provenance trial can be used to predict relative performance at later ages.

Based on the first analysis involving fourteen provenances, it was found that variation among the provenances contributed about 28.3 per cent while differences among trees contributed about 58.0 per cent to the observed variation in height growth. For girth growth, provenance variation accounted for about 27.5 percent while variation among trees accounted for about 65.6 per cent of the observed variation.

Differences among the provenances were more expressed in girth than in height growth. Genetic variance $(\sigma^2 p)$ in girth was more than eight times greater than that of height growth. The variance among trees was also greater in girth than in height growth. This shows that in a genetic improvement programme involving growth characteristics, more gain will be expected in girth than in height.

Implications to Genetic Improvement of Eucalyptus camaldulensis in the Savanna Region of Nigeria

The results obtained indicate that great genetic differences exist among the provenances of Eucalyptus camaldulensis tested for height and girth growth. It has also been reported that variation in stem form exists among provenances of the species (Jackson and Ojo, 1973; Kemp, 1970). All these show that genetic gain in volume production and form is possible through proper provenance selection. A high degree of variation among trees within provenance was also obtained. For height growth, variation among trees contributed about 58.0 per cent to the observed variation while about 65.6 per cent of the observed variation in girth was accounted for by variation among trees. In each case the value was more than double that of provenance variation. Although no formal assessment was made of stem form and crown characteristics it was observed that there was some degree of variation among individual trees within provenance for these characteristics. The existence of these variations among trees offers a great opportunity for further improvement of the species following a careful provenance selection.

Since evidence of strong juvenile-mature correlation with respect to growth of *Eucalyptus camaldulensis* has been established for the Afaka site, recommendations based on 5-year growth of the provenances (Jackson and Ojo, 1973) can still be said to be valid at age 13 years. Thus provenances recommended for planting in the different savanna zones are as follows:

- (a) Sudan zone Katherine provenance.
- (b) Northern Guinea Zone Petford followed by Katherine provenance.
- (c) Jos Plateau (Petford), Katherine provenance.
- (d) Lake Chad Basin (where the experiment was conducted under irrigation because of the arid condition there) — Mundiwindi followed by Wohlpooer provenance.

References

AINSLIE, J. R.: Exotics. Report to 4th British Empire Forestry Conference, S. Africa (1935). - Banks, J. C. G. and Hillis, W. E.: The characterization of populations of Eucalyptus camaldulensis by chemical features. Aust. Jour. Bot. 17: 133-146 (1969). - BLAKELY, W. F.: A key to the Eucalyptus. 2nd. ed. Forestry and Timber Bureau, Canberra (1955). - Burley, J., Wood, P. J. and Hans, F. A.: Variation in leaf characteristics of Eucalyptus camaldulensis Dehnh. grown in Zambia. Aust. Jour. Bot. 19: 237-249 (1971). HALL, N., JOHNSTON, R. D. and CHIPPENDALE, G. M.: Forest Trees of Australia. 3rd. ed. Dept. of National Development, Forestry and Timber Bureau, Canberra (1970). - Jackson, J. K. and Ojo, G. O. A.: Provenance trials of Eucalyptus camaldulensis in the savanna region of Nigeria. Research Paper No. 14. Sav. For. Res. Series, Samaru - Zaria. 22pp. (1973). — Karschon, R.: Ecotypic variation in Eucalyptus camaldulensis Dehnh. Contrib. on Eucalyptus in Israel 3: 25-53 (1967). - Kemp, R. H.: Trials of exotic tree species in the savanna region of Nigeria. Part I. Aims, procedure and summary of results. Research paper No. 4 of the Savanna For. Res. Station, Samaru, Zaria. 15pp. (1969). — Kemp, R. H.: Trials of exotic tree species in the Savanna region of Nigeria. Part II. Short notes on selected species. Research Paper No. 6 of the Savanna For. Res. Station, Samaru, Zaria. 62pp. (1970). - Ken-NEDY, J. D.: Exotic trees in Nigeria. Research Record No. 18. 1/5, Fed. Dept. For. Research, Ibadan, Nig. (unpublished) (1932). -PRYOR, L. D. and BYRNE, O. R.: Variation and taxonomy in Eucalyptus camaldulensis. Silv. Gen. 18: 64-71 (1969). - Schultz, Jr. E. F.: Rules of thumb for determining expectations of mean squares in analysis of variance. Biometrics 11: 123-135 (1955). - Sikes, S.: Lake Chad. Eyre Methuen, London (1972).

Nutrient Use Efficiency of Clones of Picea sitchensis and Pinus contorta

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Summary

The total nutrient uptake of 8-year-old clones of *Picea sitchensis* and *Pinus contorta* were determined from the nutrient concentrations and dry weights of all aboveground parts, plus fallen needles. Seven clones (raised from cuttings) were harvested of each species at a lowland fertile site, and needle samples were analysed from the same clones growing at an upland peaty-gley site.

P. sitchensis had a relatively high demand for Ca, K and P compared with P. contorta and P. contorta had a high demand for Mg. N concentrations were similar in both species.

Clonal differences of 10—30% were found in 'nutrient use efficiencies' defined as the amounts of dry matter produced over the 8 years per unit of nutrient taken up (omitting roots). These differences were related to three tree characteristics. (a) Clones with inherently low needle nutrient concentrations had high efficiencies, because the needles took over 50% of most of the nutrients absorbed. (Clonal differences in needle nutrient concentrations were consistent between sites). (b) Clones which partitioned a large proportion of dry matter to stems (i.e. were sparsely branched) had high nutrient use efficiencies, because the nutrient requirement for a unit increment in stem dry weight was usually less than half of that for a unit increment of branches, and only about 5—15% of that for a

unit increment of needle dry weight. (c) Clones that retained their needles longest tended to have high nutrient use efficiencies.

It was concluded that genotypes with those three characteristics may make the smallest demands on soil nutrients during their early years of growth, and so may be well-suited to grow on nutrient-poor sites.

Key words: Nutrition, clones Picea sitchensis, Pinus contorta, ideotype.

Zusammenfassung

Es wurde die Gesamtnährstoffaufnahme 8jähriger Stecklingsklone von Picea sitchensis und Pinus contorta aus Nährstoffkonzentrationen und dem Trockengewicht aller oberirdischen Teile und abgefallener Nadeln untersucht. Für die Untersuchung wurden sieben Klone jeder Art auf einem fruchtbaren Tieflandstandort herangezogen, sowie Nadelproben der gleichen Klone von einem anmoorigen Gley-Standort im Hochland.

P. sitchensis hatte einen relativ hohen Bedarf an Ca, K und P im Vergleich zu P. contorta. Dagegen hatte P. contorta einen hohen Bedarf an Mg. Die N-Konzentrationen waren bei beiden Arten ähnlich. Im Wirkungsgrad der Ausnutzung von Nährstoffen, der als die Menge der Trokkensubstanz definiert wurde, die im Verlaufe des von acht Jahren pro Einheit aufgenommenen Nährstoffs unter Ausschluß der Wurzeln gebildet wurde, wurden Klondifferenzen von 10-30% gefunden. Diese Unterschiede standen zu drei Baumeigenschaften in Beziehung. (a) Klone mit erblich geringen Nährstoffkonzentrationen hatten hohe Wirkungsgrade, weil die Nadeln mehr als 50% der absorbierten Nährstoffe aufwiesen (Klondifferenzen in den Nährstoffkonzentrationen der Nadeln waren zwischen den Standorten konsistent.) (b) Klone, die einen großen Anteil an Trockensubstanz im Stamm aufwiesen, (d. h. diese waren nur spärlich verzweigt), hatten eine hohe Effizienz der Nährstoffausnutzung, weil der Nährstoffbedarf für eine Zunahmeeinheit an Stammtrockengewicht i. a. weniger als halb so groß war, wie der für eine Zunahmeeinheit an Trockengewicht der Zweige und nur etwa 5-15% einer Zunahmeeinheit im Nadeltrockengewicht. (c) Klone, die ihre Nadeln am längsten behielten, tendierten zu einer hohen Effizienz bei der Nährstoffausnutzung.

Es wurde daraus geschlossen, daß Genotypen mit diesen drei Eigenschaften während des frühen Wachstums die geringsten Anforderungen an Bodennährstoffe stellen und auf diese Weise gut angepaßt sein können, um auf nährstoffarmen Standorten zu wachsen.

Introduction

In a previous paper (Cannell et al., 1983) we reported differences among seven clones (rooted cuttings) of *Picea sitchensis* (Bong.) Carr and *Pinus contorta* Dougl. in the distribution of aboveground dry matter, and in the amount of stemwood produced per unit area and dry weight of foliage. The clones were aged 8, and were growing in a nursery in Scotland. Height, sparse branching, and the allocation of a large proportion of dry matter to stems, were the most important characteristics associated with large, efficient stemwood production per unit of needles.

In this paper we report the nutrient concentrations and contents in the aboveground parts of those same clones. In particular, we examine clonal differences in 'nutrient use efficiency', defined as the weight of aboveground dry matter produced per unit weight of nutrient element taken up over 8 years (including litterfall).

Differences in 'nutrient use efficiency' might be associated with differences in, (a) nutrient concentrations in tree tissues, (b) nutrient partitioning among tree parts, or

(c) nutrient retranslocation and within-tree cycling. In horticulture, it is well-known that fruit-tree rootstocks differ in their ability to supply nutrients to scions, giving rise to differences in nutrient concentrations in scion tissues (see Kennedy et al., 1980). Blackmon et al., (1979) found that a Louisiana seed source of Populus deltoides growing in Mississippi produced more dry matter by age 11 per unit of N and K taken up than Mississippi and southern Illinois seed sources. They concluded that the Louisiana seed source might be better suited to grow in poor soils. Pope (1979) described similar differences among four seed sources of Pinus taeda. Clonal differences in needle nutrient concentrations have been reported in 3-year-old nurserygrown Picea abies (Kleinschmit and Sauer, 1976; Kleinschmit, 1982) and in both young and mature clones of Pinus radiata (e.g. Burdon, 1976; Knight, 1978; Raupach and Nicholls, 1982); needle nutrient concentrations were not closely related to clonal growth rates, and there were often significant clone X site interactions. Nevertheless, the existence of inherent differences in tissue nutrient concentrations indicated a potential to select for greater "nutrient use efficiency". The whole-tree analyses reported here enable that potential to be quantified and examined in detail on Picea sitchensis and Pinus contorta.

Methods

Seven clones (established from rooted cuttings) contrasting in height and branching habit, of both Picea sitchensis and Pinus contorta, were analysed (Table 1). The clones were planted in April 1973 in agricultural loam near Edinburgh, Scotland (Roslin, 55°50'N, 184 m alt.) and the destructive analysis were done in August 1981, at age 8. One tree was felled of each of the 7 clones from each of three replicate blocks. Additionally, clone X site interactions in needle nutrient concentrations were examined by sampling one and two-year-old needles, in September 1982, from all levels in the crowns, from the same clones growing in a replicate trial in a peaty-gley soil on a northfacing upland site near Peebles, Scotland (Cloich, 55°40'N, 310 m alt.). This site was more acid (pH 4.6 compared with 5.2 at Roslin), had lower levels of available P and N, and a much lower base status, particularly with respect to Ca than the Roslin site. Cahalan (1981) reported differences in clone heights, branching characteristics and phenology between the Roslin and Cloich sites.

Table 1. — Clones of Picea sitchensis and Pinus contorta that were destructively analysed at age 8, at a lowland site in Scotland (Roslin). Dry weights and wood specific gravities were reported by Cannell et al. (1983).

	Picea sitchensis		<u>Pinus</u> contorta					
4	Origin	+	Origin					
A	'Plus' tree 8013 ^{##}	J	North Bend C (43°N)					
В	San Juan C (49°N)	L	North Bend A (43°N)					
С	'Plus' tree 8010 ^{##}	м	Skagway D (59 ⁰ N)					
D	Skidegate A (53°N)	Q	Skagway C (59 ⁰ N)					
E	Sitka D (57 ⁰ N)	R	Queen Charlotte Is. A (54°N)					
F	Queen Charlotte Is. (54°N)	s	Anahim Lake A (52°N)					
G	Cordova D (61°N)	T	Anahim Lake B (52°N)					

† Clone name used in the text and figures in this paper. †† Candidate élite tree of Queen Charlotte Islands provenance.

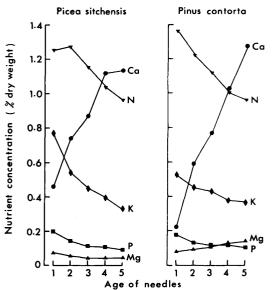


Figure 1. — Mean concentration of nutrients in needles of different ages on 8-year-old trees of *Picea sitchensis* and *Pinus contorta* growing at a lowland site in Scotland (Roslin). These are the means of all the needles on the trees, and the means of 7 clones per species, expressed as a percentage nutrient element per unit needle dry weight.

The felled trees at the lowland site (Roslin) were divided, and estimates were made of the dry weights of aboveground tree parts as described previously (Cannell *et al.*, 1983).

Mean concentrations of N, P, K, Ca and Mg were determined for the needles of ages 1, 2, 3, 4 and 5, for the branches as a whole, and for the stems, on each of the 42 trees (2 species, 7 clones, 3 replicate blocks). The needles of each age were bulked and subsampled. The branches (including bark) of each age were bulked and subsampled, and each age was analysed separately: mean branch concentrations were determined from the dry weights of branches of each age. The stems, which were divided into annual height sections, were sampled by drilling six 12 mm cores per section. The core shavings included the bark. Mean stem concentrations were determined from the dry weights of each annual height section.

Subsamples were finely ground, oven-dried and extracted using the wet oxidation procedure of Parkinson and Allen (1975). Total N and P were determined colorimetrically, K by flame photometry, and Ca and Mg by atomic absorption spectrophotometry. Nutrient concentrations were expressed as a percentage of the sample dry weight.

Total nutrient contents were obtained by multiplying concentrations by dry weights, and estimates of the amounts of nutrients lost in needle litterfall were made by multiplying the dry weight of fallen needles by the nutrient concentrations in 5-year-old needles.

Analyses of variance were done on each variate at the Roslin site)7 clones, 3 replicates) and on needle nutrient concentrations across the two sites (7 clones, 2 sites, 3 replicates).

Results

It was estimated that, over their lifetime, the trees took up 65, 9, 34, 40 and 6 g tree $^{-1}$ of N, P, K, Ca and Mg, respectively, averaged for the two species and including fallen needles. The needles had a greater concentration of all nutrients than the woody parts, and on average the living needles on these 8-year-old trees contained 68%,59%,

55%, 60% and 48% of the total N, P, K, Ca and Mg per tree, respectively. The greatest concentration of N, P, and K occurred in the one and two-year-old needles, and, because these made up 73% of the total needle dry weight in both species (Cannell et al., 1983), these young needles contained 52%, 47% and 43% of the N, P and K per tree, respectively. By contrast, the highest concentrations of Ca in both species, and Mg in *Pinus contorta*, occurred in the older needles (*Figure 1*).

Picea sitchensis compared with Pinus contorta

When comparing the nutrient content of the two species it has to be borne in mind that the *Picea sitchensis* trees had similar stem dry weights to the *Pinus contorta* trees, but they had only 56% as much branch wood dry weight, and only 61% as much needle dry weight (*Figure 2*). Consequently, the *Picea sitchensis* trees would be expected to contain smaller total amounts of nutrients than the *Pinus contorta* trees.

The N concentrations in the needles, branches and stems were similar in the two species. However, *Picea sitchensis* had markedly greater concentrations of K in both its needles and woody parts than *Pinus contorta*, and considerably greater concentrations of Ca and P in its young needles, branches and stems (*Figures 1* and 2). Consequently, the *Picea sitchensis* trees, despite being 30% lighter in dry weight than the *Pinus contorta* trees, took up only 9%, 17% and 26% less Ca, K and P, respectively (*Figure 2*). Thus, for the nutrients Ca, K and P it could be said that *Picea*

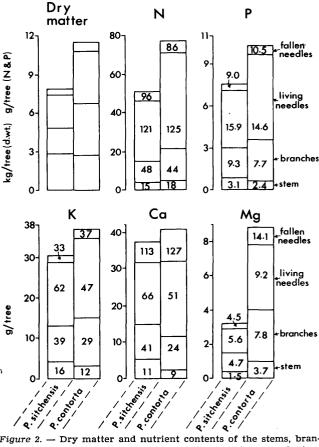


Figure 2. — Dry matter and nutrient contents of the stems, branches and needles of 8-year-old trees of *Picea sitchensis* and *Pinus contorta* growing at a lowland site in Scotland. The concentrations of the nutrients are given on each histogram times 100, e.g. 96 = 0.96% dry weight. These are the means of 7 clones per species. Individual clone values are given in Figure 3.

Table 2. — Mean 'nutrient use efficiencies' of Picea sitchensis and Pinus contorta. That is, the mean weight of dry matter produced to age 8 per unit weight of nutrient element taken up, including estimates of the weights and nutrient contents of fallen needles, but excluding roots. These are the means of 7 clones per species; individual clone values are given in Figure 4.

		g d.w	t./g nu	trient	
	N	Р	К	Ca	Mg
Picea sitchensis Pinus contorta	162 151	1094 1137	270 312	237 282	2612 1332

sitchensis had a smaller 'nutrient use efficiency' than Pinus contorta in terms of the amount of dry matter produced per unit of nutrient taken up (Table 2). By contrast, the Picea sitchensis trees had a high 'nutrient use efficiency' for the element Mg; their stems, branches and needles had much lower concentrations of Mg than those of Pinus contorta, and overall the Picea sitchensis trees took up less than half as much Mg as the Pinus contorta trees (Table 2 and Figure 2).

Clonal differences within species

There were highly significant differences between clones within each species in the concentrations of all five nutrients in all tree parts. That is, clonal repeatabilities were high. Because of differences in nutrient concentrations the larger, heavier clones did not necessarily contain most nutrients and, including fallen needles, the larger clones did not necessarily take up most nutrients over the 8 years.

Differences between clones in the concentrations of nutrients in the one and two-year-old needles (which contained most of the tree nutrients) were reasonably consistent between the lowland site (where the whole-tree analysis was conducted) and the upland site, although there were a few significant clone \times site interactions (Table 3). The similarity between sites existed despite a 2 to 3-fold difference in tree height (Cannell et al., 1983) and despite a difference in the time of year at which the needles were sampled (August at the lowland site, September at the upland site). Clearly, there were inherent, site-independent clonal differences in needle nutrient concentrations, and all of the instances mentioned below of clones having unusually high or low needle nutrient concentrations were true at both sites.

Within Picea sitchensis, clones C and F (the third and sixth largest in dry weight) had a relatively small demand for N, P and K (Figure 3). These clones could be characterized in the following ways: (a) they were relatively sparsely branched, and partitioned a large proportion of their total dry matter to stems rather than to branches and needles (48% and 43%, respectively, of their total dry weight was in stems at age 8, Figure 3); (b) both had good needle retention, so that, at age 8, 34% and 37%, respectively, of their needle mass was over 2 years old (Figure 3); and (c) clone F had an unusually low concentration of N in its needles (Figure 3 and Table 3) and, because much of the needle biomass of clones C and F was over 2 years old the mean concentrations of N, P and K in their foliage were either average or below-average compared with those in the other clones (Figure 3). Over the 8 years, clones C and F had produced significantly more stem, and 10 to 30% more total dry matter (including fallen needles) per unit of N, P and K taken up than the other Picea sitchensis clones (Figure 4).

By contrast, *Picea sitchensis* clones D and E (the fourth and fifth largest in weight) had a relatively large demand for N, P and K. They partitioned more of their dry matter

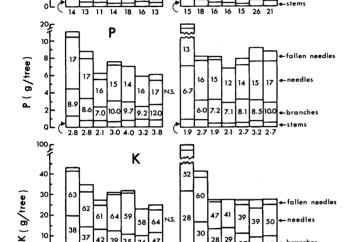
Table 3. — Concentrations (% dry weight) of N, P, K, Ca and Mg in one- and two-year-old needles of 8-year-old trees of 7 clones (A, B, C . . .) of *Picea sitchensis* and *Pinus contorta* growing at a lowland site (Roslin) and an upland site (Cloich) in Scotland. The boxes mark those values that were notably high or low at both sites.

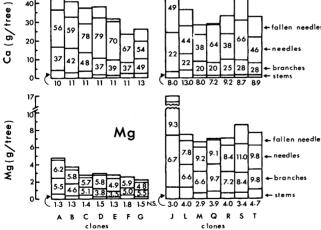
					rov	LAND SI	TE (ROS	SLIN)					UPI	AND SIT	E (CLO	CH)				
										Picea s	itchensi	s								
			A	В	С	D	E	F	G	LSD P=0.05	A	В	С	D	E	F	G	LSD P=0.05	rt	F++
N	Age	1 2	1.27	1.23	1.27	1.21	1.34	1.15	1.25	0.09 0.14	1.27	1.15 0.99	1.34	1.24	1.22	1.03	1.12	0.14 0.12	0.61	2.1
P	Age	: 1 2	0.21 0.15	0.21 0.14	0.21 0.14	0.18 0.13	0.18 0.12	0.22 0.15	0.20 0.14	0.04 0.02	0.22 0.16	0.23 0.14	0.24 0.17	0.22 0.15	0.21	0.26	0.23 0.15	0.04 0.04	0.78 0.64	0.6 1.9
K	Age	1 2	0.75 0.56	0.76 0.53	0.83 0.52	0.75 0.58	0.77 0.49	0.80 0.52	0.74 0.59	0.11 0.07	0.69 0.53	0.78 0.41	0.72 0.38	0.69 0.49	0.74 0.44	0.83	0.74 0.52	0.12 0.08	0.32 0.62	0.9 1.5
Ca	Age	1 2	0.40 0.66	0.40 0.67	0.59 0.76	0.53	0.45 0.80	0.47 0.69	0.39 0.61	0.07 0.07	0.26 0.41	0.29 0.47	0.40	0.40	0.32 0.57	0.34 0.58	0.29 0.47	0.08 0.12	0.95 0.86	0.7 2.1
Mg	Age	2	0.072 0.055	0.062 0.059	0.075 0.048	0.064 0.056	0.056 0.044	0.077 0.056	0.052 0.043	0.009 0.009	0.079 0.056	0.091 0.050	0.109 0.089	0.095 0.069	0.089 0.064	0.099 0.068	0.072 0.035	0.02 0.02	0.64 0.10	1.9 4.1*
										Pinus	contorta									
			J	L	M	Q	R	s	т	LSD P=0.05	J	L	м	Q	R	s	T	LSD P=0.05	rt	_F ††
N	Age	1 2	1.27	1.13	1.51	1.31	1.27	1.59	1.45	0.12 0.13	1.14	1.24	1.49	1.39	1.28	1.56 1.56	1.43 1.36	0.20 0.18	0.87 0.82	1.0
P	Age	2	0.18 0.11	0.19 0.15	0.19 0.13	0.16 0.11	0.16 0.13	0.16 0.14	0.19 0.15	0.03 0.014	0.19	0.23	0.19 0.14	0.18 0.16	0.17 0.14	0.18 0.17	0.18 0.14	0.04 0.02	0.60 0.48	2.0 6.0*
ĸ	Age		0.55	0.59	0.53	0.57 0.37	0.45	0.48	0.51	0.05	0.65	0.70	0.49	0.54	0.51	0.49	0.49	0.14	0.70 0.70	1.6 2.8*
Ca	Age	1 2	0.18 0.53	0.18 0.55	0.22 0.49	0.24 0.65	0.16 0.44	0.31	0.28 0.60	0.04 0.13	0.11 0.31	0.09 0.24	0.16 0.37	0.21 0.48	0.11	0.17	0.15 0.39	0.05 0.12	0.68 0.90	3.1 1.3
Mg	Age	1 2	0.083 0.091	0.064 0.075	0.084 0.088	0.077 0.083	0.071 0.081	0.092 0.120	0.085 0.102	0.011 0.016	0.072 0.070	0.053 0.046	0.088 0.079	0.105 0.072	0.077 0.070	0.076 0.075	0.069 0.072	0.02 0.012	0.30 0.52	3.7* 3.9*

[†] Correlation coefficients between sites (5 d.f.).

the Variance ratio of site × clone interaction in analyses of variance.

^{*}Significant at P < 0.05.





Ca

Figure 3. — Dry matter and nutrient contents of the stems, branches and needles of 7 clones of Picea sitchensis and Pinus contorta at age 8. The numbers on the histograms for N, P, K, Ca and Mg are the mean percentage concentrations of the nutrient elements in the stems, branches and living needles times 100, e.g. 12 = 0.12% dry weight. Significant clonal differences at P < 0.01 existed for the concentrations of all nutrients as indicated by F-ratios in analyses of variance, except for those marked N. S.

Percentage of total living needle mass over 2 years old. ## Stem dry weight as a percentage total tree dry weight.

to nutrient-rich needles and branches than the other *Picea sitchensis* clones, and they had poor needle retention (*Figure 3*). Over the 8 years, clones D and E produced significantly less stem and less total dry matter (including fallen needles) per unit of N, P and K taken up than the other *Picea sitchensis* clones (*Figure 4*).

Considering the 7 clones of *Picea sitchensis* together, their 'nutrient use efficiency' in terms of the weight of dry matter produced per unit weight of nutrient taken up over the 8 years, was (a) positively correlated with the percentage of dry matter in the stems, (b) positively correlated with the percentage of needles over 2 years old on the 8-year-old trees, and (c) negatively correlated with the mean nutrient concentration in the needles as a whole, although not necessarily negatively correlated with the nutrient concentration in the one and two-year-old need-

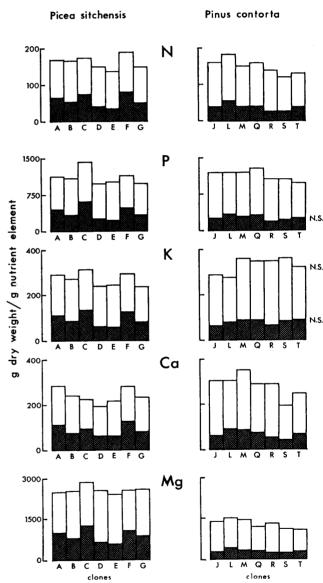


Figure 4. — The 'nutrient use efficiencies' of 7 clones of Picea sitchensis and Pinus contorta. That is, the mean weights of dry matter produced to age 8 per unit weight of nutrient element taken up including estimates of the weights and nutrient content of fallen needles, but excluding roots. Values are given for (a) total tree dry weight produced/nutrient absorbed (shaded plus unshaded, and (b) stem dry weight produced/nutrient absorbed (shaded only). Significant differences among clones existed at P < 0.01 for both (a) and (b) unless marked N.S.

10

75_[

Table 4. — Correlation coefficients (r) between 'nutrients use efficiency' and other tree characteristics among 7 clones of *Picea sitchensis* and *Pinus contorta*. Nutrient use efficiency is defined as the total net dry matter increment over 8 years including fallen needles divided by the weight of nutrient taken up over the same period.

		Stem/total dry weight at age 8	Mean nutrient concentration in all needles [†]	Mean nutrient concentration in 1-&2-year old needles	Percentage of needles > 2 yrs old
Ficea tchensis	N	0.76*	-0.68	-0.52	0.72
20	P	0.81*	-0.21	0.45	0.77*
rrcea tchens	K	0.82*	-0.67	0.27	0.82*
7 to	Ca	0.57	-0.68	-0.64	0.36
28	Mg	0.80*	-0.60	0.32	0.55
	N	-0.12	-0.76*	-0.89*	0.91*
, t	P	-0.36	-0.24	-0.47	0.90*
Pinus contorta	K	0.37	-0.75*	-0.48	-0.78*
	Ca	-0.34	-0.84*	-0.81*	0.75
	Mg	-0.30	-0.80*	-0.66	0.68

- † Taking into account the different weights of needles of different ages.
- * Significant at P < 0.05.

les (*Table 4*). These correlations existed for Ca and Mg as well as for N, P and K, although the clonal differences were not as clear-cut (*Table 4*, *Figure 4*).

Within *Pinus contorta*, the four heaviest clones, J, L, M and Q, had a relatively small demand for N, P and Ca in proportion to their size. That is, they had a relatively large 'nutrient use efficiency' in terms of the total dry matter produced per unit of N, P and Ca taken up (Figure 4). Clones J, L, M and Q had much better needle retention than the other three *Pinus contorta* clones (32—35% of their needles were over 2 years old, Figure 3), and clones J and L had unusually low concentrations of N in their needles (Figure 3, Table 3).

By contrast, the two lightest *Pinus contorta* clones, S and T (of Anahim Lake, British Columbian interior origin) had a relatively large demand for N, P and Ca. They produced a relatively small dry weight per unit of N, P and Ca taken up (*Figure 4*). These two clones had very poor needle retention (only 10% and 17% of their needles were over 2 years old, respectively, *Figure 3*), and their stems, branches and/or needles contained above-average concentrations of N, P and Ca (*Figure 3*, *Table 3*).

Similar differences among the *Pinus contorta* clones to those described for *Picea sitchensis* occurred with regard to Mg. However, K behaved very differently, because clones J and L, which were otherwise efficient nutrient users, had unusually large concentrations of K in their needles (*Figure 3, Table 3*), and, for this element, clones J and L produced relatively little dry matter per unit of nutrient taken up (*Figure 4*).

Considering the 7 clones of *Pinus contorta* together, their 'nutrient use efficiency' was (a) <u>not</u> closely correlated with the percentage of dry matter in the stems, but was (b) positively correlated with the percentage of needles over 2 years old, except for K, and (c) negatively correlated with the mean nutrient concentration in both the one and two-year-old needles, and in the total needle biomass at age 8.

Discussion

This study supported work on other woody species in showing that tree tissue nutrient concentrations are partly under genetic control, and that large inherent differences exist in dry matter production per unit of nutrient taken up. Before interpreting our findings on 'nutrient use efficiency', it is important first to observe some general points concerning the nutrient status of the trees.

Tissue nutrient concentrations

Nutrient concentrations in the current-year's needles, at both the lowland and upland sites, were well above the deficiency levels defined for *Picea sitchensis* and *Pinus contorta* needles sampled after the period of shoot elongation (Swan, 1972; Everard, 1973; Morrison, 1974). Our August-September sampling dates were 1—2 months sooner than the dates recommended for testing foliage nutrient levels (e.g. MacLean and Robertson, 1981), but we are confident that the values reported here reflect inherent levels and not temporary seasonal values. Shoot elongation had ceased in July, and the major clonal differences were consistent between sites. Our whole-tree study does not suffer from errors introduced by sampling needles within trees, which can be important where clones partition nutrients differently within their crowns (e.g. Burdon, 1976).

The differences we observed in the nutrient concentrations of different tree tissues, and the changes in nutrient concentrations with age in the needles, were generally in agreement with published values for comparable tree species (e.g. Rodin and Bazilevich, 1967; Shoulders, 1980; Comerford, 1981). However, it should be borne in mind that we did not separate stemwood from stem bark.

The markedly greater concentrations of Mg found in *Pinus contorta* tissues compared with *Picea sitchensis* parallels observations in two other studies. Christersson (1974) found that young *Pinus sylvestris* had much higher foliar Mg concentrations than young *Picea abies*, when both were grown in a clay soil, whereas they had similar levels of N, P and K. Clayton and Kennedy (1980) found that mature trees of *Pinus ponderosa* had stemwood Mg concentrations of 0.019 to 0.028% compared with only 0.003 to 0.007% in comparable *Pseudotsuga menziesii*. The reasons for such species differences are unclear, although it is recognized that species differ in their ability to regulate ion uptake (e.g. Ingestad, 1962).

Nutrient use efficiency

This study demonstrated that there were clonal differences of 10—30% in the amount of dry matter produced per unit weight of nutrients taken up ('nutrient use efficiency'). These differences existed within both *Picea sitchensis* and *Pinus contorta*, and they occurred over the first 8 years of the life of the trees, when plantation forests make the greatest demands on soil nutrients (e.g. Miller, 1979). In *Picea sichensis* clonal differences in N use efficiency were parallelled by similar differences in P and K, whereas in *Pinus contorta* K behaved somewhat differently from N and P, owing to high K concentrations in the needles of clones J and L.

Clonal differences in 'nutrient use efficiency' were closely related to the three tree characteristics listed in the Introduction. The first, and most obvious, was the nutrient concentration in the needles. In both species there were clones which had usually low concentrations of N in their needles, of all ages, and at both sites (Table 3). Similar clonal differences existed for the other nutrients, although not necessarily in the same clones. Because the needles took over 50% of most of the nutrients absorbed by the trees over 8 years, differences in needle nutrient concentrations were strongly reflected in differences in 'nutrient use efficiency'.

The second characteristic affecting 'nutrient use efficiency' was the proportion of dry matter partitioned to stems as opposed to branches and needles. The N, P and K requirement for a unit increment in stem dry weight (including bark) was usually less than half of that for a unit increment of branches, and only about 5—15% of that for a unit increment of needle dry weight. Thus, relatively small differences in partitioning to stems increased the ratio of total dry matter producion per unit of nutrient taken up, all else being equal. Differences also existed in stem nutrient concentrations, perhaps reflecting differences in wood/bark ratios or the efficiency of nutrient withdrawal from woody tissues before they died. However, these differences had much less impact on clonal nutrient use efficiencies than the large differences in stem-crown partitioning.

The third characteristic related to 'nutrient use efficiencies' was needle longevity. In both species, clones that retained their needles longest tended to produce most dry matter per unit of nutrient taken up (Table 4). We can think of two reasons why this might be so: (a) clones that retained their needles longest produced most photosynthate per unit of nutrient invested in needle construction and (b) clones with the largest needle biomass possessed the largest pool of the mobile nutrients which could be circulated within the trees, thereby lessening the demand on soil nutrients. However we could find no evidence that clones which retained their needles longest withdrew most nutrients from them before they were shed.

Conclusions

We conclude from this study that there are important opportunities to select conifer clones with relatively small demands on soil nutrients during their early years of growth. The 'ideotype' for high 'nutrient use efficiency' seems to be a tree with an inherently low nutrient concentration in its foliage, which partitions a high proportion of its new dry matter to stem, and which has good needle retention. Such trees may be well-suited to grow on nutrient-poor sites.

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References

BLACKMON, B. G., BAKER, J. B. and Cooper, D. T.: Nutrient use by three geographic sources of eastern cottonwood. Can. J. For. Res. 9, 532—534 (1979). — Burdon, R. D.: Foliar macronutrient concen-

trations and foliage retention in radiata pine clones on four sites. N. Z. J. For. Sci. 5, 250-259 (1976). - Cahalan, C. M.: Provenance and clonal variation in growth, branching and phenology in Picea sitchensis and Pinus contorta. Silvae Genet. 30, 40-46 (1981). CANNELL, M. G. R., SHEPPARD, L. J., FORD, E. D. and WILSON, R. H. F.: Clonal differences in dry matter distribution, wood specific gravity and foliage "efficiency" in Picea sitchensis and Pinus contorta. Silvae Genet. 32, 195—202 (1983). — Christersson, L.: Seasonal ionic fluctuations and annual growth rates in stands of Pinus silvestris and Pinus abies Karst. (L.) Plant and Soil 41, 343-340 (1974). - CLAYTON, J. L. and KENNEDY, D. A.: A comparison of the nutrient content of Rocky Mountain Douglas-fir and Ponderosa pine trees. Research Note. USDA For. Serv. INT-281, Intermountain Forest and Range Expt. Stn., Ogden, Utah (1980). Comerford, N. B.: Distributional gradients and variability of macroelement concentrations in the crowns of plantation grown Pinus resinosa (AIT.). Plant and Soil 63, 345-353 (1981). - EVERARD, J.: Foliar analysis. Sampling methods, interpretation and application of the results. Q. J. For. 67, 51-66 (1973) -- INGESTAD, T .: Macro-element nutrition of pine, spruce and birch seedlings in nutrient solutions. Medd. Stat. Skogsof. Inst. 51, 1—50 (1962). Kennedy, A. J., Rowe, R. W. and Samuelson, T. J.: The effects of apple rootstock genotypes on mineral content of scion leaves. Euphytica 29, 477—482 (1980). — Kleinschmit, J.: Variation in mineral nutrient content between young plants of Norway spruce provenances and clones. Silvae Genet. 31, 77-80 (1982). - Klein-SCHMIT, J. and SAUER, A.: Variation in morphology, phenology and nutrient content among Picea abies clones and provenances, and its implications for tree improvement. In: Tree Physiology and Yield Improvement. Ed. M. G. R. CANNELL and F. T. LAST, pp 503-517. Academic Press, London and New York (1976). - KNIGHT, P. J.: Foliar concentrations of ten mineral elements in nine Pinus radiata clones during a 15-month period. N. Z. J. For. Sci. 8, 351-368 (1978). - MACLEAN, K. S. and ROBERTSON, R. G.: Variation in the major element content of red spruce foliage with season, crown position, tree and tissue age. Commun. Soil Sci. Plant Analysis 12, 39-49 (1981). - MILLER, H. G.: The nutrient budgets of even-aged forests. In: The Ecology of Even-aged Plantations. Ed. E. D. Ford, D. C. Malcolm and J. Atterson. pp. 221-256. Institute of Terrestrial Ecology, Monks Wood, Hunts, England (1979). — Morrison, I. K. Mineral nutrition of conifers with special reference to nutrient status interpretation: a review of literature. Environment Canada, Forest Service, Ottawa (1974). PARKINSON, J. A. and Allen, S. E.: A wet oxidation procedure suitable for the determination of N and mineral nutrients in biological material. Commun. Soil Science and Plant Analysis 6, 1-11 (1975). - POPE, P. E.: The effect of genotype on biomass and nutrient content in 11-year-old loblolly pine plantations. Can. J. For. Res. 9, 224—230 (1979). — RAUPACH, M. and Nicholls, J. W. P.: Foliar nutrient levels and wood densitometric characteristics in clones of Pinus radiata D. Don. Aust. For. Res. 12, 93-103 (1982). - Rodin, L. E. and Bazilevich, N. I.: Production and mineral cycling in terrestrial vegetation. Oliver and Boyd, London and Edinburgh (1967). DERS, E.: Concentration and distribution of selected elements in aboveground biomass of 8-year-old slash pine. Proc. First Biennial Southern Silvicultural Research Conference, Atlanta, Georgia. p. 254-258 (1980). - Swan, H. S. D.: Foliar nutrient concentrations in lodgepole pine as indicators of tree nutrient status and fertilizer requirement. Woodlands Report WR-42. Pulp and Paper Research Institute of Canada (1972).

Research on in vitro-techniques within the framework of poplar breeding – results and future trends

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Summary

In co-operation with the KWS Kleinwanzlebener Saatzucht AG at Einbeck we have been able to reproduce on a large scale by in vitro-cultures aspen clones bred at this institute and registered for trade. The extent to which the

new propagation method contributes to the practical use of breeding success is explained.

In the field of resistance-breeding cheap and simple infection methods may be used by means of in vitro-culture techniques. The example of bacterial canker on black and