

**REGENERATION ECOLOGY OF
BROADLEAVED TREES IN CALEDONIAN
FOREST**

TANYA OGILVY

**THESIS SUBMITTED FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY**

UNIVERSITY OF EDINBURGH

2004

DECLARATION

I hereby declare that this thesis has been composed by myself and that the work presented herein is my own unless otherwise stated. All sources of information have been acknowledged by means of reference to the authors. This work has not been submitted for any other degree or professional qualification.

T.K. Ogilvy

ABSTRACT

This thesis quantifies aspects of shade tolerance in tree seedlings of species native to the Caledonian pinewood ecosystem of Glen Affric (Highland Region, Inverness-shire). Growth, allocation and morphological responses of 15 species to irradiance under simulated forest canopy light were investigated in a nursery-based shade house experiment. The same responses of four of the 15 species (*Ilex aquifolium*, *Alnus glutinosa*, *Sorbus aucuparia* and *Betula pubescens*) to different developmental stages of *Pinus sylvestris* woodland were investigated in the field. The spatial and temporal growth responses of naturally regenerating *S. aucuparia* seedlings to shade and gap microhabitats were also studied. Data from the shade house experiment enabled further detailed exploration of the relationship between relative growth rates (RGR) and irradiance and potential cross-overs of ranks of growth in high and low light conditions.

The main findings were: i) species displayed typical responses to shade such as decreases in RGR and net assimilation rate (NAR), increases in specific leaf area (SLA) and leaf area ratio (LAR) and reduction in the root:shoot ratio; ii) despite similar responses to shade, species specific differences were clearly reflected in significant species-light interactions or species-stand interactions for all growth variables; iii) variation in RGR in low light could be explained by LAR and variation in high light explained by NAR in the nursery, but this pattern was not so clear in the field; iv) most species maximised growth rates at intermediate light levels rather than in full daylight conditions; v) Ellenberg's original light indicator values underestimate the light demand of some species in the nursery but conform better to responses in the field; vi) natural regenerating *Sorbus aucuparia* seedlings persist under the shade of old-growth *P. sylvestris* canopy up to 14 years; vii) responses of both planted and natural regenerated *S. aucuparia* seedlings reflect intermediate shade tolerant behaviour; viii) there was no clear evidence of an inhibitory effect of the abundance of *Calluna vulgaris* on seedling growth but low levels in shade were associated with a high abundance of *S. aucuparia* seedlings and successful growth and performance of *I. aquifolium* seedlings.

Recommendations for restoration or rehabilitation within the Glen Affric Caledonian pinewood include growing *A. glutinosa*, in the open and old-growth woodland patches. *B. pubescens* and *S. aucuparia* are best planted on the edges of well-drained old growth stands and *I. aquifolium* under more shade (15% PAR) protected from extensive *C. vulgaris* cover, leaf miner and frost.

ACKNOWLEDGEMENTS

I would especially like to thank Colin Legg, for his endless patience, interest and commitment to this project. I am very grateful for all of his advice and enthusiasm, which has been instrumental in the production of this thesis.

I would also like to thank Jonathan Humphrey and his colleagues from Forest Research (Forestry Commission) for their advice and support. I would particularly like to thank Tom Connolly, for his statistical advice and his kind patience in explaining various models of analysis. Forestry Research provided an essential vehicle for fieldwork, as well as many man days of technical support from the team at Newton. The use of the tree nursery at the Northern Research Station provided facilities and space for seedling preparation and the shade house trial.

I fear if I start listing all the Edinburgh University undergraduates that helped on this project over three years of fieldwork, I will accidentally miss someone out which I would not want to do. Without their company and help, the Glen Affric midges and ticks and the months and months of root washing would have been unbearable.

I am grateful to all fellow PhD students and staff at the Institute of Atmospheric and Environmental Science for fruitful conversations and encouragement during the PhD. Meg Pollock was very kind in reading over chapters in the final stages. Finally, I would like to thank Susan Ogilvy and James Edwards for their field assistance in Glen Affric, and especially for their moral support.

ABBREVIATIONS

| | |
|----------------------------------------------|--------------------------------------------------------------------------------------------------------------------|
| RGR ($\text{g g}^{-1}\text{week}^{-1}$) | Relative growth rate per week: the rate of dry mass increase per unit plant dry mass. |
| RHG ($\text{mm mm}^{-1}\text{ week}^{-1}$) | Mean relative height growth rate per week |
| RDG ($\text{mm mm}^{-1}\text{ week}^{-1}$) | Mean relative diameter growth rate per week |
| LMR (g g^{-1}) | Leaf mass ratio: ratio between total leaf dry mass per plant and total dry mass per plant. |
| SMR (g g^{-1}) | Stem mass ratio: ratio between total stem dry mass per plant and total dry mass per plant. |
| RMR (g g^{-1}) | Root mass ratio: ratio between total root dry mass per plant and total dry mass per plant. |
| R:S (g g^{-1}) | Root to shoot ratio: ratio between total root dry mass per plant and total shoot (leaf + stem) dry mass per plant. |
| SLA ($\text{m}^2 \text{g}^{-1}$) | Specific leaf area: ratio between leaf area and leaf mass. |
| LAR ($\text{m}^2 \text{g}^{-1}$) | Leaf area ratio: ratio between total leaf area per plant and total dry mass per plant. |
| NAR ($\text{g m}^{-2}\text{ week}^{-1}$) | Net assimilation rate: rate of dry mass production of a plant expressed per unit of total leaf area. |
| SSL (mm g^{-1}) | Specific stem length: ratio between stem length per plant and total dry stem mass per plant. |
| d:h ratio | Basal diameter : stem height ratio |
| Stem mass (g) | Total stem mass (including petioles and rachis) per plant |
| Root mass (g) | Total root mass per plant |
| Plant mass (g) (W_2) | Total plant mass (leaf, stem and root mass) at final harvest |
| Leaves | Total number of leaves per plant |
| PAR | Photosynthetic Active Radiation |
| PPFD | Photosynthetic Photon Flux Density |
| R:Fr | Red : Far-red ratio |
| CPI | Cross Over Point Irradiance |
| CP% | Percentage of cross-overs between shade and gap irradiances |
| S.E. | Standard error |
| STDEV | Standard deviation |
| CI | Confidence interval |
| LSD | Least significant difference |
| ANOVA | Analysis of variance |
| d.f. | Degrees of freedom |
| P | Probability value |
| F | Variance ratio |

TABLE OF CONTENTS

| | Page no. |
|------------------------------------------------------------------------------------------------------------|-----------------|
| Declaration | ii |
| Abstract | iii |
| Acknowledgements | iv |
| Abbreviations | v |
| 1.0 Introduction to the research | 1 |
| 1.1 Research aims..... | 1 |
| 1.2 The Caledonian Forest..... | 1 |
| 1.2.1 Definition, history & conservation value..... | 1 |
| 1.2.2 Composition and structure..... | 3 |
| 1.2.3 Dynamics..... | 3 |
| 1.2.4 Regeneration..... | 6 |
| 1.2.5. Shade tolerance..... | 7 |
| 1.2.6 Ellenberg light indicator values..... | 11 |
| 1.3 Restoration policy and practices..... | 12 |
| 1.4 Practical implications of the research..... | 14 |
| 1.5 Presentation of the thesis and its objectives..... | 14 |
| 2.0 Description of study sites | 17 |
| 2.1 Introduction..... | 17 |
| 2.2 Glen Affric field site..... | 17 |
| 2.2.1 Climate, geology and soils..... | 17 |
| 2.2.2 Woodland types and vegetation..... | 19 |
| 2.2.3 Native tree species..... | 20 |
| 2.2.4 Woodland history..... | 20 |
| 2.2.5 Land use and management history..... | 21 |
| 2.2.6 Forest management..... | 22 |
| 3.0 Growth, allocation and morphological responses of 15 Scottish woody species to irradiance | 25 |
| 3.1 Introduction..... | 25 |
| 3.2 Methods..... | 28 |
| 3.2.1 Study site and species..... | 28 |
| 3.2.2 Seedling stock..... | 29 |
| 3.2.3 Experimental soils..... | 29 |
| 3.2.4 Experimental design..... | 30 |
| 3.2.5 Light..... | 30 |

| | | |
|------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------|
| 3.2.6 | Temperature and humidity..... | 31 |
| 3.2.7 | Establishment..... | 31 |
| 3.2.8 | Survival & growth measurements..... | 32 |
| 3.2.9 | Harvesting..... | 32 |
| 3.2.10 | Statistics..... | 34 |
| 3.3 | Results..... | 34 |
| 3.3.1 | Micro-climatic conditions in the shade houses..... | 34 |
| 3.3.2 | Plant size (Primary data)..... | 35 |
| 3.3.3 | Relative growth rates, morphology and physiology..... | 38 |
| 3.3.4 | Biomass allocation and partitioning patterns..... | 39 |
| 3.3.5 | Interrelationships between growth variables..... | 44 |
| 3.4 | Discussion..... | 50 |
| 3.5 | Summary..... | 60 |
| 4.0 | Exploration of the relationship between growth rates in woody species and irradiance..... | 61 |
| 4.1 | Introduction..... | 61 |
| 4.2 | Methods..... | 63 |
| 4.2.1 | Statistical analysis..... | 64 |
| 4.3 | Results..... | 65 |
| 4.3.1 | Plots of RGR gap Vs RGR understorey..... | 65 |
| 4.3.2 | Cross-over Point Irradiance Approach..... | 65 |
| 4.3.3 | Relationships between seed mass, shade tolerance and growth..... | 71 |
| 4.4 | Discussion..... | 72 |
| 4.5 | Summary..... | 76 |
| 5.0 | Growth, allocation and morphological responses of four broadleaved species to different developmental stages of <i>Pinus sylvestris</i> woodland...77 | |
| 5.1 | Introduction..... | 77 |
| 5.2 | Methods..... | 80 |
| 5.2.1 | Study site..... | 80 |
| 5.2.2 | Experimental design..... | 80 |
| 5.2.3 | Species and establishment..... | 80 |
| 5.2.4 | Climate data..... | 81 |
| 5.2.5 | Light..... | 81 |
| 5.2.6 | Stand assessment..... | 82 |
| 5.2.7 | Other environmental variables..... | 82 |
| 5.2.8 | Growth, performance and survival measurements..... | 83 |

| | | |
|------------|--------------------------------------------------------------------------------------------------------------------------------|------------|
| 5.2.9 | Harvesting..... | 84 |
| 5.2.10 | Statistical analysis..... | 85 |
| 5.3 | Results..... | 87 |
| 5.3.1 | Climatic data..... | 87 |
| 5.3.2 | Light..... | 88 |
| 5.3.3 | Stand structure and management..... | 88 |
| 5.3.4 | Competition..... | 89 |
| 5.3.5 | Other environmental variables..... | 90 |
| 5.3.6 | Plant size (Primary data)..... | 91 |
| 5.3.7 | Seedling architecture..... | 95 |
| 5.3.8 | Relative growth rate, morphology and physiology..... | 95 |
| 5.3.9 | Biomass allocation and partitioning patterns..... | 97 |
| 5.3.10 | Survival and vigour..... | 98 |
| 5.3.11 | Interrelationships..... | 99 |
| 5.4 | Discussion..... | 104 |
| 5.5 | Summary..... | 113 |
| 6.0 | Spatial and temporal growth patterns of <i>Sorbus aucuparia</i> within old growth <i>Pinus sylvestris</i> woodland..... | 115 |
| 6.1 | Introduction..... | 115 |
| 6.2 | Methods..... | 117 |
| 6.2.1 | Study site..... | 117 |
| 6.2.2 | Experimental design..... | 118 |
| 6.2.3 | Spatial distribution patterns..... | 118 |
| 6.2.4 | Site measurements..... | 119 |
| 6.2.5 | Seedling measurements..... | 120 |
| 6.2.6 | Statistical analysis..... | 120 |
| 6.3 | Results..... | 121 |
| 6.3.1 | Mapping..... | 121 |
| 6.3.2 | Aspect, altitude and slope..... | 125 |
| 6.3.3 | Light..... | 125 |
| 6.3.4 | Understory vegetation..... | 125 |
| 6.3.5 | Seedling abundance..... | 126 |
| 6.3.6 | Seedling size and growth measurements..... | 126 |
| 6.3.7 | Interactions between <i>C. vulgaris</i> and light..... | 127 |
| 6.3.8 | Age of seedlings..... | 128 |
| 6.3.9 | Temporal growth patterns..... | 128 |
| 6.4 | Discussion..... | 132 |

| | | |
|------------|------------------------------------------------------------|------------|
| 6.5 | Summary..... | 136 |
| 7.0 | Discussion..... | 139 |
| | References..... | 159 |
| | Appendix.1: Experimental designs..... | 185 |
| | Appendix 2: Statistics & ANOVA tables..... | 189 |
| | Appendix 3: Hemispherical photography..... | 209 |
| | Appendix 4: Ecological Site Classification..... | 217 |
| | Appendix 5: pH, moisture and aeration of soils..... | 223 |
| | Appendix 6: Data tables..... | 225 |

