

FRI/INDUSTRY RESEARCH COOPERATIVES

## EUCALYPT BREEDING COOPERATIVE

FOREST RESEARCH INSTITUTE  
PRIVATE BAG 3020  
ROTORUA

Variation in susceptibility to Possum  
Defoliation in Two Populations of  
*Eucalyptus nitens*

Phil Cannon

Report No. 7

January 1993

Variation in susceptibility to Possum  
Defoliation in Two Populations of  
*Eucalyptus nitens*

Phil Cannon

Report No. 7

January 1993



# VARIATION IN SUSCEPTIBILITY TO POSSUM DEFOLIATION IN TWO POPULATIONS OF *EUCALYPTUS NITENS*

By Phil Cannon

## SUMMARY

Possum defoliation of *Eucalyptus nitens* is recognised as a potentially severe cause of growth loss in forest plantations, particularly in some parts of New Zealand which are near native bush. One means by which damage can be reduced is to plant tree genotypes which are least preferred by possums.

During the winter of 1992, a possum population at Poronui Station (30 km east of Lake Taupo at 700 masl) fed on two sets of a single-tree-plot progeny test involving 79 families of *Eucalyptus nitens*. The families in Set 1 were all of central Victorian origin. In Set 2, all families were from central Victoria except for six which came from New South Wales.

The feeding on this test was moderately heavy and obviously discriminatory; some trees were more heavily browsed than were others. On average trees closest to the native bush and in areas where weed control was best were most affected, but these patterns could not account for more than a part of the variation.

To determine the genetic influence on the degree of browsing, each tree in this progeny test was evaluated for the percentage of defoliation. The narrow sense heritability of individual values for possum resistance ( $h^2$ ) was determined to be 0.30 for set 1 and 0.38 for set 2.

The sizeable difference in heritabilities between these sets is attributed mainly to the presence of six New South Wales families in Set 2 which, on average, had had 28% more of their foliage removed by possum feeding than individuals from central Victoria.

At a selection intensity of 1 in 200, the expected reduction in possum defoliation using combined selection is 37% for Set 1 and 27% for Set 2. Means of using this information practically in an ongoing breeding programme of *Eucalyptus nitens* and in conjunction with other possum control measures are considered.

## INTRODUCTION

Defoliation by possums is a major cause of growth loss and stem deformation in many plantations of many species in New Zealand. Finding means of reducing the impact of this animal could therefore be quite important. Several approaches have been tried to do just this; most of these have been aimed at controlling the possum population (Peters, 1974; Warburton, 1981) or chemically altering the palatability of the leaves (Crozier, 1991). These techniques have worked to varying degrees. Often they depend on the intensity to which they are applied and the costs associated with an adequate intensity can make them unaffordable.

Of considerable appeal is an approach to contain possum damage through the planting of genotypes which are unpalatable to possums. Variation in susceptibility to possum defoliation has often been observed at the species level and has been observed at the provenance level as well (e.g. in *Pinus contorta* by Shelbourne and Miller [1976]).

*Eucalyptus nitens* is now recognised as having considerable potential as a commercial forest plantation species in New Zealand. However, it is moderately susceptible to possum defoliation, and, especially where possum populations are large and voracious, defoliation and growth loss to *E. nitens* trees can be heavy. If possible, it would be useful to have resistant *E. nitens* seed which could be deployed to planting situations with a high risk of possum attack. This current study has the objective of studying the genetic variation in possum defoliation between and among families of *Eucalyptus nitens* as a basis for determining how best to breed for unpalatability.

## METHODS

A progeny trial of central Victorian *E. nitens* which had recently been ravaged by a number of possums was selected for the purposes of this study. This trial, which includes 79 families represented mainly by 24 progeny each\*, was established as a sets in replication design single-tree-plot test in November, 1990.

---

\* Note due to a lack of stock at planting time, some families are represented by a smaller number of progeny.

The families were divided into two nearly equally-sized sets to keep the number of trees per rep set reasonably small. In total the experiment has 24 replications of each set, and, overall, was rectangular in shape. Table 2 lists the source of each family represented in each set.

After 17 months, grassy weeds had become quite abundant and the herbicide Gardoprim was applied in one-metre wide strips that ran in the direction of the columns of this experiment. This application, for reasons unknown, produced quite variable responses; some columns were totally free of weeds, others were essentially unaffected by the herbicide, while still other columns had intermediate weed kill.

At about 17 months it was noticed that there was some possum defoliation at the top of experiment which is close to a 50-metre-wide strip of manoa scrub which separates the experiment from an extensive area of native scrub and forest. Measures were taken to control these possums, and, although several were killed, this was not sufficient to reduce the population adequately. In the ensuing hard winter which followed possums caused variable but often severe defoliation. At 22 months of age, (Oct. 1992) the trial was visited and defoliation was assessed. At that time it was noticed that defoliation was generally greatest towards one corner of the experiment and in columns where weed control had been most effective. However, there were also large differences in defoliation of individual trees which could not be accounted for by these patterns.

Defoliation of each tree in the test by possums was assessed with scores of 0, 1, 2, 3, 4 or 5 which correspond to 0%, 20%, 40%, 60%, 80% and 100% defoliation respectively. The level of weed control was also recorded at each plot with scores of 1, 2 and 3 representing no weed control, intermediate weed control and total weed control, respectively. These data were read into a computer. Then first order regressions were run using SAS regression procedures (PROC REG) to determine the relationship between the intensity of possum defoliation ( $Def_o$ ) and the level of Weed Control ( $W$ ).

$$Def_o = b_o + b_1 (W)$$

Similar regression procedures were used to determine the relationship between the intensity of possum defoliation ( $Def_o$ ) and the proximity of the tree in the experiment relative to the most heavily attacked rows ( $R$ ) and columns ( $C$ ) of the experiment (i.e. those in the upper right corner of the experiment):

$$\text{Def}_O = b_0 + b_1 (R)$$

$$\text{Def}_O = b_0 + b_1 (C)$$

(There was no evidence to suggest that either row or column position had any influence on the effectiveness of the weed control).

The  $b_1$  coefficients of these regression equations were then used to transform the original data using the equation.

$$\text{Def}_T = \text{Def}_O - b_W W - b_R R - b_C C$$

where:

$\text{Def}_T$	=	The transformed value for defoliation
$\text{Def}_O$	=	The defoliation level measured on individual trees in the experiment
$W$	=	The effectiveness of weed control as assessed for each tree
$R$	=	The row number of a trees position (beginning from the top)
$C$	=	The column number of a trees position (beginning from the right)
$b_W$	=	The $b_1$ coefficient in the equation $\text{Def}_O = b_0 + b_1 W$
$b_R$	=	The $b_1$ coefficient in the equation $\text{Def}_O = b_0 + b_1 R$
$b_C$	=	The $b_1$ coefficient in the equation $\text{Def}_O = b_0 + b_1 C$

These transformed defoliation scores of each set were then subjected to an analysis of variance to document the family differences in possum defoliation and to determine the significance of this variation using the GLM procedure of SAS. These data were also subjected to a Student-Newman-Keuls test (SAS) for family means. Finally, variance components were estimated using the VAR COMP procedure of SAS. These were used to calculate the narrow sense heritability ( $h^2$ ) for possum defoliation, the interclass correlation coefficient ( $t$ ), and the heritability of family means ( $h_F^2$ ). This genetic information for each set was then used to determine the amount of reduced possum defoliation which could be expected using family selection and combined selection techniques. Reasons and formula for calculating each of these parameters are developed in Federer (1989) and are summarised in Appendix I of this report.

## RESULTS

The results of the analyses of variance of each set (Table 1) indicate that there are statistically significant differences between families for possum defoliation. However, when these families were subjected to the Student-Newman-Keuls test (Table 2) it can be seen that it is only the most and least susceptible families which have statistically significant differences in susceptibility.

A summary of the genetic properties of the populations of the *E. nitens* families represented in the two sets is given in Table 3. The full mathematical determination of each of these properties is given in Appendix I.

**TABLE 3: A summary of genetic properties associated with possum defoliation of *Eucalyptus nitens* families in the two sets of the Poronui progeny test. The calculations of these properties are given in Appendix II**

Parameter	Set 1	Set 2
t	0.076	0.095
$h^2$	0.30	0.38
$h_f^2$	0.735	0.806
$R_{f_5}$	0.207*	0.227*
$R_{f_{20}}$	0.534*	0.583*
$R_{c_{100}}$	1.72*	1.25*
$R_{c_{200}}$	1.87*	1.37*

- where:
- t = The interclass correlation coefficient.
  - $h^2$  = The heritability of individual values.
  - $h_f^2$  = The heritability of family means.
  - $R_{f_5}$  = The expected mean response (predicted gains) when the best family out of 5 was chosen.
  - $R_{f_{20}}$  = The expected mean response when the best family out of 20 was chosen.
  - $R_{c_{100}}$  = The expected mean response when combined selection is used to identify the best individual tree in the better families choosing one tree out of 100.
  - $R_{c_{200}}$  = The expected mean response when combined selection is used to identify the best individual tree in the better families choosing one tree out of 200.

\* A unit of 1.0 corresponds to a difference of 20% in defoliation.

**TABLE 1a: Analysis of variance and variance component estimates  
for *Eucalyptus nitens* families in Set 1**

**General Linear Model Procedure (SAS)**

Dependent Variable: POSSUM					
Source	DF	Sum of squares	Mean square	F Value	Pr > F
Model	56	184.30770863	3.29120908	2.49	0.0001
Error	674	889.71489893	1.32005178		
Corrected Total	730	1074.02260757			
R-Square		C.V.	Root MSE	Possum mean	
0.171605		521.9054	1.1489351	0.2201424	
Source	DF	Type I SS	Mean square	F Value	PR > F
REP	23	64.19987321	2.79129884	2.11	0.0018
FAMILY	33	120.10783543	3.63963138	2.76	0.0001
Source	DF	Type III SS	Mean square	F Value	Pr > F
REP	23	65.81239485	2.86140847	2.17	0.0013
FAMILY	33	120.10783543	3.63963138	2.76	0.0001
VARCOMP Procedure (SAS)					
Variance Component	Estimate				
Var (REP)	0.04802167				
Var (FAMILY)	0.10826892				
Var (Error)	1.32005178				



**TABLE 1b: Analysis of variance and variance component estimates for *Eucalyptus nitens* families in Set 2**

**General Linear Model Procedure (SAS)**

Dependent Variable: POSSUM					
Source	DF	Sum of squares	Mean square	F Value	Pr > F
Model	63	203.07094323	3.22334831	2.91	0.0001
Error	621	687.31141818	1.10678167		
Corrected Total	684	890.38236141			
R-Square		C.V.	Root MSE	Possum mean	
0.228072		307.1813	1.0520369	0.3424807	
Source	DF	Type I SS	Mean square	F Value	PR > F
REP	22	80.57271149	3.66239598	3.31	0.0001
FAMILY	41	122.49823174	2.98776175	2.70	0.0001
Source	DF	Type III SS	Mean square	F Value	Pr > F
REP	22	77.24514616	3.51114301	3.17	0.0001
FAMILY	41	122.49823174	2.98776175	2.70	0.0001
VARCOMP Procedure (SAS)					
Variance Component		Estimate			
Var (REP)		0.08496569			
Var (FAMILY)		0.11652005			
Var (Error)		1.10678167			

TABLE 2a: Origin and mean defoliation of each *Eucalyptus nitens* family in Set 1 and results of the Student-Newman-Keuls test. (Note: M, T and R designate MacAlister, Toorongo and Rubicon provenances, respectively; all of these provenances are in central Victoria, Australia)

Means with the same letter are not significantly different

SNK Grouping	Mean*	N†	Family Code
A	1.1494	22	880 Connors Plain M
B A	0.9115	23	617 Mt Toorongo T
B A C	0.8511	21	664 Loch Valley T
B A C	0.8272	24	649 Connors Plain M
B A C	0.8136	23	615 Mt St Gwinear T
B A C	0.5832	23	685 Rubicon R
B A C	0.5570	12	852 Mt St Gwinear T
B A C	0.5333	12	899 Powellton T
B A C	0.4987	24	669 MMBW
B A C	0.4592	18	627 MacAlister M
B A C	0.4082	24	623 Link Rd T
B A C	0.3827	24	731 Rubicon R
B A C	0.3431	23	659 Mt Toorongo T
B A C	0.3406	24	646 Tweed Spur R
B A C	0.3081	11	104 Mt St Gwinear T
B A C	0.2532	12	56 Mississippi T
B A C	0.1604	23	648 Rubicon R
B A C	0.1221	24	723 Rubicon R
B A C	0.1109	24	854 Mt Erica T
B A C	0.0963	23	637 Mt Toorongo T
B A C	0.0852	23	719 Rubicon R
B A C	0.0714	22	651 Connors Plain M
B A C	0.0579	21	636 Mt Toorongo T
B A C	0.0535	23	652 MacAlister M
B A C	0.0317	24	666 Loch Valley T
B A C	0.0273	22	881 Toorongo Plateau T
B A C	-0.0305	22	671 Little Boys Creek T
B A C	-0.0855	23	718 Rubicon R
B A C	-0.1801	21	720 Rubicon R
B C	-0.2111	23	722 Rubicon R
B C	-0.2984	22	634 Toorongo T
B C	-0.4124	24	625 Toorongo T
B C	-0.4316	24	619 Mt Erica T
B C	-0.4668	23	658 Mt St Gwinear T

\* Mean defoliation score after transformation, a unit of 1.0 corresponds to a difference of 20% in defoliation.

† The number of progeny in the test for the indicated family.

TABLE 2b: Origin and mean defoliation of each *Eucalyptus nitens* family in Set 2 and results of the Student-Newman-Keuls test. (Note: M, T, R, sNSW and nNSW designate MacAlister, Toorongo, Rubicon, southern New South Wales and northern New South Wales, respectively; the first three of these are from central Victoria)

Means with the same letter are not significantly different

SNK Grouping			Mean*	N†	Family Code	
	A		1.5378	7	919	Nitens Rd sNSW
B	A		1.4384	11	15	Nimmitabel sNSW
B	A		1.0961	24	901	Royston Dam R
B	A	C	1.0437	6	909	Majors Pt. nNSW
B	A	C	0.9426	22	955	Tweed Spur R
B	A	C	0.8377	11	949	Spring Hill M
B	A	C	0.7933	19	939	Tweed Spur R
B	A	C	0.7854	16	904	Majors Pt. nNSW
B	A	C	0.7537	21	628	Toorongo T
B	A	C	0.7354	20	952	Tweed Spur R
B	A	C	0.6950	21	941	Connors Plain M
B	A	C	0.6392	18	897	Mt Erica T
B	A	C	0.5319	11	19	Nimmitabel sNSW
B	A	C	0.5235	7	957	Mt Torbreck R
B	A	C	0.5119	21	831	Rubicon R
B	A	C	0.5073	16	916	Tallaganda sNSW
B	A	C	0.4643	23	826	Federation R
B	A	C	0.4050	17	903	Tweed Spur R
B	A	C	0.4024	21	813	Cathedral R
B	A	C	0.3240	6	716	MacAlister M
B	A	C	0.3197	15	931	MacAlister M
B	A	C	0.2616	21	937	MacAlister M
B	A	C	0.2525	16	642	MacAlister M
B	A	C	0.2316	11	948	Spring Hill M
B	A	C	0.2181	21	891	Mt Erica T
B	A	C	0.1563	18	877	Mt Horsfall T
B	A	C	0.1392	22	868	Mississippi T
B	A	C	0.0753	12	912	Quartz Link R
B	A	C	0.0696	11	958	Mt St Gwinear T
B	A	C	0.0496	23	834	Connors Plain M
B	A	C	0.0438	22	732	Rubicon R
B	A	C	0.0438	23	889	Mt Horsfall T
B	A	C	0.0190	6	932	Little Boys Creek T
B	A	C	0.0170	15	943	Bamawall Plains R
B		C	-0.0325	21	946	Serpentine Ck M
B		C	-0.0387	10	920	Mt Shillinglaw M
B		C	-0.0514	23	928	Snobs Creek R
B		C	-0.1935	15	712	Mt Erica T
B		C	-0.3066	23	929	Mt Shillinglaw M
B		C	-0.4050	20	964	Mt Torbreck R
B		C	-0.4792	7	714	Mt Erica T

\* Mean defoliation score after transformation, a unit of 1.0 corresponds to a difference of 20% in defoliation.

† The number of progeny in the test for the indicated family.

## DISCUSSION

The results of this study indicate that if the best family in 20 was selected for each set, the reductions in defoliation would only be 10.7% and 11.7% for sets 1 and 2, respectively. However, very sizeable reductions in the amount of defoliation by possums could be obtained by combined selection (choosing the least affected individual trees in the least affected families) for families in both sets of this *Eucalyptus nitens* experiment. At a selection intensity of one tree in 200, the amount of foliage removed by possums would be 37% less from selections made in set 1 and 27.4% less from selections made in set 2.

Therefore, it could be concluded that breeding for possum damage using combined selection could greatly reduce the level of possum defoliation. However, there are several practical aspects which are worth considering. The trees in this particular experiment were, overall, seriously affected by possums, but in most other parts of New Zealand, possum defoliation would be expected to be much less and, on average, would affect growth rate and form to only a minor degree. Therefore, at present, possum resistance in *E. nitens* would not appear to be a trait that would need to be incorporated into the main breeding programme and seed orchards of *Eucalyptus nitens* which will be serving the majority of the country. In this light, a simple and appropriate approach might be just to select the most outstanding individual from each of the 4 best families (fastest growth, no record of serious frost damage and least affected by possums) in this Poronui test, clone each of these individuals approximately eight times apiece, and plant them at random in one corner of *E. nitens* seed orchard so that seed collected from these clones could be segregated and used as a "possum-resistant" lot.

Of course, this situation with respect to possums could change. Recent indications are that possum populations are increasing very fast in several parts of the country. If this trend continues then a larger area of "possum-resistant" *E. nitens* in the clonal orchard may be required. In a worst case scenario (where possums maintain their currently high rates of population increase for as long as a decade) it might be necessary to actually select for possum resistance in the breeding population and to select more clones for possum resistance from a larger number of individuals and families. It is unlikely that this will happen, but if it does, this study indicates that there is a good prospect for gains from selection for resistance to possum defoliation using a combined selection breeding approach.

In this test, families *E. nitens* from New South Wales suffered 28% more defoliation than families from central Victoria. In an adjacent planting at Poronui of largely New South Wales sources of *E. nitens* but with deliberate intermittent planting of central Victorian sources the same trend was noticed (average defoliation scores were 10% less in the central Victoria *E. nitens*). This information suggests that if these two sources were assessed as having equal growth potential for a given site, and if there is high risk of possum damage, then central Victorian sources should be planted.

One thing that should be recognised is that the planting of possum-resistant *E. nitens* genotypes rather than the average *E. nitens* genotype (e.g. the most resistant genotypes in set 1 had 37% less defoliation than the average tree in set 1) does not ensure that the amount of damage will be less by as much as it was in this test. Failing the presence of their preferred genotypes, hungry possums may be able to settle for second best.

Finally, since the level of resistance attainable is only partial, and not complete, the use of possum resistant *E. nitens* genotypes should be viewed as only one arm in an integrated possum management scheme; shooting, baiting, trapping, chemical deterrents and other possum management techniques will continue to play an important role in minimising of defoliation by these animals. There may also be future discoveries, like the finding in this study, that possums feed more on trees where herbicide treatment had killed the surrounding grass (presumably because in approaching such trees do not get their bellies wet) which will also help in designing a better control of these animals. It is not known what might be the best overall strategy for combating possums, but the analysis of this serendipitous attack on a *Eucalyptus nitens* progeny test at Poronui station indicates that there is a substantial amount of heritable genetic variation in possum defoliation that can (if need be) be drawn on to help in the reduction of possum defoliation of this species.

## REFERENCES

- Crozier, E.R. 1991. Practical animal repellents for tree seedlings: a success story. In: Menzies, M.I., Parrot, G.E. and Whitehouse, L.J. Efficiency of Stand Establishment Operations. FRI Bulletin 151, pp. 173-177.
- Federer, D.S. 1989. Introduction to Quantitative Genetics. Longman Scientific and Technical. 438 pp.
- Peters, J.A. (1974). Chemical control of vertebrate pests – a perspective. NZJF 19 (1), pp. 233-245.
- Shelbourne, C.J.A. and Miller, J.T. 1976. Provenance variation in *Pinus contorta* – 6 year results from IUFRO seedlots in New Zealand. Proc. XVI World Congress. Div. II, pp. 140-145.
- Warburton, B. 1981. Possum traps – an assessment, FRI What's New No. 101.



## APPENDIX I

## Calculations used for the construction of Table 1\*

The variance components estimates for sets 1 and 2 are as follows:

	Set 1	Set 2
Var (Rep)	0.04%	0.085
Var (Family)	0.108	0.1165
Var (Error)	1.320	1.1068

From this, the interclass correlation coefficients (t) can be calculated by the formula:

$$t = \frac{\sigma_F}{\sigma_F + \sigma_W}$$

so:

$$t_1 = \frac{0.108}{0.108 + 1.320}$$

$$= 0.076$$

$$t_2 = \frac{0.1165}{0.1165 + 1.1068}$$

$$= 0.095$$

Also, the heritability of individual values ( $h^2$ ) is determined by the formula  $h^2 = t/r$ .

The values for t are given above, and  $r = \frac{1}{4}$  for open pollinated populations, therefore:

$$h_1^2 = 0.30$$

$$h_2^2 = 0.38$$

The heritability of family means is given by the formula:

$$h_f^2 = \frac{1 + (n-1) r}{1 + (n-1) t} h^2$$

\* The formula used in these calculations come from Federer, 1989.

Assuming that n is 24, which is not exactly correct because not all families were represented in each replication, these heritabilities are:

$$\begin{aligned}
 h_{f1}^2 &= \frac{1 + (23) \frac{1}{4}}{1 + (23) (0.076)} h^2 = \frac{6.75}{2.75} \cdot 0.30 & h_{f2}^2 &= \frac{1 + (23) \frac{1}{4}}{1 + (23) (0.095)} h^2 = \frac{6.75}{3.18} \cdot 0.38 \\
 &= 2.45 \cdot 0.30 & &= 2.12 \times 0.38 \\
 &= 0.735 & &= 0.806
 \end{aligned}$$

The expected responses to breeding\* under family selection can be calculated by the following formula:

$$R_f = i \sigma_p h^2 \left( \frac{1 + (n-1) r}{\sqrt{[n(1 + (n-1) t)]}} \right)$$

Here we will calculate at two levels of intensity, one family in 5 which gives an i value of 0.7 and one family in 20 which gives an i value of 1.8.

$$\begin{aligned}
 R_{f_{15}} &= i \sqrt{.108 + 1.322} h^2 \left( \frac{1 + 23 (0.25)}{\sqrt{1 + 23 (0.076)}} \right) & R_{f_{25}} &= i \sqrt{.108 + 1.322} h^2 \left( \frac{1 + 23 (0.25)}{\sqrt{1 + 23 (0.076)}} \right) \\
 &= 0.7 (1.19) 0.3 \left( \frac{6.75}{8.12} \right) & &= 0.7 (1.106) .38 \left( \frac{6.75}{8.74} \right) \\
 &= 0.207 & &= 0.2272 \\
 R_{f_{120}} &= 0.534 & R_{f_{220}} &= 0.583
 \end{aligned}$$

And the expected responses to breeding under combined selection can be determined by the formula:

$$R_c = i \sigma_p h^2 \sqrt{1 + \frac{(r-t)^2}{(1-t)} \times \frac{n-1}{1 + (n-1) t}}$$

Here considerably greater numbers of individuals can be screened for selection, therefore the intensity of selection might be one individual in 100 or one individual in 200 which correspond to i values of 2.5 and 2.75 respectively.

So:

$$\begin{aligned}
 R_{c1_{100}} &= 2.5 (1.19) 0.3 \sqrt{1 + \frac{(0.25 - 0.076)^2}{(1 - 0.076)} \times \frac{23}{1 + 23 (0.076)}} \\
 &= 2.5 (1.19) 0.3 \sqrt{1 + \frac{.030}{.924} \times \frac{23}{2.748}} \\
 &= 2.5 (1.19) 0.3 (1.93) \\
 &= 2.5 (0.68) \\
 &= 1.72
 \end{aligned}$$

and  $R_{c1_{200}} = 1.87$

$$\begin{aligned}
 \text{and } R_{c2_{100}} &= 2.5 (1.106) 0.38 \sqrt{1 + \frac{(0.25 - .095)^2}{(1 - .095)} \times \frac{23}{1 + 23 (.095)}} \\
 &= 2.5 (1.106) 0.38 \sqrt{1 + \frac{0.024}{0.905} \times \frac{23}{3.185}} \\
 &= 2.5 (1.106) 0.38 (1.19) \\
 &= 1.25
 \end{aligned}$$

and  $R_{c2_{200}} = 1.375$

\* It will be noted that a response of 1.0 corresponds to a difference in defoliation of 20%.