UPPER MID-CROWN YELLOWING IN *PINUS RADIATA*: SOME GENETIC AND NUTRITIONAL ASPECTS ASSOCIATED WITH ITS OCCURRENCE

P. N. BEETS

New Zealand Forest Research Institute,
Private Bag 3020, Rotorua, New Zealand

and E.J. JOKELA

School of Forest Resources & Conservation,
University of Florida, Gainesville, Florida, United States.

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ABSTRACT

Upper Mid-Crown Yellowing (UMCY), needle retention, and foliar chemistry were determined for *Pinus radiata* D.Don clones at the Kaingaroa Seed Orchard in the central North Island of New Zealand. These clones had been propagated as rooted cuttings and grafts. UMCY was found to be under both environmental and genetic control, with clone accounting for around half of the variation at this site. The broad-sense heritability of UMCY was 59%.

Nutrient concentrations in two needle age-classes from the upper and lower crown were measured in four ramets of each of 17 clones selected to cover the range of UMCY severity. There was a negative correlation between UMCY and magnesium ($r = -0.60$, $n = 17$, $p = 0.01$), and a positive correlation with potassium ($r = 0.56$, $n = 17$, $p = 0.05$) and nitrogen ($r = +0.75$, $n = 17$, $p = 0.01$) in upper crown foliage, with the correlations based on clone means. UMCY was absent in clones where foliar magnesium concentrations in 1-year-old needles from the upper crown exceeded 0.10%, but increased with decreasing foliar magnesium, particularly in clones with high foliar potassium or nitrogen. Unknown clonal factors were also involved in UMCY.

Broad-sense heritabilities of foliar nutrients were high for potassium, magnesium and calcium (particularly in the lower crown position of trees grown from cuttings), and moderate for other nutrients. Clone means of foliar nutrients differed by more than a factor of two for potassium, magnesium, calcium, boron, and manganese. Marked differences were found between upper and lower crown positions for most nutrients. The scion played a major role in determining foliar magnesium, potassium, manganese, and copper concentrations, while the root stock/graft union played a major role for calcium, zinc, and to a lesser extent nitrogen and phosphorus.

Needle retention was also highly clonal, with a broad-sense heritability of 68%. Clones with low needle retention had higher potassium concentrations, both in upper and lower crown foliage, and significantly more UMCY than healthy clones.

Part of the clonal variation in diameter at breast height (dbh) was related to UMCY, with healthy clones being larger in mean dbh than clones with severe UMCY. Dbh

increased with increasing needle retention, while the concentrations of foliar nitrogen, phosphorus, and potassium correspondingly decreased.

We conclude that some genotypes of *P. radiata* are pre-disposed to UMCY at this site, owing to the high K:Mg and N:Mg ratios in upper crown foliage. Large clonal variation in UMCY indicates that considerable opportunity exists for improving tolerance to UMCY through vegetative propagation of tolerant *P. radiata* genotypes.

Keywords: broad-sense heritability; clones; ion antagonism; magnesium; nitrogen; potassium; stress tolerance; rooted cuttings; grafts.

INTRODUCTION

Reports by forest health observers that Upper Mid-Crown Yellowing (UMCY), a form of crown dieback, is widespread and appears to be increasing throughout the country (Forest Research Institute 1991) have raised concerns regarding possible adverse effects on growth. Historical records indicate that UMCY has occurred for several decades in *P. radiata* stands in New Zealand (Beets *et al.* 1993). Explanations advanced to explain UMCY include: physical damage from possums, wind, snow, land subsidence; needle pathogens such as *Cyclaneusma minus* (Butin) DiCosmo *et al.*; root diseases such as Armillaria (causal organisms *Armillaria novae-zelandiae* (Stevenson), *A. limonea* (Stevenson) Boesewinkel), and site limitations due to poor drainage and nutrient deficiency (Beets *et al.* 1993).

It has been hypothesised that magnesium deficiency is the cause of UMCY in older stands (Forest Research Institute 1991). In support of this hypothesis the following observations were made by Beets *et al.*(1993):

(1) Yellow needle-tipping in the upper crown is a symptom of magnesium deficiency;

(2) Young stands with magnesium deficiency symptoms (Will 1966) are often found near older stands with UMCY;

(3) Within-stand variation in foliar magnesium is large (Mead & Will 1976), and so is within-stand variation in UMCY;

(4) Clonal differences occur in *P. radiata* foliar nutrient levels, including magnesium, in New Zealand and elsewhere (Forrest & Ovington 1971; Burdon 1976; Knight 1978; Raupach & Nicholls 1982). Magnesium deficiency symptoms were evident in clones which ranked low in foliar magnesium (Knight 1978);

(5) Photographic records for Puruki Experimental Catchment show a progression over time from magnesium deficiency symptoms in young trees to UMCY symptoms in older trees.

The last observation provided the most direct evidence linking UMCY with foliar magnesium levels.

Knight (1978) showed that clone rankings by magnesium concentration were maintained despite magnesium concentrations fluctuating seasonally (foliar magnesium concentrations were at their lowest level in spring). This consistency in ranking for magnesium is particularly pertinent, because an association between UMCY and foliar magnesium measured in clonal *P. radiata* in spring would be expected to apply at other times of the year. The association between UMCY and magnesium needs further examination so that appropriate

remedies can be developed. UMCY can most easily be scored in spring, and foliar nutrient concentrations in clones were examined at the same time.

The objectives of this study were to examine the severity of UMCY in clones of *P. radiata* at the Kaingaroa Seed Orchard, and to determine the relative amounts of variation within and between clones for UMCY, foliar nutrient concentration in spring (by crown position and needle age), needle retention, and tree diameter, and their inter-correlations.

MATERIALS AND METHODS

The study was conducted in part of the Kaingaroa Seed Orchard, which was planted in 1978 after the harvest of a previous crop of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Soils were derived from rhyolitic flow-tephra (Kaingaroa loamy sand) and had low cation exchange capacity and available magnesium (Metson 1974). Detailed descriptions of the climate and soil of this series have been reported by Rijkse (1988). The seed orchard was at an altitude of 550 m. Precipitation averaged 1500 mm annually, with an annual average temperature of 11°C. Site productivity was high, although drainage was restricted and frosts could occur at any time of year. The site was windrowed before cuttings and grafts of selected *P. radiata* clones were planted.

The clones were of phenotypically selected trees with superior growth rate and form, subsequently re-selected on the basis of progeny test performance. Physiological age of ramets was about 14 years at time of planting. Ramets of individual clones were planted in a single-tree-plot layout, designed to minimise the likelihood of pollination by members of the same clone. Spacing was 8 × 5 m at time of planting, or 250 trees/ha. Roguing reduced the stocking to approximately 90 trees/ha by 1992, when the trees were essentially under open-grown conditions. Windrows were located at 48-m intervals, and were oriented parallel with the rows of trees. These were planted on top, immediately adjacent to, and away (as three intervening rows) from windrows.

UMCY Assessment

A survey of tree health in blocks 262/4, 14, 24 was made during October and November 1992. Blocks were each about 4 ha in area. These blocks had been treated in 1984 with 500 kg dolomite/ha and 500 kg diammonium phosphate/ha, and in 1985 with 500 kg dolomite/ha (T.G.Vincent pers. comm.). The blocks were composed either entirely of cuttings, or of cuttings and grafts growing in mixture. Each tree was mapped according to clonal identity and propagation method (rooted cutting *v.* grafted on seedling root stock).

UMCY severity was estimated by separate observers positioned on lines at right angles to each other and at least 20 m from the base of the tree. A single score was recorded after agreement had been reached—a process instituted to reduce errors associated with scoring large trees. Modifications to the original scoring system outlined by Beets and others (Forest Research Institute 1991) were made to expand the number of severity classes:

A+ Healthy upper crowns.

A– Yellow needle tips sub-apically; full upper crowns with high retention of 2-year-old needles.

B+ Yellow needle tips and thin crowns sub-apically, with poor retention of 2-year-old needles.

B– Yellow 1- and 2-year-old needles and thin upper crowns with low needle production and retention on secondary branches.

C+ Hollow zone caused by death of secondary branches occupying less than half the width of the upper crown.

C– Hollow zone as for C+, but occupying more than half the width of the upper crown.

D+ As for C–, but with one or more dead primary branches also present in UMCY zone.

D– Zone with dead primary branch whorls in upper crown—sometimes also associated with top death.

For statistical analysis, severity classes were assigned numerical values ranging from 1 (for A+ trees) to 8 (for D– trees). UMCY severity was not scored when evidence of stem breakage was observed, even if the tree top had recovered. In total, 809 trees divided among 86 clones were scored.

To test whether biotic factors were associated with UMCY, additional observations and measurements were made on individual trees. At this site needle retention in the lower crown indicates susceptibility to defoliation by *C. minus*—a needle-cast fungus which is prevalent at Kaingaroa. A needle retention score of 0 (if the lower crown was dead) to 3, increasing by one unit for every more-or-less complete needle age-class retained in the lower crown, was allocated to each tree. The incidence (0 = absent, 1 = present) of branch-terminal death caused by *Diplodia pinea* Desm. Kickx invasion (associated with physical damage that occurred during cone picking) was recorded. Root-collar girdling with Armillaria disease (expressed as percentage circumference affected) was recorded for each tree in 17 clones (*see below*) sampled for foliar nutrient analysis. Tree diameter (dbh) was measured at breast height (1.4 m).

Foliar Analysis

Seventeen of the 86 clones examined were selected to cover the range in UMCY severity observed at the seed orchard. Ten clones were represented by both cuttings and grafts and seven by cuttings only. Four ramets of each propagation type were sampled per clone. Three trees sampled for foliar nutrient concentration were on windrows, which were otherwise avoided to minimise environmental variation in foliar nutrients.

Two 2-year-old secondary twigs were collected from the upper and lower crown of each ramet. Four foliage samples per tree—two needle age-classes from each of two crown positions—were prepared for chemical analysis. The upper crown sampling position corresponded closely with the standard sampling position for *P. radiata* foliage (Will 1985), but samples were collected in November, when needle yellowing in the UMCY zone was most evident, rather than during the standard sampling period (February–March).

Samples were ground and analysed for total nitrogen, phosphorus, potassium, calcium, magnesium, boron, manganese, zinc, and copper, using methods described by Nicholson (1984), and concentrations were expressed on a oven-dry weight basis.

Statistical Analysis

Clonal and environmental effects on UMCY, needle retention, and dbh were examined using analysis of variance (ANOVA) of the survey data (Tables 1–3). Significance tests were restricted to clones with four or more ramets per clone/propagation method. In ANOVA Tables 1–3, Type I effects depend on the order that variables are fitted, while Type III do not. However, in studies involving clones, both Type I and III mean squares (MS) should be examined if the broad-sense heritability of a trait is high. In this case, environmental sources of variation may not be significant after clone effects are accounted for (Type III MS). Reliance must then be placed on the Type I results, which are more difficult to interpret correctly.

Broad-sense heritability, h^2_{bs} reflects the relative amounts of variation between and within clones, and was estimated for UMCY, needle retention (Cyclaneusma), dbh, and Diplodia using the equation:

$$h^2_{bs} = s^2_{clone}/(s^2_{clone} + s^2_{within\ clone})$$

TABLE 1–ANOVA of UMCY severity scores for radiata pine clones at the Kaingaroa Seed Orchard. Propagation method (Propag.) included rooted cuttings and grafts.

		Type I		Type III	
Source	df	MS	F value	MS	F value
Block	10	3.73	4.30***	1.82	2.10*
Windrow	2	5.88	6.77**	3.62	4.17*
Needle ret.	3	5.97	6.89***	3.52	4.06**
Diplodia	1	31.7	36.6 ***	2.95	3.39ns
Clone	49	13.1	15.1 ***	8.46	9.75***
Propag.	1	3.50	4.07*	5.55	6.40*
ClonexPropag.	23	1.77	2.04**	1.77	2.04**
Between ramets within clones	653	0.868			

* F-values significant at p = 0.05
** p = 0.01
*** p = 0.001

TABLE 2–ANOVA of needle retention (Cyclaneusma) scores for *Pinus radiata* clones at the Kaingaroa Seed Orchard.

		Type I		Type III	
Source	df	MS	F value	MS	F value
Block	10	1.21	3.26***	1.21	3.27***
Windrow	2	0.25	0.69ns	0.87	2.34ns
UMCY	7	1.79	4.83***	0.45	1.20ns
Diplodia	1	3.25	8.76***	0.78	2.11ns
Clone	49	8.50	22.8 ***	6.10	16.4 ***
Propag.	1	0.06	0.16ns	0.00	0.00ns
ClonexPropag.	23	0.52	1.40ns	0.52	1.40ns
Between ramets within clones	649	0.37			

* F-values significant at p = 0.05
** p = 0.01
*** p = 0.001

TABLE 3–ANOVA of dbh for *Pinus radiata* clones at the Kaingaroa Seed Orchard.

Source	df	Type I		Type III	
		MS	F value	MS	F value
Block	10	43.4	2.28*	37.7	1.98*
Windrow	2	392.9	20.6 ***	478.6	25.1 ***
UMCY	7	61.9	3.25**	12.8	0.67ns
Needle ret.	3	591.4	31.0 ***	92.9	4.87**
Diplodia	1	230.0	12.1 ***	159.7	8.38**
Clone	49	206.2	10.8 ***	139.8	7.34***
Propag.	1	30.6	1.60ns	117.1	6.14*
Clone×Propag.	23	44.5	2.33***	44.5	2.33***
Between ramets within clones	636	19.1			

* F-values significant at p = 0.05
** p = 0.01
*** p = 0.001

The variance components (s^2_{clone} = variance between clones, $s^2_{within\ clone}$ = variance within clones) were estimated using ANOVA, in which the effect of clone was examined after block and windrow effects had been taken into account. Differences between clones tested under environmental conditions as uniform as possible probably reflect genotypic differences.

Foliar nutrient data were subjected to ANOVA after logarithmic transformation of calcium, magnesium, boron, manganese, and phosphorus concentrations. Broad-sense heritability was estimated for each element using ANOVA by needle age, crown position, and propagation method. Clone was the only variable included in the ANOVA. Heritability estimates are normally based on samples selected from a population at random (Burdon 1976); however, the heritability estimates for the nutrient data were based on clones selected to cover the range in UMCY severity. Our heritability estimates for nutrient data are not strictly comparable with those from other studies. Heritabilities are likely to be over-estimates for nutrients correlated with UMCY.

Multiple regression analysis was used to examine the relationship of UMCY with foliar nutrient concentrations as affected by needle age and crown position. This analysis was based on clone means to meet statistical requirements. In order to examine the role of clone on UMCY more fully, individual tree foliar nutrient data were analysed both before and after fitting clone. These analyses were intended to indicate to what extent UMCY is associated with non-clonal (environmental) variation in nutrient availability, and whether clonal factors were additionally implicated.

The information contained in the nutrient correlation matrix (for nitrogen, phosphorus, potassium, calcium, magnesium, boron) was examined using multivariate methods. The reported analyses were based on tree mean (upper and lower crown) nutrient concentrations in 1-year-old needles, with cuttings and grafts combined. The 2-year-old needles were not used because data were frequently missing, owing to low needle retention in the lower crown. The upper and lower crown positions, when examined separately, gave similar results to those reported here. Principal component and factor analysis (using the Varimax rotation

method, SAS) were used. Results were interpreted based on correlations of principal components and factors with UMCY, needle retention, Diplodia, and dbh, and results are given by propagation method.

RESULTS

UMCY Assessment

Results are presented on a tree and clone mean basis. Of the 809 trees, 67% were classified in category A, 23% in B, 8% in C, and 1% in D. Of the 86 clones, 38%, 38%, 12%, and 12% were classified in A, B, C, and D categories, respectively. Some clones were consistently free of UMCY symptoms, receiving "A" scores for both cuttings and grafts, while others consistently exhibited severe UMCY symptoms with "C" or "D" scores for cuttings and grafts. Intermediate clones varied in UMCY severity, although variation within clone was quite low, as indicated by the broad-sense heritability estimate for UMCY (59%). These results indicate that clones with low UMCY severity were better represented (i.e., more ramets per clone) at the seed orchard than clones with high severity rating. Fifty clones were represented by at least four ramets per clone and propagation method.

UMCY varied significantly in relation to clone, block, windrow, and needle retention, and was also associated with the method of propagation (Type III Mean Square, Table 1). Clone explained about half of the total variation in UMCY severity at this site. Variation between ramets-within-clones (the error term of this model) accounted for 40% of the total variation, and was therefore the major source of environmental variation that was not accounted for by block and windrow. The latter environmental sources of variation (block and windrow) together accounted for less than 5% of the total variation. UMCY was more severe in trees with intermediate needle retention (1 or 2 years) than in trees with high (3 years) or low (0 years) needle retention both among trees and within clones. Diplodia, which had a broad-sense heritability of 29%, was associated with UMCY (Type I MS, Table 1), but not after clone effects were accounted for. The effects of propagation method were significant, but explained only a small proportion of the total variation. UMCY was more severe in grafts than cuttings, particularly in clones with severe UMCY, as indicated by the significant clone × propagation-method interaction (Table 1). UMCY symptoms were more severe adjacent to than away from windrows.

Needle retention in the lower crown was associated mainly with clone (Table 2), which accounted for about 66% of the total variation in the lower crown needle retention. The broad-sense heritability estimate was 68%. A significant block effect was also apparent, but none of the other variables tested was related to needle retention after clone effects had been taken into account.

Dbh varied spatially within the seed orchard, as indicated by the significant block effect, and trees adjacent to windrows were 5% larger in dbh than trees away from windrows. Dbh was significantly associated with UMCY after block and windrow effects were accounted for (Type I MS, Table 3), but not after clone had been taken into account (Type III MS, Table 3). Dbh was related to needle retention both among and within clones. The broad-sense heritability of dbh was 54%.

The incidence and severity of sub-lethal Armillaria was very low (Mark Self pers. comm.), and was neither clonal nor associated with UMCY severity.

Foliar Nutrient Levels

The effects of clone, sampling position (upper *v.* lower crown), foliage age-class (1- *v.* 2-year-old), and propagation method (cuttings *v.* grafts) on foliar nutrient concentrations are summarised in Table 4. Almost all nutrients varied significantly ($p = 0.01$) with respect to sampling position, foliage age, and clone, while nitrogen, phosphorus, calcium, boron, and zinc also varied with propagation method. With the exception of clone × propagation-method, few significant interactions were found.

The means and ranges of foliar nutrient concentrations in 1-year-old upper-crown needles differed widely among the 17 clones examined (Table 5). Cation and micronutrient concentrations varied by a factor of two or more, while nitrogen and phosphorus exhibited considerably lower levels of variation. Foliar nutrient concentrations of calcium, magnesium, boron, manganese, and zinc decreased with sampling height within crown while other nutrients, except copper, increased. Copper concentrations did not vary with crown position (Tables 4 and 5). Significant clone × crown-position interactions were found for potassium,

TABLE 4–Summary of ANOVA on effects of sampling position (upper or lower crown), foliage age (1- or 2-year-old needles), clone, and propagation method on foliar nutrient concentrations.

Source of variation	N	P	K	Ca	Mg	B	Mn	Zn	Cu
Crown position (P)	**	**	**	**	**	**	**	**	ns
Foliage age (A)	**	*	**	**	**	ns	**	ns	**
P × A	ns	*	ns	*	ns	*	ns	**	ns
Clone (C)	**	**	**	**	**	**	**	**	**
C × P	ns	ns	**	ns	ns	*	ns	*	ns
C × A	ns	ns	ns	ns	ns	ns	ns	ns	ns
Propag. method (M)	*	*	ns	**	ns	**	ns	**	ns
M × P	ns	ns	ns	ns	ns	ns	ns	ns	ns
M × A	ns	ns	ns	ns	ns	ns	ns	ns	ns
C × M	**	**	ns	ns	ns	*	*	*	**

* F-values significant at $p = 0.05$
** $p = 0.01$
*** $p = 0.001$

TABLE 5–Overall means of nutrient concentrations of 1-year-old needles in the upper and lower crown, together with minimum and maximum clone means (upper crown), of *Pinus radiata* cuttings.

Nutrient (oven dry weight basis)	Upper crown mean	Lower crown mean	Min. clonal mean	Max. clonal mean
Nitrogen (%)	1.27	1.22	1.07	1.51
Phosphorus (%)	0.12	0.11	0.10	0.15
Potassium (%)	0.80	0.74	0.55	1.08
Calcium (%)	0.33	0.57	0.23	0.52
Magnesium (%)	0.07	0.13	0.04	0.10
Boron (ppm)	9	14	6	16
Manganese (ppm)	269	391	183	403
Zinc (ppm)	67	76	54	90
Copper (ppm)	3.3	3.3	2.6	4.1

boron, and zinc (Table 4), and so the summary by crown position for these nutrients (Table 5) only indicates overall trends.

In both cuttings and grafts, the broad-sense heritability estimates for phosphorus, potassium, calcium, and magnesium concentrations in most foliage material were highly significant. This was rarely the case for other nutrients examined (Table 6). Heritability estimates were similar in 1- and 2-year-old needles, but generally decreased with crown height. For potassium, calcium, and magnesium, the 1-year-old needles provided the highest estimates of heritability, which ranged between 0.76 and 0.83 in the lower crown and between 0.50 and 0.62 in the upper crown. These results suggest that within-tree sampling error is larger in the upper crown than in the lower crown. Almost without exception, heritabilities for foliar nutrients were lower in grafts than in cuttings.

TABLE 6–Clonal broad-sense heritability of foliar nutrient concentrations of *Pinus radiata* at the Kaingaroa Seed Orchard, in relation to propagation method (rooted cuttings *v.* grafts), sampling position (upper *v.* lower crown), and needle age.

Material	Nutrient								
	N	P	K	Ca	Mg	B	Mn	Zn	Cu
Cuttings									
Upper 1 year	**0.42**	**0.44**	**0.62**	**0.54**	**0.50**	**0.57**	0.34	0.30	**0.48**
Upper 2 year	0.36	**0.41**	**0.62**	**0.59**	**0.51**	0.31	0.36	**0.51**	0.37
Lower 1 year	0.40	**0.51**	**0.83**	**0.76**	**0.77**	0.35	0.34	**0.50**	0.40
Lower 2 year	0.42	**0.66**	**0.84**	**0.74**	**0.71**	**0.52**	0.39	**0.62**	0.35
Grafts									
Upper 1 year	0.28	**0.53**	**0.55**	0.23	0.24	0.39	**0.47**	0.24	**0.56**
Upper 2 year	0.41	**0.44**	**0.45**	0.26	0.33	0.35	0.38	0.33	**0.48**
Lower 1 year	0.27	0.33	0.33	**0.53**	**0.51**	0.37	0.35	0.10	0.25
Lower 2 year	0.16	0.29	**0.52**	0.38	**0.53**	**0.59**	0.31	0.27	0.36

Bold numbers are significant at 0.05 probability level.

When examined across all clones, foliar concentrations of certain nutrients were significantly inter-correlated, though the correlations were not always consistent among crown positions, age classes, and propagation methods. Of the 36 possible nutrient inter-correlations only Ca-Mg, Ca-Zn, Ca-Mn, P-Mg, P-Cu, N-Cu, N-P, and B-Zn were found to be consistently significant ($p = 0.05$), occurring in at least six of the eight possible sampling categories (i.e., 2 crown-positions × 2 needle-age-classes × 2 propagation-methods), while P-K and Mg-Zn were always significant in the upper crown. The correlations noted above were positive with an average value of 0.5. The strongest correlations were those between calcium and magnesium, both within and among clones.

The severity of UMCY increased as foliar concentrations of magnesium decreased and those of nitrogen and potassium increased. For example, the correlation coefficient (r) between clone mean nutrient concentration in 1-year-old upper crown needles and clone mean UMCY score in cuttings was high and significant for nitrogen ($r = +0.75$; $n = 17$, $p = 0.0005$), potassium ($r = +0.56$; $n = 17$, $p = 0.02$), magnesium ($r = -0.60$; $n = 17$, $p = 0.01$), K:Mg ($r = +0.65$, $n = 17$, $p = 0.004$), and N:Mg ($r = +0.67$, $n = 17$, $p = 0.003$). The correlation between UMCY and magnesium is shown in Fig. 1. UMCY was also correlated with foliar magnesium, potassium, and the K:Mg ratio in the lower crown position, but not with nitrogen

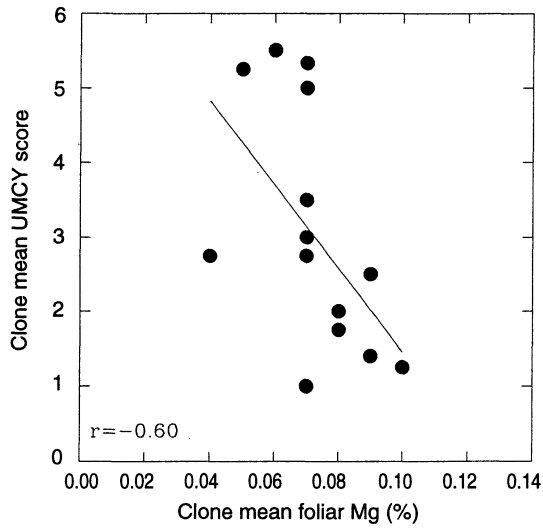

FIG. 1–Relationship between clone mean UMCY severity score and foliar magnesium (Mg) concentration in *Pinus radiata*, based on 1-year-old needles from the upper crown of four trees per clone. Nutrient concentrations are expressed on an oven-dry weight basis.

or the N:Mg ratio. A similar pattern of correlation between UMCY, foliar magnesium, potassium, and nitrogen emerged irrespective of needle age and propagation method. While magnesium and calcium were always strongly inter-correlated, correlations between UMCY and foliar calcium were significant in only two of the eight possible sampling categories, even though calcium and magnesium were highly inter-correlated in all eight sampling categories. Furthermore, no visual calcium deficiency symptoms were observed.

Three principal components ("all nutrients", magnesium *v.* potassium, and boron) and three factors (N|P|K, Ca|Mg, and B) were identified. In cuttings, UMCY was correlated with the magnesium *v.* potassium component ($r = 0.46$, $n = 67$, $p = 0.0002$), the N|P|K factor ($r = 0.26$, $n = 60$, $p = 0.04$), and the Mg|Ca factor ($r = -0.42$, $n = 60$, $p = 0.0007$). These results show that UMCY was more closely related to magnesium *v.* potassium (which is equivalent to the K:Mg ratio) than to either N|P|K or Mg|Ca. In grafts, UMCY was weakly correlated with the Mg|Ca factor ($r = -0.30$, $n = 38$, $p = 0.07$).

The multivariate analyses also showed that dbh was negatively correlated with the N|P|K factor ($r = -0.25$, $n = 67$, $p = 0.04$ in cuttings, and $r = -0.33$, $n = 36$, $p = 0.05$ in grafts). Diplodia was correlated with the "all nutrients" component ($r = 0.33$, $n = 67$, $p = 0.006$) in cuttings but not in grafts, and the Mg|Ca factor ($r = 0.27$, $n = 67$, $p = 0.03$) in cuttings. Needle retention was correlated with the magnesium *v.* potassium component ($r = -0.27$, $n = 67$, $p = 0.03$) in cuttings and with the N|P|K factor ($r = -0.24$, $n = 67$, $p = 0.05$) in cuttings but not significantly ($r = -0.24$, $n = 38$, $p = 0.15$) in grafts, possibly because the sample size was small.

A multiple-regression model designed to predict clone mean UMCY score from the clone mean foliar magnesium and potassium (in the upper crown) was highly significant, with a coefficient of determination r^2 of 52%. When foliar nitrogen (in the upper crown position) was included in this multiple regression model the r^2 increased to 67%. The model shows that UMCY can be predicted from the clone mean concentrations of foliar magnesium, potassium,

and nitrogen, with UMCY increasing markedly as the concentration of magnesium in needles decreases below 0.10% (Fig. 1).

A multiple regression model designed to predict individual tree UMCY from foliar magnesium, potassium (in 1-year-old needles in the upper crown), and clone, in an analysis which included only these three variables, explained 80% of the variation in UMCY in cuttings, and 60% in grafts. Clone accounted for about 66% of the variation explained by this model, so it appears that additional clonal factors besides foliar total magnesium and potassium concentration were associated with UMCY. When clone was fitted before magnesium and potassium, these nutrients explained none (using upper crown magnesium and potassium) or only a small but significant proportion (lower crown magnesium and potassium) of the variation in UMCY, which indicates that clonal variation in UMCY was related mostly to clonal variation in magnesium and potassium.

Foliar nitrogen concentrations were higher in the upper than in the lower crown of trees showing severe UMCY (Fig. 2). In contrast, the ratios of upper:lower crown magnesium and potassium were not correlated with UMCY (Fig. 2).

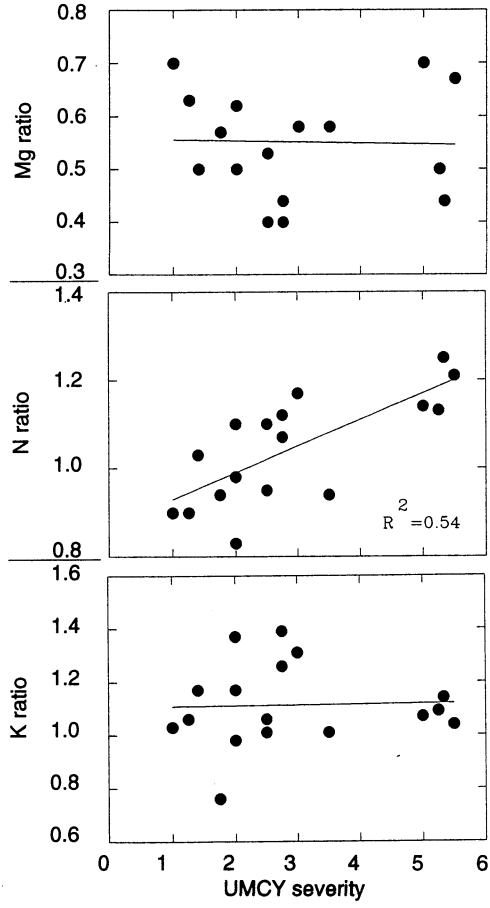

FIG. 2–Upper:lower crown ratios of foliar nutrient concentrations and their relationship with UMCY severity (based on clone means) in *Pinus radiata* clones.

UMCY was not associated with propagation method in the subset of clones used for nutrient analysis (ANOVA not shown), while foliar calcium, zinc, nitrogen, and boron were significantly higher in cuttings and phosphorus was higher in grafts (Table 4).

DISCUSSION

Nutrients Associated with UMCY

Information on the cause of UMCY in *P. radiata* is required in order to develop remedial action. The relationship between UMCY and magnesium deficiency in *P. radiata* has been described by Beets and others (Forest Research Institute 1991), who suggested that nutritional factors were the likely cause of UMCY. The seed orchard study showed that severe UMCY was associated with low foliar magnesium, and high foliar potassium and nitrogen concentrations in the upper crown. This supports the view that nutritional factors are involved. Foliar calcium was also associated with UMCY, although visual calcium deficiency symptoms were not observed. Yellow needle-tips in *P. radiata* were previously associated with magnesium deficiency (Will 1966). At the seed orchard, an imbalance between foliar K:Mg and N:Mg seems to influence UMCY symptoms.

The decrease in foliar magnesium with height contributed most to the increase in K:Mg and N:Mg ratios in the upper crown, and occurred in all clones. The latter finding is particularly important, as it indicates that low foliar magnesium in the upper crown is the cause of UMCY, although not, as a single factor, a symptom (Fig. 2). The inability of some clones to concentrate foliar magnesium in all crown positions predisposes them to varying degrees of crown die-back at this site.

High N:Mg ratios in the upper crown resulted in part from high concentrations of foliar nitrogen in trees with UMCY. Presumably, nitrogen demands for growth in the UMCY zone of trees exhibiting crown die-back would be reduced. This could explain why the upper:lower crown nitrogen ratio increased from 0.9 to 1.25 with increasing UMCY severity (Fig. 2). Foliar nitrogen concentrations were significantly correlated with UMCY after the effects of magnesium and potassium were accounted for. Excess availability of nitrogen has previously been associated with tree ill-health (Abrahamsen *et al.* 1994). Evidence from agricultural crops suggests that nitrate-nitrogen may play an antagonistic role with potassium in protein synthesis (Flowers & Dalmond 1992). Non-protein nitrogen has been found to accumulate in magnesium-deficient plants, and nitrate-nitrogen is commonly associated with high foliar potassium (Marschner 1986).

High concentrations of potassium observed in upper-crown needles were associated with increased severity of UMCY in clones with low foliar magnesium (Fig. 1). In contrast to foliar nitrogen, the ratio of upper:lower crown potassium did not increase with the severity of UMCY (Fig. 2). We suspect that death of branches in the UMCY zone results from interruption of protein synthesis owing to insufficient magnesium. Both magnesium and potassium are essential for the correct sequencing of amino-acids during protein synthesis. When either magnesium is low or potassium is high, protein synthesis ceases (Marschner 1986).

Foliar magnesium concentrations below 0.07% during February/March were identified as being critical, in a study based on seedlings (Will 1985). The seed orchard clones were assessed in spring, when foliar magnesium concentrations can be expected to be at a low

point, based on the pattern of seasonal fluctuations given by Knight (1978). The critical magnesium level appears to be too low for semi-mature *P. radiata* at this site.

Other clonal factors besides foliar concentrations of magnesium and potassium were associated with UMCY. These factors appeared to have an important influence on the apparent utilisation efficiencies of magnesium and potassium, with some clones developing more severe UMCY than others as foliar magnesium decreased below 0.10%. If magnesium, potassium, and perhaps nitrogen are causally related to UMCY, it is curious that foliar nutrient concentrations were only comparatively weakly associated with UMCY. Foliar total magnesium and potassium may be too crude to provide a precise index of UMCY. If the physiology of protein synthesis is involved, definition of nutrient distribution within the foliage may be needed to improve the prediction of UMCY.

The broad-sense heritabilities of foliar magnesium and potassium concentrations in the upper and lower crown were very high (Table 6), though broadly in line with the results of Knight (1978). More work is needed on the extent to which foliar concentrations of these nutrients are under genetic control. While propagation method (cuttings *v.* grafts) significantly influenced the concentration of some nutrients, foliar magnesium and potassium were largely unaffected. This suggests that the genotype of the scion may be important in determining the concentration of nutrients associated with UMCY.

Non-genetic clonal effects (the "c"-effects of Burdon & Shelbourne 1974), such as poor rooting ability, do not appear to influence UMCY. Results from grafted clones show that the scion's genotype, rather than the root stock/graft union, largely determines UMCY—though heritabilities of nutrient concentrations and UMCY were lower in grafts than in cuttings. This may have been due to the non-clonal nature of root-stocks in grafted clones and to graft incompatibility. While UMCY was more severe in grafts than in cuttings of affected clones, information from another site suggests that cuttings are no more prone to UMCY than seedlings. For example, at Puruki, where cutting and seedling trees occur in mixture (Beets & Brownlie 1987), the severity of UMCY and the concentrations of magnesium and potassium in needles were similar in cuttings and seedlings, suggesting that "c"-effects may not apply to foliar nutrients and UMCY (Beets unpubl. data).

No significant relationships between UMCY and root disease were found at the seed orchard. Although Armillaria disease was present at low levels in the seed orchard, it was not associated with UMCY. Sub-lethal infection by *Armillaria* spp. was found in green-crowned trees in a study conducted nearby (Hood & Sandberg 1993). The visual effects of Cyclaneusma needle-cast (which was highly clonal) could be readily distinguished from UMCY, but the incidence of the two conditions was correlated—apparently through their common association with foliar nitrogen and potassium.

Like UMCY in *P. radiata*, the poor health of forests in parts of Norway and Germany has been ascribed primarily to magnesium deficiency. In particular, a reduction in exchangeable magnesium is held to be responsible (Abrahamsen *et al.* 1994; Roberts *et al.* 1989). The effect of magnesium deficiency on growth was confounded with increased availability of nitrogen in Norway and Sweden, where growth rates increased over time, even though the forests exhibited symptoms of ill-health (*see* Abrahamsen *et al.* 1994 for a recent review of acid rain research). Similarly, we found higher tree growth rates and more severe UMCY symptoms in trees adjacent to windrows.

UMCY—Likelihood of Growth Loss

Some effect of UMCY on growth could be expected to result from loss in leaf area associated with severe UMCY. In the present study, the absence of a significant relationship between UMCY severity and dbh in the analysis conducted within-clone (i.e., after removing effects of block, windrow, and clone) was surprising, given the severity of UMCY in some trees, the high precision expected when using clonal material, and the low stocking at the seed orchard (where growth compensations among trees would have been minimal). It may be due to the low within-clone variation in UMCY: the large effect of needle retention on dbh was found to be diminished after clone effects were accounted for. Severe UMCY was associated with certain clones which had a smaller dbh than trees without UMCY. More research is required to determine the relationship between growth loss on a unit area basis and UMCY severity.

Severe magnesium-deficiency in young *P. radiata* (and by inference UMCY in semi-mature trees) is not easily remedied by fertiliser treatment. Very slow increase in foliar magnesium (over several years), and slow growth response to magnesium fertilisers are thought to be related to slow regeneration of fine roots and total leaf area (Hunter *et al.* 1986; Payn 1991). Growth reductions associated with magnesium deficiency in *Pinus resinosa* Ait. were slow to develop, even with advanced symptom expression (Leaf 1968). The effects of magnesium deficiency on tree nutritional status and growth rate are in marked contrast to those commonly reported for nitrogen deficiency.

An increase in K:Mg ratio in *P. radiata* foliage has been observed after repeated harvesting on some pumice soils of the central North Island (Will 1961; Ballard 1978). This suggests that UMCY will probably increase in commercial plantation forest. Changes in foliar nutrient concentrations and balances seem to reflect the impacts of organic matter removals on exchangeable pools of potassium and magnesium (Ballard 1978; Dyck & Skinner 1990). Will & Knight (1968) cautioned that the existing supplies of magnesium were insufficient to maintain high productivity and health in *P. radiata* grown on volcanic ash soils for more than two rotations.

Strategies for Reducing Incidence and Severity of UMCY

In addition to developing appropriate site management techniques (e.g., organic matter management and fertiliser treatment), selection for increased tolerance to UMCY should be considered. At the seed orchard, 100 kg elemental magnesium/ha as dolomite was insufficient to prevent UMCY in some clones. Magnesium fertiliser treatment in conjunction with selection of UMCY-tolerant genotypes may be more cost-effective in the long-term.

Clonal forestry offers an opportunity for rapid development of UMCY tolerance if clonal differences in UMCY are not site-specific. Information on clone × site interaction effects on UMCY is not available. Limited data on clone/site effects exist for foliar nutrients. In one study of nitrogen, phosphorus, potassium, calcium, and magnesium in *P. radiata*, nitrogen was the only nutrient showing consistency in concentrations within clones planted on different sites (Burdon 1976). This suggests that a regionalised approach may be necessary.

CONCLUSIONS

Foliar nutrient levels and UMCY severity were found to be characteristics of certain *P. radiata* clones and are inter-correlated. It can be inferred that they are both controlled by

genetic factors. Severe UMCY was associated with nutritional imbalance involving low concentrations of magnesium and high potassium and nitrogen in upper crown needles. Imbalances among these nutrients have elsewhere been associated with reduced plant protein synthesis, which is consistent with foliage yellowing and branch death symptoms observed in this study.

Clonal variation in foliar cation concentrations and UMCY suggests that selection for increased tolerance to nutritional imbalance involving magnesium, potassium, and possibly nitrogen should be pursued as a possible strategy for reducing the incidence of UMCY. Selection of UMCY-tolerant clones combined with magnesium application may be more cost effective in the long term than magnesium fertiliser treatment alone.

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