Model forest system: even-aged Douglas fir plantation with invasive Rhododendron

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Abstract

This thesis investigated the ecology and dynamics of Douglas fir (Pseudotsuga menziesii var. menziesii) dominated plantations at Coed-y-Brenin, Wales, whose transformation to continuous cover forestry has been delayed due to the presence of non-native invasive rhododendron (Rhododendron ponticum L). The literature review highlighted the complementary evolution of silviculture and modelling concepts to meet societal expectations and advance knowledge and understanding. It highlighted the development of hybrid, individual-based models, facilitated by advances in technology and complex systems theory to address contemporary pressures on forests. Three permanent sample plots of different ages, collectively covering 1.6ha of forest, were resurveyed in 2011, producing a 5-year growth series of mensuration data to parameterise an individual-based spatially-explicit forest growth model, SORTIE-ND. Vegetation, soil and light were surveyed to construct a statistical model of rhododendron seedling establishment and determine Ecological Site Classification. The limiting factors identified by the ecological site classification were a slightly dry Soil Moisture Regime and a poor Soil Nutrient Regime with moderate to high phosphorus and low nitrogen availability. SORTIE-ND was successfully parameterised using a maximum likelihood technique and simulated annealing. Parameterised relationships achieved an excellent level of fit to the data (R2 of 0.785 to 0.971), and the stand simulations produced DBH density plots comparable to observed size distributions. A Bayesian statistical model of rhododendron seedling establishment was produced. The cross-validated model predicted 81.3% of 24 survey stations with rhododendron seedlings, and 75% of 16 stations without seedlings, with an overall accuracy of 77.5%. Seedling establishment probability increased with soil O layer depth and decreased with increasing summed tree height in a 12x12 m neighbourhood. SORTIE-ND was then parameterised, using published literature, for the rhododendron

lifecycle, to highlight knowledge gaps and as the novel first step towards full parameterisation from field data and the creation of decision support systems enabling foresters to interrogate the impact of different harvest regime scenarios on rhododendron invasion vulnerability.

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Chapter 1: Introduction

1.1 Research background

Silvicultural practices change in tandem with social and/or environmental conditions, such as economic demands, modified cultural and philosophical attitudes, and increased scientific understanding (Cotta, 1902, Puettmann et al., 2008). The advent of modern forest practice began with the realisation that resources were finite and that management was a logical progression from the use of the 'commons' (Pretzsch, 2000, Kimmins, 2008). Modern forestry concepts are moving away from the idea of silviculture as analogous to agriculture towards ecosystem management, where a forest ecosystem is managed holistically, for multiple benefits and services aside from timber production (Mason et al., 1999, Puettmann et al., 2008, Bugmann et al., 2010).

Conceptual shifts during the mid-20th Century integrated the interrelationship of ecology and the idea of forests as ecosystems into the silvicultural literature (Kimmins, 2004, Gratzer et al., 2004). A changing silvicultural focus from even-aged monocultures to multi-aged and mixed-species stands began, which sought to include management goals other than sustained growth and yield. Though these ideas were not new (Troup, 1927), interest surged in response to sustainable forest management requirements defined as a consequence of the 1992 United Nations conference on Environment and Development, in Rio de Janeiro (Pommerening & Murphy, 2004, Hahn & Knoke, 2010, Mäkelä et al., 2012).

The last thirty years have seen an unprecedented change in the cost, power, complexity, availability and portability of technological systems (Hilbert & Lopez, 2011). Alongside the changes to silvicultural theory the information demand has moved away from mean stand-level attributes to single-tree dimensions that underlie forest stands (Pretzsch, 2000, Porte & Bartelink, 2002).

The most common models used in forest management today are Yield Tables. First developed in 18th Century Germany (Vanclay, 1994, Pretzsch, 2000, Porte & Bartelink, 2002), they were originally designed as tools to assist with taxation and planning over large areas, and further developed to inform silvicultural management decisions (Pretzsch, 2000, Sonmez et al., 2009). Yield Tables relate site conditions to reference stands, and are indexed by site conditions and mean tree height at a particular stand age (Hasenauer, 2006). These empirically-based historical bioassay models are reliable and believable under constant environmental and managerial conditions, however usage is otherwise limited, and more importantly, in today's climate, they are unable to provide robust predictions under changing circumstances (Kimmins, 2004).

Modern paradigms of forestry, along with the looming pressure of climate shifts and factors such as insect infestation and invasive species, mean that these models are increasingly unable to cope with the demands of modern ecosystem management. Contemporary spatially-explicit individual-based models of forest growth and dynamics are now capable of much more than yield predictions. Modern silviculture favours complex structured, uneven-aged, mixed-species systems, but lacks a historic theoretical background to assist implementation. Models can provide insight into the necessary fine-scale dynamics of forest systems without the long time scales expected of traditional forest trials (Coates, 2000, Coates et al., 2003, Canham et al., 2004, Canham & Uriarte, 2006).

Human-caused global environmental change, whether intentional introduction of species or the consequence of climate change, affects a variety of biogeochemical factors including the chance of biological invasions (Vitousek et al., 1997). Invasive rhododendron *(syn.* Pontian rhododendron, *Rhododendron ponticum* L.), introduced to Great Britain as an ornamental plant during the 18th Century (Erfmeier & Bruelheide, 2010), is now designated as one of eight highest threat invasive species (Edwards, 2009). Ensuring the development of robust management policies and actions requires the prediction and understanding of invasion processes, a task for which computer modelling is ideally suited (Gallien et al., 2010).

Increases in technology have facilitated the use of new methods of data analysis, for example, maximum likelihood estimation (Kobe et al., 1995, Kneeshaw et al., 2006) and Bayesian methods (Ellison, 2004, Van Oijen et al., 2005), that require computationally expensive recursive structures (for instance Monte-Carlo Markov Chains) for fitting. The use of these analysis techniques allowed the development of models, such as SORTIE-ND, that can be directly coupled to field data (Canham & Uriarte, 2006).

SORTIE-ND is an individual based model of forest dynamics that was originally developed in 1996 as SORTIE, and was initially parameterised for use in the northeastern United States transitional oak hardwood forests (Pacala et al., 1996). Later development and application to other research particularly by scientists from the British Columbia Forest Service Research Section (Coates et al., 2003) led to the addition of further sub-models, restructuring and re-programming in C++. Rebranding as SORTIE-ND highlighted the focus on local neighbourhood dynamics. SORTIE-ND is available for use under an open-source license as a pre-compiled user version or as source code for development and modification complete with user and developer documentation. (Canham, 2012).

1.2 Study overview

The initial goal of this study was to parameterise a forest growth model, SORTIE-ND, (Pacala et al., 1996, Kobe et al., 1997) from three Douglas fir (*Pseudotsuga menziesii* var. menziesii) dominated permanent sample plots within Forestry Commission plantations at Coed-y-Brenin, North Wales. The final goal was then the incorporation of invasive *R.*

ponticum into the forest growth model as a first step towards the prediction of establishment probabilities under changing management scenarios.

The main thesis objectives are to:

(1) carry out a literature review that highlights the interrelationship of advances in silvicultural theory and practice, and forest modelling practices and theory (Chapter 2).

(2) investigate the demographic dynamics of Douglas fir and sub-component trees species at three permanent sample plots within Coed-y-Brenin forest park by completion of a five-year growth survey (Chapter 3);

(3) systematically survey the ground flora, a range of abiotic factors (e.g. soils, climate and light) and non-native rhododendron present within the largest permanent sample plot (CyB5) (Chapter 3);

(4) determine the ecological site classification of CyB5 to gain insight into the relationship between site conditions and rhododendron invasion (Chapter 3);

(5) parameterise the spatially-explicit individual-based forest simulator SORTIE-ND (Pacala et al., 1996, Kobe et al., 1997) for the dominant tree species, Douglas fir, for Coed-y-Brenin forest (Chapter 4);

(6) identify and construct a statistical model of rhododendron seedling establishment with data collected from the surveys of the Coed-y-Brenin permanent sample plots (Chapter 3) that are potentially compatible with inclusion in a spatially-explicit individual-based model (e.g. SORTIE-ND) (Chapter 5).

(7) parameterise SORTIE-ND for *R. ponticum,* with data from published sources, to highlight gaps in the understanding of the *R. ponticum* lifecycle and its interaction with other plant species (Chapter 6).

1.3 Layout of the thesis

The literature review presented in chapter 2 highlights the historical linkage between advances in silvicultural theory and practice, and forest modelling. It reviews how traditional forestry techniques, based on the 'Normal forest concept and sustainable yield', were developed in Germany in the 18th Century. The chapter details how this German method spawned the first practical forest models, Yield Tables, and spread throughout the world. The 20th Century saw a technological revolution occur alongside shifting forestry paradigms that involved management of forests as more than crops. Paradigms that required complex models that dealt with individual trees. The chapter concludes with a discussion of complex systems theory in relation to ecosystem modelling, new data streams related to remote sensing, and the next generation of hybrid forest models (Chapter 2).

The fieldwork necessary for completion of the project is detailed in Chapter 3. There were three main objectives to the fieldwork. In order to investigate the demographics of Douglas fir and the sub-component tree species it was necessary to resurvey the permanent sample plots to complete a five-year mensurational growth series and to include the extra data to parameterise the forest growth model. The final objective of the fieldwork was to carry out a systematic soil and vegetation survey throughout the largest PSP (CyB5) to characterise the level of rhododendron invasion and to carry out an ecological site classification survey.

Chapter 4 details the parameterisation of the SORTIE-ND model for the study location. Data collected from the permanent sample plots was used along with parameter values from published literature (Coates 2012). The model was parameterised for the dominant tree species Douglas fir using a maximum likelihood technique and simulated annealing.

Chapter 5 utilises data from the vegetation, mensuration and soil surveys in 2011 and a LiDAR collected as part of a NERC Airborne Research and Survey Facility survey in March 2010. This generated 42 factors used as potential covariates for a Bayesian statistical model of rhododendron seedling establishment probability. The objective of this chapter was to highlight covariates that could be combined with a forest growth model (e.g. SORTIE-ND) to predict rhododendron establishment probabilities under changing management scenarios.

The final chapter (Chapter 6) combines several literature sources featuring characteristics of *R. ponticum* dispersal (Stephenson et al., 2007), establishment (Ninaber, D., 2009), growth (Erfmeier & Bruelheide, 2004) and allometric relationships (Nadezhdina et al., 2004) to formulate an initial step in the parameterisation of SORTIE-ND. This model was then tested in simulations with equal tree densities to the largest permanent sample plots in order to highlight strengths, weaknesses and gaps in the literature and model structure. Further work to improve the parameterisation of SORTIE-ND with field data for *R. ponticum* is then discussed in Chapter 7.

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Chapter 2: The dual evolution of forestry practices and forest modelling

2.1 Introduction

Changing silvicultural practices and management approaches can be viewed alongside concomitant cultural, societal and economic developments. Developments including changes in forest commodity demand, improved scientific understanding and altered spiritual, cultural and philosophical attitudes towards forests have resulted in radical changes in forest practices. Silviculture has changed very little during periods of reasonably constant social and environmental conditions, for example from the 1950s through to the 1970s (Puettmann et al., 2008).

Forestry can be defined as “the art (skill), practice, science and business of managing forested landscapes to sustain a desired balance of values and environmental services from those landscapes” (Kimmins, 2002, p. 264). Kimmins (2002, 2004, 2005) and Pretzsch et al. (2008) describe several stages in the development of forestry within a society that can be used to outline model development (Figure 2.1). In the early stages of human development, *Preforestry*, forests were simply a feature of the landscape and their use was essentially unregulated. Pretszch et al. (2008) terms this early phase as *Multiple use* forestry with typical uses including: animal grazing, hunting, wood-felling and extraction of non-timber forest products. Kimmins (2004, 2005) further breaks this stage in to two distinct methods of exploitation: sustainable and non-sustainable. Sustainable exploitation continues while human population and technological levels are low, relying on local experience-based knowledge. Unsustainable exploitation inevitably occurs with population and/or technological increases and/or through colonisation by persons without local knowledge, leading to resource depletion and degradation.

The first true 'forestry' stage occurs after unsustainable exploitation and is characterised by the implementation of rules and regulations, generally to sustain supplies of one or more resources (Kimmins et al., 2005). Pretzsch et al. (2008) describes this paradigm as *dominant use* while Kimmins (2004) again breaks it into two distinct sections (Figure 2.1). The initial stage is termed *Administrative forestry* and typically lacks ecological sensitivity to varying forest conditions and is industrially focused not site specific. The lack of ecological basis means that this paradigm eventually fails to meet its objectives and is supplanted by the next forestry stage, *ecologically based timber management*, which is site-specific and usually succeeds in sustainable provision of conventional forest products and sustains ecosystem function (Kimmins, 2004). However, it does not support all the requirements of an affluent post-industrial society as it is still primarily timber focused.

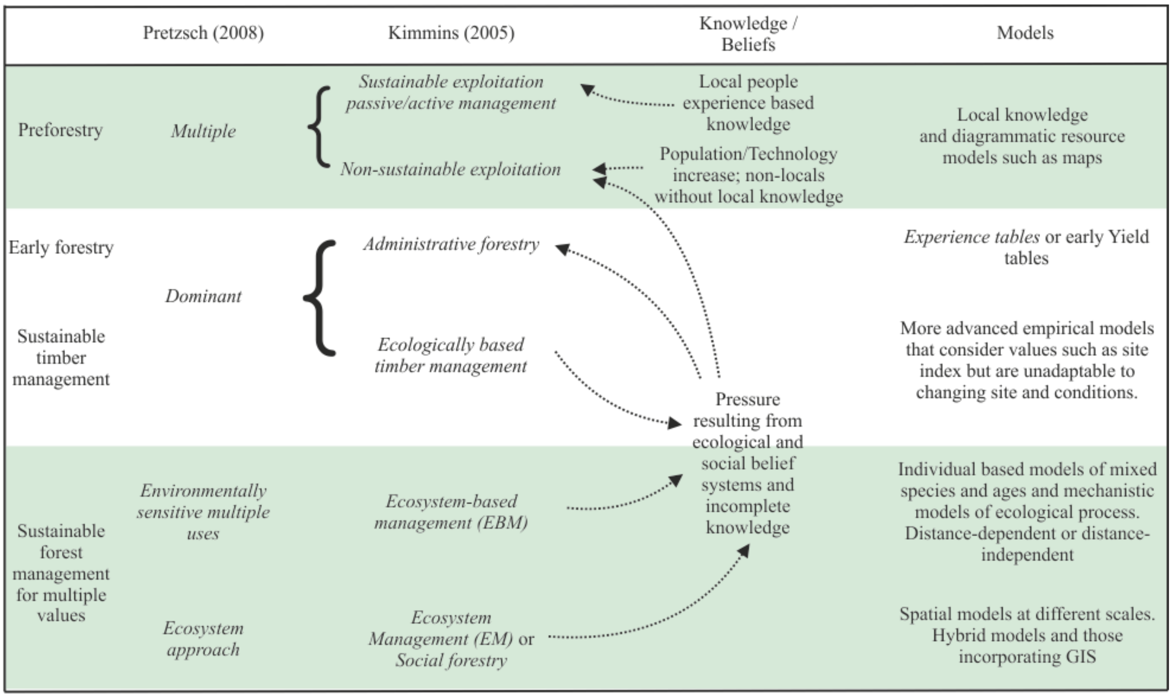

Figure 2.1. The evolution of forestry after Kimmins et al. (2005) and Pretzsch et al. (2008). Dotted arrows link knowledge and belief held with the related forestry stage. Parentheses relate Kimmins (2005) nomenclature to Pretzsch et al (2008).

The progression within a society, for inclusion of alternative factors than timber production to forest management, encourages the shift to the next paradigm, which Pretzsch (2008) terms *environmentally sensitive multiple use* and Kimmins et al. (2005) *ecosystem-based management*. *Environmentally sensitive multiple use* combines the production of timber with supply maintenance of other forest goods and services (such as recreation, biodiversity maintenance and/or water quality) (Pretzsch 2008). Kimmins' (2005) definition of ecosystem-based management is somewhat more expansive and incorporates multiple uses/values, mostly in terms of biophysical processes, but not as a complete ecological system. Within this paradigm, different agencies manage the various individual system values from separate management plans, leading to a disconnect and suboptimal ecosystem management, possibly resulting in conflict between resources and values.

Kimmins et al. (2005) and Pretzsch et al. (2008) view the next stage as ecosystem focused (Figure 2.1). Pretzsch's *ecosystem approach* paradigm takes a bio-centric viewpoint considering the vulnerability of ecosystem processes to anthropogenic effects such as climate shift and acid rain. Under this paradigm conservation and sustainable use are considered of primary value, furthering system understanding. Likewise, the required biophysical and social values are paramount in Kimmins et al. (2005) *ecosystem management* paradigm; however he extends the definition to necessitate forest ecosystem management under a single, sustainable framework. and Pretzsch et al. (2008) also includes a further definition that extends beyond forest management to 'ecoregional management', essentially shifting the perspective away from a forests biota and species composition to regional scale interactions, for example, the interaction between different land cover types such as grassland, moorland and forest.

Forest management objectives change alongside societal needs, environmental and economic conditions and shifts in our understanding of the needs of forest resource management (Hahn & Knoke, 2010). It is not suggested that these forest paradigms are sequential or linear in process (Pretzsch et al., 2008). Figure 2.1 highlights how societal knowledge and beliefs change expectations and goals of forest management. Likewise the historical development of models encapsulating forest growth has not followed a linear progression of continuously improving models replacing subordinates. Rather, it has involved the simultaneous development of differing model types with varied concepts and intentions representing the state of contemporary forest knowledge at the time of creation. Major changes in model conception have taken place that are closely related to these changing objectives and societal perceptions, greatly affecting the quality of the generated information. The expansion of forest growth science and knowledge can therefore be documented through advances in forest growth modelling (Pretzsch 2000).

2.1.1 Aim of study

The aim of this study is to evaluate the historical changes to silvicultural practices in the context of model development and these forestry paradigms (Figure 2.1). The initial focus is on the development and spread of the German traditions through Europe and to North America. The current state of the art is discussed and future directions and challenges are highlighted.

2.2 The start of active management and administrative forestry

In Europe, *multiple use* forestry or *preforestry*, continued until the 17th Century and included activities such as hunting, livestock grazing, tree-felling and timber extraction (Kimmins et al., 2005, Pretzsch et al., 2008). The earliest ecosystem models were maps showing the location and availability of resources, for instance forests, commons, hunting-grounds and bee-hives (Pretzsch et al., 2008).

Demand for construction timber after the 30 year war (1618 – 1648) and wood for furnaces and firewood, led to the implementation of regulations designed to sustain resources, the primary stage of institutionalised forestry (the *dominant use* or *administrative forestry* paradigms (Figure 2.1)). In general the rules at this stage fail to maintain ecosystem integrity, as they are rarely based on an understanding of the ecosystem and the desired values (Kimmins et al., 2005).

Though evidence of planted trees in British orchards or gardens goes back to Anglo-Saxon, and possibly Roman times, it was not common for trees to be planted in the landscape until the 13th Century. Even then the majority were related to hedgerows or parks, rather than the commencement of contemporary forestry (Rackham, 1990). Coppicing-with-standards was well established by 1086 and had spread to nearly all woods by 1251. Coppice wood was mainly used for fencing, whilst the standards were utilised for building (Rackham, 1990). Evidence also shows that Coppice management was already practiced in Germany by the 12th Century and possibly earlier (Warde, 2006). German foresters were planting conifer species around Nurnberg as early as 1378 with seed trade taking place in the 1420s, and by the 1510s had been introduced to the Netherlands. By the 16th Century conifer planting was widespread in central Europe (Warde, 2006). The first documented appearance of wood in a marketing context was in the 15th Century and until the 17th Century forest products were used locally or sold in local principality regulated markets (Puettmann et al., 2008).

2.2.1 The Normal forest concept

With the Enlightenment in Germany came the introduction of the Cameral sciences (*Kameralwissenschaft*) subjecting a variety of social, administrative and economic practices to 'scientific' scrutiny. Introduced into Prussian universities in 1727, within 30 years it was an established part of the curriculum. Forest management was scrutinised in an attempt to use economic rationalisation to turn existing knowledge into a system and previous activities into science. Cameral officials sought to describe the forest quantitatively before applying economic reason, and mathematics was a prominent subject, especially in the first two years of study (Lowood, 1990).

Before the 18th Century, forests were a stable component of the regional European economy supported by management practices (Puettmann et al., 2008). A precise demarcation of the forest had previously been discouraged by traditional communal privileges and its continued use for grazing, mast and various agricultural purposes. From the 1760s, the idea that forest could be precisely defined and objectively studied was promoted by trained officials who now had access to publications in which to exchange ideas (Lowood, 1990). By the late 18th Century estate managers and 'calculating foresters' were paying increasing attention to yield (Warde, 2006) and forest goals shifted to maximise land-owners profits (Puettmann et al., 2008).

By the end of the 18th Century three concepts linking the regulated forest with the focus on measurement and calculation were apparent in silvicultural writings: *minimum diversity*, *the balance sheet* and *sustainable yield* (Puettmann et al., 2008). Arguably the two most influential pioneers of forest science were Georg Ludwig Hartig and Johann Heinrich Cotta, both Germans. One of the first dedicated forestry schools in Europe was founded by Hartig at Hungen (1789) in Hesse; Johann Heinrich Cotta founded the Royal Saxon Academy of Forestry in Tharandt, Saxony (1816) (Ciancio & Nocentini, 2000). Minimum diversity became apparent in the new units of forest computation: *standard tree* (*Normalbaum)*, *size class* (*Stärkeklasse*), *sample plot* (*Probemorgen*), and *age class* (*Periode, Altersklasse),* with Hartig and Cotta both advocating removal of details that might confuse calculations from the sample plot (Puettmann et al. 2008).

The concept of a *Normal* forest arose from these conditions and its effect on silviculture is still visible in today's landscape (Puettmann et al., 2008). Devised as a conceptual model for the calculation of sustainable harvest levels and the formulation of ideas relating to growing stock and growth and yield relationships; its use was not limited to this intention and instead was interpreted as the desirable goal for a managed forest. The normal forest was assumed to be composed of stands (units) that had homogeneous monocultures or species mixtures, site conditions and size, full stocking and wood quality, and a spatial organisation that facilitated harvesting without risk of catastrophe or natural damage. The rotation length influenced stand characteristics, with one age class harvested and regenerated every year to provide constant increment and volume, with the assumption of similar species mixture, tree densities, site and tree qualities (Puettmann et al., 2008).

Two prominent schools of thought emerged in central Europe. The *Bodenreinertrag*'s philosophy was that economic interest was the sole purpose of forestry. Where previous forestry decisions were based on forest structure of fully stocked stands, defined by area or volume, they were now replaced by criteria related to productivity. The *Waldreinertrag* recognised the landowner's social responsibility to the community so that management goals maximised annual profits without including interest rates and as a consequence optimal rotations were generally longer. The different approaches partially reflect societal values with regards to social responsibility and private property: in North America *Bodenreinertrag* was more favoured whilst most emphasis was on *Waldreinertrag* in Europe (Puettmann et al., 2008).

2.2.2 The Development of yield tables in Germany

Though many texts state that the concept can be identified as far back as the "Lung Ch'uan codes" in 4th Century China (Vanclay, 1994), yield tables (as used today) were first developed in 18th Century Germany (Vanclay, 1994, Pretzsch, 2000, Porte & Bartelink,

2002) and closely reflect the *Normal* forest concept. Initially a basis for planning and taxation in large regions, further development led to regional and site-specific yield and growth models being used to explore management alternatives, silvicultural options and inform decision making (Vanclay, 1994, Pretzsch, 2000, Porte & Bartelink, 2002). Stocking rates and mean stand development are provided along with an estimation of site quality related to mean dominant tree height. Each forest is related to a "reference stand" (analogous to the *Normal* forest) of a particular yield table by indexing the site in relation to its mean total height at a given age (Hasenauer, 2006).

Pretzsch (2000), highlights key 18th and 19th Century researchers, among them Hartig (G.L.) (1795), Paulsen (1795) and von Cotta (1821) as creating the first generation of yield tables, described as *experience tables* due to their basis on estimation or limited data sets. These tables soon highlighted gaps in scientific knowledge and led to the creation of experimental areas for long-term data collection that are still managed and surveyed today (Pretzsch, 2000).

Categorised as historical bioassay models, Yield tables are reliable as long as ecological conditions remain constant however their use is limited under changing environmental conditions and management scenarios. The empirical approach used in these mensurational models assumes that the way forests have grown in the past is the best indicator of how they will grow in the future. If ecological conditions remain constant, and the data set is accurate, historical bioassay models are reliable and believable. However, under differing site and managerial conditions they provide poor predictions and cannot provide explanations to the mechanisms of growth (Kimmins, 2004).

Pretzsch (2008) highlights four generations of yield tables. After *experience tables,* the second generation were those produced between the end of the 19th Century and the 1950s, following construction principles, with a strong empirical basis, proposed in 1874 by the Association of Forestry Research Stations which later became the International Union of Forest Research Organisations (IUFRO) (Pretzsch, 2000).

In the 1930s a shift stressing the influence of site conditions and ecological relationships to forest development emerged (Puettmann et al. 2008) and mixed species stands have gradually become the focus of forest research over the last century, particularly due to studies by Karl Gayer (1886) and others (Pretzsch, 2000). The first mixed stand yield tables were built in the 1930s and 1940s by Wiedemann, however he was prevented from finishing their development by the Second World War (Pretzsch 2000, Porte and Bartelink 2002). The Prussian Research Station provided data from approximately 200 experimental areas, facilitating the development of even-aged mixed stand models for pine and spruce, oak and beech, pine and beech and spruce and beech (Pretzsch, 2000). Although widely used, models of this type were confined to specific age structures, mixed patterns and site conditions (Pretzsch 2000) as, even with a two-species mixture, the possible number of compositions was immense and difficult to calculate (Porte and Bartelink 2002).

In the early 1900s Gehrhardt (1909 and 1923 in Pretzsch et al., 2008) developed yield tables that influenced a move away from purely empirical models to a third generation of yield tables based on biometric equations and theoretical principles. At the core of the models that followed are flexible functions based around natural growth relationships that are statistically parameterised. Many of these have been adapted to computer programs that predict stand development (Pretzsch et al., 2008).

The fourth generation of yield tables highlighted by Pretzsch (2008) are models that simulate stand growth and development for different site conditions, planting densities and thinning regimes. Again they are empirically parameterised and reflect wide ranging management scenarios. Yield tables still form the basis of sustainable forestry management, particularly for plantations, despite the drawbacks discussed earlier and their impact on forest science was hugely important (Porte and Bartelink 2002, Pretzsch 2000).

2.2.3 The spread of the German method in Europe and North America

2.2.3.1 Europe

French reforms under Louis XIV (reign 1643 – 1715) resulted in the *plans de forêts* and the concept of annual cutting areas. New statutes, inventories and re-organisations were prompted by Jean-Baptistes Colbert’s ambitious plans for reform in 1669, however scientific forest management did not establish until the 1820s when it was imported from Germany (Lowood, 1990). The French forestry academy founded in Nancy in 1825 by Bernard Lorentz (a friend of Hartig) was particularly influenced by Cotta's Saxon school at Tharandt (Ciancio & Nocentini, 2000, Warde, 2006). The French in turn provided the model for Spanish forestry. The Russians had sought foresters from Germany as early as 1732 and were later trained at Hartig's school at Eberswalde near Berlin (Warde, 2006).

The start of English forestry as a tradition began in 1611 with publication of *The Commons Complaint* by Arthur Standish (1611). Though mostly advisory the pamphlet outlined a national planting plan complete with directions and economic information (Rackham, 1990). *Sylva: Or a discourse of forest trees and propagation of timber* was published by John Evelyn in 1664 and was heavily influenced by Standish’s work. Though it had most relevance to plantations, which were still considered a hobby for gentleman, the work was a standard for 150 years (Rackham, 1990). The majority of these early plantations were coppices, intended to supplement woodlands, not replace them. The area of plantations did not surpass that of woodlands until the 20th Century in England, though it happened in the 18th Century in Scotland, and possibly Ireland, due to state planting orders (Rackham, 1990). By the middle of the 17th Century British foresters were attempting to make yields more predicable by standardising stands. Realising that tree growth varied and that there were differences between compartments they attempted to calculate particular trees growth patterns and the yield of specific areas by adjusting compartment size (Warde, 2006).

Despite concerns raised in publications, such as Evelyn (1664), a forest inventory was not carried out until a board of agriculture was established in 1793 (Lowood, 1990). The shift in the 18th Century was to the combination of practical experience and statistical and mathematical techniques, inspired by German foresters, for more dynamic woodland management (Warde, 2006). English forestry then developed in three ways during the Victorian era (1837 – 1901): firstly with the incorporation of German practices, via India and Cyprus, from German foresters such as Dietrich Brandis and William Schlich, who were involved in British Imperial forestry and later worked in England; secondly with an increasing theoretical and scientific basis to forest practices, particularly regarding economics, as forestry became a financial endeavour; and lastly with the commitment to plantations and the annexing of moorland and farmland by foresters (Rackham, 1990, Lewis, 1999).

2.2.3.2 North America

Along with granting land rights to the Aboriginal people, Canada's first forest policies were dictated by British and French colonial administrators. For example, in 1610 Newfoundland enacted a policy of forest protection banning the use of fire as a management practice. For most of the 17th and 18th Century Canadian colonial forest policy limited timber based industries to supplying domestic demand and reserved certain tree species for naval use. A timber export trade, fuelled by loyalist refugees from the U.S. during the early 1800's, grew on the Atlantic coast of current day Canada, primarily exporting squared timbers and hand-hewn spars to England and British colonies. 'Broad-arrow' laws throughout North America reserved certain trees for Royal Naval use and

Britain relied heavily on Canadian timber for masts and spars during its wars of 1812 with the United States and France (Apsey, 2003).

The rapid development of the colonial forest industry and the establishment of new laws to regulate it laid the foundations for forest policies that still exist today (Drushka, 2003). During the 19th Century Canadian forest policy was primarily concerned with stimulating the growth of the milled timber (termed *lumber* in North America) industry (Apsey, 2003). The U.S. civil war ended in 1865 and the Canadian confederation was formed two years later. With an increase in demand for milled timber from North America a thriving saw mill industry developed in Canada's Atlantic Provinces, which coincided with Britain dropping its mercantile colonial policy and its declining demand for hand-sawn timber (Apsey, 2003). Colonial forest exploitation and liquidation ended with Canadian Confederation in 1867, coinciding with a period of rapid industrialisation and a new era of forest impact (Drushka, 2003).

This industrialisation during the last half of the 19th Century and the first quarter of the 20th, impacted forests mostly via the uptake of steam powered machinery (Drushka, 2003). Logging and milling operations were speeded up by the mechanisation of the industry and that combined with the availability of steam locomotives impacted the Canadian forests in a multitude of ways: line construction used huge quantities of timber that had to be replaced every three to four years; a continental rail system expanded in the U.S.; the increased infrastructure meant that more land was settled, particularly damaging the southern boreal region and was responsible for the most extensive forest liquidation in Canadian history. Another consequence of the use of steam engines was the amount and extent of accidentally started fires (Drushka, 2003).

In the U.S., Franklin B. Hough, who had overseen two New York state censuses (1855 and 1865) and the 1870 federal census noticed trends related to declining timber supplies. In his 1873 speech to the American Association for the Advancement of Science, *On the duty of governments in the preservation of forests,* he associated the increasing tendency of destructive floods and periods of drought to the clearing of woodlands (Hough, 1873). Hough (1873, p. 2) highlighted the country's complete dependence on timber and drew parallels with, mainly European, countries (including Germany and British India) that had instigated 'systems of management and regulation of national forests, as a measure of governmental policy and public economy'. The speech resulted in the creation of a committee to lobby congress and in 1876 Hough was appointed, within the United States department of Agriculture (USDA), as the first *special forestry agent* tasked with investigation of the national forest lumbering situation (U.S. Forest Service, 2004). When the division of Forestry became a permanent part of the USDA in 1886, Bernhard E. Fernow was appointed as its chief. Fernow, a German national educated at the Royal Prussian Academy of Forestry, Münden, began research programs in tree planting, forest products, wood technology, forest pathology and silviculture. Fernow was in office until 1898 and, along with his staff, produced in excess of 200 forestry articles and associated literature. A key part of Fernow's forestry ethos was sustainable yield and the conservation of natural resources (U.S. Forest Service, 2004).

In 1898, Carl Alwin Schenck, a German forester, opened the first U.S. school of forestry, the Biltmore Forest School, in North Carolina (Schenck, 1974). Schenck had originally started work on the Biltmore estate in 1895 to replace Gifford Pinchot. Pinchot had graduated from Yale in 1889 and travelled to Europe to study forestry, where he was encouraged to enrol at the French Forest School at Nancy by Dietrich Brandis. Returning to the U.S. in 1891, Pinchot began work at the Biltmore estate later that year (Lewis, 1999). Upon leaving the Biltmore estate in 1898 Gifford Pinchot succeeded Fernow as chief of the USDA forestry division.

Fernow left to become the founding head of the New York State College of Forestry at Cornell University in close collaboration with Schenck, whose school he had visited prior to taking the post at Cornell. In correspondence between Schenck and Fernow dated April 17, 1898, Fernow asked if Cornell students could carry out summer courses at Biltmore Forest School to provide practical demonstration, and if Schenck will visit as an occasional lecturer (Gardner, 2002).

These two schools, along with others including the Yale School of Forestry, established in 1900 from an endowment by the Pinchot family (Lewis, 1999), exposed Canadian foresters to the German methods when they went there to train (Drushka, 2003). With Canada's first forest congress in 1906 the early twentieth Century saw various Canadian provinces establish forest services, an introduction of laws relating to the prevention of forest fires, diseases and insect infestations and the establishment of forest schools in Toronto (1907), Fredericton (1908) and Quebec City (1910) (Gibson, 1946, Apsey, 2003). The founding dean of Toronto's forest school was Bernhard E. Fernhow (Drushka, 2003); Cornell's forestry program had collapsed in 1903 mainly due to a need to earn revenue (Lewis, 1999).

In the decade before WWI the Canadian federal government passed legislation allowing reserves it had already established to be managed under scientific methods, tree-planting programs were started on the prairies, forest product research laboratories were established in Vancouver and Montreal in 1917, and around the same time forest research facilities were opened (Drushka, 2003). The Forest Service was disseminating considerable amounts of advice in the form of Agricultural and Technical bulletins and other journals by this time. Though the influence of European forestry was acknowledged, some leading foresters were questioning the applicability of European methods to North American forests. Mustian (1978) highlights Henry S. Graves in his 1908 paper titled

‘Present condition of American silviculture’ acknowledging the principles and results of European forestry, but stating that there were difficulties in applying the methods to American situations, along with the lack of fundamental information on the silviculture of American tree species such as reproduction, tolerance and response to release.

2.3 Ecologically based timber management

Development of timber-focused silviculture with an ecological foundation is the first major modification of administrative forestry (Kimmins et al., 2005). Hartig (1791) and Cotta (1817) provided the first documentary evidence in Europe of a scientific understanding of silvicultural and ecological issues. These documents are essentially the initiation of silvicultural science and ecology became an established science shortly afterwards (Puettmann et al. 2008). By the mid-19th Century forest inventory and planning systems dominated silvicultural writings, but the scientific basis for silvicultural decision-making was not formally acknowledged until the early twentieth Century (Puettmann et al. 2008).

Kimmins (2004) defines ecologically-based timber management as forestry for the “sustained production of timber and other conventional products” (Kimmins 2004, p.15) (Figure 2.1). A later definition alters this to *ecologically based timber management* and adds an interim stage between this and s*ocial forestry*, that of *ecosystem-based management*. Under *ecosystem-based management* the forest is managed for multiple individual values (not solely timber), but different stakeholders manage different aspects, which leads to a disconnection in system management and, consequently, sub-optimal utilisation of resources and potentially conflicting of objectives (Kimmins et al., 2005).

2.3.1 Growth and yield modelling

By the mid-20th Century silvicultural literature had integrated the interrelationship of ecological components and the view of forests as ecosystems. Of particular importance during the latter half of the 20th century was Watt's (1947) synthesis *pattern and process in the plant community*, an important milestone in spatio-temporal dynamics, using the development of forests' spatial patterns to provide insight into the functioning of ecosystem dynamics (Gratzer et al., 2004).

The theory of patch dynamics built on Watt's work to describe the spatio-temporal dynamics of a system by the demographic analysis of patches as opposed to individuals. This theory reduced ecosystems to mosaics of discrete patches, created by disturbance events, that were internally homogenous (Gratzer et al., 2004). At the time Watt had found describing plant communities in terms of individuals and their spatial relations impractical. However recent advances in spatial ecology demonstrate the importance of community dynamics, local processes and the effect of individuals. Neighbourhood-oriented perspectives of plant community dynamics are now widely acknowledged (D'Amato et al., 2011).

Alongside these conceptual shifts major changes were also taking place in how forest growth was modelled. Before the 1960s the stand had been the base unit upon which all modelling forecasts were made (Porte and Bartelink 2002). With the silvicultural focus shifting from even-aged monocultures to mixed species stands and management goals moving to incorporate other values than growth and yield (Porte and Bartelink 2002), alongside increasing computational availability and power, the information demand for forestry changed away from stand growth models based on mean stand variables towards the single-tree dimensions of nominated parts of the stand (Pretzsch 2000). The first single tree growth and yield model was developed for pure Douglas fir (*Pseudotsuga* spp.) stands in North America by Newnham for his PhD thesis in 1964 (Hasenauer 2006, Shugart 2001, Pretzsch 2000). Whilst spatially explicit and comprehensive it did not explicitly account for height growth of an individual and was intended to model stand growth rather than that of an individual (Newnham, R.M., 1964). A trend towards eco-physiological models also occurred in the 1960s that provided insight into the complexity of causal relationships and predicted forest growth under varying ecological conditions (Pretzsch 2008).

2.4 Uneven-aged silviculture and Ecosystem-based management

2.4.1 Dauerwald (continuous forest)

The German, back-to-nature movement, led by Karl Gayer in the late 19th Century, argued for natural regeneration and uneven aged forest forms as opposed to even aged stands (Mustian, 1978). An uneven-aged stand can be defined as containing trees with many ages (usually three or more age-classes), whether grouped or mixed, whereas an even-aged stand contains trees from a single age class (O'Hara & I. Valappil, 1999). Troup (2000) stated that the term Dauerwald gained prominence from an article published in 1920 and 1921 by Dr. Alfred Möller titled *Kiefern-Dauerwaldwirtschaft*, which can be translated as *continuous pine forest* (Helliwell, 1997). The idea of Dauerwald arose after the late 18th Century and early 19th Century's extensive implementation of clear-felling with artificial regeneration obsession in Germany, and through their influence, other countries. In many places the idea of sustained yield contrasted with the silvicultural requirements of the species applied, and soil-degradation and unhealthy crops had occurred. Möller applied the term Dauerwald to any system that didn't involve clear-felling and soil exposure, essentially dividing existing forest treatments into two distinct groups (Troup, 1927).

The main principles of the Dauerwald treatment aim to maintain soil fertility by avoiding clear-fell through the continuous tending of forest cover: everything that is vigorously producing timber is retained and everything that isn't, is removed. The *Normal* forest ideas of age-class distribution and rotation are disregarded to allow a more elastic practice that gains maximum production. A key factor is the encouragement of regeneration through favourable conditions, rather than using planting as a system driver, with the aim that artificial regeneration is used only where necessary. Calculations to periodically measure increment were also used in place of calculations to determine annual yield (Troup, 1927).

The concept of “continuous forest” or “dauerwald” was last explored in the UK in the 1950s and 1960s. Now in an era when alternative forestry objectives to timber production are being explored Continuous Cover Forestry (CCF) is a realistic option (Mason et al., 1999). In North America, harvesting methods that only removed a stand’s largest trees have been practised since the 1930s and various terminology is used to define uneven-aged silviculture, including uneven-aged regeneration (selection) methods, variable retention and staged clearcut (O’Hara, 2001).

In 1898, De Liocourt described the tendency of ‘natural’ uneven-aged stands to show a reverse J-shaped diameter distribution (Figure 2.2) (Peng, 2000). This typical diameter distribution became apparent in uneven-aged stands as area increased; with smaller areas potentially having more irregular distributions (Peng, 2000). De Liocourt also quantified the geometric progression of the size classes by the ratio of trees in one size class to trees in the next largest class and termed this the *q constant* (Peng, 2000).

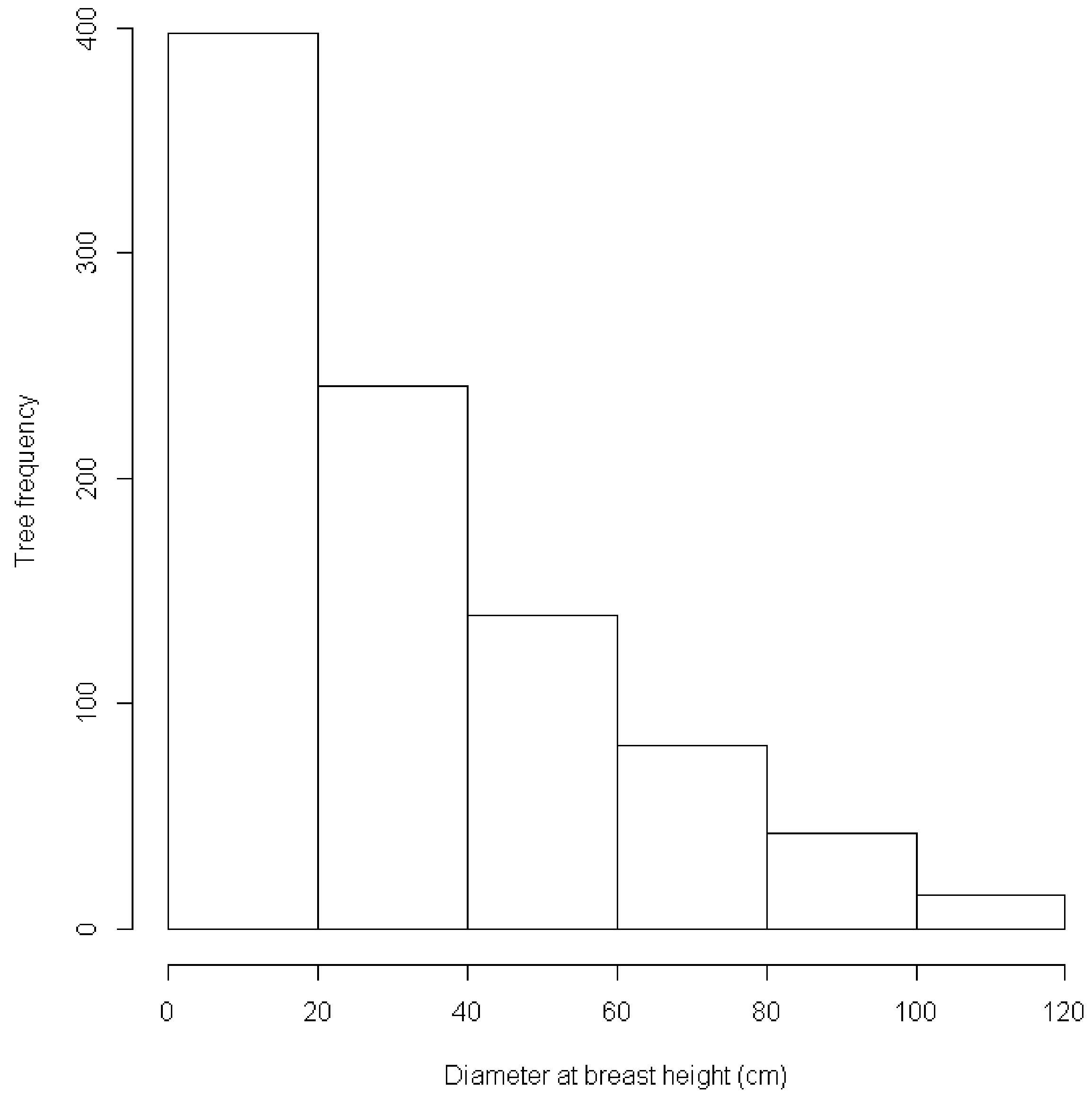

Figure 2.2. Reverse-J shaped diameter distribution

With discussion about management, foresters in general tended to assume that striving for a reverse-J distribution was the only way to achieve uneven-aged stands (Mason et al., 2003). There is also a potential misconception that ‘natural’ uneven-aged stands are all-aged as events beneficial for regeneration do not take place every year (O'Hara, 2002). Within the British Forestry Commission, Kerr (2001) suggested that uneven-aged silvicultural systems were perceived by foresters to be too labour intensive and suggests an alternative to the J-shaped distribution of defining equilibrium growing stock: a theoretical state where a size-class frequency distribution remains largely constant generating sustainable timber increment. In uneven-aged modelling studies a sustainable, equilibrium or steady state structure has been related to the concept of balance defined by Meyer (1952). Where a balanced uneven-aged structure is one where the structure and volume is maintained by periodic removal of a constant yield (Peng, 2000).

2.4.2 Contemporary Model classifications

Contemporary models are generally classified according to the method of calculating growth: empirical, mechanistic or hybrid models combining elements of both (Figure 2.3). However Korzukhin et al (1996) challenged the view of separating mechanistic and empirical and instead suggested that all models have elements of the others to different degrees, existing on a continuum from purely statistical to purely mechanical rather than process and empirical models being mutely exclusive (Makela et al., 2000, Monserud, 2003). Peng (2000) identify and describe these historical classifications delineating modelling philosophies.

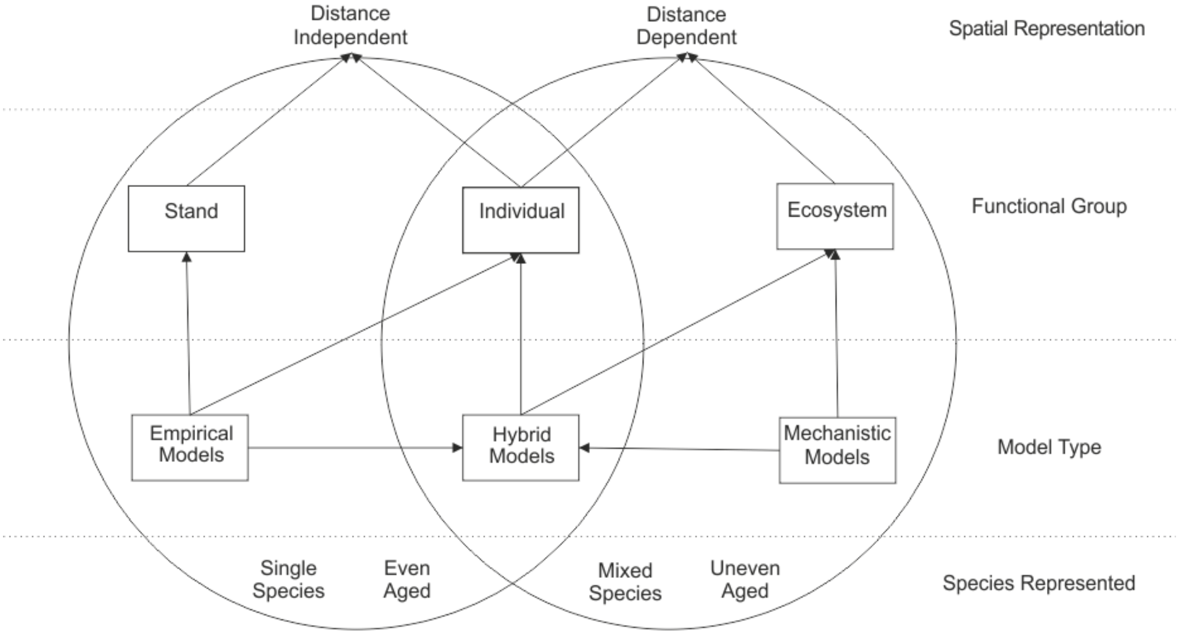

Figure 2.3. Generalised model classifications separated by function, spatial arrangement, manner of species representation and model type.

2.4.2.1 Empirical growth and yield models

Empirical growth and yield models emerged through German forest mensurationists in the late 1700s and are the origin of contemporary forest management Decision Support Systems (DSS). Such tools fall down when environmental conditions are not constant or when dealing with the prediction of novel silvicultural systems for which we lack experience (Fontes et al., 2010, Kimmins et al., 2008).

Empirical models are generally calibrated from long-term experiments or inventory data. While historical models are not suited to changing environments several new developments can accommodate changing environmental conditions including management and climate change (Fontes et al., 2010). Two approaches to empirical models that may address these issues are a dynamic state-space approach (Nord-Larsen & Johannsen, 2007) and productivity-environment relationships (Tyler et al., 1996, Seynave et al., 2005, Fontes et al., 2010). The dynamic state-space approach assumes that at any given time the system contains the information to predict its future behaviour. The current system state is then taken as the accumulation of past information, with future behaviour predicted by the application of information about the present (Nord-Larsen & Johannsen, 2007). Temporal stand and site variations alongside site potential, genetically determined potential and management effects are accounted for by this prediction of future system states through the iteration and application of a transition operator to an n-dimensional state vector (Nord-Larsen & Johannsen, 2007, Fontes et al., 2010). Minimum assumptions of allometric relations are used, but the use of stand specific calibration for the transition operator is fundamental to ensure the linkage between predictions and mensurational variables (Fontes et al., 2010). The most common site productivity measurement in forestry is site index, however this is only applicable to even-aged single species stands (Seynave et al., 2005). Productivity-environment relationship models attempt to make empirical models more applicable to changing environmental conditions by isolating the key environmental factors of site index by statistically regressing site index against environmental co-variates. (Seynave et al., 2005, Fontes et al., 2010).

2.4.2.2 Mechanistic Process models

Variously termed mechanistic models, causal models, process-based models (PBMs), biogeochemical models or matter balance models these consider the processes that directly influence the development and long-term dynamics of forests (Fontes et al., 2010). Functional components interact with each other and the environment to provide derivations of system behaviour (Vacchiano et al., 2012) with many explicitly modelling transpiration, respiration and/or photosynthesis (Fontes et al., 2010) alongside other biogeochemical processes such as the carbon or nitrogen balance (Pretzsch 2002).

Originally designed for research, and most commonly used for scientific explanation as opposed to prediction (Monserud, 2003), process-based models are more responsive to changes in site conditions and the environment than empirical models (Pinjuv et al., 2006) and are considered particularly useful for the investigation of forest dynamics under changing environmental conditions (Fontes et al., 2010). However, modelling of the underlying causal processes can be complex (Taylor et al., 2009) and though they are based on the underlying growth mechanism they include many uncertainties and can be difficult to parameterise (Pinjuv et al., 2006). Their complexity also makes it difficult to isolate behaviours and the specific causal processes responsible (Fontes et al., 2010).

Forest management seldom utilises PBMs as practical tools because they are commonly considered to contain excessive uncertainty, requiring excessive parameters to produce reliable projections in contrast to empirical models (Fontes et al., 2010, Makela et al., 2000). The attraction of PBMs is the possibility of applying generic components, representing underlying principles, across various species and situations (Vanclay, 2012).

A key PBM paradigm, relevant to deciduous and coniferous trees, is the *pipe model theory* developed by Shinozaki et al (1964). They found that, within a plant community, above a certain horizontal level, the sum of the cross-sectional area of stems and branches at a given level were proportional to the amount of leaves at that level. Plant form was then conceptualised as *unit pipes* able to support a unit quantity of photosynthetic organ. Landsberg and Waring (1997), Makela et al. models (2000), Monserud (2003) and Fontes et al. (2010) provide further reviews of PBMs.

2.4.2.3 Hybrid models

The integration of information provided by empirical forestry data and PBMs in the form of hybrid models (Makela et al., 2000) attempts to create growth models capable of adapting to changing environmental conditions in a way that purely empirical models are unable to do (Monserud, 2003). The combination attempts to avoid the shortcomings of both (Pinjuv et al., 2006, Taylor et al., 2009)for example the models require decreased levels of parameterisation compared to PBMs and contain greater biological realism than empirical models (Pinjuv et al., 2006).

Another key advantage of Hybrid models over empirical models, for forest management scenario planning, is their flexibility. They are less constrained to site-specific conditions and can be re-parameterised to cope with changing environmental conditions (Taylor et al., 2009). So far Hybrid models have been explored in two different ways: either existing models have been coupled or new models containing both concepts have been developed (Fontes et al., 2010).

2.4.3 Stand and individual based models

Aside from model type, forest growth models can be defined by the base unit of representation: whole stand or individual tree models, and by their spatial representation: distance-dependent and distance-independent (Figure 2.3). Stand models simulate growth and yield through parameters that define the underlying diameter distribution, for instance, volume density and basal area, whereas individual based models hold each tree as the fundamental unit acting through establishment, growth and mortality (Porte and Bartelink 2002).

A system of equations controls each tree's growth according to its placement in the stand (Pretzsch 2000). Competition indices predict growth form (e.g. diameter, height, etc.) and quantify growth spatially through assessment of past and current competition (Hasenauer, 2006). Control parameters defining single-tree and environmental attributes are provided at the instantiation of the simulation. Usually this data originates from plot inventories and after processing of the tree list, changing growth conditions are defined, influencing the next growth period (Pretzsch 2000). Emergent system level properties can then be studied from the adaptive behaviour of these individuals (Grimm et al. 2006). This information can then be aggregated and summarised to provide stand data and is scalable to address a wide variety of issues from that individual upwards (Pretzsch 2000, Busing and Mailly 2004). Fundamentally the transition to single-tree growth models from stand-level predictions removed any predefined limits on species mixture, age or silvicultural treatment (Porte & Bartelink, 2002, Hasenauer, 2006, Hasenauer & Pietsch, 2009).

It is possible to further separate individual tree models spatially (Figure 2.3) into distance dependent and independent (Peng, 2000). Independent models do not consider spatial distribution when calculating competition. Distance dependent tree models came about as a response to the demand for more detailed spatial representation of growth and succession (Taylor et al., 2009). A further overview of tree and stand level models is provided by Peng (2000).

2.4.3.1 Gap models

Gap models are a subset of individual based models that describe collections of gaps or patches defined by lists of individual trees (Botkin et al., 1972, Pretzsch, 2000, Porte & Bartelink, 2002). The first gap model, JABOWA, simulated the dynamics of a mixed broadleaved forest as part of the Hubbard Brook Ecosystem study in New England U.S.A (Peng, 2000, Porte & Bartelink, 2002). Botkin et al (1972, p. 849) stated that before JABOWA no one had "successfully reproduced the major characteristics of a mixed-species, mixed-age forest from a conceptual basis". Tree establishment, growth and mortality were formalized by the development of several keys: the abstraction of the stand into a composite of several small patches of land, each potentially having a different successional stage and age. Patch (gap) size was defined as dominated by a large individual organism and tree position within each patch was not modelled. Consequently each patch was horizontally homogenous and all tree crowns extended horizontally across the whole patch with leaves represented by a thin disk at the top of each stem (Figure 2.4, b). Patches did not interact and so successional processes were independent (Bugmann et al., 2001). A large range of forest gap models were created after Botkin et al's (1972) JABOWA, with the concept also applied to other vegetation types (Bugmann et al., 2001).

Most gap models utilize patches in the area of 100 – 1000 m^2 (Bugmann et al., 2001) and gap size is generally equivalent to the crown size of a dominant tree (Botkin et al., 1972, p. 849). This Creates horizontally homogenous gap conditions (Porte & Bartelink, 2002), which can cause shading issues of understorey trees in some models (Bugmann et al., 2001). Each tree is independently simulated and two features are emphasized that are important to describe vegetation dynamics: an individual's response to the environmental conditions and the effect of the individual on those conditions (Shugart, 2002). An individual's recruitment, growth and mortality are the basis for the modelling of dynamics and a species-specific function, related to diameter at breast height (DBH), represents genetic potential under non-limiting conditions (Shugart, 2002). Growth predictions can then be modified by environmental conditions such as available light, soil moisture, soil nutrients and temperature (Kimmins, 2004). Each individual tree's response to light is simulated at height intervals throughout the plot and shading effects are modelled using a light extinction equation (Figure 2.4, c) (Shugart, 2002).

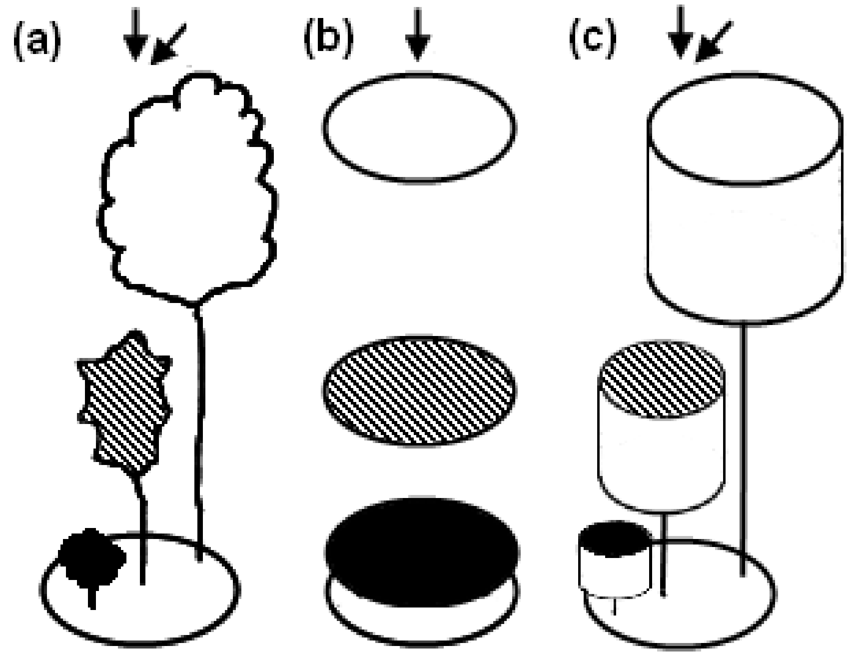

Figure 2.4. Crown representations (a) reality, (b) Gap model and (c) SORTIE-ND; after Busing and Mailly (2003).

The ZELIG model (Urban, 1990) introduced the first gap model patch interactions allowing for three modes of functionality: no patch interaction; a one-dimensional 'transect' mode with linearly arranged patches that consider the sun angles and a rectangular grid of patches in a two-dimensional mode. The latter two modes directly considered the light regime and availability to each tree (Bugmann et al., 2001). Models such as ZELIG and SORTIE shifted the focus to interactions between individual organisms away from discrete patches (Gratzer et al., 2004).

SORTIE is a contemporary individual based model that builds on the gap model approach and is capable of modelling much larger areas of forest (Bugmann, 2001). It differs from previous models in that it is spatially explicit, utilising a Cartesian co-ordinate system to model interactions and includes a complex light model that calculates the light regime by considering the daily and seasonal movement of the sun (Figure 2.4, c). SORTIE is well known for its capability to include interspecific variation in growth and mortality and for its linkage to site conditions through rigorous calibration from field data. The design uses measurements of fine scale processes to project community dynamics (Busing & Mailly, 2004) and individual sub-models are empirically parameterized and validated with species-specific data (Taylor et al., 2009). SORTIE also builds on FORET (a modification of JABOWA describing foliage distribution) in its representation of tree crowns as cylinders as opposed to homogenous disks (Figure 2.4, b, c) and the ability to model canopy light transmission. Though this light management provides increased realism there is a computational and parameterization-effort cost (Bugmann, 2001).

Criticisms of gap models are based on their underlying structure which despite improvements and modifications are (in some cases) crude and generalised (Pacala et al., 1996, Kimmins, 2004). Ease of parameterisation is key to the success of IBMs and, although JABOWA was unrealistic in some aspects, it was conceptually simple and the data needed to parameterise it was easily accessible (Berger et al., 2008). Also little attention has been paid to physiology and ecosystem functioning (such as carbon, nitrogen and water cycling) in traditional gap models, which instead focus on forest composition and structure (Bugmann et al., 2001). Overviews of gap models are provided by Bugmann (2001) and Shugart (1996).

2.4.4 Uneven-aged/CCF Modelling challenges

Modelling contemporary forest systems with diverse species mixtures and age ranges increases complexity and requires adequate representation of regeneration, growth, competition and mortality (Mendoza & Vanclay, 2008). Regeneration is an essential component of real world CCF and is necessary if models are to run over any appreciable length of time (Vanclay, 2012). Busing and Mailly (2004) highlight the difficulty in modelling regeneration and identify three potential weaknesses with current methods: the compounding of stages from dispersal to establishment; an assumption of universal seed availability and discounting the impact of pathogens or animals (Busing & Mailly, 2004). A requirement of uneven-aged management, and a disadvantage of individual based models, is the need to model mortality. Mortality is difficult to predict and removing an individual from a simulation has consequences for the remaining trees (e.g. Taylor & MacLean, 2007). In effect meaning that models are stochastic which has implications affecting their implementation in forest management (Vanclay, 2012).

2.5 Social forestry/Ecosystem management (EM)

Kimmins (2004) describes *social forestry*, later termed *ecosystem management* (Kimmins et al., 2005) as forestry that sustains the desired social values and forest conditions that ecological forestry lacks; sustainable management of the forest as a complex, integrated system with one management plan that meets multi-value targets, based on diverse values and the social and biophysical sciences (Figure 2.1).

The view of forest ecosystems as a whole organism was proposed as a management strategy as early as 1923 (Puettmann et al., 2008) but mainstream thinking did not take to the idea. Franklin (1989), among others, suggested that it was necessary to shift focus to the maintenance of complex forest ecosystems and called for a shift of silvicultural focus away from the regeneration of trees, towards ecosystem complexity and the retention of biological legacies that maintained ecological consistency.

Scientists now advocate a paradigm shift to EM, considering goods and services at greater spatial scales than current silviculture (Bugmann et al., 2010), in combination with the increased significance of non-timber forest attributes, e.g. conservation, ecosystem services, resilience to climate change and recreation (Diaci et al., 2011). Kimmins (2007) highlights several basic attributes of EM, among them a requirement for sound ecological models. A key theme highlighted was that management should cross over levels of biological organisation and integration to manage forests ecosystems as a whole (Kimmins, 2007).

2.5.1 Sustainable development, Sustainable Forest Management, Criteria & Indicators

The principle of sustainable development has become widely accepted during the last 20 years (Hahn & Knoke, 2010). The Brundtland report on the politics of sustainable development defined it as: “development that meets the needs of the present without compromising the ability of future generations to meet their own needs” (Brundtland, 1987, p. 41). Effective management of natural resources is a core part of sustainable development but a wide gap exists between the objectives of sustainability and current natural resource management practices due in part to the limitations of “static (management) approaches based on standard economical models” such as maximum sustainable yield (Rammel et al., 2007). The Brundtland report effectively began a shift in paradigm from sustained yield to sustainable forestry (Monserud, 2003).

The 1992 United Nations conference on environment and development (UNECD), in Rio de Janeiro, established a link between participatory decision-making and the achievement of sustainable development (Hahn & Knoke, 2010). Potentially the most important document was the *Non-legally binding authoritative statement of principles for global consensus on the management, conservation, and sustainable development of all types of forests* otherwise known as the *Forest principles.* Annex 22.1 within this, *Managing forested landscapes for socio-ecological resilience*, became the basis for international sustainable forest management (SFM) frameworks through the development of criteria and indicators (C&I) that integrated the social, economic and ecological functions of forests (Reed et al., 2010, Corona & Scotti, 2011, Menzel et al., 2012, Mäkelä et al., 2012).

The Ministerial Conference on the Protection of Forests in Europe (MCPFE) subsequently applied sustainable development to European forests and defined *sustainable forest management* along with specific C&I. Concurrent and comparable international initiatives occurred in other countries e.g. the Montreal process (Monserud, 2003, Mäkelä et al., 2012), an internationally agreed working group for the establishment of C&I for sustainable management of temperate and boreal forests. The working group consists of 13 member countries (including the U.S., Canada, Australia and New Zealand), however approximately 150 countries worldwide are engaged in other regional or international criteria and indicator processes (Sato, 2009)

Sustainable forestry can be defined as embodying various management techniques that provide long-term social, ecological, economic and cultural benefits to future generations without reduction in the health and integrity of the forest ecosystem. Though all encompassing, this multi-faceted definition is not easily quantified by science (Monserud, 2003). The purpose of C&I is therefore as quantitative and qualitative measures of sustainable forestry (Monserud, 2003, Wolfslehner & Seidl, 2010). The indicators are periodically assessed elements demonstrating the level and direction of change in relation to each criterion. However, it is not necessarily the case that the link between stand condition and indicators is properly understood and Mäkelä et al. (2012) state that indicator choice is often driven by data availability rather than theoretical concerns. Studies investigating the use of C&I at the operational scale of SFM include: Popp et al (2001), Wintle and Lindemayer (2008) and Muys et al. (2010).

The inclusion of C&I is also an important challenge for modellers (Auclair, 2010) and forest growth models, whilst valid for SFM, require important developments in both model outputs, in relation to assessment of sustainability, and methods to evaluate management operations to better represent the C&I (Mäkelä et al., 2012). The MCPFE defined six sustainability criteria and their indicators that encapsulated social, economic and ecological attributes of forests (Pretzsch, 2006). Mäkelä et al (2012) group these indicators into four stand level modelling related categories: those that can be derived directly from model outputs; those that are derived from scaling up stand level results; those that directly refer to sustainable management practices and those that refer to current land-use and regional or national statistics. They suggest that a broad suite of models would be necessary to encapsulate growth and yield alongside the other pivotal aspects of ecosystem functioning related to the sustainability criteria and indicators (Mäkelä et al., 2012).

2.5.2 Ecosystem Management

The Millennium Ecosystem Assessment (MEA) (2005) brought together more than one thousand natural and social science experts to conduct a systematic review of the state of the world's ecosystems. The MEA (2005) found that there had been substantial and largely irreversible loss of Earth's diversity, many ecosystem services were degraded and the risk of non-linear change had increased. It was stated that new approaches to the management of social and natural capital were needed, based on an understanding of ecosystem function, to maintain ecosystem services (Reed et al., 2010). Forestry has shifted management from sustained-yield to ecosystem approach in an effort to preserve ecological integrity and ensure future resource provision (Taylor et al., 2009), evolving to a situation that attempts to ensure long-term maintenance of ecosystem functionality that retains other social and economic benefits (Auclair, 2010). The central tenet of this change is that it is no longer acceptable or possible to manage forests for a single aim; multiple objectives other than timber production are now necessary. These multiple objectives are generally termed ecosystem services and encapsulate broad services such as provisioning (food, water), regulating (water catchment), cultural (aesthetic, recreational) and supporting (nutrient cycling, biodiversity maintenance) (Auclair, 2010, Fontes et al., 2010).

Undoubtedly heavy-handed industrial silvicultural practices reduce the heterogeneity of forest ecosystems (Puettmann et al. 2008). However with finite land, and an increasing demand for timber, plantation forestry has needed to intensify at a time when there is a greater expectation for producers to increase emphasis on non-timber goods and services (Vanclay, 2003). Expectations are that within 20 years, plantations will provide half the world's wood fibre, half from the tropics and sub-tropics (Lee et al., 2011), however concerns about disappearing forests and climate change, coupled with greater public and scientific perception, are forcing silviculturists to accommodate wider ecological and societal values (Puettmann et al. 2008). Historic data and climate models show clear increases in temperature and atmospheric CO2 concentrations that will inevitably have effects on natural vegetation dynamics and range distribution (Auclair, 2010). In 2011 the IUFRO board stated that the major challenge for the forestry sector and forest research was the adaptation of forestry and forests to climate change (Lee et al., 2011). The report highlighted forest events that impacted livelihoods worldwide including: large-scale mortality, dieback, and changes in growth, productivity, tree physiology and biodiversity. Within Europe, an increased frequency of extreme events such as droughts and floods is deemed to be due to regional precipitation regime changes and increased temperatures induced by a changing climate (Bugmann et al., 2010). With further temperature rises and shifting patterns of precipitation predicted under climate change scenarios the weather and climate variations present uncertainty to the management of forest systems. (Reed et al., 2010, Puettmann, 2011).

Ecosystem management holds the concept of integration as a central characteristic. European forests, generally, fulfil a multitude of objectives at each site as opposed to practices elsewhere in the world where forestry plantations are separated from other functions such as conservation and recreation. This integrated approach involves the consideration of social, economic and ecological functionality, managing trade-offs to achieve multipurpose objectives that do not need to be so actively considered where forestry is segregated. Planning and decision making increase in difficulty as demands on forest services diversify, highlighting, among other considerations, the necessity of effective knowledge transfer from science to practice (Peng, 2000).

2.5.3 Resilience

Historical theories of natural resource management have generally been based around the adaptation of species, populations, communities and ecosystems to disturbance (Lee et al., 2011). Complex dynamics can result from disturbance events, altering landscape structure, successional pathways and ecological processes at a multitude of scales (Sharik et al., 2010). The expectation that ecosystems recover depends on how narrowly its properties are defined and, if considering the whole, it is not necessarily the case. Research into ecosystem recovery after disturbance has gained prominence due to the influence of climate change and human intervention (Sharik et al., 2010).

Theories of nonlinear ecosystem regime shifts are gaining credibility. Threshold effects were discussed in the MEA (2005) where regime shifts, as non-linear changes, occur in response to one or several drivers, often associated with biodiversity shifts (Auclair, 2010). Ecological resilience relates to how much stress a system can absorb before a regime shift to an alternative structure or mode of function (D'Amato et al., 2011). It can be described as the capacity to buffer disturbance and reorganise, whilst changing, to maintain continuity of identity, structure and function (Folke et al., 2004, Reed et al., 2010). Reduction of ecosystem diversity and interruption of processes reduce the resilience of ecosystems and increase the likelihood of unwanted regime shifts (Folke et al., 2004).

Bio-diversity is suggested as key to the evaluation of a system's stability with increases in the horizontal and vertical structural heterogeneity of a stand linked to a higher number of species. Within an ecosystem undergoing change, the diversity of functional groups, and species within those groups, has a substantial relationship to the level of resilience and maintenance of desirable states (Elmqvist et al., 2003). This can be described in terms of the diversity of responses to environmental change, among species, when considering the same ecosystem function (e.g. primary production) (Elmqvist et al., 2003, D'Amato et al., 2011). Reduced response diversity increases vulnerability of an ecosystem to disturbance or climate shift, increasing the likelihood of detrimental changes to ecosystem services and attributes such as yield and biodiversity (D'Amato et al., 2011). Theoretically then, a system is able to respond or adapt to climate change by maintaining elevated levels of structural, compositional and functional complexity in line with theories of ecological resilience (D'Amato et al., 2011).

Forest management is evolving to support adaptation through maintenance of compositional and structural diversity (D'Amato et al., 2011) with the resilience and adaptability of managed forests believed to be improved by the integration of complexity into silvicultural prescriptions (Mizunaga et al., 2010). The benefits of silviculturalists moving towards management paradigms that embrace the idea of complex systems include allowing the forests to respond to change (Puettmann et al., 2008).

Achieving complex stand structures potentially requires more intervention though that results in greater expense or necessitates more advanced treatments (Mizunaga et al., 2010). However the benefit of maintaining ecosystem resilience to factors such as climate change or invasion from exotic species can be easily understood (Puettmann et al., 2008). *Rhododendron ponticum* is an important invasive species in the British Isles that is receiving considerable modelling attention regarding its spread in to forested areas. *R. ponticum* shrubs can quickly spread by layering, forming dense shaded thickets with toxic foliage and acid litter that impede the regeneration of other species (Nadezhdina et al., 2004). Ground flora is also shaded obstructing regeneration cycles and affecting forest replanting (Rotherham, 2001). The case for *R. ponticum* is discussed in Chapter 4.

Theoretical literature related to resilience is abundant, however guidance on implementation is an emerging research field (Reed et al., 2010). The theoretical basis of resilience management is supported by work in fields such as chaos theory and complexity studies, which, in combination with increases in computational capacity, has led to investigations of emergent behaviours related to parts and processes of ecological systems (Reed et al., 2010). If resilience is the goal it is necessary for managers to understand what allows an ecosystem to maintain its integrity when perturbed (Levin, 2005). A future direction for disturbance research is assessing the impacts of disturbance dynamics at varying scales to determine the scale sensitive thresholds for specific interactions (Sharik et al., 2010).

2.5.4 Complex Adaptive Systems

Within the natural and social sciences awareness is increasing that socio-economic, physical and ecological systems have common characteristics to complex adaptive systems

(Rammel et al., 2007). Evolutionary biology studies during the 1920s highlighting the connections between elements and feedback loops, as opposed to cause and effect relationships between single elements, formed the basis of systems-thinking (Reed et al., 2010). Complex adaptive systems can be defined as ‘being composed of populations of adaptive agents whose interactions result in complex non-linear dynamics, the results of which are emergent phenomena’ (Brownlee, 2007, p. 1). The study of complex adaptive systems relates to how interaction patterns and complex structures can form from chaos via simple but powerful change-based rules. Levin (2005) states the essential elements as: individuality of constituent parts; interactions at local scales; “an autonomous process that selects from among those” constituent parts, ‘based on the results of local interactions, a subset for replications or enhancements’ (Levin, 1998, p. 432).

Ecosystems are often used as primary examples of complex systems (Kimmins et al. 2005). The global biosphere and ecosystems can be defined as complex adaptive systems because macroscopic system properties, e.g., nutrient flux patterns, productivity-diversity relationships and trophic structure emerge from interactions between components and (potentially) feedback, influencing the consequential interactions (Anand et al., 2010, Levin, 1998, Levin, 2005). Three main characteristics define the emergent properties in ecological systems: i) they don’t exist as isolated subsystems, ii) at higher levels they are a result of interactions in the subsystems, and iii) it is not possible to deduce the properties at one level by investigating the lower levels (Breckling et al., 2005). The simplified structures of heavily managed systems are imposed exogenously rather than arising endogenously. Therefore they are not purely CAS and without adaptive responses they are exposed to single stresses, such as insect infestation (Rottier, 1984).

With social demands on ecosystems continuing to change, future demands may be completely different without historical equivalent: *no-analog* systems. A consequence of this is that future managers may not be able to rely on their knowledge and experience of past ecological functioning (Puettmann 2011). Future silviculturalists may encourage forests towards a desired window of possible states rather than to a specific condition. New technologies that integrate a forest ecosystems temporal and spatial range would be necessary to account for the uncertainty. If we accept that forest ecosystems are in a non-equilibrium state then managing for resilience implies that changes in one ecological process can cause non-predictable emergent behaviours in others (Reed et al., 2010). Complex systems theory is potentially one way to address issues of non-linearity in ecosystem management (Auclair, 2010). Guidance from complex systems theory can be used in order to develop new forest management systems (Reed et al., 2010). For managers to accept emergent behaviours and a certain lack of predictability within future forest management systems is a dramatic shift from conventional forestry practices that focus on predictable constrained outcomes (Reed et al., 2010, Puettmann et al., 2008). The expectation is that traditional "command and control" paradigm management must be replaced by integrated, innovative methodologies that encapsulate the inherent complexity of social and ecological systems (Parrott et al., 2012).

2.5.5 Adaptive management

Increasingly diverse and intense societal demands placed upon forests, alongside rapidly (relative to the preceding few centuries) shifting abiotic influences, require complex and adaptive management scenarios (Pretzsch, 2006, Fontes et al., 2010, Reed et al., 2010, Lee et al., 2011). A systems adaptive capacity is its potential to adapt to the effects of perturbations. Exceed this capacity results in changes that are a natural function of ecosystem dynamics, but potentially undesirable from an anthropocentric viewpoint (Hahn & Knoke, 2010).

Adaptive management is an emerging field as contemporary issues of sustainable forestry move beyond the scope of traditional knowledge and management tools alone (Wolfslehner & Seidl, 2010). Planning must now also incorporate the values and objectives of multiple stakeholders in a transparent consistent process, rather than solely the application of technical knowledge (Wolfslehner & Seidl, 2010). Adaptation is not only about coping with negative future states but also about maximising future opportunities. Avoidance of risk can be implemented by increasing ecosystem resistance to disturbance or by maximising resilience to allow a system to return to (near) its initial state. Both strategies are valid, and risk avoidance is necessary to some degree, but what is the optimal situation that consequently allows maximisation of opportunity (Hahn & Knoke, 2010).

2.5.6 Decision Support

Significant consequences of management actions can take 50 years or more to develop (Kimmins et al., 2008) therefore effective management and planning requires the use of quantitative models that project responses to natural and human disturbances (Busing & Mailly, 2004). Scenarios developed as part of the MEA call for the use of advanced decision support tools that are increasingly proactive to issues of interest including changing climate (Auclair, 2010). The projection of management scenarios across differing spatial and temporal scales is critical for strategic planning to achieve sustained yields whilst maintaining expected ecological and social conditions (Taylor et al., 2009). Simulation is therefore a key component of decision support as models are capable of predicting potential outcomes of management decisions, allowing the formulation and investigation of alternatives (Muys et al., 2010).

Whatever models are constructed for, adoption is crucial to utilisation. To be adopted models need to be accessible, available and ready to be used (Vanclay, 2003). Forest resource trend analysis by forestry sector governmental planners and policy makers increasingly makes use of simulations (Muys et al., 2010) and future model development solutions could involve the coexistence of various modelling approaches that allow different intuitive decisions at different scales. Fontes et al (2010) use the context of climate change to review forest models as tools for aiding forest management. Other previous reviews include: (King, 1993, Korzukhin et al., 1996, Makela et al., 2000, Robinson & Ek, 2000, Landsberg, 2003, Van Oijen et al., 2005).

2.5.7 Ecosystem models

As early as 2000 it was suggested that biome shift and forest succession models were valuable tools in the investigation of global change and forest ecosystems (Pretzsch, 2000). Forest ecosystem simulation models facilitate a deeper understanding of the functioning between key ecosystem components and help predict how the processes of a forest landscape affect the state variables of a dynamic system (Vacchiano et al., 2012). Various levels of spatial or temporal resolution can be used with spatial scales varying from cells to the global carbon production and temporally from seconds upwards (Pretzsch, 2000).

A recent trend in landscape modelling has been the integration of GIS with forest models, mostly only loosely coupled for visualisation or basic data processing, but further integration is possible (Mendoza & Vanclay, 2008). Landscape modelling integrates computer simulation and GIS technology with the fields of quantitative and landscape ecology. Forest ecosystem models developed during the 1990s are capable of simulating processes at multiple scales. Among them was LANDIS a spatially explicit grid based model capable of simulating landscape forest changes and natural (e.g. hurricane, fire) and anthropogenic (e.g. felling) disturbances. It has been used to simulate landscape dynamics at large (> 10^5 ^{h}a) scales, including climate change, seed dispersal, succession, management and carbon cycling (Xi et al., 2009). Xi et al (2009) provide a listing of commonly used models detailing their features, key research questions and application.

2.5.8 Data and Technology

Data has shifted from the early modelling situation where data was scarce and computers were more powerful than could be utilised, to the current point where large amounts of data are now available and underutilised. We now record so much data that much of it is wasted, and consequently reduced in value due to difficulties in identifying important factors (Vanclay, 2003).

Large scale spatial data analysis grew in the 1980s, driven particularly by the adoption of Landsat Thematic Mapper satellite images, GIS software and increases in computational speed and storage capacity (Xi et al., 2009). Global vegetation monitoring is now possible using high spatial and temporal resolution satellite systems. The foundation technology of these endeavours is remote sensing and key quantifiable indices, aside from land conversion rates and types, include: biomass, vegetation cover (%), net primary production and net ecosystem production ("the net effect on C storage of gains through photosynthesis and losses through ecosystem respiration" (Turner, 2011, p. 4). The United Nations Food and Agriculture Organisation (UNFAO) has recently supported the Integrated Global Observing System in a move towards developing a more integrated global monitoring system aiming to provide comprehensive coverage of oceans, land and climate (Turner, 2011).

Models can be used to explore management scenarios, engaging stakeholders and educating them to a systems complexity. Hybrid models that integrate GIS with agent or individual based methodologies are increasingly used, based at a low structural level. For example, an individual or landscape unit with higher level functions emerging as properties of the lower (Parrott et al., 2012).

There is also potential for innovation with forest growth modelling using new technologies including automated data collection, animation of model outputs and modelling software. Satellite data and forest machines provide avenues to collect traditional growth and yield data as well as new data types. LiDAR has the ability to survey large areas rapidly and to record individual tree measurements (e.g. Hill & Broughton, 2009). Also with increasing mechanisation of harvesting operations many feller-bunchers used for harvesting contain on-board computers and GPS combined with harvesting heads that are capable of recording information about each stem harvested: biomass (from a load cell in the hydraulic arm), diameter, length etc. along with coordinates from the GPS (Vanclay, 2003). The combination of airborne LiDAR and data collected from feller-bunchers (tree GPS location, diameter etc.) during forestry operations can be added as census data to recalibrate "learning models" capable of refining estimates of plantation productivity (Vanclay, 2003). Online integration of the harvesting technology, growth models, and harvesting information systems would allow real time updating of the felling operation to easier complete felling requirements and ensure that management was optimised by only felling what was absolutely necessary (Vanclay, 2003).

2.6 Discussion

Trade-offs exist in natural science modelling between a desire for realism, accuracy of simulation and model generalisation. Though our conceptual and computational models of ecosystems have become increasingly complex as our understanding of their complexity increased (Kimmins et al., 2008) it has been suggested that simulation models have not fulfilled their potential for expanding our understanding of ecology, due to inadequate representation of the complexity of the modelled systems (Grimm, 1999, Kimmins et al., 2008). As theoretical ecology, mathematical and modelling concepts have developed, alongside increases in computational capacity, modelling interest in the concept of ‘complexity’ has grown. The implementation of ecosystem models is one area that is highlighting the challenges involved in modelling complex systems, much the same as the construction of yield tables highlighted gaps in early foresters understanding of system dynamics (Auclair, 2010).

Strategic forest management planning is required to ensure successful implementation of ecosystem management, including being able to evaluate and forecast the future composition of forest units (Taylor et al., 2009). Lack of practical experience in novel management techniques (e.g. CCF) and the need to compensate by using scientific tools to produce management guidelines has been recognised by silviculturalists (Mason et al., 2003). Ecological models are valuable because rather than predict the future they assist in our understanding of nature’s patterns and processes through the exploration of complex, explicitly stated assumptions (Bugmann et al., 2001). However one model shouldn’t necessarily be expected to cover all management objectives and to be applicable models need to be integrated within decision support systems that potentially include multi-criteria decision methods, optimisation techniques, participatory tools and visualisations. The increasing need to address complexity in forestry and forest ecosystems requires management models that are capable of more than traditional systems (Kimmins, 2007).

Makela et al. (2000) summarise the outcome of the 1998 IUFRO meeting *Process-based models for forest management* held at Saariselkä, Finland by highlighting that the implementation of such models would be accelerated with the general acceptance that empirical models and process models will be mutually improved by integration of components as hybrid models. A further point stated the necessity for cooperation between forest managers and modellers for the ideas to be incorporated into operational situations.

With modellers required to take the initiative and cooperate with forest managers in order to make progress (Monserud, 2003).

One solution for further research involves the coexistence of empirical and PBMs for forest management fulfilling different roles: eco-physiological models would guide long-term decision making processes and conventional growth and yield models would fulfil operational requirements (Pretzsch, 2006). However a more intuitive approach and the likely future direction lies with hybrid models (Mendoza & Vanclay, 2008).

The selection of parameters and construction of models requires different source data when changing from models with low resolution tree and stand management to increasingly complex eco-physiological models. This data base can only really be provided by inter-disciplinary cooperation and widening experimental concepts (Pretzsch, 2000). The production of models of value to practitioners, can guide scientists' research priorities and also provide a platform for discussion between differing modelling methodologies (Makela et al., 2000).

Experience and empirical data are a reliable basis when faced with constant or slowly changing conditions. However, to provide management scenarios when faced with changing or uncertain conditions, it becomes necessary to combine experience with scientific understanding of system processes. Kimmins (2005) believes that forestry has not incorporated science to the extent that is possible for three main reasons. Firstly a lack of consensus among scientists about the best policy or practice adds confusion. Also, in general, science is viewed to be about the biological and physical sciences, marginalising the now apparent social science elements of forestry (people's values, needs and desires). Lastly confusion exists about how science works, with many people expecting that science provides single correct solutions to problems when in fact the reality is much more complicated.

Ecological history has followed a path of increasing complexity in theory and explanation. In tandem the path of modelling has moved from relatively simple bioassay models to the simulation of complex ecosystem dynamics (Kimmins, 2008). The idea of complexity appears to contradict the concept of parsimony that has dominated modelling theory. A translation of Occam's razor "do not posit complexity more than necessary" is echoed in the words of Albert Einstein "make everything as simple as possible but not simpler", summed by Kimmins (2008) to "As simple as possible but as complex as necessary".

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Chapter 3: Coed-y-Brenin permanent sample plot forest mensuration and ecological site classification

3.1 Introduction

The natural range of coastal Douglas fir (*Pseudotsuga menziesii* var. *menziesii*) covers 18.8 Mha (Hermann & Lavender, 1999) and extends from central British Columbia (western North America) into California via the Pacific mountains. One of the earliest imports of Douglas fir seed to the United Kingdom was by the Forestry Commission in 1921, sourced from the Lower Fraser Valley, British Columbia, Canada (Phillips, 1993). The United Kingdom is one of the European countries with the largest share of Douglas fir plantations outside of North America, alongside France, Germany and the Netherlands (Hermann & Lavender, 1999). The 1995-1999 National Inventory of Woodlands and Trees (NIWT) recorded 45,224 ha across GB (Smith & Gilbert, 2003), equating to 3% of all conifer cover. Douglas fir can occur as monocultures or as mixed plantations (< 80% Douglas fir), and is commonly grown with Sitka spruce (*Picea sitchensis* [Bong.] Carr.), a popular commercial tree. Mixtures are favoured by current policies designed to diversify conifer plantations (Mason & Britain, 2006). An assessment of the suitability of Douglas fir in future climate scenarios by Ray et al. (2002) indicated that Douglas fir will remain "Very Suitable" in southwest and east Wales, while becoming more Suitable across the whole of Scotland, making it an important commercial forestry species.

Patch clearfelling is the primary silvicultural system in use in Britain and, in 1999, was employed in approximately 90% of managed forests (Mason et al., 1999). A contemporary goal of Great Britain's regional forest strategies is the increase of woodland resources that are sustainably managed for timber, biodiversity, amenity and recreation. These strategies have created a paradigm shift towards more sustainable and diverse management practices, leading the Forestry Commission of Scotland and Wales to designate areas for low impact silvicultural systems, such as Continuous Cover Forestry (CCF) (England (Forestry Commission, 1999), Scotland (Forestry Commission, 2006) and Wales (Forestry Commission, 2001)). The Welsh Assembly intend to convert ≥50% of its woodlands to CCF by 2020 (Forestry Commission, 2001). This shift has increased research into CCF systems, containing Sitka spruce and Douglas fir, within the Forestry Commission (Mason et al., 1999, Malcolm et al., 2001, Kerr et al., 2002, Mason et al., 2003) and in academia (Pommerening & Murphy, 2004, Schütz & Pommerening, 2013). A particular concern with conversion to CCF is the possibility of increased vulnerability to *Rhododendron ponticum* invasion[1].

Rhododendron (*Ericaceae*), was repeatedly introduced to Great Britain from 1763 onwards from the Black Sea region and Iberian Peninsula (Erfmeier & Bruelheide, 2010) with re-colonisation originating from a Gibraltan seed by plant collectors from Kew Gardens (Rotherham, 2001). A survey of chloroplast DNA variation in 260 naturalised populations indicated that 89% contained genetic material unique to Spain and 10% contained genetic material unique to Portuguese populations (Milne & Abbott, 2000). Though present during the inter-glacial periods, this plant is now categorised as a naturalised non-native species. Widely established but especially invasive in Snowdonia, Scotland, western England and areas of Ireland (Rotherham, 2001, Harris et al., 2009), *R. ponticum* is now one of eight non-native terrestrial plant species in Great Britain designated as the highest invasive species threat (Edwards, 2009). The majority of Welsh invasive stands are in Snowdonia where blanket bogs, heath and woodlands, some designated at the European level as Special Areas of Conservation, are threatened. Though control can be effective, the main barrier is the associated cost (£150 to £10,000 per

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[1] Aled Thomas, FC Wales Local Area Manager, Dolgellau

hectare) (Harris et al., 2009). The cost of eradication in Snowdonia national park alone has been estimated at £10 million (Jackson, 2008).

In forestry terms, invasive interference with stand development has an associated economic cost that varies in relation to the level of invasion (Harris et al., 2009). Thriving in areas with high rainfall and humidity, and light, acidic soils (Peterken, 2001), *R. ponticum* shrubs can quickly spread, forming dense shaded thickets that imped the regeneration of other species (Nadezhdina et al., 2004). Dark shade and potentially allelopathic effects break the natural regeneration cycle, restricting the germination and establishment of native tree seedlings, ground flora and many bryophytes (Peterken, 2001, Rotherham, 2001). Overall biodiversity loss continues as native species are suppressed leading to a consequential reduction in reliant fauna (Harris et al., 2009). The leaves and roots of *R. ponticum* are allelopathic to other species (Jackson, 2008) with sufficient quantities of phenols to deter herbivores (Rotherham, 2001). Examples of poisoning of vertebrates and invertebrates also exist (Rotherham & Read, 1988, Judd & Rotherham, 1992, Rotherham, 2001).

The Forestry Commission ecological site classification decision support system (ESC-DSS) tool for Great Britain implements a multi-dimensional approach to site classification that matches site conditions and woodland communities to tree species in order to assist with sustainable forest management (Ray, 2003). The most suitable National Vegetation Classification (NVC) woodland communities for a site (Pyatt et al., 2001, Ray, 2003) are predicted based on vascular plant surveys, soil (soil moisture regime and soil nutrient range) and climate factors (temperature, moisture deficit, windiness and continentality) (Pyatt et al., 2001).

The objectives of this study are to (i) investigate the demographic dynamics of Douglas fir and sub-component tree species at three permanent sample plots established within Coed-y-Brenin forest, (ii) systematically survey the ground flora and invasive non-native *R. ponticum,* (iii) measure a range of abiotic factors (soils, climate, light) critical to stand development, and (iv) determine the ecological site classification to gain insight into the relationship between site conditions and invasive potential of rhododendron. The data from this study will also be used to parameterise a forest growth model for Douglas fir (Chapter 3) and contribute to a statistical model of *R. ponticum* establishment (Chapter 4).

3.2 Materials and methods

3.2.1 Coed-y-Brenin forest park

This study utilises three permanent sample plots (PSPs) in Douglas fir dominated plantations within Coed-y-Brenin (The Kings Forest) forest park, North Wales (52.824361, -3.8961077) (Figure 3.2) Situated at the southern edge of Snowdonia National Park, Coed-y-Brenin is approximately 10 miles in land from the Irish Sea and contains the confluences of the Afon (river) Wen, Mawddach, Gamlan and Eden. The climate has maritime influences, with an annual rainfall of 1216.8 mm and temperature range of 1.7°C to 19.8°C (mean 9.9°C) based on MetOffice 1981-2010 climate normals for Trawsgoed (Figure 3.1), which is situated ~54 miles south of the study site and at an altitude (63 m) similar to the PSPs (Table 3.1).

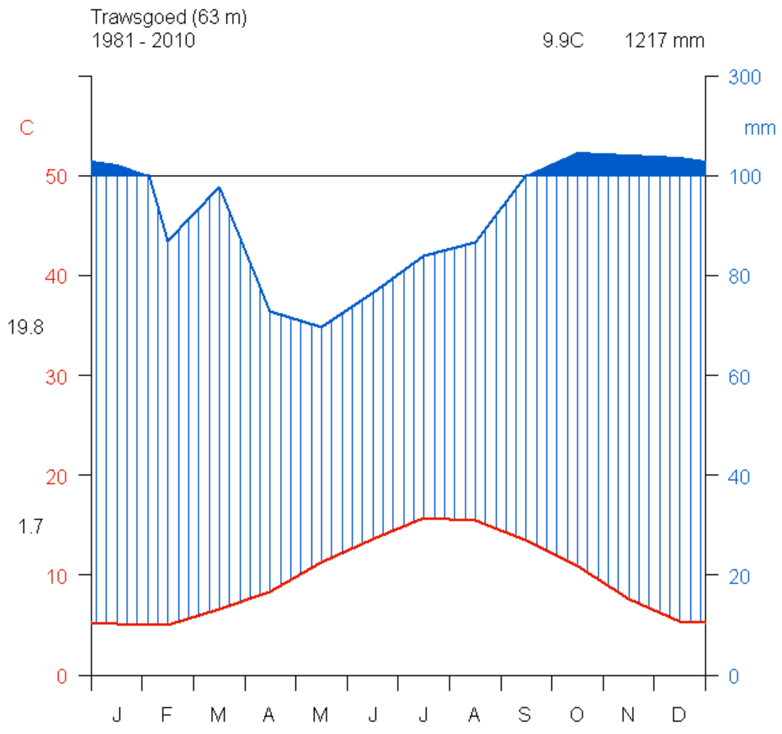

Figure 3.1. Monthly precipitation (blue line) and temperature (red line) based on 30 year climate normals (1981-2010) for Trawsgoed weather station (52.344, -3.947, 63m above mean sea level). Source: MetOffice, 2013

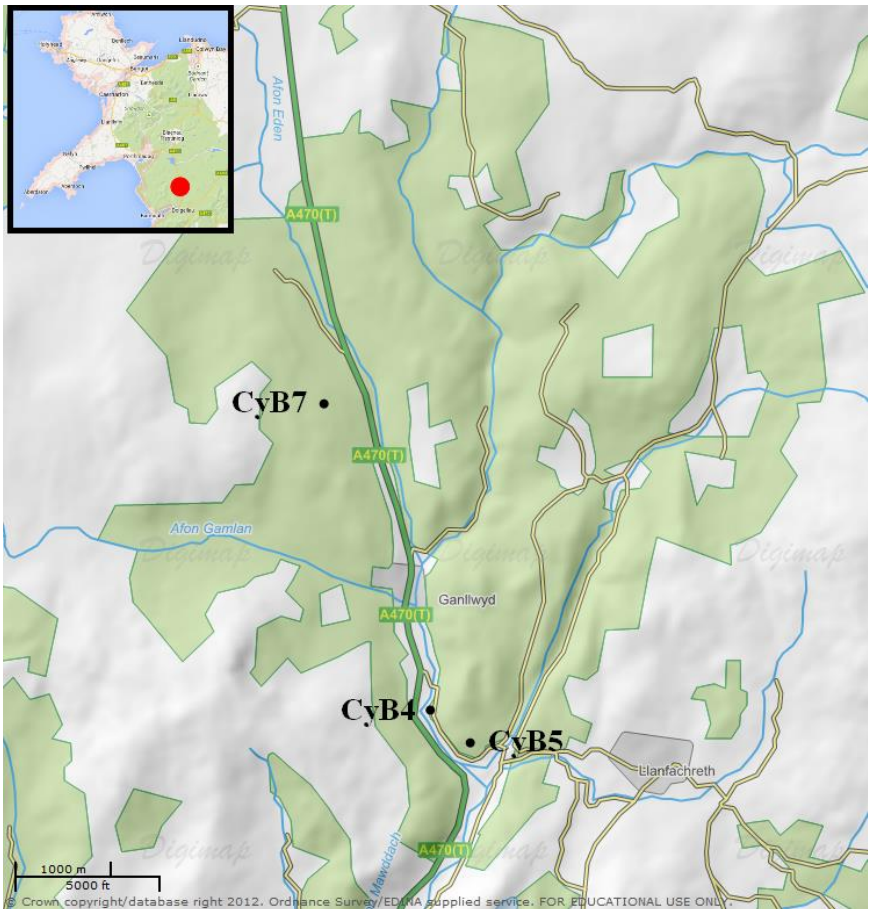

Figure 3.2 Location of the three permanent sample plots (CyB 4, 5, 7) in Douglas fir dominated plantations at Coed y Brenin, Wales. Grey shading shows relief of the land (Source: Edina Digimap). Inset: location of Coed-y-Brenin forest (Source: Google maps).

Table 3.1. Key characteristics of the three permanent sample plot (PSPs) at Coed y Brenin (CyB) at plot establishment.

	Permanent sample plot		
	CyB4	CyB5	CyB7
Establishment year	1928	1929	1985
Age in 2006 (years)	78	77	21
Latitude[a]	52.790440	52.787262	52.818528
Longitude[a]	-3.8867	-3.88016	-3.89987
Plot size (ha)	0.403	0.992	0.162
Elevation range (m)	46-66	73-84	152-163
Number of trees in 2006	108	292	387
Density in 2006 (trees ha)	268	294	2389
Douglas fir in 2006 (%)	74.07	65.75	69.25

[a] GPS coordinates for the SW corner of the plot

3.2.2 Tree demographic surveys

3.2.2.1 PSPs establishment in 2006

The three PSPs (Table 3.1) were established in 2006 by Dr. Arne Pommerening[2] as part of a Continuous Cover Forestry trial. Data was collected on tree, stand and site characteristics that covered a range of stand ages with the aim to establish a growth series of planted semi-natural forests in Wales (Pommerening et al., 2002). All trees with a diameter at breast height (DBH) of ≥ 5 cm were spatially mapped to a Cartesian co-ordinate system in the X, Y, Z planes, using a Topcon Total station, running PenMap software. PSP size varied between the three sites, with CyB5 the largest and CyB7 the smallest (and youngest), but most densely stocked (Table 3.1). All mapped trees were painted with a DBH line at 1.3 m above ground level (uphill side on slopes), given a unique numeric tag, and tree species, tree height and crown base height recorded with a vertex (Vertex III and Transponder T3, Haglof, Sweden AB).

The youngest PSP, CyB7, was planted in 1985 and is the most densely populated of the three plots. At plot establishment it was intended to be used as part of a thinning trial though no management has been carried out (Pommerening, pers. Comm., 2011). Detailed management data for CyB4 and CyB5 was lost during a transfer from paper to digital records (Thomas, A. pers. comm.). It is known that both PSPs were planted in the late 1920s. In forestry terms a normal rotation of Douglas fir is 45 – 60 years (Malcolm et al., 2001) and maximum mean annual increment is achieved at 50-65 years (Savill, 2013), by this definition, both CyB4 and CyB5, at 82-83 years, are over mature. They are both undergoing the understorey reinitiation phase of Franklin et al. (2002).

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[2] Formerly of University of Wales, Bangor.; now: Bern University of Applied Sciences

3.2.2.2 PSP resurvey in 2011

The PSPs were re-surveyed in 2011 for the purposes of this study. Existing trees were designated survivor growth (SG). Trees that had grown into the 5 cm DBH threshold were recorded as ingrowth (IG), numbered and marked according to the establishment protocol (Pommerening et al., 2002). Ingrown trees were mapped to the existing Cartesian co-ordinate system by measuring the distances and angles from existing neighbouring trees, using a Haglof Vertex. Distances and angles were then converted to radians and coordinate transformed. Canopy radius (metres) was recorded in four cardinal directions (N, E, S, W) using a compass clinometer (Suunto) and measuring tape for each tree above the 5 cm threshold to parameterise the tree growth model.

A systematic survey of trees less than 5 cm DBH trees was carried out through the establishment of 25, 4 by 4 m equidistant survey stations, arranged in a grid system within each PSP. Stations were subdivided into four 2m by 2m quadrats and species, diameter at 10 cm height, height and DBH (if present) were recorded.

GPS data was collected at six locations through CyB5 with a Leica 1200 I dual-frequency DGPS. The DGPS data was then post processed using surrounding RINEX reference stations (ADAR, ASAP, HOLY, MACY, SHRE) to improve position and height quality to 10-13 cm. A total station (Leica TCRP1205) survey mapped the GPS points to the surrounding trees and the Cartesian coordinate system to permit transformation of the PSP Cartesian coordinate system into Ordnance Survey GB grid references in ArcGIS 10 using the three best DGPS data points (ESRI, 2011).

3.2.3 CyB5 ground flora and invasive non-native rhododendron surveys in 2011

Vegetation was surveyed in two, 2 by 2 m, quadrats that were randomly[3] selected for each station (Figure 3.3, red squares). Vegetation was vertically stratified into ground flora (<1.3 m height) and understorey (≥1.3 m height). Species, abundance (percentage coverage), and density (number of individuals) (where appropriate) were then recorded.

3.2.4 CyB5 abiotic surveys of soil and light

3.2.4.1 Soil

The type of substrate and its abundance (percentage cover) was recorded for the two quadrats. O layer depth was measured at three locations within the stations and then soil samples were taken from the O and E layers at the same three locations. Collected soil samples were analysed for soil moisture percentage and organic matter content. Each sample was weighed, dried and re-weighed to calculate percentage moisture lost. The remaining sample was then sieved at 2 mm, ground and then baked for two hours in a furnace at 550° C. The cooled samples were reweighed to yield the percentage of organic matter lost on ignition (Davies, 1974). Soil data was then interpolated, using ordinary kriging, in Surfer 9 (Golden, 2009) to produce soil maps for the entire plot.

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[3] Using random.org, a ‘true’ random number generator that uses atmospheric noise, rather than pseudo-random number generators.

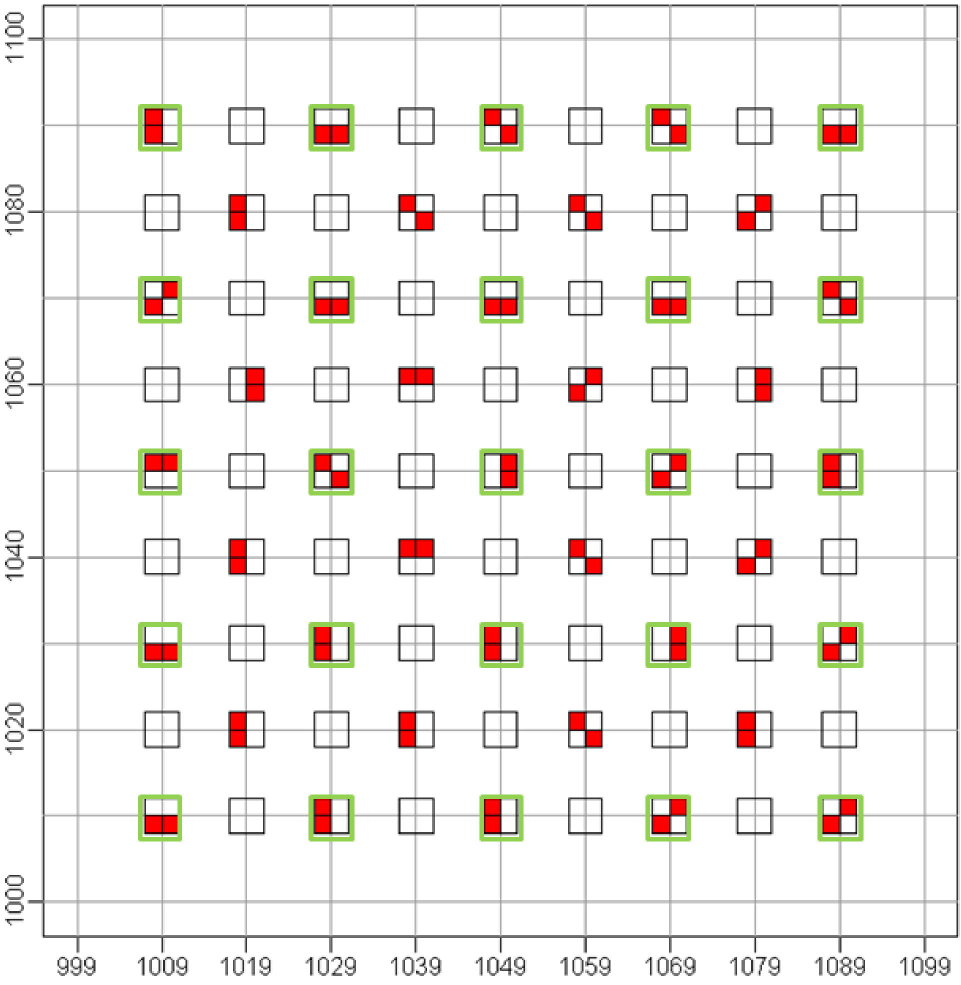

Figure 3.3 Layout of 81 equidistant stations on survey grid in CyB5; green edging indicates 25 4x4m tree regeneration stations and red shading 82 2x2m ground flora and rhododendron quadrats.

3.2.4.2 Light

Digital hemispherical photographs were captured at the centre of each of the 81 equidistant survey stations (Figure 3.3) using a CanonEOS1000D SLR with a Sigma/C 4.5mm f/2.8 EX DC HSM circular fisheye lens mounted on a tripod set to 1.3 m in height (floor to mount). Photos were taken on automatic settings with autofocus during periods of uniform, white cloud cover. A compass clinometer was used to ensure that the camera was level and oriented North to South.

The digital photographs were analysed with Gap Light Analyser (Frazer et al. 1999) using standardised techniques to calculate Global Light Index (GLI), a percentage measure of combined diffuse and direct radiation penetrating canopy gaps throughout the growing season (Canham et al., 1994, Pacala et al., 1994, Wright et al., 1998, Canham et al., 1999, Boivin et al., 2011). Hemispherical photographs are digitised, and a manual black and white threshold applied to distinguish sky from canopy components (Figure 3.4).

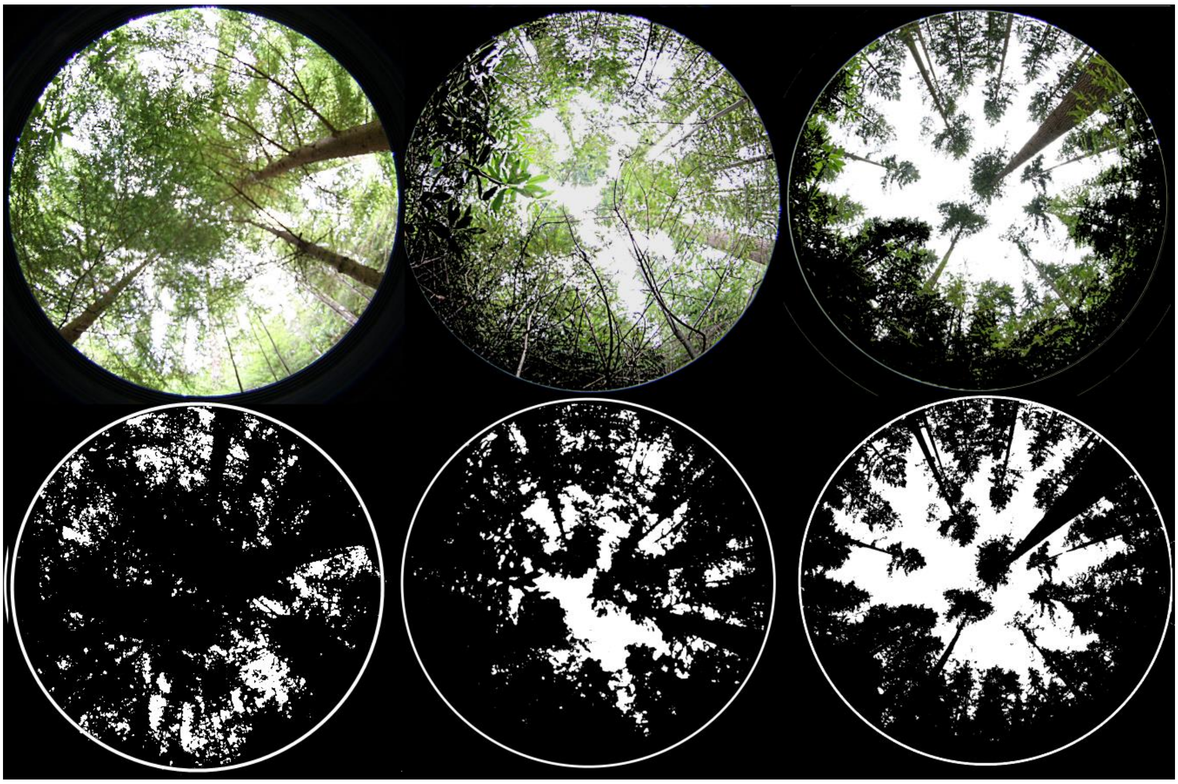

Figure 3.4. Examples of original hemispherical photos (top) and thresholded images (bottom) used in the Gap Light Analyzer software for CyB5 (Frazer et al., 1999)); Canopy transmittance from left to right: 10.29%, 32.86%, 50.93%. White outline around thresholded images (bottom) manually added to aid comparison with originals (top).

Canopy openness is computed by dividing the number of sky pixels by the total number of pixels. GLI is then calculated according to canopy openness and above-canopy growing season solar radiation defined by the following region specific parameters: the *Solar constant* (W/m^2), the total radiant flux of the sun on a perpendicular surface situated outside the atmosphere at a mean distance of one astronomical unit (kept at the recommended 1367 W/m^2); the *Cloudiness index* (Kt), a site specific measure of cloudiness, defaulting to 0.5; *Spectral fraction* and the fraction of global solar radiation incident on a ground level horizontal surface falling within a limited range of the electromagnetic spectrum (0.25 µm to 25.0 µm). Spectral fraction defaults to 0.45; the desired Units, defaulting at the incident photon flux density of Photosynthetically Active Radiation (mols/ m^2/d); and *beam fraction*, a ratio of direct (beam) to total (global) spectral radiation incident on a ground level horizontal surface over a distinct temporal period (e.g. hour, day, month, etc.). Cloudiness index was computed for the region by:

$$Kt = \frac{H}{Ho} \tag{3.1}$$

where *H* is the amount of global radiation incident on the ground and *Ho* is the amount of extraterrestrial radiation incident on a horizontal surface outside the atmosphere. *H* was obtained directly from the Centre for Environmental Data Archive for two locations: RAF Valley, Anglesey (53.275138, -4.500179; Alt. 22 m) and Cwmystwyth, Aberstwyth (52.351283, -3.778910; Alt. 243 m). *Ho* was modelled from within the GLA software to give:

$$Kt = \frac{11.35}{23.52} = 0.482 \tag{3.2}$$

Spectral fraction was computed as:

$$\frac{R_p}{R_s} = 1 - e^{-0.499 * Kt^{-0.219}} \tag{3.3}$$

R_p is the ratio of total daily global PAR to total daily global radiation (total shortwave). Giving:

$$\frac{R_p}{R_s} = 1 - e^{-0.499 * 0.482^{-0.219}} = 0.444 \tag{3.4}$$

Beam fraction is then calculated in a similar manner:

$$\frac{H_b}{H} = 1 - e^{-3.044*Kt^{2.436}} \tag{3.5}$$

Where H_b/H is the fraction of total daily direct global solar radiation incident on a horizontal surface, giving:

$$\frac{H_b}{H} = 1 - e^{-3.044*0.482^{2.436}} = 0.399 \tag{3.6}$$

3.2.5 Data analysis

3.2.5.1 Species classes and size classes

For the purposes of this document *recruitment* refers to all trees with a DBH less than 5 cm. As some trees do not have a DBH (those under 1.3 metres in height) Diameter at 10 cm height (cm) has been used as a reference metric. This measurement is also used for the SORTIE-ND forest model relevant to this study (Pacala et al., 1996). For the purposes of this document *adults* refers to trees with DBH ≥ 5 cm, this data includes *survivor growth* (adults with DBH ≥ 5 cm in 2006) and *ingrowth* data (adults with DBH ≥ 5 cm in 2011, but not in 2006).

For the purposes of this study tree species were grouped to provide sufficient numbers for model parameterisation. The four species groups were: Douglas fir (DF) (*Pseudotsuga menziesii,* recruitment: n = 1593; ingrowth: n = 152; survivor growth: n = 511)); the SNS species group consisting of Sitka (*Picea sitchensis,* dominant (recruitment: n = 240; ingrowth: n = 49; survivor growth: n = 55) and Norway spruce, *Picea abies* (recruitment: n = 1; ingrowth: n = 1; survivor growth: n = 16)); hardwoods (HWD), consisting of birch (*Betula spp.* dominant (recruitment: n = 35; ingrowth: n = 15; survivor growth: n = 74)), beech (*Fagus sylvatica* (recruitment: n = 1; ingrowth: n = 18; survivor growth: n = 5)), oak (*Quercus spp*. (recruitment: n = 16; ingrowth: n = 3; survivor growth: n = 5)), rowan (*Sorbus spp* . (survivor growth: n = 4)), hazel (*Corylus spp*. (recruitment: n

= 9; ingrowth: n = 4)), sycamore (*Acer pseudoplatanus* (survivor growth: n = 2)), willow (*Salix spp*. (survivor growth: n = 4)) and holly (*Ilex aquifolium* (recruitment: n = 18; ingrowth: n = 2; survivor growth: n = 1)). All remaining conifers were grouped into a softwood species group (SWD) consisting of western hemlock (*Tsuga heterophylla,* dominant (recruitment: n = 23; ingrowth: n = 82; survivor growth: n = 65)) Grand fir (*Abies grandis* (recruitment: n = 4; ingrowth: n = 14; survivor growth: n = 1)), Japanese larch (*Larix kaempferi* (survivor growth: n = 1)), scots pine (*Pinus sylvestris* (survivor growth: n = 1), and western red cedar (*Thuja plicata* (recruitment: n = 6; ingrowth: n = 8; survivor growth: n = 2)).

3.2.5.2 Ecological site classification

An ecological site classification was carried out following the guidelines from the Forestry Commission (Pyatt et al., 2001). The ESC-DSS calculates accumulated temperature, moisture deficit, windiness and continentality through a set of climate models, and soil moisture regime and soil nutrient range from more detailed site specific information such as: plant indicator species, humus form, tree rooting depth, soil texture and stoniness (Ray, 2003). Measures of soil quality are formed through a combination of the moisture and nutrient regimes to form a *soil quality grid*. The aim of the ESC is then to identify site type and consider the ecological or silvicultural options suited to that site (Pyatt et al., 2001).

The climate models (apart from windiness) calculate climatic factors from Meteorological Office data for the period 1961 – 90 that covers each 10 x 10 km square of Britain. The data consists of basic meteorological variables, such as monthly rainfall and monthly mean temperature. Accumulated temperature provides a measure of summer warmth and is calculated as the day-degrees above a 5°C growth threshold. Moisture deficit emphasises growing season dryness, rather than year wetness, by balancing potential evaporation and rainfall. Monthly rainfall is subtracted from monthly evaporation and summed throughout the year. The moisture deficit is the peak value (in mm) reached that year. Continentality, seasonal climatic variation, is negligible in Britain's maritime climate. Windiness is calculated by *DAMS*, an interpolation of tatter flag data that provides a representation of strong wind frequency and mean wind speed (Quine & White, 1994, Quine, 2000). *DAMS* scores range from 3 to 36, separated into nine classes (Pyatt et al., 2001)

In the ESC *Soil Moisture Regime (SMR)* is estimated in terms of eight classes that cover the wide range of soils suitable for tree growth: *very dry, moderately dry, slightly dry, fresh, moist, very moist, wet and very wet.* Climate, topography and edaphic conditions influence the soil moisture regime with moisture deficit an indicator of likely soil moisture regime. Part of the assessment of soil available water capacity is an assessment of soil texture which once defined is then related to and modified by depth and stoniness of the rooting zone. Soil available water capacity is then correlated with the moisture deficit to provide the soil moisture regime of freely draining soils (Pyatt et al., 2001).

The *Soil Nutrient Regime (SNR)* is divided into six arbitrary classes: *Very poor (VP), poor (P), medium (M), rich (R), very rich (VR) and carbonate (C)*. These arbitrary classes express nutrient availability for plant growth, along with pH and other possible nutrient problems. Lithology can refine the relationship between nutrient regime and soil type though it cannot be precisely defined given the variability within geological strata. Humus form is then used to locally adjust the soil nutrient regime, reflecting the breakdown of organic matter by organisms, providing an indicator of the soil itself (Pyatt et al., 2001).

Species suitability is assessed by fitting smoothed response curves for each of the climatic and soil quality factors. With an unsuitable rating in any one forcing an overall unsuitable rating. The ESC-DSS also matches NVC native woodland sub-community types to the ESC site type, and output the results, in a similar manner (Pyatt et al., 2001, p10).

The ESC classification requires ten quadrats. Ten stations were selected, forming a systematic grid of the site, and then a single quadrat within each was chosen using a random number generator (as previously).

3.2.6 Statistical analysis

Chi-square tests of association between rhododendron and surveyed species were carried out using a 2 x 2 contingency table to investigate associations. The critical threshold for a 2 x 2 contingency table is 3.84; values higher than the critical threshold indicate a significant negative or positive association. A comparison of the observed versus the expected value provides the direction of association (Fowler et al., 1998, p. 111 - 113).

3.3 Results

3.3.1 Tree demographics (2006 to 2011)

A total of 1135 adult trees were inventoried and mapped in the three plots,153 in Cyb4 (379. 65 trees ha^{-1}), 594 in CyB5 (598.79 trees ha^{-1}) and 388 (2395.05 trees ha^{-1}) in CyB7 (Figure 3.5, Table 3.1, Table 3.2). Stem locations and crown extents are shown in Figure 3.5.

As can be seen from the stem maps CyB7 is the densest and smallest stand (Figure 3.5, c) with considerably smaller crown widths relative to CyB4 and CyB5 (Figure 3.5, a and b respectively). CyB4 and CyB5 have larger areas of white space between crowns affecting understorey conditions.

Table 3.2. Basal area and stem density in 2006 for the three PSPs by size class and species. Values in brackets indicate percent of size class.

	Stem density (n ha^{-1})			Basal area (m² ha^{-1})		
	CyB4	CyB5	CyB7	CyB4	CyB5	CyB7
a. Recruitment (<5cm DBH in 2011)						
DF	1129.03 (67%)	1136.09 (90%)	67.90 (85%)	0.25	0.12	0.05
SNS	389.58 (23%)	84.68 (7%)	0.00 (0%)	0.15	0.01	0.00
HWD	134.00 (8%)	23.19 (2%)	12.35 (15%)	0.04	0.01	0.03
SWD	32.26 (2%)	20.16 (1%)	0.00 (0%)	0.01	0.01	0.00
All	1684.86	1264.11	80.25	0.45	0.15	0.08
b. Ingrowth (>5cm DBH in 2011)						
DF	39.70 (35%)	137.10 (45%)	0.00 (0%)	0.11	0.45	0.00
SNS	7.44 (7%)	47.38 (16%)	0.00 (0%)	0.02	0.20	0.00
HWD	9.93 (9%)	37.30 (12%)	6.17 (100%)	0.03	0.15	0.01
SWD	54.59 (49%)	82.66 (27%)	0.00 (0%)	0.24	0.45	0.00
All	111.66	304.44	6.17	0.40	1.25	0.01
c. Survivor growth (>5cm DBH in 2006)						
DF	196.03 (75%)	193.55 (66%)	1481.48 (68%)	41.12	29.39	27.38
SNS	29.78 (12%)	35.28 (12%)	148.15 (7%)	9.32	1.26	4.24
HWD	7.44 (3%)	5.04 (2%)	537.04 (24%)	0.06	0.04	5.19
SWD	27.30 (10%)	57.46 (20%)	12.35 (1%)	0.36	0.89	0.36
All	260.55	291.33	2179.02	50.86	31.58	37.17
d. Mortality (>5cm DBH in 2006)						
DF	2.48 (33%)	0.00	172.84 (82%)	0.86	0.00	0.62
SNS	4.96 (67%)	2.02 (67%)	6.17 (3%)	1.15	0.01	0.00
HWD	0.00	0.00	30.86 (15%)	0.00	0.00	0.10
SWD	0.00	1.01 (33%)	0.00	0.00	0.00	0.00
All	7.44	3.02	209.88	2.01	0.01	0.72

Species codes: DF, Douglas fir, HWD, Hardwood; SNS, Sitka and Norway Spruce; SWD, softwood.

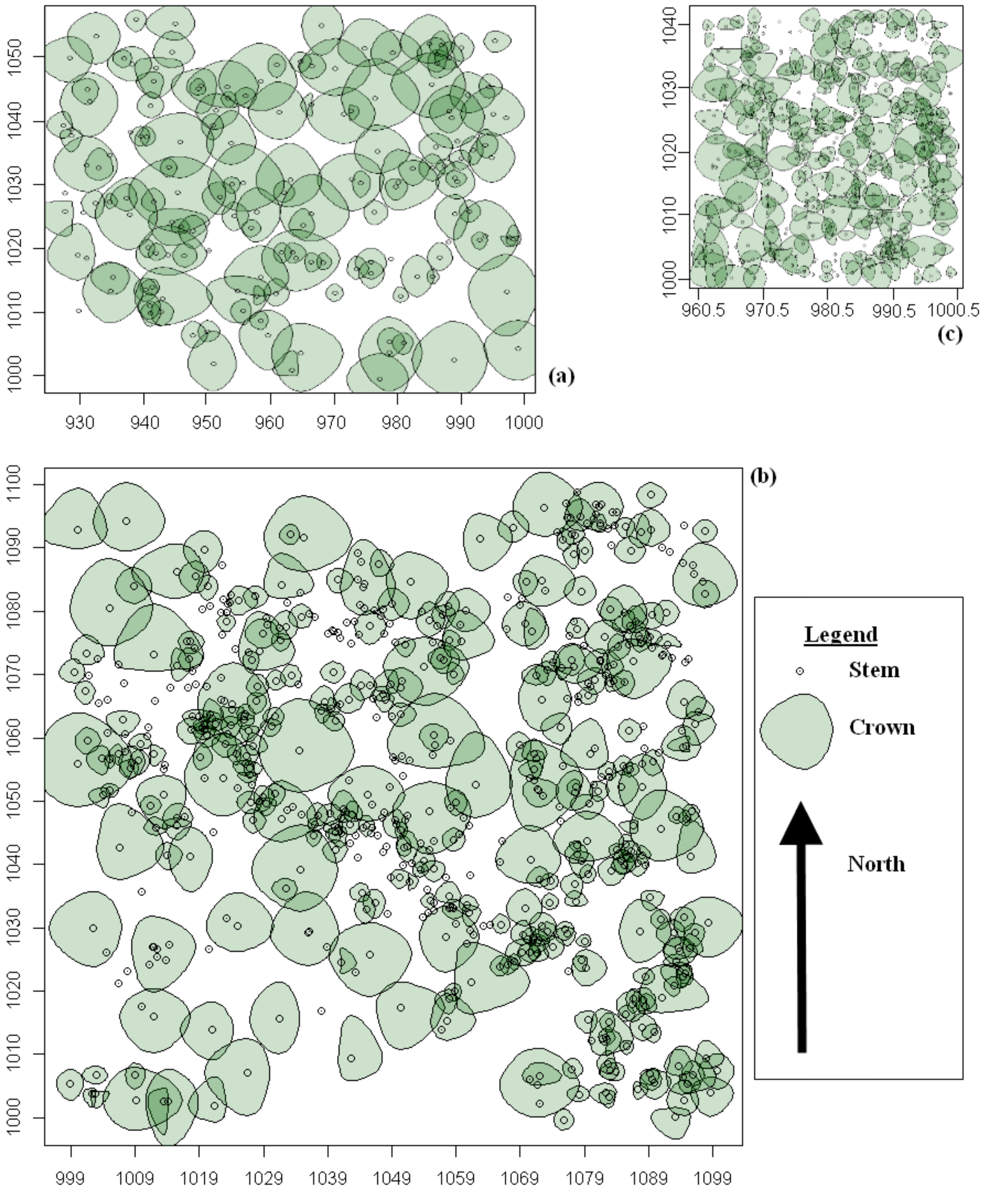

Figure 3.5. Permanent sample plots: CyB4 (a), CyB5 (b) and CyB7 (c) showing scale, stem locations and crown extent.

3.3.1.1 Recruitment

Recruitment was abundant in CyB4 and CyB5, and negligible in CyB7 in terms of both basal area and density (Table 3.2, Figure 3.6). CyB4 has the largest recruitment basal area of all the plots (Table 3.2), reflecting the shallow attrition of recruitment density across the size classes (Figure 3.6). Though CyB5 had a marginally greater number of DF recruits, CyB4's basal area was twice as large. Total recruitment stem density was also larger in CyB4 due to an abundance of SNS in the first two smallest size classes (0 to 1.5 cm and 1.5 to 3 cm diameter at 10 cm height) (Figure 3.6). Recruitment exhibited a classic J-shaped curve for both CyB4 and CyB5, with decreasing density across the diameter size classes. CyB7 did not exhibit any trend over the size class, and although sparse, DF was the dominant recruitment tree (Figure 3.6).

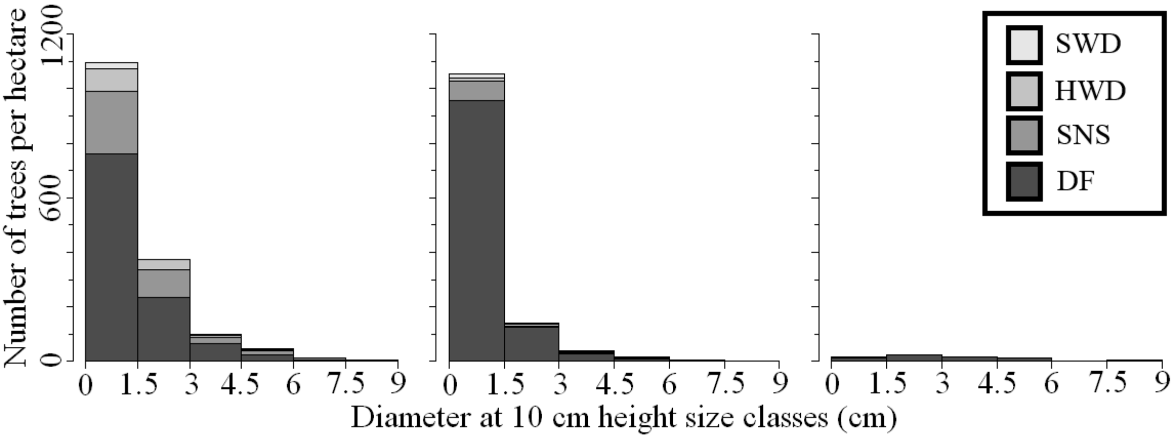

Figure 3.6. Diameter at 10 cm height size class distribution from the 2011 survey for CyB4 (left), CyB5 (middle) and CyB7 (right) of trees with DBH < 5 cm.

3.3.1.2 Ingrowth

Again CyB5 had the most abundant ingrowth with three times as many stems per hectare as CyB4 (137.10 to 39.70) (Table 3.2). CyB7 had very low ingrowth of only 6.17 HWD trees ha^{-1}. The distributions for CyB4 and CyB5 show a sharp tapering of density from the smallest to the larger size classes (Figure 3.7). No individuals were present in the largest two size classes of CyB4.

DF is the 45% of the ingrowth in CyB5 but only 35% of CyB4, with SWD the dominant ingrowth in CyB4. A strong cohort of SWD is present throughout the distributions for CyB4 (49%) and CyB5 (27%) with individuals present through all size classes, contrasting with the lack of SWD recruitment (Table 3.2, Figure 3.7). SWD is the second most abundant species in CyB5 but with basal area equal to the dominant species (DF). SNS is only present in the lowest size class of CyB4 but is present through most of CyB5, though much less densely than SWD.

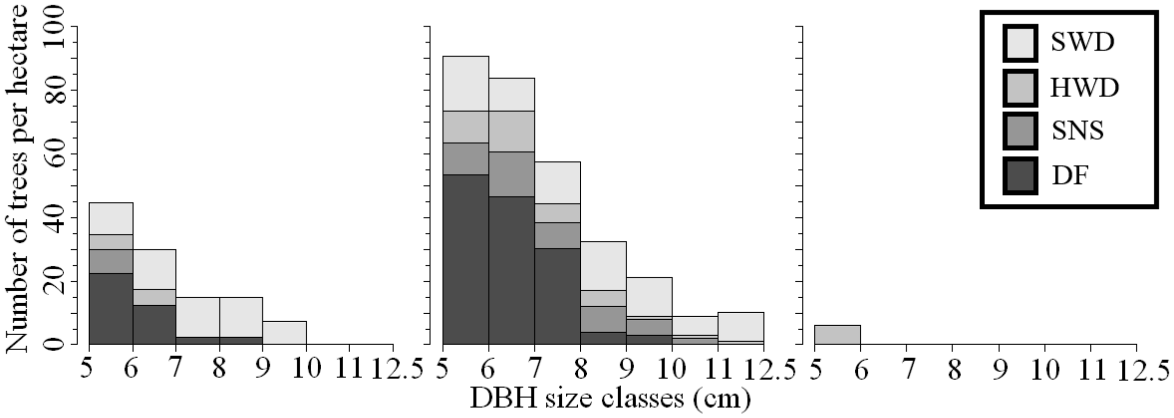

Figure 3.7. Ingrowth DBH (cm) size classes for CyB4 (left), CyB5 (middle) and CyB7 (right).

3.3.1.3 Survivor growth

The comparisons of survivor growth clearly highlighted the density of CyB7 (1481.48 trees ha^{-1}) in relation to CyB4 (196.03 trees ha^{-1}) and CyB5 (193.55 trees ha^{-1}) (Figure 3.8, Table 3.2). CyB4 has the highest overall basal area (50.86 m² ha^{-1}) with 81% of that DF. This is evidenced by the greater numbers of trees in the largest size classes than CyB5 or CyB7. DF is the dominant species in all plots however CyB7 has considerable numbers (circa 500 trees ha^{-1}) in the lower two size classes (5 to 15 cm DBH) while CyB4 and CyB5 have approximately 100 trees ha^{-1} in the 5 to 10 cm DBH range and less than 50 trees ha^{-1} in the 10 to 15 cm DBH range. No plots follow the expected reverse-J distribution of an uneven-aged stand and there is a clear two storey division shown in CyB4 and CyB5 with the absence of trees in the central size classes (Figure 3.8).

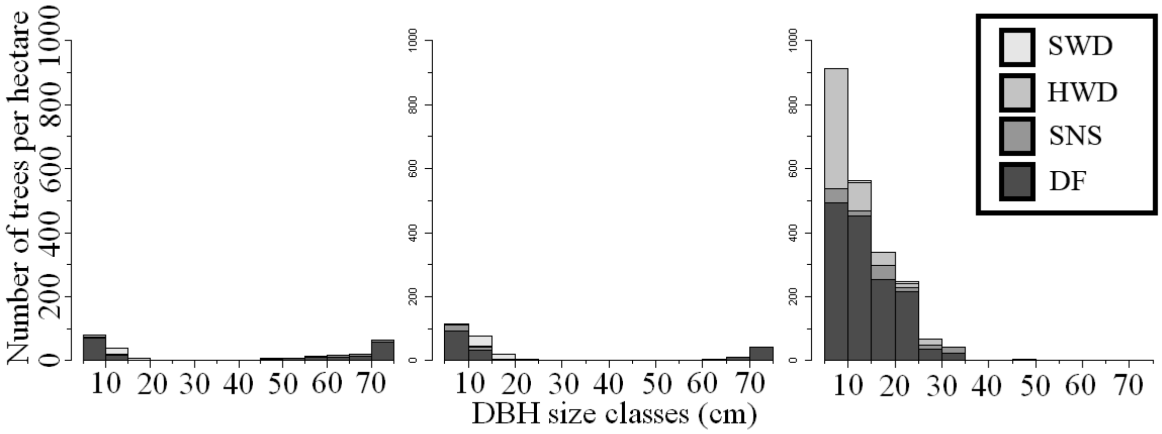

Figure 3.8. Survivor growth DBH size class distribution from the 2011 survey for CyB4 (left), CyB5 (middle) and CyB7 (right) of trees ≥ 5 cm DBH

3.3.1.4 Mortality

During the five year period CyB7 had the highest mortality rate losing 172.84 DF trees ha^{-1} and 30.86 HWD trees ha^{-1} (Table 3.2). Mortality in CyB4 and CyB5 was low (7.44 trees ha^{-1} and 3.02 trees ha^{-1}) respectively.

3.3.2 Ground flora and rhododendron status

R. ponticum was present in 47 of the 82 quadrats, with seedlings in 24 quadrats and adults in 33 (Figure 3.9, Table 3.2). *R. ponticum* was only recorded present in a quadrat if it was rooted, whether layering in or grown. Of the remaining quadrats 15 had some *R. ponticum* growing over, but not rooting inside. Though *R. ponticum* is present throughout the site the central to south eastern section did not have seedlings or adults present in any quadrats (Haffenden pers. observation).

Rhododendron seedlings and adults were significantly associated ($X^2_{(1)}$ = 9.80). The observed association (10.00) was lower than the expected (13.76) and we can conclude that there is a significant negative association between seedling adult. Wood sorrel (*Oxalis acetosella*) was the most associated of the other species ($X^2_{(1)}$ = 8.71). Again the observed association (21.00) was lower than the expected (27.51) concluding that the association is negative. Broad Buckler fern (*Dryopteris dilatata*) was also significantly negatively associated with rhododendron (observed 25.00, expected 30.95). Conversely Spruce (*Picea spp.*) was positively associated with rhododendron (observed 15.00, expected 10.89). Spruce is not directly identified to species as Norway and Sitka are present on the site and it was not possible to positively differentiate between all individuals in the field given the small seedling sizes. Due to the differences in abundance at the site (Sitka spruce had 33 individuals and Norway spruce had 4 actual individuals > 5 cm DBH, within CyB5) it can be inferred that the association is with Sitka spruce (See appendix 1 for tables).

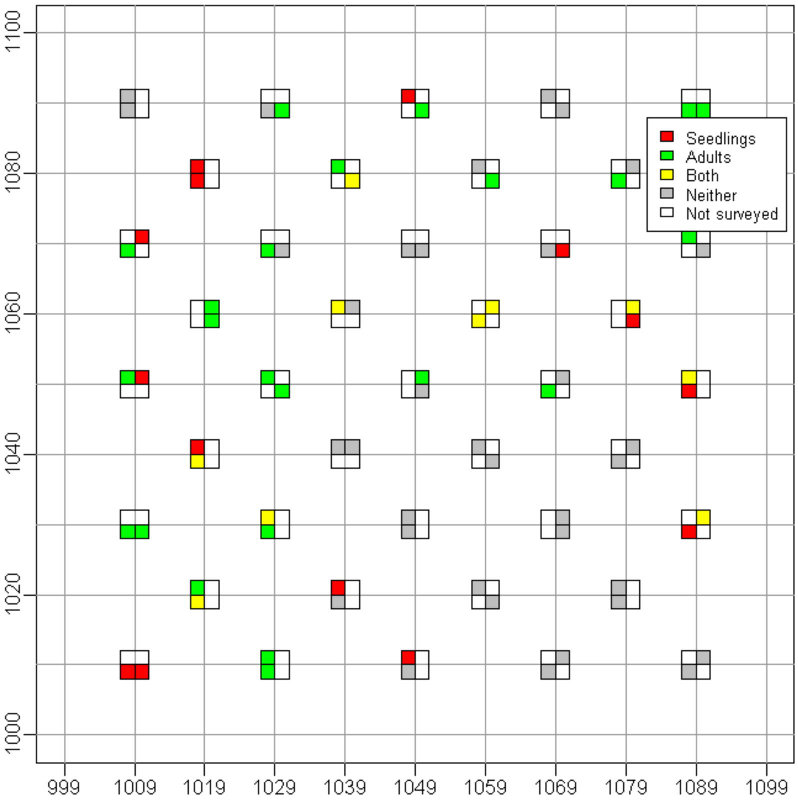

Figure 3.9. CyB5 vegetation survey stations detailing locations where *R. ponticum* was found. Red squares represent those locations containing seedlings (≤ 30 cm height); green squares adults (> 30 cm height); yellow squares seedlings and adults, grey squares are survey locations where no *R. ponticum* was encountered and white squares were not surveyed.

Table 3.3. Ground flora list, ESC NIV (Wilson) scores and quadrat data: total quadrats with species, quadrats with and without rhododendron seedlings; the Chi Square statistic of association between the target species and rhododendron. For rhododendron the Chi square represents the association between seedling and adult.

			Quadrats with species				
Species	Common name	NIV (Wilson)	Total	with RP seedlings	with RP adults	with RP seedlings and adults	Chi square
Rhododendron ponticum	rhododendron	NA	47	24	33	10	9.80
Oxalis acetosella	Wood Sorrel	3.74	48	12	13	4	8.71
Dryopteris dilatata	Broad Buckler fern	3.94	54	16	15	6	7.85
Picea spp.	Spruce	NA	19	10	11	6	4.73
Abies grandis	Grand fir	NA	2	0	0	0	NA
Illex spp.	Holly	4.33	4	1	0	0	1.8
Blechnum spicant	Hard fern	3.48	62	16	25	8	1.74
Dryopteris affinis	Scaly male fern	3.74	22	8	6	4	1.73
Tsuga heterophylla	Western Hemlock	NA	2	1	1	0	NA
Sorbus spp.	Rowan	NA	8	1	2	0	1.42
Chamerion angustifolium	Rosebay Willow Herb	5.09	1	0	0	0	NA
Viola spp.	Dog violet	3.74	1	0	0	0	NA
Pseudotsuga menziesii	Douglas fir	NA	54	20	22	9	0.93
Pteridium	Bracken	3.69	13	3	4	1	0.79
Geum rivale	Water avens	0	1	0	1	0	NA
Thuja plicata	Western Red Cedar	NA	1	0	1	0	NA
Quercus	Oak	NA	9	2	3	1	0.68
Athyrium felix-femina	Lady fern	4.67	7	2	1	0	0.65
Fagus spp.	Beech	NA	5	1	1	0	0.65
Rubus fruticosus	Bramble	4.6	39	11	14	4	0.37
Erica spp.	Heath	NA	9	4	3	1	0.36
Empetrum nigrum	Crowberry	0	3	2	0	0	0.11
Calluna spp.	Heather	NA	3	1	2	1	0.11
Hedera spp.	Ivy	NA	3	2	0	0	0.11
Potentilla	Tormentil	2.58	8	3	2	0	0.1
Vaccinium myrtillus	Cowberry/ Bilberry	2.7	69	20	29	9	0.08
Betula spp.	Birch	NA	17	6	8	4	0.02
	Mean	3.36					

3.3.3 CyB5 abiotic surveys of soil and light

3.3.3.1 Soil

The minimum O layer depth recorded was 3 cm, maximum 16 cm and the mean 7.04 cm. The interpolation (Figure 3.10, a) showed a concentration of high depth in the central east of the plot though this is likely the influence of one station. A shallower section was apparent through the central mid-section of the plot towards the south-east corner and also in the upper north-east.

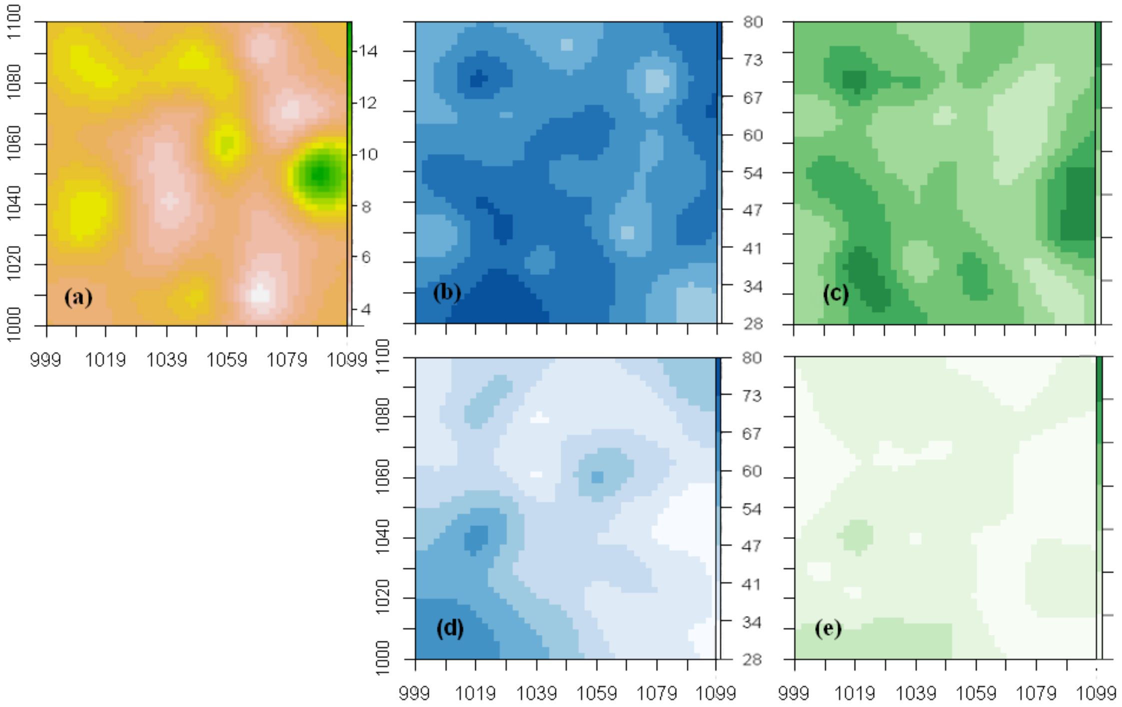

Figure 3.10. Interpolated (Surfer, Golden Inc.) soil maps from field survey: (a) O layer depth (cm); (b) O layer moisture (%); (c) O layer soil organic matter (%); (d) E layer moisture (%); (e) E layer soil organic matter (%)

The O layer wetness ranged from a minimum of 45.57% to a maximum of 85.39% with a mean of 65.78%. Though the mean of the E layer was similar at 43.91% the maximum, 67.20%, and the minimum, 28.29%, were lower. Comparison of the interpolations (Figure 3.10, O layer (b); E layer (c)) demonstrate the difference between the two layers, with E drier overall.

The range of soil organic matter was broader in the O layer (minimum 30.50%, maximum 80.13%) than the E layer (minimum 12.60%, maximum 38.64%). The E layer soils averaged (22.01%), less than half the organic matter of the O layer (51.70%).

3.3.3.2 Light

Global light index determined from thresholded hemispherical photos ranged from 10.29% to 50.93% (Figure 3.11). Examples of hemispherical photos and the relative thresholded images are shown in Figure 3.4. The distribution exhibits a non-normal distribution, bi-modal at 25-30% and 40-45% with a median value of 35%. Light levels greater than 45% and less than 25% were relatively uncommon, representing approximately 8.5% and 12% of the 81 stations, respectively.

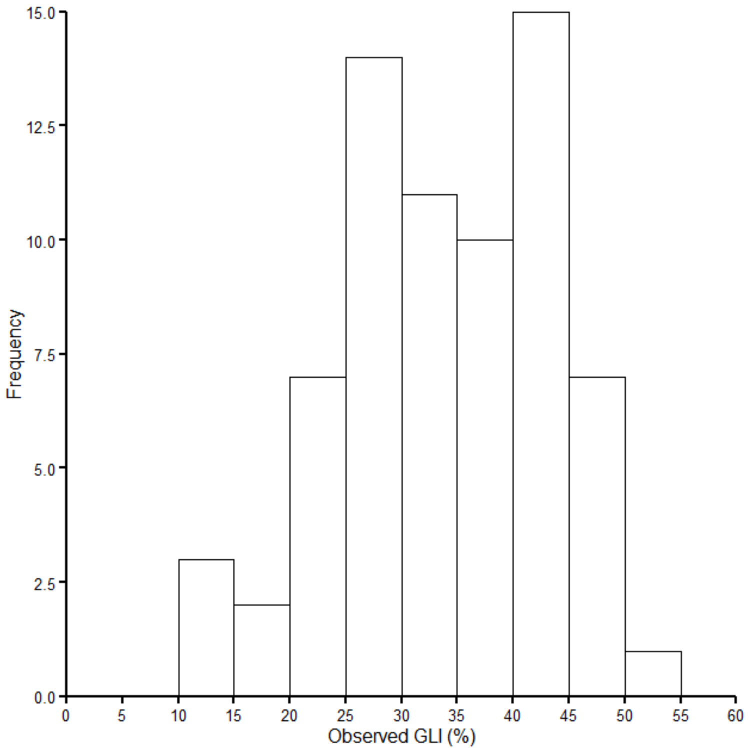

Figure 3.11. Histogram of canopy transmittance (GLI) (%) calculated by Gap Light Analyzer (Frazer et al., 1999)

3.3.4 Ecological site classification

The ESC-DSS models output accumulated temperature (1690°C), moisture deficit (142 mm), windiness (9) and continentality (7) from grid reference and elevation (Table 3.4). Providing the soil type (Brown earth) (Table 3.4) yielded a *fresh* rating for SMR and a *medium* rating for SNR (Table 3.4). The soil was defined as purely *Brown earth* and no phase was specified. Table 3.3 provides a breakdown of all identified species in the quadrats. *Calluna vulgaris* and *Hedera helix* were not used for the ESC classification because they were not present in the quadrats selected. Other species that were not used were tree species. Of these *Pseudotsuga menziesii* was the most abundant (54 of 82 quadrats). See appendix 2 for the Field layer ESC indicator plant species results.

Table 3.4. Top: ESC data. Left hand column is data provided to the ESC-DSS; right hand column is climatic factors output by the ESC-DSS;

Bottom: Soil moisture and soil nutrient regime values with progression (left to right) of modification by soil type, soil phase (default), site and geology, humus and plant layer

Data input to ESC		Output climatic factors	
Grid Reference	SH733228	Accumulated Temperature	1690
Elevation(m)	84	Moisture Deficit (mm)	142
Root depth	100 cm (default)	Windiness (DAMS)	9
Stoniness	30%	Continentality (Conrad)	7
Texture class	Sandy/silty loam (3)		
Lithology	65 - Middle Cambrian sediments		
Soil type	Brown earth (1)		
Humus	Moder-like mull		

Data	Soil type	Soil phase	Site/Geology	Humus	Plants
SMR	F	Not set	SD	-	-
SNR	M	M	R	M	P

Inclusion of site specifics: root depth, texture class and lithology further refined the assessment to a final s*lightly dry* for SMR and *rich* for SNR (Table 3.4). Overall many roots were present from approximately 10 cm depth, ranging from, (mostly) very fine and 1 – 2 mm, to the occasional 1 – 2 cm width. Stoniness was above 30% for all locations and in terms of texture, dampened soil from three sites did not roll to a cylinder (loamy sand), and two sites did not roll to a thread (sandy loam). Root depth was also left at the default 100 cm due to lack of data (Table 3.4).

SMR was further refined through the inclusion of the humus characteristics and characteristics of the plant layer (Table 3.4). Humus was classified as *moder-like mull* due to the presence of fresh and fragmented, discoloured litter and three stations had mycelia present though neither faecal pellets or earth worms were seen. It was distinguished from *Oligomull* by the presence of an H layer in places. With the inclusion of indicator plants the Wilson indicator values provide a final *Poor* rating for the site nutrient class.

3.3.4.1 Tree species suitability

The dominant adult species, Douglas fir and Sitka spruce*,* were both found to be *very suitable* and *suitable* respectively for the site. Western Hemlock, (dominant species in SWD) as the most abundant in the ingrowth, was also found to be *very suitable* (Table 3.5) and had the highest potential yield (21 m^3 ha^{-1} yr^{-1}). The limiting factor for each species was different with the SMR having the most impact on Sitka (Table 3.5).

Table 3.5. Predicted suitability and yield for dominant canopy and ingrowth trees.

Species	Suitability	Yield scale (m^3 ha^{-1} yr^{-1})	Limiting factor
Douglas fir	Very suitable	19	SNR[a]
Sitka spruce	Suitable	18	SMR[b]
Western hemlock	Very suitable	21	MD[c]

[a] Soil Nutrient Regime; [b] Soil Moisture Regime; [c] Moisture Deficit

From the ESC-DSS the most applicable native woodland type to the site was an oak, birch and wavy-hair grass woodland designated NVC woodland number W16 (

Table 3.6).

Table 3.6. Top suitable *native* woodlands output as suitable by the ESC-DSS with NVC type, suitability score (0 to 1) and NVC reference code number.

NVC Woodland type	Suitability score	NVC woodland code number
Oak with birch and wavy-hair grass	1	W16
Oak with birch and wood sorrel	0.7	W11
Birch with oak and rowan	0.5	W17

3.4 Discussion

3.4.1 Demographic dynamics of Douglas fir and sub-component tree species

3.4.1.1 CyB7 overview

The biomass accumulation / competitive exclusion stage of forest growth occurs once a cohort is established and canopy closure is completed. This stage is characterised by exclusion, through competition (e.g. for light), of other organisms, and rapid biomass accumulation and growth (Franklin et al., 2002). Canopy closure reduces light levels to such an extent that herbaceous vegetation is less than one percent of what it would attain at the seedling sapling stage (Alaback, 1984).

It is clear from the DBH histograms (Figure 3.6, Figure 3.7, Figure 3.8) that CyB7 is at a different developmental stages than CyB4 and CyB5. Young, natural, Douglas fir stands have densely closed canopies and gaps that occur during normal successional growth (e.g. by self- thinning or pathogens) are short-lived, rapidly closed by lateral branch growth (Spies & Franklin, 1989). From the greater relative density, lack of ingrowth and high mortality in CyB7 (Table 3.2, Figure 3.7) it is apparent that understorey regeneration is excluded except for sparse DF scattered throughout the site, and HWD with low basal area (Table 3.2). The only ingrowth to CyB7 was HWD and this, combined with a lack of recruitment would suggest that the majority of the adult HWD were pioneer species, outcompeted by the DF now present in the canopy. The lack of SWDs in this stand could be due to a lack of adult trees in the surrounding environment however the reality is currently unknown; all SWDs in CyB4 and CyB5 have invaded from other locations.

3.4.1.2 CyB4 and CyB5 overview

Once maximum height in a stand has been reached by the pioneer cohort (in this case planted trees), the understorey, including shade-tolerant trees, re-establishes.

Typically, as the vertical structure begins to diversify intermediate and co-dominant canopy positions are filled by shade-tolerant trees such as western hemlock (Franklin et al., 2002). CyB4 and CyB5 are both over-mature in forestry terms (Malcolm et al., 2001) with only a year between them (Table 3.1). Both plots were planted as even-aged, predominantly Douglas fir, with some Sitka spruce.

Neither plot follows a typical *J shaped* curve due to a distinct lack of individuals in the central size classes suggesting that the understorey is in the process of re-establishing itself as outlined by Franklin (2002). In a comparison of CyB4 and CyB5: CyB4 has low ingrowth and high adult biomass; CyB5 has high ingrowth and low adult biomass. The majority of this difference in biomass is in the larger size classes inferring increased canopy cover in CyB4 and possibly explaining the reduced ingrowth (in comparison to CyB5).

3.4.1.3 Ingrowth and western hemlock

The 2011 ingrowth (Figure 3.7) can be described as the product of historic recruitment. Given the close proximity, relative ages and similar species mixtures at planting it could be expected that CyB4's future ingrowth would resemble CyB5's current (Figure 3.7, centre), with greater numbers of individuals steadily populating each larger and larger size class.

Old-growth Douglas fir and western hemlock coexist in stands over their natural range, though most in the Pacific Northwest not on public lands have been logged (DeBell & Franklin, 1987). DeBell and Franklin (1987) found that dominance gradually shifted from a Douglas fir dominated stand to western hemlock within a stand with similar well-drained sandy loam soils to CyB5. They suggest that, in the Pacific North-west, a common pattern within a stand would show that Douglas fir contributed a larger volume, whilst Western Hemlock would contribute a greater density of trees. This observation is supported by

Kimmins (2004) description of a typical pattern of autogenic ecosystem change present in some low elevation forest ecosystems in British Columbia.

In stands following heavy disturbance or clearcuts, Douglas fir, as a shade intolerant pioneer, will dominate. However it does not readily regenerate in small gaps where western hemlock, a more shade tolerant species can invade and after time dominate (Spies & Franklin, 1989). Western hemlock is the most shade tolerant of its seral group and though it can regenerate without canopy gaps, it may require small openings to reach the overstorey (Spies & Franklin, 1989). A combined Douglas fir and western hemlock canopy in their native range typically reduces understorey light levels to <5% of full sunlight (Spies & Franklin, 1989). Douglas fir as shade intermediate trees require in excess of 40% full light (achieved from gaps approximately larger than 0.15 ha) to sufficiently develop (Schütz & Pommerening, 2013). Studies in Douglas fir dominated forests in areas where western hemlock is the climax species demonstrated that young Douglas fir can, after severe fire, develop near pure even-aged stands (Spies et al., 1990). Generally though stands over 200 years old demonstrate overstorey codominance with western hemlock (Spies et al., 1990).

The presence of western hemlock dominated, SWD ingrowth, would appear to suggest two possible reasons: the first that the stands had only (relatively) recently been invaded and that the species group was moving very rapidly through it. Though if this was the case then individuals would be present throughout the recruitment size classes, however SWD is only present in the lowest recruitment size classes and with less individuals and basal area than any other species (including HWD) (Figure 3.1, Table 3.2) suggesting that regeneration is not taking place.

A second possibility is that SWD seeds or recruitment were present in the stand and were released as the canopy grew, earlier in CyB5 and later in CyB4, with all individuals that were released having now grown through the 5cm threshold; evidenced by the fact that they are present throughout the lower size classes. At a certain point no further SWD were released, probably due to competition with the herbaceous layer, which outcompeted and suppressed it. Studies have found Sitka spruce and western hemlock regeneration inhibited by competition from herbs and mosses on the forest floor (Spies & Franklin, 1989). Potentially the initial cohorts were sufficiently advanced to outcompete the herbaceous layer and now further seedlings cannot establish. Seed availability may also contribute to the lack of regeneration though with the present cohort could be the product of a mast year from neighbouring stands.

Hemlock-spruce forests do typically occur throughout Oregon and Washington, BC's, coastal mountains, and south eastern Alaska. The area has high precipitation, moderate temperatures and mild-winters (DeMars, 2000). These forests generally occur on well-drained soils at low elevations. (Alaback, 1982). Sitka spruce is much less shade tolerant than western hemlock. Hemlock has the ability to rapidly grow and release after small scale disturbances that follow from removal of the overstorey (Deal & Tappeiner, 2002). In a comparison of Sitka and hemlock after removal of overstorey, Deal and Tappeiner (2002) found that Sitka responded with rapid and sustained growth, consistently accruing more diameter increment than hemlock. However in the Sitka-hemlock forests of their natural range, hemlock usually dominates with Sitka colonising following the creation of large canopy gaps (Alaback, 1984). A recent study at Artist's Wood, Gwydyr forest, North Wales (approximately 25 miles north of Coed-y-Brenin), found that Douglas fir and Sitka spruce had an equivalent shade tolerance, at 87 % of a reference species (Norway spruce); western hemlock had 95% of the shade tolerance of Norway spruce (Schütz & Pommerening, 2013).

Aside from the central gap in the adult DBH size classes Douglas fir is present throughout the recruitment and ingrowth for both stands, suggesting that there is steady regeneration taking place, which is to be expected in a healthy stand, as DF is the dominant species.

SNS recruitment in CyB4 looks healthy there are individuals through the majority of recruitment size classes (Figure 3.6) and though ingrowth was low (9 trees ha^{-1}) this could be attributed to the beginning of stem inclusion. The picture in CyB5 is different, though there was more ingrowth than CyB4, SNS is very poorly represented in all recruitment size classes except the smallest, (Figure 3.6) suggesting that regeneration is possibly being suppressed by the herbaceous layer as with the SWD species group.

3.4.2 Site survey and rhododendron status

The negative association between rhododendron seedlings and adults is to be expected with dispersed seeds travelling away from the parent. Rhododendron's evergreen status and known capacity for over-shading competitors would ensure that any seeds landing close to an adult bush would be at a competitive disadvantage regarding the likelihood of sufficient light for germination and primary production. Either seedlings or adults were found in 58% of the 81 quadrats. Seedlings were present in 24 quadrats and adults 33. The low ratio of quadrats with seedlings to adults (0.7) would appear to suggest that site invasion is not advancing rapidly, however the broad definition of adults in this study does not provide any information about sexual maturity. It may be that plants defined here as adults are yet to reach maturity, with a sharp increase in seed production and invasion potential when this occurs.

Rhododendron had a negative association with wood sorrel and with broad buckler fern. Wood sorrel is a perennial, low-growing herb, that is widely distributed in the British Isles (Proctor, 2013), on a wide variety of soils, mostly within woodlands but also other habitats that do not suffer from considerable droughting (Packham, 1978) . It is commonly regarded as a shade plant, growing well in woodlands and bryophyte communities (Packham & Willis, 1977, Packham, 1978). Packham and Willis (1977) found that optimum growth was achieved in reduced light levels (27% of available light) and that growth under heavy shade (6% of available light) was better than in high light (70% of available) where heavy watering was required. Plants grow well in a range of pH though it is most common between 4.0-6.0 and grows well in conifer plantations, particularly Sitka spruce, in areas with adequate rainfall (Packham, 1978). Broad buckler fern is also widespread and very common in the British Isles at altitudes up to 1125 m over a range of humidity levels from relatively dry to high (Rhind & Evans, 2001, Rünk et al., 2012). A woodland shade tolerant species with optimum light levels reported to be between 5-10% of relative illumination. It typically grows in deep, moderately fertile, mineral soils with deep humus that are permanently moist but not wet. Rarely found in soils with pH > 6.5 and most common in acidic soils pH < 5.0 (Rünk et al., 2012).

The ESC only predicted the site to be *suitable* for Sitka spruce with the limitation the *soil moisture regime* which was *slightly dry*. The positive association result of the Chi square, between Sitka spruce and rhododendron, supports earlier work by Edwards and Taylor (2008) that examined the relationship between rhododendron status and ESC class in Argyll and Bute, Scotland. The analysis revealed site suitability for Sitka spruce may be associated with site suitability for rhododendron on the basis of bush cover type ($F_{[2,1398]}$ = 0.46, p<0.001), however the data could be confounded by length of occupancy. This suggests that the ESC Sitka spruce model may be a useful analog for rhododendron, and could be used to predict sites susceptible to rhododendron invasion and expansion.

3.4.3 Ecological site classification and site conditions

Accumulated temperature (day-degrees above 5° C) is divided into nine bands from < 175 to > 1800. The models prediction of 1690 sits within the 1475 – 1800 band (Table 3.4). Likewise moisture deficit is in nine bands from < 20 mm to > 200 mm. Our accumulated temperature and moisture deficit suggest that within this scale the area is relatively warm and dry. A windiness (DAMS) score of 9 is in the lowest banding (< 10) indicating that the area is sheltered. The range of continentality within Britain is from 1 to 13 (Pyatt et al., 2001) therefore a value of seven would suggest that the site has an average continentality.

The inclusion of lithology, root depth (which was default) and stoniness (Table 3.4) resulted in a *Soil Moisture Regime (SMR)* of *Slightly Dry (SD). Slightly Dry* is defined as 'soil profile not wet within 70 cm depth for more than 30 days in' at least 15 out of 30 years (Pyatt et al., 2001, p. 10). In terms of the *Soil Nutrient Regime (SNR)*, a Poor rating suggests that in the upper 25 cm pH will be between 3 and 4 with moderate to high phosphorus (P) availability and low nitrogen (N) availability, mainly in the form of ammonium (NH_4) with some nitrate (NO_3).

Another feature of the ESC-DSS is that it predicts suitable native woodlands from site characteristics. The predicted sites (W16, W11 and W17) are very acidic to strongly acidic, with pH rarely above 4, with free draining or strongly leached soils (Hall et al., 2001).

The limiting factor for Douglas fir on CyB5 was the *soil nutrient regime*. In UK forests it needs deep, well-drained, relatively moist and moderately fertile soils. (Savill 2013). Mean yield class over British regions ranges between 10 to 15 m^2 ha^{-1} yr^{-1}, the predicted 19 is close to the maximum of 21 m^2 ha^{-1} yr^{-1} (Savill 2013). That hemlock was *very suitable* for the site and Sitka spruce was found to be only *suitable* may, as previously stated, have implications for regeneration and for rhododendron invasion.

The ecological site classification has provided important detail on the ecosystem structure and plant communities of CyB5 that, combined, with the tree species dynamics, provide insight into the future pattern of growth without management. It is clear that there is a heavy rhododendron presence within CyB5, but it is difficult to see how that presence will change over time: if the population is stable or if the site will continue to be invaded, with or without management. Likewise it is difficult to gauge how silvicultural activities will impact the rhododendron population.

Forest growth models are an important tool for predicting forest dynamics. SORTIE-ND is a stochastic individual based model that is parameterised from field data. Its individual, spatially-explicit methodology makes it ideal for studying the dynamics involved with small scale silvicultural operations (Pacala et al., 1993, Menard et al., 2002).

Studies have been carried out that discuss *R. ponticum's* invasive potential (Erfmeier & Bruelheide, 2010) and relate its establishment to environmental variables in a heterogeneous woodland (Stephenson et al., 2006). There is discussion around the ideal conditions for *R. ponticum* establishment, moisture, moss, woody debris but the question remains as to why CyB5 is only patchily invaded. Some microsite effects must be in play. Further work involves the relationship of forest structure to the establishment potential of *R. ponticum* through the outlined modelling techniques.

3.4.4 Study limitations and further work

Forest growth models are an important tool for predicting forest dynamics. SORTIE-ND is a stochastic individual based model that is parameterised from field data. Its individual, spatially-explicit methodology makes it ideal for studying the dynamics involved with small scale silvicultural operations (Pacala et al., 1993, Menard et al., 2002).

A limitation of this study is the static nature of the inventory and the lack of data on trees < 5 cm DBH from the 2006 survey to compare it to. This is especially a limitation given the invasion of this stand by the western hemlock cohort and rhododendron. A future aim to address this would be to continue collecting data for the growth series at five yearly intervals for all trees. This would be an interesting opportunity to monitor understorey reinitiation within a plantation if no felling takes place. Likewise now that a firm baseline of the stand conditions has been established, including vegetation cover, soil moisture, organics and substrate, it will be possible to directly compare felling effects to the species compositions after management. A limitation in this respect is the lack of comparable sub-canopy data for CyB4 and CyB7. The case of CyB7 particularly, as it has very little vegetation, would make an interesting case study to monitor the effects of any silvicultural treatment on the understorey composition. A comparable survey of light distribution and canopy transmittance alongside soil and vegetation sampling could be used to investigate management and understorey effects to gauge the impact on biodiversity.

With regards to the ecological site classification, rooting depth was estimated (at 100 cm) and this could be included in later work to fine tune the classification of the *Soil Moisture Regime*. Work to further support the ecological site classification would involve direct measurement of soil pH and the use of Ion chromatography or standard colourimetric techniques to determine soil phosphorous (P) and nitrogen (N) availability, including ammonium (NH_4) and nitrate (NO_3) levels.

The ecological site classification has provided important detail on the ecosystem structure and plant communities of CyB5 that, combined, with the tree species dynamics, provide insight into the future pattern of growth without management. It is clear that there is a heavy rhododendron presence within CyB5 but it is difficult to see how that presence will change over time: if the population is stable or if the site will continue to be invaded, with or without management. Likewise it is difficult to gauge how silvicultural activities will impact the rhododendron population. Studies have been carried out that discuss *R. ponticum's* invasive potential (Erfmeier & Bruelheide, 2010) and relate its establishment to environmental variables in heterogeneous woodland (Stephenson et al., 2006). There is discussion around the ideal conditions for *R. ponticum* establishment, moisture, moss, woody debris but the question remains as to why CyB5 is only patchily invaded. Some microsite effects must be in play. Further work involves the relationship of forest structure to the establishment potential of *R. ponticum* through the outlined modelling techniques. Expanding the understorey survey and ecological site classification to CyB4 and CyB5

3.4.5 Conclusion

To conclude, this chapter provides a comprehensive three dimensional cross-section of CyB5, the largest permanent sample plot, at our study location. This baseline will be used to provide data for the parameterisation of the SORTIE-ND model of forest dynamics and to build a Bayesian statistical model of rhododendron establishment predication. The study's depth of focus provides a unique snapshot of a Welsh forest plantation commencing its understory reinitiation phase. This data provides a sound base for further research into the effects of management scenarios on biodiversity and rhododendron invasion.

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Chapter 4: Parameterisation of SORTIE-ND forest model for three Douglas fir dominated stands

4.1 Introduction

Contemporary silviculture is moving away from an agricultural model of tree production towards forest management based on ecology and ecosystem dynamics (Coates et al., 2003). Clearfell systems of forest management are no longer popular and ideas of sustainable management of forests as complex ecological systems are gaining force (Coates & Burton, 1999, Coates, 2000, Kimmins et al., 2008). Long-time scales involved in forest management make field-studies difficult with considerable lag between treatment and result (Coates et al., 2003). With a move towards more complex stand structures and management techniques (e.g. continuous cover forestry), coupled with the threat posed by climate change and invasive species (e.g. *Rhododendron ponticum*), more complex predictive models are required (Coates, 2000).

Traditional empirical models of growth and yield have a strong historical foundation and are ideal for even-aged stands under conditions that remain constant (Peng, 2000, Pretzsch, 2000, Pretzsch et al., 2008, Pretzsch, 2009). By contrast, uneven-aged systems, such as continuous cover forestry, requiring multi-entry harvesting over the life of the stand, often involving multiple species, are more complex and can be composed of a multitude of spatial arrangements, species configurations and life-history stages (Malcolm et al., 2001). Partial harvesting also creates spatial patterns in understorey light conditions that have implications for regeneration and the invasion potential of exotic species (Canham et al., 2006). Purely empirically based, non-spatial models cannot capture the challenges of managing these structurally complex stands with dynamic spatial structures and more competitive resource environments (Canham et al., 2004).

Spatially-explicit individual-based models can provide insight into neighbourhood dynamics within forest systems capturing the fine-scale dynamics that decide demography. These dynamics provide an interface between neighbourhood and ecosystem processes allowing practitioners to investigate different silvicultural and management pathways (He & Mladenoff, 1999, Leroy et al., 2009).

SORTIE-ND is a spatially-explicit individual-based forest growth model that combines mechanistic, stochastic and empirical behaviours to model tree growth over complex structured multi-species stands (Loehle, 2000, Bulkley Valley Research Centre, 2009). Population dynamics are provided through prediction of an individual tree's life-cycle and its interaction with neighbouring trees via resource depletion and mechanistic competition. The original implementation combined sub-models that predicted an individual tree's dispersal, recruitment, growth and mortality alongside resource availability (specifically light) (Pacala et al., 1993, Pacala et al., 1996). The model extrapolates from these quantifiable short-term and fine-scale interactions to predict long-term and large scale forest dynamics. Light is the only resource currently modelled in SORTIE however it is potentially the most heavily manipulated by partial felling and an essential determinant of forest growth and composition (Coates & Burton, 1999).

The design of SORTIE was inspired by the construction of the JABOWA (Botkin et al., 1972, Botkin et al., 1972) model and its progeny FORET (Shugart & West, 1977). These early models were not spatially explicit, consisting of cells containing many individuals with unspecified locations, and were designed so that the growth, mortality and recruitment submodels could be parameterised from published literature. SORTIE was designed so that it could be parameterised from components directly estimated from field measurements (Pacala et al., 1993). Initially developed for oak-dominated hardwood forests in north-eastern North America, the name SORTIE acknowledges its use of high-level sorting algorithms and its descent from FORET, the sub-heading ND stands for Neighbourhood Dynamics (Pacala et al., 1993). Both SORTIE and FORET are able to predict the structure and dynamics of forests. However, SORTIE differs in that it is spatially explicit, contains a complex light model, recruitment is closed (produced only by trees within the model) and the dispersal, growth and mortality sub-models are calibrated and site specific through its parameterisation with field data (Pacala et al., 1993).

The validity of submodels in SORTIE are supported by parameterisation from field data, and extensive statistical analysis and testing detailed through peer review and publication (Pacala et al., 1993, Canham et al., 1994, Ribbens et al., 1994, Kobe et al., 1995, Kobe et al., 1997, Menard et al., 2002, Kunstler et al., 2009). The linkage between model and data promotes confidence in the simulations and models can essentially be seen as complementary tools to field studies (Menard et al., 2002)

SORTIE-ND has been globally implemented to a wide range of forest types and scenarios. For example: Uriarte et al. (2009) predicted tropical forest dynamics as part of a larger project investigating how changes in land use and climate affect the environment in Luquillo, Puerto Rico. Coomes et al. (2009) and Kunstler et al. (2009) investigated the impacts of different herbivores for a range of forest types in Waitutu, New Zealand. The Labrador Forest Management Model Integration Project combined several models into what they term a “Sustainable Forest Management Toolkit” utilising the SELES programming environment to bind the BAP model for habitat assessment with SORTIE at the stand level, and LANDIS model at the landscape level (Papaik et al., 2010). SORTIE-ND has also been used to model the effect of strip-cutting on boreal lowland black spruce (*Picea mariana*) forests located in north-eastern Ontario, Canada (Thorpe et al., 2010). While Belsky and Canham (1994) used it to investigate patch dynamics in tropical savanna ecosystems and Arii et al. (2008) constructed a selection harvesting algorithm for implementation within SORTIE-ND and other spatially explicit individual based models. Climate change scenarios have been investigated by linking SORTIE-ND to a mechanistic species distribution model (TACA) to analyse the responses of trees to biophysical and phenological variables driven by climate (Nitschke et al., 2012). The responses of a temperate forest ecosystem's spatial diversity and community structure to increased CO_2 levels were also investigated by parameterisation of SORTIE-ND with seedling greenhouse data on biomass accumulation (Bolker et al., 1995).

This movement to spatially-explicit individual-based models has in part been facilitated by new methods of data analysis. Through information-theoretic methodologies, such as maximum likelihood estimation (Kobe et al., 1995, Kobe, 1996, Uriarte et al., 2004, Kneeshaw et al., 2006), a coupling is possible between directly parameterised models and collected data creating the mechanisms to quantify uncertainty in model parameterisation and model prediction (Canham & Uriarte, 2006).

The use of information-theoretic methods allow parameter estimation and model selection in terms of 'best fit' and parsimony by focusing on statistical evidence and avoiding distinctions such as significant or non-significant (Burnham & Anderson, 2004). Maximum likelihood estimation returns parameter values that have the maximum probability of obtaining the data observed. The Akaike Information Criterion (AIC) can then be used to select between models in terms of their likelihood and number of parameters (McCarthy, 2007, Hilborn & Mangel, 1997).

Parameterisation with likelihood analysis involves four general steps: 1) model specification, 2) parameter estimation using maximum likelihood techniques and an optimisation algorithm (such as simulated annealing), 3) comparison of competing models, and 4) model evaluation (Canham & Uriarte, 2006). This follows Burnham and Anderson's (2004) statement of the problem of valid inference as: the formulation of candidate models, the selection of the model to be used, estimation of the model parameters, and the estimation of model precision. Models within SORTIE-ND are pre-specified requiring only selection of candidate models to be parameterised and compared.

The aim of this study is to parameterise and validate (i) the underlying tree allometry, (ii) the neighbourhood basal area linked growth submodel and (iii) the light resource submodel of SORTIE-ND for Douglas fir (*Pseudotsuga menziesii*) with data collected from permanent sample plots at Coed-y-Brenin forest park, North Wales; the final objective of this chapter it to run initial simulations of the parameterised model and compare them to the collected data.

Chapter 6 then continues the parameterisation of SORTIE-ND for *Rhododendron ponticum* from published data as the first step towards a working model to investigate the impact of forest management techniques on *R. ponticum* invasion. Chapter 7 completes the discussion regarding field data collection for a full parameterisation of SORTIE-ND for *R. poncticum.*

4.2 Methods

4.2.1 Study sites and data

This study uses data from three permanent sample plots in Coed-y-Brenin forest, Snowdonia, North Wales. The plots were established in 2006 and re-surveyed in 2011 for this study. See Chapter 3 for further details. Douglas fir (DF) is the dominant species at all sites (65-84% trees) and is the focus of this chapter. Minor components of other species are interspersed in the DF stands, but are poorly represented and therefore had only minor influence on stand dynamics. To ensure sufficient sample size (n>15 trees), other species were grouped as Sitka spruce (*Picea Sitchensis*)- Norway spruce (*Picea abies*) (SNS), other conifers (SWD) and hardwoods (HWD). It was not possible to stratify either the HWD or SWD group by light requirements. Sitka spruce dominated the SNS group, western hemlock (*Tsuga heterophylla* (Raf.) Sarg) dominated the SWD group, and silver birch (*Betula pendula*) dominated the HWD group. See Chapter 3 for a full breakdown of species composition and appendix 5 for the model parameter files including SNS, SWD and HWD.

The simulation of SORTIE-ND used four life-history stages (seedling, sapling, adult and snag) based on height and diameter at 10cm and 1.35m thresholds to provide continuity from seedlings to adults **(**Table 4.1**)**. Only dead standing adult trees (>10cm DBH) are classified as snags, smaller diameters are not reported (Table 4.1). As the base unit of representation, a tree's attributes contain all relevant information within the model, including life-history stage and a discrete spatial location. Progress through each stage is a function of a tree's allometry and its allocated behaviours to simulate growth, development and mortality.

Stands were split into north and south quadrants as this captured the full range of environmental gradients and ensured comparable datasets in terms of life history and DF metrics for parameterisation (North quadrant) and validation (South quadrant) (Table 4.1).

Table 4.1. SORTIE-ND life-history stages and associated sample sizes for parameterisation and validation datasets

Life-history stage	Diam. 10 cm height (cm)	Diam. 1.35 m height (cm)	Height (m)	Parameterisation dataset (N quadrant)		Validation dataset (S quadrant)	
				No. individuals	DF (%)	No. individuals	DF (%)
Seedling	> 0	NA	< 1.35	417	81	865	84
Sapling	> 0	< 10	> 1.35	317	74	300	86
Adult	NA	≥ 10	> 1.35	243	78	183	65
Snag	NA	≥ 10	> 1.35	0	0	0	0

Notes: NA, not applicable

4.2.2 Maximum likelihood parameter estimation and Simulated Annealing

Given a random sample from an unknown population, e.g. the data vector y = (y_i, …, y_n), the goal of statistical modelling is to identify the most likely population to have generated the sample. Each population is identified by a probability distribution and each model parameter has a unique value associated to each probability distribution. As parameter values change the probability distributions are altered. The probability density function (PDF) specifying the probability of observing the data y, given the parameter w, is written f(y|w). Values of w, in combination with the corresponding PDF, demonstrate that some data have a higher probability of appearing in y. However we have y (the data) and do not have w (the parameter value(s)), constituting an inverse problem. The likelihood function is then found by reversing the parameters, w and the data vector, y to give f(y|w), i.e.

$$\text{Likelihood}(w|y) = f(y|w) \tag{4.1}$$

which describes the likelihood of parameter w given the data y. For a one parameter model the likelihood function will be a curve; in general terms for a model with k parameters, the likelihood function Likelihood(w|y), is in the form of a k-dimensional surface (Hilborn & Mangel, 1997, Myung, 2003).

The maximum likelihood estimation (MLE) corresponds to the parameter vector found by searching the parameter space to find the values that make the observed data the "most likely", maximising the likelihood function. Computationally it is more convenient to obtain the MLE by maximising the log-likelihood function, ln(Likelihood(w|y)). Maximising either ln(Likelihood(w|y)) or Likelihood(w|y) gives the same MLE as the two functions are monotonically related (Myung, 2003). In practice, models can be highly non-linear and involve many parameters, making a formal solution to MLE estimates difficult and necessitating optimisation algorithms involving iterative trial and error steps to seek a solution (e.g. Monte Carlo Markov chains and simulated annealing methods) (Goffe et al., 1994, Myung, 2003).

Optimisation algorithms essentially attempt to improve on parameters specified or randomly assigned by the user. With each iteration a new parameter set is generated that considers the previous iterations results, continuing until the MLE is reached. One issue is convergence on a local, as opposed to global maximum. In general, optimising algorithms start at a random or user-specified point and find the best direction to head 'uphill', sometimes assuming that a local optimum is the global optimum (Goffe et al., 1994). One optimisation algorithm that attempts to overcome this local maxima problem is Simulated Annealing (Myung, 2003). *Annealing* is rooted in thermodynamics and is defined as heating and gradually cooling to prevent or remove internal stress in metals (Oxford University Press, 2013). In much the same way, simulated annealing attempts to find the global maximum by moving in large steps to gain a rough surface view and gradually decreasing the step-length, with the algorithm drawn to a specific area whilst still being able to escape a local maxima through downhill movement. The algorithm should then eventually converge on a functions global maximum (Goffe et al., 1994).

Support limits are calculated for all parameter maximum likelihood estimates to assist with evaluation of the support strength for each parameter’s MLE. They “are the values above and below the maximum likelihood estimate that cause the likelihood to drop by a given number of units, while holding all other parameters at their maximum likelihood values. Two units is standard, and 1.92 units roughly corresponds to a 95% confidence interval” (Murphy, L., 2012, p. 19).

4.2.3 Comparison of competing models

In model selection likelihood and parsimony compete; multi parameter models can be expected to have higher likelihood estimates (Canham, C.D. & Cayuela, L., 2011). Akaike's Information Criterion (AIC) was derived as a way to choose between competing models that considered both MLE and parsimony by relating the likelihood to the Kullback–Leibler distance, which defines the hypothetical distance between a model and reality (Burnham & Anderson, 2002, Canham, C.D. & Cayuela, L., 2011). Once the models log-likelihood has been found the AIC values can be calculated as:

$$\mathrm{AIC} = -2\ln \mathrm{L} + 2\mathrm{d} \tag{4.2}$$

where *L* is the fitted model's likelihood and *d* is the number of parameters (Morgan, 2008)

If the model has too many parameters in relation to sample size the AIC may perform badly. A second order variant of AIC with a bias-correction term to over-come this problem, AICc selection criteria, can then be used:

$$\mathrm{AICc} = \mathrm{AIC} + \left(\frac{2\mathrm{K}(\mathrm{K}+1)}{\mathrm{n}-\mathrm{K}-1}\right) \tag{4.3}$$

where *n* is the sample size and *K* the number of parameters. The use of AICc is recommended with small n/K ratios (approx. < 40). For a stated analysis either AICc or AIC must be used consistently and can only be compared when used with the same combination of data. AIC values are normally positive however negative values can occur due to shifts caused by additive constants. The AIC value itself is not important, rather the relative values over all considered models and their differences (Burnham & Anderson, 2004). Canham and Cayuela (2011) suggests some general rules of thumb for assessing strength of model choice in relation to AIC values(denoted by Δ): a model with Δ within 1 or 2 of the *best* model shows considerable support; a Δ value of 4 to 7 shows less, and Δ >10 can be excluded.

4.2.4 Model evaluation

The final stage of parameterisation requires evaluation of the model in terms of *goodness of fit* and bias (Canham et al., 2006).

4.2.4.1 Goodness of fit and bias

The R^2 value is the proportion of variance accounted for by the statistical model in relation to the mean of the data, in the form:

$$R^2 = 1 - \frac{SS_{err}}{SS_{tot}} = 1 - \frac{\sum_{i=1}^{N}(y_i - \hat{y_i})^2}{\sum_{i=1}^{N}(y_i - \bar{y})^2} \tag{4.4}$$

where SS_{err} is the residual sum of squares and SS_{tot} is the total sum of squares, y_i are the observed values, $\hat{y}_i$ the predicted and $\bar{y}$ the mean of observed values. R^2 is not bounded by 0 and 1; if SS_{err} is greater than SS_{tot} the mean of the observed data has a superior fit to the estimated model. R^2 can be negative where $SS_{err} > SS_{tot}$ (Murphy, L., 2012, Canham, C.D. & Cayuela, L., 2011)

The square of the correlation co-efficient (r^2) is a measure of the linear dependence between two variables and is bounded between 0 and 1. A biased model will have low or negative R^2; r^2 will give an indication of the goodness of fit after accounting for bias. Model bias can be either proportional, where the slope is not equal to one, or systematic, where the intercept is not equal to zero (Canham, C.D. & Cayuela, L., 2011). Once the residuals are plotted it is important to check that they fit the probability density function used.

4.2.5 Allometrics

Allometry determines the inter-relationship of size and shape attributes. SORTIE-ND requires parameterisation for the following allometric relationships: DBH (or diameter at 10 cm height) to height relationship (seedlings, saplings, adults); DBH to diameter at 10 cm height relationship (saplings); Crown depth to tree height (adults); and Crown radius to DBH (adults) (Murphy, 2010).

4.2.5.1 Diameter to height relationships

A linear function was used for seedlings (4.5) and SORTIE's *standard* function was used for saplings and adults (4.6). The seedling linear function:

$$\text{seedling height} = \alpha + \beta * \text{diam}_{10} \tag{4.5}$$

where *height* is tree height in metres, α is the intercept, β is the slope and diam_{10} is tree diameter at 10 cm height, in cm. The intercept in this model was fixed at 0.1 m (Coates, K.D., 2012). The 'Standard' function for sapling and adults utilises DBH rather than diam_{10}:

$$\text{sapling and adult height} = 1.35 + (\text{h\_max} - 1.35) * (1 - e^{-\beta * \text{DBH}}) \tag{4.6}$$

h_max is the maximum possible tree height (m). Sapling and adult data were combined for this model. See appendix 3.1 and 3.2 for R scripts.

4.2.5.2 DBH to diameter at 10 cm height relationship (saplings only)

To maintain continuity between the seedling and adult life-history stages SORTIE-ND uses a DBH to diameter at 10 cm height relationship for saplings:

$$\text{DBH} = (\text{diam}_{10} * \beta) + \alpha \tag{4.7}$$

The intercept for was fixed at zero (Coates, K.D., 2012). See appendix 3.3 for R script.

4.2.5.3 *Crown depth to tree height and crown radius to DBH (saplings and adults)*

The *standard* relationships used to relate crown attributes to stem are very similar. Crown depth, the distance from the top to the bottom of the crown cylinder (m), is calculated as:

$$\mathrm{Crown\ depth} = \mathrm{C} * \mathrm{height}^{\mathrm{b}} \tag{4.8}$$

where height is the tree height (m), C is the slope and b is the exponent. See appendix 3.4 and 3.5 for R scripts.

For Crown radius (m), DBH (cm) replaces height, and is constrained to limit crown radius to a maximum of 10 meters. Canham et al. (1998) utilise an 'effective' crown radius of 50% the maximum measured in the field in a coarse attempt to model the crown as a cylinder with a vertical cross-sectional area equivalent to a cone. This is applied in SORTIE-NZ (Kunstler, 2011) by rescaling the crown radius exponent (C from (4.**8**)) by 0.57. This conversion was also applied to the CyB data.

4.2.6 Behaviour submodels

4.2.6.1 *Recruitment - Dispersal*

The *disperse* behaviour stores and distributes seeds within the plot via a *dispersed seeds grid* at a cell resolution of 4 x 4 m, equivalent to the survey stations (see Chapter 3. Fieldwork). Actual seed positions within the cell are not stored (Murphy, 2010).

The *gap spatial disperse* behaviour was implemented using data provided from another study at Date Creek in the interior western redcedar (*Thuja plicata* Donn ex D. Don in Lamb) –western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) forests of northwestern British Columbia (Coates, K.D., 2012, pers. comm.). Species were not an exact match so proxies with similar traits were used: Hybrid spruce, (*Picea glauca* (Moench) x *Picea* *sitchensis* (Bong.)), was deemed to be the closest match to the DF and SNS species groups, which have equivalent shade tolerance based on a recent study of Welsh plantations (Schütz & Pommerening, 2013). Western hemlock, was used to represent the SWD species group as the dominant species; Paper birch (*Betula papyrifera*) was used as a proxy for Silver birch, the dominant species of the HWD group.

The behaviour considers forest cover (i.e., gap or closed-canopy) when calculating the number and placement of seeds. A gap is a cell in the *dispersed seeds grid* that meets the criteria of the *maximum adults allowed in a gap cell* parameter (currently set to zero). Seed placement is then calculated according to a Weibull probability distribution function:

$$R_i = \frac{STR}{n} \sum_{k=1}^{T} \left(\frac{DBH_k}{30}\right)^{\beta} e^{-Dm_{ik}{}^{\theta}} \tag{4.9}$$

where:

$$n = \int_0^{\infty} e^{-Dm_{ik}{}^{\theta}} \tag{4.10}$$

R_i is seedling density (#/m^2) at a point i, STR, *standardized total recruits*, is the number of seedling recruits produced by a 30 cm DBH parent tree, DBH_k is the DBH of the K = 1 to T parent trees within a specified radius, D is the dispersal parameter (species-specific), m_{ik} is the distance from point i to the k$^{\text{th}}$ parent tree and β and θ are disperse parameters (canopy and gap). The number of seeds produced by each tree with a DBH greater than the reproductive age is calculated by:

$$\text{seeds} = \text{STR} * (\text{DBH}/30)\beta \tag{4.11}$$

Once seeds have established the establishment behaviour turns them into seedlings with a randomised diameter at 10 cm height A proportional behaviour was used for seed establishment as no data was available that related light, substrate or density to establishment at this site.. The proportion for establishment was set at 0.05 for all species (Thomas, P.A., 2012, pers. comm.)

4.2.6.2 Growth

Seedlings and saplings

Growth series data for the PSP's only covered trees with DBH of 5 cm or above (minimum DBH of the original survey). Therefore parameter values from a study by Wright et al (2006) at sites in British Columbia (Lat. 54º01' – Long. 54º40') with the same proxy species as the g*ap spatial disperse* behaviour were used (Coates, K.D., 2012, pers. comm.). The *non-limited absolute growth radial increment* sub-model used in this study (Lischke & Loeffler, 2006) utilises a modified Michaelis-Menton function that incorporates parameters for suppression and release:

$$\mathrm{Y} = \left(\frac{\mathrm{a} * \mathrm{GLI}}{\frac{\mathrm{a}}{\mathrm{s}} + \mathrm{GLI}}\right)\mathrm{SF} \tag{4.12}$$

Where Y is $\log_{10}$(radial growth +1), a is the asymptotic diameter growth, s is the slope of the growth response, GLI is the *global light index* (light section, below) and SF is the suppression factor (4.13) (Murphy, 2010). The a value can be considered as a measure of potential growth at high light and the s parameter a measure of growth at low light. Generally shade intolerant species are expected to have higher s values than shade-tolerant species (Coates & Burton, 1999).

To calculate the suppression factor radial growth thresholds were defined corresponding to a sapling mortality rate of 10%, over a three year period (Wright et al., 2000). Suppression was defined as periods of at least four consecutive years below that threshold. A 10% rate was chosen because a steep rise in the probability of mortality, as a function of recent growth, occurred after that threshold (Kobe & Coates, 1997) (found by use of the *BC mortality function* (4.18) that must be used in tandem (Wright et al., 2000)). The suppression factor rate is multiplicative. Trees that aren't suppressed are given a suppression factor of one. The suppression factor is calculated as:

$$\mathrm{SF} = e^{((g*\mathrm{YLR})-(d*\mathrm{YLS}))} \tag{4.13}$$

where *g* is the length of current release factor, *YLR* is the length of last, or current, release period, in years; *d* is the length of the last suppression factor, and *YLS* is the length of the last (or current) suppression period, in years. Diameter growth is compounded over time as:

$$\mathrm{G} = \frac{\left((10^{y} - 1) * 2\right)}{10}\mathrm{T} \tag{4.14}$$

where Y is $\log_{10}$(radial growth +1) (4.12); radial growth is log-transformed to stabilise the variance.

Adult

SORTIE-ND uses a regression analysis of an individual's growth as a function of neighbours abundance and distribution to mechanistically model the link between above and below-ground competition, and spatial distribution, size and abundance of neighbours (Murphy, 2010). This approach is deemed to be more broadly relevant and phenomonologically based in comparison to modelling resource use or limitation. The model incorporates three terms: the maximum growth that a tree can attain (diameter increment in cm yr^{-1}) and two scalar modifiers, ranging from 0 to 1, that relate maximum growth to the size of the target tree (DBH, cm) and the effect of neighbourhood crowding (Canham et al., 2006):

$$\mathrm{Growth} = \mathrm{Max\,Growth} * \mathrm{SE} * \mathrm{CE} \tag{4.15}$$

Max growth (cm yr^{-1}) is the potential maximum diameter growth the target tree can attain. The model assumes that the crowding effect (CE) reduces the growth potential inherent in a free growing tree. Size effect (SE) provides the variation in diameter growth due to actual DBH. Potential Radial Growth relates observed growth to the variation due to the Crowding Effect (Canham et al., 2004). Size Effect is calculated as:

$$\mathrm{SE} = e^{-0.5*\left[\frac{\ln\left(\frac{\mathrm{DBH}}{\mathrm{X_o}}\right)}{\mathrm{X_b}}\right]^2} \quad (4.16)$$

The form of the function allows that when X_o is very small the shape will be monotonically decreasing and increasing when very large. X_b determines the functions breadth (Canham et al., 2006).

Crowding Effect is calculated as:

$$\mathrm{CE} = \exp^{\left(-\mathrm{C}*\left(\mathrm{DBH}^{\gamma}\frac{\mathrm{BA_n}}{\mathrm{BADiv}}\right)^{\mathrm{D}}\right)} \quad (4.17)$$

C is the slope; DBH (cm) is the target tree; γ is the target tree species sensitivity; D is the steepness; BA_n (cm^2) is the sum of all eligible neighbours basal areas and BADiv is a divisor parameter (set to 1000 in SORTIE-ND).

The growth function was parameterised and assessed for two models, one with *size effect* and *crowding effect*, the other with *size effect* alone. The maximum radius for influential neighbours was also parameterised during this process.

4.2.6.3 Mortality

Seedlings and Saplings

Growth and mortality are fundamental aspects of forest dynamics with juveniles of different species having differing capacity to survive suppression events. In forest systems that rely on gap-phase dynamics or low impact silvicultural systems reliant on gap creation, individuals may be subjected to various periods of suppression and release, incurring different growth and mortality rates (Kobe et al., 1995, Kobe & Coates, 1997, Wright et al., 2000). The growth based mortality behaviour *BC mortality* is implemented in conjunction with the a*bsolute growth radial increment* (Kobe & Coates, 1997, Wright et al., 2000) designated:

$$M = 1 - e^{-(T*m_1)e^{-m_2 G}} \tag{4.18}$$

Where *M* is the mortality probability (%), *T* is the number of years in a timestep, *m1* is mortality at zero growth (%), *m2* is the light dependent parameter and *G* is the amount of radial growth (mm yr^{-1}). This behaviour is implemented in tandem with the *absolute growth radial increment* model and utilises the same proxy species (Kobe & Coates, 1997, Wright et al., 2000).

Juveniles and adults

The *juvenile stochastic mortality* and the *adult stochastic mortality* behaviours are also implemented. They provide a background mortality rate and, where applicable, individuals are randomly selected to die at a specified rate. This rate is currently set to 0.01 in line with previous studies (Coates, K.D., 2012, pers. comm.).

4.2.6.4 Light

As the key resource in SORTIE, light calculations are sophisticated and take up a large proportion of computation time. In this implementation light directly affects the growth of seedlings and saplings, and consequentially adults. The sky is simulated at the beginning of a run. The model considers the plot location (latitude is set to 52.47° for CyB5) and calculates the amount of light from each part of the sky, accounting for the suns' position throughout the growing season running from 15th April until 15th September (Coates et al., 1997, Canham et al., 1999). The sky is divided into a hemispheric grid (36 azimuth and 9 zenith regions) and tracks total amount of direct beam and diffuse radiation for each region. At the start of each timestep SORTIE simulates a fisheye photograph at mid-crown height to calculate the amount of light each tree received through consideration of the sky grid and position of neighbours. Two methods describe the type of light a tree receives: *global light index* (GLI, described in 3.2.4.2) is the percentage of full sun at a given point and *sail light index* is the proportion of shade experienced at a given point (from zero to total) (Murphy, 2010). The *quadrat based GLI light* behaviour assigns GLI values to trees through the use of a grid object (quadrats). A GLI value is calculated for each grid cell that contains a tree and all trees in the cell are assigned the same value, GLI grid maps can then be saved and inspected (Murphy, 2010).

Calculation of GLI requires specification of a *canopy openness* parameter for each species. Canopy openness is defined as the ratio of white to black pixels within a black and white binary image of a specific tree crown. Boivin et al. (2011) detail a method and R package, Crown Delineator, that standardises this approach using seven different algorithms for defining the crown outline and one method that treats a crown as opaque (Figure 4.1 a). Five of the seven methods define the crown outline as that corresponding to the trace left by an imaginary circular disk rolling around the crown edge. Each of the five use a different radii (in pixels) for the disk: 20, 40, 80, 160 and 320; with the smallest radii relating to the finest crown delineation (Boivin et al., 2011). The final two methods define the smallest convex hull and the smallest rectangle that include the entire crown (Figure 4.1). Crowns were separated from hemispherical photographs (see Figure 3.4) and thresholded black and white (Figure 4.1 b and c). The canopy openness was then calculated as the ratio of white pixels to the total number within the crown outline. These values are given the variable names CO_{20}, CO_{40}, CO_{80}, CO_{160}, CO_{320}, CO_{CH}, CO_{rect} (Boivin et al., 2011).

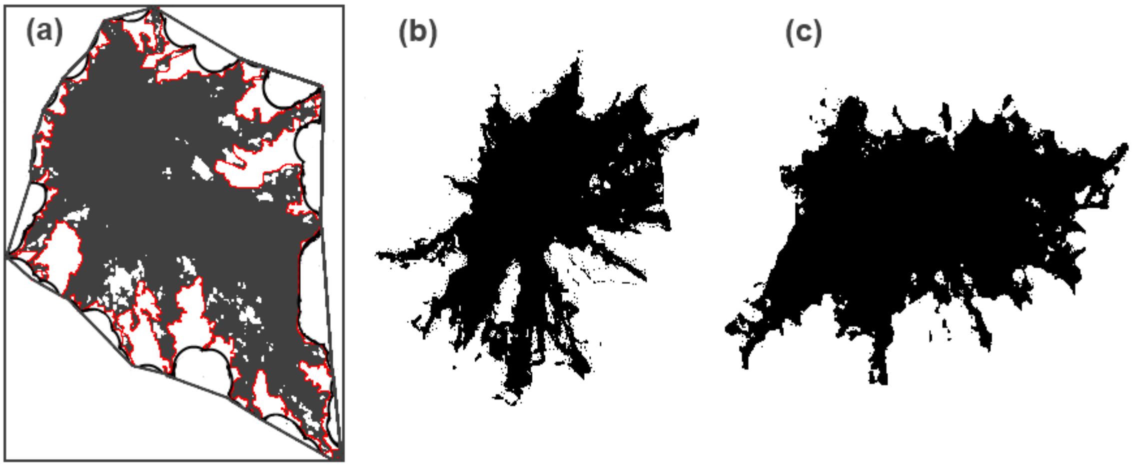

Figure 4.1. (a) Example of binary colour crown image demonstrating four of seven crown outlines delineated by Crown Delineator (Boivin et al., 2011). The outer rectangle, CO_{rect}, is the smallest rectangle that contains the entire crown; the dark grey convex hull outline is the smallest convex polygon that encompasses the crown dripline; the final two outlines (black and red) are derived using geometrical buffers corresponding to the outline of a disk with a specified radius moving around the crown; (b) and (c) examples of images passed through Crown Delineator software demonstrating variation in crown size and shape.

To validate the light model, the Gap Light Index values computed in Chapter 4 were compared with the predicted values from the same locations, output from SORTIE after a one-year timestep using the *GLI Points File Creator* behaviour. The behaviour takes a series of locations, and heights of GLI computation (1.35 m) as inputs, and outputs GLI values.

4.2.7 Initial model runs

In terms of successional studies Pacala et al. (1993)suggest that with a lack of long-term regeneration data only three options remain to evaluate a model: (i) data from a successional sere; (ii) historical forest reconstruction from old-stumps, tip-up mounds and the pollen record; (iii) a short chronosequence of data. Seral information would need to encompass the transition from even-aged plantation to uneven-aged stand, data which is currently unavailable. Forest reconstruction from historical data is not possible for this site as all records relating to management (except planting date) were lost during a transition from paper-based to computerised records for this site.

Therefore the (current) best option is to evaluate the model over a short chronosequence of data (in this case the five year growth series) by assessing if the model adequately represented growth of the 2006 survey trees to the 2011 conditions.

4.2.7.1 Model starting conditions

The 2006 survey data was used as the initial tree map for the model scenario (Table 4.2). The scenario was then run for 30 iterations, each for a five year period, in one year timesteps. At the end of the five year period average values for density (total number of trees), DBH and BA (m^2) were statistically compared with the 2011 survey data using the Wilcoxon signed-rank test (wilcox.test in R). The test is a non-parametric statistical paired difference test that can be used as an alternative to the paired Student's t-test when the population cannot be assumed to be normally distributed.

Only trees greater than five centimetres DBH in the 2006 survey were assessed with the resulting outputs compared to the 2011 survey data. Comparisons were made over individual plots (CyB4, CyB5 and CyB7).

4.2.8 Statistics

All analyses were carried out in R (R Development Core Team, 2012). Standard analyses used the built in *stats* package. Maximum likelihood estimations using simulated annealing were conducted with the *likelihood* package (Murphy, 2010).

Table 4.2 Plot characteristics in 2006 of all trees ≥ 5 cm DBH.

	No. individuals	DBH (cm) (mean ±Standard Deviation)	BA(m^2/ha) (summed)
CyB4			
All	108	37.44 ±29.8	19.35
DF	80	39.13 ±30.5	15.41
SNS	14	57.01 ±16.8	3.86
HWD	3	7.43 ±2.4	0.01
SWD	11	8.38 ±2.4	0.07
CyB5			
All	292	21.37 ±27.0	27.16
DF	192	27.54 ±31.0	25.83
SNS	37	12.05 ±14.2	0.99
HWD	5	7.22 ±2.9	0.02
SWD	58	8.08 ±2.2	0.32
CyB7			
All	387	11.30 ±5.0	4.65
DF	268	11.92 ±5.0	3.50
SNS	25	13.62 ±6.6	0.45
HWD	92	8.77 ±3.7	0.65
SWD	2	15.95 ±2.8	0.04

4.3 Results

4.3.1 Allometry

4.3.1.1 Seedling height to diameter linear relationship

Table 4.3. Model parameters and evaluation for the DF seedling height to diameter at 10cm height linear relationship

MLE	α	β	β Support intervals	AICc	R^2
-684.312	0.1	1.077	1.012 – 1.1148	1372.660	0.786

Linear model based on equation (4.5). Abbreviations: AICc, Akaike's information criterion correction; MLE, Maximum likelihood estimate.

The seedling height to diameter at 10cm height linear relationship had a good level of fit, with only 21.4% of variance unaccounted for by the statistical model (Table 4.3). Comparison of predicted seedling heights to observed heights yielded a good fit for the parameterisation dataset despite the influence of two outliers from CyB5 with greatly underestimated seedling heights. The slope of the line (β = 0.787) deviates from 1 and intercepts the 1:1 line at 0.45m (Figure 4.2a), above which the model underestimates seedling height as shown by the negative residuals (Figure 4.2c). For example, an observed height of 1.2m was predicted as 1.05m (Figure 4.2a). The model fit for the validation dataset is slightly poorer (R^2 = 0.681), with a large number of seedlings predicted to have 0.1m height compared to observed heights of 0-0.6m (Figure 4.2b). The intercept between the regression line and 1:1 relationship occurred at 0.2m (Figure 4.2b), and the regression line slope was closer to 1 (Figure 4.2b). Overall, the residuals were evenly dispersed, with the greatest range of values for mid-range predicted heights (Figure 4.2c,d).

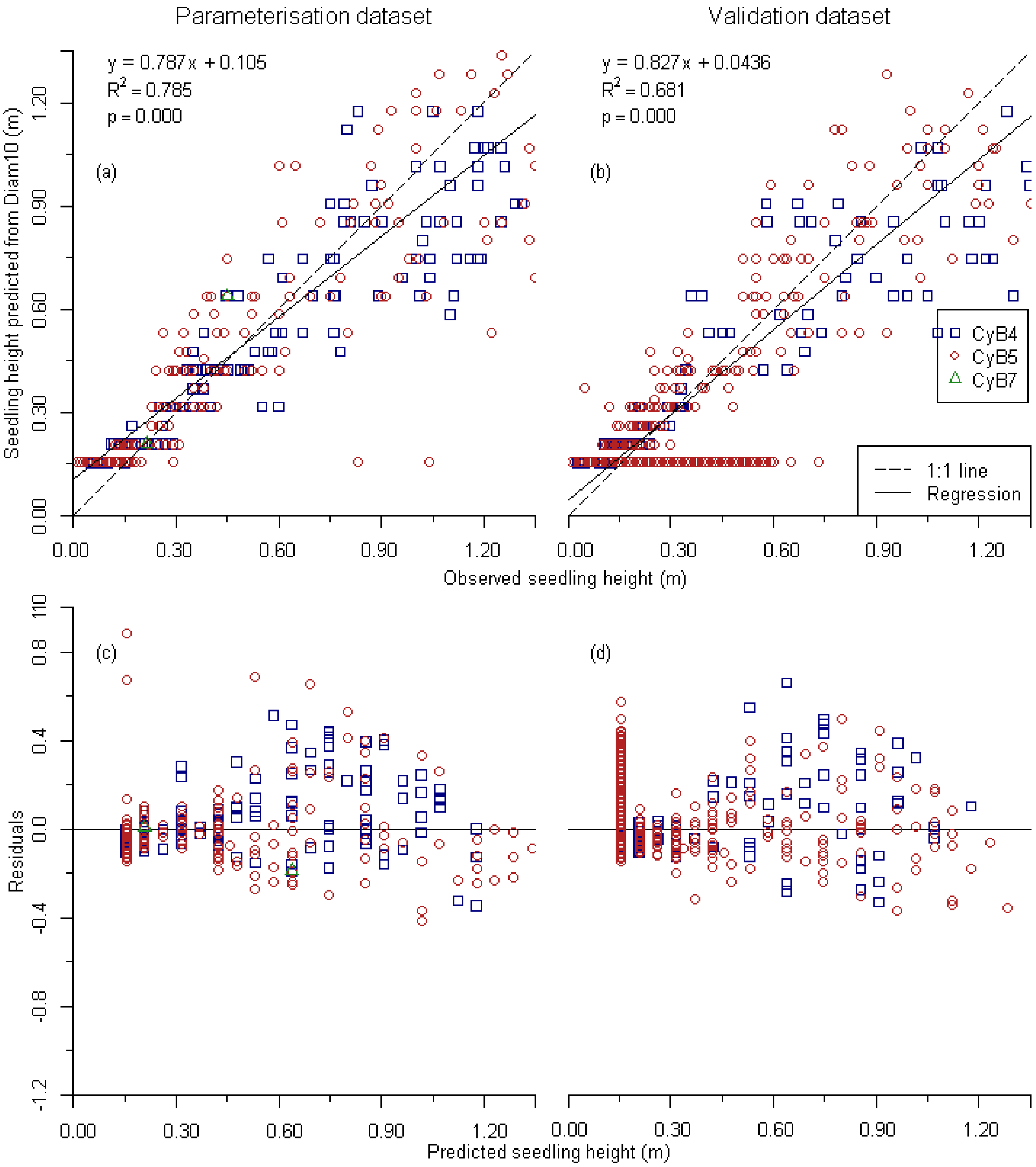

Figure 4.2. Seedling height relationship based on predictions from diameter at 10cm for the parameterisation and validation datasets: a + b, comparison of observed and predicted seedling heights, note deviation of solid regression line from the dashed 1-1 relationship line; c + d, residual plots.

4.3.1.2 Saplings DBH to Diameter at 10 cm height

Table 4.4. Model parameters and evaluation for the DF sapling DBH to diameter at 10cm height relationship

MLE	α	β	β Support intervals	AICc	R^2
-89.478	0	0.599	0.575 – 0.623	183.009	0.839

Linear model based on equation (4.7). Abbreviations: AICc, Akaike's information criterion correction; MLE, Maximum likelihood estimate.

There was a good level of fit for the sapling DBH to diameter at 10cm height relationship with the statistical model accounting for all but 16.1% of the variance (Table 4.4). Comparing observed DBH to the predicted yielded a reasonable fit for the parameterisation dataset though systematic and proportional bias are present, causing an increasing underestimation of DBH at higher values. The proportional bias (β = 0.68) deviates from 1 and intercepts the 1:1 line at 1.25 cm (Figure 4.3a), above which the model underestimates sapling DBH, evidenced by positive residuals (Figure 4.3c). For example, an observed DBH of 4 cm is predicted at 3 cm (Figure 4.3a). The model fit for the validation dataset is slightly poorer (R^2 = 0.789), however the systematic bias is slightly less (β = 0.64) with an observed DBH of 3 cm predicted at 2.25 cm (Figure 4.3b). The intercept between the regression line and 1:1 relationship occurred at 1 cm (Figure 4.3b). The residuals were more evenly dispersed, with the greatest range of values for the larger DBH's (Figure 4.3 c,d).

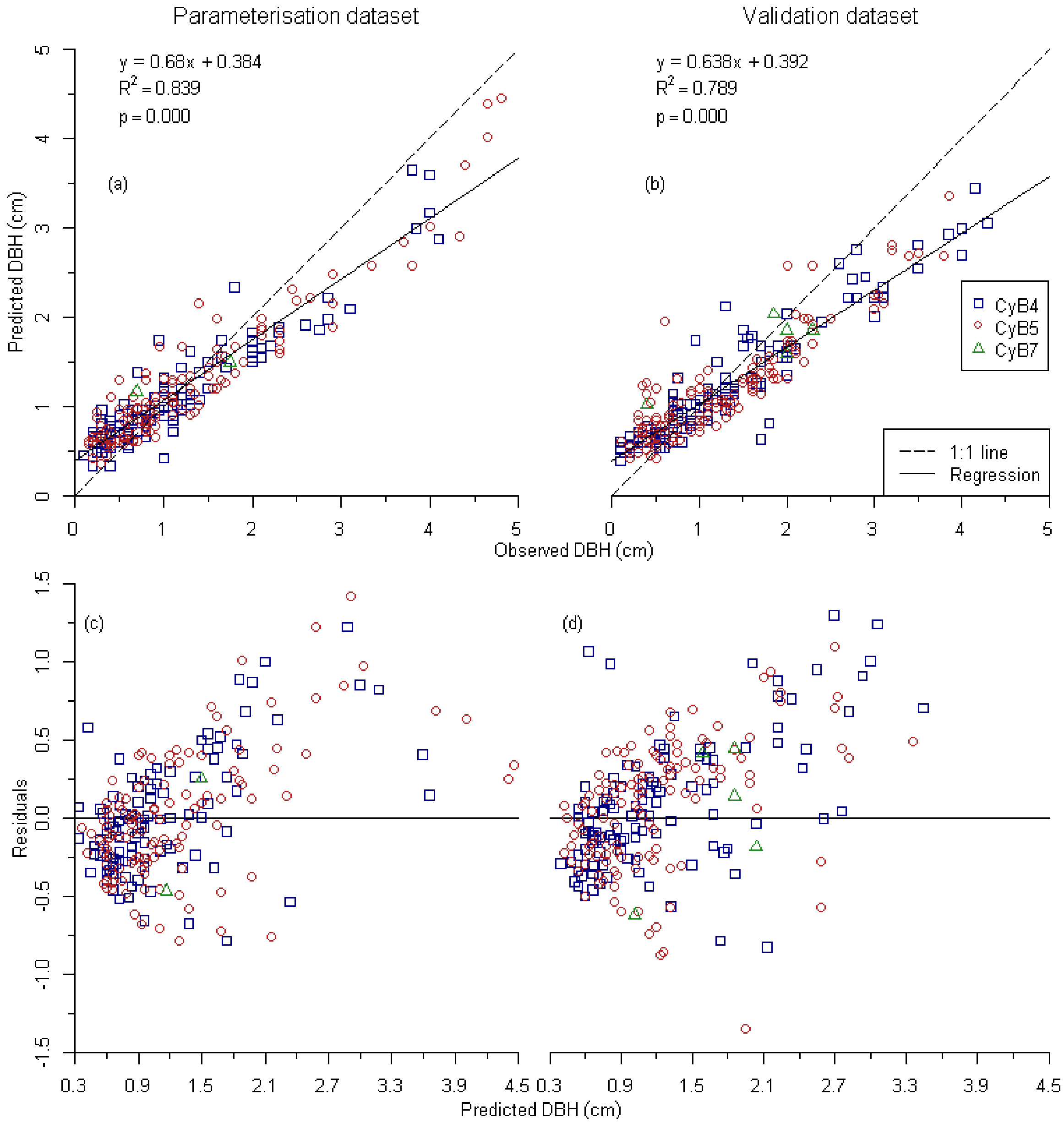

Figure 4.3. Sapling DBH to diameter at 10cm height relationship for the parameterisation and validation datasets: a + b, comparison of observed and predicted sapling DBH's, note deviation of solid regression line from the dashed 1-1 relationship line; c + d, residual plots.

4.3.1.3 Sapling and Adult Standard tree height to DBH

Table 4.5. Model parameters and evaluation for the DF sapling and adult height to DBH standard relationship

MLE	h_max	h_max support intervals	β	β Support intervals	AICc	R^2
-932.131	70.329	69.626 – 71.033	0.015	0.014 – 0.015	1870.304	0.971

Model based on equation (4.6). Abbreviations: AICc, Akaike's information criterion correction; MLE, Maximum likelihood estimate.

The combined sapling and adult height to DBH relationship had a very good level of fit, with only 2.9% of unaccounted variance from the statistical model (Table 4.5). When compared to the observed heights, the predicted heights were a good fit with negligible bias (Figure 4.4) despite an outlier from CyB5 and one from CyB7. The slope of the line ($\beta = 0.971$) only marginally deviated from 1 and crossed the 1:1 line at 15m (Figure 4.4a), above which the model underestimates adult height slightly. For example, an observed height of 55 m was predicted as 57 m (Figure 4.4a). The model fit for the validation dataset is slightly better ($R^2 = 0.974$), with less systematic and proportional bias (Figure 4.4b). The two story canopy status is obvious in the comparisons of observed and predicted heights (Figure 4.4a, b) and also in the model residuals (Figure 4.4 c,d) though they are otherwise scattered aside from the two outliers in the parameterisation data.

The structural difference between CyB7, and CyB4 and CyB5 is demonstrated clearly. Both parameterisation and validation datasets show a strong band of CyB7 trees between 10and 25 m. The understorey trees of CyB4 and CyB5 reach a maximum of 15 – 20 m and then leave a clear gap until the 35 m point, outlier aside (Figure 4.4a, b).

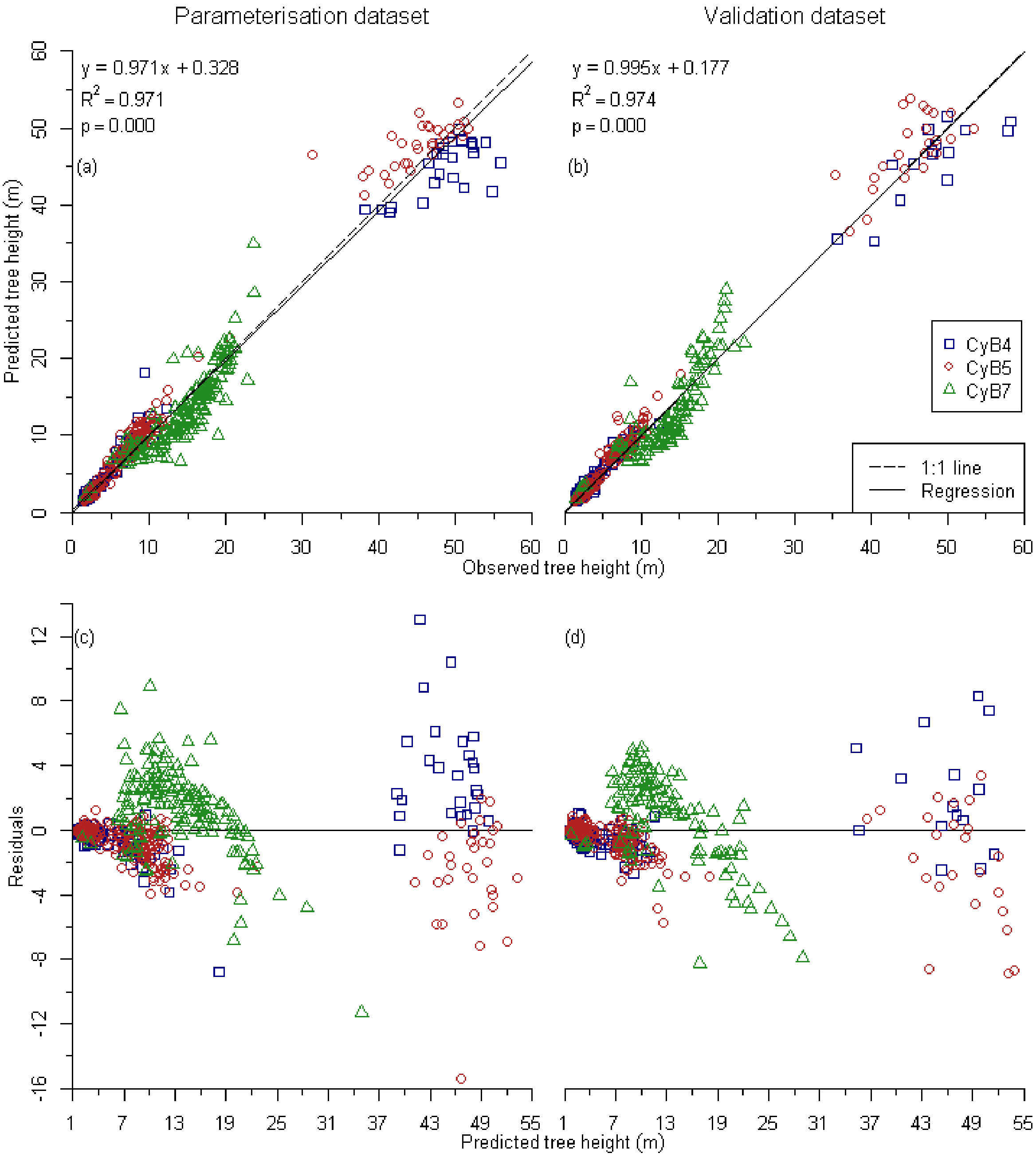

Figure 4.4. Sapling and adult tree height to DBH relationship for the parameterisation and validation datasets: a + b, comparison of observed and predicted tree heights, note close match of regression line and 1-1 relationship line; c + d, residual plots.

4.3.1.4 Crown depth to tree height (saplings and adults)

Table 4.6. Model parameters and evaluation for the DF sapling and adult crown depth to tree height standard relationship

MLE	b	b Support intervals	C	C Support intervals	AICc	R^2
-453.233	1.092	1.092 – 1.092	0.416	0.402 - 0.427	912.602	0.913

Model based on equation (4.8) Abbreviations: AICc, Akaike's information criterion correction; MLE, Maximum likelihood estimate.

Parameterisation of the crown depth to tree height relationship showed a good fit level with only 11.2% of variance unaccounted for (Table 4.6). Predicted crown depth was close to the observed values with only slight systematic bias (0.764) and marginal proportional bias (0.941) (Figure 4.5, a). The 1:1 line intercepted the regression at 12 m after which depths were slightly underestimated e.g. an observed crown depth of 31.5 m was predicted as 29.75 m (Figure 4.5, a). At the lower crown depths data from CyB7 were central to 1:1 line whilst CyB5 data was offset (Figure 4.5, a). This can be seen in the residuals as the majority of CyB5 data is above the zero line. Otherwise the residuals were scattered though the two storey system is still apparent (Figure 4.5, c)

The validation set goodness of fit was only slightly poorer, and still strong (R^2 = 0.87). The proportional bias (0.91) is more pronounced with the intercept between the regression line and 1:1 relationship occurring at a lower crown depth (10.5 m) (Figure 4.5b), creating a larger underestimation of crown depth afterwards (for example, an observed value of 28 is predicted as 24.5 m) (Figure 4.5b).

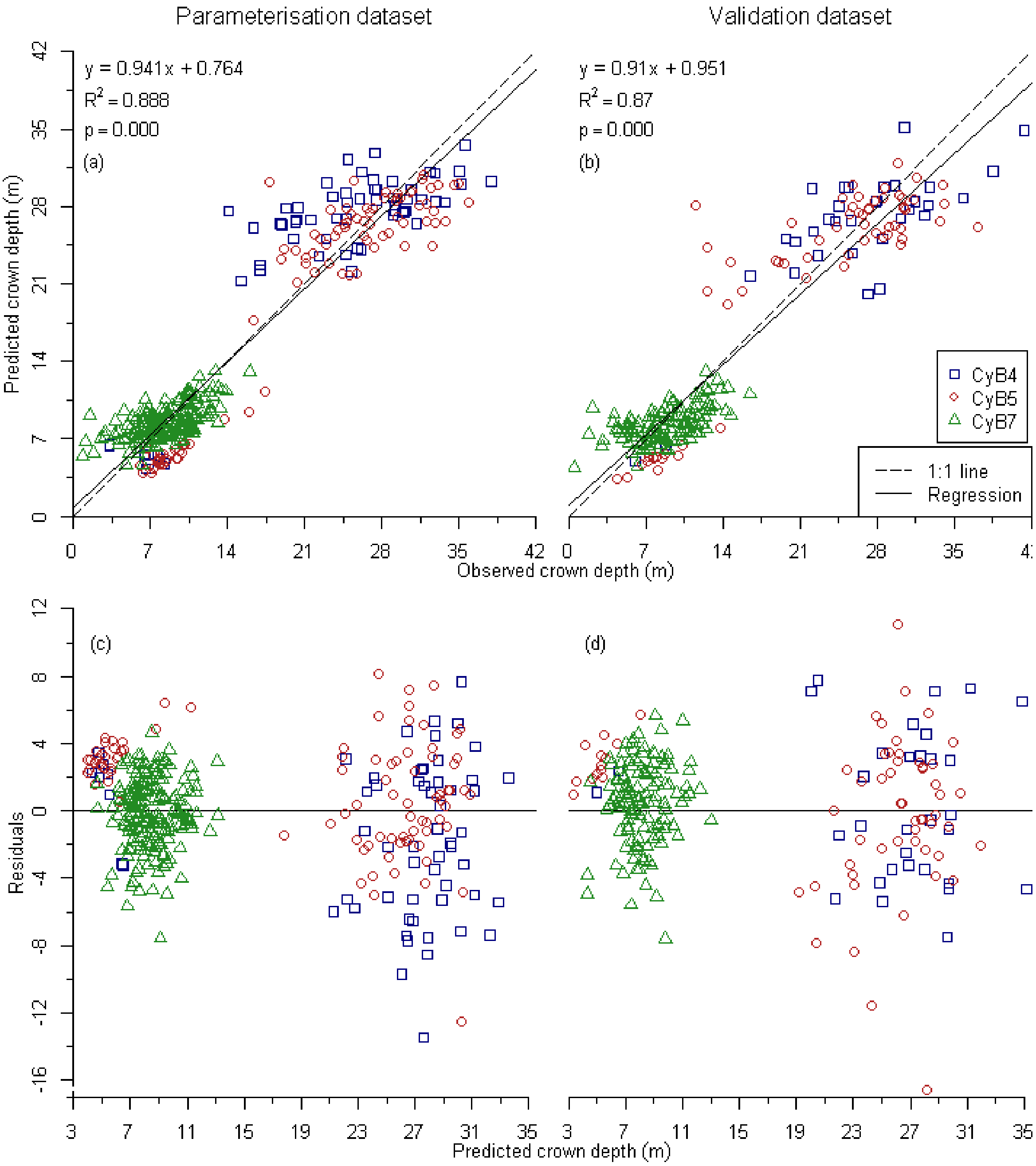

Figure 4.5. Sapling and adult crown depth to tree height relationship for the parameterisation and validation datasets: a + b, comparison of observed and predicted tree heights, note close match of regression line and 1-1 relationship line; c + d, residual plots.

4.3.1.5 Crown radius to DBH (saplings and adults)

Table 4.7. Model parameters and evaluation for the DF sapling and adult crown radius to tree height standard relationship

MLE	b	b Support intervals	C	C Support intervals	C scaled	AICc	R^2
-187.368	0.598	0.592 – 0.604	0.351	0.340 – 0.363	0.200	380.865	0.785

Model based on equation (4.8) Abbreviations: AICc, Akaike's information criterion correction; MLE, Maximum likelihood estimate.

The crown radius to DBH relationship had a good level of fit (0.785) for the parameterisation data, though the validation dataset fit was higher (0.846) (Table 4.7, Figure 4.6). The comparison of observed to predicted crown radius was relatively poor with smaller observed radii overestimated and larger underestimated, for example an observed radius of 2 m was predicted at 5 m and an observed of 7.5 m was predicted at 5 m. The proportional bias ($\beta = 0.754$) deviated from 1, intercepting the 1:1 line at 2. 5 m (Figure 4.6a), there was also considerable systematic bias (0.652). The residuals for the larger values were considerably spread and, as with crown depth, CyB7 datapoints appear to have monopolised the fit at the lower values (Figure 4.6c). Comparison of the predictions against observed for the validation dataset were not as poor but the 1:1 line was intercepted at 2 m after which radii were still underestimated, e.g. an observed of 6 m was predicted at 4.5 m (Figure 4.6b). Overall, the residuals were more evenly dispersed than the parameterisation dataset (Figure 4.6 c,d).

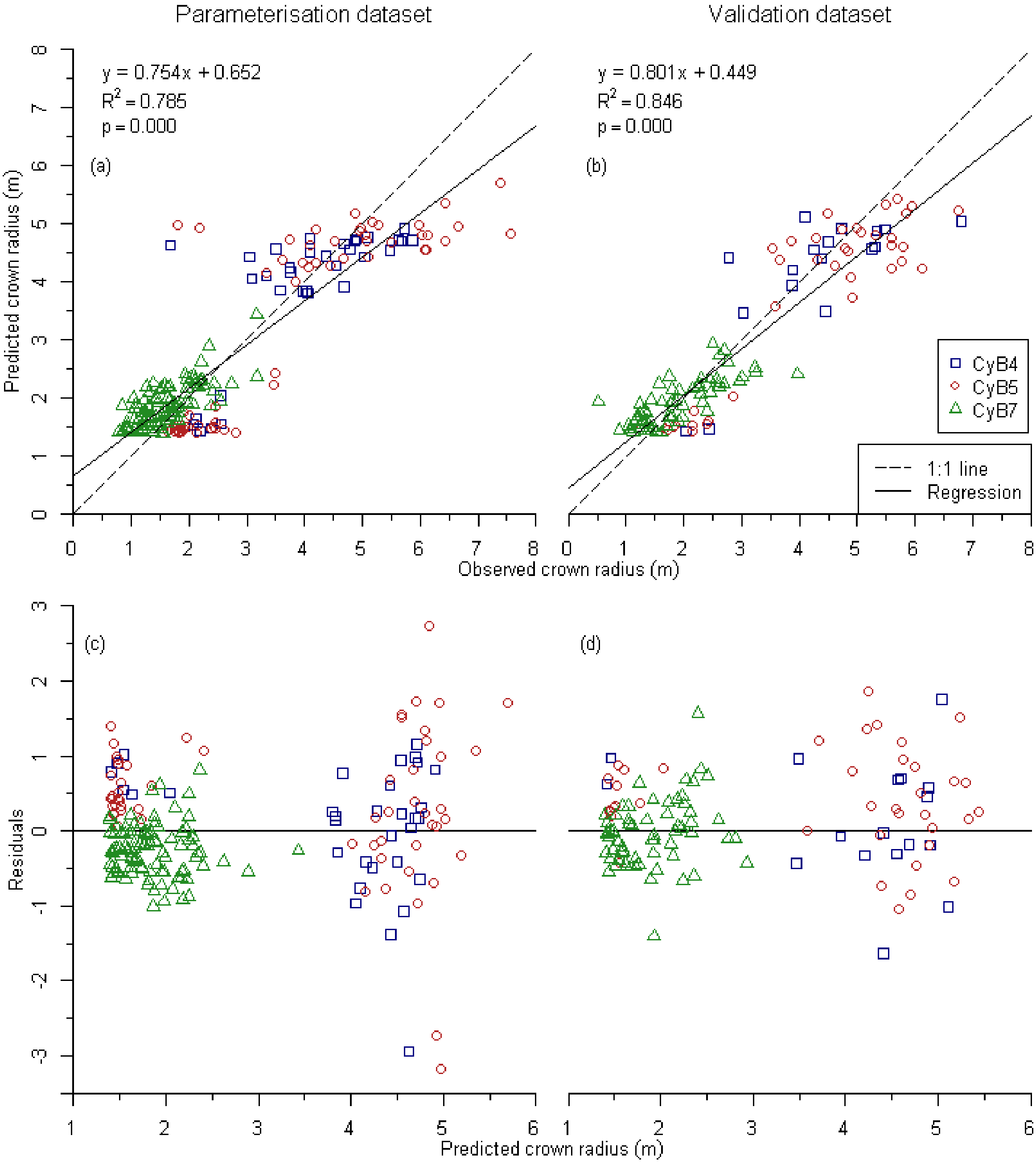

Figure 4.6. Sapling and adult crown radius to DBH relationship for the parameterisation and validation datasets: a + b, comparison of observed and predicted tree heights, note close match of regression line and 1-1 relationship line; c + d, residual plots.

The slope of the asymptotic crown radius was scaled as with SORTIE-NZ by a factor of 0.57 to 0.200.

4.3.2 Adult growth submodel

The slope of the regression is much shallower than the slope of the 1:1 relationship (Figure 4.7a). It is apparent from comparisons of the parameterisation data observed against predicted, and the residual plots (Figure 4.7a, c) that four outliers (two from CyB5 and two from CyB7) have had an overriding influence on the parameterisation. From the residuals it is clear that without the bias imposed by the outliers, the fit would be greatly improved. Whilst goodness of fit was low for both datasets ($R^2 = 0.301$ for parameterisation and $R^2 = 0.304$ for validation) the correlation between observed and predicted was highly significant, $p = 0.000$. Currently the parameterisation data set greatly underestimates fit above 0.75 cm yr^{-1} e.g. an observed growth of 1 cm yr^{-1} is predicted at 0.75 cm DBH yr^{-1}. Between 0 growth and 0.75 cm yr^{-1} it is underestimated by up to 0.41 cm yr^{-1}. The majority of datapoints fall between 0 growth and 1.25 cm yr^{-1} for both parameterisation and validation datasets. The same lack of fit is apparent in the validation dataset which includes another outlier with underestimated growth (2.4 cm as 0.75 cm).

Table 4.8. Results of parameterisation for Basal area NCI with competition effect (right) and without (left).

	Size Effect		Crowding effect	
Parameter	Value	Support intervals	Value	Support intervals
max radius	NA	NA	10.515	9.043 - 12.602
max growth	0.971	0.884 -1.061	1.213	1.104 - 1.325
Xo	37.346	35.105 -40.225	42.306	39.768 - 45.914
Xb	0.783	0.729 - 0.843	0.838	0.780 - 0.883
C	NA	NA	4.489E-03	2.738E-03 - 6.867E-03
D	NA	NA	0.707	0.630 - 0.776
MLE	-54.559		-50.823	
AICc	117.383		116.403	
R^2	0.209		0.316	

Model based on equation (4.15) Abbreviations: AICc, Akaike's information criterion correction; MLE, Maximum likelihood estimate.

The AICc value showed support for both models (Table 4.8), however the model with *crowding effect* had a better overall fit (though still low) and lower MLE, and was selected for use in the final model (Table 4.8). The maximum likelihood estimate of maximum radius of neighbourhood influence was 10.515 m which is in line with the limit of crown extent built into the model (Table 4.8).

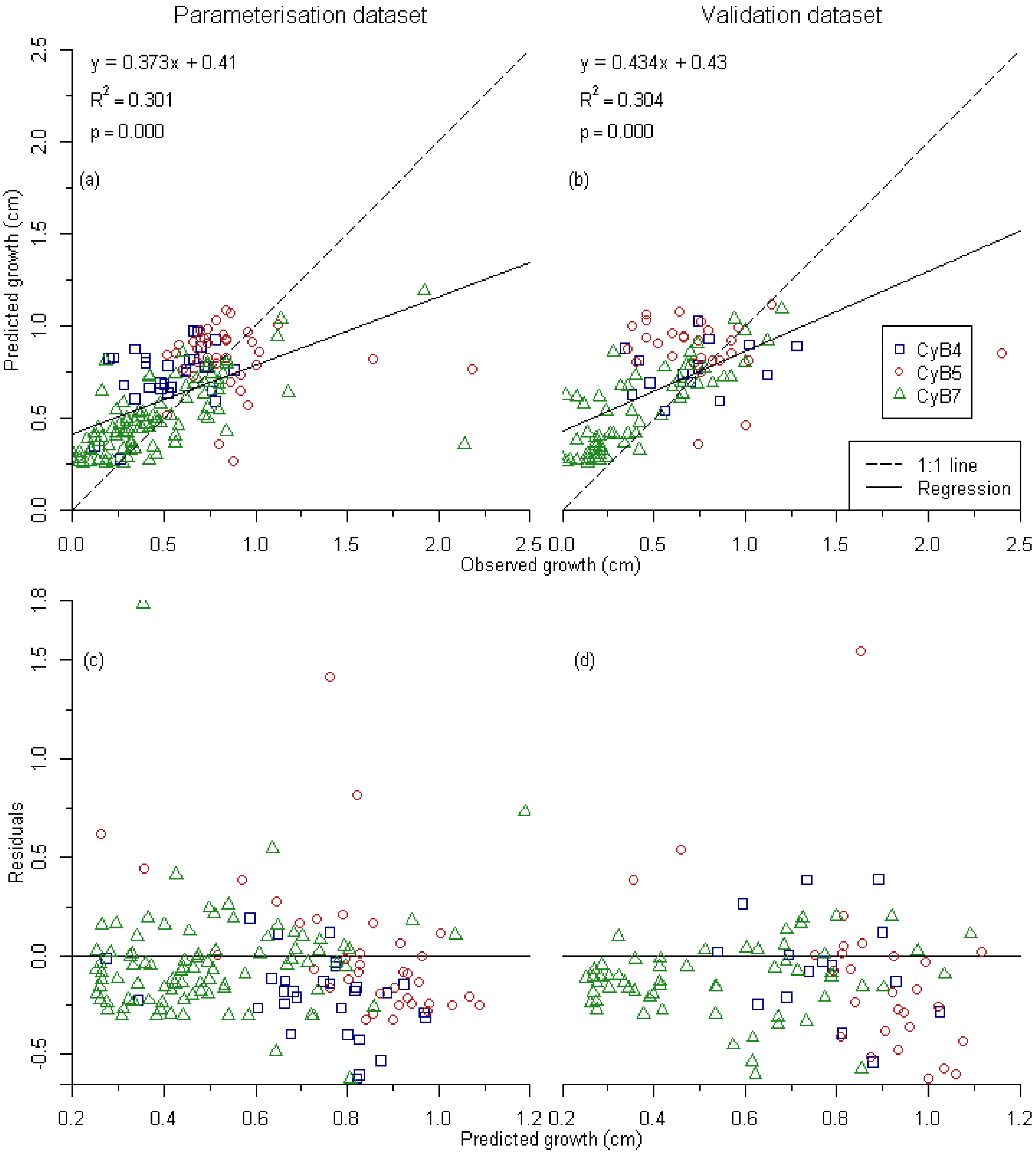

Figure 4.7. Predicted growth (cm yr^{-1}) against observed growth (cm yr^{-1}) for the basal area NCI growth behaviour, classified by PSP, for the (a) parameterisation dataset and (b) validation dataset. Bottom: Residual plots for (c) Parameterisation and (d) Validation datasets.

4.3.3 Light submodel

The canopy openness values calculated from 65 DF individuals by the Crown Deliminator software (Boivin et al., 2011) ranged from 0.111 ±0.01 (11.1%) for CO20 to 0.547 ±0.06 (54.7%) with CO_{rect} (Table 4.9).

Table 4.9. Canopy openness values determined by the Crown Delineator software from 65 Douglas fir (Boivin et al., 2011)

Outline	Canopy Openness Value	Standard Deviation	Confidence Interval
CO20	0.111	0.039	0.010
CO40	0.154	0.045	0.011
CO80	0.203	0.057	0.014
CO160	0.246	0.064	0.016
CO320	0.283	0.069	0.017
CO_{CH}	0.355	0.074	0.018
CO_{rect}	**0.547**	**0.060**	**0.015**

The CO_{rect} method had the best one to one fit to the observed data (p = 000; adj. R^2 = 0.764) (Figure 4.8). All other crown delineation methods provided values far below those actually found (Figure 4. 9).

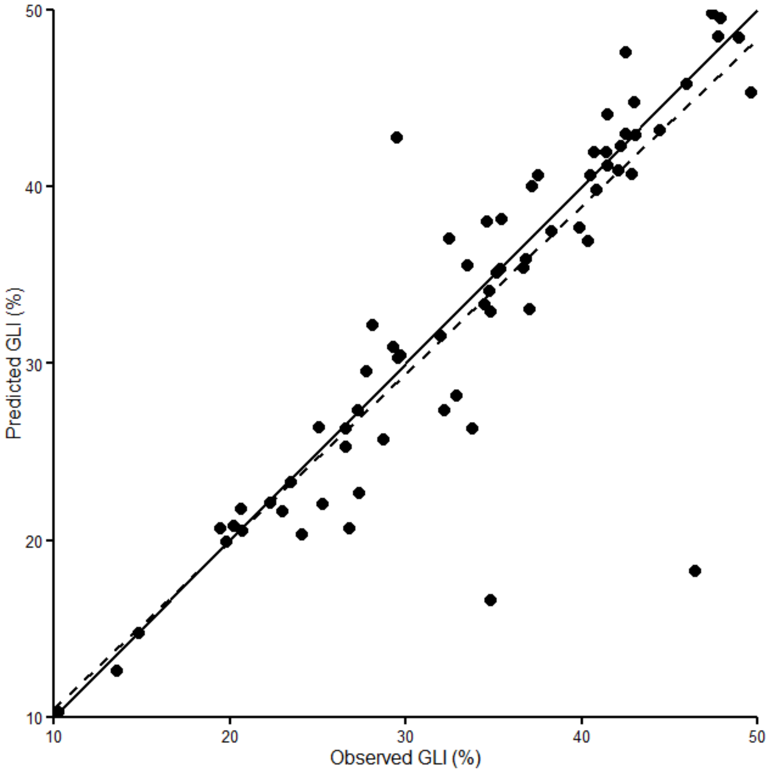

Figure 4.8. Observed GLI (%) vs predicted. Solid line is one to one, dashed line is the regression.

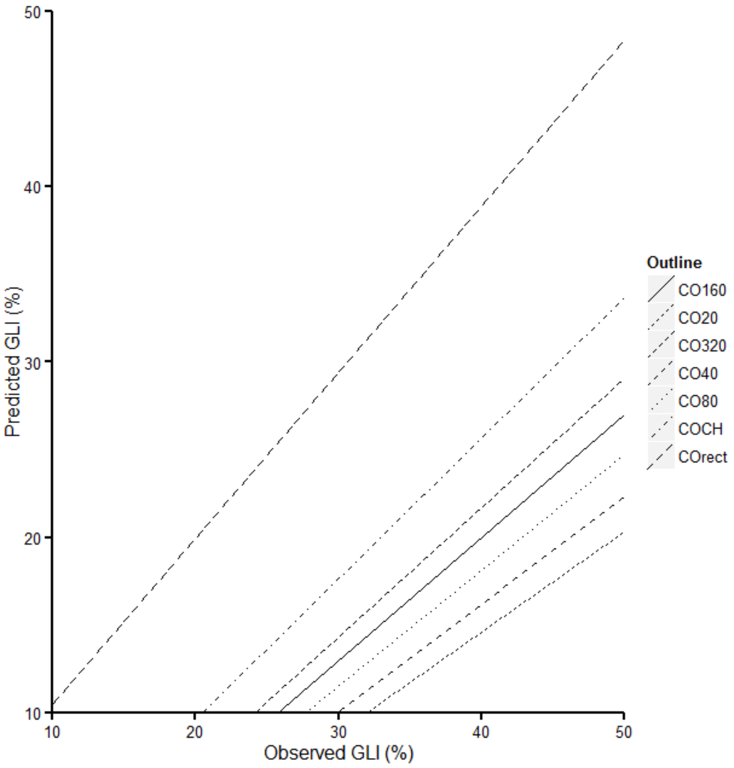

Figure 4. 9. One to one plot of observed GLI (%) vs predicted for all seven canopy openness algorithms.

4.3.4 Initial model runs

4.3.4.1 CyB4

From the 2006 survey of 108 individuals, the CyB4 2011 PSP survey showed 105 individuals as survivor growth (SG): one DF had died (felled, reason unknown), two SNS had suffered mortality, and all HWD and SWD survived. The average survivor growth DBH increased by 2 cm and the total BA increased by 1.15 m²/ha. The average DBH of DF increased by 1.98 cm and the total basal area also increased by 1.16 m²/ha (Table 4.10a).

Total number of SG trees were consistent between model outputs (104±1.42) and PSP data (105). Likewise the overall average DBH of 40.63 (± 30.78 cm) and a total BA of 21.33 m²/ha (± 0.20) were consistent with field data. The DBH density diagram (Figure 4.10a) demonstrates the adequacy of the model output. This is further supported by the Wilcox test comparisons of DBH for all species, combined and separately (Table 4.10a). In terms of density all species groups suffered mortality and growth consistent with the PSP data, except for SNS which was slightly over represented, with model outputs of 13.87 ± 0.35 stems to PSP data of 12, approximately two trees difference. CyB5

CyB5 had 292 trees in total of which 192 were DF in 2006 (Table 4.2). This had decreased to 289 SG with two SNS and 1 SWD mortality (Table 4.10b). The average surveyed DBH increased to 25.22 ± 27.8 from a 2006 average of 21.37 ± 27.0. Total basal area had increased from 27.16 m²/ha in 2006, for all species, to 31.33 m²/ha in 2011.

CyB5 model outputs were less consistent with the PSP data than CyB4. Tree density was reduced to 278.97 ±2.99 with DF suffering the bulk of the mortality (Table 4.10b). DF numbers averaged a difference of approximately 8 trees between observed and predicted. However comparison with a Wilcox test found this to be significantly different for all 30 runs. SWD was also significantly different for all 30 runs whereas HWD and

SNS were not. From the density diagram (Figure 4.10b) it is apparent that this difference is results from a reduced progression through the lower size classes (5 to 15 cm) where modelled outputs are compared to PSP data (Figure 4.10b).

Table 4.10. Comparison of stand characteristics (mean ± st dev) for 2011 PSP input data and SORTIE output data (See Table 4.2 for 2006 data)

	Observed 2011 PSP data			Predicted model outputs			
	N	DBH	BA	N	DBH	BA	Wx[a] DBH
(a) CyB4							
All	105	39.44 ± 30.6	20.50	104.90 ±1.42	40.63 ± 30.78	21.33 ± 0.20	0/30
DF	79	41.11 ± 31.5	16.57	77.67 ± 1.30	42.26 ± 31.69	16.94 ± 0.21	0/30
SNS	12	60.42 ± 19.2	3.76	13.87 ± 0.35	60.55 ± 15.93	4.26 ± 0.11	0/30
HWD	3	9.87 ± 2.6	0.02	2.73 ± 0.52	9.09 ± NA	0.02 ± NA	0/30
SWD	11	12.71 ± 2.3	0.14	10.63 ± 0.49	10.87 ± 3.63	0.11 ± 0.01	0/30
(b) CyB5							
All	289	25.22 ± 27.8	31.33	278.97±2.99	23.99±28.39	30.21±0.19	30/30
DF	192	30.61 ± 32.0	29.15	184.43±2.80	30.14±32.48	28.35±0.22	30/30
SNS	35	15.65 ± 15.2	1.25	34.93±0.98	13.56±15.90	1.18±0.08	0/30
HWD	5	9.90 ± 2.4	0.04	3.43±0.82	9.62±NA	0.03±NA	0/30
SWD	57	13.93 ± 3.1	0.88	56.17±1.37	11.2±4.81	0.65±0.01	30/30
(c) CyB7							
All	353	13.24 ± 6.5	6.02	343.43±3.26	13.72 ± 6.44	6.19 ± 0.02	0/30
DF	240	13.99 ± 6.3	4.44	252.03 ± 2.53	14.05 ± 6.31	4.69 ± 0.02	0/30
SNS	24	16.93 ± 9.0	0.69	22.07 ± 0.91	18.05 ± 8.46	0.68 ± 0.03	0/30
HWD	87	10.01 ± 4.8	0.84	67.33 ± 2.63	10.86 ± 4.83	0.74 ± 0.01	30/30
SWD	2	18.85 ± 5.6	0.06	2 ± 0.00	21.85 ± 2.91	0.08 ± 0.01	0/30

[a] Results of a Wilcoxon (Mann-Whitney) ranked sum test. Number of runs (out of 30) that were statistically ($p < 0.05$) different.

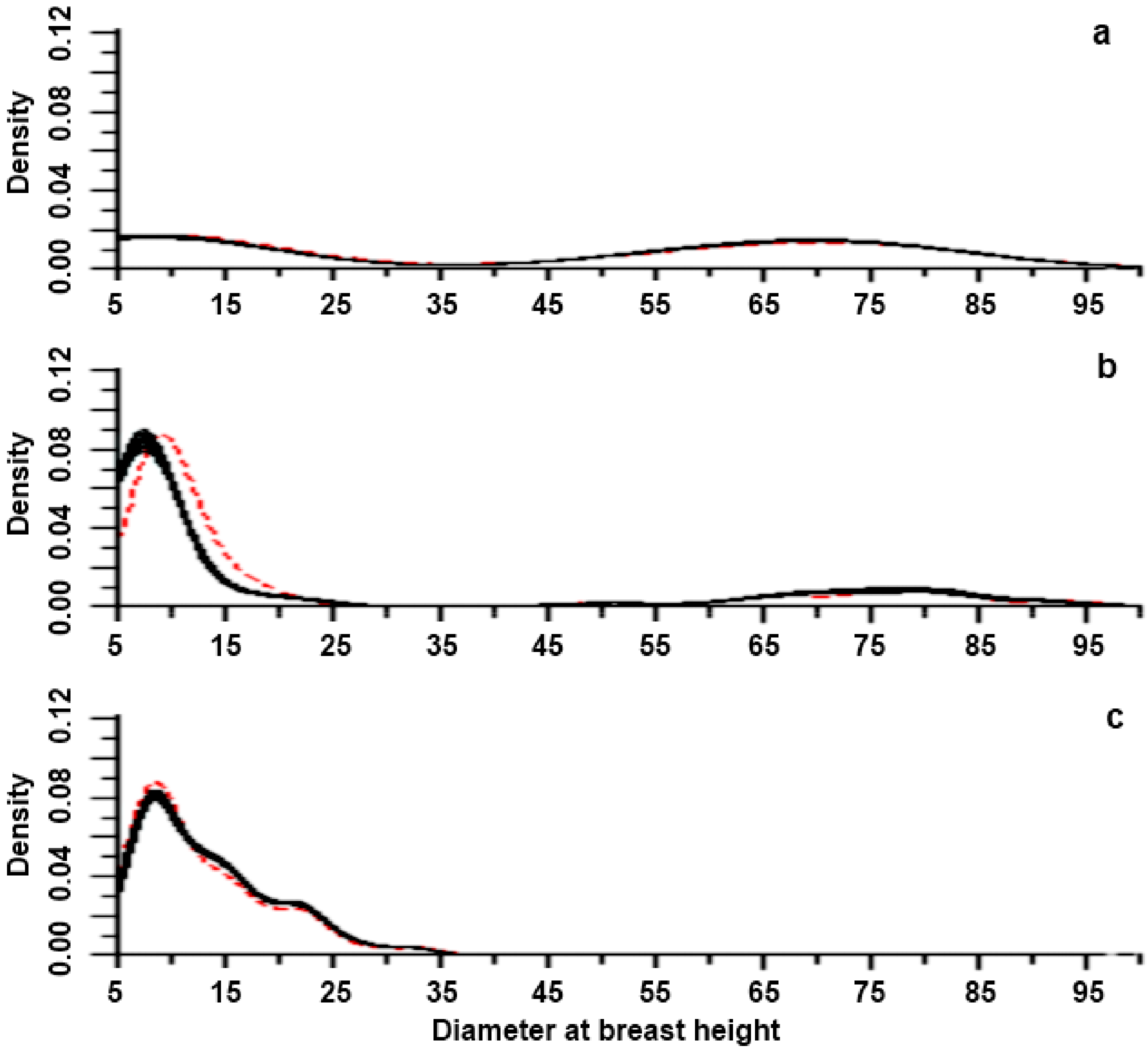

Figure 4.10. DBH density diagrams from 30 model for (a) CyB4, (b) CyB5 and (c) CyB7. Red dotted line is PSP data from 2011; black lines are simulation runs.

4.3.4.2 CyB7

As the densest stand, CyB7 suffered the greatest mortality of all three PSPs over the growth period with a total reduction of original trees from 387 in 2006 (Table 4.2) to 354 (Table 4.10). DF suffered 28 fatalities, SNS 1, HWD 4 and SWD zero. Over all species, average DBH increased by 1.9 cm and basal area was increased 1.37 m²/ha between 2006 and 2011. The average DBH of DF increased by 2.05 cm with a concurrent increase in basal area by 94 m²/ha (Table 4.10a).

With all species combined, the model runs were not significantly different than the PSP data mortality (Table 4.10c) however density was lower for model outputs (343.43

±3.26) than for field data (353). This difference was accounted for by a reduction in HWD from 87 individuals to 67.33 (± 2.63) and an increase in the number of DF from 240 to a modelled 252 (± 2.53). Only the HWD species group had a modelled average DBH that was significantly different from the PSP data.

4.4 Discussion

4.4.1 Allometrics

The estimated parameter values for DF compare well to previous studies (Kunstler, 2011, Coates, K.D., 2012). The study of Interior Cedar Hemlock forests at Date Creek (ICH-DC) (Canham et al., 1999, Coates, K.D., 2012) provides parameter estimates of directly comparable species, western hemlock and hybrid spruce (Table 4.11). Hybrid spruce is the cross of white spruce (*Picea glauca* (Moench) Voss), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and sometimes Engelmann spruce (*Picea engelmannii* Paary ex Engelm.)) (Canham et al., 1999).

A further study at the Waitutu Forest, Southland, New Zealand (Coomes et al., 2005, Kunstler, 2011), parameterised the model SORTIE-NZ for local native species using similar allometric and growth relationships, including two conifer species: *Podocarpus halli* or *Podocarpus cunninghamii, (*there is controversy over the scientific name) is a stout endemic conifer that grows to approximately 20 m (NZ Plant Conservation Network, 2013). *P. halli* is denoted here as PODHAL following the authors convention. The other species, *Dacyrydium cupressinum,* is an endemic evergreen conifer that grows to between 35 – 60 m in height (NZ Plant Conservation Network, 2013). *D. cupressinum* is likewise denoted here as DACCUP (Table 4.11).

Douglas fir had a sharper slope of the relationship between seedling height and diameter at 10 cm height than all the compared studies (Table 4.11, a, beta parameter) and was closer to the SORTIE-NZ values than the ICH-DC. This is not unreasonable though and the model tended to underestimate the relationship for both parameterisation and validation datasets (Figure 4.2). The lower values for the slope of the linear function suggest that Douglas fir seedlings gain more height at a smaller diameter than the compared species though many of the seedlings encountered were growing along the ground (Haffenden pers. obs.).

The ICH-DC DBH to Diam_{10} parameter value for hybrid spruce (0.693) is very close to the parameterised DF value and its upper support limit (0.599, range from 0.575 – 0.623) (Table 4.4, Table 4.11, b) . The slope of Western hemlock is steeper than either Douglas fir or hybrid spruce suggesting a larger DBH at a smaller height. Comparisons of radial growth increment in relation to percentage of full light, between western hemlock and hybrid spruce, along various climatic gradients at Date Creek, found a greater radial increment at lower light levels for western hemlock (Wright et al., 1998). The intercepts for the SORTIE-NZ parameterisation were not fixed at zero however DACCUP gained the greatest DBH for diameter at 10 cm height and PODHAL was equivalent to western hemlock in its relationship. DF accrued the lowest DBH to diam_{10} of all the species suggesting that it is the slowest growing.

Predicted maximum achievable height of DF (70.329 m) was considerably higher than any of the comparison species (Table 4.5, Table 4.11). Next tallest was hybrid spruce at 45 m. However the Gymnosperm database (Earle, 2012) states that Douglas fir reaches 90 m in height if not larger. White spruce is predicted to reach 50 m in height (Earle, 2012) and Sitka 80 m (Earle, 2012). The data suggests that Douglas fir seedlings, saplings and adults are slower growing than western hemlock and hybrid spruce, but if parameters from the Date Creek site are representative (Coates, K.D., 2012), then it attains greater height over time.

The crown depth parameters DF compare well to both the Date Creek and SORTIE-NZ study (Table 4.11). The Date Creek parameterisation was carried out with the *b* parameter fixed at 1. A comparison of the graphed relationships (Figure 4.11) predicts that DF will have deeper crowns for height than the other species. For example, at western hemlocks predicted maximum height (39.480 m), it will have a crown depth of 15.36 m and Douglas fir will have a crown depth of 23.03 m (Figure 4.11). The goodness of fits reported for SORTIE-NZ were considerably less convincing than this study (Data Creek data is not available).

The goodness of fit for the Standard crown radius relationship (0.785) (Table 4.11), though low, was greater than that reported for the PODHAL and only slightly less than DACUP (Kunstler, 2011). Again the *b* parameter was fixed at 1 for the Date Creek study, making numerical comparisons difficult. The fitted values (Figure 4.12) for DF are similar in shape and amplitude to DACCUP. Hybrid spruce appears to accrue crown radius very slowly. Western hemlock may be equivalent to DF with the inclusion of the *b* term was parameterised (Figure 4.12).

The separation in the data that is apparent in the sapling and adult DBH to tree height and crown metric relationships supports the findings of the fieldwork chapter (chapter 3), that the stands are at different stages of succession. The largest individuals in the lower group, for all three allometric relationships, are from CyB7. CyB7 as the youngest stand, in the process of stem exclusion, does not have any of the larger more mature trees present in CyB4 and CyB5 (the larger separated group). The other individuals present in the lower group (from CyB4 and CyB5) are the beginning of the stand reinitiation phase.

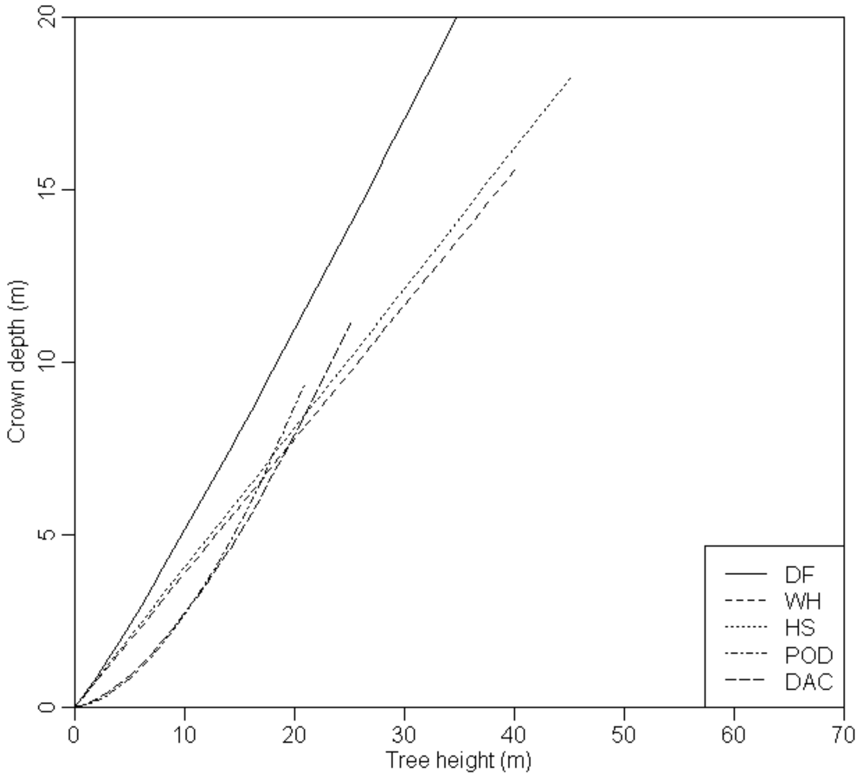

Figure 4.11. Comparison of DF crown depth to tree height relationship parameter estimates to species from other studies: western hemlock and hybrid spruce (Coates, K.D., 2012), and PODHAL and DACCUP (Kunstler, 2011) (Table 4.11).

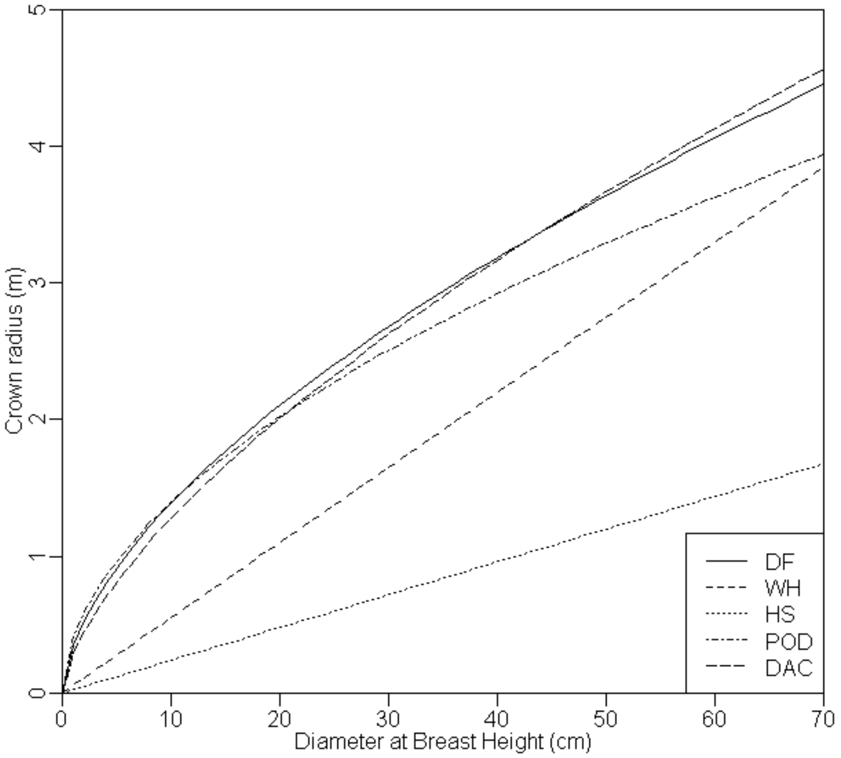

Figure 4.12. Comparison of DF crown radius to DBH relationship parameter estimates to species from other studies: western hemlock and hybrid spruce (Coates, K.D., 2012), and PODHAL and DACCUP (Kunstler, 2011) (Table 4.11).

Table 4.11. Allometric parameter estimates in comparison to other models and published data demonstrating parameter estimate, goodness of fit, species and related study.

Parameter	Estimate	Parameter	Estimate	R^2	Species	Study
(a) seedling height to diameter at 10 cm height						
alpha	0.100	beta	1.077	0.786	DF	This study
	0.100		0.034	NK	western hemlock	Coates 2012
	0.100		0.029	NK	hybrid spruce	Coates 2012
	0.100		0.832	0.832	PODHAL	Kunstler 2011
	0.100		0.717	0.890	DACCUP	Kunstler 2011
(b) sapling DBH to diameter at 10 cm height						
alpha	0.000	beta	0.599	0.839	Douglas fir	This study
	0.000		0.801	NK	western hemlock	Coates 2012
	0.000		0.693	NK	hybrid spruce	Coates 2012
	-0.551		0.815	NK	PODHAL	Kunstler 2011
	-0.933		0.939	NK	DACCUP	Kunstler 2011
(c) standard tree height to DBH						
h_max	70.329	beta	0.015	0.971	DF	This study
	39.480		0.030	NK	western hemlock	Coates 2012
	45.000		0.026	NK	hybrid spruce	Coates 2012
	20.950		0.066	0.519	PODHAL	Kunstler 2011
	25.279		0.054	0.886	DACCUP	Kunstler 2011
(c) standard crown depth						
b	1.092	C (slope)	0.416	0.913	DF	This study
	1.000		0.389	NK	western hemlock	Coates 2012
	1.000		0.405	NK	hybrid spruce	Coates 2012
	1.690		0.055	0.760	PODHAL	Kunstler 2011
	1.541		0.078	0.669	DACCUP	Kunstler 2011
(d) standard crown radius						
b	0.351	C (slope)	0.598	0.785	DF	This study
	1.000		0.055	NK	western hemlock	Coates 2012
	1.000		0.024	NK	hybrid spruce	Coates 2012
	0.532		0.411	0.743	PODHAL	Kunstler 2011
	0.654		0.284	0.826	DACCUP	Kunstler 2011

4.4.2 Growth submodel

No published data was available to directly compare the parameter values for the *basal area NCI growth* behaviour. Yearly maximum growth compares favourably with the data from Date Creek (Coates, K.D., 2012), and from SORTIE-NZ (Kunstler, 2011), in terms of magnitude (Table 4.12). DF is predicted to have the potential for 0.32 cm greater DBH growth than western hemlock, and 0.031 cm DBH growth more than hybrid spruce.

Both the SORTIE-NZ species had greater potential growth than DF (Table 4.12). The maximum radii of competitors were larger for hybrid spruce and western hemlock in the Date Creek study but not excessively (Coates, K.D., 2012). The SORTIE-NZ values were closer but these were specified in relation to plot size rather than parameterised. The model goodness of fit was affected by four outliers in this study but no obvious reason to exclude them is apparent in the data. However the values (1.64, 1.92, 2.14 and 2.18 cm DBH growth per year) are all greater than the predicted maximum growth and seem excessively high. Poage and Tappeiner (2002) in a study of long term growth patterns for Douglas fir in western Oregon found yearly diameter increment of between 0.6 and 1.54 cm yr^{-1} for trees older than 100 years.

Table 4.12. Basal area growth model parameter estimates in comparison to SORTIE-NZ

Species	max radius	max growth	R^2	Study
DF	10.515	1.213	0.316	This study
Western hemlock	13.134	0.893	NK	Coates 2012
Hybrid spruce	15.000	1.182	NK	Coates 2012
PODHAL	11.28	1.461	0.052	Kunstler 2011
DACCUP	11.28	1.529	0.023	Kunstler 2011

4.4.3 Light submodel

The Douglas fir canopy openness of 0.547 (±0.060) (54.7%) is higher than that found for any of the proxy species used. (Pacala et al., 1996, Canham et al., 1999). In the initial parameterisation of SORTIE, Pacala et al (1999) recorded a range of openness between 0.064 (±0.014) (6.4%) for American beech and eastern hemlock to 0.399 (±0.004) (39.9%) for various species including yellow birch (*Betula alleghaniensis*). The range of values found in the Interior Cedar Hemlock forest study ranged from 0.058 (5.8%) for paper birch to 0.206 (20.6%) for trembling aspen and included western hemlock, 0.08 (8%) and hybrid spruce, 0.114 (11.4%) (Canham et al., 1999).

However the resultant best fit for the CO_{rect} algorithm is in line with that shown by Boivin et al. (2011) during their pilot study of a boreal mixed wood forest. The canopy openness values for deciduous species (pin cherry, aspen and paper birch) ranged between 0.7 (70%) and 0.8 (80%) with the only conifer species, balsam fir, slightly lower but within the same range, at 0.7 (70%).

Discrepancies in this study may be due to comparisons of stands at different stages and in different locations. The over-mature status of CyB5 alone would potentially allow more developed crowns and larger trees than would normally be found within a plantation. A second possibility, as discussed by Boivin et al. (2011), is that the process of crown delineation with software such as the Gap Light Analyzer is described imprecisely and inconsistently in the literature. Likewise thresholding within the GLA software is subjective to the operator, there are no clear guidelines, and best carried out by one person for a study due to the variation in possible results (Beaudet et al. 2011). Much is left to interpretation, making comparisons between studies difficult (Boivin et al., 2011).

4.4.4 Initial model runs

With all three PSPs at different levels of stand development it is useful to compare their structure and model outputs to identify possible reasons for the discrepancies in the runs. The results of the initial runs for CyB4 are the most consistent with the PSP data whilst CyB7 appears consistent except for the HWD species group. There are low numbers of HWD SG in the other stands (3% of survivor growth in CyB4 and 2% in CyB5), while it is 25% of CyB7. However, the basal area of HWD trees in CyB7 is only 5.19 m^2 ha^{-1} (SNS which is 7% of total trees has a basal area of 4.24 m^2 ha^{-1}), which suggests that the majority of HWD are understory trees. The density of trees in CyB7 (2179 n ha^{-1}) compared to CyB4 and CyB5 (260.6 No. ha^{-1} and 291.3 No. ha^{-1} respectively) and the mortality of understory HWD trees suggests that the discrepancies between the model outputs of CyB4 and CyB7 are related to either the proxy values used for understory trees or the application of suppression and mortality parameters to saplings, which includes trees 5 ≤ 10 cm DBH as well as seedlings.

This may then explain the difference in outcomes between CyB4 and CyB5 given their greater similarity to each other rather than CyB7. CyB5 has a greater density of survivor growth (291.33 No. ha^{-1}) than CyB4 (260.55 No. ha^{-1}) but a considerably smaller basal area (31.58 m^2 ha^{-1} compared to 50.86 m^2 ha^{-1}). The density diagram from Figure 4.10b supports this hypothesis that smaller trees are being overly suppressed compared to the PSP data in CyB5 and suppressed to mortality in CyB7 (Figure 4.10c).

4.4.5 Study limitations and further work

Parameterising the models with data from three stands and two growth stages creates a more robust model over a range of stand conditions. Coates et al. (2009) found that growth models parameterised from narrow competitive ranges and successional stages were not able to predict a range of successional stages robustly. However, there are inherent gaps in the data due to the structure of the stands. The data used to parameterise DF is clearly separated into two layers (Figure 4.4a, b; Figure 4.5a, b; Figure 4.6a, b). The central data gap is perhaps not so much of an issue as there is sufficient data to predict the relationship. However, there is a trade-off in the parameterisation between the regeneration from CyB4 and CyB5 and the more densely packed planted trees of CyB7. Effectively the tree density of CyB7 swamps the crown allometrics of the regeneration from the other stands, as can be seen from the residual plots (Figure 4.5c; Figure 4.6c). A more robust fit would be acquired with the inclusion of data to fill the missing values over the central range.

There was insufficient data collected to be confident in the parameterisation of the sub-component species groupings. Though these sub-components are relatively minor compared to DF, there is the potential for a shift in dynamics over time, particularly with the advancing cohorts of SWD in CyB4 and CyB5 (Chapter 3). Also the majority of data collected for the SWD and HWD species groups are from the sub-canopy and so are not representative of the complete growth range as can be seen by comparison of the tree height to DBH parameterised relationships (Figure 4.13). It would be expected that HWD and possibly SWD would not have as high a height to DBH ratio as DF, but the limitations of the data preclude confidence in the relationships for predictions of future growth.

Removal of the outliers from the parameterisation data (Figure 4.7) for the *basal area NCI growth* relationship increased the fit by 10.7% to 0.423. However with no obvious reason to exclude them further work would be required to confirm the validity of the measurements and to inspect any other factors that may have caused extreme growth. These outliers may be due to erroneous data or may have exhibitied unusual growth due to extremes of environmental variation.

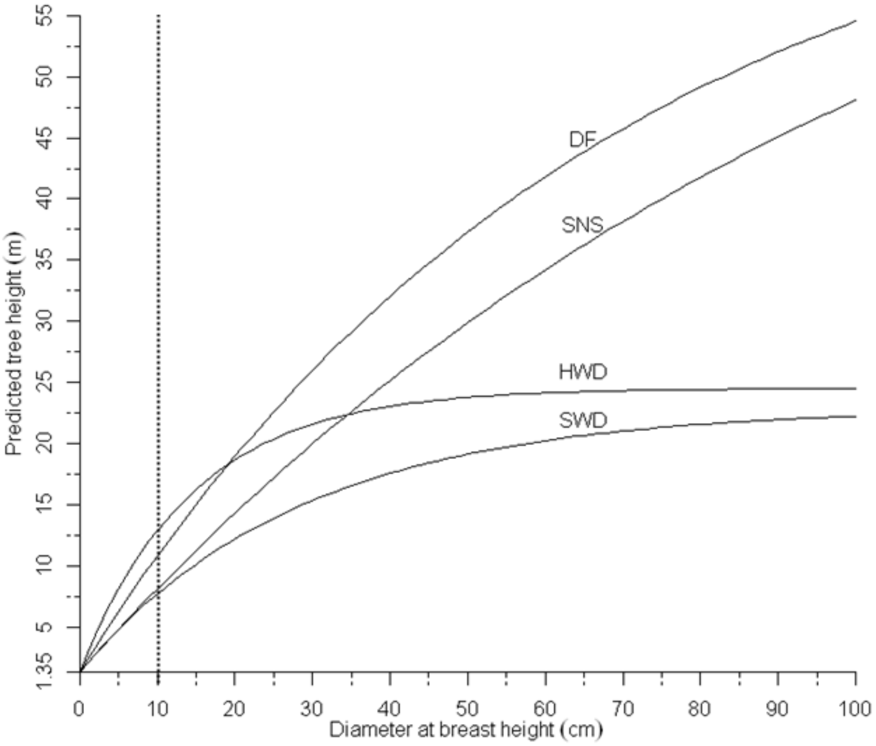

Figure 4.13. Predicted tree height to DBH for all species groups saplings and adults. Dotted line is transition point between saplings and adults (10 cm DBH).

Seedling and sapling growth and mortality are limited by the use of proxy species in relation to the *non-limited absolute growth radial increment* and the *BC mortality* behaviours that was necessary due to the lack of site specific data. These behaviours both rely on the light model to effectively function and it is difficult to assess whether or not the relationships are adequate for Coed-y-Brenin. Further data needs to be collected to parameterise the seedling and sapling growth sub-models for Coed-y-Brenin. The data can then be validated alongside the proxy species data from the Date Creek study (Coates, K.D., 2012) that is currently in use.

The use of proxy data (Coates, K.D., 2012) for dispersal is another area where it is difficult to quantify how much impact the lack of site and species-specific parameters has on the model. Ribbens et al. (1994) highlight the impact of parent tree spatial arrangement in seedling recruitment. While this may not be an issue for Douglas fir, as the dominant species at our study sites, it may become important as western hemlock or more Sitka spruce reach canopy status (or when moving to complex stands where natural regeneration is the forest driver).

Capacity exists within SORTIE-ND for the inclusion of substrate effects on seedling recruitment; an aspect of the model that may also be important for rhododendron establishment. Data was collected on substrate and seedling abundance throughout CyB5 (Chapter 3) and could be used to investigate relationships in the same manner as rhododendron is investigated in Chapter 5. LePage et al. (2000) characterised seedling abundance of deciduous and conifer species under a range of canopy types to model the relationship between substrate type and seedling dispersion and establishment. The parameter values would be applicable as proxies within Coed-y-Brenin but it would be important to parameterise the sub-models for our site given the potential impact of harvesting on disturbance and micro-site creation. A 1993 study of 22 southern Britain

Douglas fir stands found denser seedling regeneration in the presence of bryophytes and lower numbers in areas dominated by bracken (*Pteridium aquilinu*m), shrubs (particularly *R. ponticum*), brambles (*Rubus* spp.) and grasses (Schlicht & Iwasa, 2004). This sub-model could also be parameterised for *R. ponticum* regeneration.

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Chapter 5: Bayesian model of *Rhododendron ponticum* establishment probabilities

5.1 Introduction

Two different concepts are used to explain plant invasion patterns: invasibility of habitat or community and invasiveness of species. Invasibility is associated with availability of resources, physical environmental characteristics (particularly climate) and absence of competitors, or some complementary mix (Lonsdale, 1999, Lamarque et al., 2011). Though plant ecophysiological traits affect invasiveness, landscape invasibility, determined by its influence on the germination and establishment of a species, also plays its part. Invasiveness is determined by specific attributes or ecophysiological traits, such as high seed production or increased growth rates (Sakai et al., 2001, Erfmeier & Bruelheide, 2010).

Non-native *Rhododendron ponticum* L. occupies 2238 of the 3844 10 km^2 grid cells that make up the British Isles (Dehnen-Schmutz et al., 2004), but the distribution is restricted and in places it is rare and vulnerable (Rotherham, 2001). For many species the ability to adapt to natural selection within the new range influences their invasion success (Erfmeier & Bruelheide, 2010). Previous studies have attributed the successful spread of rhododendron to increased environmental suitability and/or the range of suitable habitats in the new regions (Stephenson et al., 2006, Erfmeier & Bruelheide, 2010). It has also been suggested that an invasive genotype exists with genotypic differences between invasive and native species (Erfmeier & Bruelheide, 2005).

Established rhododendron plants do not appear to suffer from Snowdonia's climatic extremes except at altitude, where few plants have been recorded higher than 400 m except in sheltered locations (Jackson, 2008). Most soil conditions within Snowdonia will support established *R. ponticum*, though permanently wet sites are required for seedlings to establish. Growth is reduced in deep shade and although plants can tolerate low light levels (2% daylight) they cannot survive under un-thinned conifer canopy (Nadezhdina et al., 2004). Light is considered essential to germination with experiments carried out by Cross (1981) showing a linear decline of seed viability to a maximum survival of 160 days. Plants flower from around 12 years of age and produce seeds prolifically, up to one million wind dispersed seeds annually, and can also propagate vegetatively (Mejias et al., 2002, Erfmeier & Bruelheide, 2004, Erfmeier & Bruelheide, 2010). As with most ericaceous plants mycorrhizal interactions assist nutrient competition in deficient soils (Xu et al., 2009), enabling rhododendron to outcompete other plants in low nutrient environments (Wolter et al., 2009).

It has been suggested that the habitats favoured by British rhododendron are similar to that in disturbed native areas (Rotherham, 2001) and the occurrence of ‘safe sites’ have been shown in a number of studies to be crucial to the success of rhododendron. Mejias et al. (2002) found recruitment in Spanish populations was low despite high fruiting rates, and *safe sites* were restricted to the humid soils and bryophyte carpets of river contact zones. This was confirmed by Erfmeier and Bruelheide (2004) in an investigation of two Spanish populations at the waterline. Cross (1975) suggests that seedlings are easily smothered by low vegetation and litter having little competitive ability until well established. The abundance of bryophyte safe sites in Killarney woods were suggested by Cross (1981) as the most important factor, after unpalatability, for rhododendron’s success.

Rhododendron seedlings are vulnerable to desiccation and browsing, and require mossy or bare ground and damp conditions. Suitable regeneration sites are key to seedling establishment and opportunities to invade are commonly provided by disturbance (Rotherham, 2001). Though seed dispersal is extensive, rapid site invasion does not usually occur due to a lack of establishment facilitation and critical questions are raised by the invasion of established communities in one location, but not others (Rotherham, 2001).

Stephenson et al. (2006) state there is great potential to use spatially explicit simulation models to investigate rhododendron spread in forest habitat, types but the models require quantitative data as opposed to the majority of available qualitative data.

Harris et al. (2009) devised a simplified individual-based model of establishment in relation to habitat, that investigated the effects of containment by completely unsuitable habitats and other individual-based models have been developed that assess rhododendron's spread through different habitats (Harris et al., 2011) but no work has related establishment probability to stand structure.

This study aims to identify and construct a statistical model of rhododendron establishment with data collected from the surveys of the Coed-y-Brenin permanent sample plots (Chapter 3) that are potentially compatible with inclusion in a spatially-explicit individual-based model (e.g. SORTIE-ND) (Chapter 5). The overall objectives are: i) to identify potential factors based upon a literature synthesis, examination of field surveys and integration of field surveys important to rhododendron establishment, (ii) to reduce those factors to a suite of independent orthogonal candidate variables, (iii) to assess them for spatial autocorrelation and (iv) to construct a Bayesian model of rhododendron establishment and quantify the degree of fit. The associated hypothesis is that light will be an important factor in predicting locations of rhododendron seedling establishment. Future work would then combine this model with the parameterised SORTIE-ND model for this site to investigate establishment probabilities under changing management scenarios.

5.2 Material and Methods

5.2.1 Study site

The study was based on a 100 m x 100 m permanent sample plot (CyB5) Coed-y-Brenin, Forest Park, Snowdonia. The Douglas fir (*Pseudotsuga menziesii*) and Sitka spruce (*Picea sitchensis*) dominated plantation was established in 1929. Felling of the plantation was on hold due to an extensive rhododendron presence[4]. Rhododendron is present throughout the site with a lower, clearer, central section that is heavily infested. There is evidence of previous rhododendron management in the form of cut stumps and areas of herbicide application, though this is isolated and not recent as evidenced by resprouting. The aspect is predominantly south easterly across the Afon (river) Eden valley. The north and south boundaries of the plot are delineated by a footpath and mountain bike trail, respectively, and a footpath also cuts through the Eastern half of the site. The data used in this study were taken from a forest survey and a vegetation survey of the permanent sample plot, CyB5 using 4 by 4 m quadrats as depicted in Figure 3.8 and Figure 5.1. See Chapter 3 for further details on the study site, data collected and the collection methods.

For the purpose of the establishment model, seedlings were classified as individual stems (not layered) of less than or equal to 29 cm in height (79 individuals; mean = 10cm). Given the small seedling size and lack of site intervention it can be assumed that the covariates measured will not have changed significantly in the seedlings lifetime.

5.2.2 Aerial survey and data analysis

Further to the field data an aerial LiDAR survey was carried out on 10th March 2010 by the NERC Airborne Research and Survey Facility (ARSF) using a Leica ALS50 Airborne Laser Scanner. The LiDAR was sectioned to CyB5, height-filtered to classify

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[4] Aled Thomas, FC Wales Local Area Manager, Dolgellau

ground and non-ground points, and a bare-earth Digital Elevation Model was produced using the ENVI 4.8 (Exelis Visual Information Solutions, Boulder, Colorado) BCAL LiDAR tools 1.5.2 (BCAL LiDAR Tools,). Height-filtering (Streutker & Glenn, 2006) enabled output of raster products that consist of bare-earth topographic (Stage & Wykoff, 1998), vegetation (Evans et al., 2009) and intensity metrics. Raster layers were output in 1x1 m pixels to allow extraction of the metrics at each staggered survey station. The field and LiDAR data was then rasterised

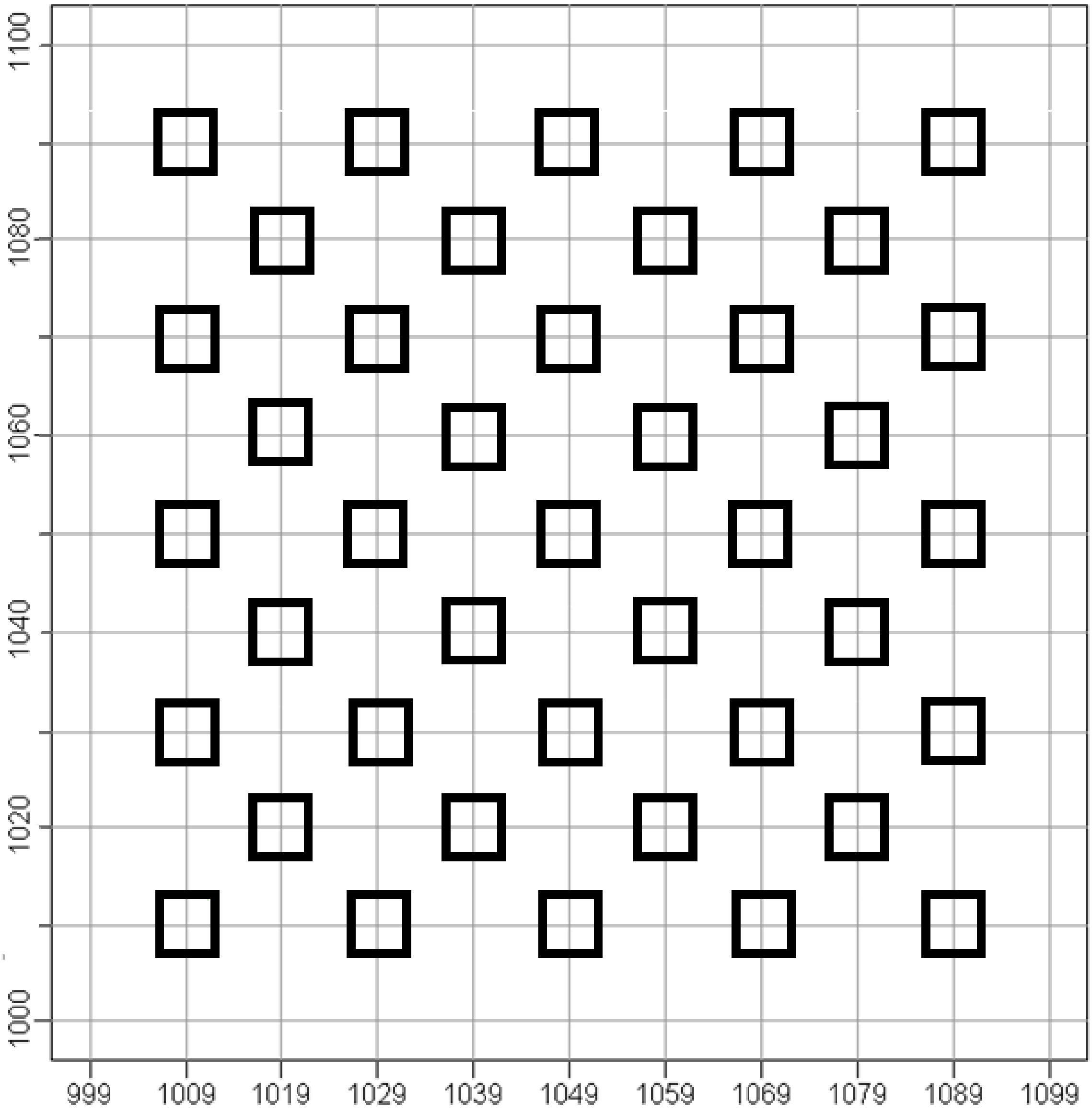

Figure 5.1. Locations of four by four m quadrats used for establishment model.

to match the extent and resolution of CyB5 and the data sectioned to survey stations. The required transforms were all carried out using the R raster package (Hijmans & van Etten, 2013).

5.2.3 Model construction and selection

Candidate models were constructed using a manual stepwise approach. The initial step was the assessment of likely data from the large pool of available variables. The data was separated into those with rhododendron seedlings present and those without and then compared statistically. Those variables with a significance of $p \leq 0.1$ were considered for the model and are indicated with an asterisk in Table 5.2. Tree attributes were significantly correlated ($c > 0.5$), therefore only one parameter was selected in turn from data group a (Table 5.2) for inclusion in the model runs. O layer depth and O layer moisture content were not correlated. The LiDAR vegetation metrics were not correlated except for total percentage of vegetation cover returns and percentage of vegetation cover between 0 and 1 m, hence these two variables were loaded separately. The abundance of moss, tree litter and deadwood, and the presence of buttresses were incorporated into the model as candidate data separately and as interaction terms, even though they were not found significant during trials, as they were deemed significant in Stephenson et al.'s (2006) investigation of rhododendron establishment.

The candidate models were fitted using Bayesian inference and Gibbs sampling in OpenBugs (Lunn et al., 2009) with the R2WinBugs package (Sturtz et al., 2005). Gibbs sampling has its roots in Markov chain theory and is a technique that calculates random variables from a specified distribution. The generated Markov chain sequence is then used to obtain the parameter distributions (Casella & George, 1992). Time series plots and Rhat values were used to check for chain convergence within a stationary distribution. Rhat is a convergence diagnostic based on the Gelman-Rubin statistic that uses a technique similar to analysis-of-variance to assess between and within chain variance. Convergence is indicated by values close to one, with 1.1 an adequate threshold (Kéry, 2010). Models were fit for three chains running 50,000 iterations with a 1,000 burn-in to avoid any bias from the starting locations. The prior distributions used were uninformative normal distributions with a mean of 0 and a standard deviation of 0.001.

Support for model parameters was assessed by visualisation of their posterior densities. Any parameter that had a possible zero value within the 95% credible intervals was discarded. The 95% credible intervals used were bounded by the 2.5 and 97.5 percentile of the parameters posterior distribution (Kéry, 2010, Lu et al., 2012). Frequentist confidence intervals and Bayesian credible intervals are generally numerically equivalent when uninformative priors are used (McCarthy, 2007)

Pearson residuals, posterior predictive distributions and the Bayesian p-value were calculated to assess goodness-of-fit. Pearson residuals were computed on each iteration as:

$$pearson\ residual = \frac{D - E}{\sqrt{E}} \tag{5.1}$$

where *D* is the observed data and *E* is the estimated data.

The posterior predictive check compares the model lack of fit for the actual ‘real’ data to the model lack of fit for replicated ‘ideal’ data. This ‘ideal’ data is generated from the parameter estimates gained from the analysis of the ‘real’ data and conforms exactly to the assumptions made about the model. A replicate dataset is created at each MCMC iteration using the same model that is fitted to the ‘real’ data, and using the parameter values from the current iteration. The sum-of-squares discrepancy measure is then computed for the ‘ideal’ and the ‘real’ dataset. The Bayesian *p-value* is calculated as the number of times that the ‘ideal’ datasets discrepancy measure is greater than the ‘real’ dataset. A Bayesian p-value of close to 0.5 indicates a good fit, while values close to 0 or 1 are a poor fit (Kéry, 2010). See appendix 4 for R scripts.

For model selection the Deviance information criterion (DIC) is computed automatically in OpenBugs (Lunn et al., 2009). The DIC is a Bayesian analog to the Akaike's Information Criterion (AIC), that incorporates a penalisation to the model fit for the introduction of more parameters (Spiegelhalter et al., 2002, Kéry, 2010). A similar rule of thumb was used as suggested by Canham (2011) in relation to AIC values (denoted by Δ): considerable support was shown for a model with Δ within 1 or 2 of the 'best' model; less support for a Δ value of 4 to 7 and no support for models with Δ greater than 10.

To compare model predicted presence and absence with observed data it was necessary to convert predicted values to zero or one based on a threshold value. The mean of the fitted values was used to generate a threshold rather than 0.5, as classifications using 0.5 can be biased towards the larger group (Stephenson et al., 2006).

5.2.4 Model evaluation

Leave-one-out cross-validation is an implementation of *K* fold cross-validation used when data is sparse, as even small changes to the data are likely to affect the fitted model (Cawley & Talbot, 2004). *K* fold cross-validation partitions data into *K* distinct, equally sized sets. One of the *K* subsets is retained for model validation and the other *K*-1 subsets are then used to parameterise the model. The process is then repeated with each of the *K* subsets as validation data (Cawley & Talbot, 2004, Wenger & Olden, 2012). Of the 41 locations sampled across the study area there were 17 presences and 24 absences. Station 31 was excluded from the analysis as the south-west quadrat had a section of path running through it and the effects were apparent in the model, reducing the available number of stations with seedling present to 16 out of 40 stations. Therefore for our model validation $K = 40$. To assess the model fit the fully fitted model rate of prediction was compared with the rate of prediction for the (40) excluded values from the cross-validation.

5.2.5 Statistics

Data was investigated to assess the normality, centring and spread of values and to check for outliers visually and statistically using boxplots, boxplots conditional on seedling presence/absence, histograms and the Shapiro-Wilk test of normality (R packages stats and base (R Development Core Team, 2012). Bivariate scatterplots and Pearson correlation coefficient were used to investigate the degree of correlation between variables (Revelle, 2011). Variables with a correlation ≥ 0.5 were not loaded into the same model. Wilcoxon Rank Sum Test (equivalent to the Mann-Whitney test) were carried out using the wilcox.test in R. All statistical analyses (except for the Bayesian calibration) were carried out in R version 2.14.1 (R Development Core Team, 2012).

Spatial autocorrelation can occur in ecological data through intrinsic factors, such as distance related processes (i.e. dispersal) or extrinsic processes that generally result from environmental forcing (Wintle & Bardos, 2006, Kissling & Carl, 2008). Moran I is a commonly used, robust statistic, for analysing spatial autocorrelation (Sokal & Oden, 1978, Fortin et al., 2006, Rangel et al., 2006, Dormann, 2007). A Moran value of ±1 indicates a strong positive/negative spatial autocorrelation, while a value of zero indicates a random pattern (Sawada, 2009). Regression tests assume that errors are independently distributed and spatial autocorrelation may inflate type I errors in this case, hence an spatial autocorrelation test was carried out on the residuals of regression models (Kissling & Carl, 2008).

Two separate Moran tests were carried out on the dependent variable and model residuals to confirm the results (moran.test and moran.mc, R package spdep (Bivand, 2013). Maximum distance was computed using a k nearest neighbour approach (knn2nb in R package spdep). The dependent variable (Moran's I = -0.265 (and p = 0.908 for run 1, and I = -0.2647 and p = 0.915 for run 2) and residuals (Moran I = -0.096 and p = 0.754 for run 1, and I statistic = -0.096, p = 0.69 for run 2) were both randomly distributed, and therefore spatial autocorrelation was not a factor in the model.

5.3 Results

5.3.1 Rhododendron seedling presence predictive model

The final model included three covariates and converged with a Rhat value of 1.00 (Table 5.1). The Bayesian p-value of 0.43 calculated from comparisons of the 'real' and 'ideal' data indicated a good fit (Table 5.1).

Table 5.1. Mean parameter values of covariates with Rhat convergence metric and overall Deviance Information Criterion and Bayesian p-value

Covariates	Type[a]	Parameter Coefficient			pD	DIC	Bayesian p -value
		Mean ±Stdev	CI (2.5-97.5%)[b]	Rhat			
alpha	I	-3.68±1.55	-7.17 to -1.16	1.00	3.99	39.11	0.43
Rhododendron adult present	C	3.43±1.54	0.77 to 6.79	1.00			
O layer depth (cm)	Q	1.53±0.63	0.42 to 2.90	1.00			
Sum tree height (m)	Q	-2.78±0.99	-5.02 to -1.15	1.00			

[a] Variable type: C, categorical; Q, quantitative; I, intercept
[b] 95% Credible Intervals (CI) are insignificant if range includes zero

The model predicted that the probability of seedling presence was positively influenced by presence of an adult bush and depth of the O soil layer and negatively influenced by the summed tree heights in a 144 m² (12x12m) neighbourhood (Table 5.2). The rhododendron adult presence and O layer depth posterior density distributions both crossed the zero thresholds, however the 95% Credible Intervals did not include zero, hence there is a 95% probability that the true parameter values (μ and σ) lie within that interval (Figure 5.2).

Table 5.2 Median (min-max range) of candidate variables in the presence and absence of rhododendron, grouped by variable type. All variables with p =< 0.1 were considered for the model

Candidate variables[a]	Rhododendron seedling status		Wilcox Rank Sum[b]	
	Present (n=16)	Absent (n=24)	W Statistic	p value.[c]
a. Tree attributes in 12x12 m neighbourhood				
*Crown radius sum (m)	7.10 (0.0-16.1)	10.50 (2.8-28.3)	107.5	0.01
*Crown depth sum (m)	34.15 (0.0-73.5)	45.77 (10.0-85.2)	118	0.02
*Tree height sum (m)	53.40 (0.0-113.8)	73.40 (11.6-156.4)	118.5	0.02
*DBH sum (cm)	83.00 (0.0-199.7)	114.75 (0.0-210.4)	121.5	0.03
Total basal area sum (m^2)	0.39 (0.0-1.1)	0.52 (0.0-1.3)	152.5	0.18
b. Substrate in 4x4 m quadrat				
*Moss (%)	55.00 (30.0–85.0)	66.25 (10.0-97.5)	170.5	0.38
*Litter (%)	27.50 (0.0–70.0)	22.50 (0.0 - 81.3)	236.5	0.4
*Deadwood (%)	8.75 (3.8-27.5)	11.63 (0–50)	185.5	0.63
Stump buttress (categorical)[d]	17	24		
c. Soil in 4x4 m quadrat				
*O layer depth (cm)	7.67 (4.8–16.0)	6.50 (3.0-9.5)	285.5	0.03
*O layer moisture (%)	69.50 (52.1-85.4)	64.70 (45.5-80.6)	277.5	0.05
O layer soil organic matter (%)	56.14 (30.5-80.1)	49.93 (32.5-75.5)	251	0.22
E layer soil organic matter (%)	21.00 (12.6-28.6)	20.18 (16.0-32.2)	246	0.28
E layer moisture (%)	47.40 (28.3-85.4)	40.85 (33.8-58.6)	244.5	0.29
d. LiDAR intensity in 4x4 m quadrat				
*Mean return intensity	68.93 (20.0-151.4)	42.25 (19.1-99.3)	289	0.02
Mean bare-earth intensity	10.82 (0-101.6)	7.98 (0.0-81.3)	223	0.62
Mean vegetation intensity	75.13 (-0.7-108.9)	83.24 (27.6–109.0)	153	0.18
e. LiDAR vegetation in 4x4 m quadrat				
Vegetation 0 - 1 m (%)	6.66 (0.0-100.0)	0.09 (0.0-88.1)	227.5	0.09
Vegetation 1 - 2.5 m (%)	0.00 (0.0-100.0)	3.99 (0.0-90.1)	175	0.95
*Vegetation 2.5 - 10 m (%)	0.00 (0.0-19.8)	5.28 (0.0–100.0)	114.5	0.06
Vegetation 10 - 20 m (%)	0.00 (0.0-45.5)	0.00 (0.0-76.5)	183.5	0.66
*Vegetation 20 - 30 m (%)	0.00 (0.0 - 60.4)	10.06 (0.0-84.0)	115	0.08
Vegetation 30 m (%)	27.73 (0.0-98.2)	2.32 (0.0-89.0)	188.5	0.63
Height 5th percentile	1.37 (0.0-31.8)	1.66 (0.1-31.7)	174	0.44
Height 10th percentile	1.37 (0.0-31.8)	2.13 (0.1-31.7)	172	0.41
*Height 25th percentile	1.60 (0.0-42.6)	2.90 (0.1-31.7)	188	0.7
Height 50th percentile	2.35 (0.0-44.8)	10.88 (0.3-34.0)	154	0.19
Height 75th percentile	2.25 (0.0-45.4)	11.79 (0.5-39.0)	182	0.57
Height 90th percentile	2.25 (0.0- 45.4)	15.10 (0.5-38.9)	180	0.53
Height 95th percentile	2.25 (0.0-45.4)	15.15 (0.5-39.0)	181	0.56
Mean height (m)	2.20 (0.0-41.6)	8.68 (0.5-31.7)	169	0.37
Height range (m)	0.10 (0.0-35.2)	7.65 (0.0-32.1)	183.5	0.6
*Vegetation returns (%)	58.40 (0.0-99.0)	83.71 (0.5-100.0)	162	0.06
Mean vegetation return intensity	75.13 (-0.71-108.9)	83.24 (27.6-109.0)	153	0.18
f. bare-earth products				
Elevation mean (m)	74.86 (61.9-84.6)	73.56 (61.0-88.9)	193	0.78
Aspect	124.42 (8.7-339.3)	131.09 (3.0-345.5)	193	0.78
Slope	17.66 (2.9-49.7)	16.91 (3.7- 49.3)	198	0.89
g. light products				
Total light transmission (%)	12.41 (5.4-18.8)	10.81 (4.9-18.4)	252	0.21
n. Adult rhododendron in quadrat				
Abundance (%)	25.50 (0.0-57.5)	1.25 (0.0-95.0)	246	0.20
*Presence (categorical)[d]	17	24		
n. Adult rhododendron in quadrat				
Abundance (%)	25.50 (0.0-57.5)	1.25 (0.0-95.0)	246	0.20
*Presence (categorical)[d]	17	24		

[a] Parameters used as candidates for the model are indicated by asterisks.

[b] Non-parametric Wilcoxon rank sum test was used as some variables were not normally distributed.

[c] Significance level: *, p<0.05; **, p<0.01; ns, non-significant.

[d] Number of stations with presence of feature

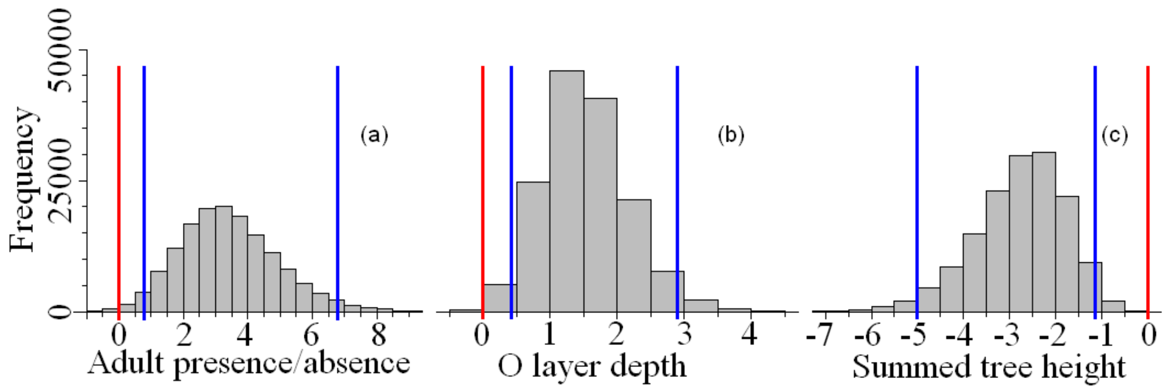

Figure 5.2. Posterior density distributions for model coefficients of (a) adult presence/absence, (b) depth of the soil O layer and (c) summed tree height

5.3.1.1 Cross-validation and prediction probability

The predicted outcomes for the fully fitted model were classified using the mean of the fitted values (0.4003785). Those greater than the mean were classified as presences and those less than, as absences. The fully fitted model classified 79.17% (19 of 24) of the absences correctly and 100% (16 of 16) of the presences, with an overall prediction rate of 87.5% (35 of 41) (Table 5.3).

Table 5.3 Observed versus predicted model outcomes from the fully fitted model (left) and the excluded data from the leave-one-out cross-validation (right).

	Number (% observed)[a]	
	Full model	Cross validation
a. All	35 (87.5% of 40)	31 (77.5% of 40)
b. Correct model fit		
Observed absent – predicted absent	19 (79.2% of 24)	18 (75.0% of 16)
Observed present – predicted present	16 (100.0% of 16)	13 (81.3% of 24)
c. Incorrect model fit		
Observed absent – predicted present	5 (20.8% of 24)	6 (25.0% of 24)
Observed present – predicted absent	0 (100.0% of 16)	3 (18.8% of 16)

[a] Proportion of observed that are correctly predicted by the model.

The predictions for the excluded stations were summarised from the cross-validation, resulting in reduced prediction probabilities for both absences: 75% (18 of 24); presences: 81.25% (13 of 16) and with an overall prediction rate of 77.5% (31 of 41)

(Table 5.3). Classification of the cross-validation used the relevant mean of the fitted values from each run.

The five stations incorrectly classified from the full dataset were all absences classified as presences: 2, 5, 14, 36 and 41 (Figure 5.3, red triangles; Table 5.4. top). The cross-validation also failed to correctly identify station 33 as an absence and stations 17, 35 and 39 as presences, that were correctly identified in the full model (Figure 5.3, blue circles; Table 5.4, bottom).

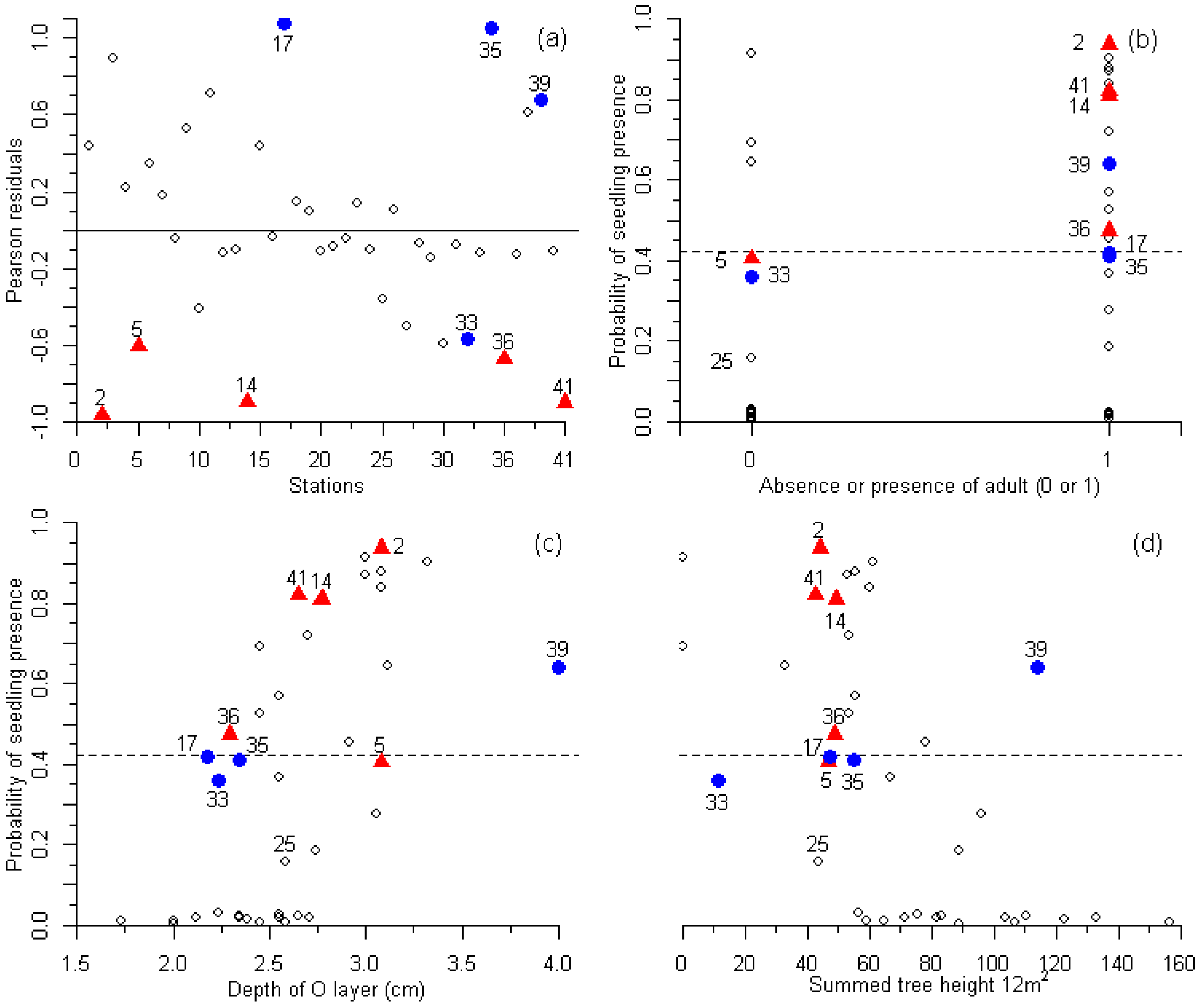

Figure 5.3. (a) Model residuals for Bayesian logistic regression, full model. (b) Predicted probability of seedling presence against presence/absence of an adult. (c) Predicted probability of seedling presence against O layer depth (cm) (d) Predicted probability of seedling presence against summed tree height within 12 m² of the survey quadrat. Red points are those incorrectly classified in the full model, blue points are additional points incorrectly classified during cross-validation.

During the cross-validation runs the means for the three presences classified as absences are lower than in the full model by 0.28 (station 39), 0.11 (station 17) and 0.8 (station 35). The inclusion of station 39 had considerable effect on its parameter mean. All stations incorrectly classified as absences by the cross-validation have credible intervals that include the classification mean though the mean of the posterior distributions are low. For the full fitted model all three stations credible intervals span the range of values and stations 17 and 35 classifications are borderline though classified correctly. Though the mean of station 39 is higher it is still not a tight classification.

Table 5.4. Incorrectly identified locations from full and cross-validation (cross-validation errors extra to the full model in bold): Predicted station (Stn.), correct absence classification percentage (0 %), correct presence classification percentage (1 %), total correct classification percentage (Total %), prediction mean (2.5 and 97.5 percentiles), mean fitted values used for classification.

Station	Rhododendron status		Total % (n)	Parameter mean (2.5% - 97.5%)	
	Absent % (n)	Present % (n)		Full model	Cross-validation
a. Presence classified as absence					
17	**83.33 (20)**	**87.50 (14)**	**85.00 (34)**	**0.42 (0.10 - 0.79)**	**0.31 (0.05 - 0.72)**
35	**79.17 (19)**	**87.50 (14)**	**82.50 (33)**	**0.41 (0.13 - 0.74)**	**0.33 (0.08 - 0.68)**
39	**79.17 (19)**	**87.50 (14)**	**82.50 (33)**	**0.64 (0.08 - 0.99)**	**0.36 (0.00 - 0.97)**
b. Absence classified as presence					
2	88.33 (20)	87.50 (14)	85.00 (34)	0.94 (0.78 - 1.00)	0.98 (0.902 - 1.00)
5	75.00 (18)	87.50 (14)	80.00 (32)	0.40 (0.06 - 0.84)	0.53 (0.09 - 0.94)
14	83.33 (20)	100.00 (16)	90.00 (36)	0.81 (0.57 - 0.96)	0.87 (0.65 -0.98)
33	**75.00 (18)**	100.00 (16)	**85.00 (34)**	**0.36 (0.05 - 0.79)**	**0.46 (0.07 - 0.90)**
36	79.17 (19)	100.00 (16)	87.50 (35)	0.47 (0.16 -0.80)	0.55 (0.19 - 0.87)
41	83.33 (20)	100.00 (16)	90.00 (36)	0.82 (0.57 - 0.97)	0.88 (0.66 - 0.99)

Station 17 was incorrectly classified as an absence by two absence stations (2 and 5) and four presence stations (11, 17, 35 and 38). The seedling here was borderline in size. Even though it met the < 30 cm height criteria, at 20 cm, it was 9 cm x 12 cm wide and older than three years (aged through counting growth points). Adult rhododendron was also present layering into the station from outside.

Station 35 was also incorrectly classified as an absence during cross-validation by two stations (2 and 5) and six presences (3, 6, 11, 17, 35 and 38). This station had adult rhododendron present and had two seedlings in the North-East quadrat and nine in the South-East, both growing from needle litter. The South-East quadrat had very little other vegetation.

Station 39 was the only station where O depth was not an important factor, the 2.5% CI crossed zero. Station 39 was also only incorrectly classified by itself suggesting that it is a strong influence on the model fit. This is supported by it having the largest difference in mean posterior distributions of the presences classified as absences. Station 39 was classified correctly in the full model however it had the deepest O layer (Figure 5.3c) and the largest summed tree height (Figure 5.3d) of all the presences.

Stations 2, 14 and 41 were strongly classified as presences instead of absences, with tight credible intervals a significant margin from the classification mean. Stations 2, 14, 41 were wrongly classified by all cross-validation runs. Station 36 was also wrongly classified by all runs except run 17. These four stations all have adult rhododendron present in the quadrat. Station 2 SW is 95 – 100% covered by a RP thicket of three bushes, SE is 95 – 100% covered with three bushes as well. one in each flowering. Station 14 has adult RP in the SE quadrat and some on periphery. Station 41 has adult RP layering in to plot but only between 2 – 5 %. Station 36's NE quadrat is dominated by a multi-stemmed bush with an abundance of 55 – 60 %. The SW quadrat has 30 – 35% RP on the ground and 25 – 30 % in understorey.

The predicted distribution for station 5, 33 and 36 have wide posterior distributions that span almost the full range of values with means close to 0.5 for both the fully fitted model and the cross-validations.

Station 5 was incorrectly classified by 11 of 16 presences and 18 of 24 absences however a path runs through almost the entire North-West quadrat and part of the South-West. Station 33 was incorrectly classified as a presence by two absence stations (5 and 33) and one presence (39). No adult rhododendron was present in this plot however it was almost completely dominated by a western hemlock (*Tsuga heterophylla*) understorey, 95 – 100 % abundance North-West and 65 – 70 % South-West, with very little other vegetation in the North-West quadrat.

5.4 Discussion

Light has been cited as a key factor affecting the likelihood of rhododendron germination (Cross, 1981, Stephenson et al., 2006, Ninaber, D., 2009) and it was therefore hypothesised that it would be an influential factor in the prediction of establishment sites. This was not the case and light did not have any influence on the model

Numerous studies stress the importance of substrate, in particular thin bryophytes for seedling establishment (Cross, 1975, Cross, 1981, Mejias et al., 2002, Rotherham, 2001, Erfmeier & Bruelheide, 2004, Stephenson et al., 2006). In Killarney oak woods, Ireland, rhododendron seedling distributions appeared to follow the distribution of bryophytes (Cross, 1981). Stephenson et al (2006) found that the probability of establishment was significantly higher for moss and litter substrates on dead tree material in comparison to litter alone and some evidence that it was higher than moss alone. However, no support for moss, litter, deadwood or any combination was found for the model at this location. Incorporation of deadwood in the model worsened the fit when combined with moss, as did litter. Moss on its own did not improve or decrease the model fit. This may have been due to the abundance of moss at the study site not being a limiting factor as moss was present in all quadrats (mean 59.13, range from 10.0-97.5%)

In the Killarney population drought was a significant factor in seedling death with plants in deeper soils, in open locations, less affected (Cross, 1981). Rhododendron is described as thriving in moist habitats (Harris et al., 2009) and moisture was found to be a limiting factor for Spanish populations (Mejias et al., 2002, Erfmeier & Bruelheide, 2004). However, again no direct relation to moisture in the soil O or E layer was found in the model for CyB5.

A positive model relationship with adult presence may be related to proximity to seed source. Controlled release experiments of rhododendron seed in open conditions found that 99.8% of seeds were found on traps within 10 m of the release point (Stephenson et al., 2007). The probability of seedling presence decreased as distance from adults decreased with 85% of seedlings found <5 m from adults (Stephenson et al., 2006) and most travel <10 m from a parent (Stephenson et al., 2007). An alternate possibility for the relationship may be that the presence of an adult is an indicator of a suitable establishment site. This result appears to contrast with the predicted negative association between rhododendron seedlings and adults returned by the Chi-square test in Chapter 3. The difference in result is due to the different scales involved: the model was parameterised on 4x4 m quadrats whereas the Chi-square test was carried out over the 2x2 m sub-quadrats. Within the smaller quadrats seeds will have been excluded by the adults and with the short dispersal distance of rhododendron seedlings would be likely to establish in neighbouring quadrats.

Although the direct use of soil moisture was not an important factor in the model, the depth of the O layer may be acting as a proxy. Soil surveys were carried out over one day, providing a snapshot of soil moisture content and allowing a relative comparison between stations. Investigation of the site for completion of the ecological site classification (Chapter 3) classified the stoniness of the soil at 30%. It is possible that the O layer depth is important for all plants at the site given the generally shallow soil (Table 5.2) and underlying stoniness. While a soils O layer may contain higher levels of organic Carbon and Nitrogen than lower layers (Leiros et al., 1999) it would not be expected that seedlings would be affected by this at establishment. However Cross (1975) found occurrences of germination on brown earths of circa. 40 %, however subsequent development was slight due to a nutrient imbalance. Depth of the O layer may be representative of the year round moisture holding content of the uppermost soil layer. Moisture and bryophytes are related to the concept of ‘safe sites’ crucial to rhododendron establishment (Cross, 1975, Cross, 1981, Mejias et al., 2002, Erfmeier & Bruelheide, 2004).

The negative association of summed neighbourhood tree height may be related to seed dispersal. Rhododendron seeds are primarily wind dispersed and though prolific (around 20 000 g yr^{-1}) most seeds fall within 10 m of the parent tree (Harris et al., 2011). With lower wind speeds under canopy than in the open (Harris et al., 2011), the probability of establishment would be expected to decrease with increasing tree density. This may be the reason that the presence or absence of an adult tree is a strong positive factor. Cross (1975) also found that seed dispersal within woodlands was ineffective in comparison to open areas. Edwards and Taylor (2008) modelled rhododendron at the landscape scale and adjusted ease of seed movement according to the habitat type: seed dispersal was restricted to 5 m in woodlands, 10 m in young plantations, 20 m in recently felled woodlands and built up areas, and 100 m for open habitats (e.g., agricultural lands). Harris et al. (2011) found that invasion densities were very low in evergreen woodland with high canopy cover from simulations of invasion spread that combined a mechanistic model of seed dispersal with demographic traits and habitat covariates. Though densities were low, evergreen woodland had the fastest invasion spread due to a related increase in rhododendron plant height. Increases in canopy cover resulted in reduced invasion potential. It is also suggested that low numbers of propagules are produced in evergreen woodlands with the probability of reproduction, given reproduction in the previous year, a third lower in dense evergreen forest than in open areas. Taylor (unpublished data) found that 18-33% of terminal rhododendron stems had flowers in deciduous woodland, compared to 54.5-81.8% on bushes growing on south facing edge of the woodland, and flowers dropped to 0-18% in conifer woodlands at Keele University.

The model predicted 81.3% of presences correctly during cross-validation (Table 5.3). Stations 2, 14 and 41 were incorrectly classified as presences however the distributions are convincing classifications (Figure 5.4) suggesting that there is a high probability of presence. Given the unambiguity of the classifications it is possible that these three stations are likely colonisation sites or already contain seedlings that were missed during the data collection.

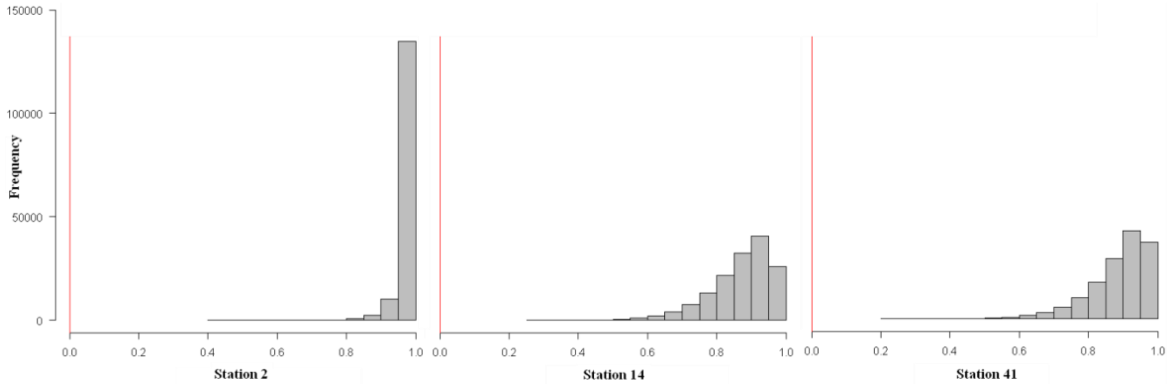

Figure 5.4. Posterior density distributions from cross-validation for excluded stations: station 2 (left); station 14 (middle); station 41 (right).

Factors that were expected to be important, such as light and substrate, were not, potentially indicating that there may not have been sufficient differences in the microclimate of the study location to draw inferences about optimum conditions. However it is likely that the entire study plot is suitable for establishment and the controlling factors are not related to microclimate or *safe sites* at this location.

SORTIE-ND was considered to be the ideal candidate for modelling the forest ecosystem with the expectation that light would be an important factor in rhododendron seedling establishment. That aside SORTIE-ND is still an excellent candidate for this model and the important factors lend themselves well to the model structure. Development of the complete model including the statistical model parameters are discussed in Chapter 6.

5.4.1 Study limitations and future work

LiDAR data provides considerable potential that was not sufficiently explored within this work. The importance of summed tree height was not reflected by the LiDAR vegetation data which raises three initial questions: why is summed tree height important? Why only at that scale? What about it is different to the LiDAR vegetation metrics?

The measurement error with ground collected data is reasonably easy to quantify, the techniques are known and tools are straightforward. The introduction of technological data collection systems do not necessarily reduce that, in fact they aim to greatly improve the ease and accuracy. However, several different technologies were combined to connect the LiDAR data to the PSP data (Digital GPS, total station, LiDAR), each introducing a measurement error. The LiDAR pixel size is 2x2 m, the survey station size was 4x4 m and the correlation of the two involves some generalisation of the surrounding conditions. Without several fixed ground points to reference, or further processing of the LiDAR data to delineate canopy, it is difficult to explicitly state the error for the LiDAR data.

Summed tree height requires further investigation to ascertain exactly what its influence is. The plot is divided between large canopy trees and smaller understorey trees.

The expectation is either that the negative effect of summed height refers, in the main, to the surrounding understorey trees, and the errors in prediction relate to those locations where a canopy tree is present. Or that it relates in some way to the presence of large trees that is not captured by the inclusion of the buttress categorical variable.

The use of two quadrats at each survey station potentially reduced the sensitivity of the data collected however further data collection wasn't feasible given the field constraints at the time. Using each quadrat as a separate location would almost definitely have introduced spatial autocorrelation issues that would have needed to be addressed. However the incorporation of data from CyB4 and CyB7 would be a useful cross comparison. This study has captured a snapshot of the situation at CyB5 and future work to incorporate the findings into an individual based forest growth model would enable longer term investigation of the ecological dynamics relating forests and rhododendron.

CyB7 is currently free from rhododendron and, as a stand currently undergoing stem exclusion, would be a useful test-bed for a combined thinning/rhododendron establishment trial[5]. Experimentation could be carried out to assess germination under different canopy cover along with assessment of competition effects on rhododendron seedlings. Cross (1975) suggests that seedlings are easily smothered by low vegetation and litter, having little competitive ability until well established.

5.5 Conclusions

In conclusion the results of the modelling study appear to place emphasis on forest structure through the inclusion of summed tree height though micro-climate is a factor through the inclusion of O depth. If as cross suggests rhododendron seedlings are poor

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[5] Rhododendron was added to Schedule 9 (2) of the Wildlife and Countryside Act in 2010 and cannot be intentionally planted in forest however dispensation can be provided (Parliament, 1981).

competitors until well established the increased nutrients associated with a deeper O horizon may play an important part. With the combined negative importance of summed neighbourhood tree height and positive influence of adult presence It is possible then that the major impact of clearfelling on rhododendron establishment is the facilitation of dispersal rather than release of seedlings. If seedlings are poor competitors (Cross, 1975) then release from clear-felling would increase understorey competition.

5.6 References

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Chapter 6: Towards an individual based model of Rhododendron ponticum growth and forest dynamics

6.1 Introduction

There has been a concurrent development of forestry practice alongside conceptual and theoretical models as development and circumstance in one area informed and advanced the other (Chapter 2). The implementation of policy decisions that support low impact silvicultural systems (Forestry Commission, 1999, Forestry Commission, 2001, Mason & Britain, 2006, UKWAS, 2008) illustrate the contemporary shift towards perceptions of forests as ecosystems (Kimmins, 2004, Gratzer et al., 2004, Bugmann et al., 2010) and a focus on ecosystem services (Auclair, 2010, Bugmann et al., 2010, Fontes et al., 2010). With unprecedented increasing biological invasions occurring in forest stands (Dehnen-Schmutz et al., 2004, Dehnen-Schmutz & Williamson, 2006), the inclusion in forest models is warranted.

There is a wide recognition of the negative impact that invasive species have on native species biodiversity and ecosystem functioning (Sakai et al., 2001), an impact that is expected to increase with global climate change (Vitousek et al., 1996). With the major role that forests play in landscape composition, regulation of ecosystem services and biodiversity maintenance, tree species are a major focus of research into the prediction and modelling of species range shifts expected under future climate change scenarios (Morin & Thuiller, 2009). The likelihood of unwanted regime shifts increases in ecosystems that suffer from interruptions of key processes (such as regeneration) and a reduction in biodiversity (Folke et al., 2004).

The transformation of an even-aged forest plantation (e.g. PSP CyB5 at Coed-y-Brenin from this study) to an in irregularly structured low impact silvicultural system (e.g.

Continuous Cover Forestry) is a long and difficult process (Schütz, 2001). Once a forest is transformed management is required that ensures the continuitity of regeneration and recruitment balanced with sustainable and continuous harvesting (Pommerening & Murphy, 2004). The encouragement of natural regeneration is crucial to maintain the necessary temporal and spatial variation of a multi-structured ecosystem (Schütz, 2001); Mason et al. (2003, p. 42) state that 'freedom from vegetation competition' is a fundamental requirement of natural regeneration in relation to Continuous Cover Forestry in British forests. As discussed (Chapters 3 and 5) invasion of forest stands by *Rhododendron ponticum* results in loss of biodiversity through the interruption of natural regeneration cycles (Peterken, 2001, Rotherham, 2001). Spread of *R. ponticum* is facilitated by prolific seed production and, in some regions, by short-distance vegetative layering (Stout, 2007). Seed establishment requires specific conditions to occur and studies have highlighted the important role of disturbance in increasing invasibility (Davis et al., 2000, Stephenson et al., 2006). An issue with CCF in areas populated by *R. ponticum* is a need to increase site access to carry out multi-entry management that may increase site disturbance and actively encourage invasion (Stephenson et al., 2006).

Much of the early work describing the functioning of *R. ponticum* was informative but anecdotal (e.g. Cross, 1975, Cross, 1981). More recent work has sought to quantify aspects of the organisms lifecycle. Simple allometric relationships were derived by Nadezhdina et al. (2004) from destructive sampling of two Belgium *R. ponticum* populations as part of an investigation into biomass allocation, leaf-area index and branching patterns. Other studies have investigated leaf-level photosynthetic plasticity (Niinemets et al., 2003) and the relationship between seed size and leaf shape (Cornelissen, 1999). Erfmeier and Bruelheide (2004) compared natural and invasive populations from Georgia (Caucasus) and Ireland contrasting leaf characteristics and growth of shoots and stem. A further genetic comparison of invasive and native *R. ponticum* populations by the same authors (Erfmeier & Bruelheide, 2005) found that Irish populations responded faster to germination treatments. Several other studies have identified other key aspects of *R. ponticum* ecology and invasiveness, such as dispersal (Stephenson et al., 2007) and establishment (Stephenson et al., 2006, Ninaber, D., 2009).

Two recent studies using a spatially-explicit individual-based framework have modelled different aspects of *R. ponticum* invasion. The first investigated different strategies for the control of *R. ponticum* (Harris et al., 2009). This model was parameterised with individuals that had different age related dispersal kernels. The invasion front was then investigated along with plant removal strategies. The second model investigated invasion potential over different habitats with plant height and seed release height as the main driver to invasion spread (Harris et al., 2011).

The rise of spatially-explicit individual-based models has in part been facilitated by new methods of data analysis (Kobe et al. 1995, Kobe 1996, Uriarte et al. 2004, Kneeshaw et al. 2006). Providing a coupling between directly parameterised models and collected data creates mechanisms to quantify uncertainty in model parameterisation and model prediction (Canham and Uriarte 2006). This linkage promotes confidence in the simulations and models can essentially be seen as complementary tools to field studies (Menard et al. 2002b). A particular strength of the spatially-explicit individual-based forest growth model SORTIE-ND is its ability to model an individual's complete lifecycle and community dynamics. Coupled with field data this is a powerful tool to aid functional understanding and to highlight areas where knowledge is weak or absent.

The aim of this study is to model *R. ponticum* individuals within the SORTIE-ND context. The specific objectives are to (i) parameterise SORTIE-ND for *R. ponticum* using available published data on allometry, growth and dispersal, (ii) carry out initial runs combined with the tree model data from Chapter 4, using the Douglas-fir dominated CyB5 permanent sample plot, and (iii) discuss the limitations of available data. Areas where knowledge is required to enable robust parameterisation of SORTIE-ND for *R. ponticum* and field data collection methods are outlined in Chapter 7 further work.

6.2 Methods

6.2.1 Forest model structure

SORTIE-ND simulations describe four life-history stages (seedling, sapling, adult and snag). Only dead standing adult trees (>10cm DBH) are classified as snags, smaller diameters are not reported. Population dynamics are modelled through the prediction of an individual's lifecycle as defined by its allometric structure, growth and mortality, dependent on its interaction with neighbours and resources (Light in this context) (Pacala et al., 1993, Pacala et al., 1996). As the base unit of representation, a tree's attributes contain all relevant information within the model, including life-history stage and a discrete spatial location. Progress through each stage is a function of a tree's allometry and its allocated behaviours simulating (in this case) dispersal, establishment, growth and mortality.

6.2.2 *Rhododendron ponticum* parameterisation

The primary processes necessary for individuals in SORTIE-ND are allometry, dispersal, establishment, growth and mortality. To work within the current confines of SORTIE-ND with *R. ponticum* it is necessary to define key parameters for the seedling, sapling and adult life cycle stages: minimum adult DBH, minimum DBH for reproduction and maximum seedling height. The allometric relationships necessary for SORTIE relate diameter to tree height (DBH, or diameter at 10cm height for seedlings), crown depth to tree height and crown width to DBH. Continuity of progression through life history stages is maintained by a DBH to diameter at 10 cm height relationship.

6.2.2.1 Diameter to tree height and DBH to diameter at 10 cm height

Linear relationships describing the relationship of diameter at 10 cm height to stem height have been defined by Nadezhdina et al. (2004) as part of a biomass and leaf area study of Rhododendron in sparse Scots pine (*Pinus sylvestris*) stands in Belgium. Where:

$$\text{stem height} = 0.53 * \text{Diam}_{10} + 0.1 \tag{6.19}$$

stem height is in metres and Diam_{10} is in cm. The data in Nadezhdina et al's (2004) study ranged from 0.5 - 2.3 m in height.

Stem (trunk) diameter is a key attribute within SORTIE, its increase per year is calculated and this drives the respective increase in height. Diameter and height then, in turn, affect crown width and crown depth. However stem diameter is not a meaningful relationship for *R. ponticum*, given that it is (usually) multi-stemmed and has high plasticity, similar to plant species such as common heather (*Calluna vulgaris* (L.) Hull) (Figure 6.1) Previous studies of *R. ponticum* have tended to measure diameter at soil level (Erfmeier and Bruelheide 2004) or at 10 cm height (Nadezhdina et al. 2004). With a model requirement for DBH and the use of the Diam_{10} to DBH relationship to maintain continuity, the DBH to Diameter at 10 cm height relationship was set as a 1 to 1 relationship; effectively making the trunk a cylinder and the diameter value a generalised relation to woody biomass rather than actual stem width.

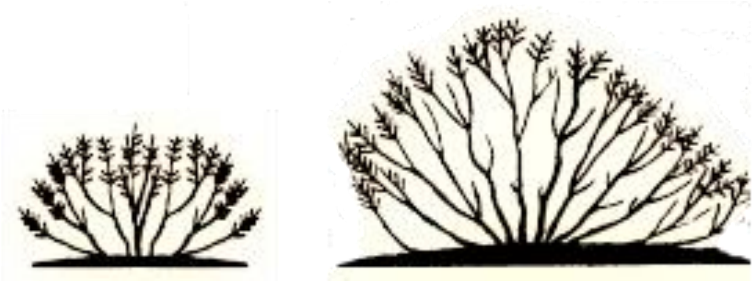

Figure 6.1. Growth form stages of *Calluna vulgaris* demonstrating multi-stemmed growth structure similar to *Rhododendron ponticum* (after Watt, 1955).

A secondary issue is the need to fix a maximum bush (tree) height. This was fixed at 6 m for *R. ponticum* (Nadezhdina et al., 2004). However it is necessary for stem diameter to continue to increase once maximum bush height had been reached. In order to maintain continuity of the diameter to height relationship, past the 6 m maximum tree height, dummy data that assumed continual height increase at an equivalent rate was used.

This ensured that, in the final model, once the bush height reached 6 m, the diameter continued to increase at the same rate.

6.2.2.2 Crown radius and depth

Tree crowns within SORTIE-ND are represented as cylinders with a depth and a radius. Allometric crown relationships do not exist for *R ponticum* however Nadezhdina et al. (2004) derived a leaf area relationship to stem height:

$$\text{leaf area in m}^2 = 1.96 * \text{stem height in meters} - 0.52 \tag{6.20}$$

Early forest gap models (Figure 2.4) defined tree crowns as flat disks at the top of a tree. Usually these flat 'crowns' covered the entirety of the gap. This has been adapted for use with *R. ponticum* with the leaf area relationship (6.2) translated into tree crowns defined only by crown radius (flat disks).

The dummy data used to maintain continuity of diameter after maximum tree height was again used to ensure the linear increase in leaf area was maintained, keeping the relationship constant. Only saplings and adults have crowns in SORTIE-ND. The SORTIE standard relationship used for Crown radius is:

$$\text{Crown radius} = \text{C} * \text{diameter}^{\text{b}} \tag{6.3}$$

Where C is the slope and b is the exponent of the relationship. Parameters were estimated using maximum likelihood techniques and simulated annealing in the R likelihood package (Murphy, L., 2012).

6.2.2.3 Growth

Erfmeier and Bruelheide (2004) calculated median basal diameter increase at the soil surface of 6.1 mm y^{-1} for invasive *R. ponticum* individuals growing in Ireland. Though measured at the soil level rather than the required 10 cm height specified by SORTIE, with stem set to a uniform diameter in this model, basal diameter gives a proxy for diameter increase per year. Erfmeier and Bruelheide (2004) also found a median stem elongation of between 17.1 and 20.7 cm yr^{-1} with this population.

SORTIE-ND uses a constant radial growth model that adjusts diameter based on a radial increment and auto-updates height in relation to the allometric relationship. This was parameterised as:

$$Y = \left(\frac{g4}{10}\right) * 2 * T \tag{6.4}$$

Where Y is the amount of diameter growth, in cm, to add to the tree (0.61 cm); g4 is the Adult Constant Radial Growth in mm yr^{-1} parameter (3.05 mm) and T is the number of years per timestep (can be varied per run).

6.2.2.4 Allometrics and growth combined

Table 6.1. details the diameter, height and crown radius for each life-stage allometric relationship derived from the literature.

Table 6.1. Ranges of life-history traits for *R. ponticum* with relevant simulated diameters for seedling, sapling and adult individuals.

	Diameter (cm)		Stem height (m)		Crown radius (m)	
Life-stage	Min.	Max.	Min.	Max.	Min	Max.
Seedling	0.1	2.35	0.15	1.35	0	0.82
Sapling	2.35	7.32	1.35	3.98	0.82	1.56
Adult	7.32	NA	3.98	6	1.53	NA

.

Maximum seedling height was defined as 1.35 m in line with the tree species. Stephenson et al. (2006) state average time to reproduction for *R. ponticum* as 12 years. With a deterministic growth function of 0.61 cm yr^{-1} (6.4), minimum adult DBH and minimum DBH for reproduction were both set to 7.32 cm (an increase of 0.61 cm yr^{-1} for 12 years). A maximum seedling height of 1.35 m equates to a maximum seedling diameter of 2.35 cm. Saplings therefore have a diameter of between 2.35 cm and 7.32 cm (Table

6.1). A rhododendron bush then has a height of ≈ 4 m as it transitions between sapling and adult and spends 4 years as a seedling, 8 years as a sapling with maximum height reached after 18 years.

6.2.2.5 Dispersal

The SORTIE-ND spatial dispersal behaviour contains two key components: the shape of the dispersal kernel and number of seeds produced as a proportion of those produced by a 30 cm DBH adult:

$$\mathrm{R}_i = \left(\frac{\mathrm{STR}}{\mathrm{n}}\right)\sum_{K=1}^{T}\left(\frac{DBH_k}{30}\right)^{\beta} e^{-Dm_{ik}{}^{\theta}} \tag{6.5}$$

Where:

$$n = \int_0^{\infty} -Dm_{ik}{}^{\theta}\, dm \tag{6.6}$$

$\mathrm{R_i}$ is the density of seedlings (#/m^2) at a given point i. STR, the 'standardised total recruits' is defined as the total seeds produced by a 30 cm DBH tree. This is then modified by the β dispersal parameter. In this case β was set to 0 so that the STR value was directly applied according to the remaining parameters: *m* is the distance from the *i*th parent tree; *D* and θ are modified parameters that affect the shape of the dispersal kernel.

Data for *R. ponticum* seed dispersal distances were collected by Stephenson et al. (2007) from controlled and natural release trials. The controlled release set seed traps at 0.5, 1, 2, 5, 10, 20, 50 and 100 m from a wooden platform in eight compass directions. Wind speed was measured and seeds were released from two heights. The natural release trial captured seeds released over 6.5 weeks from an established *R. ponticum* stand, with individual traps covering an identical area to the controlled release trial. This study found that the majority of seeds (99.8% and 97.1% respectively) were found within 10 m of the release point. Only 0.001% (controlled) and 0.02% (natural) travelled to 50 m. The greatest number of seeds were found at 5 m (controlled) and 1 m (natural) (Stephenson et al., 2007). To account for the reducing effect of the surrounding forest on windspeed, distance values were halved for parameterisation of the dispersal model with the majority of seeds (≈ 99%) falling within 5 m and the remainder at up to 25 m (Edwards & Taylor, 2008).

Limited studies have been carried out in relation to number of seeds produced by *R. ponticum*. A key text by Cross (1975) found that a bush growing in a semi-open location with 2 m height and 10 m canopy circumference bore 233 buds. Inspection of 10 racemes yielded 268 ± 88 seeds per capsule and 18.3 ± 3.4 capsules per raceme; equating to 4900 ± 1900 seeds per raceme or the potential for over one million seeds if production was similar for each bud. However, given that this individual was growing in a semi-open location it is difficult to directly relate this to the growth and seed production of an individual growing in a forest habitat. For the purposes of this study we have assumed that each adult individual, regardless of age, produces 4900 seeds per year, equating to one raceme (STR set at 4900). The benefit of this is that without specific data we can assume each stem has one flower and remove confounding assumptions. STR can then simply be varied for later model runs to assess influence.

6.2.3 Establishment

6.2.3.1 Light dependent seed survival

Photosynthetically Active Radiation (PAR) and photosynthetic photon flux density (PPFD) are used interchangeably in the literature (Gullo et al., 2014, Kang et al., 2014, Kumar et al., 2014). Light in SORTIE is calculated as GLI, a measure of the percentage of PAR transmitted to a specific point through the canopy or a canopy gap (Canham, 1988). A study to quantify the 1:1 relationship between GLI and %PPFD observed that GLI slightly overestimated %PPFD with an R^2 of 0.77 (Battaglia et al., 2003). This would suggest that GLI, %PPFD and PAR are acceptably comparable.

Ninaber (2009) conducted experiments on the germination rate of *R. ponticum* under combinations of substrates (tall moss, sown grass and bare earth) and variation in forest floor light variations using green, 20 % PPFD, grey, 20 % PPFD and clear, 90 % PPFD. Green was shown to represent canopy, grey shadow and clear open or gap light. *Rhododendron ponticum* germination rates were observed of 14.8 %, 29.3 % and 23.7 % respectively. Seedling survival was likewise affected with 11.7 %, 34.7 % in grey and 46.8 % survinng under the respective light conditions (Table 6.2).

To incorporate light dependent seed survival in SORTIE-ND requires parameters for: an optimum GLI (GLI_{opt}), the point where 100% of seeds survive; a slope parameter below optimum GLI (SL_{lo}); a slope above optimum GLI (SL_{hi}) (Figure 6.2).

Table 6.2. Filters used in study of *R. ponticum* germination under different light conditions by Ninaber (2009) with PPFD of each, percentage of seedlings that germinated, percentage of seedlings that survived and proportion of final seedlings that survived (per 100).

Filter	PPFD (%)	Simulates	Germination (%)	Survival (%)	Final seed
Green	20	Canopy shade	14.8	11.7	1.73 per 100
Grey	20	Shadow	29.3	34.7	
Clear	90	Open	23.7	46.8	11.09 per 100

* Assuming a 1:1 relationship of GLI to PPFD

The grey and green filters used had the same PPFD value (Table 6.2) and so only green and clear were used. The clear filter represented the optimum GLI for establishment (clear sky). Under the clear filter, 23.7% of seedlings germinated and 46.8% of those survived, leaving 11.09/100 final surviving seedlings. Under the green filter, 14.8% of seedlings germinated with 11.7% of those surviving, leaving 1.73/100 final seedlings surviving.

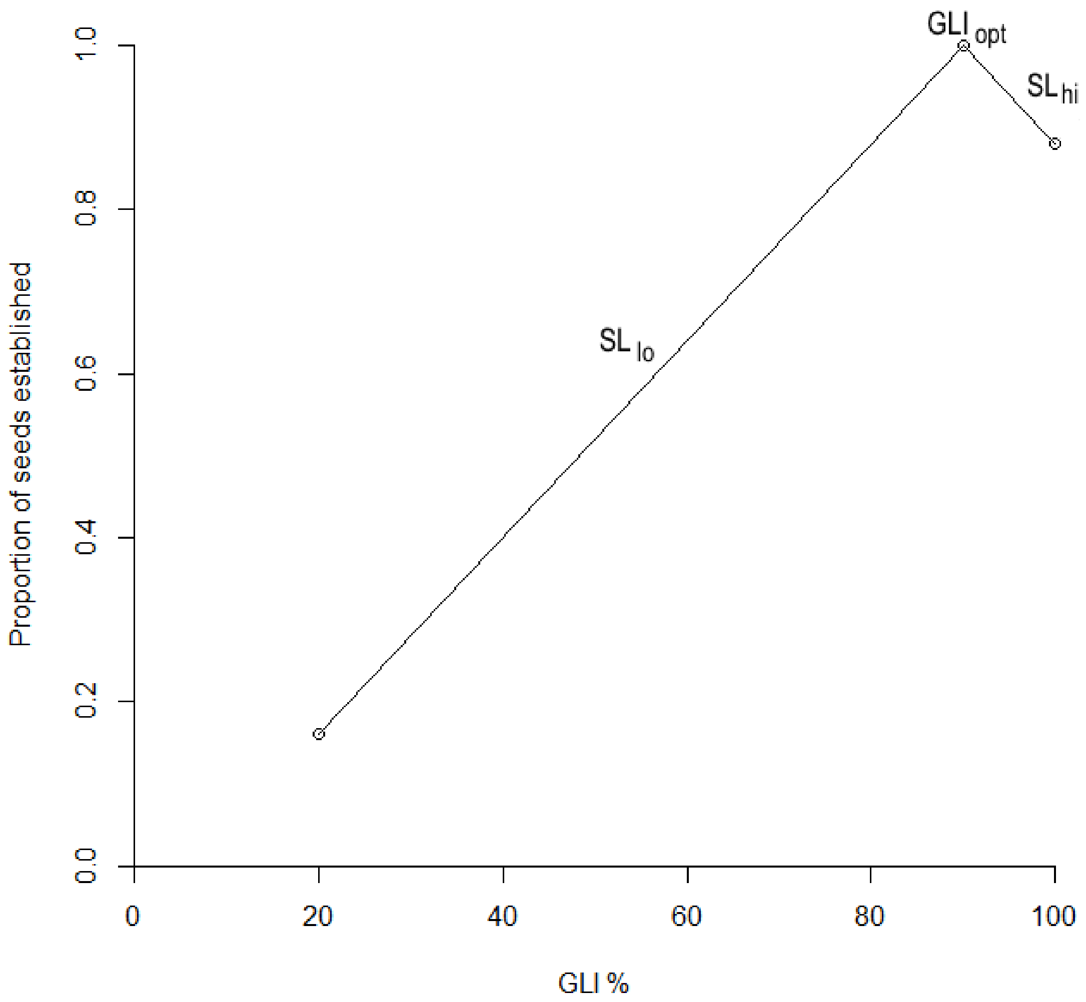

Figure 6.2. Up scaled light dependent seed establishment showing optimum establishment (GLI_{opt}) at 90% GLI, reduction, slope of 0.01206 (SL_{lo}) and -0.01206 (SL_{hi}) away from optimum.

To translate the clear filter value to GLI_{opt}, where 100% of seeds survive, it was necessary to scale up the data from 11.09% survival at 90% GLI under clear glass by a multiplication of 9.017133. The green survival rate of 1.73% was scaled by the same factor to 15.59964 %. These points were then used to obtain the slope from GLI_{opt} to SL_{lo}, the slope below optimum (Figure 6.2). Slope above optimum (SL_{hi}) was set to the reverse of SL_{lo} as no data was available.

The resultant proportion of surviving seeds were then reduced to the original scale using the ‘proportional seed survival’ behaviour by a multiplication factor of 0.1109.

6.2.4 Canopy transmission

Previous studies have found that the distribution and size of neighbourhood trees had the greatest effect on understory light variation (Canham et al., 1999, Kucharik et al., 1999) with inter-crown gaps responsible for much of the light variation (Stadt et al., 2007). In studies where no species-specific light transmission data was available crowns have been assumed to be opaque (zero canopy light transmission) (Canham et al., 2004, Stadt et al., 2007, Boivin et al., 2011). Therefor without specific data for *R. ponticum* canopy transmittance this study has assumed crowns to be opaque.

6.2.5 Modelling scenarios

Two different scenarios were used to compare and investigate the model function in the context of spread through the 100 by 100 m CyB5 plot for 100 years: the first was a baseline plot using the 2011 CyB5 tree map and density distribution and recorded tree species understory only. The second included a lone individual of *R. ponticum* at plot centre. A lone individual at plot centre was used to allow quanitification of spread without contamination from other individuals and to avoid confusion from edge effects by SORTIE's torus shape. Plots were then analysed for changes in all species seedling, sapling and adult density over time.

Each modelling scenario was run over 100 years using 1 year timesteps. Ten replicates of each scenario was run, averaged and then investigated at 25 year intervals.

6.3 Results[6]

6.3.1 Rhododendron allometrics

The combination of the diameter to height relationships (Nadezhdina et al., 2004) and the growth relationship (Erfmeier & Bruelheide, 2004) (Equations (6.19 and (6.4) caused the maximum bush height of 6 m to be reached after 18 years (Figure 6.3).

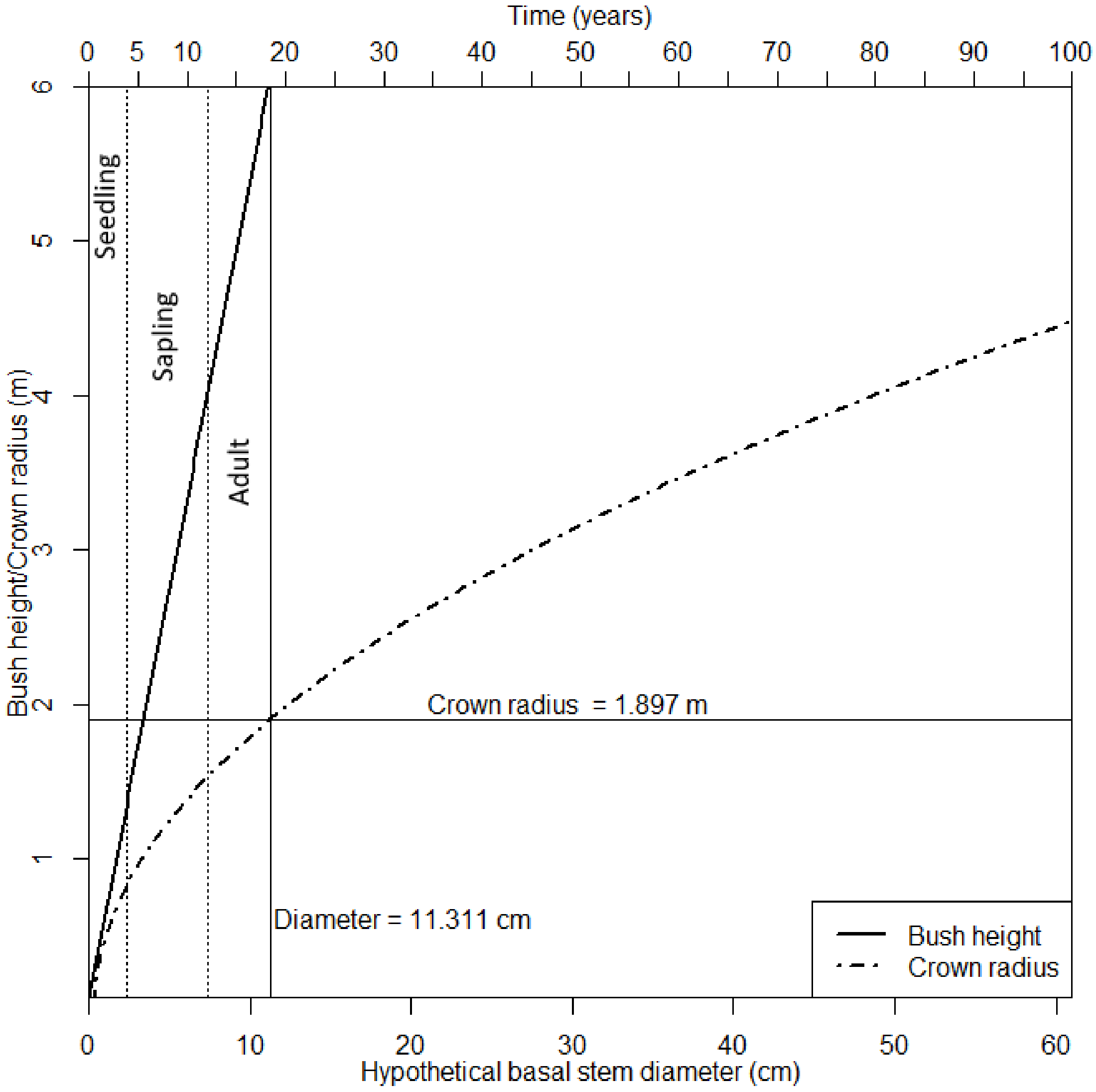

Figure 6.3. Crown radius and bush height (m) to Diameter (cm) relationship showing years to maximum height (6 m), crown radius and basal stem diameter. Dotted lines show transition from seedling to sapling and sapling to adult. Line intercept details crown radius (1.897 m) and basal stem diameter (11.311 cm) at maximum height.

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[6] See appendix 5 for parameter values.

Upon reaching maximum height a bush would have a diameter of 11.31 cm and a crown radius of 1.897 m (Figure 6.3).

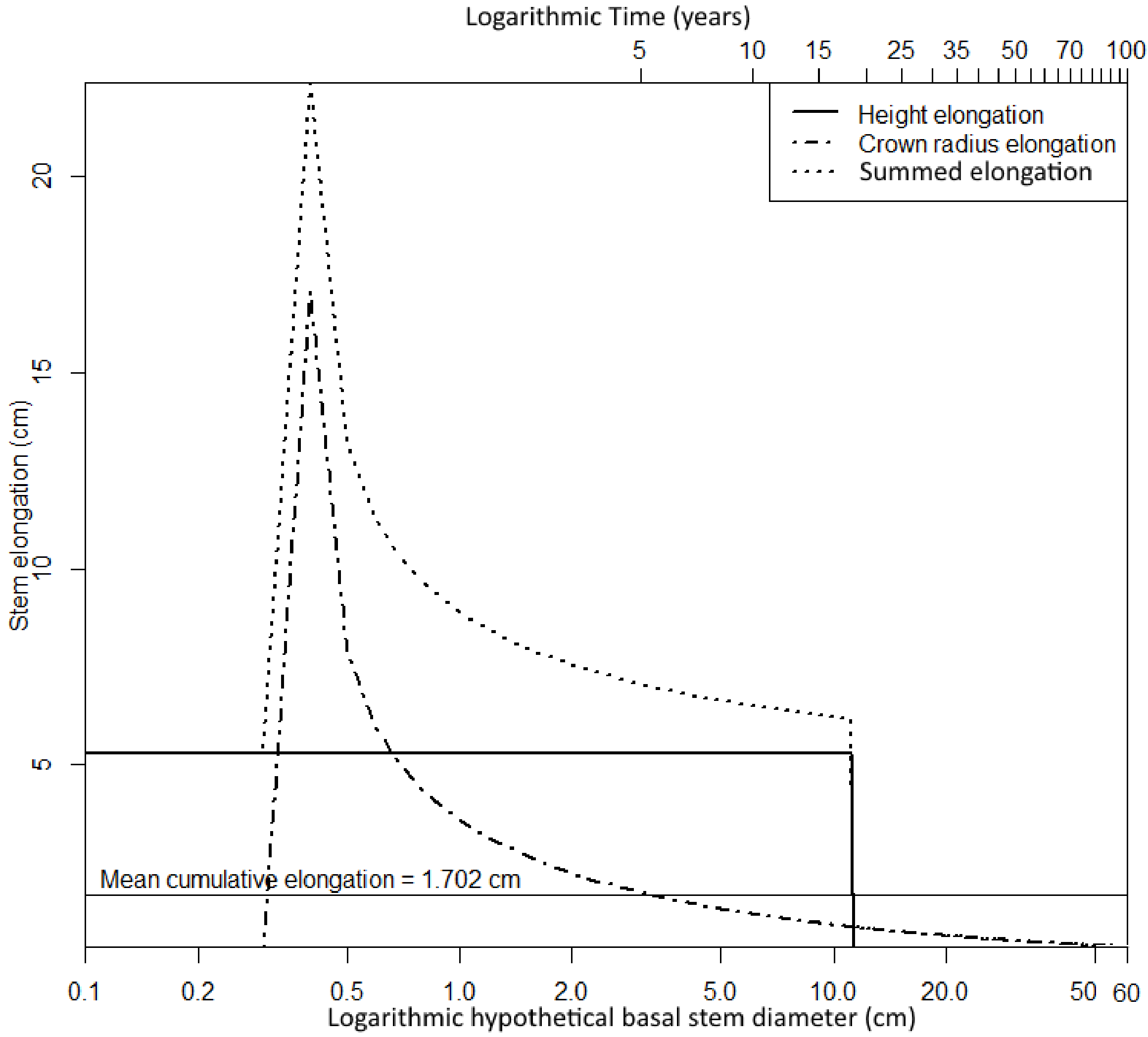

Figure 6.4. Stem elongation for height, crown and summed (horizontal and vertical) in relation to stem diameter and time. Height elongation shown as solid dark line, terminating at bush reaching maximum height.

6.3.1.1 Growth and Stem elongation

Erfmeier and Bruelheide (2004) estimated median stem elongation of 17.1-20.7 cm yr^{-1} for invasive rhododendrons growing in Ireland. The combination of the growth equation, the height diameter relationship and leaf area relationship (crown expansion) resulted in a mean cumulative elongation (vertically and horizontally) of 1.702 cm over a 100 year period (Figure 6.4). Elongation rates similar to those described by Erfmeier and

Bruelheide (2004) were only experienced in the early stages of development (Figure 6.4). However the artificial crown shape and growth form inherent in SORTIE do not accurately represent the spatial development of *R. ponticum* individuals whilst maintaining the linear growth and leaf area described previously.

6.3.1.2 Dispersal

Parameterisation of the dispersal function reproduced the expected results with the majority of seeds (≈ 99%) falling within 5 m of the dispersal point however the model failed to accurately capture the minority distribution of seeds over greater distances and up to 25 m (Edwards & Taylor, 2008). Comparisons of model runs with differing STR values of 100 and 1000 (to ease percentage calculations) (Figure 6.5 a and b) demonstrated that STR purely affected number of seeds distributed without affecting the shape of the dispersal kernel. It is then possible for later runs to incorporate variation of seed production, by varying STR, to assess impact on expansion rates.

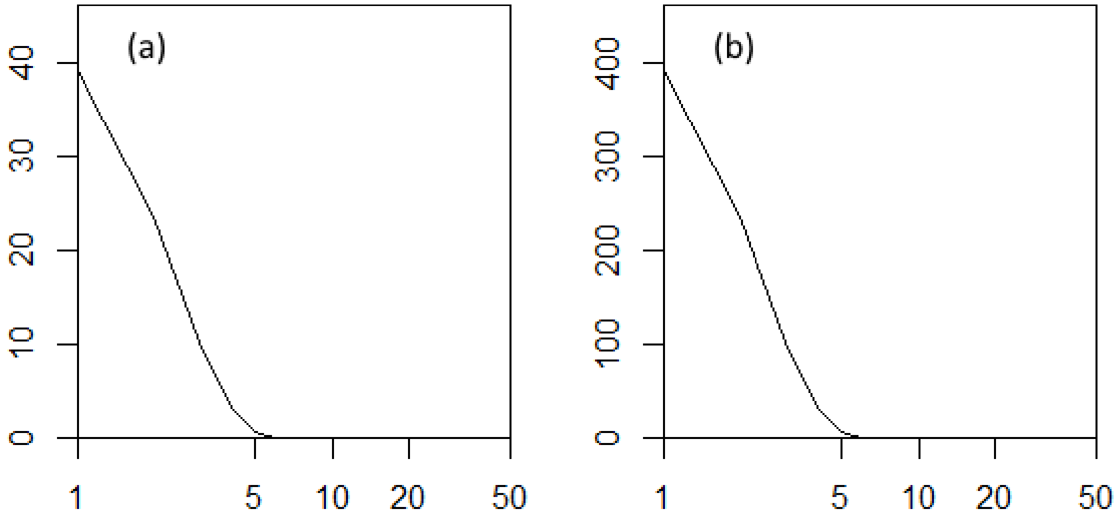

Figure 6.5. Weibull dispersal kernal with STR of 100 (a) and 1000 (b) demonstrating proportional distribution of seeds remains constant in relation to distance and that the STR parameter does not affect distribution.

6.3.1.3 Establishment

The impact of the light-dependent seedling establishment and proportional seed reduction three runs were investigated using two timesteps (Figure 6.6 a and b), with STR set at 1000. Seed establishment was compared seed establishment without any reduction, with reduction only due to light, and with light-dependent plus proportional reduction.

Without any reduction in seed numbers (Figure 6.6, red circles) seed establishment can be seen at approximately 50, 60, 80 and 90 % GLI. The variation in numbers of seeds established at this point is purely due to location of seeds and the number of seeds that fall there. Nothing can be inferred from this except perhaps distance to parent.

Runs with light dependent seed establishment (black triangles) demonstrate that at the 50 and 60 % GLI seed numbers are considerably reduced and more so at the lower light level. At the higher GLI

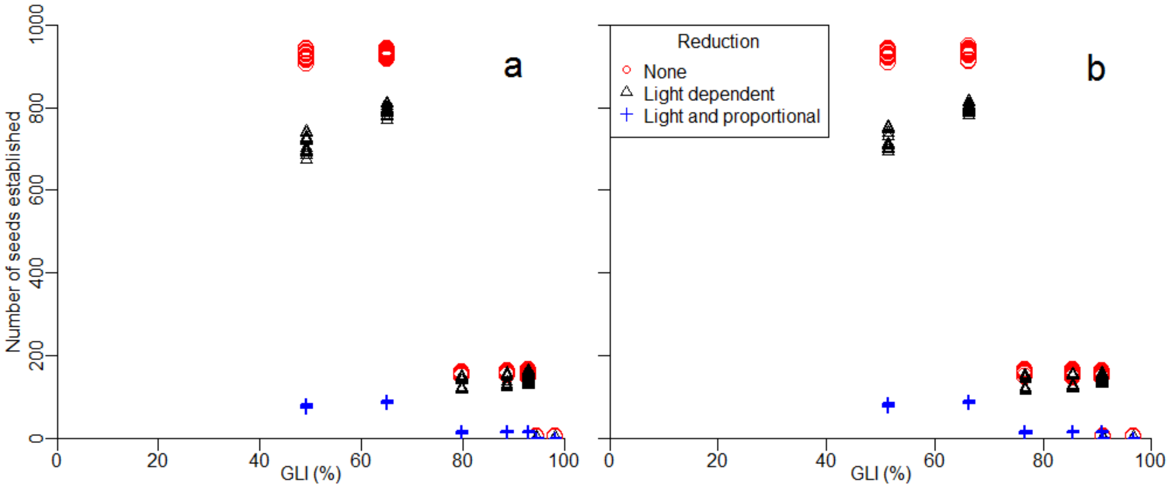

Figure 6.6. Comparisons of seed establishment numbers over two timesteps (a and b) for seed establishment with no reduction (red circles), seed establishment with light dependent reduction (black triangles) and seed establishment with light dependent reduction and proportional establishment (blue crosses).

A greater reduction due to light can clearly be seen at the lower GLI levels (40 – 60 %, Figure 6.6 a and b) than at the higher levels (80 to 100 %). Similarly the tailing reduction from ≈ 70 % GLI ≈ 50% GLI (black triangles) is apparent. The further proportional reduction (blue crosses) effectively reduces the established seeds to the expected values.

6.3.2 Modelling scenarios

6.3.2.1 Effect on tree species at the 25 year timestep

With inspection of the data after 25 years, both seedling scenarios had very similar distributions. Relatively few seedlings of any species had emerged by this point, after an initial drop off of DF numbers caused by the stand being in the stem exclusion stage of development (Franklin et al., 2002) (Figure 6.8). Overall tree seedlings had declined by 10.5 % with the addition of *R. ponticum,* with SWD hardest hit (35.3 % reduction). Although HWD numbers had increased by 20 %, this only equated to 1 tree ha^{-1} (Table 6.a). Overall seedling numbers had suffered a sharper decline than the sapling numbers by approximately 3 %.

In terms of saplings the introduction of *R. ponticum* had the greatest effect on the HWD and SWD species groups (Table 6.b). SWD was reduced by a third, equating to 35 trees ha^{-1}, whilst HWD numbers increased. DF and SNS numbers were also reduced slightly.

Excluding DF, the adult tree species had almost opposite interaction effects with *R. ponticum* than the seeding and saplings. SNS and SWD experienced marginal increases in numbers (6 and 7 %) and HWD a slight decline (Table 6.c). Adult numbers in general increased by 0.5 %, though DF numbers were still decreasing.

At 25 years there were very few *R. ponticum* saplings (11 ±3.6) or adults (25 ±10.6) (Table 6.3) though from Figure 6.9 it is apparent that prior to the 25 year mark there was a cohort that increased to around 30 or 40 saplings and subsequently declined.

6.3.2.2 Effect on tree species at the 50 year timestep

At the 50 year timestep the introduction of *R. ponticum* had caused a reduction in all tree species seedlings except HWD, which remained the same (Table 6.3). As with the snapshot at the 25 year timestep, SWD seedlings had been hardest hit, reduced by almost 50 %. On average there were over 3.5 times as many *R. ponticum* seedlings at 50 years as there were at 25.

There was an identical reduction in the overall numbers of tree seedlings and saplings at this stage. All sapling tree species were reduced with SWD hardest hit (reduced by 36.4 %), and HWD only slightly reduced (by 4 %) (Table 6.). In comparison to the 25 years timestep the average total number of saplings had been reduced by around 5 %.; the proportion that the DF species had reduced by had doubled, and for SNS it had tripled. There were over 20 times as many *R. ponticum* saplings at 50 years as there were at 25 years.

Adult numbers declined overall with the inclusion of *R. ponticum* (though only by 2 %) due to a 46 % reduction in the SWD species group. Numbers for all other species were relatively consistent over both scenarios (Table 6.).

The number of *R. ponticum* adults had increased by around 30 times compared to 25 years. However, it can be seen that by this point the standard deviations for *R. ponticum* seedlings (and saplings and adults) are considerably larger than that for any of the tree species at all life stages (Table 6.). By this stage an emergent oscillation in the production of seedlings (Figure 6.8) has occurred that is not represented by the 25 and 50 year snapshots. These oscillations then resonate through the sapling growth stage (Figure 6.9) and result in the beginning of a stepped increase in adult numbers (Figure 6.10).

6.3.2.3 Effect on tree species at the 75 year timestep

Seedling numbers for all tree species were heavily impacted by the addition of *R. ponticum* after 75 years (Table 6.3a) with total numbers reduced by almost 30 %. The SWD species group continued to be hardest hit, by 76 %. The average number of *R. ponticum* seedlings had also declined by 63 % though standard deviations here were still high and numbers were clearly increasing though not to the levels of the previous peak between 50 and 75 years (Figure 6.8).

Tree sapling numbers continued to decline in scenarios containing *R. ponticum* with a reduction of 23.3 % overall compared to 13.2 % at 50 years (Table 6.b). The SWD species group was reduced by almost 60 % and DF by over 20 %. *Rhododendron ponticum* numbers, 485 (±444.7), are actually the tail end of a larger peak towards 1250 individuals (Figure 6.9).

Average adult density was largely unaffected by the increasing trend of *R. ponticum* invasion (Figure 6.10). In line with previous timesteps SWD was in decline (by 41.2 %) and HWD increasing (by 33%); though HWD numbers were still marginal at 8 trees ha^{-1} (Table 6.3c).

6.3.2.4 Effect on tree species at the 100 year timestep

All tree seedling numbers were reduced by the 100 timestep stage (Table 6.c). Though DF seedlings were reduced by 31.4 % there were an increase in numbers in relation to the 75 year mark. Likewise though HWD and SWD were reduced in comparison to the non-*R. ponticum* scenario, numbers had remained constant over the preceding 25 years. At the 100 year timesteop zero *R. ponticum* seedlings were present and numbers had been close to zero for approximately the previous 20 years (Figure 6.8)

Sapling numbers are reduced by 34.3 % with the inclusion of *R. ponticum* at 100 years and almost halved in relation to numbers at 75 years (Table 6.b). SWD is reduced by the largest margin and HWD the least, though, on average, at this stage only 1 HWD individual remains and only 2 seedlings are present. Rhododendron numbers are reduced to an average of 4 saplings ha^{-1}.

Adult numbers continued to be largely unaffected apart from SWD (Table 6.c) and *R. ponticum* levels appeared relatively stable for the previous 15 years (Figure 6.10). Howver, As can be seen from a graphic of *R. ponticum* spread, taking one run as an example (Figure 6.7 a to d), and from the number of adults surviving after 100 years (4400 ±1529.94) (Table 6.) an improbable number of individuals are confined within a small area.

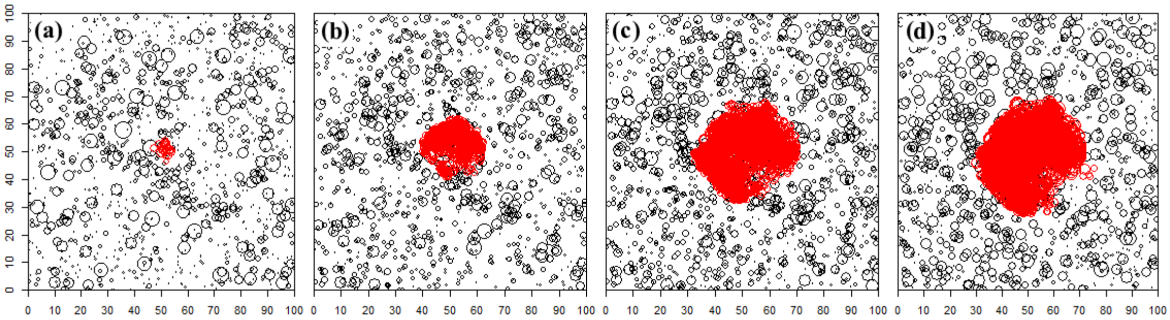

Figure 6.7. Spread of *R.ponticum* throughout CyB5 from a representative run of one individual placed at centre plot, after 25 years (a), 50 years (b), 75 years (c) and 100 years (d). Images depict crown radii with tree species in black and *R. ponticum* in red.

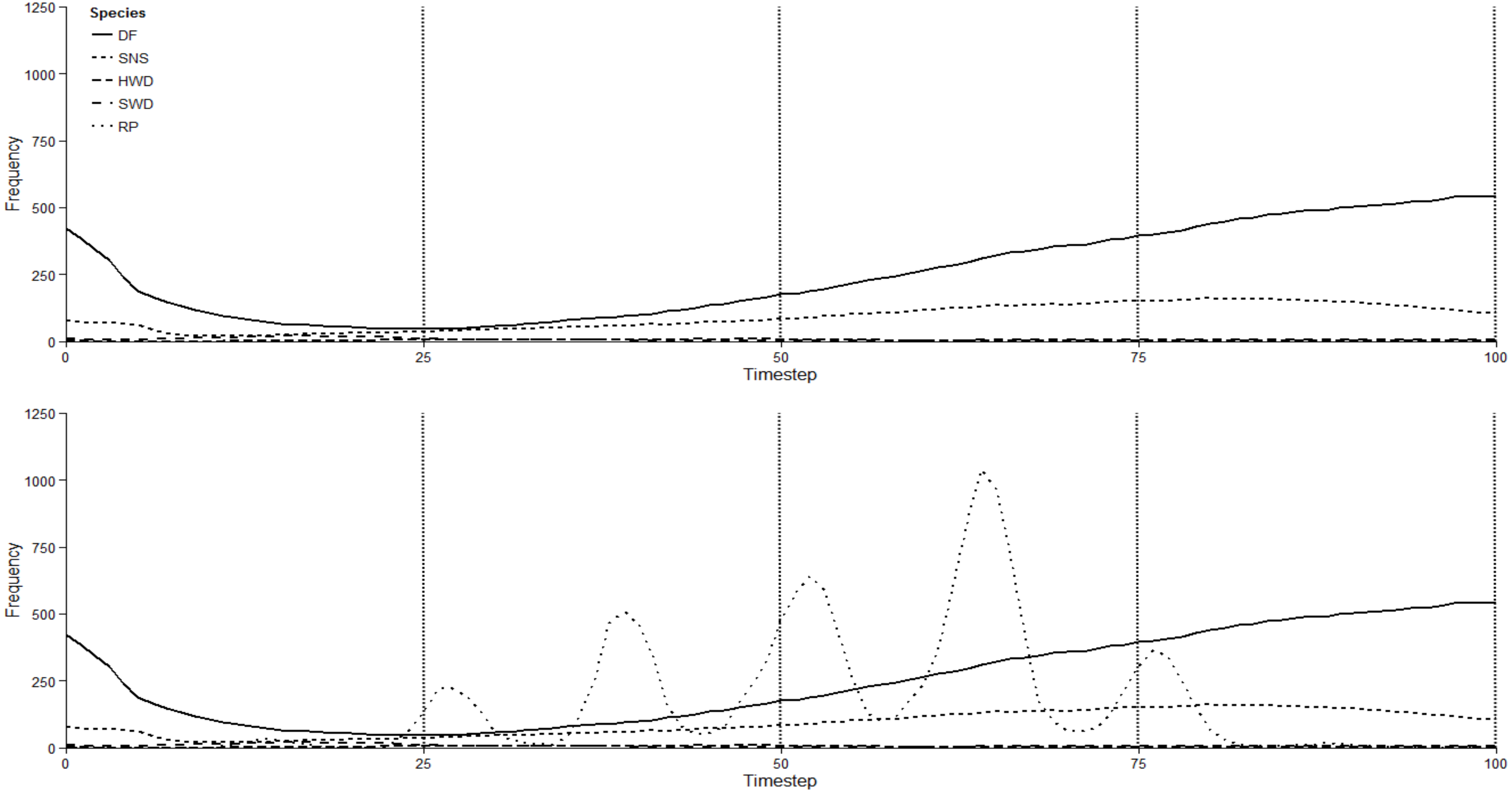

Figure 6.8. Average number of stems per hectare for plot seedlings over 100 years in the absence (a) and presence of ***R. ponticum*** (b).

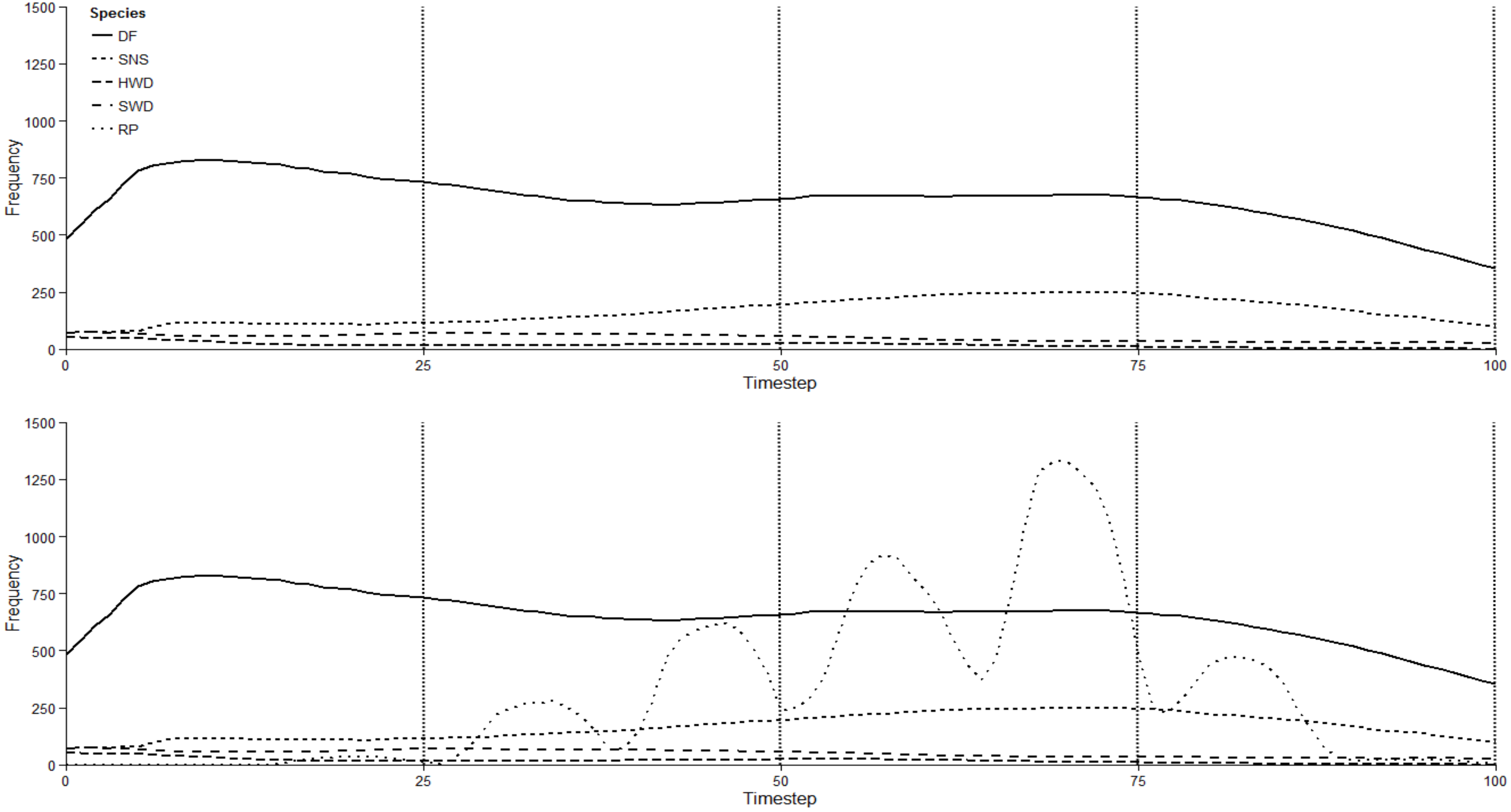

Figure 6.9. Average number of stems per hectare for plot saplings over 100 years in the absence (a) and presence of *R. ponticum* (b).

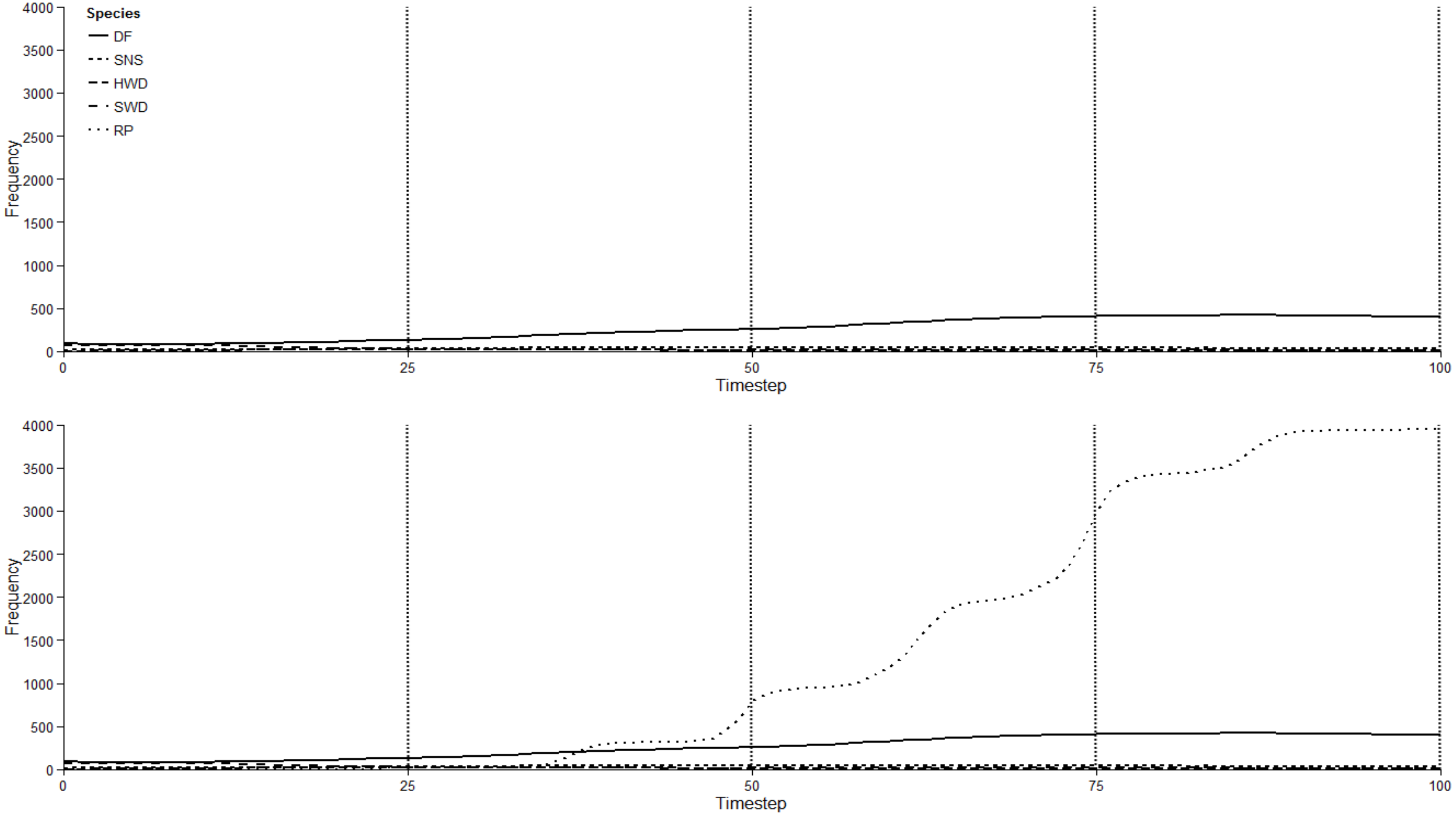

Figure 6.10. Average number of stems per hectare for plot adults over 100 years in the absence (a) and presence of *R. ponticum* (b).

Table 6.3. Average absolute densities (number per hectare) and standard deviation of runs with tree species only (Trees) and with *R. ponticum* (RP) at 25, 50 and 75 years timesteps for seedling, sapling and adult life-history stages.

		25 yrs.		% change	50 yrs.		% change	75 yrs.		% change	100 yrs.		% change
	Species	Trees	With RP		Trees	With RP		Trees	With RP		Trees	With RP	
a. Seedling	DF	50 ±11.4	50 ±9.4	0.0	204 ±14.1	177 ±14.1	-13.2	556 ±18.4	398 ±28.5	-28.4	791 ±49.1	543 ±27.7	-31.4
	SNS	43 ±4.2	36 ±3.5	-16.3	97 ±12.5	86 ±8.7	-11.3	195 ±16.4	152 ±9.9	-22.1	174 ±17.6	110 ±11.6	-36.8
	HWD	5 ±2.0	6 ±2.2	+20.0	8 ±3.6	8 ±2.7	0.0	2 ±1.4	4 ±2.5	+100.0	3 ±1.6	2 ±1.5	-33.3
	SWD	17 ±4.0	11 ±2.3	-35.3	9 ±2.8	5 ±2.5	-44.4	25 ±7.9	6 ± 3.8	-76.0	22 ±6.7	6 ±2.4	-72.7
	Total	114 ±12.3	102 ±12.1	-10.5	318 ±18.8	276 ±15.9	-13.2	778 ±30.5	561 ±29.3	-27.9	990 ±41.4	661 ±27.3	-33.3
	RP	NA	136 ±36.5	NA	NA	483 ±265.9	NA	NA	306 ±362.7	NA	NA	0 ±0.0	NA
b. Sapling	DF	772 ±37.7	733 ±27.7	-5.1	745 ±38.3	658 ±20.4	-11.7	862 ±38.3	668 ±15.6	-22.5	522 ±75.5	357 ±31.2	-31.6
	SNS	120 ±6.7	116 ±7.3	-3.3	217 ±13.2	196 ±15.5	-9.7	297 ±25.0	246 ±12.2	-17.2	121 ±25.3	102 ±16.1	-15.7
	HWD	13 ±3.7	16 ±4.5	+30.0	25 ±7.9	24 ±3.4	-4.0	11 ±2.8	11 ±3.3	0.0	1 ±1.1	1 ±0.8	0.0
	SWD	105 ±11.2	70 ±5.6	-33.3	88 ±10.8	56 ±9.1	-36.4	80 ±12.2	34 ±9.1	-57.5	97 ±14.1	27 ±9.0	-72.2
	Total	1010 ±44.8	935 ±25.3	-7.4	1075 ±32.0	933 ±25.1	-13.2	1250 ±37.8	959 ±11.0	-23.3	741 ±88.2	487 ±43.2	-34.3
	RP	NA	11 ±3.6	NA	NA	239 ±166.7	NA	NA	485 ±444.7	NA	NA	4 ±5.3	NA
c. Adult	DF	134 ±4.1	132 ±4.9	-1.5	256 ±9.7	259 ±8.6	+1.2	414 ±9.81	411 ±13.6	-0.7	403 ±8.6	399 ±11.4	-0.0
	SNS	32 ±1.2	34 ±0.9	+6.3	44 ±3.5	47 ±3.5	+6.8	40 ±2.17	42 ±2.7	+5.0	32 ±3.7	33 ±3.4	+3.1
	HWD	23 ±2.9	22 ±2.5	-4.4	12 ±3.6	14 ±2.8	+16.7	6 ±1.95	8 ±2.3	+33.3	4 ±2.3	5 ±2.3	+25.0
	SWD	26 ±3.4	28 ±1.7	+7.7	30 ±3.3	16 ±2.6	-46.7	34 ±6.04	20 ±4.6	-41.2	15 ±3.0	9 ±3.1	-40.0
	Total	215 ±4.1	216 ±4.2	+0.5	343±9.4	336 ±9.6	-2.0	495 ±13.0	481 ±11.8	-2.8	454 ±8.8	446 ±13.7	-1.7
	RP	NA	25 ±10.6	NA	NA	790 ±181.3	NA	NA	2989 ±1214.5	NA	NA	3955 ±1529.9	NA

*See chapter 3 for species acronyms

6.4 Discussion

From a purely practical point of view this study has shown that it is possible to parameterise an individual-based model, such as SORTIE-ND, from published literature for *R. ponticum*. However, it has also shown that certain manipulations and assumptions were necessary to parameterise the model and receive useful outputs, and that data necessary to adequately model a full plant lifecycle is absent.

Applying published allometric and growth relationships (Nadezhdina et al., 2004, Erfmeier & Bruelheide, 2004) with SORTIE-ND's inbuilt functions only approximate *R. ponticum* functioning. The manner in which SORTIE-ND simplifies an individual tree's structure is one of its key strengths in forest modelling. The allometric relationships and submodels allow conceptualisation of idealised individual trees in a parsimonious but useful way. A key challenge to incorporate *R. ponticum* further in this type of model is the design of an idealised but sensible conceptual structure for *R. ponticum* with key, easily measurable variables that provide a similar functionality.

A further downside of parameterisation from literature sources, rather than field data as SORTIE-ND was designed, is the impossibility of quantifying parameter uncertainty. It is apparent that a cylindrical crown shape, and in turn the flat disk used in this study, will not adequately mimic the complexity of *R. ponticum* crown form. However, questions of quantification must be asked in terms of model usage and required goals. In this context, to carry out an initial investigation into the interaction between species in terms of reproduction and establishment due to light conditions, representation of leaf-surface area may be sufficient.

There is an inherent trade-off between the systems of equations to facilitate modelling. It has been shown that the crown representation, minimum-height and maximum attainable height do not produce the stem extensions witnessed by Erfmeier et al. (2004) a further issue compounded by the enforced tree structure. Life-history stages blur and with purely mechanistic growth it is impossible to model system dynamics in a more robust manner. Again as stated previously DBH is not a sensible metric for *R. ponticum* and diameter at 10 cm height (or even soil height) is difficult to measure and perhaps not usefully indicative. As highlighted by Erfmeier et al. (2004), bush height is easier to survey in the field as is bush diameter, however this leads back to bush and crown representation in a cylindrical or semi-cylindrical form.

An essential component absent from this simplistic *R. ponticum* representation is any mortality other than the implied seed mortality present in the establishment behaviours. It is likely that, in-line with other vascular plants, *R. ponticum* is affected by changing light conditions in terms of growth suppression and eventual mortality, at the very least in the seedling stages. Studies exists investigating leaf-plasticity (Niinemets et al., 2003) but no work directly related to plasticity of growth or natural mortality under varying conditions.

Parameterisation of dispersal with the available data and dispersal models failed to adequately represent long distance spread of a small percentage of seeds for *R. ponticum*. It was not possible to adequately contain 99% of the seeds within 5 m and still allow long distance spread. Whilst only small numbers of seeds (between 0.001% and 0.02% (Stephenson et al., 2006) were found to travel longer distances, this has potential to change the extent of the current plant distribution (Figure 6.7) and create satellite groups throughout the plot. An obvious solution to correct the problems with the dispersal distribution would be to provide an implementation of the WALD model within SORTIE. The WALD model (Katul et al. 2005) is a mechanistic model that incorporates complex windspeed and turbulence interactions, and was identified by Stephenson et al. (2007) to best represent the less frequent long-distance dispersal of *R. ponticum* seeds.

The oscillation of seedling production is an interesting and unexpected outcome of the model scenario. Even with relatively simple establishment rules it demonstrates the complexity of reproduction in a dynamic environment. Substrate is cited as a key factor in *R. ponticum* establishment and whilst included indirectly in the data from Ninaber (2009) explicit incorporation would provide greater insight into factors affecting *R. ponticum* colonisation. This explicit incorporation would require modification of the SORTIE-ND establishment submodel but could utilise the establishment results of Chapter 5 or published data from Stephenson et al. (2006).

One of the key questions at Coed-y-Brenin and of Rhododendron invasion is why more seedlings are not present when seeds are so abundantly produced. In the survey of 41 quadrats at CyB5 (Figure 5.1) only 79 seedlings were found. A possible indicator to an explanation could be that in the later model runs with large number of adults (≈ 4000) did not allow any seeds to establish for two decades with potential seed production of 20 million seeds per year. However, this may only be a peculiarity of the current model set up with the majority of individuals in dense areas unable to establish however it is an area for further investigation.

Study limitations are discussed in Chapter 7.

6.5 Conclusion

Simulation models are increasingly used to predict invasive species expansion and explore management scenarios (Frid et al 2013). Species distribution models (SDM) have commonly been used to predict locations where species will occur under future climate scenarios but often function independently of biotic interactions and rarely consider competition between non-native and native species (Capinha et al. 2013, Wisz et al. 2013). Equally SDMs are more generally used at regional or continental scales to identify areas most susceptible to invasion according to climatic or environmental suitability (Gallardo and Aldridge 2013). A failing of these broader scale models is their inability to capture differences between similar habitats over these large ranges. With increasing technological capability individual-based models are capable of examining emergent patterns at increasing scales (Gallien et al. 2010).

In relation to invasive species, individual-based models have variously been used to describe the invasion process in a qualitative manner (e.g. Travis et al. 2007) or as a quantification of the invasion process (e.g. Nehrbass and Winkler 2007). The novel, individual-based, approach described in this chapter combines *R. ponticum's* invasion dynamic with a forest model and presents several benefits to purely demographic models. Firstly, an explicit description of interaction and competition results in a more mechanistic understanding of the underlying processes and potentially results in an increased predictive capacity within the studied environment. Secondly, quantification of structure and functioning in this manner provides insight into the related impacts on ecosystem services such as biomass accumulation (Carbon storage) and reduction of biodiversity.

This study demonstrates an important first step in the integration of *R. ponticum* into contemporary models of forest dynamics. Without precedent it is apparent that, unlike the tree species historically used in such models, published relationships do not adequately contain the *R. ponticum* lifecycle. However it is shown that SORTIE-ND and similar models have the potential to become a useful tool in the investigation of *R. ponticum's* dynamic neighbourhood relationships.

6.6 References

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Chapter 7: Overall discussion and synthesis

7.1 Introduction

This study responds to the need to model complex plantations undergoing transformative management under pressure from an invasive species, *R. ponticum*. SORTIE-ND (Pacala et al., 1996, Kobe et al., 1997) is an appropriate model due to its spatially-explicit, individual-based framework and strong focus on modelling understorey light conditions. Fieldwork involved the resampling of three forest permanent sample plots, established in 2006 at Coed-y-Brenin, Wales, to complete a five year mensurational growth sequence of 787 trees. Ingrowth was recorded and measured (348 trees) and unique data collected on regeneration (1,939 seedlings), understorey allometrics and crown geometry. Geo-spatial data (total stations and digital GPS) was collected to geo-reference the plots and an ecological site classification carried out as per Forestry Commission guidelines (Chapter 3). The SORTIE-ND forest model was parameterised for Douglas fir (*Pseudotsuga menziesii* var. *menziesii*) with maximum likelihood techniques and simulated annealing to characterise the species allometric relationships and growth (Chapter 4). A regression model of invasive non-native rhododendron *(syn.* Pontian rhododendron, *Rhododendron ponticum* L.) seedling establishment probability was parameterised using habitat covariates reflecting soil attributes, forest structure and parent location (Chapter 5). SORTIE-ND was then parameterised for *R. ponticum* from literature sources to assess feasibility and highlight areas for further development for future inclusion in models of forest growth and dynamics (discussion in this Chapter).

The aim of this chapter is to bring together information from the previous research chapters to build a cohesive picture of the dynamic relationships between the dominant tree species and rhododendron, to critique the methodological approach and to provide recommendations for the next stage of this research. The overall thesis objectives and relevant chapters are listed in Table 7.1.

7.2 Summary of results

7.2.1 Fieldwork and data collection

Chapter 3 had three main aims: to describe the demographics of the tree species present within the permanent sample plots (PSPS), to quantify the vegetation structure of the vascular plant species and abiotic characteristics of the sites to gain insight into the status of rhododendron invasion and to carry out an ecological site classification. This field study provided a baseline assessment of the site conditions, data for the parameterisation of an individual-based forest-growth model (Chapter 4), a statistical model of rhododendron establishment (Chapter 5) and a for the combination of the parameterised model from Chapter 4 with data for *R. ponticum* individuals (Chapter 6).

The three PSPs ranged in size from 0.162-0.992 ha and were located in Douglas fir (DF) dominated stands planted 28 to 85 years ago, capturing the *stem exclusion* and *understorey reinitiation* stand development stages of Franklin et al. (2002). This ensured a range of variation in tree structure was incorporated into model parameterisation. Tree data were categorised into four species groups: Douglas fir (DF) focal species, Sitka and Norway spruce (SNS), hardwoods (HWD), and softwoods (SWD); and three size categories: survivor growth (SG) in 2006), ingrowth (IG) in 2011 and recruitment (R) in 2011.

CyB7, the youngest stand (26 years at plot initiation Table 3.1), was at the *stem exclusion* stage (Franklin et al., 2002). Stem density (2185.18 trees ha^{-1}) and mortality (209.88 trees ha^{-1}) was highest and recruitment the lowest (80.25 trees ha^{-1}) of the three plots. Aside from low recruitment there was very little understorey vegetation, apart from bryophytes within CyB7, in comparison to CyB4 and CyB5 (Haffenden pers. observation).

Whilst all of the ingrowth to CyB7 was HWD (6.17 trees ha^{-1}), DF made up 85% of the recruitment and HWD the remainder.

CyB4 and CyB5 had entered the *understorey reinitiation stage,* characterised as the point where vertical structure begins to diversify, typified by infilling of intermediate and co-dominant canopy positions by shade-tolerant trees, such as western hemlock (Franklin et al., 2002). Recruitment was abundant in CyB4 and CyB5 exhibiting a classic reverse J-shaped distribution. However both plots also exhibited a distinct two-story separation between the canopy and sub-canopy (Figure 3.7, Figure 4.4, Figure 4.5, Figure 4.6), suggesting that understorey reinitiation was not complete. A key feature of the reinitiation was a cohort of the SWD species group, which was dominated by invasive western hemlock (94% of stems) in the ingrowth of CyB4 and CyB5 (Table 3.2, Figure 3.7). In their natural range, old-growth Douglas fir and Western Hemlock coexist (DeBell & Franklin, 1987) as do hemlock-spruce forests (DeMars, 2000). Western hemlock, as the most shade tolerant of its seral group can regenerate without canopy gaps though it may require small openings to reach the overstorey (Spies & Franklin, 1989). A recent study (Schütz & Pommerening, 2013) at Artist's Wood, Gwydyr forest, North Wales (approximately 25 miles north of Coed-y-Brenin), found that Douglas fir and Sitka spruce had an equivalent shade tolerance of 87% compared to Norway spruce, which was used as a reference species. By contrast, western hemlock had 95% of the shade tolerance of Norway spruce (Schütz & Pommerening, 2013).

A systematic grid of 81 stations was established in CyB5 to survey vegetation and abiotic attributes. Vegetation abundance, substrate type and abundance, soil depth, soil moisture and soil organic content were recorded in two randomly selected 2x2 m quadrats at 41 of the stations (Figure 3.3). The O layer averaged 7.04 cm deep and tended to be wetter (65.8 vs. 43.9%) and have a higher organic content (51.7 vs. 22.0%) than the E layer; though moisture content is purely relative as it is heavily dependent on time since last rain. Hemispherical photographs obtained at a height of 1.3 m for 81 stations, yielded a post-processed canopy transmittance of 11.53% (Figure 3.4)

Rhododendron ponticum was present in 57% of 82 surveyed quadrats, with seedlings in 24 quadrats and adults in 33 (Figure 3.9). A Chi-square test of association between *R. ponticum* (seedlings combined with adults) and surveyed species found a negative association with broad buckler fern (*Dryopteris dilatata*) and wood sorrel (*Oxalis acetosella*). *Rhododendron ponticum* seedlings and adults were also negatively associated with each other. The most abundant species was Cowberry (*Vaccinium myrtillus*) present in 69 quadrats (Table 3.3) and did not have a significant association with *R. ponticum* because of this.

The negative association between *R. ponticum* seedlings and adults is to be expected, with dispersed seeds travelling away from the parent. Rhododendron's evergreen status and known capacity for over-shading competitors would ensure that any seeds landing close to an adult bush would be at a competitive disadvantage regarding the likelihood of sufficient light for germination and primary production. The negative association with wood sorrel and broad buckler fern may also be due to shading effects, though wood sorrel is described as requiring heavy watering in high light levels so there may be some competition for moisture (Packham & Willis, 1977) and broad buckler also required permanently moist soils (Rünk et al., 2012).

A positive association was found with Sitka spruce supporting earlier work by Edwards and Taylor (2008). This suggests that the ESC Sitka spruce model may be a useful analogue for *R. ponticum*, and could be used to predict sites susceptible to invasion and expansion. The ESC predicted the site to be *suitable* for Sitka spruce (Douglas fir and western hemlock were *very suitable*) and specified the limitation as the *soil moisture* *regime* which was *slightly dry*. This suggests that moisture may also be a limiting factor for *R. ponticum* at the site.

To meet the requirements of the ecological site classification ten stations that formed a systematic grid on the site were selected and then a single quadrat within each was chosen at random. The site overall was classified as *poor* in terms of the *Soil Nutrient Regime,* which is classified as having a pH of between 3 and 4 in the upper 25 cm with moderate to high phosphorus (P) availability and low nitrogen (N) availability. The *Soil Moisture Regime (SMR)* was classed as *Slightly Dry,* which is defined as 'soil profile not wet within 70 cm depth for more than 30 days in' at least 15 out 30 years (Pyatt et al., 2001, p. 10). The ecological site classification also provides an indication of climatic conditions in terms of accumulated temperature (1690°C), moisture deficit (142 mm), windiness (9) and continentality (7). Western hemlock, was predicted to have the highest potential yield (21 m^3 ha^{-1} yr^{-1}) for the site which may be an important indicator of suitability of conditions for the SWD species group. The common characteristics for suitable native woodlands were very acidic to strongly acidic soils, with pH rarely above 4 that are free draining or strongly leached (Hall et al., 2001).

7.2.2 SORTIE-ND parameterisation

The overall objective of Chapter 4 was to parameterise and validate the Douglas fir allometry, growth and light submodels for the SORTIE-ND individual-based spatially-explicit model of forest growth. The PSP tree and light field data (Chapter 3) were separated into species groups and the SORTIE life-history stages: seedling, sapling and adult based on height, diameter at 10cm and 1.35m height thresholds (Table 4.1) to parameterise the allometrics and submodels. The data was then further split into a parameterisation (Northern half) and validation (Southern half) dataset to ensure that the models were not tested on the data that they were parameterised on.

7.2.2.1 Allometrics

The parameterised allometric relationships were validated with the second dataset and then compared to two studies that utilised the same relationships: a study of the Interior Cedar Hemlock forests at Date Creek (ICH-DC) (Canham et al., 1999, Coates, K.D., 2012) and study at the Waitutu Forest, Southland, New Zealand (Coomes et al., 2005, Kunstler, 2011). SORTIE-NZ is a recent example of a study that was parameterised with the same allometric relationships and submodels. Though the species are not as directly comparable as the Date Creeks study they provide a good indication of parameter ranges.

The seedling height to diameter at 10cm height linear relationship had a good level of fit ($R^2 = 0.786$) (Table 4.3), though there was a tendency to underestimate seedling height at larger diameters (Table 4.3). The model was closer to the parameter values from SORTIE-NZ (Kunstler, 2011), with a steeper slope than the other seedling models, suggesting that Douglas fir seedlings gained more height at a smaller diameter.

The DBH to diameter at 10cm height model accounted for all but 16.1% of the variance in the data (Table 4.4) even with an increasing proportional underestimation of DBH. The model parameters were closest to those of hybrid spruce (which has been used as a proxy for seedling and sapling growth) from the ICH-DC study (Coates 2012). DF had the lowest DBH at a given $diam_{10}$ of all the species, suggesting that it is the slowest growing.

The combined sapling and adult height to DBH relationship had a very good level of fit, with only 2.9% of unaccounted variance from the statistical model (Table 4.5). The estimated maximum height (70.329 m) was greater than the comparison species, but not unfeasibly.

The DF crown depth relationship compares well to both the Date Creek and SORTIE-NZ study and had a good level of fit ($R^2 = 0.888$) to the parameterisation and validation ($R^2 = 0.870$) data. DF has the potential for deeper crowns for a given height than the comparison species. The SORTIE-NZ goodness-of-fits were considerably less convincing than this study. The goodness of fit for the Standard crown radius relationship was lower for the parameterisation dataset (0.785) than for the validation (0.846). The fitted values for DF were similar in shape and amplitude to *Dacrydium cupressinum,* a New Zealand endemic evergreen (Figure 4.12) (Coomes et al., 2005, Kunstler, 2011).

7.2.2.2 Basal area NCI Growth

Parameterised yearly maximum growth (1.213 cm yr^{-1}) compares favourably with the data from Date Creek (Coates, K.D., 2012), and from SORTIE-NZ (Coomes et al., 2005, Kunstler, 2011) and with published values for trees in western Oregon with yearly diameter increment of between 0.6 and 1.54 cm yr^{-1} (Poage & Tappeiner, 2002). The goodness of fit is low ($R^2 = 0.316$), potentially due to four outliers (1.64, 1.92, 2.14 and 2.18 cm DBH growth per year) that are all greater than the predicted maximum growth.

7.2.2.3 Light submodel

It has been commented that the process of crown delineation with the software used, Gap Light Analyzer (Frazer et al., 1999), is imprecisely and inconsistently described in the literature, with much left to interpretation (Boivin et al., 2011). Image thresholding is subjective and crown delineation methods are open to interpretation. In this respect the use of the Crown Delineator software developed by Boivin et al. (2011) provided a standard, quantifiable method and greatly reduced the uncertainties found in other methods described in the literature. It was found that delineating the crown with a bounding rectangle (CO_{rect}) provided the best fit to the data. This is potentially due to a combination of SORTIE-ND defining crowns as cylinders and the long limb extension on the over-mature Douglas fir trees used for parameterisation.

7.2.2.4 Initial model runs

Initial model runs to investigate the results of parameterisation over a five year growth period yielded mixed results: CyB4 and CyB7, both strikingly different in terms of structure and age, returned results that demonstrated that the model outputs were not statistically different to the actual demographics for all 30 runs (Table 4.10; Figure 4.10). For CyB5, although the physical DBH distribution appeared convincing (Figure 4.10,b) there were statistical differences for the DF and SWD species groups due to slower growth rates at low DBH.

7.2.3 Bayesian model of *Rhododendron ponticum* establishment probabilities

The aim of Chapter 5 was to identify and construct a Bayesian statistical model of rhododendron establishment capable of inclusion within a spatially-explicit individual-based model (e.g. SORTIE-ND). Candidate data was selected from the field study of the Coed-y-Brenin permanent sample plots and the LiDAR airborne survey (Chapter 3). The two hypotheses were that light would be an important factor driving rhododendron seedling establishment and that rhododendron was not limited by the occurrence of *safe sites* (Cross, 1975, Cross, 1981, Mejias et al., 2002, Erfmeier & Bruelheide, 2004) within CyB5.

A positive model relationship with the presence of an adult rhododendron was found, which may be related to proximity to seed source or alternately an indicator of site suitability. The model analysis and result from the Chi-square test in Chapter 3 appear to contradict each other however the analyses were both carried out at different scales: the Chi-squared test used all 81 of the 2x2 m quadrats and the model parameterisation used the

41 4x4 m quadrats. The implication being that exclusion would have occurred between adult and seedling at the smaller scale (negative relationship) and seed dispersal would have meant a positive relationship with neighbouring quadrats. Inclusion of substrate within the model had no effect on establishment probabilities. Investigations of deadwood, litter moss, and the presence of a buttress alone or in combination had no effect on prediction, however the depth of the soil O layer was positively associated with the presence of rhododendron seedling. Whilst the O layer depth may not be important in terms of nutrients it is potentially a proxy for soil moisture with a deeper O layer being more efficient at moisture retention.

The negative influence of summed neighbourhood tree height indicates the influence of forest structure on seedling establishment. Rhododendron seeds are primarily wind dispersed and fall close (with 10 m) of the parent tree (Harris et al., 2011). The negative impact of forest structure may indicate why adult presence is important at this location. Ease of seed movement was adjusted by habitat type in landscape scale models of rhododendron seed movement to 5 m in woodlands and 10 m in young plantations (Edwards & Taylor, 2008). The overmaturity of CyB5 and its increased understory diversity is more like a woodland than an understory free plantation.

Although cited as a key factor affecting the likelihood of rhododendron germination by many studies (Cross, 1981, Stephenson et al., 2006, Ninaber, D., 2009), light was not an influential factor in the prediction of establishment sites within CyB5. The probable reason for this was that there was insufficient variation between the locations surveyed. Total light transmittance within the site was homogeneous, with relatively little difference between the stations with and without rhododendron (12.41% vs. 10.81%, respectively, Figure 3.11).

Along with other soil parameters recorded from samples taken from the site the O layer moisture (percentage) was also tested as a possible covariate and not found to be important. Soil samples were taken over one day and moisture levels would provide a better indication of relative moisture at each station rather than seasonal moisture levels.

The cross-validated model predicted 81.3% of presences correctly and 75.0% of absences (77.5%, 31 of 40 correct overall).

7.2.4 SORTIE-ND parameterisation for *Rhododendron ponticum*

The SORTIE-ND model was parameterised using data and relationships adapted from published studies. Allometrics relationships were adapted from Nadezhdina et al. (2004), the growth and crown radius relationships from Erfmeier and Bruelheide (2004), dispersal from Stephenson et al. (Stephenson et al., 2007) and establishment from Ninaber (2009).

With maximum height set at 6 m and reproduction commencement at 12 years, individuals were classified as seedlings between 0.10 and 2.35 cm in diameter and saplings up to 7.32 cm diameter (Table 6.). Maximum bush heights were 1.35 m for seedlings, 3.98 m for saplings and 6 m for adults. Due to SORTIE's representation of crown shape as a cylinder the leaf area function from Erfmeier and Bruelheide (2004) was adapted to represent a flat disk (a cylinder with zero depth) at the respective height. Though not ideal, for an initial test run of model functioning, this was seen as the best compromise between a multitude of possible crown height and depth relationships. Maximum crown radius was 0.82 m for seedlings and 1.56 m for saplings.

The expectation that ≈ 99% of dispersed seeds would fall within 5 m of the parent bush was well reproduced however dispersal was minimal at larger distances and consequently spread throughout the test plot was slow, even with zero mortality after establishment.

The light dependent and proportional seed establishment behaviours resulted in an unexpected oscillation of seed establishment potentially explained by a high density of individuals limiting light for reproduction. It is possible that individuals at the edges of the invasion front were too juvenile to reproduce seeds and the interior too dark for them to establish, however numbers were low for a period of approximately 20 years.

7.3 Study limitations

7.3.1 Permanent sample plots

The data from the permanent sample plots (PSPs) underpins the entire thesis and as such it is limited by the spatial and temporal extent of the three plots. CyB4 and CyB5 are relatively similar in their development, location and altitude (46-84 m), and although CyB7 is 68-117m higher in elevation, climate effects would not be expected to differ significantly. Only three PSPs were surveyed, with a total area of 1.557 ha, and data for part of the study was restricted to CyB5 (i.e. ecological site classification, rhododendron, light and soil measurements), which at 0.992 ha was the largest plot surveyed. The PSPs are located in plantations that were planted in the 1920s and 1980s, for which very limited historical information is known. A consequence of this is that the data set is limited to two stages of stand development (stem exclusion and understorey reinitiation), and there is a distinct gap in the data between tree heights of 25-40 m (Figure 4.4), reflecting a vertical zone between the understory and overstorey components of the stands, which will reduce the models applicability to this range as the stand progresses.

Essentially the data is from three stands that are in extreme situations for plantations: CyB7 is densely populated and a pre-commercial thinning was not carried out hence the stand is overstocked and density-driven competition between trees is very high; CyB4 and CyB5 are overmature by approximately 20 years (Malcolm et al., 2001) and therefore would normally have been harvested by now. It would have been useful to know stocking densities at the time of establishment and the timing of any interventions to reverse engineer the plot as part of the testing methodology. Unfortunately the loss of management information for CyB4 and CyB5 removes any information other than year of establishment, and the current 5-year measurement period only provides a static snapshot over which to determine much longer-term stand dynamic processes and mortality levels. Also, a DBH threshold of 5 cm DBH for trees to be inventoried at plot establishment in 2006, means the level of regeneration that established over the subsequent 5-year period has to be estimated. Clearly a longer dataset is necessary to truly understand the stand dynamics.

With only 1,095 total trees ≥5 cm DBH inventoried in 2006, of which Douglas fir constituted approximately 60% (663 trees), splitting the data into parameterisation and validation datasets reduced the data quality. The lumping of sub-component species into mixed species groups was an attempt to make up for the lack of data, but even then parameterisation was not convincing. This also resulted in species with different ecological requirements (e.g. shade-tolerant and intolerant hardwoods) placed together in a single group, further confounding meaningful results. Unfortunately these species groups, HWD and SWD in particular, were the main understorey components suffering mortality in the initial model runs.

Future consideration is necessary to reduce the impact of edge effects into model runs. The delineation of sample plot boundaries contains stems, but generally includes the crowns of surrounding trees whose stems are not captured. These crowns then are not accounted for in plot maps and result as white space (Figure 7.1). This is equally the case where plots are bounded by man-made features (e.g. paths, roads) as is the case with CyB5. SORTIE-ND attempts to counter edge effects by constructing a torus shaped plot. However when using tree-maps of existing plots similar to CyB5 (Figure 7.1) the result is the mirrored amplification of gaps created by missing crowns (Figure 7.1, shaded area). To circumvent this issue a boundary equivalent to the maximum predicted crown radius (6m) should be implemented.

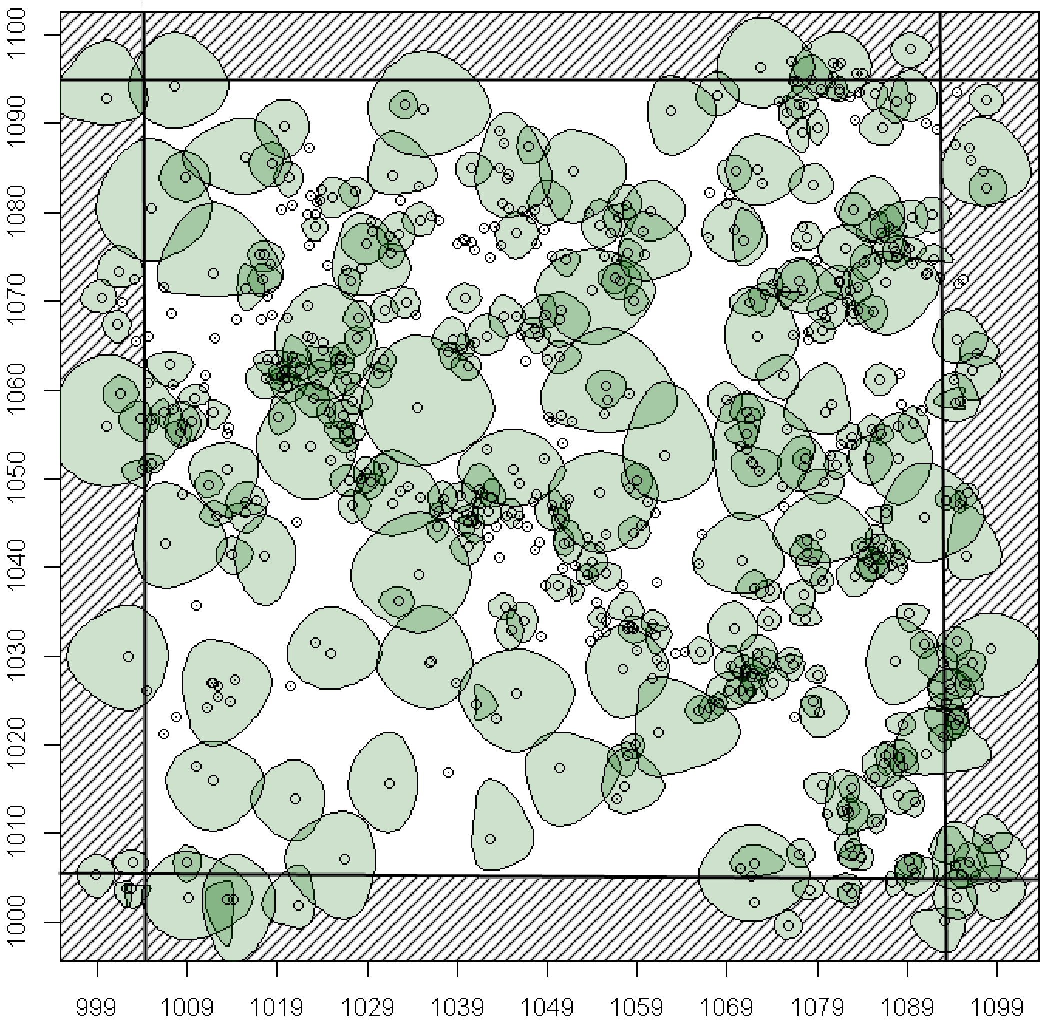

Figure 7.1. PSP CyB5 showing edge effects and (shaded) area of overlapping crowns and 6 metre exclusion zone.

7.3.2 Rhododendron invasion dynamics

The relationship between forest structure and adult rhododendron presence in the predictive model highlights an important assumption of this study, that rhododendron seed is abundant across the entire site (i.e., saturated levels) and an important limitation. The heavy presence of rhododendron throughout the plot and surrounding locality is apparent

(Haffenden pers. obs.), but not quantified here. However, within the model the distinction between seedling and adult is made from field observations (i.e. size, stem width and number, leaf morphology) rather than an ecological basis. Equally in terms of adults there is no distinction of reproductive capacity. A logical progression of this project would be the development of a spatial model of rhododendron establishment incorporating distance to adult and also differentiating sexually mature adults.

7.4 Future work

7.4.1 Legacy of permanent sample plots

The three PSPs that form the basis of this study represent an amazing resource that needs to be preserved and maintained. The plots form a larger network of plots established in 2006 as part of a continuous cover study (Schütz & Pommerening, 2013), including two plots at Artists wood 25 miles north of the Coed-y-Brenin plots. The Artists wood plots were not utilised in this study as they fell outside the area surveyed in 2010 by the NERC Airborne Research Survey Facility. However, a useful continuation of this study would be to parameterise the SORTIE-ND models with the full CyB dataset and validate it against Artists wood. Stand dynamics require the collation of long-term datasets, therefore the future of these plots needs to be ensured, and a regime of 5-year inventories established so that better estimates of growth and mortality can be gauged. Measurements should follow the original protocol of Pommerening et al. (2002) to ensure consistency, with the addition of ingrowth as per this study, and regeneration survey extended to all plots using the gridding system adopted for CyB5. Since historical management information is not available, the extraction of increment cores from trees outside the plot would permit the creation of a master dendrological chronology to confirm the age of the plantation and identify any pre-commercial thinning events that may have taken place, which would be discernible as post-entry rapid growth events (Druckenbrod, 2005).

Dendrochronologies have been utilised in many studies to capture past histories, including the impact of insect outbreaks (Taylor & MacLean, 2007), mode of action of pollutants (Fairchild et al., 2009) and prehistoric bog fires (Chambers et al., 1997). In order to account for edge effects, a 5m buffer could be added to the perimeter of plots to capture stems falling outside the plot whose crowns fall within the plot area. Since the mean crown radius is 2.67 m and the predicted maximum crown radii was 6m (Figure 4.6) this would minimise edge effects, and enable the impact of neighbouring boundary trees on target trees within the plot to be accounted for.

7.4.2 Remote sensing as a means of capturing invasive species extent

Since the rhododendron model included the presence of adult rhododendron, a rapid means of gaining this data is required. Repeated field-based studies are a time-consuming and expensive means of detecting, monitoring and documenting the spatial distribution of invasive plants, even for a region as small as a county (He et al., 2011). Hyperspectral images that acquire images with narrow spectral bands in the visible, near-infrared (IR) and mid-IR regions of the electromagnetic spectrum are currently the most heavily used imaging source for studies of non-native plants (He et al., 2011, Huang, 2009, Wang & Cumming, 2009). Taylor et al. (2011) developed a logistic regression model of absolute reflectance at five key wavelengths (490, 550, 610, 1040 and 1490 nm) based on *ex situ* dark room measurements of destructively sampled leaves to determine the success of discriminating rhododendron from three other shrubby species likely to be encountered in woodlands during the winter. The logistic regression model was highly significant ($p < 0.001$), with 93.5% of 246 leaf sets correctly identified as rhododendron or non-rhododendron (i.e. cherry laurel (*Prunus laurocerasus*), holly (*Ilex aquifolium*), and beech (*Fagus sylvatica*)) (Taylor et al., 2011). Hyperspectral data was collected as part of the 2010 NERC Airborne Remote Sensing Facility surveys across the Coed y Brenin study site. This study only utilised the LiDAR component to capture information on vegetation biometrics (e.g., top height) and surface intensities. Hence there is the potential to investigate the potential of the hyperspectral data to predict adult rhododendron distribution using the rhododendron status at 81 stations in CyB5 as a means of validation.

7.4.3 *Rhododendron ponticum* field data collection for SORTIE-ND parameterisation

The *R. ponticum* model requires parameterisation and validation with field data. There are five key areas where development is needed: growth and mortality, dispersal, establishment and allometry, which will be addressed in turn.

7.4.3.1 Growth and mortality

As discussed in Chapter 6 the current model implementation does not utilise any mortality, and growth functions are linear. The use of the *non-limited absolute growth radial increment* sub-model (equation 4.12) and the *BC mortality* sub-model (equation 4.18) for seedlings and saplings would allow incorporation of growth as a function of GLI alongside growth and mortality modification for periods of suppression and release. Both sub-models can be parameterised from field data as detailed by Kobe and Coates (1997) for mortality and Wright et al. (1998, 2000) for growth.

For the mortality parameterisation, Kobe and Coates (1997) selected sites where they expected a wide variety of response in the predictor variable (recent individual growth) to occur: locations with discontinuous overstorey; young self-thinning stands without mature canopy and self-thinning stands in canopy gaps. They then collected three sets of field data from randomly stratified samples within the heterogeneous light environment at each site: number of dead and live individuals (using quadrats to sub-sample) and random samples of live and dead individuals, harvested at 10 cm above the root collar, to provide growth measurements from a digital ring analyser.

Mortality is parameterised as a likelihood function that considers the probability that dead saplings are encountered within the total population, the probability density function of growth rate prior to death and the density function for growth of live individuals (Kobe et al., 1995, Kobe & Coates, 1997).

Growth data can be collected concurrently, though requiring extra samples, by sampling total height, DBH and past 6 years leader length. Wright et al. (2000) suggest selecting the best growing sample at a given light level to represent optimum growth. Trees are harvested at 10 cm above the ground and growth analysed with a digital ring analyser (Wright et al., 1998, Wright et al., 2000). Hemisperical photos would also need to be taken above each cut stump at a height of 1 to 2 metres as detailed in Chapter 3.

The adult growth functions within SORTIE-ND are designed for canopy trees or trees that will assume canopy status. In this respect they may not be suitable for use with *R. ponticum.* A possible solution is to collect data for mortality and growth similar to seedlings and saplings and parameterise the same functions. This would provide a growth function linked to environmental conditions rather than a purely deterministic, linear representation.

Growth models may also need to take account of vegetative clonal spreading (layering) of collapsed lateral branches from parent plants, which can enable bushes to persist for 200-400 years in Turkey (Colak et al., 1998). Layering was typical in native Georgian populations, but not native Spanish or invasive Irish populations (Erfmeier & Bruelheide, 2004). However, Mejías et al. (2002) noted that excavation of the soil frequently revealed a layering origin for bigger plants. Similarly, Pornon et al. (2000) detected high levels of layering on mature alpenrose (*Rhododendron ferrugineum*), whereas at best it was only weakly developed in younger populations. Excavation of the soil surface was used to distinguish seedlings from layered plants in this study, but no attempt was made to gauge annual expansion of bushes by layering from parent bushes, despite it being a major driver of colonisation in sites unfavourable for invasion by seedlings (Edwards 2006). In their model of rhododendron invasion in Argyll and Bute, Edwards and Taylor (2008) permitted expansion rates of 2m y^{-1} for rhododendrons growing in broadleaf woodland in Argyll and Bute, and assumed layering was zero in all other habitats including conifer plantations. This assumption needs to be verified with real field data.

7.4.3.2 Dispersal

Stephenson et al. (2007) compared two mechanistic models of *R. ponticum* seed dispersal. Whilst the more complex WALD model tended to slightly overestimate the tail of the dispersal distances, they suggest that it provides a precautionary implementation suited to invasive species. The adaptation of an existing SORTIE dispersal submodel for the WALD dispersal model would greatly increase the relative application of this methodology.

Work by Travis et al. (2011) and Harris et al. (2009) experimented with simulated seed movement using a spatially-explicit individual-based model incorporating varying seed numbers and release heights from a distribution related to age. With this implementation the dispersal kernel varied according to bush height and number of seeds released with increasing age. Implementation of this approach could be incorporated within SORTIE-ND along with the WALD dispersal model discussed previously. The current implementation provides for a fixed amount of dispersed seeds which lacks ecological realism. Clearly it should be expected that flower numbers, and therefore seed numbers, would increase with age and size of a mature individual. Adjustment for individual height and the effect on the dispersal kernel would implement the expectation that seeds released from a greater height would travel a greater distance.

7.4.3.3 Germination and Establishment

Stephenson et al. (2006) and this study (Chapter 5) identified key co-variates in the establishment of *R. ponticum.* An important part of any future parameterisation of SORTIE-ND for *R. ponticum* would be the incorporation of these key co-variates such as substrate type and depth (Stephenson et al., 2006). Further investigation is required to determine the influence of tree structure on establishment probabilities as highlighted in Chapter 5.

SORTIE-ND provides a substrate based establishment behaviour based on a favourability index for substrate mixtures and it would be possible to follow the protocol of LePage et al. (2000) to parameterise this aspect for *R. ponticum*. In their study field data was collected in 1 m quadrats along line transects over four site types: full canopy, partial canopy (no distinct gaps), large logging gaps and clearcut (LePage et al., 2000). All distributed through old-growth and mature forests. In each quadrat area an estimate of abundance for each substrate type, to the nearest 5%, was recorded, each summing to 100% and including ten different substrate types ranging from mineral soil to rock were included (LePage et al., 2000). This sampling was combined with a survey of seedlings that had survived 1 to 3 years since germination. The number of recruits by substrate type were then recorded for each quadrat.

7.4.3.4 Allometry

In order to parameterise more generalised allometric relationships it would be necessary to collect a range of field data from a variety of habitats and life-history stages. Analysis would then be required to define potential alternatives to the DBH-based functions defined within SORTIE. Height and canopy size are easier to access in dense areas of *R. ponticum* however given the high plasticity it may be difficult to define generalised functions.

7.5 Conclusions

This study is the first to produce a UK model of SORTIE-ND parameterised for Douglas fir dominated stands with a subcomponent of Sitka spruce. Such stands are the focus of a UK wide government policy to convert softwood plantations from a single entry clear cut regime to a multiple entry harvesting regime and achieve ‘continuous cover’.

The final modelling chapter is the first work in this field to integrate an individual-based spatially-explicit model of forest and invasive species growth, and neighbourhood dynamics. Incorporation of the full species lifecycle highlights the knowledge gaps necessary to understand how this species invades and interacts with its adopted environment; as the earliest yield-tables highlighted the gaps in foresters scientific knowledge and led to the development of further experimental work (Chapter 2, Pretzsch, 2000).

SORTIE-ND is capable of implementing complex silvicultural treatments and the inclusion of *R. ponticum* provides a mechanism to investigate the impact of different management activities on its likely establishment and growth. Spatially explicit models such as the model developed for this study, provide a means of forecasting spatiotemporal stand structure changes resulting from multiple harvest entries. Multiple harvesting systems may result in stands that are more vulnerable to *R. ponticum.* An understanding of the factors affecting its lifecycle within a forest ecosystem can inform decisions regarding cutting intensity and spatial configuration of plots. Incorporation into individual-based models of forest dynamics will lead to deeper understanding of the processes hidden by investigation in isolation, and is key to formulating management plans that minimise risk and ensure resilience of forests to change.

Table 7.1. Thesis objective and relevant study results by chapter

Thesis objectives	Study results - key points from each chapter
Chapter 2: The dual evolution of forestry practices and forest modelling: children of necessity	
To carry out a literature review highlighting the interrelationship between advances in silvicultural theory and practice, and forest modelling practices and theory	The 18th Century advent of the *Normal forest* concept and the introduction of yield tables. Two practices which shaped forest management and are still in use today. Incorporation of ecological thinking into Silviculture; increases in computing power; creation of the first single tree growth and yield models in the 20th Century Changing societal perceptions; ecosystem management and low-impact silviculture; hybrid models
Chapter 3: Coed-y-Brenin permanent sample plot forest mensuration and ecological site classification	
To investigate demographic dynamics at three permanent sample plots within Coed-y-Brenin forest park by completion of a five-year growth survey	CyB4 and CyB5 in understorey reinitiation stage; CyB7 in stem exclusion stage DF dominant species in all stands; SWD (western hemlock) an invasive cohort in CyB4 and CyB5 ESC found the site *very suitable* for Douglas fir and western hemlock, and *suitable* for Sitka spruce
To systematically survey the ground flora, a range of abiotic factors (e.g. soils, climate and light) and non-native *R. ponticum* present within the largest permanent sample plot (CyB5)	Rhododendron was present in 47 of the 81 quadrats. Only 10 quadrats contained seedlings and adults Negative association between rhododendron seedlings and adults; wood sorrel and broad buckler fern were negatively, Sitka spruce positively, associated with the presence of rhododendron.
To determine the ESC of CyB5 to gain insight into the relationship between site conditions and *R. ponticum* invasion	Soil Moisture Regime designated as Slightly Dry, *Soil Nutrient Regime* (SNR) designated as Poor.
Chapter 4: Parameterisation of SORTIE-ND forest model for three Douglas fir dominated stands	
To parameterise the model allometric relationships	Allometric relationships were parameterised with R^2 (goodness of fit) between 0.79 and 0.97.
To parameterise the adult growth submodel	Adult growth submodel was parameterised with a goodness of fit of 0.32.
To parameterise the light submodel	Fit with light model is poor and further work is required to calibrate the model – outlined in discussion
Chapter 5: Rhododendron ponticum establishment model	
Construction of statistical model of *Rhododendron ponticum* establishment	Full model correctly predicted 87.5% of presences absences; Cross-validation correctly predicted 77.5% of presences and absences
Identification of covariates compatible with inclusion in a spatially-explicit individual-based model (e.g. SORTIE-ND)	Model parameterised with presence/absence of an adult rhododendron, summed neighbourhood tree height and depth of soil O layer
Chapter 6: Parameterisation of SORTIE-CyB for Rhododenderon pontcum	
To parameterise SORTIE-ND for R. ponticum using available published data on its allometry, growth and dispersal	Model parameterised for seedling, sapling and adult lifestages with data adapted from publications
To carry out initial runs for *R. ponticum* using tree densities from CyB5	Initial runs demonstrated establishment, growth and spread of *R. ponticum* through a simulated Douglas fir dominated plantation.
To discuss the limitations of the available data	No clear definition of allometric relationships and progression through life-history stages. Work needed on response to suppression and quantification of mortality processes.

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Appendices

Appendix 1 – Chi square tables for rhododendron and associated species

Table for:	RP seedlings and adults									
	RP adults +			RP adults -		Row tot			Chi sq	9.80
RP seed +	O	10.00		O	14	O	24			
	E	13.76		E	10.24	E	24			
	(O-E)^2	14.11		(O-E)^2	14.11					
	X^2	1.03		X^2	1.38					
RP seed -	O	23.00		O	35	O	58			
	E	33.24		E	24.7561	E	58			
	(O-E)^2	104.94		(O-E)^2	104.94					
	X^2	3.16		X^2	4.24					
Col tot	O	33		O	49			O	82	
	E	47		E	35			E	82	
						O	82			
						E	82			

Table for:	Wood sorrel									
	RP +			RP -		Row tot			Chi sq	18.80
sp +	O	21.00		O	27	O	48			
	E	27.51		E	20.49	E	48			
	(O-E)^2	42.41		(O-E)^2	42.41					
	X^2	1.54		X^2	2.07					
sp -	O	26.00		O	8	O	34			
	E	19.49		E	14.51	E	34			
	(O-E)^2	42.41		(O-E)^2	42.41					
	X^2	2.18		X^2	2.92					
Col tot	O	47		O	35			O	82	
	E	47		E	35			E	82	
						O	82			
						E	82			

Table for:	BB fern								
	RP +			RP -		Row tot		Chi sq	7.85
sp +	O	25.00		O	29.00	O	54		
	E	30.95		E	23.05	E	54		
	(O-E)^2	35.42		(O-E)^2	35.41				
	X^2	1.14		X^2	1.54				
sp -	O	22.00		O	6	O	28		
	E	16.05		E	11.95	E	28		
	(O-E)^2	35.42		(O-E)^2	35.42				
	X^2	2.21		X^2	2.96				
Col tot	O	47		O	35			O	82
	E	47		E	35			E	82
						O	82		
						E	82		

Table for:	Spruce								
	RP +			RP -		Row tot		Chi sq	4.73
sp +	O	15.00		O	4.00	O	19		
	E	10.89		E	8.11	E	19		
	(O-E)^2	16.89		(O-E)^2	16.89				
	X^2	1.55		X^2	2.08				
sp -	O	32.00		O	31.00	O	63		
	E	36.11		E	26.89	E	63		
	(O-E)^2	16.89		(O-E)^2	16.89				
	X^2	0.47		X^2	0.63				
Col tot	O	47		O	35			O	82
	E	47		E	35			E	82
						O	82		
						E	82		

Appendix 2 - Field layer ESC indicator plant species results

Plant name	NIV Wilson	NIV Hill	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8	Q9	Q10
Vaccinium myrtillus	2.7	4	35	1	10	0	30	0	25	2	25	0
Dryopteris dilatata	3.94	9	4	2	2	5	0	5	2	2	0	30
Blechnum spicant	3.48	6	10	0	0	45	0	20	10	5	2	25
Oxalis acetosella	3.74	8	0	0	0	5	15	15	15	5	0	5
Rubus fruticosus	4.6	12	1	0	0	5	0	5	0	5	0	1
Dryopteris affinis	3.74	10	0	0	0	0	15	0	0	5	0	0
Pteridium aquiline	3.69	6	0	0	0	0	0	25	0	15	0	0
Athyrium felix-femina	4.67	11	0	0	0	0	0	10	0	0	0	1
Potentilla erecta	2.58	5	2	0	0	0	0	10	0	0	0	0
Ilex aquifolium	4.33	10	0	0	1	0	0	0	0	0	0	0
Empetrum nigrum	0	3	2	0	0	0	0	0	0	0	0	0
Chamerion angustifolium	5.09	11	0	0	0	0	0	2	0	0	0	0
Geum rivale	0	10	0	1	0	0	0	0	0	0	0	0
Viola riviniana	3.74	9	0	0	0	0	0	1	0	0	0	0
Abundance weighted mean NIV	3.36	6.42										

Appendix 3.1 – Simulated annealing R script for seedling height to diameter relationship

```
#=================================================================
# Simulated annealing to find maximum likelihood estimates of model parameters
# for SORTIE-ND standard diameter to height relationship for seedlings
#Modified from annealing1 and annealing2 with Canham/Murphy likelihood package
#by Austin Haffenden 14Dec11
#23Mar12: Modified to include revised data split (North/South)
#               Modified to save a copy of the output file and the workspace to new file
#               structure.
#               Modified to include Hessian Matrix in the annealing/likelihood estimation
#               for use in calculation of confidence intervals.
#               Modified to save result as matrix of lists
#=================================================================
rm(list=ls())
#Required librarys
library(likelihood)
#===================================================================
# Set working directory
# Seedlings:
#PC
setwd("E:/Documents/Projects/SORTIE_ND/parameterisation/data/Juvenile")
#===================================================================
#Read in Juvenile data file
juv_data <- read.csv("juvenile_data_complete.csv", sep = "\t", header=TRUE)
#Subset to working data and to seedlings and then merge
#Subset to DatasetA
cyb4_n <- subset(juv_data, plot=="CyB4"&North_South=="North"&height_m<=1.35 )
cyb5_n <- subset(juv_data, plot=="CyB5"&North_South=="North"&height_m<=1.35 )
cyb7_n <- subset(juv_data, plot=="CyB7"&North_South=="North"&height_m<=1.35 )
#part merge then full
part_dataA <- merge(cyb4_n, cyb5_n, all=TRUE)
in_dataA <- merge(part_dataA, cyb7_n, all=TRUE)

#Data transformations
dataA <- data.frame(plot = as.vector(in_dataA$plot),
                                     sp_gp = as.vector(in_dataA$sp_gp),
                                     assm = as.vector(in_dataA$assm),
                                     Diam10 = as.vector(in_dataA$diam10_cm),
                                     #DBH = as.vector(in_dataA$dbh_cm),
                                     Height = as.vector(in_dataA$height_m),
                                     WE = as.vector(in_dataA$West_East),
                                     NS = as.vector(in_dataA$North_South)        )
#=================================================================
#Subset to DatasetB
#cyb4_s <- subset(juv_data, plot=="CyB4"&North_South=="South"&height_m<=1.35 )
#cyb5_s <- subset(juv_data, plot=="CyB5"&North_South=="South"&height_m<=1.35 )
#cyb7_s <- subset(juv_data, plot=="CyB7"&North_South=="South"&height_m<=1.35 )
##part merge then full
#part_dataB <- merge(cyb4_s, cyb5_s, all=TRUE)
#in_dataB <- merge(part_dataB, cyb7_e, all=TRUE)

#Data transformations
#dataB <- data.frame(plot = as.vector(in_dataB$plot),
#              spe = as.vector(in_dataB$sp),
#              assm = as.vector(in_dataB$assm),
#              Diam10 = as.vector(in_dataB$diam10_cm),
#              DBH = as.vector(in_dataB$dbh_cm),
#              Height = as.vector(in_dataB$height_m),
```

```
#                    WE = as.vector(in_dataB$West_East),
#                    NS = as.vector(in_dataB$North_South)       )
#=========================================================================
# Species groups
#DF
#species_group <- "DF"
df_dataA <- subset(dataA, sp_gp=="1")
#SS_NS
#species_group <- "SSNS"
sns_dataA <- subset(dataA, sp_gp=="2")
#Hardwoods
#species_group <- "Hwood"
hwd_dataA <- subset(dataA, sp_gp=="3")
#Softwoods
#species_group <- "Swood"
swd_dataA <- subset(dataA, sp_gp=="4")
#
#modify this line to choose the dataset list
# data_in <- list(df_dataA, sns_dataA, hwd_dataA, swd_dataA)
# #data_in <- list(df_dataB, ssns_dataB, Hwood_dataB, Swood_dataB)
# species_groups <- c("DF", "SNS", "HWD", "SWD")
#=====================================================================
#for loop data structures
data_in <- list(     df_dataA,
                      sns_dataA,
                     hwd_dataA,
                     swd_dataA )

species_groups <- c(  "DF",
                        "SNS",
                        "HWD",
                        "SWD")
#===================================================================
# Create model functions where height is the dependent variable
stan_fun <- function (beta, Diam10) {
  0.1 + 30*( 1 - exp((-beta/1000) * Diam10 ) )
}
#=========================================================================
#Create new dnorm for variance function
new_dnorm <- function(x,mean,c,Diam10,log)
{ sd <- sqrt(c*Diam10)
  dnorm(x,mean,sd,log)
}
#==========================================================================
# Create parameter list and
# set initial values for a and c and indicate
# that Diam10 comes from the column marked "Diam10"
# in the dataset
par <- list(beta = 400, c=0.05)
# Create a place to put all the other values
var <- list(Diam10 = "Diam10")

#Set bounds
par_lo<-list(beta = 0, c = 0)
par_hi<-list(beta = 1000, c = 100)

# Using the normal probability distribution function -
# add the options for it to our parameter list
# "x" value in PDF is observed value
var$x<-"Height"
```

```
# Mean in normal PDF
var$mean<-"predicted"
#var$sd<- varfun

# Have it calculate log likelihood
var$log<-TRUE
#============================================================================
#Create dataframe to store the summary output to later save as .csv
#
# #names of parameters to be returned and used as column headers
# summary_param_names <- c(    "MLE",
#                            "beta",
#                            "c",
#                            "aic",
#                            "aic_corr",
#                            "R2",
#                            "iterations" )
#
repetitions <- 1 # 1st dimension
#=====================================================================================
# Set output directory
setwd("C:/DocumentsandSettings/red74/MyDocuments/Projects/SORTIE_ND/parameterisation/allometrics/
Simulated_annealing/Diameter Height Relationships/Standard/outputs/seedling")
# Open graphics window
x11()

#for (i in 1:length(data_in) ) {
i <- 1
    #Remove NAs from datafile
    dataset <- subset(data_in[[i]], Diam10!="NA"&Height!="NA")

#====================================================================================
#Call the linear model and store the results
        for (j in 1:repetitions) {
            result  <- anneal(  model = stan_fun,
                        par = par,
                        source_data = dataset,
                        pdf = new_dnorm,
                        dep_var = "Height",
                        max_iter = 100000,
                        min_change = 0.001,
                        min_drops = 600,
                        hessian = TRUE )
                cat("iteration: ",i,":",j, "\n")


        current_time <- format(Sys.time(), "%d_%m_%Y__%H_%M_%S")
        model_n_life_stage <- paste("rescale_stan_height_dbh", "seedling", sep="_")
        #set filename
        output_file <- paste(species_groups[i],current_time, model_n_life_stage, "csv", sep=".")
        write_results(result, output_file)


    }#==========================================================================
}
```

Appendix 3.2 – Simulated annealing R script for sapling and adult height to diameter relationship

```
## Simulated annealing to find maximum likelihood estimates of model parameters
## for SORTIE-ND standard diameter to height relationship for saplings
##Modified from annealing1 and annealing2 with Canham/Murphy likelihood package
#by Austin Haffenden 14Dec11
#Modified 23Mar12: To include sapling and adult data
# to include: revised data split (North/South)
#                   Modified to save a copy of the output file and the workspace to new file
#                   structure.
#                   Modified to include Hessian Matrix in the annealing/likelihood estimation
#                   for use in calculation of confidence intervals.
#Modified 24Mar12: to include max iteration, 0.001 min change, 600 max drop
#=======================================================================
#Need to:
rm(list=ls())
#Required librarys
library(likelihood)
#=====================================================================
# Set working directory
# Saplings:
#PC
setwd("E:/Documents/Projects/SORTIE_ND/parameterisation/data")
#Read in Juvenile data file
juv_data <- read.csv("Juvenile/juvenile_data_complete.csv", sep = ",", header=TRUE)
adult_data<- read.csv("Adult/CyB_all_adult_combined_complete.csv", sep = ",", header=TRUE)
#======================================================================
#Subset to working data and to saplings and then merge
#Dataset A
sub_juv_A <- subset(        juv_data,
                            height_m > 1.35 &
                            (plot=="CyB4"&North_South=="North"|
                    plot=="CyB5"&North_South=="North"|
                    plot=="CyB7"&North_South=="North" ) &
                            assm==2011)

dataA_juv <- data.frame(    plot = as.vector(sub_juv_A$plot),
                            spe = as.vector(sub_juv_A$sp),
                            assm = as.vector(sub_juv_A$assm),
                            Diam10 = as.vector(sub_juv_A$diam10_cm),
                            DBH = as.vector(sub_juv_A$dbh_cm),
                            Height = as.vector(sub_juv_A$height_m) )

sub_adult_A <- subset(      adult_data,         (plot=="CyB4"&North_South=="North"|
                    plot=="CyB5"&North_South=="North"|
                    plot=="CyB7"&North_South=="North" ) &
                            assm==2011 )

dataA_adult <- data.frame( plot = as.vector(sub_adult_A$plot),
                            spe = as.vector(sub_adult_A$species),
                            assm = as.vector(sub_adult_A$assm),
                            DBH = as.vector(sub_adult_A$dbh),
                            Height = as.vector(sub_adult_A$h_mean) )

dataA <- merge(dataA_juv, dataA_adult, all=TRUE)

#============================================================================
##Dataset B
#sub_juv_B <- subset(juv_data,      height_m > 1.35 &
```

```
#                              (plot=="CyB4"&North_South=="North"|
#                              plot=="CyB5"&North_South=="North"|
#                              plot=="CyB7"&North_South=="North" ) )
#
#dataB_juv <- data.frame( plot = as.vector(sub_juv_B$plot),
#                       spe = as.vector(sub_juv_B$sp),
#                       assm = as.vector(sub_juv_B$assm),
#                       Diam10 = as.vector(sub_juv_B$diam10_cm),
#                       DBH = as.vector(sub_juv_B$dbh_cm),
#                       Height = as.vector(sub_juv_B$height_m) )
#
#sub_adult_B <- subset(adult_data, dbh < 10 &
#                       (plot=="CyB4"&North_South=="North"|
#                       plot=="CyB5"&North_South=="North"|
#                       plot=="CyB7"&North_South=="North" )
#
#dataB_adult <- data.frame(plot = as.vector(sub_adult_B$plot),
#                       spe = as.vector(sub_adult_B$species),
#                       assm = as.vector(sub_adult_B$assm),
#                       DBH = as.vector(sub_adult_B$dbh),
#                       Height = as.vector(sub_adult_B$h_mean) )
#
#
#dataB <- merge(dataB_juv, dataB_adult, all=TRUE)
#
#==============================================================================
#species groups
#DF
#df_dataA <- subset(dataA, spe=="DF")
#df_dataB <- subset(dataB, spe=="DF")
#SS_NS
#ssns_dataA <- subset(dataA, spe=="SS"|spe=="NS")
#ssns_dataB <- subset(dataB, spe=="SS"|spe=="NS")
#Hardwoods
hwood_dataA <- subset(dataA,
spe=="BE"|spe=="BI"|spe=="HOL"|spe=="HZL"|spe=="OK"|spe=="ROW"|spe=="SY"|spe=="WIL")
#hwood_dataB <- subset(dataB,
spe=="BE"|spe=="BI"|spe=="HOL"|spe=="HZL"|spe=="OK"|spe=="ROW"|spe=="SY"|spe=="WIL")
#Softwoods
swood_dataA <- subset(dataA, spe=="GF"|spe=="WH"|spe=="WRC"|spe=="SP")
#swood_dataB <- subset(dataB, spe=="GF"|spe=="WH"|spe=="WRC"|spe=="SP")
#==============================================================================
#for loop data structures
data_in <- list( df_dataA,
         ssns_dataA,
         hwood_dataA,
         swood_dataA )
#data_in <- list( ssns_dataA )
species_groups <- c(  "DF",
           "SNS",
           "HWD",
           "SWD")

#==============================================================================
# Create model function where height is the dependent variable
#h_max needs to be hard wired into this function for each species group
stan_fun <- function (beta, h_max, DBH) {
  1.35 + (h_max - 1.35)*( 1 - exp(-((beta/1000)*DBH) ))
}
#==============================================================================
```

```
# Create variance function
#varfun <- function(c, DBH) {sqrt(c * DBH)}
#==============================================================================
new_dnorm <- function(x,mean,c,DBH,log)
{ sd <- sqrt(c*DBH)
  dnorm(x,mean,sd,log)
}
# Create parameter list and
# set initial values for beta, h_max and c and indicate
# that DBH comes from the column marked "DBH"
# in the dataset
par <- list(beta=0.01, h_max= 50, c=0.05)
# Create a place to put all the other values
var <- list(DBH = "DBH")

#Set bounds
par_lo<-list(beta = 0, h_max = 0, c = 0)
par_hi<-list(beta = 200, h_max = 80 , c = 5)

# Using the normal probability distribution function -
# add the options for it to our parameter list
# "x" value in PDF is observed value
var$x<-"Height"

# Mean in normal PDF
var$mean<-"predicted"
#var$sd<- varfun

# Have it calculate log likelihood
var$log<-TRUE
#==============================================================================
#Create dataframe to store the summary output to later save as .csv

#specify dataframe paramets
repetitions <- 5 # 1st dimension
no_params <- length(summary_param_names) # 2nd dimension
no_species <- length(species_groups) # 3rd dimension

# result_summary <- array(data = NA,
#                          dim= c(repetitions, no_params, no_species),
#                         dimnames = list(NULL,summary_param_names, NULL ) )
#==============================================================================
# Set output directory
setwd("C:/Documents and Settings/red74/My Documents/Projects/SORTIE_ND/parameterisation/allometrics/Simulated_annealing/Diameter Height Relationships/Standard/outputs/sap_adult")

# Open graphics window
x11()

for (i in 1:length(data_in) ) {

                #Remove NAs from datafile
                dataset <- subset(data_in[[i]], DBH!="NA"&Height!="NA")

#==============================================================================
#Call the linear model and store the results

                for (j in 1:repetitions) {
```

```
                    result  <- anneal(  model = stan_fun,
                                        par = par,
                                        var = var,
                                        source_data = dataset,
                                        par_lo,
                                        par_hi,
                                        pdf = new_dnorm,
                                        dep_var = "Height",
                                        max_iter = 100000,
                                        min_change = 0.001,
                                        min_drops = 600,
                                        hessian = TRUE )

                    cat("iteration: ",i,":",j, "\n")


#                   results_complete[,j,i] <- result

                    current_time <- format(Sys.time(), "%d_%m_%Y__%H_%M_%S")
                    model_n_species <- paste("stan_height_dbh", "sapling_adult", sep=".")
                    #set filename
                    output_file <- paste(species_groups[i],current_time, model_n_species, "csv", sep=".")
                     write_results(result, output_file)


                    }
#==================================================================
}
#set timestamp
current_time <- format(Sys.time(), "%d_%m_%Y__%H_%M_%S")
model_n_species <- paste("stan_height_dbh", "sapling_adult", sep=".")
#set filename
output_file <- paste(current_time, model_n_species, sep=".")



#Save workspace
setwd("C:/Documents and Settings/red74/My
Documents/Projects/SORTIE_ND/parameterisation/allometrics/Simulated_annealing/Diameter Height
Relationships/Standard/workspaces")
#setwd("D:/R_workspace/SORTIE_ND/allometrics/outputs")
image_file <- paste(output_file, "RData", sep=".")
save.image(file = image_file  )
```

Appendix 3.3 – Simulated annealing R script for sapling DBH to diameter relationship

```
## Simulated annealing to find maximum likelihood estimates of model parameters
## for SORTIE-ND DBH to Diam10 relationship for saplings
##Modified from annealing1 and annealing2 with Canham/Murphy likelihood package
#by Austin Haffenden 14Dec11
# 23Mar12:Modified to include revised data split (North/South)
#                   Modified to save a copy of the output file and the workspace to new file
#                   structure.
#                   Modified to include Hessian Matrix in the annealing/likelihood estimation
#                   for use in calculation of confidence intervals.
#Modified 24Mar12: to include max iteration, 0.001 min change, 600 max drop
# 05 Feb 13: alpha set to 0 as per DC's param file
#===========================================================================
==
#Need to:
rm(list=ls())
#Required librarys
library(likelihood)
#===========================================================================
===
# Set working directory
# Saplings:
#PC
setwd("C:/Documents and Settings/red74/My Documents/Projects/SORTIE_ND/parameterisation/data")
#Read in Juvenile data file
juv_data <- read.csv("Juvenile/juvenile_data_complete.csv", sep = ",", header=TRUE)
adult_data<- read.csv("Adult/CyB_all_adult_combined_complete.csv", sep = ",", header=TRUE)
#==========================================================================
#Subset to working data and to saplings and then merge
#Dataset A
sub_juv_A <- subset(juv_data,  height_m > 1.35 &
        (        plot=="CyB4"&North_South=="North"|
                 plot=="CyB5"&North_South=="North"|
                 plot=="CyB7"&North_South=="North" ) )

dataA_juv <- data.frame(   plot = as.vector(sub_juv_A$plot),
                           spe = as.vector(sub_juv_A$sp),
                           assm = as.vector(sub_juv_A$assm),
                           Diam10 = as.vector(sub_juv_A$diam10_cm),
                           DBH = as.vector(sub_juv_A$dbh_cm),
                           Height = as.vector(sub_juv_A$height_m) )

sub_adult_A <- subset(     adult_data, dbh < 10 &
                           plot=="CyB4"&North_South=="North"|
                           plot=="CyB5"&North_South=="North"|
                           plot=="CyB7"&North_South=="North" ) )

dataA_adult <- data.frame( plot = as.vector(sub_adult_A$plot),
                           spe = as.vector(sub_adult_A$species),
                           assm = as.vector(sub_adult_A$assm),
                           DBH = as.vector(sub_adult_A$dbh),
                           Height = as.vector(sub_adult_A$h_mean) )

dataA <- merge(dataA_juv, dataA_adult, all=TRUE)

#===========================================================================
##Dataset B
```

```
#sub_juv_B <- subset(juv_data,       height_m > 1.35 &
                                (            plot=="CyB4"&West_East=="East"|#
                                             plot=="CyB5"&North_South=="South"|
                                             plot=="CyB7"&West_East=="East" ) )

#dataB_juv <- data.frame( plot = as.vector(sub_juv_B$plot),
#                                            spe = as.vector(sub_juv_B$sp),
#                                            assm = as.vector(sub_juv_B$assm),
#                                            Diam10 = as.vector(sub_juv_B$diam10_cm),
#                                            DBH = as.vector(sub_juv_B$dbh_cm),
#                                            Height = as.vector(sub_juv_B$height_m) )
#
#sub_adult_B <- subset(adult_data,  dbh < 10 &
#                                            (plot=="CyB4"&West_East=="East"|
#                                             plot=="CyB5"&North_South=="South"|
#                                            plot=="CyB7"&West_East=="East" ) )
#
#dataB_adult <- data.frame(           plot = as.vector(sub_adult_B$plot),
#                                            spe = as.vector(sub_adult_B$species),
#                                            assm = as.vector(sub_adult_B$assm),
#                                            DBH = as.vector(sub_adult_B$dbh),
#                                            Height = as.vector(sub_adult_B$h_mean) )

#dataB <- merge(dataB_juv, dataB_adult, all=TRUE)
#
#============================================================================
#species groups
#DF
#species_group <- "DF"
df_dataA <- subset(dataA, spe=="DF")
#df_dataB <- subset(dataB, spe=="DF")
#SS_NS
#species_group <- "SSNS"
ssns_dataA <- subset(dataA, spe=="SS"|spe=="NS")
#ssns_dataB <- subset(dataB, spe=="SS"|spe=="NS")
#Hardwoods
#species_group <- "Hwoods"
hwood_dataA <- subset(dataA,
spe=="BE"|spe=="BI"|spe=="HOL"|spe=="HZL"|spe=="OK"|spe=="ROW"|spe=="SY"|spe=="WIL")
#hwood_dataB <- subset(dataB,
spe=="BE"|spe=="BI"|spe=="HOL"|spe=="HZL"|spe=="OK"|spe=="ROW"|spe=="SY"|spe=="WIL")
#Softwoods
#species_group <- "Swoods"
swood_dataA <- subset(dataA, spe=="GF"|spe=="WH"|spe=="WRC"|spe=="SP")
#swood_dataB <- subset(dataB, spe=="GF"|spe=="WH"|spe=="WRC"|spe=="SP")
#============================================================================
#for loop data structures
data_in <- list( df_dataA, ssns_dataA, hwood_dataA, swood_dataA )
species_groups <- c("DF", "SSNS", "Hwood", "SWD")
#============================================================================
# Create model function where height is the dependent variable
DBH_Diam10_fun <- function (Diam10, beta) {
  (Diam10*beta) + 0 #alpha is 0 in DC's param file
}
#============================================================================
# Create variance function
varfun <- function(c, Diam10) {sqrt(c * Diam10)}
#============================================================================
# Create parameter list and
# set initial values for beta, h_max and c and indicate
```

```
# that Diam10 comes from the column marked "Diam10"
# in the dataset
par <- list(beta=1, c=0.05)
# Create a place to put all the other values
var <- list(Diam10 = "Diam10")

#Set bounds
par_lo<-list(beta = 0, c = 0)
par_hi<-list(beta = 5, c = 10)

# Using the normal probability distribution function -
# add the options for it to our parameter list
# "x" value in PDF is observed value
var$x<-"DBH"

# Mean in normal PDF
var$mean<-"predicted"
var$sd<- varfun

# Have it calculate log likelihood
var$log<-TRUE
#================================================================================
#Create dataframe to store the summary output to later save as .csv

#names of parameters to be returned and used as column headers
summary_param_names <- c(       "MLE",
                                "beta",
                                "c",
                                "aic",
                                "aic_corr",
                                "R2",
                                "iterations" )

#specify dataframe paramets
repetitions <- 5 # 1st dimension
no_params <- length(summary_param_names) # 2nd dimension
no_species <- length(species_groups) # 3rd dimension

# result_summary <- array(       data = NA,
#                                dim= c(repetitions, no_params, no_species),
#                                dimnames = list(NULL,summary_param_names, NULL ) )
#================================================================================
#Create the list matrix to store results in the workspace
#this will (prob) need to be changed if anneal( Hessian = FALSE )
full_param_names <- c(    "best_pars",
                          "var",
                          "iterations",
                          "source_data",
                          "par_lo",
                          "par_hi",
                          "par_step",
                          "support_interval_range",
                          "upper_limits",
                          "lower_limits",
                          "initial_temp",
                          "temp_red",
                          "ns",
                          "nt",
                          "pdf",
                          "note",
```

```
            "model",
            "std_errors",
            "var_covar_mat",
            "max_likeli",
            "aic_corr",
            "aic",
            "slope",
            "R2",
            "likeli_hist" )

results_complete <- array( list(NULL),
            c(length(full_param_names), repetitions, length(species_groups) ),
            dimnames = list(full_param_names, NULL, species_groups) )
#=======================================================================
#Directory for outputs
setwd("C:/Documents and Settings/red74/My
Documents/Projects/SORTIE_ND/parameterisation/allometrics/Simulated_annealing/DBH_to_Diam10/outp
uts") #PC

#open window
x11()

for (i in 1:length(data_in) ) {

    #Remove NAs from datafile
    dataset <- subset(data_in[[i]], DBH!="NA"&Diam10!="NA")

#===========================================================================
#Call the linear model and store the results

    for (j in 1:repetitions) {

        result  <- anneal(  model = DBH_Diam10_fun,
                par = par, var = var,
                source_data = dataset,
                par_lo,
                par_hi,
                pdf = dnorm,
                dep_var = "DBH",
                max_iter = 1000000,
                min_change = 0.001,
                min_drops = 600,
                hessian = TRUE )

        cat("iteration: ",i,":",j, "\n")

    results_complete[,j,i] <- result
    #set timestamp
    current_time <- format(Sys.time(), "%d_%m_%Y__%H_%M_%S")
    #set filename
    output_file <- paste(current_time, species_groups[i], "dbh_to_diam10", "sapling", "csv", sep=".")
    write_results(result, output_file)

    }#===================================================================
}
#set timestamp
current_time <- format(Sys.time(), "%d_%m_%Y__%H_%M_%S")
#set filename
output_file <- paste(current_time, "dbh_to_diam10", "sapling", sep=".")
```

```
# #Save data summary file
# for (i in 1:length(data_in) ) {
#
#	setwd("C:/Documents and Settings/red74/My Documents/Projects/SORTIE_ND/parameterisation/allometrics/Simulated_annealing/DBH_to_Diam10/outputs") #PC
#	#setwd("D:/R_workspace/SORTIE_ND/allometrics/outputs") #Tims machine
#	write.csv(result_summary[,,i], file = paste(output_file, species_groups[i], "csv", sep=".") )
# }

#Save workspace
setwd("C:/Documents and Settings/red74/My Documents/Projects/SORTIE_ND/parameterisation/allometrics/Simulated_annealing/DBH_to_Diam10/workspaces") #PC
#setwd("D:/R_workspace/SORTIE_ND/allometrics/workspaces") #Tims machine
image_file <- paste(output_file, "RData", sep=".")
save.image(file = image_file  )
```

Appendix 3.4 – Simulated annealing R script for sapling and adult crown depth to tree height relationship

```
## Simulated annealing to find maximum likelihood estimates of model parameters
## for SORTIE-ND stamdard Canopy depth to crown height relationship for adults
##Modified from annealing1 and annealing2 with Canham/Murphy likelihood package
#by Austin Haffenden 14Dec11
#23Mar12: Modified to include revised data split (North/South)
#                 Modified to save a copy of the output file and the workspace to new file
#                 structure.
#                 Modified to include Hessian Matrix in the annealing/likelihood estimation
#                 for use in calculation of confidence intervals.
#Modified 24Mar12: to include max iteration, 0.001 min change, 600 max drop
#Modified 25Mar12: to include par_lo and par_hi
#=============================================================================
#Need to:
rm(list=ls())
#Required librarys
library(likelihood)
#=============================================================================
# Set working directory
# Seedlings:
#PC
setwd("C:/Documents and Settings/red74/My
Documents/Projects/SORTIE_ND/parameterisation/data/Adult")
#Tims machine
#setwd("D:/R_workspace/SORTIE_ND/data/Adult")
#E:
#setwd("E:/Temp_working docs/Parameterisation13Jan/Data/Adult")
#=============================================================================
#Read in Adult data file
adult_data <- read.csv("CyB_all_adult_combined_complete.csv", sep = ",", header=TRUE)
#
# #Subset to working data and to seedlings and then merge
sub_adult_A <- subset(    adult_data,     dbh >= 10 &
                          assm == "2006" &
                          North_South=="North" &
                          (plot=="CyB4"&North_South=="North"|
                          plot=="CyB5"&North_South=="North"|
                          plot=="CyB7"&North_South=="North" ) )

dataA <- data.frame(      plot = as.vector(sub_adult_A$plot),
                          sp_gp = as.vector(sub_adult_A$sp_gp),
                          assm = as.vector(sub_adult_A$assm),
                          crown_depth = as.vector(sub_adult_A$crown_depth),
                          Height = as.vector(sub_adult_A$h_mean) )
#
# sub_adult_B <- subset(  adult_data, dbh >= 10 &
#                         assm=="2011" &
#                         North_South=="South" &
# #                       (plot=="CyB4"&North_South=="South"|
# #                       plot=="CyB5"&North_South=="South"|
# #                       plot=="CyB7"&North_South=="South" ) )
#
# dataB <- data.frame(    plot = as.vector(sub_adult_B$plot),
#                         sp_gp = as.vector(sub_adult_B$sp_gp),
#                         assm = as.vector(sub_adult_B$assm),
#                         crown_depth = as.vector(sub_adult_B$crown_depth),
#                         Height = as.vector(sub_adult_B$h_mean) )
#species groups
```

```
#DF
df_dataA <- subset(dataA, sp_gp==1)
#df_dataB <- subset(dataB, sp_gp==1)
#SS_NS
ssns_dataA <- subset(dataA, sp_gp==2)
#ssns_dataB <- subset(dataB, sp_gp==2)
#Hardwoods
hwood_dataA <- subset(dataA, sp_gp==3)
#hwood_dataB <- subset(dataB, sp_gp==3)
#Softwoods
swood_dataA <- subset(dataA, sp_gp==4)
#swood_dataB <- subset(dataB, sp_gp==4)
#=========================================================================
#for loop data structures
#data_in <- list( df_dataA, ssns_dataA, hwood_dataA, swood_dataA )
data_in <- list(hwood_dataA)
#data_in <- list( df_dataB, ssns_dataB, hwood_dataB, swood_dataB )
#species_groups <- c("DF", "SSNS", "Hwood", "Swood")
species_groups <- c("HWD")
#=========================================================================
#Data structures for for loop
#data_list <- list( df_dataA, ssns_dataA, hwood_dataA, swood_dataA )
data_list <- list(hwood_dataA)
#data_list <- list( df_dataB, ssns_dataB, hwood_dataB, swood_dataB )
#species_groups <- c("DF", "SSNS", "Hwood", "Swood")
#=========================================================================
# Create model functions where height is the dependent variable
stan_fun <- function (alpha, beta, Height) {
   alpha*Height^beta
}
#=========================================================================
# Create variance function
#varfun <- function(c, Height) {sqrt(c * Height)}
#=========================================================================
new_dnorm <- function(x,mean,c,Height,log)
{ sd <- sqrt(c*Height)
  dnorm(x,mean,sd,log)
}
# Create parameter list and
# set initial values for beta, h_max and c and indicate
# that Height comes from the column marked "Height"
# in the dataset
par<-list(alpha = 1, beta = 1, c = 0.05)
# Create a place to put all the other values
var <- list(Height = "Height")

#Set bounds
par_lo <- list( alpha = 0, beta = 0, c = 0)
par_hi <- list( alpha = 5, beta = 5, c = 10)

# Using the normal probability distribution function -
# add the options for it to our parameter list
# "x" value in PDF is observed value
var$x<-"crown_depth"

# Mean in normal PDF
var$mean<-"predicted"
#var$sd<- varfun

# Have it calculate log likelihood
```

```
var$log<-TRUE
#==========================================================================
#Create dataframe to store the summary output to later save as .csv
#names of parameters to be returned and used as column headers
summary_param_names <- c(        "MLE",
                                 "alpha",
                                 "c",
                                 "upper_limits_alpha",
                                 "lower_limits_alpha",
                                 "aic",
                                 "aic_corr",
                                 "R2",
                                 "iterations" )

#specify dataframe paramets
repetitions <- 10 # 1st dimension
no_params <- length(summary_param_names) # 2nd dimension
no_species <- length(species_groups) # 3rd dimension

# result_summary <- array(         data = NA,
#                                  dim= c(repetitions, no_params, no_species),
#                                  dimnames = list(NULL,summary_param_names, NULL ) )
#
#==========================================================================
# #Create the list matrix to store results in the workspace
# #this will (prob) need to be changed if anneal( Hessian = FALSE )
# full_param_names <- c(  "best_pars",
#                         "var",
#                         "iterations",
#                         "source_data",
#                         "par_lo",
#                         "par_hi",
#                         "par_step",
#                         "support_interval_range",
#                         "upper_limits",
#                         "lower_limits",
#                         "initial_temp",
#                         "temp_red",
#                         "ns",
#                         "nt",
#                         "pdf",
#                         "note",
#                         "model",
#                         "std_errors",
#                         "var_covar_mat",
#                         "max_likeli",
#                         "aic_corr",
#                         "aic",
#                         "slope",
#                         "R2",
#                         "likeli_hist" )
# results_complete <- array( list(NULL),                                  #
        c(length(full_param_names), repetitions, length(species_groups) ),
#        dimnames = list(full_param_names, NULL, species_groups) )
# Output directory
setwd("C:/Documents and Settings/red74/My
Documents/Projects/SORTIE_ND/parameterisation/allometrics/Simulated_annealing/Crown Depth Tree
Height/Standard/outputs") #PC
```

```
for (i in 1:length(data_in) ) {

        #Remove NAs from datafile
        dataset <- subset(data_in[[i]], crown_depth!="NA"&Height!="NA")

#=============================================================================
#Call the linear model and store the results

        for (j in 1:repetitions) {

                result  <- anneal(  model = stan_fun,
                                    par = par, var = var,
                                    source_data = dataset,
                                    par_lo,
                                    par_hi,
                                    pdf = new_dnorm,
                                    dep_var = "crown_depth",
                                    max_iter = 100000,
                                    min_change = 0.001,
                                    min_drops = 600,
                                    hessian = TRUE )

                cat("iteration: ",i,":",j, "\n")

#               result_summary[j,,i]<- c(   result$max_likeli,
#                                           result$best_pars$alpha,
#                                           result$best_pars$beta,
#                                           result$best_pars$c,
#                                           result$upper_limits$alpha,
#                                           result$lower_limits$alpha,
#                                           result$aic,
#                                           result$aic_corr,
#                                           result$R2,
#                                           result$iterations   )

        #set timestamp
        current_time <- format(Sys.time(), "%d_%m_%Y__%H_%M_%S")
        #set filename
        output_file <- paste(species_groups[i], current_time, "standard_CD", "adult", "csv", sep=".")
        write_results(result, output_file)

        #results_complete[,j,i] <- result

        }
#=============================================================================

}


# #Save data summary file
# for (i in 1:length(data_in) ) {
#       setwd("C:/Documents and Settings/red74/My Documents/Projects/SORTIE_ND/parameterisation/allometrics/Simulated_annealing/Crown Depth Tree Height/Standard/outputs") #PC
#       #setwd("D:/R_workspace/SORTIE_ND/allometrics/outputs") #Tims mach
#       write.csv(result_summary[,,i], file = paste(output_file, species_groups[i], "csv", sep=".") )
# }

#Save workspace
```

```
setwd("C:/Documents and Settings/red74/My Documents/Projects/SORTIE_ND/parameterisation/allometrics/Simulated_annealing/Crown Depth Tree Height/Standard/workspaces") #PC
#setwd("D:/R_workspace/SORTIE_ND/allometrics/workspaces") #Tims mach
image_file <- paste(output_file, "RData", sep=".")
save.image(file = image_file )
```

Appendix 3.5 – Simulated annealing R script for sapling and adult crown radius to DBH relationship

```
## Simulated annealing to find maximum likelihood estimates of model parameters
## for SORTIE-ND stamdard CR to DBH relationship for adults
##Modified from annealing1 and annealing2 with Canham/Murphy likelihood package
#by Austin Haffenden 11Dec11
#23Mar12: Modified to include revised data split (North/South)
#                   Modified to save a copy of the output file and the workspace to new file
#                   structure.
#                   Modified to include Hessian Matrix in the annealing/likelihood estimation
#                   for use in calculation of confidence intervals.
#========================================================================
#Need to:
rm(list=ls())
#Required librarys
library(likelihood)
#========================================================================
# Set working directory
# Seedlings:
#PC
setwd("E:/Documents/Projects/SORTIE_ND/parameterisation/data/Adult")
#========================================================================
#Read in Adult data file
adult_data <- read.csv("CyB_all_adult_combined_complete.csv", sep = ",", header=TRUE)

#Subset to working data and to seedlings and then merge
sub_adult_A <- subset(    adult_data,       dbh >= 10 &
                          (plot=="CyB4"&North_South=="North"|
                          plot=="CyB5"&North_South=="North"|
                          plot=="CyB7"&North_South=="North" ) )

dataA <- data.frame(      plot = as.vector(sub_adult_A$plot),
                          spe = as.vector(sub_adult_A$species),
                          assm = as.vector(sub_adult_A$assm),
                          crown_radius = as.vector(sub_adult_A$crown_radius),
                          DBH = as.vector(sub_adult_A$dbh) )

#sub_adult_B <- subset(data_list,    dbh >= 10 &
#                         (plot=="CyB4"&North_South=="South"|
#                         plot=="CyB5"&North_South=="South"|
#                         plot=="CyB7"&North_South=="South" ) )

#dataB <- data.frame(     plot = as.vector(sub_adult_B$plot),
#                         spe = as.vector(sub_adult_B$species),
#                         assm = as.vector(sub_adult_B$assm),
#                         crown_radius = as.vector(sub_adult_B$crown_radius),
#                         DBH = as.vector(sub_adult_B$DBH) )
#species groups
#DF
df_dataA <- subset(dataA, spe=="DF")
#df_dataB <- subset(dataB, spe=="DF")
#SS_NS
ssns_dataA <- subset(dataA, spe=="SS"|spe=="NS")
#ssns_dataB <- subset(dataB, spe=="SS"|spe=="NS")
#Hardwoods
#hwood_dataA <- subset(dataA,
spe=="BE"|spe=="BI"|spe=="HOL"|spe=="HZL"|spe=="OK"|spe=="ROW"|spe=="SY"|spe=="WIL")
#hwood_dataB <- subset(dataB,
spe=="BE"|spe=="BI"|spe=="HOL"|spe=="HZL"|spe=="OK"|spe=="ROW"|spe=="SY"|spe=="WIL")
```

```
#Softwoods
swood_dataA <- subset(dataA, spe=="GF"|spe=="WH"|spe=="WRC"|spe=="JL"|spe=="LP"|spe=="SP")
#swood_dataB <- subset(dataB, spe=="GF"|spe=="WH"|spe=="WRC"|spe=="JL"|spe=="LP"|spe=="SP")
#===========================================================================
#Data structures for for loop
data_list <- list( df_dataA, ssns_dataA, swood_dataA )
species_groups <- c("DF", "SSNS", "Swood")
#===========================================================================
# Create model functions where height is the dependent variable
stan_fun <- function (alpha, beta, DBH) {
        alpha*DBH^beta
}
#===========================================================================
# Create variance function
#varfun <- function(c, DBH) {sqrt(c * DBH)}
#===========================================================================
new_dnorm <- function(x,mean,c,DBH,log)
{ sd <- sqrt(c*DBH)
  dnorm(x,mean,sd,log)
}
# Create parameter list and
# set initial values for beta, h_max and c and indicate
# that DBH comes from the column marked "DBH"
# in the dataset
par<-list(alpha = 2, beta = 5, c = 0.05)
# Create a place to put all the other values
var <- list(DBH = "DBH")

#Set bounds
par_lo <- list( alpha = 0, beta = 0, c = 0)
par_hi <- list( alpha = 5, beta = 10, c = 10)

# Using the normal probability distribution function -
# add the options for it to our parameter list
# "x" value in PDF is observed value
var$x<-"crown_radius"

# Mean in normal PDF
var$mean<-"predicted"
#var$sd<- varfun

# Have it calculate log likelihood
var$log<-TRUE
#===========================================================================
repetitions <- 10 # 1st dimension
no_params <- length(summary_param_names) # 2nd dimension
no_species <- length(species_groups) # 3rd dimension

# set output directory
setwd("C:/Documents and Settings/red74/My
Documents/Projects/SORTIE_ND/parameterisation/allometrics/Simulated_annealing/Crown Radius
DBH/Standard/outputs") #PC

# open graphics window
x11()

for (i in 1:length(data_list) ) {

        #Remove NAs from datafile
        dataset <- subset(data_list[[i]], crown_radius!="NA"&DBH!="NA")
```

```
#==============================================================================
#Call the linear model and store the results

        for (j in 1:repetitions) {

                result  <- anneal(  model = stan_fun,
                                    par = par, var = var,
                                    source_data = dataset,
                                    par_lo,
                                    par_hi,
                                    pdf = new_dnorm,
                                    dep_var = "crown_radius",
                                    max_iter = 100000,
                                    min_change = 0.001,
                                    min_drops = 600,
                                    hessian = TRUE )

                cat("iteration: ",i,":",j, "\n")

#               result_summary[j,,i]<- c(   result$max_likeli,
#                                           result$best_pars$alpha,
#                                           result$upper_limit$alpha,
#                                           result$lower_limit$alpha,
#                                           result$best_pars$c,
#                                           result$aic,
#                                           result$aic_corr,
#                                           result$R2,
#                                           result$iterations   )
#
#               results_complete[,j,i] <- result

                #set timestamp
                current_time <- format(Sys.time(), "%d_%m_%Y__%H_%M_%S")
                #set filename
        output_file <- paste(species_groups[i], current_time, "standard_CR", "adult", "csv", sep=".")

        write_results(result, output_file)
        }#=====================================================================
}
#set timestamp
current_time <- format(Sys.time(), "%d_%m_%Y__%H_%M_%S")
#set filename
output_file <- paste(current_time, "standard_CR", "adult", sep=".")

#Save data summary file
# for (i in 1:length(data_list) ) {
#       setwd("C:/Documents and Settings/red74/My
Documents/Projects/SORTIE_ND/parameterisation/allometrics/Simulated_annealing/Crown Radius
DBH/Standard/outputs") #PC
# #     setwd("D:/R_workspace/SORTIE_ND/allometrics/outputs") #Tims mach
#       write.csv(result_summary[,,i], file = paste(output_file, species_groups[i], "csv", sep=".") )
# }

#Save workspace
setwd("C:/Documents and Settings/red74/My
Documents/Projects/SORTIE_ND/parameterisation/allometrics/Simulated_annealing/Crown Radius
DBH/Standard/workspaces") #PC
#setwd("D:/R_workspace/SORTIE_ND/allometrics/outputs") #Tims mach
image_file <- paste(output_file, "RData", sep=".")
save.image(file = image_file  )
```

Appendix 3.6 –Simulated annealing R script for adult diameter growth

```
##Basal area NCI Growth modified from annealing2 package(neighlikeli) and Crown radius/depth
#Using Size Effect and crowding effect
##27 Jan 12
#==========================================================================
#Clear the workspace
rm(list=ls())
#==========================================================================
#import the librarys(s)
library(neighlikeli)
#==========================================================================
# Set up our datasets:
#====================
# Set working directory
#PC
setwd("C:/DocumentsandSettings/red74/MyDocuments/Projects/SORTIE_ND/parameterisation/data/Adult")
##====================
#Take in the adult (neighbours) dataset
neigh_in <- read.csv("CyB_all_adult_combined_complete.csv", header=TRUE)
#Take in the adult growth (target) file
targ_in <- read.csv("CyB_all_adult_growth.csv", sep=",", header=TRUE)
##====================
#Subset Neighbours to 2006
sub_neigh <- subset(neigh_in,      x!="NA"&BA_cm2!="NA"&assm=="2006"&North_South=="North")
#Species is grouped here for use in for loop
neighbours <- data.frame(  species = as.vector(sub_neigh$sp_gp),
                           plot_yr = as.vector(sub_neigh$plot_yr),
                           X = as.vector(sub_neigh$x),
                           Y = as.vector(sub_neigh$y),
                           BA = as.vector(sub_neigh$BA_cm2),
                           Site =as.vector(sub_neigh$plot))
#====================
#Seperate DF for targets
df_sub_target <- subset(targ_in, sp_gp==1&dbh_growth_cm_yr>=0&North_South=="North"&dbh_06>=10)
#transform to dataframe
df_target <- data.frame(   sp = as.vector(df_sub_target$sp_gp),
                           X = as.vector(df_sub_target$x),
                           Y = as.vector(df_sub_target$y),
                           DBH = as.vector(df_sub_target$dbh_06),
                           Growth = as.vector(df_sub_target$dbh_growth_cm_yr),
                           Site = as.vector(df_sub_target$plot) )

df_target <- df_target[1:153,]
#====================
#Seperate SSNS for targets
ssns_sub_target <- subset(targ_in,
sp_gp==2&dbh_growth_cm_yr>=0&North_South=="North"&dbh_06>=10)
#transform to dataframe
ssns_target <- data.frame( sp = as.vector(ssns_sub_target$sp_gp),
                           X = as.vector(ssns_sub_target$x),
                           Y = as.vector(ssns_sub_target$y),
                           DBH = as.vector(ssns_sub_target$dbh_06),
                           Growth = as.vector(ssns_sub_target$dbh_growth_cm_yr),
                           Site = as.vector(ssns_sub_target$plot) )
#====================
#Seperate Hwood for targets
hwood_sub_target  <- subset(targ_in,
sp_gp==3&dbh_growth_cm_yr>=0&North_South=="North"&dbh_06>=10)
#transform to dataframe
```

```
hwood_target <- data.frame(sp = as.vector(hwood_sub_target$sp_gp),
                           X = as.vector(hwood_sub_target$x),
                           Y = as.vector(hwood_sub_target$y),
                           DBH = as.vector(hwood_sub_target$dbh_06),
                           Growth = as.vector(hwood_sub_target$dbh_growth_cm_yr),
                           Site = as.vector(hwood_sub_target$plot) )
#====================
#Seperate Swood for targets
swood_sub_target  <- subset(targ_in,
sp_gp==4&dbh_growth_cm_yr>=0&North_South=="North"&dbh_06>=10)
#transform to dataframe
swood_target <- data.frame(sp = as.vector(swood_sub_target$sp_gp),
                           X = as.vector(swood_sub_target$x),
                           Y = as.vector(swood_sub_target$y),
                           DBH = as.vector(swood_sub_target$dbh_06),
                           Growth = as.vector(swood_sub_target$dbh_growth_cm_yr),
                           Site = as.vector(swood_sub_target$plot) )
#====================
#Data structures for for loop
data_in <- list(   df_target ,
                   ssns_target,
                   hwood_target,
                   swood_target )
species_groups <- c(       "DF",
                           “SNS",
                           "Hwood",
                           "Swood")
#===========================================================================
# Create our basal area growth model function Size Effect ONLY
model <- function (max_growth, Xo, Xb, C, DBH, gamma, N, BADiv, D) {
        max_growth *
        exp( -0.5*( log(DBH/Xo)/ Xb )^2 ) *
        exp( -C * ( ( DBH ^ gamma ) *  (N / BADiv) )^D )
}

# Create our neighbor summing function - refer to test2.R
sumfun <- function (BA) { BA }

#===========================================================================
# Create variance function
#varfun <- function(c, DBH) {sqrt(c * DBH)}
        new_dnorm <- function(x,mean,c,DBH,log)
{ sd <- sqrt(c*DBH)
  dnorm(x,mean,sd,log)
}
# Create a place to put our parameters and
# set initial values
par<-list(max_growth = 3, Xo = 1, Xb = 1, C = 2, D = 2, c = 0.05, max_radius = 5)
var<-list(N = sumneigh, DBH = "DBH", BADiv = 1000, gamma = 1)

# Set the summing function parameters
var$BA<- neighbours$BA

# Put in the parameters for sumneigh
var$targetx<-"X"
var$targety<-"Y"
var$neighborx<-"X"
var$neighbory<-"Y"
var$targetsite<-"Site"
var$neighborsite<-"Site"
```

```
var$sumfun<-sumfun
#var$target_data<-target
var$neigh_data<-neighbours

# Set bounds
par_lo <-list(max_growth = 0, Xo = 0, Xb = 0,  C = 0, D = 0, c = 0, max_radius = 0)
par_hi <-list(max_growth = 5, Xo = 300, Xb = 10, C = 10, D = 5, c = 10, max_radius = 20)

# We'll use the normal probability distribution function -
# add the options for it to our parameter list
# "x" value in PDF is observed value
var$x<-"Growth"

# Mean in normal PDF
var$mean<-"predicted"
#var$sd <- varfun

# Have it calculate log likelihood
var$log<-TRUE
#==========================================================================
# Number of runs
no_runs <- 5
#Loop through data sets
for (j in 1:length(species_groups)) {

#Assign the target data
dataset <- data_in[[j]]
var$target_data<-dataset

#Get name of species group for filename
species_group <- species_groups[j]

# Folder for output
#setwd("C:/DocumentsandSettings/red74/My
Documents/Projects/SORTIE_ND/parameterisation/behaviours/growth/Basal_area_NCI_growth/outputs")
setwd("D:/R_workspace/SORTIE_ND/behaviours/output")
#Start the timer
ptm <- proc.time()
#Call the standard model and store the results
for (i in 1:no_runs) {

  results<-anneal(            model,
                              par,
                              var,
                              dataset,
                              par_lo,
                              par_hi,
                              new_dnorm,
                               "Growth",
                              max_iter= 100000,
                              min_change = 0.001,
                              min_drops = 600,
                              hessian=FALSE )

  #Output summary
        cat("Run: ",i, "\n")
        cat("MLE: ", results$max_likeli, "\n")
        cat("max_growth: ", results$best_pars$max_growth, "\n")
        cat("Xo: ", results$best_pars$Xo, "\n")
        cat("Xb: ", results$best_pars$Xb, "\n")
```

```
            cat("C: ", results$best_pars$C, "\n")
            cat("D: ", results$best_pars$D, "\n")
             cat("max_radius: ", results$best_pars$max_radius)
            cat("aicc: ", results$aic_corr, "\n")
            cat("R2: ", results$R2, "\n")
            current_time <- format(Sys.time(), "%d_%m_%Y__%H_%M_%S")
            output_file <- paste(species_group, "BA_NCI_growth_SE_and_CE", current_time, "csv", sep=".")
            write_results(results,  output_file)

} #end i
#Output elapsed time
print("Elapsed time : ")
proc.time() - ptm
#           #Save data summary file
#setwd("C:/Documents and Settings/red74/MyDocuments/Projects/SORTIE_ND/parameterisation/behaviours/growth/Basal_area_NCI_growth/outputs")
#   #setwd("D:/R_workspace/SORTIE_ND/behaviours/output")
#           current_time <- format(Sys.time(), "%d_%m_%Y__%H_%M_%S")
#           output_file <- paste(species_group, "BA_NCI_growth_SE_and_CE", current_time, "csv", sep=".")
#           write.csv(result_df, file = output_file)
}#end j
```

Appendix 4 – R and Winbugs script for Bayesian calibration of rhododendron seedling establishment logistic regression

```
# WinBugs minus station 31
################################################################
rm(list=ls())
library("R2WinBUGS")
library("mass")
#library("lme4")
# Take in data
setwd("E:/Documents/Projects/RP_GLM/data/workspaces")
#setwd("/Users/greybeard/Documents/RP_GLM/workspaces")
load("field_candidate_data.RData")
load(file = "LiDAR_candidate_data.RData")

field <- field_cand_data
lidar <- lidar_cand_data

field$seed_bin <- as.numeric(levels(field$seed_bin))[field$seed_bin]
field$ad_bin<-as.numeric(levels(field$ad_bin))[field$ad_bin]
field$butt<-as.numeric(levels(field$butt))[field$butt]
#================================================================
# From exploratory analysis data to use is:
# field$Height_sum_1, field$CD_sum_1, field$CR_sum_1, field$sq_o_depth, field$DBH_sum_1
# lidar$log_intens_mean
#====
# other possible data that is not significant but is close is:
# lidar$log1p_perc_2.5_10, field$o_moist, lidar$veg_cover
#====
# field$ad_bin and field$butt should be tried as well
#================================================================
# Some data transforms
model_data <- data.frame( seed_bin = as.vector(field$seed_bin),
                  ad_bin = as.vector(field$ad_bin),
                  butt = as.vector(field$butt),
                  height = as.vector(field$Height_sum_1),
                  CD = as.vector(field$CD_sum_1),
                  CR = as.vector(field$CR_sum_1),
                  o_depth = as.vector(field$sq_o_depth),
                  DBH = as.vector(field$DBH_sum_1),
                  intens = as.vector(lidar$log_intens_mean),
                  perc = as.vector(lidar$log1p_perc_2.5_10),
                  o_moist = as.vector(field$o_moist),
                  veg_cov = as.vector(lidar$veg_cov),
                  moss = as.vector(field$moss_av_perc),
                  litter = as.vector(field$sq_litter),
                  dwood = as.vector(field$sq_dwood),
                  ad_perc = as.vector(field$ad_perc))
#================================================================
# Centre and Standardise

mod <- model_data[1:3]
mod$height <- (model_data$height - mean(model_data$height))/ sd(model_data$height)
mod$CD <- (model_data$CD - mean(model_data$CD)) / sd(model_data$CD)
mod$CR <- (model_data$CR - mean(model_data$CR)) / sd(model_data$CR)
mod$o_depth <- (model_data$o_depth - mean(model_data$o_depth)) / sd(model_data$o_depth)
mod$DBH <- (model_data$DBH - mean(model_data$DBH)) / sd(model_data$DBH)
mod$intens <- (model_data$intens - mean(model_data$intens)) / sd(model_data$intens)
mod$perc <- (model_data$perc - mean(model_data$perc)) / sd(model_data$perc)
mod$o_moist <- (model_data$o_moist - mean(model_data$o_moist)) / sd(model_data$o_moist)
```

```
mod$veg_cov <- (model_data$veg_cov - mean(model_data$veg_cov)) / sd(model_data$veg_cov)
mod$moss <- (model_data$moss - mean(model_data$moss)) / sd(model_data$moss)
mod$litter <- (model_data$litter - mean(model_data$litter)) / sd(model_data$litter)
mod$dwood <- (model_data$dwood - mean(model_data$dwood)) / sd(model_data$dwood)
mod$ad_perc <- (model_data$ad_perc - mean(model_data$ad_perc)) / sd(model_data$ad_perc)
mod <-mod[-31,]
#================================================================
# all tree attributes are correlated. Height was most significant so trying that
#================================================================
# Candidate model

### 13.4. Analysis using R
glm_cand_2 <- glm(mod$seed_bin ~ mod$ad_bin +
                        mod$o_depth +
                        mod$height,
                        family = binomial) # Fit the model
summary(glm_cand_2)      # logistic regression
# Call:
#   glm(formula = mod$seed_bin ~ mod$ad_bin + mod$o_depth + mod$height,
#       family = binomial)
#
# Deviance Residuals:
#   Min       1Q   Median       3Q      Max
# -2.3038  -0.3304  -0.1202   0.7221   1.2988
#
# Coefficients:
#   Estimate Std. Error z value Pr(>|z|)
# (Intercept)  -2.9733     1.3506  -2.201  0.02771 *
#   mod$ad_bin    2.8035     1.3524   2.073  0.03817 *
#   mod$o_depth   1.2227     0.5476   2.233  0.02555 *
#   mod$height   -2.2488     0.8651  -2.600  0.00933 **
#   ---
#   Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
#
# (Dispersion parameter for binomial family taken to be 1)
#
# Null deviance: 53.841  on 39  degrees of freedom
# Residual deviance: 30.744  on 36  degrees of freedom
# AIC: 38.744
#
# Number of Fisher Scoring iterations: 6
anova(glm_cand_2, test = "Chisq") # Likelihood ratio test (LRT)
# Analysis of Deviance Table
#
# Model: binomial, link: logit
#
# Response: mod$seed_bin
#
# Terms added sequentially (first to last)
#
#
# Df Deviance Resid. Df Resid. Dev  Pr(>Chi)
# NULL                        39     53.841
# mod$ad_bin   1   2.5751        38     51.266 0.1085542
# mod$o_depth  1   5.7238        37     45.542 0.0167368 *
# mod$height   1  14.7976        36     30.744 0.0001197 ***
# ---
# Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
stepAIC(glm_cand_2)
# Start:  AIC=45.07
```

```
# mod$seed_bin ~ mod$ad_bin + mod$o_depth + mod$height
#
# Df Deviance    AIC
# <none>            37.069 45.069
# - mod$ad_bin   1   40.229 46.229
# - mod$o_depth  1   42.091 48.091
# - mod$height   1   48.571 54.571
#
# Call:  glm(formula = mod$seed_bin ~ mod$ad_bin + mod$o_depth + mod$height,
#           family = binomial)
#
# Coefficients:
#   (Intercept)   mod$ad_bin  mod$o_depth   mod$height
# -1.7141       1.6599       0.9302      -1.5985
#
# Degrees of Freedom: 40 Total (i.e. Null);  37 Residual
# Null Deviance:      55.64
# Residual Deviance: 37.07            AIC: 45.07
#=================================================================
### 13.5. Analysis using WinBUGS
# Define model
setwd("E:/Documents/Projects/RP_GLM/outputs/cand_2")
sink("bayes_cand_2_minus_31.txt")
cat("
   model {

   # Priors
   alpha ~ dnorm(0,0.001)
   beta_1 ~ dnorm(0,0.001)
   beta_2 ~ dnorm(0,0.001)
   beta_3 ~ dnorm(0,0.001)

   # Likelihood
   for (i in 1:n) {

   seed_bin[i] ~ dbern(lambda[i])
   logit(lambda[i]) <- alpha + beta_1*ad_bin[i] + beta_2*o_depth[i] + beta_3*height[i]

   # Fit assessments
   Presi[i] <- (seed_bin[i] - lambda[i]) / sqrt(lambda[i]) # Pearson residuals

   seed_bin.new[i] ~ dbern(lambda[i])          # Replicate data set
   Presi.new[i] <- (seed_bin.new[i] - lambda[i]) / sqrt(lambda[i]) # Pearson resi
   D[i] <- pow(Presi[i], 2)
   D.new[i] <- pow(Presi.new[i], 2)
   }

   # Add up discrepancy measures
   fit <- sum(D[])
   fit.new <- sum(D.new[])
   }
   ",fill=TRUE)
sink()

# Bundle data
win.data <- list( seed_bin = mod$seed_bin,
                 ad_bin = mod$ad_bin,
                 height   = mod$height,
                 o_depth  = mod$o_depth,
                 n        = nrow(mod) )
```

```r
# # Inits function
inits <- function(){ list(alpha=rlnorm(1),
                          beta_1=rnorm(1),
                          beta_2=rnorm(1),
                          beta_3=rnorm(1))}

# Parameters to estimate
params <- c("lambda", "alpha",
            "beta_1",
            "beta_2",
            "beta_3",
            "Presi", "fit", "fit.new")

# MCMC settings
nc <- 3
ni <- 50000
nb <- 1000
nt <- 2

# Start Gibbs sampler
bayes_cand_2 <- bugs(data=win.data, inits = inits, parameters.to.save=params,
                     model.file="bayes_cand_2_minus_31.txt", n.thin=nt, n.chains=nc, n.burnin=nb,
                     n.iter=ni, debug = TRUE)

out <- bayes_cand_2

#==================================================================
### 13.5.1. Check of MCMC convergence and model adequacy
print(out, dig = 3)

x11()

which(out$summary[,8] > 1.1)
# which value in the 8th column is > 1.1 ?
# named integer(0)

hist(out$summary[,8], col = "grey", main = "Rhat values")
savePlot(filename = "Rhat", type ="png")

plot(out$mean$Presi, las = 1)
abline(h = 0)
savePlot(filename = "Presi", type ="png")

plot(out$sims.list$fit, out$sims.list$fit.new, main =
       "Posterior predictive check \nfor sum of squared Pearson residuals",
     xlab = "Discrepancy measure for actual data set",
     ylab = "Discrepancy measure for perfect data sets")
abline(0,1, lwd = 2, col = "black")
savePlot(filename = "Pos_predi", type ="png")

# Bayes p value
mean(out$sims.list$fit.new > out$sims.list$fit)

# DIC
out$DIC

# pD
out$pD
```

```
hist(out$sims.list$beta_1, col = "grey", las = 1, xlab = "Coefficient for ad_bin", main = "")
abline(v = 0, lwd = "2", col = "red")
abline(v = c(out$summary["beta_1", "2.5%"], out$summary["beta_1", "97.5%"]), lwd = 3, col = "blue")
#savePlot(filename = "ad_bin_density", type ="png")

hist(out$sims.list$beta_2, col = "grey", las = 1, xlab = "Coefficient for O depth", main = "")
abline(v = 0, col = "red")
abline(v = c(out$summary["beta_2", "2.5%"], out$summary["beta_2", "97.5%"]), lwd = 3, col = "blue")
#savePlot(filename = "o_depth_density", type ="png")

hist(out$sims.list$beta_3, col = "grey", las = 1, xlab = "Coefficient for tree height", main = "")
abline(v = 0, col = "red")
abline(v = c(out$summary["beta_3", "2.5%"], out$summary["beta_3", "97.5%"]), lwd = 3, col = "blue")
#savePlot(filename = "height_density", type ="png")
#================================================
#save.image(file = "cand_2_data.RData")
```

Appendix 5 - SORTIE-ND parameter file for Coed-y-Brenin PSPs CyB4, CyB5 and CyB7 and DF, SNS, HWD, SWD and *Rhododendron ponticum* (RP)

Plot

Number of Timesteps	100
Current Timestep	0
Random Seed	0
Number of years per timestep	1
Plot Length in the X (E-W) Direction, in meters	100
Plot Length in the Y (N-S) Direction, in meters	100
Plot Latitude, in decimal degrees	52.47
Plot title	CyB_all

Allometry

	DF	SNS	HWD	SWD	RP
Slope of DBH to Diameter at 10 cm Relationship	0.5989	0.4667	0.5968	0.6600	1.0000
Intercept of DBH to Diameter at 10 cm Relationship	0.0000	0.0000	0.0000	0.0000	0.0000
Maximum Tree Height, in meters	70.3292	80.0000	24.5249	22.8858	6.0000
Slope of Asymptotic Height	0.0147	0.0090	0.0688	0.0350	NA
Slope of Height-Diameter at 10 cm Relationship	1.0770	0.8453	0.7280	0.8897	0.5300
Intercept of Height-Diameter at 10 cm Relationship	0.1000	0.1000	0.1000	0.1000	0.1000
Slope of Asymptotic Crown Radius (a)	0.2000	0.6293	0.0484	0.3826	0.5184
Crown Radius Exponent (b)	0.5984	0.3014	1.0000	0.4850	0.5283
Slope of Asymptotic Crown Depth (a)	0.4156	1.1085	1.5480	1.1459	0.0000
Crown Depth Exponent (b)	1.0915	0.8382	0.6755	0.8620	0.0000
Adult linear function slope	NA	NA	NA	NA	0.5300
Adult linear function intercept	NA	NA	NA	NA	0.1000
Sapling linear function slope	NA	NA	NA	NA	0.5300
Sapling linear function intercept	NA	NA	NA	NA	0.1000

Tree Population

New Seedling Diameter at 10 cm	0.1
Seedling Height Class 1 Upper Bound, in cm	20
Seedling Height Class 2 Upper Bound, in cm	30
Tree Map To Add As Text	

	DF	SNS	HWD	SWD	RP
Minimum Adult DBH	10	10	10	5	7.32
Max Seedling Height (meters)	1.35	1.35	1.35	1.35	1.35

Light

Beam Fraction of Global Radiation	0.3
Clear Sky Transmission Coefficient	0.65
First Day of Growing Season	92
Last Day of Growing Season	288
Number of Azimuth Sky Divisions for Quadrat Light Calculations	36

Number of Altitude Sky Divisions for Quadrat Light Calculations	9
Minimum Solar Angle for Quadrat Light, in rad	0.785
Height at Which GLI is Calculated for Quadrats, in meters	0.675
Height of Fisheye Photo	Mid-crown
Quadrat GLI - Always Calculate All GLIs	FALSE
Upper Age (Yrs) of Snag Light Transmission Class 1	7
Upper Age (Yrs) of Snag Light Transmission Class 2	17
Number of Azimuth Sky Divisions for GLI Light Calculations	18
Number of Altitude Sky Divisions for GLI Light Calculations	12
Minimum Solar Angle for GLI Light, in rad	0.785
Sail Light Minimum Solar Angle, in degrees	30
Sail Light Maximum Shading Neighbor Distance, in meters	15
Calculated Crown Depth	All height

	DF	SNS	HWD	SWD	RP
Amount Canopy Light Transmission (0-1)	0.5474	0.5840	0.058	0.4810	0.000
Snag Age Class 1 Amount Canopy Light Transmission (0-1)	0.446	0.446	0.695	0.446	0.000
Snag Age Class 2 Amount Canopy Light Transmission (0-1)	0.502	0.502	0.755	0.502	0.000
Snag Age Class 3 Amount Canopy Light Transmission (0-1)	0.673	0.673	0.883	0.673	0.000

Growth

Mortality Threshold for Suppression	0.1
Years Exceeding Threshold Before a Tree is Suppressed	3
NCI DBH Divisor (q)	1000
Include Snags in NCI Calculations	FALSE

	DF	SNS	HWD	SWD	RP
Asymptotic Diameter Growth (A)	0.6230	0.6230	0.6880	0.8580	NA
Slope of Diameter Growth Response (S)	0.0170	0.0170	0.0440	0.0270	NA
Length of Last Suppression Factor	0.0000	0.0000	0.0160	0.0000	NA
Length of Current Release Factor	0.0260	0.0260	0.0150	0.0000	NA
NCI Maximum Potential Growth, cm/yr	1.2127	1.1875	0.6501	2.1520	NA
NCI Maximum Crowding Distance, in meters	10.5150	0.2820	0.0000	5.2007	NA
NCI Alpha	2.1349	2.0212	2.2397	3.4140	NA
NCI Beta	0.8677	0.6394	0.6782	0.2153	NA
NCI Size Sensitivity to NCI (gamma)	1.0000	1.0000	1.0000	1.0000	NA
NCI Crowding Effect Slope (C)	0.0045	0.0163	0.0000	0.2626	NA
NCI Crowding Effect Steepness (D)	0.7073	3.3174	0.0000	0.3043	NA
NCI Neighbor Storm Damage (eta) - Medium (0-1)	1	1	1	1	NA
NCI Neighbor Storm Damage (eta) - Complete (0-1)	1	1	1	1	NA
NCI Minimum Neighbor DBH, in cm	5	5	5	5	0.0

	DF	SNS	HWD	SWD	RP
NCI Size Effect Mode, in cm (X0)	42.3061	27.3363	19.6605	113.6954	NA
NCI Size Effect Variance, in cm (Xb)	0.8385	0.7404	0.5305	9.7224	NA
NCI Shading Effect Coefficient (m)	1.0040	0.3661	0.9255	0.0000	NA
NCI Shading Effect Exponent (n)	1	1	1	1	NA
NCI Damage Effect - Medium Storm Damage (0-1)	1	1	1	1	NA
NCI Damage Effect - Complete Storm Damage (0-1)	1	1	1	1	NA
Western Hemlock NCI Lambda Neighbors	1.0000	0.1869	0.1017	0.2187	NA
Western redcedar NCI Lambda Neighbors	0.7303	0.3422	0.0072	1.0000	NA
Amabalis Fir NCI Lambda Neighbors	0.4385	1.0000	0.1000	0.6427	NA
Subalpine Fir NCI Lambda Neighbors	0.8381	0.9088	1.0000	0.4594	NA
Hybrid spruce NCI Lambda Neighbors	0.0000	0.0000	0.0000	0.0000	NA
Lodgepole Pine NCI Lambda Neighbors	0.0000	0.0000	0.9854	0.3166	NA
Trembling Aspen NCI Lambda Neighbors	0.0000	0.0165	0.0095	0.1154	NA
Black Cottonwood NCI Lambda Neighbors	0.5372	0.1152	0.5164	0.2839	NA
Paper Birch NCI Lambda Neighbors	0.0104	0.0000	0.9669	0.9330	NA

Mortality

DBH of Maximum Senescence Mortality Rate, as an integer in cm	200

	DF	SNS	HWD	SWD	RP
Mortality at Zero Growth	1	1	1	1	NA
Light-Dependent Mortality	5.913	5.913	2.0931	11.544	NA
Senescence Mortality Alpha	-3.7	-3.7	-3.7	-3.7	NA
Senescence Mortality Beta	0.12	0.12	0.2	0.135	NA
DBH at Onset of Senescence, in cm	63	72	22	20	NA
Adult Background Mortality Rate	5.00E-04	5.00E-04	9.00E-03	5.00E-04	NA
Juvenile Background Mortality Rate	0.01	0.01	0.01	0.01	NA
Weibull Annual "a" Parameter for Snag Size Class 1 Mortality	0.05	0.05	0.05	0.05	NA
Weibull Annual "a" Parameter for Snag Size Class 2 Mortality	0.05	0.05	0.05	0.05	NA
Weibull Annual "a" Parameter for Snag Size Class 3 Mortality	0.05	0.05	0.05	0.05	NA
Weibull Annual "b" Parameter for Snag Size Class 1 Mortality	2.5	2.5	2.5	2.5	NA
Weibull Annual "b" Parameter for Snag Size Class 2 Mortality	2.5	2.5	2.5	2.5	NA
Weibull Annual "b" Parameter for Snag Size Class 3 Mortality	2.5	2.5	2.5	2.5	NA
Weibull Upper DBH of Snag Size Class 1	8	8	8	8	NA
Weibull Upper DBH of Snag Size Class 2	20	20	20	20	NA

Disperse

Maximum Parent Trees Allowed in Gap Cell	0
Seed Distribution	Deterministic

	DF	SNS	HWD	SWD	RP
Minimum DBH for Reproduction, in cm	15	15	10	10	7.32
STR/n for Stumps	0	0	0	0	NA
Beta for Stumps	0	0	0	0	NA
Seed Dist. Std. Deviation (Norm. or Log.)	0	0	0	0	NA

	DF	SNS	HWD	SWD	RP
Seed Dist. Clumping Parameter (Neg. Binomial)	0	0	0	0	NA
Canopy Function Used	Weibull	Weibull	Weibull	Weibull	Weibull
Gap Function Used	Weibull	Weibull	Weibull	Weibull	NA
Weibull Canopy Annual STR/n	3.4412	3.4412	3.2012	3.865	5000.0000
Weibull Canopy Beta	2	2	2	2	0.0000
Weibull Canopy Theta	3	3	3	3	5.0000
Weibull Canopy Dispersal	3.00E-05	3.00E-05	2.33E-04	1.76E-04	0.0100
Weibull Gap Annual STR/n	2.3828	2.3828	3.832	1.2816	NA
Weibull Gap Beta	2	2	2	2	NA
Weibull Gap Theta	3	3	3	3	NA
Weibull Gap Dispersal	6.93E-06	6.93E-06	7.76E-06	1.14E-06	NA
Lognormal Canopy Annual STR/n	0	0	0	0	NA
Lognormal Canopy Beta	0	0	0	0	NA
Lognormal Canopy Xb	0	0	0	0	NA
Lognormal Canopy X0	0	0	0	0	NA
Lognormal Gap Annual STR/n	0	0	0	0	NA
	DF	SNS	HWD	SWD	NA
Lognormal Gap Beta	0	0	0	0	NA
Lognormal Gap Xb	0	0	0	0	NA
Lognormal Gap X0	0	0	0	0	NA
Slope Mean Non-Spatial Seed Rain, seeds/m2/ha of BA/yr	0	0	0	0	NA
Intercept of Mean Non-Spatial Seed Rain, seeds/m2/yr	0	0	0	0	NA

Establishment

	DF	SNS	HWD	SWD	RP
Proportion germinating between 0 and 1	0.05	0.05	0.05	0.05	0.1109
GLI of Optimum Establishment, 0 – 100	NA	NA	NA	NA	90.0
Slope of Dropoff Below Optimum GLI	NA	NA	NA	NA	0.01206
Slope of Dropoff Above Optimum GLI	NA	NA	NA	NA	-0.01206