 0.017y for Massachusetts.

Distribution of dry matter

Of the 98 clones at Bush, four were chosen for growth analysis from each of four contrasting latitudes at coastal sites less than 100m altitude. They were: Haines and Juneau, Alaska, at a mean of 58⁰ 54' N; lower Skeena River, British Columbia, 54⁰ 36' N; lower Fraser River, B.C., at a mean of 49⁰ 12' N; and Castlerock, Woodland and Camas, Washington State, at around 46⁰ 00' N. Single-node cuttings were rooted in a glasshouse in 2" peat pots of loam in March 1973, and transferred to 12" whale hide pots of loam which were buried in nursery beds at Bush in April, 1973. Clones were assigned randomly to plots within each of four blocks. One plant of each clone, representing each latitude zone, was removed from each block (total of 4 plants per

Fraser River and Washington clones, respectively (signif. different P < 0.05). Taking the 16 clones separately, root : shoot weight ratios were negatively correlated with dates of height growth cessation, and positively with their latitudes of origin, both with r = 0.81.

Allometric relationships

Relationships between log shoot dry weights and log root dry weights were significantly linear over the period of the experiment, and the regression (or allometric) coefficients for the clones decreased with latitude of origin *(Table 1)*. That is, the Alaskan clones developed greater root : shoot ratios than the Washington clones, because their ratios of root relative growth rates: shoot relative growth rates in-
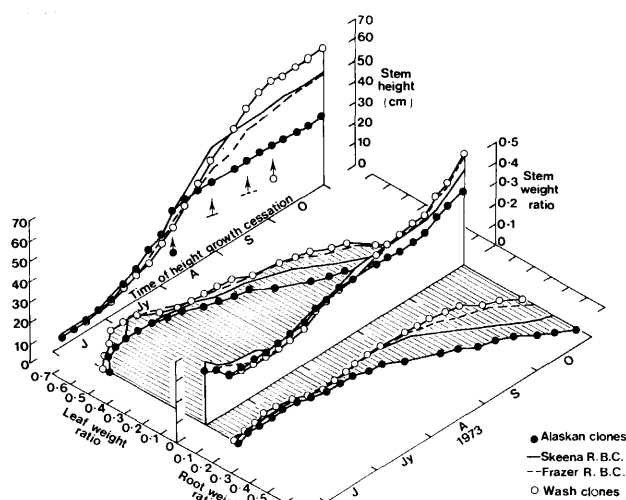
Figure 2. — Seasonal changes in the proportion of the total dry weight of *Populus trichocarpa* clones which occurred in the leaves, stems and roots, shown in relation to their increase in height. Each point is a 3-week moving mean of 4 plants sampled per week, representing 4 clones from a given latitude zone, grown in buried containers in a nursery at Bush, Scotland.

calculated to be 0.21, which was not significantly different from the coefficients calculated for *Populus trichocarpa* (legend to *Figure 1*). That is, the mean change in apparent daylength response with provenance latitude of origin was similar for the two species. KRAUS and LINES (1976) showed how local variations were superimposed on this general pattern for *Picea sitchensis*.

Distribution of dry matter

Seasonal changes in dry matter distribution in *Picea sitchensis* were monitored for 18 months after germination by sequential destructive sampling. Four provenances were compared: Cordova, Alaska (60⁰ 30' N); Sitka, Alaska (57⁰ 05' N); Skidegate, Queen Charlotte Is., B.C. (53⁰ 13' N), and Denmark, Oregon (42⁰ 51' N), all from less than 100 m altitude. Two hundred stratified seeds of each provenance were germinated individually in paper pots of sand : peat : loam (1 : 1 : 1) in June 1972, and transferred to 4" pots in August 1972. They were then grown in natural daylengths at Bush, protected inside an open-ended polythene tunnel. Sixty plants per provenance were placed in each of four randomized blocks which were ranked according to plant size. One plant of each provenance was taken from each block on 14 occasions between September 1972 and Feb-

Table 1. — Regression equations relating log. shoot dry weight to log. root dry weight (mg) of *Populus trichocarpa* clones from four latitudes (<100 m alt.) grown from single-node cuttings outdoors at Bush, Scotland, between June and October 1973. The regression coefficients approximate the 'allometric' or 'relative growth' coefficients (LEDIG *et al.* 1970; WAREING and PATRICK 1975). Each is based on 21 values.

Clone origins (see text)	Correlation coefficient r	Intercept	Regression coefficient ± S.E.
Alaska	0.97	1.13	0.77 ± 0.033
Lower Skeena River, B.C.	0.99	1.06	0.85 ± 0.038
Lower Fraser River, B.C.	1.00	0.94	0.93 ± 0.037
Washington State	0.99	0.88	0.97 ± 0.033

creased after height growth cessation, and not because they were different in total weight from the Washington clones.

Picea sitchensis (BONG.) CARR.

Periods of shoot elongation

Picea sitchensis ranges from Alaska to California, mostly within 100 miles of the sea, and below 100 m altitude. Recent studies by KRAUS and LINES (1976) on I.U.F.R.O. seed collections growing at Bush have substantiated that the date of height growth cessation of seedlings in their second year is under temperature-modified photoperiodic control, (see also ALDHOUS, 1962; LINES and MITCHELL, 1966; ROCHE, 1969; MALCOLM and CALDWELL, 1971). Photoperiod regulates shoot elongation as long as the plants are able to produce 'free' growth (POLLARD, TEICH and LOGAN, 1975). The relationship at Bush between (y), the day after January first when seedlings completed 80% of their height growth, and (x), their latitudes of seed origin in ⁰N, was y = 352 — 2.03x (r = —0.91, KRAUS and LINES, 1976). The same relationship calculated for 32 *Populus trichocarpa* clones from lowland seaboard regions in W. America growing at Bush was: y = 350 —2.12x (S.E. ± 0.16, r = —0.92). The regression coefficients are not significantly different. Furthermore, KRAUS and LINES' regression coefficient for *Picea sitchensis*, relating the time of height growth cessation in terms of daylength (in minutes) with latitude of provenance origin, was

ruary 1973. The remaining seedlings were transferred to 9" pots of the same compost and plunged in a nursery bed, again in 4 randomized blocks ranked by size. Sampling was then continued at 1—2 weekly intervals until December 1973. Each sampled seedling was measured in height, divided, dried and weighed.

As expected, shoot extension terminated about 8 weeks sooner on the Alaskan seedlings than on the Oregon ones, and there was a marked increase in root weight ratios (root dry weight : total plant dry weight) after shoot elongation ceased, provided this occurred before about mid-October. Consequently the Alaskan provenances developed proportionately heavier root system than the Oregon provenance during late summer, and had greater root : shoot weight ratios throughout the winter. However, following early spring root growth, the Alaskan provenances began extending their shoots before the southerly provenances, and retained virtually all their dry matter gain in their new shoots. Consequenty their root : shoot ratios fell abruptly, and for about 5 weeks in May-June their root : shoot dry weight ratios were similar to those of the Oregon provenance *(Figures 3 and 4)*.

Root : shoot weight ratios

Of the 64 I.U.F.R.O. provenances studied by KRAUS and LINES (1976) 32 were sampled from nursery seedbeds at the end of their first growing season at Bush (1973) and 22 were sampled from transplant lines at the end of their
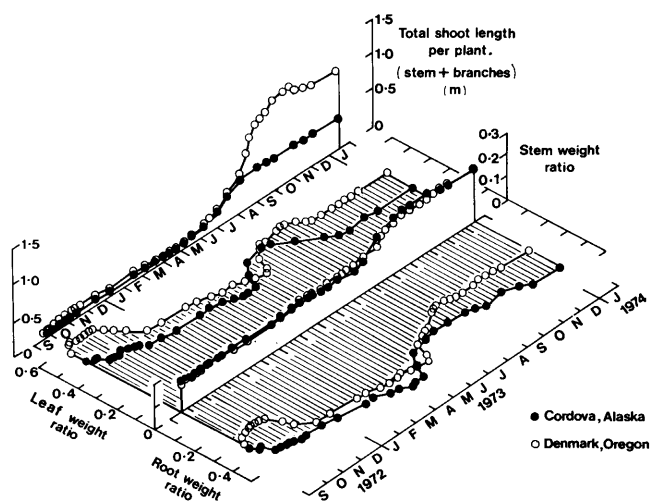
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Figure 3. — Seasonal changes in the proportion of the total dry weight of *Picea sitchensis* seedlings of two provenances which occurred in the needles, stems and roots, shown in relation to their increase in shoot length. The seedlings germinated in June 1972. Each point is a moving mean of 1—3 weekly samplings of 4 plants, grown in an unheated polythene tunnel at Bush in 1972 and in a nearby nursery in 1973.

not be explained by differences in the total weights of the seedlings *(Figure 7 a)*. It seemed that northerly provenances maintained relatively heavy root systems compared with southerly provenances, although there was little evidence for a difference in the 'allometric coefficient' describing the slope of the relationship between shoot and root dry weights *(Figure 7 a)*. However, these measurements described the situation only at the end of each growing season.

Turning now to the four provenances that were sampled continuously, it is clear that the allometric relationships between shoot and root dry weights changed during each growing season. During the late summer and autumn of their first and second growing seasons, the northerly provenances had relatively rapidly growing root systems compared with southerly provenances, as suggested in *Figures 3 and 4*. However, during the spring and early summer, when the shoots increased in weight rapidly, the northerly provenances had relatively faster growing shoots than the southerly provenances *(Figure 7 b)*. Consequently, the allometric coefficients became temporarily similar for all provenances during the summer, before differences in dry matter distribution were set-up again as a result of differences in dates of height growth cessation. Insofar as they are meaningful, the slopes of linear regressions of shoot and root dry weights recorded from germination to the end of the second year, were not significantly different between the four provenances (coefficients 0.99 to 1.06 ± 0.04). Thus, the apparent 'imbalance' in root : shoot ratios that occurred as a result of the differing periods of autumn root growth were temporarily fully compensated in spring and summer when the shoots were active dry matter sinks.

second growing season. On both occasions about 20 seedlings were taken per provenance, and their roots and shoots were separated, dried and weighed.

At the end of the first and second growing seasons the mean root : shoot weight ratios of these I.U.F.R.O. provenances were positively correlated with their latitudes of seed origin (r = 0.65 in 1973, and 0.60 in 1974, overall relationship in *Figure 5)*, and negatively correlated with the dates when they completed 85% of their height growth in their second year *(Figure 6)*. About 40% of the total variance in root : shoot weight ratios could be accounted for by either provenance latitudes and/or their dates of height growth cessation.

Allometric relationships

The differences in root : shoot dry weight ratios among the I.U.F.R.O. provenances were weakly positively correlated with their total dry weights (r = 0.28), but could

Pinus contorta DOUGL.

Pinus contorta ranges from Alaska to California (subsp. *contorta*) and inland over the Rockies in British Columbia (subsp. *latifolia*) and the Cascades in Washington and Oregon (subsp. *murrayana*).

Periods of shoot elongation

LONGMAN (1960) showed that *Pinus contorta* is photoperiodically sensitive, and CRITCHFIELD (1957) and HAGNER (1970) found relationships between the dates when 1—2
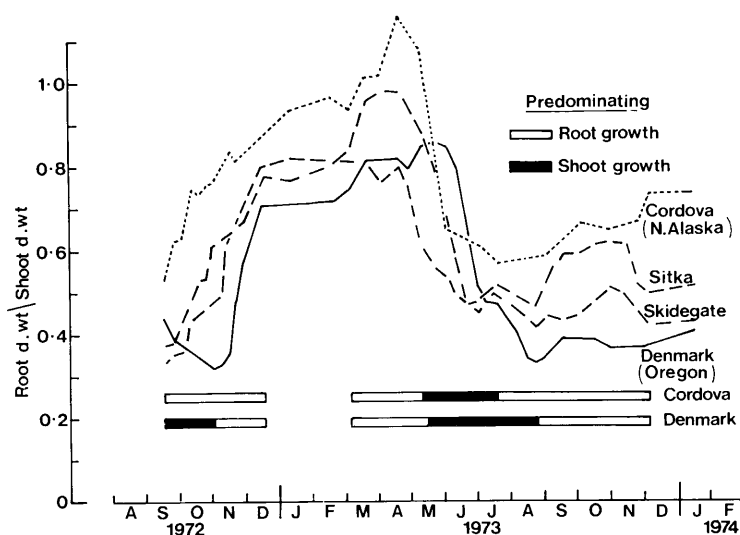

Figure 4. — Seasonal changes in the root : shoot dry weight ratios of *Picea sitchensis* seedlings of four provenances. Based on 1—3 weekly samplings of 4 plants per provenance, as for *Fig. 3*. Cordova, 60° 30' N; Sitka, 57° 05' N; Skidegate, 53° 13' N; Denmark, 42° 51' N.

Figure 5. — Relationship between (a) the root : shoot dry weight ratios of *Picea sitchensis* provenances sampled from a nursery at Bush, Scotland at the end of their first (○) and second (●) growing seasons, and (b) their latitudes of origin. Each point is the mean of about 20 seedlings. r = 0.67; y = —1.28 + 3.77x. Some provenances were sampled in only one growing season, while others were sampled from two blocks in one growing season. The I.U.F.R.O. identity numbers are given for each provenance: 3009—3018 from Oregon and Willapa Bay, Washington; 3001—3008 and 3052—3067 British Columbia; 3026—3068 Northern B.C. and Alaska. See KRAUS and LINES (1976) for a detailed listing.

Figure 6. — Relationship between the root : shoot dry weight ratios of *Picea sitchensis* provenances and the dates when they completed 85% of their height growth in their second growing season. See legend to Fig. 5. r = —0.61, y = 1.16 — 3.30x.

year-old provenances stopped growing in height and their latitudes and elevations of origin. The trends were similar to those shown in *Figure 1* for *Populus trichocarpa*.

However, these relationships are meaningful only in the first and, possibly, second years, because, in contrast to *Picea sitchensis*, these are the only years when there is substantial 'free' or lammas growth. In the third year, the total number of needle fascicles on *Pinus contorta* is mostly 'predetermined' the year before; the buds are, in effect, telescoped shoots, and elongate in early summer over relatively brief periods, irrespective of daylength or provenance. Northerly and montane provenances may finish elongating their shoots sooner than southerly provenances, but only because their pre-formed shoots (buds) have fewer stem units (Cannell, *et al.*, 1976). Because of the early onset of predetermined growth, studies on root : shoot weight relationships in *Pinus contorta* were continued until the end of the third year.

Distribution of dry matter

Dry matter distribution was monitored by sampling containergrown seedlings as described for *Picea sitchensis*. Seven provenances were studied spanning the latitude range: Skagway, Alaska, 59° 28' N, 150 m; Anahim Lake, Central Interior B.C., 52° 28' N, 1220 m; Nanaimo, Vancouver Is., 49° 10' N, 100 m; Masset, Queen Charlotte Is., 54° 00' N, 150 m; Clearwater, Southern Interior B.C., 51° 40' N, 460 m; Hauser Dunes, Oregon, 43° 30' N, 30 m; Cascadia (to S.E. near Lapine), Interior Oregon, c. 42° N, 300 m.

The treatments, experimental lay-outs, and measurements were the same as those in the *Picea sitchensis* experiments. Seedlings which had been treated identically to those sampled during their first year in a polythene tunnel, and during their second year in a nursery, were transferred individually into 15" buckets of nursery loam and plunged 50 cm apart in the Bush nursery for sampling throughout their third year (1974). In this year there were

the first year and produced considerable lammas growth in the second year *(Figures 8 and 9)*. The southerly provenances not only produced a proportionately greater weight of needles, but also relatively large weights of stems and branches *(Figure 8)*. As with *Picea sitchensis* there was evidence of early spring root growth before the shoots elongated appreciably. Also, like *P. sitchensis*, the roots grew very little while the shoots were elongating, especially on the Alaskan and inland provenances. During June-July the root : shoot weight ratios of the latter provenances were similar to, or smaller than, those of the southerly lowland provenances *(Fig. 9)*. Thus, provenances which had relatively heavy root systems during the winter could 'overcompensate', and produce relatively heavy shoots, the following summer.

In the third year all provenances stopped elongating their pre-formed shoots within the same 2 weeks in late July, and all produced a similar small amount of lammas
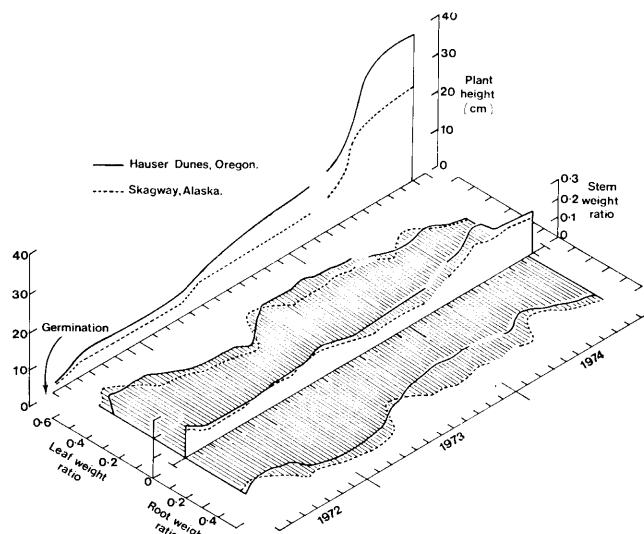
Figure 7. — Relationships between shoot and root dry weights of *Picea sitchensis* seedlings growing at Bush, Scotland. (a) I.U.F.R.O. provenances sampled from a nursery at the end of their first and second growing seasons; (b) fourth degree polynomials fitted through 37—45 values (each a mean of 4 plants) obtained for each of four provenances throughout their first two growing seasons. The regression coefficents were significantly different between Denmark and the others, and in all cases over 95% of the total variance was accounted for.

5 blocks, each with 33 plants of each provenance. One plant of each provenance was lifted from each block on 22 occasions between March 19 and November 12, 1974.

The pattern of distribution of dry matter during the first two years was similar to that described for *Picea sitchensis*. Those provenances which had brief periods of shoot elongation produced relatively heavy root systems during late summer and autumn compared with southerly provenances which had prolonged periods of shoot extension in

Figure 8. — Seasonal changes in the proportion of the total dry weight of *Pinus contorta* seedlings of two provenances which occurred in the needles, stems and roots, shown in relation to their increase in height. Lines are drawn through 3-date moving means of 4 plants sampled at 1—3 weekly intervals. The plants were grown in an unheated polythene tunnel at Bush in 1972, and in a nearby nursery during 1973 and 1974.
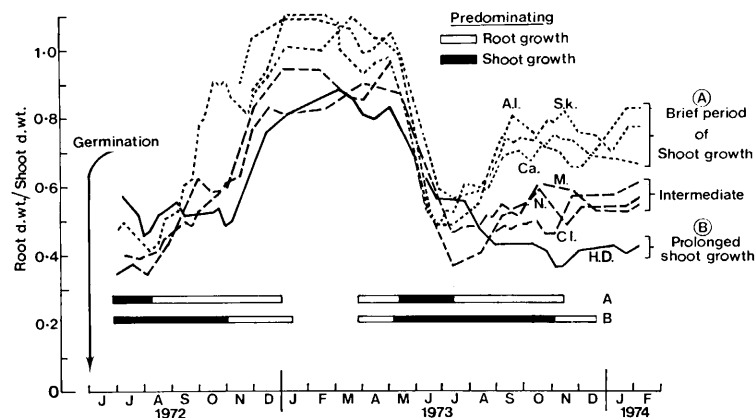

Figure 9. — Seasonal changes in the root : shoot dry weight ratios of *Pinus contorta* seedlings of seven provenances. Based on 1—3 weekly samplings of 4 plants per provenance as for *Fig. 8*. A.L. — Anahim Lake; Sk. — Skagway; Ca. — Cascadia; M. — Masset; N. — Nanaimo; Cl. — Clearwater; H.D. — Hauser Dunes.
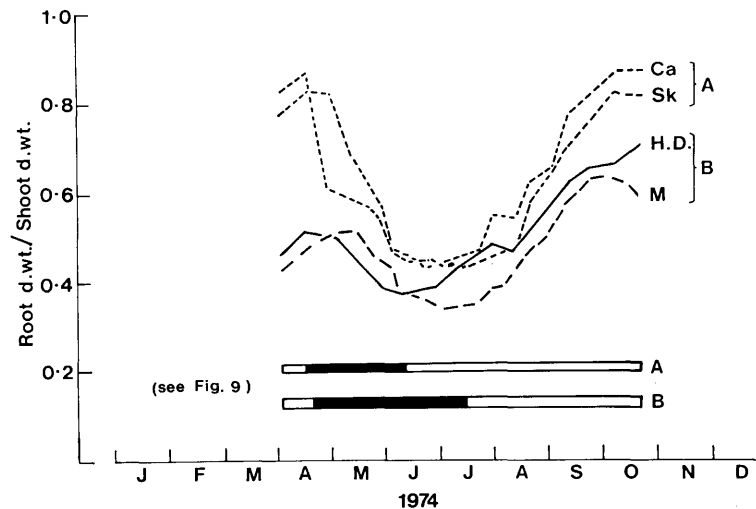
54

Figure 10. — Root : shoot dry weight ratios of *Pinus contorta* provenances during their third year. See legend to *Fig. 9.* Anahim Lake followed the same pattern as Cascadia (Ca.) and Skagway (Sk.), and Nanaimo and Clearwater did not differ appreciably from Masset (M.) or Hauser Dunes (H.D.).

growth in August. Consequently, they all had similarly long periods of root growth in late summer and autumn. Even so, the Alaskan and inland provenances which had small pre-formed shoots (Skagway, Anahim Lake and Cascadia) maintained and developed relatively large root-shoot ratios *(Fig. 10).*

Root : shoot weight ratios

LINES (1971) determined the root : shoot dry weight ratios of 18 provenances of *Pinus contorta* at the end of their first and second growing seasons. Nine seedlings were uprooted from each of two replicate nursery beds at Bush, Scotland, at the end of the first growing season, and five transplants were taken per provenance from each of four blocks growing in a nursery at Inchnacardoch, Invernesshire, Scotland, at the end of the second growing season.

In general, southerly provenances had smaller root : shoot dry weight ratios than northerly ones, and low-elevation provenances had smaller root : shoot weight ratios than high-elevation ones *(Fig. 11).* This is as expected from the trends in dates of height growth cessation for 1—2 year old seedlings of *Pinus contorta* (HAGNER, 1970). The latitude and elevation of origin of the provenances accounted for 67% of the variation in root : shoot dry weight ratios observed. Also, the provenances were ranked similarly in the two samplings (see LINES, 1971).

Allometric relationships

As with *Picea sitchensis (Fig. 7 a)* graphs of shoot against root dry weights for the provenances sampled at the end of their first and second growing seasons by LINES (1971) showed that the provenance differences were not due to differences in total dry weights. Root : shoot ratios were poorly correlated with total plant weights in both years (r < 0.20). However, these end-of-season data ignore the changes in allometry during the year.

During their first and second years the provenances with prolonged periods of late summer root growth (Skagway, Anahim Lake and Cascadia) had relatively rapid rates of root dry weight increase, compared with provenances with brief periods of root growth. This situation was reversed the following spring and early summer when the shoots were extending *(Fig. 12).* The roots of most prove-

nances actually decreased in dry weight at this time (May-June). Linear regressions, relating root and shoot dry weights, calculated for the whole period shown in *Fig. 12,* were not significantly different between provenances (coefficients ranged from 1.04 to 1.15 ± 0.028 to 0.044).

In their third year the differences in root : shoot weight ratios that developed among the *Pinus contorta* provenances could not be explained by differences in the relative durations of shoot and root growth, nor by differences in total plant weights. Even so, Skagway, Anahim Lake and Cascadia had significantly greater ratios of 'root to shoot relative growth rates' than the other provenances during the summer; that is, the slopes of the regressions relating shoot and root dry weigths were significantly different *(Fig. 13).* Also, the differences in shoot : root allometry indicated in *Fig. 13* occurred equally for relationships between needle and root dry weights. An explanation is
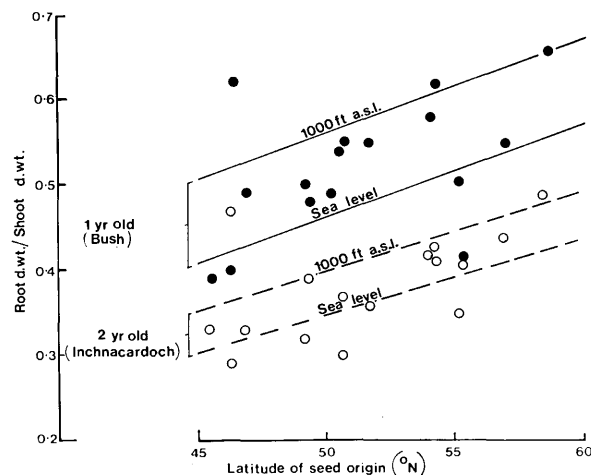

Figure 11. — Relationship between the root : shoot dry weight ratios of 16 provenances of *Pinus contorta* seedlings and their latitudes and elevations of origin. Data after LINES (1971).
● Bush nursery, Midlothian, Scotland, at the end of their first growing season. Root : shoot ratio = —0.093 + 0.018 lat. (mins) + 0.00010 elevation (ft); r (lat.) = 0.81; r (elev.) = 0.29.
o Inchnacardoch nursery, Invernesshire, Scotland, at the end of their second growing season. Root : shoot ratio = —0.116 + 0.015 lat. (mins) + 0.00005 elevation (ft); r (lat.) = 0.84; r (elev.) = 0.21.
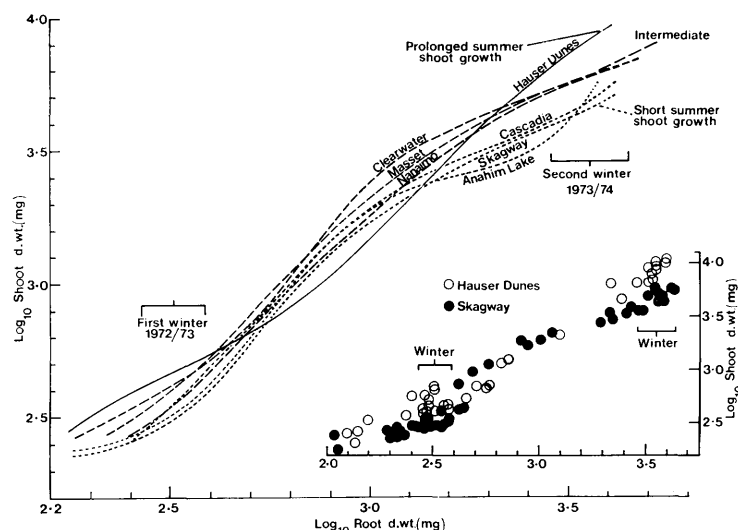
Figure 12. — Relationships between shoot and root dry weights of *Pinus contorta* seedlings of 7 provenances during their first two growing seasons. Fourth degree polynomials are fitted through up to 48 values (each a mean of 4 plants) obtained for each provenance as shown in the inset graph. Regression coefficients were significantly different between provenances with differing types of line in the figure.

that Skagway, Anahim Lake and Cascadia all had relatively small preformed shoots and hence smaller total commitments to shoot growth than the other provenances, although all the preformed shoots elongated over the same period of time. Thus, Skagway, Anahim Lake and Cascadia had shorter leaders and/or fewer branches than the other provenances and developed smaller stem as well as needle weight ratios *(Table 2).*

Table 2. — Mean shoot growth characteristics of *Pinus contorta* provenances following their main 'flush' of shoot elongation in their third growing season in a nursery at Bush, Scotland. Means of 48 plants sampled per provenance between July 23 and November 12.

Provenance (see text)	Height (cm)	Number of branches/plant	Proportion of total dry weight in:	
			stem	needles
Skagway	25.2	7.9	0.198	0.408
Cascadia	28.3	6.7	0.214	0.389
Anahim Lake	27.0	6.7	0.211	0.408
Nanaimo	35.3	7.9	0.238	0.420
Masset	28.9	9.4	0.219	0.457
Clearwater	34.8	6.8	0.233	0.434
Hauser Dunes	37.7	8.4	0.229	0.415
Least significant difference P = 0.05	2.01*	1.10*	0.0146**	0.0509**

* 269 d.f.   ** 55 d.f.

Discussion

The unexpected finding of these studies was that there were no marked, lasting differences in allometry between roots and shoots among provenances of *Populus trichocarpa, Picea sitchensis,* and *Pinus contorta* as judged by root and shoot dry weight relationships. That is, there was little evidence for inherent provenance differences in the relative 'activity' (as mineral nutrient and carbon sources) of the root and shoot masses. This was so even though there were provenance differences in the relative growth rates of the roots and shoots within each growing season, producing significant differences in root : shoot weight ratios at the end of each year.

Seasonal differences in dry matter distribution reflected inherent differences in shoot growth phenology as regulated, in particular, by temperature-modified photoperiodic responses. Provenances which were photoperiodically adapted such that they had prolonged periods of shoot elongation in Scotland, developed relatively less root than those with brief periods of shoot elongation. The relationship between dates of height growth cessation and end-of-season root : shoot weight ratios in young plants of all three species studied were as shown in *Figure 14.* In the case of 3-year old *Pinus contorta* with preformed shoots, the phenomenon was similar, but may be regarded as having occurred over two years. In the first year the shoot apices developed needle initials over brief or prolonged periods depending
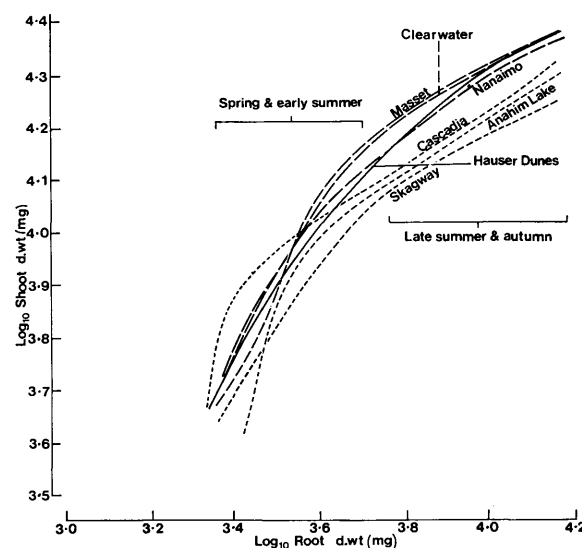

Figure 13. — Relationships between shoot and root dry weights of *Pinus contorta* of 7 provenances during their third growing season. Fourth degree polynomials are fitted through 13 mean values obtained for each provenance. Regression coefficients were significantly different between (a) Skagway, Anahim Lake and Cascadia and (b) the other provenances.

on the provenances' daylength and temperature sensitivity (CANNELL and WILLETT, 1975) and in the following year the trees developed correspondingly small or large shoot systems, irrespective of the potential size of the root sink. In Alaskan and inland provenances potential shoot growth was small compared with potential root growth and their root : shoot dry weight ratios became large compared with southerly provenances. However, during the following year's flush of shoot growth the root : shoot ratios of all provenances became similar because the shoots apparently monopolized current assimilates to differing extents and probably mobilized stored carbohydrates from the stems and roots. Teleologically speaking, apparent 'imbalances' in root and shoot masses that developed each summer and autumn were 'corrected' each spring or early summer, and the larger the 'imbalances' the greater the 'corrections'. There was little evidence that provenance differences in root : shoot masses were compounded each year as a result of differences in allometry.
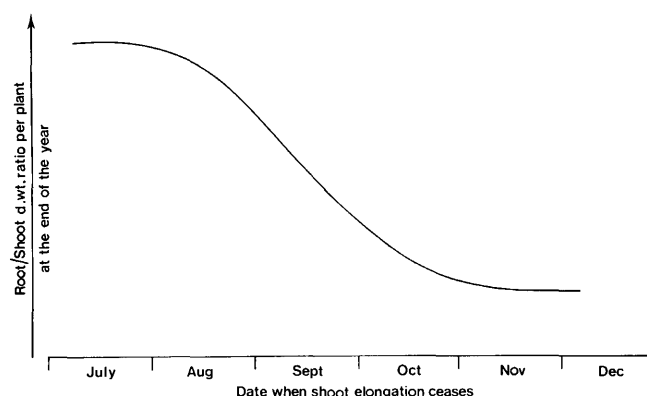

Figure 14. — General relationship, for young *Populus trichocarpa* plants and seedlings of *Picea sitchensis* and *Pinus contorta*, between the time of height growth cessation and end-of-season root : shoot dry weight ratios (see also *Fig. 6*).

This conclusion is supported by excavations of over 500 trees in five forest experiments by the U.K. Forestry Commission. These have shown that slow-growing Alaskan and inland provenances of *Pinus contorta* have end-of-season root : shoot fresh weight ratios 10% greater than southern coastal provenances, both as seedlings and young trees (LINES, pers. comm.), the important point being that this difference did not increase with age up to 8 years after planting. If there were differences in allometric coefficients between these provenances, there would be ever-increasing differences in root : shoot ratios as the trees increased in weight.

The seasonal trends in dry matter distribution were as expected (RUTTER, 1957; LYR and HOFFMANN, 1965; GORDON and LARSON, 1968; HOFFMANN, 1973). The roots (a) started growing in spring before the shoots, (b) grew more slowly, or lost weight, when 'predetermined' shoots began to grow, (c) grew faster as shoot growth slowed, and (d) continued to grow for varying periods of time after shoot growth ceased. Clearly, any homeostatic mechanisms between the shoots and roots operated only as long as they were competing sinks, and accordingly the only period when the allometric coefficients of all the provenances of one species were similar was during or after the periods of active shoot growth, usually in July. Thereafter the shoot : root allometric coefficients remained large if the shoots continued to demand a relatively large proportion of the total sum-

mer photosynthate, or decreased if the roots became the only major dry matter sinks, both as growth and storage organs. Evidently, photosynthesis continued long after the shoots had stopped elongating and were receiving relatively short photoperiods.

The end-of-season differences in root : shoot ratios reported here and elsewhere for photoperiodic ecotypes are, in a sense, artifacts. If the patterns of shoot development were not so rigidly fixed by adaptations to photoperiod and temperature regimes, but were able to fill the available growing seasons, it seems that the allometric coefficients of all provenances would be close to unity for most of the year. That is, the regression lines in *Figures 7 (b)* and *12* would be straight.

The mean allometric coefficients for the *Picea sitchensis* and *Pinus contorta* seedlings calculated over periods of 18 months varied little from 1.0. For instance, *Picea sitchensis* values varied from 0.99 for Sitka to 1.06 for Denmark, and *Pinus contorta* values in their first two years varied from 1.04 for Skagway to 1.15 for Hauser Dunes, and in their third year from 0.90 for Anahim Lake to 1.23 for Hauser Dunes (S.E. in the range 0.03—0.04). This suggests again that, for many provenances, root : shoot dry weight ratios will remain similar from year to year, irrespective of their seasonal changes and increase in total dry weight.

LEDIG and PERRY (1965) and LEDIG et al. (1970) concluded, from their reviews, that root : shoot ratios of tree seedlings increased with increase in tree weight. This would have been the conclusion in all these studies if the distribution of dry matter was monitored over only one season, simply because the roots became important dry matter sinks in the autumn. JONES (1968), reviewing the European literature, concluded that end-of-season root : shoot weight ratios of *Pinus* and *Picea* nursery seedlings decreased from year to year, and this tendency was demonstrated for mature *Pinus sylvestris* by OVINGTON (see LEDIG et al., 1970). In our studies root : shoot ratios were large at the end of the first year *(Figures 4 and 9)*, and thereafter the trends from year to year for *Pinus contorta* were less important than both the changes during each year, and the provenance differences. In any case, comparisons of root : shoot ratios can be misleading. Absolute values will depend on the rooting volume and medium, the method of extracting the roots and the presence of mycorrhizas, as well as gross features of the environment. All seedlings in these studies were well-watered, suffered no detectable mineral deficiency and the conifers had mycorrhizas, but inevitably the roots grew around the bottom of the pots by the end of all the experiments.

Practical implications

1. The thesis of this paper is that end-of-season provenance differences in root : shoot weight ratios may be temporary phenomena, which reflect the extent to which provenances are phenologically adapted to the length of the growing season in which they are grown. The size of the shoot sink is even when the shoots are preformed in buds, limited by the provenances' daylength and temperature sensitivity, whereas the roots are potential dry matter sinks throughout the growing season. Provenances with small shoot sinks in relation to total seasonal dry matter production will develop large root : shoot dry weight ratios and *vice versa*. However, in all but extreme cases, these differences do not reflect the allometric or functional balance between the roots and shoots (as sources of minerals or

carbohydrates) and will be compensated by relatively slow or rapid root growth during the following year's flush of shoot growth. That is, differences in root : shoot ratios are purely seasonal. Because seedling differences in end-of-season root : shoot weight ratios reflect only seasonal differences in allometric relationships, root : shoot ratio differences cannot be expected to increase in subsequent years.

2. Provenances with large root : shoot ratios will tend to be those which produce small shoot dry weights in long growing seasons. The desirable combination of a large amount of shoot growth with a large end-of-season root : shoot ratio is unlikely to be found among provenances, but could be sought among progenies or clones.

3. End-of-season differences in root : shoot dry weight ratios that occur between provenances, although temporary, do last throughout the autumn and winter when wind damage is most likely in Britain. Inherent differences of 10—30% in root : shoot dry weight ratios found in young trees in this study and by others, very probably contribute to differences in wind stability after planting, if not by differences in root anchorage, then by differences in shoot development and 'sail area'.

Summary

Dry matter distribution was monitored over 1—3 years on photoperiodic ecotypes of Populus trichocarpa, Picea sitchensis and Pinus contorta. Seedlings or cuttings were grown in pots in nursery conditions and sampled at 1—3 weekly intervals.

The shoots were priority dry matter sinks while they were elongating, whereas the roots became major sinks after height growth ceased. Provenances which stopped increasing in height early in the growing season had relatively long periods available for root growth and consequently developed relatively large root : shoot weight ratios by the end of each year. In this way end-of-season root : shoot ratios were correlated negatively with times of height growth cessation and positively with latitudes of origin. Also, conifer provenances with large preformed shoots developed less root than those with small preformed shoots, even though their periods of shoot elongation were similar.

The ratios of root relative growth rates (g g^{-1} wk^{-1}) to shoot relative growth rates (the allometric coefficients) increased, to different extents on the different provenances, during late summer and autumn, and decreased the following spring. Both the root : shoot ratios and allometric coefficients were temporarily similar for all provenances while the shoots were elongating. Large and small root : shoot ratios were then compensated by lesser or greater root growth. Allometric coefficients were the same for all provenances of Picea sitchensis and Pinus contorta when they were averaged over 12—18 months, and provenance differences in end-of-season root : shoot ratios did not increase in successive years.

It seems that differences in end-of-season root : shoot weight ratios found among provenances do not reflect inherent differences in allometry (the functional balance between roots and shoots). Instead they reflect the extent to which shoot growth is adapted to the climatic regime in which the provenances are grown.

Key words: allometry, root growth, photoperiodism, ecotype, wind stability, growth analysis, physiological genetics.

Zusammenfassung

An 62 Herkünften von Populus trichocarpa, 54 Herkünften von Picea sitchensis und 7 Herkünften von Pinus contorta, jeweils aus dem gesamten Verbreitungsgebiet von Alaska bis Kalifornien bzw. Oregon wurde die gewichtsmäßige Verteilung der Trockensubstanz auf Wurzel und Sproß über 3 Jahre hinweg untersucht. Hierbei hat sich gezeigt, daß während des Sproßwachstums höhere Trockensubstanzgewichtsanteile in den Sproßteilen gefunden werden, während danach höhere T.-anteile in der Wurzel festzustellen waren. Oekotypen mit frühem Abschluß des Triebwachstums hatten relativ lange Wurzelzuwachsperioden und demzufolge am Jahresende höhere T.-anteile in der Wurzel. Das Ausmaß des relativ verstärkten Wurzelwachstums im Spätsommer und Herbst war für die einzelnen Provenienzen unterschiedlich. Ebenso konnten Provenienz-Unterschiede im Nachlassen des Wurzelwachstums gegen das nächste Frühjahr hin festgestellt werden.

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Composition and Genetics of Monoterpenes from Cortical Oleoresin of Norway Spruce and their Significance for Clone Identification

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Introduction

A considerable portion of the oleoresin found in conifers consists of the monoterpenes, commonly classified as secondary metabolites. Depending on their molecular stability, as well as their inter- and intraspeciifc variability, these compounds are frequently utilized for studies in the fields of taxonomy, population genetics, and genecology. In particular, the characteristics of qualitative and quantitative variation in monoterpene composition among individuals and populations enable an estimation of population heterogeneity, a determination of intraspecific variation patterns, and a specific characterization of individuals and populations, e.g. races, provenances (see for review Lever and Burley 1974). The latter possibility has recently become particularly attractive in forestry research with respect to clonal and provenance identification, since, in many cases, morphological and physiological characters do not possess a sufficient specificity. In addition, the efficiency of such biochemical characters increases, if they can be found to be under strong genetic control, since then phenotypic differences directly indicate genetic variants. The findings, that several monoterpene components in pine species are controlled by relatively simple genetic systems (Hanover 1966, 1971, Squillace 1971, Baradat et al. 1972, Rockwood 1972, Hiltunen et al. 1975), demonstrate the suitability of these metabolites for identification studies and furthermore indicate a possible application as so-called gene markers in population genetic investigations and tree breeding programs.

The monoterpene composition of Norway spruce (Picea abies) has been determined by v. Schantz (v. Schantz 1965, v. Schantz and Juvonen 1966) by means of GLC analyses of needle oils and wood extracts, and by Schuck and Schütt (1975) through the study of volatile compounds from wood samples. In our investigations with Norway spruce reported in the present paper, cortical oleoresin collected from exuded drops was used for GLC analyses of monoterpene composition. A study of the intra- and interclonal variation should examine the possibility of clonal identification, and the data obtained from several full-sib families were scored with respect to inheritance patterns of individual monoterpene components. Furthermore, it was considered whether the monoterpene patterns are appropriate for constructing a mathematical method for clonal identification (differentiation).

Materials and Methods

a) *Plant material*

The 22 clones of Norway spruce (*Picea abies* (L.) Karst.) available for this study had three different origins: 9 of them were 10-year-old trees grown from cuttings of the Hessische Forstliche Versuchsanstalt, Hann. Münden; 9 were 6-year-old trees from cuttings of the Institut für Forstgenetik und Forstpflanzenzüchtung, Schmalenbeck; and 4 were 8-year-old clones originated from grafts of the Niedersächsische Forstliche Versuchsanstalt, Escherode.

For studies of the genetics of individual monoterpenes of cortical oleoresin, four full-sib families containing 16—22 progenies each have been analyzed. The following controlled crossings were available:

We 40—7	× We 40—7	selfing
We 47—1	× We 40—7	intraspecific crossing
We 48—5	× We 40—7	intraspecific crossing
P. abies var. acrocona	× We 40—7	intervarietal crossing

Five-year-old progenies are growing in Holzerode on the plantation of the Niedersächsische Forstliche Versuchsanstalt.

b) *Collection and pretreatment of oleoresin samples*

Oleoresin samples were collected for gas-liquid-chromatographic (GLC) analyses of monoterpene composition (MTC) in each plantation during one day in summer. The samples were sucked into micropipettes (5 μl) from cuts