

**Detection And Genetic Mapping Of Quantitative Trait Loci Influencing Stem  
Growth Efficiency In Radiata Pine**

**Livinus Chinenye Emebiri**

Department of Forestry  
Australian National University

A thesis submitted for the degree of Doctor of  
Philosophy of The Australian National University

January 1997

## Declaration

The work presented in this thesis is my own. Assistance and specific contributions by others are referred to in the text and acknowledgments.

L. C. Emebiri

January 1997

Department of Forestry

School of Resource and Environmental Management

Faculty of Science

The Australian National University

The following papers are based on this dissertation:

Emebiri, L. C., Devey, M. E., Matheson, A. C. and Slee, M. U. (1997) Linkage of RAPD markers to NESTUR, a stem growth index in radiata pine seedlings. *Theoretical & Applied Genetics* (in press).

Emebiri, L. C.; Devey, M. E.; Matheson, A. C. and Slee, M. U. (1995) On genetically remodelling radiata pine: identification of QTLs influencing NESTUR by use of bulked segregant analysis. Paper presented at the Conifer Biotechnology Working Group 7th International Conference, 26-30 June 1995, Surfers Paradise, Queensland, Australia.

Emebiri, L. C.; Devey, M. E.; Matheson, A. C. and Slee, M. U. (1995) Detection and mapping of QTLs influencing NESTUR in radiata pine. Paper presented at the sixth Australasian Gene Mapping Workshop & New Zealand Genetical Society Conference, Nov. 27-1 Dec., 1995, University of Otago, Dunedin, New Zealand.

Emebiri, L. C.; Devey, M. E.; Matheson, A. C. and Slee, M. U. (1996). Interval mapping of NESTUR, a stem growth efficiency index in radiata pine. Poster presentation submitted for the Scientific Regional Information Exchange Group (SRIEG) Conference, Texas A & M University, Houston, Texas, June 23-26. Abstract available at <http://mslisma.tamu.edu/staff/tom/SRIEG/srieghome.html> (manuscript in preparation).

Emebiri, L. C.; Devey, M. E.; Matheson, A. C. and Slee, M. U. (1997). Age related changes in the expression of QTL for growth in radiata pine seedlings. Submitted to *Theoretical & Applied Genetics*.

Emebiri, L. C.; Devey, M. E.; Matheson, A. C. and Slee, M. U. (1997). Interval mapping of quantitative trait loci affecting NESTUR, a stem growth efficiency index of radiata pine seedlings. Submitted to *Theoretical & Applied Genetics*.

## **Acknowledgments**

I thank my supervisory panel of Dr. M. U. Slee, Dr. M. E. Devey, and Dr. A. C. Matheson for their advice and encouragement throughout the course of my studies.

Special thanks to Dan Gardener for technical assistance with the dendrometer, and to Dane Donaldson, Nathan Caesar and Josie Morosin for assistance during NESTUR measurements. I thank David Spencer for assistance with design of field layout, planting and maintenance of the progeny evaluation.

I am especially grateful to Ms Judy Faccioni for invaluable assistance and support throughout this study. Special thanks also to Prof. Peter Kanowski for his advice and encouragement.

This study was funded by an ANU PhD scholarship from the Australian National University, Canberra, and an OPRS scholarship from the Department of Employment, Education & Training (DEET), Australia. Financial and institutional support were also provided by the Southern Tree Breeding Association (STBA), Australia, the CSIRO Forestry & Forest Products, Canberra, and by the Department of Forestry, The Australian National University, Canberra.

## Abstract

Needle-to-stem unit rate (NESTUR) is a stem growth index of conifer seedling trees that measures the efficiency of stemwood production per unit of needle growth. Five experiments were carried out in this thesis using progenies of two unrelated full-sib radiata pine crosses. The initial experiment (experiment 1) applied the bulked segregant analysis technique to determine whether RAPD analysis could be successfully extended to the development of molecular markers for NESTUR in radiata pine. The NESTUR values of 174 progenies of the full-sib family 12038 x 10946 were determined. Based on the genotypic analysis of the individuals, two quantitative trait loci (QTL) controlling NESTUR were identified at ANOVA P-levels of 0.01-0.001. An absence of RAPD fragment markers generated by primers OPE-06 and OPA-10 was associated with low NESTUR values, while primer UBC-333 generated a 550 bp band that was associated with high NESTUR values. Linkage to components of NESTUR (increments in stem diameter and stem volume) was demonstrated for one of the QTL, while the other was unique to NESTUR, and not shared with the components. There was a significant interaction between the two QTLs. Presence of OPA-10<sub>1200</sub> locus appeared to inhibit expression of the QTL linked to UBC-333<sub>550</sub>.

To further analyse the quantitative trait loci (QTLs) controlling NESTUR, a linkage map was constructed from RAPD markers segregating in 93 haploid progeny of another full sib cross (30040 x 80121) (experiment 2). Two hundred and sixty-two (262) markers were mapped to 14 linkage groups of at least 7 markers, ranging in size from 39 to 183 cM. The 14 linkage groups covered approximately 1511 cM of genetic map distance.

In experiment 3, the linkage map was used to map QTLs controlling NESTUR, as well as increments in seedling stem diameter, volume, and height and needle volume. Altogether, five putative QTLs were detected for NESTUR, with explained variation ranging from 9 to 22%. Of the five QTLs detected, 3 were coincidental with those for stem growth in height, diameter and volume. The two QTL positions that were unique to NESTUR were flanked by QTLs for the component traits. Together, effects of the five QTLs explained 48% of the total phenotypic variation for NESTUR.

Ability of identified markers to predict the phenotype and seedlings with growth potential was assessed in the cross 30040 x 80121, using six RAPD markers associated with NESTUR at ANOVA P-levels of 0.01-0.001 (experiment 4). The correlation between observed NESTUR and predicted values was 0.70. Differences in observed vs. predicted values were not large and did not indicate serious misclassifications, such as classification of an upper ranking individual into the lower group, or vice versa.

Over a two-year growth period, the ability of NESTUR to predict stem growth was strongly affected by seedling age. In contrast, markers linked to NESTUR showed a consistent ability to predict stem growth, irrespective of seedling age. Compared with the top 1% of the original population, seedlings selected for their genotypic values showed a higher stem volume growth of 103% in the first year, and 76% in the second year.

The expression of QTLs for stem volume, stem diameter, height, number of branches, number of whorls, and branches/whorl were compared at 5, 12, and 24 months of age. Two QTLs detected for height showed contrasting expression over two years, one was gradually reduced from LOD of 2.70 to 0.43 and the other

increased from 1.12 to 2.45. Compared with the pattern observed for height, LOD scan profiles for diameter and volume showed less temporal change of peaks, suggesting that the genetic control for height growth is probably more unstable than that of diameter. QTLs controlling the phenotype at the time of measurement (ie the final phenotype) showed similar magnitude of effects on that trait's respective increments (or growth rate).

## **TABLE OF CONTENTS**

<b>CHAPTER 1</b>	<b>1</b>
<b>1 INTRODUCTION</b>	<b>1</b>
1.1 LIMITED PROGRESS IN BASIC TREE BREEDING	1
1.2 AGE-AGE CORRELATION AND EARLY SELECTION	2
1.3 NEEDLE-TO-STEM UNIT RATIO (NESTUR)	3
1.4 MOLECULAR MARKER-ASSISTED SELECTION	4
1.5 QUANTITATIVE TRAIT LOCUS (QTL) ANALYSIS	6
1.6 THE AIM OF THE PRESENT STUDY	7
1.6.1 <i>Primary objectives</i>	7
1.6.2 <i>Secondary objectives</i>	7
<b>2 TYPES OF GENETIC MARKERS</b>	<b>8</b>
2.1 MORPHOLOGICAL MARKERS	8
2.2 MOLECULAR MARKERS	9
2.2.1 <i>RFLP markers</i>	10
2.2.2 <i>AFLP</i>	10
2.2.3 <i>SSR or Microsatellites</i>	11
2.2.4 <i>RAPDs</i>	11
2.3 APPROACHES TO QTL ANALYSIS IN FOREST AND TREE CROP SPECIES	18
2.3.1 <i>Bulked segregant analysis</i>	19
2.3.2 <i>Genomic mapping</i>	19
2.3.3 <i>Available mapping populations</i>	20
2.4 MARKER ANALYSIS OF QUANTITATIVE TRAITS	22
2.4.1 <i>Magnitude of QTL effects</i>	25
2.4.2 <i>QTL clustering and pleiotropic effects</i>	26
2.4.3 <i>Epistasis</i>	27
2.5 MARKER-ASSISTED SELECTION (MAS)	28
2.5.1 <i>QTL repeatability between populations.</i>	30
<b>CHAPTER 3</b>	<b>33</b>
<b>3 STRUCTURE OF THE THESIS</b>	<b>33</b>
<b>4 CHAPTER 4</b>	<b>36</b>
<b>EXPERIMENT 1: DETECTION OF RAPD MARKERS LINKED TO NESTUR BY USE OF BULKED SEGREGANT ANALYSIS</b>	<b>36</b>
4.1 INTRODUCTION	36
4.2 MATERIALS AND METHODS	36
4.2.1 <i>Plant material</i>	36
4.2.2 <i>DNA extraction and RAPD assays</i>	41
4.2.3 <i>Electrophoresis and gel documentation</i>	42
4.2.4 <i>DNA pooling and RAPD assay</i>	42
4.2.5 <i>Relationship of NESTUR with stem growth variables</i>	44
4.3 RESULTS	45
4.3.1 <i>Frequency Distribution of NESTUR values</i>	45



4.3.2 <i>Identification and genetics of marker-linked QTLs</i> -----	45
4.3.3 <i>QTL coincidence and pleiotropy</i> -----	49
4.3.4 <i>Epistatic interactions</i> -----	50
4.4 DISCUSSION-----	52
4.4.1 <i>General considerations</i> -----	52
4.4.2 <i>Limitations of bulked segregant analysis</i> -----	53
4.4.3 <i>QTL validation</i> -----	55
<b>5 CHAPTER 5</b> -----	<b>57</b>
<b>EXPERIMENT 2: CONSTRUCTION OF A RAPD-BASED GENETIC LINKAGE MAP</b> -----	<b>57</b>
5.1 INTRODUCTION -----	57
5.2 MATERIALS AND METHODS -----	58
5.2.1 <i>Plant materials</i> -----	58
5.2.2 <i>Primer screening</i> -----	58
5.2.3 <i>Nomenclature of RAPDs</i> -----	59
5.2.4 <i>Linkage analysis and error detection</i> -----	59
5.2.5 <i>Genome length estimation and marker coverage</i> -----	62
5.3 RESULTS-----	62
5.3.1 <i>Primer screening and marker scoring on mapping population</i> -----	62
5.3.2 <i>Inspection of segregation ratio</i> -----	63
5.3.3 <i>Inspection of recombination estimates and LOD scores</i> -----	64
5.3.4 <i>Linkage map construction</i> -----	65
5.3.5 <i>Map goodness-of-fit</i> -----	69
5.3.6 <i>Estimate of genome size</i> -----	71
5.4 DISCUSSION-----	71
5.4.1 <i>Reliability of RAPDs</i> -----	71
5.4.2 <i>Segregation distortion</i> -----	72
5.4.3 <i>Levels of polymorphism</i> -----	73
5.4.4 <i>Co-dominant RAPD markers</i> -----	75
5.4.5 <i>Genome size estimation and map coverage</i> -----	77
5.4.6 <i>Efficiency of mapping function and algorithm</i> -----	78
5.4.7 <i>Genetic mapping of QTLs</i> -----	80
<b>6 CHAPTER 6</b> -----	<b>81</b>
<b>EXPERIMENT 3: INTERVAL MAPPING OF QTL UNDERLYING NESTUR AND ASSOCIATED SEEDLING GROWTH TRAITS IN RADIATA PINE</b> -----	<b>81</b>
6.1 INTRODUCTION -----	81
6.2 MATERIALS AND METHODS -----	82
6.2.1 <i>Plant materials and phenotyping</i> -----	82
6.2.2 <i>Genotyping, linkage map construction, and QTL analysis</i> -----	82
6.2.3 <i>Linkage map re-construction</i> -----	82
6.2.4 <i>QTL detection methods</i> -----	83
6.3 RESULTS-----	86

6.3.1	<i>Frequency of phenotypes</i>	86
6.3.2	<i>Linkage map re-construction</i>	87
6.3.3	<i>QTL detection by single-point analyses</i>	93
6.3.4	<i>QTL detection by interval mapping</i>	95
6.3.5	<i>Epistasis between QTL</i>	100
6.3.6	<i>Trait correlations and pleiotropic effects</i>	100
6.4	DISCUSSION	102
6.4.1	<i>Linkage map calculations</i>	102
6.4.2	<i>Limitations of RAPDs for QTL dissection in out-breeding species</i>	104
6.4.3	<i>Comparison of QTL mapping methods</i>	106
6.4.4	<i>Perspective</i>	107
<b>7</b>	<b>CHAPTER 7</b>	<b>109</b>
	<b>EXPERIMENT 4: MARKER PREDICTION OF NESTUR AND SEEDLINGS WITH SUPERIOR GROWTH POTENTIAL</b>	<b>109</b>
7.1	INTRODUCTION	109
7.2	MATERIALS AND METHODS	111
7.2.1	<i>Plant materials</i>	111
7.2.2	<i>Field planting and trait measurements</i>	111
7.2.3	<i>Regression analyses</i>	112
7.2.4	<i>Comparative analyses</i>	112
7.3	RESULTS	113
7.3.1	<i>Prediction of NESTUR from linked markers</i>	113
7.3.2	<i>Classification accuracy</i>	115
7.3.3	<i>Comparison of NESTUR versus linked markers in predicting seedling growth</i>	116
7.3.4	<i>Growth performance of seedlings with high- and low-NESTUR marker alleles</i>	118
7.4	DISCUSSION	120
7.4.1	<i>Marker prediction of phenotype</i>	120
7.4.2	<i>Marker prediction of seedlings with superior growth potential</i>	122
7.4.3	<i>Potential for marker-assisted selection</i>	126
<b>8</b>	<b>CHAPTER 8</b>	<b>128</b>
	<b>EXPERIMENT 7: MARKER-BASED INFERENCES ON AGE-SPECIFIC QTL EXPRESSION IN SEEDLING GROWTH OF RADIATA PINE</b>	<b>128</b>
8.1	INTRODUCTION	128
8.2	MATERIALS AND METHODS	129
8.2.1	<i>Plant materials</i>	129
8.2.2	<i>Trait measurements</i>	129
8.2.3	<i>QTL mapping by interval method</i>	129
8.3	RESULTS	130
8.3.1	<i>QTL dissection of stem growth</i>	130
8.3.2	<i>Coincidence of stem growth QTLs</i>	134
8.4	DISCUSSION	137
8.4.1	<i>Stability of stem growth QTLs with development stage</i>	137
8.4.2	<i>Similar QTLs control stemwood variables and increments</i>	138

8.4.3 <i>Perspective on marker-assisted selection</i> -----	139
<b>9 CHAPTER 9: GENERAL DISCUSSION</b> -----	<b>140</b>
9.1 STEM GROWTH EFFICIENCY AND EARLY SELECTION -----	140
9.2 USING MARKER-ASSISTED SELECTION TO IMPROVE STEM GROWTH EFFICIENCY	141
9.2.1 <i>Detection of QTLs influencing NESTUR by bulked segregant analysis</i> -----	143
9.2.2 <i>Genomic mapping of NESTUR-linked QTLs</i> -----	144
9.2.3 <i>Marker prediction of stem growth potential</i> -----	146
9.2.4 <i>Stability of QTL expression with development stage</i> -----	148
9.2.5 <i>Potential applications of detected markers in radiata pine improvement</i> -----	149
<b>10 REFERENCES</b> -----	<b>150</b>
<b>11 APPENDIX 4.1</b> -----	<b>170</b>

## **LIST OF TABLES**

TABLE 4.1 SUMMARY OF RAPD LOCI IN LINKAGE WITH FACTORS INFLUENCING NESTUR IN RADIATA PINE FULL-SIB CROSS 12038 X 10946.....	47
TABLE 4.2 SUMMARIES OF (i) SPEARMAN RANK CORRELATIONS OF NESTUR WITH STEM GROWTH TRAITS, AND (ii) ASSOCIATIONS OF NESTUR-LINKED RAPDs WITH STEM GROWTH TRAITS. ....	50
TABLE 4.3 P-VALUES FROM 2-WAY ANALYSES OF DIGENIC EPISTASIS BETWEEN PUTATIVE QTLs, USING MARKERS AS TREATMENTS.....	51
TABLE 5.1 SCORED MARKERS, SEGREGATION DISTORTION AND MAPPABLE POLYMORPHISMS OBSERVED IN THE MAPPING POPULATION OF 30040 X 80121 CROSS.....	63
TABLE 5.2 LINKAGE GROUP, MARKER NUMBER, GENETIC LENGTH AND MEAN INTERVAL BETWEEN MARKERS IN THE RADIATA PINE RAPD-BASED LINKAGE MAP. ....	66
TABLE 6.1 NUMBER OF LINKAGE GROUPS AND GENETIC LENGTH OF LINKAGE MAPS CONSTRUCTED FROM MARKERS WITH UNKNOWN PHASE AND INFERRED. ....	89
TABLE 6.2 LINKAGE GROUP, MARKER LOCI, AND SINGLE-LOCUS EFFECTS OF RAPD MARKERS SIGNIFICANTLY ASSOCIATED WITH NESTUR AND STEM GROWTH TRAITS. ....	94
TABLE 6.3 BIOMETRICAL PARAMETERS OF DETECTED QTL AFFECTING NESTUR, SVOL GROWTH, HT GROWTH AND NVOL GROWTH IN THE RADIATA PINE FAMILY 3040 X 80121.....	97
TABLE 6.4 PHENOTYPIC CORRELATION COEFFICIENTS FOR NESTUR AND ASSOCIATED SEEDLING GROWTH TRAIT. ....	101
TABLE 6.5 LOD-SCORE CORRELATIONS FOR NESTUR AND ASSOCIATED SEEDLING GROWTH TRAITS.....	101
TABLE 7.1 COMPARISON OF GROWTH (OVER 2 YEARS) OF SEEDLING TREES WHICH SHARED SIMILAR BANDING PATTERN (PRESENCE/ABSENCE) OF 6 RAPD MARKERS LINKED TO NESTUR IN THE CROSS 30040 X 80121.....	124
TABLE 7.2 COMPARISON OF GROWTH (OVER 2 YEARS) OF THE TOP 1% OF THE PROGENIES (BASED ON NESTUR VALUES) WITH SEEDLING TREES POSSESSING HIGH FREQUENCY OF NESTUR-INCREASING RAPD MARKER ALLELES IN CROSS 30040 X 80121.....	125

TABLE 8.1 BIOMETRICAL PARAMETERS OF DETECTED QTLs AFFECTING  
SEEDLING GROWTH AT 5 MONTHS, 1 YR AND 2 YRS OF AGE IN THE RADIATA  
PINE FAMILY 30040 X 80121..... 132

## **LIST OF FIGURES**

FIGURE 4.1 RADIATA PINE SEEDLING 10 DAYS AFTER GERMINATION, SHOWING THE SEED COAT AND MEGAGAMETOPHYTE TISSUE CLOSE TO THE POINT OF BEING CAST OFF.....	38
FIGURE 4.2 IRRIGATION DRIPPERS USED IN SEEDLING CULTURE.....	38
FIGURE 4.3 MEASUREMENT OF NEEDLE VOLUME BY WATER DISPLACEMENT.....	41
FIGURE 4.4 FREQUENCY DISTRIBUTION OF LOG <sub>10</sub> TRANSFORMED NESTUR VALUES IN 174 INDIVIDUALS OF THE FULL-SIB CROSS OF RADIATA PINE (12038 X 10946).....	46
FIGURE 4.5 ELECTROPHORETIC SEPARATION OF RAPD AMPLIFICATION PRODUCTS USING PRIMERS OPE-06, OPA-10 AND UBC-333. ....	48
FIGURE 4.6 ILLUSTRATION OF EPISTASIS BETWEEN MARKER-LINKED QTL INFLUENCING NESTUR IN CROSS OF RADIATA PINE 12038 X 10946 .....	52
FIGURE 5.1 EXAMPLES OF REPEATABLY AMPLIFIED RAPD BANDS FROM TWO SEPARATE THERMOCYCLERS, THE FTS-960 THERMAL SEQUENCER (CORBETT RESEARCH) AND GENEAMP PCR SYSTEM 9600 (PERKIN ELMER CETUS).....	65
FIGURE 5.2 PLOT OF TWO-POINT RECOMBINATION ESTIMATES AND LOD SCORES OBTAINED FOR 262 MARKERS USING JOINMAP PROGRAM JMREC32.....	65
FIGURE 5.3 A RAPD-BASED GENETIC LINKAGE MAP OF RADIATA PINE, CONSTRUCTED FROM HAPLOID DNA OF 93 MEGAGAMETOPHYTES.....	68
FIGURE 5.4 DISTRIBUTION OF INTERVAL SIZES (IN CENTIMORGANS, CM) BETWEEN ADJACENT MARKERS ON RAPD-BASED RADIATA PINE LINKAGE MAP.....	69
FIGURE 5.5 PLOT OF MEAN OBSERVED VS. CALCULATED MAP DISTANCES FOR THE 14 LINKAGE GROUPS ASSEMBLED USING 262 RAPD MARKERS.....	70
FIGURE 5.6 EXAMPLES OF RAPD BANDS AMPLIFIED FROM THE SAME PRIMER, AND WHICH SHOWED LINKAGE TO THE SAME GROUP.....	74
FIGURE 5.7 EXAMPLES OF RAPD BANDS SHOWING CO-DOMINANT SEGREGATION PATTERNS.....	76

FIGURE 6.1 FREQUENCY DISTRIBUTIONS OF NESTUR AND ASSOCIATED SEEDLING GROWTH TRAITS IN THE FULL-SIB FAMILY 30040 X 80121.....	86
FIGURE 6.2 QUANTITATIVE TRAIT LOCUS (QTL) MAP OF NESTUR AND ASSOCIATED STEM GROWTH VARIABLES IN RADIATA PINE SEEDLINGS .....	92
FIGURE 6.3 SCATTER PLOT OF MARKER ORDER IN LINKAGE MAPS CONSTRUCTED WITH MARKERS OF KNOWN AND INFERRED PHASES .....	93
FIGURE 6.4 LOGARITHM OF ODDS RATION (LOD) PLOT OF SIGNIFICANT GENOMIC REGION IN GROUP 4, SHOWING SCAN PROFILES FOR NESTUR, HEIGHT GROWTH (HT GROWTH), VOLUME GROWTH (SVOL GROWTH), AND DIAMETER GROWTH (SD GROWTH).....	98
FIGURE 6.5 LOGARITHM OF ODDS RATIO (LOD) PLOT OF SIGNIFICANT GENOMIC REGION IN GROUP 3, SHOWING SCAN PROFILES FOR NESTUR, HEIGHT GROWTH (HT GROWTH), AND DIAMETER GROWTH (SD GROWTH).....	99
FIGURE 6.6 LOGARITHM OF ODDS RATIO (LOD) PLOT OF SIGNIFICANT GENOMIC REGION IN GROUP 3, SHOWING SCAN PROFILES FOR STEM DIAMETER GROWTH (SD GROWTH), VOLUME GROWTH (SVOL GROWTH) AND NEEDLE VOLUME GROWTH (NVOL GROWTH).....	103
FIGURE 7.1 PLOT OF OBSERVED AND PREDICTED NESTUR VALUES FROM LINKED RAPD MARKERS USING A MULTIPLE REGRESSION MODEL.....	114
FIGURE 7.2 NORMAL PROBABILITY PLOT OF THE CUMULATIVE DISTRIBUTION OF RESIDUALS FROM PREDICTING NESTUR USING LINKED MARKERS.....	115
FIGURE 7.3 PERCENTILE PLOT OF OBSERVED VS. PREDICTED NESTUR VALUES.....	116
FIGURE 7.4 CORRELATION COEFFICIENT BETWEEN OBSERVED STEM GROWTH OVER TWO YEARS AND PREDICTED VALUES USING NESTUR, NESTUR-LINKED MARKERS, AND A COMBINATION OF NESTUR + LINKED MARKERS.....	117
FIGURE 7.5 MEAN HEIGHT GROWTH OF SEEDLING TREES WITH BANDING PATTERNS FOR RAPD MARKERS ASSOCIATED WITH LOW-AND HIGH-NESTUR, AND THE TOP 1% OF THE PROGENIES (BASED ON NESTUR VALUES).....	121

FIGURE 8.1 MEAN OF LOD SCORES FOR STEM GROWTH TRAITS  
(HEIGHT, DIAMETER AND VOLUME) MEASURED AT VARIOUS GROWTH  
STAGES (TIME FROM GERMINATION) IN RADIATA PINE SEEDLINGS GROWN IN  
GLASSHOUSE AND UNDER FIELD CONDITIONS.....133

FIGURE 8.2 LOGARITHM OF ODDS RATIO (LOD) PLOT OF SIGNIFICANT GENOMIC  
REGION IN GROUP 6, SHOWING SCAN PROFILES FOR STEM DIAMETER,  
STEM VOLUME AND THEIR INCREMENTS OVER THREE SUCCESSIVE PERIODS.....135

FIGURE 8.3 LOGARITHM OF ODDS RATIO (LOD) PLOT OF SIGNIFICANT GENOMIC  
REGION IN GROUP 13, SHOWING SCAN PROFILES FOR HEIGHT, DIAMETER,  
STEM VOLUME AND THEIR INCREMENTS OVER THREE SUCCESSIVE PERIODS.....136