MECHANISMS OF INTERFERENCE BETWEEN KAHIKATEA AND GREY WILLOW IN THE WAIKATO

A thesis

submitted in partial fulfillment

of

the requirements for the Degree

of

Master of Science in Biological Sciences

at

The University of Waikato

by

Emma Coleman

2010

ABSTRACT

Research was undertaken to determine the nature of the coexistence between kahikatea and grey willow in the Waikato Ecological Region. Three main questions were investigated. Is grey willow inhibiting recruitment of kahikatea? If this is occurring, which mechanisms (of interference) are involved? And does anthropogenic disturbance influence this interaction?

The first and third were addressed by measuring kahikatea and grey willow populations for age, stem frequency and diameter at six sites, to assess how populations were structured, to reconstruct the population histories at each site and to determine whether kahikatea is successfully regenerating and what possible factors influence regeneration. Results indicated grey willow was establishing after kahikatea populations at all but the Totara Park site, and that once grey willow had reached the canopy, no further recruitment of kahikatea into the canopy occurred. No kahikatea saplings were present in grey willow densities above two per $10m^2$ and sapling presence did not always result in canopy emergence. Sites containing the highest sapling frequencies were those most recently exposed to moderate to large-scale disturbance, and those closest to a large seed source, rather than those with long established kahikatea populations. This suggests anthropogenic disturbance of certain scale and frequency can promote the regeneration of both species.

The second question was investigated using a range of methods. Dendrochronology was employed to compare diameter growth rates between the species at each site and found grey willow only performed marginally better than kahikatea and its competitive advantage in reaching the canopy faster is likely exerted via more rapid height growth rates. Experimental methods involved measuring annual height and diameter growth rates of forty introduced and twenty naturally established seedlings in various grey willow canopy treatments and water table heights in Totara Park, Hamilton city. Hemispherical photography and water table measurements were used to quantify seedling microhabitats. The greatest seedling diameter and height growth rates were recorded in the open canopy introduced treatment and the lowest in the closed canopy naturally established treatment irrespective of water table height. The reduction in summer light levels from a grey willow canopy regularly caused apical stem death or reduced growth rates of kahikatea seedlings.

Interference effects from allelopathy were investigated as previous research indicated kahikatea litter is toxic to its own seedlings. A trial was set up using potted grey willow cuttings and *Sinapus alba* seedlings and regularly sprayed with kahikatea litter extract. Results were inconclusive and the natural concentrations of kahikatea litter found at Totara Park did not appear to affect the growth of either species.

Overall this research suggests grey willow is inhibiting kahikatea regeneration via overtaking kahikatea growth to the canopy, shading out further recruitment, and maintaining dominance through efficient vegetative reproduction. Active management is required to ensure the return to dominance of kahikatea in Waikato swamp forests and highly disturbed sites, close to abundant seed source may provide novel opportunities for restoration.

ACKNOWLEDGEMENTS

Firstly I would like to thank my primary supervisor, Professor Bruce Clarkson, your enthusiasm for plant ecology is infectious! Thank you for introducing me to the subject of this research and providing the encouragement and opportunity necessary for me to complete this thesis. Also, my secondary supervisor, Dr. Chrissen Gemmill, for providing much needed constructive criticism of my drafts. And the University of Waikato, for funding through the Masters Research Scholarship and the FRST urban restoration programme (UOWX0501).

A big thank you to the Biological Sciences technician Toni Cornes, you were always there to help and field endless questions, supply required equipment, make pretty study site maps and stuck around the longest to help me in the field. Dr. Jacques Boubée for introducing me to the Tamahere Reserve site, and a great help in sampling it. Stu Clarke for providing access through his farm to the Kopuatai Wetland site. The DoC staff at the Waikato area office for directions on how to get to the Kopuatai site and the permit. Liz Overdyck for instruction on the method of increment coring. Dr. Mike Clearwater for training on the use of a hemispherical camera. Dr. Peter J. Morris for supplying kahikatea seedlings of local provenance. Don McLean for supplying unpublished increment core data on kahikatea at Totara Park. Mark Smale for giving us a good deal on tree tags. Stacey Foster, Claire Taylor and James Pilkington for field work support, which cannot be understated considering the nature of my study environments.

And a final thanks to my family. Dad, your awesome building skills came in handy once again when constructing increment core displays. Diane, your patience, nursery experience and contacts proved invaluable for sourcing kahikatea seedlings and growing my grey willow cuttings. Mum and Suze, for assisting me in the field, proofing my drafts, and supporting me in times of craziness.

TABLE OF CONTENTS

LIST OF FIGURES

Figure **Page**

Chapter 1

Chapter 2

Chapter 3

Chapter 4

LIST OF TABLES

Table **Page**

Chapter 1

Chapter 2

Chapter 3

CHAPTER 1: INTRODUCTION

General introduction

Plant interference encompasses all interactions that result from one plant affecting the population density of another, either through competition or allelopathy (Muller 1966, 1969; Rice 1984; Zimdahl 1999). For plants, competitive effects on the population density of another species are usually exerted via reductions in resource availabilities (Tilman 1997). Allelopathic effects are exerted via the addition of biochemicals to the immediate environment (Rice 1984). Understanding the role of interference in determining species organization in forest communities is of great interest to ecologists and still not fully understood. In the natural world, habitats are generally heterogeneous and resource availabilities tend to fluctuate, which can obscure the effects of competition and allow plants to coexist through occupying spatially separate localities and diverging in their allocation or tolerance of available resources (Fowler 1988). Direct evidence from experimental manipulation of natural forest environments is difficult to obtain (Duncan 1991) and replication and the use of adequate controls is challenging in ecological studies (Hurlbert 1984). The solution to these problems at present is to illustrate the effects of interference via changes in plant performance including growth and survival (eg. Moen & Meurk 2001), or spatial distribution, which involves testing for random vs. non random mortality caused by the closeness of conspecifics (Duncan 1991).

Before European arrival, New Zealand's tallest tree, the endemic podocarp kahikatea *Dacrycarpus dacrydioides* (A. Rich.) de Laubenfels, formed a major component of the podocarp forests of the Waikato, which covered an estimated 51.6% of the region (Harding 1997; Leathwick et al. 1995). Extensive harvesting of timber, conversion of forest to farmland and the channelization of waterways (for flood prevention) has since severely reduced this forest type (Wardle 1974; Burns *et al.* 2000), until only an estimated 0.3% of this underrepresented forest remains in the Waikato Ecological Region (Harding 1997; Leathwick *et al.* 1995). An intermittent and extensive degree of landscape disturbance (Veblen & Stewart 1980; Veblen 1992; Ogden & Stewart 1995) is required to provide the optimum large open sites for kahikatea seedlings to colonise and gain a head start in overtopping competitors, particularly faster growing angiosperms (Wardle 1974;

Beveridge 1983; Bond 1989; Duncan 1993). Because kahikatea colonises disturbed sites early, it is described as a long-lived pioneer (Ogden & Stewart 1995) that maintains dominance for hundreds of years. Pioneer species are generally not self-perpetuating (unless exposed to continuous disturbance) because the seedlings fail to mature under an adult canopy due to shade intolerance (Whitmore 1988; Veblen 1992). This makes kahikatea vulnerable to competitive effects from other pioneer species that are able to gain greater height in shorter time periods.

Since it was first recorded in 1957 in the Waikato (Champion 1994), grey willow (*Salix cinerea*) has replaced much of the true swamp forest that was once dominated by kahikatea (Champion 1988; Clarkson *et al.* 2002) and is the second most common exotic species in New Zealand after *Pinus radiata* (NWASCA 1987). The woody shrub or small tree successfully achieved dominance in many New Zealand swamps because it is fast growing and shades out most species, is able to reproduce both vegetatively and sexually, is a prolific producer of highly dispersible seed and has numerous physiological adaptations to persisting in a swamp environment (Partridge 1994; Champion 1994). In 1994, willow wetlands consisting mainly of grey and crack willow (*Salix fragilis*) species comprised 169 ha of the Waikato Ecological District (159 376 ha), comparable to the area remaining in indigenous podocarp forest (253 ha; Harding 1997; Leathwick et al. 1995). Grey willow is often found alongside Kahikatea throughout the Waikato (Clarkson *et al* 2002; Champion *et al.* 1993; de Winton & Champion 1993).

The focus of this study is to determine the nature of the coexistence between kahikatea and grey willow in the Waikato Ecological Region. What is the role of interference in structuring the populations of these two species and more specifically is grey willow inhibiting the recruitment of kahikatea? Does anthropogenic disturbance, along an urban to rural landscape gradient, influence this interaction? It is hoped the results in this study will contribute to understanding aspects of ecological competition theory and provide scientifically based recommendations for regional councils, land owners and other organizations in New Zealand who wish to promote the recruitment of kahikatea and/or the control of grey willow.

Chapter outline

The overall aim of this research was to quantify specific interactions between grey willow and kahikatea to allow further understanding of the impact grey willow has on kahikatea growth rate and regeneration. This thesis consists of five chapters. Following is a brief outline of the main aims of each chapter. Specific objectives of this research as discussed in more detail in the final section of the introduction.

Chapter one introduces the nature of this study and the research questions it seeks to answer. An ecological theoretical framework is constructed to explain the mechanisms of species coexistence and inhibition. Kahikatea and grey willow are described with reference to their taxonomic and botanical attributes and their geographic distribution. The species competitive strategies for regeneration and niche occupation are compared. Previous research findings are incorporated where they apply to the research objectives of this study.

Chapter two consists of a population analysis of kahikatea and grey willow at five swamp sites along an urban to peri-urban to rural gradient to assess whether the presence and proximity of grey willow is affecting the distribution, growth and regeneration of kahikatea and if this changes with respect to the level of disturbance at the site. A dendrochronological analysis for both species is undertaken to assist in reconstructing the demographic histories at each site.

Chapter three measures kahikatea seedling growth responses to changes in the light resource under and free of a grey willow canopy and after canopy release at Totara Park, Hamilton city. The light and water table environments at each seedling location are quantified with the aim to test for any significant effect of a grey willow canopy on kahikatea sapling growth and the possible reasons for this interaction.

Chapter four seeks to determine whether kahikatea exerts an allelopathic effect on grey willow, as kahikatea has been shown to display autotoxicity (Molloy *et al.* 1978). The chapter consists of a single experiment to assess and compare the responses of grey willow cuttings and white mustard seedlings to repetitive spraying of increasing concentrations of kahikatea litter extract. This chapter also reports on a small grey willow seed germination trial.

Chapter five summarizes the final conclusions and places them in context of the research aims. Recommendations for the management of Waikato swamp forests containing kahikatea and grey willow populations are outlined to promote kahikatea recruitment and suggestions for further research are made in the final paragraphs.

Ecological interference

Harper (1961) used the term ‘interference’ to broadly describe the loss of vigor or productivity of one individual caused by the close proximity of another. Muller (1969) incorporated both competition and allelopathy under the term of interference, which is now commonplace (Harper 1975; Rice 1984; Nilsson 1994; Zimdahl 1999; Foy & Inderjit 2001). Tilman (1997) describes competition as any negative impact on a species growth, fecundity or survival caused by another individual or group of individuals of the same or different species, that for plants is usually exerted via a reduction in resource availability and does not include allelopathy (the addition of biochemicals to the environment). Competition intensity refers to the combined effect of neighbours to reduce the ability of an individual or population to acquire a resource of limited availability (Keddy 1989). The limiting resource in turn determines the maximum growth rate attainable, which is further reduced if neighbours also consume this resource (Tilman 1997). Fundamental to the theory of competition is the concept of the ‘niche’, which is a broad term that encompasses a species environmental tolerances and habitat and resource requirements, and in the presence of vegetation associates, interference may restrict the volume of this niche (Hutchinson 1957; Slobodkin 1961a). Hardin (1960) developed the competitive exclusion principal, which asserts complete competitors cannot coexist. If a community is experiencing competition, then individuals with fewer or more distant neighbours should perform better (Weiner 1984). The key question ecologists seek to answer is how important is competition in defining community structure (Antonovics & Levin 1980)?

Mechanisms for species coexistence

Rees *et al.* (2001) outline three methods less competitive species use to avoid the negative effects of competition. These include greater tolerance of shade, greater colonization ability and/or the successful exploitation of temporally infrequent and variable regeneration opportunities such as forest gap creation. Wilson's (1990) review of the twelve mechanisms to avoid competitive exclusion includes; niche diversification, pest pressure, equal chance, gradual climate change, intermediate-timescale disturbance, life history differences, initial patch composition, spatial mass effect, circular competitive networks, cyclic succession, aggregation and stabilizing coevolution. He concludes niche diversification, gradual climate change, spatial mass effect and cyclic succession are likely the most important mechanisms to explain the occurrence of species coexistence in New Zealand forests (without competitive exclusion occurring).

Niche diversification was first defined by Connell (1978) and states divergence in a species niche (ie. geographical, resource or phenological), permits community coexistence. Clarkson *et al.* (2009) illustrated this in the coexistence of *Empodisma minus* and *Sporadanthus ferrugineus* in New Zealand raised bogs. They identified differentiation in spatial root structure which enabled the species to exploit different nutrient sources and concluded this may provide a mechanism for coexistence or at least to slow the rate of competitive displacement. The spatial mass effect (Shmida & Ellner 1984) occurs when a population is maintained in the margin habitats (e.g. edge effect) but does not increase in the patch itself because the number of immigrating individuals equals the death of individuals within the patch. Gradual climate change refers to the fact certain species are favored in particular environmental conditions over others and that the environment is dynamic. Therefore at any one time the community contains a mix of species adapted to the current environment and 'remnant' species from previous climates. Wardle (1963) refers to this when explaining the regeneration gap of New Zealand conifers, and estimates the change occurred between 1600 and 1800 AD. However the conifer regeneration gap has also been explained as a consequence of the high light requirements of podocarps (Beveridge 1983; Norton *et al.* 1988). The process of cyclic succession (Watt 1947) is similar to that of gradual climate change except involves entire communities. It is also not separable from the mechanism of intermediate-timescale disturbance because disturbance creates the opportunities involved in this mechanism (Wilson 1990). An example of this is the demonstrated autotoxicity kahikatea seedlings experience from adult litter (Molloy *et al.* 1978), thereby inhibiting kahikatea participation in later successional sequences until another catastrophic disturbance event occurs. It is possible that grey willow has the ability to prevent cyclic successional processes from progressing, due to its ability to withstand disturbance and resprout, therefore maintaining a presence in the canopy (Whitmore 1988). The mechanism of intermediate-timescale disturbance (Margalef 1963; Connell 1978) is particularly relevant for species that regenerate as cohorts (Ogden *et al.* 1987). If the disturbance event is too common, species are likely to be lost from the community, if the disturbance is not common enough it is possible competitive exclusion may occur due to the length of time competition will have to take effect. Intermediate levels promote the highest species coexistence. Picket (1980) illustrates this mechanism will create patches of species A and older patches containing species B, and within patch coexistence. Duncan (1993) uses this mechanism to explain the continuing dominance of kahikatea floodplain forest over angiosperm competitors.

Measuring competition

Experimental studies of competition between native and invasive species in forest types targeted for restoration may uncover the mechanisms for dominance by invasive species in turn aiding the development of management strategies (Menninger & Palmer 2006). However proving competition is the dominant factor limiting restoration is challenging (Seabloom *et al.* 2003). Antonovics & Levin (1980) state competition between members of a plant community can only be accurately demonstrated using perturbation analysis (species removals and/or additions), which distinguishes between whether coexistence results from an absence of competition or precedes it. Putwain & Harper (1970) recommended the use of the release technique (which is a form of perturbation analysis), whereby the response of species A is measured after the removal of species B. Keddy (1989) states it is a priority to establish whether an individual’s dominance is a result of its superior competitive ability or its ability to tolerate low resource levels, as the latter could occur in the absence of competition.

Kahikatea and grey willow

Taxonomy and botanical description

Kahikatea (*Dacrycarpus dacrydioides*) is New Zealand’s tallest tree, growing up to 60 metres tall and 1.6 metres in diameter (Salmon 1980). In forested sites the trunk is ‘often unbranched for a greater part of its height’ (Entrican 1949), with a reduced crown (Figure 1), while in full sun branches often begin lower on the trunk giving a ‘cigar’ shape (Philipson & Molloy 1990). The trunk is often fluted or buttressed and the grey, ‘hammer-marked’ bark flakes off in rounded fragments (Entrican 1949; Poole & Adams 1963; Salmon 1980; Philipson & Molloy 1990). Kahikatea passes through several morphological stages (Salmon 1980). Seedlings are distinguished by the presence of two opposite cotyledons topped by four branchlets at right angles to each other (Foweraker 1929; Philipson & Molloy 1990). Juvenile foliage generally lasts until heights of 1-2m, where it is replaced by semi-adult and adult foliage (Figure 2), and all foliage stages may be present on one tree (Salmon 1980). Juvenile leaves are long (up to 7mm), narrow (~1mm), 2-ranked, slightly curved with acute tips. Semi-adult leaves are shorter (~4mm), not so closely appressed and arranged spirally. Adult leaves are scale-like up to 2mm in length and closely appressed to the stem (Entrican 1949; Cockayne & Phillips-Turner 1967; de Laubenfels 1969; Salmon 1980; Philipson & Molloy 1990).

Like the majority of genera within the Podocarpaceae, kahikatea is dioecious (de Laubenfels 1969). Male cones are 5-8mm long and female cones are 1-2mm long (Figure 3; McEwen 1988) and both are found terminally positioned on branchlets. Pollen grains are monad (occur as single grains), heteropolar, bilateral, vesiculate and trisaccate (3 winged) and 50-70µm long (Pocknall 1981). Female cones consist of a cluster of ovuliferous scales, of which only one matures into a seed (Foweraker 1929). After pollination the receptacle begins to develop from green to yellow to orange and finally red (Salmon 1980). The mature seed is an ‘ovoid black nut’, around 4mm in length (Poole & Adams 1963).

All the New Zealand podocarps have an ancient lineage, stretching back to around 135-190 million years ago. Pollen grains of *Dacrycarpus* found in the Nelson district dated to between 100 and 135 million years ago. The likely ancestor of *D.*

Figure 1 Mature kahikatea (ages estimated between 250 to 350 years old) at Silverdale gully, Hamilton.

Figure 2 Two ranked juvenile leaves (left) and spirally arranged, closely appressed adult leaves (right).

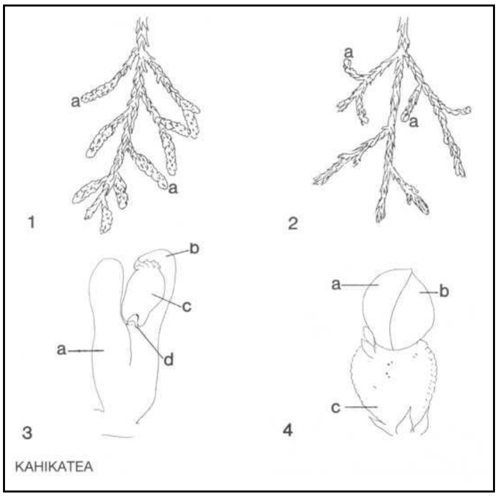

Figure 3 Kahikatea male and female cone structures (Figure produced by McEwen 1988). 1 - Male cones (terminal on branchlet, 5-8mm). 2 - Female cones (terminal, 1-2mm). 3 - Ovule (2mm) missing 10 surrounding scale leaves, a. Bract, b. Carpidium, c. Epimatium, d. Micropyle mouth. 4 - 'fruit' (8mm), a. Carpidium, b. Purple-black epimatium (surrounds seed), c. Receptacle (red).

dacrydioides was identified as *Podocarpidites ohikaensis*, fossils of which date back to around 54 – 37 million years ago (Salmon 1980; Kelch 1998). *Dacrycarpus dacrydioides* was originally classified *Podocarpus dacrydioides* by A. Rich. (1832), who based this on observations made by D´Urville in 1827. However there were additional classifications that were not legitimised. These included; *Podocarpus thujoides* by Mirb. in 1825, *Dacrydium excelsum* by Cunn in 1838 and *Nageia excelsa* also by Cunn. in 1891. The *Podocarpus* genus originally contained 8 sections and well over 100 species. Differences between species were as large as distances that separate most other genera. For these reasons de Laubenfels proposed to elevate four sections (and an additional section from *Dacrydium)* to their own genera, eventuating in the present 12 genera, including *Dacrycarpus*.

All *Dacrycarpus* lack cataphylls (differentiated bud scales at the tips of branchlets) and have juvenile 2-ranked leaves (Philipson & Molloy 1990), however their distinguishing character is the fusion of the bract between seed and seed scale on one side (de Laubenfels 1969). *D. dacrydioides* is distinguished from other species of *Dacrycarpus* by the terminal position of the pollen cones (and ovules), the development of 'short shoots' (younger trees only) from dormant buds in the axis of leaves on the proximal primary and lateral branches, scale-like foliage leaves that are longer than the involucral leaves and involucral leaves that do not enclose the seed or receptacle (de Laubenfels 1969). *D. dacrydioides* is the only temperate species of *Dacrycarpus* (de Laubenfels 1969). Hawkins & Sweet (1989) found optimum temperatures for growth and photosynthesis in New Zealand podocarps were day temperatures of 27ºC and night temperatures between 22ºC and 27 ºC. They state this provides strong evidence all New Zealand podocarps, including *D. dacrydioides* evolved in sub-tropical environments. Morphological phylogenies of the podocarpaceae place the *Dacrycarpus* genus closest to *Dacrydium* and *D. dacrydioides* is named after *Dacrydium cupressinum* (Kelch 1998). Recent molecular analysis of the family, using 18S rDNA and indels, has found *Dacrycarpus* is actually closest to the *Podocarpus* genus (Kelch 1998).

Salix cinerea, or grey willow, is a deciduous shrub or small tree, typically growing to heights of 5 to 10m. The bark is smooth, but cracks in water logged environments due to the production of lenticels (Champion 1994). The species forms dense thickets, shown in Figure 4 (Webb *et al.* 1988), and has sympodial growth, meaning after the apical meristem dies in winter, growth resumes from the lateral meristems. This increases branch angling as the individual matures with lower branches often becoming horizontal and reduces self-shading. Branches are flexible at the base and branchlets are green or greenish grey, pilose and flexible (Webb *et al.* 1988; Argus 1997). Leaves are 2 to 7cm long and 1.5 to 3.5cm across, often smaller at the base of lateral shoots, glandular and obovate to elliptic in shape (Webb *et al.* 1988; Argus 1997). The margins are serrulate to sub-entire and the undersides are grey or glaucous in colour and densely clothed in soft grey or white hairs (Webb *et al.* 1988). Petioles are short (under 1cm) and pilose (Webb *et al.* 1988).

The dioecious species produces catkins before leaves in September to October, which are 1.5 to 3.5 centimetres long and broadly cylindric to cylindric-ovate in shape (Webb *et al.* 1988). Flower bracts are brown to black with an obtuse to rounded apex. Staminate catkins contain two stamens, pilose filaments and are silvery at first but turn yellow once the pollen is released (Meikle 1984). Pistillate catkins have pedicels larger than the bracts, and stalked ovaries which are white and tomentose. There are 3 to 13 ovules per carpel, and seed is small and attached to white cotton like hairs, which aid in wind dispersal (Meikle 1984).

Figure 4 *Salix cinerea* and *S. fragilis* carr, Silverdale gully, Hamilton.

The *Salix* genus is extremely large and complex with species estimates varying from 330 (Skvortsov 1968b) to 526 (Fang 1987). As a result it has had a long history of classification (see Argus (1997) for a good summary) with modification, and a completely natural classification is still unreached. Molecular phylogenetic analysis of cpDNA using random fragment length polymorphisms (Brunsfeld *et al* 1992) and the rbcL loci (Azuma *et al.* 2000) have been undertaken, but did not resolve the evolutionary path of *Salix,* and further study using nuclear markers was recommended. The genus has been further divided into tribes, subseries, subsections, subgenera, stirpes, series, sections, rotten, groups, divisions and cohorts, but there has been little consistency in their application (Argus 1997). However there are 20 sections with more than two species which are widely acknowledged. These include; *Candidae Hastatae, Chamaetia, Cinerella*, *Cordatae*, *Diplodictyae, Geyerianae, Glaucae*, , *Herbella, Humboldtianae, Lanatae, Longifoliae, Mexicanae, Myrtilloides, Myrtosalix, Ovalifoliae, Phylicifoliae, Salicaster*, *Sitchenses* and *Villosae* (Argus 1997). *Salix cinerea* is one of 10 species belonging to the section *Cinerella*.

Salix cinerea contains two subspecies; *Salix cinerea* subsp. *cinerea* (species present in the Waikato) and *Salix cinerea* subsp. *oleifolia*. Meikle (1984) outlined the differentiation of the sub-species is based on five main characters. The former tends to be slightly shorter (ca. 5 metres), has smoother bark, the leaf undersides contain yellow-grey hairs and the stipules are large. *Salix cinerea* subsp. *oleifolia* has finer red-brown hairs on the leaf underside and small stipules. Their respective areas of origin also differ with the sub-species *cinerea* emerging from Central and Eastern Europe and Western Asia, while *oleifolia* occupied Western Europe and North Western Africa.

The highest numbers of native *Salix* species are found in China (ca. 270 sp.), the former Soviet Union (ca. 120 sp.), North America (ca. 103 sp.) and Europe (ca. 65 sp.). Native species of *Salix* are also found in Japan, Africa, the Middle East, India and Central and South America, but are only introduced or naturalized in Oceania (Argus 1997). Hybridisation and introgression is common in the Salicaceae (Brunsfeld *et al.* 1992), which is partly why the classification of this genus is so complex. For instance there are intermediate hybrids between subsp. *cinerea* and *oleifolia*, making it impractical to treat the subspecies as separate species (Webb *et al.* 1988). Polyploidy is also common, in 1926 Harrison identified *Salix cinerea* as a tetraploid and the section *Cinerella* contains species with the chromosome numbers 2n = 38, 57, 76, 95 or 114 (Argus 1997).

Distributions in New Zealand

Kahikatea occurs on all three main islands (Figure 5), but is rare on Stewart Island (Cockayne & Phillips-Turner 1967). It occurs in greatest densities on the post glacial alluvial terraces of South Westland, (Foweraker 1929; Wardle 1974) and the recent alluvial gley soils of the Waikato and Manawatu (Smale 1984; Smale et al. 2005). Kahikatea generally occurs below 100 metres above sea level (Wardle 1991), but is found at altitudes up to 600 metres (Salmon 1980), more often in the North Island (Entrican 1949). The last glacial period did not appear to negatively impact on kahikatea distribution (Kershaw & McGlone 1995), however gaps in kahikatea distribution naturally occur in the South Island along the Alps and directly east due to beech distribution and altitude and moisture gradients.

At the time of European settlement kahikatea dominant forest was a major feature in the landscape. Timber harvesting (Wardle 1974), mostly to produce butter boxes until 1946, and forest clearance for farmland has greatly reduced kahikatea populations. Maximum butter box production in the 1920’s removed 170 000 m^3

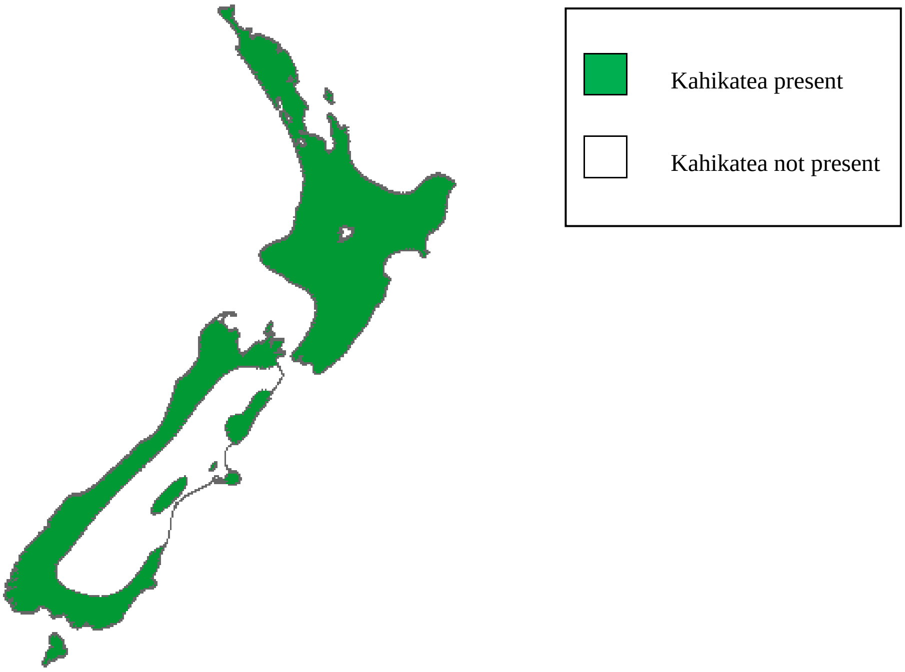

Figure 5 The geographical distribution of *Dacrycarpus dacrydioides* within New Zealand (Metcalf 2002).

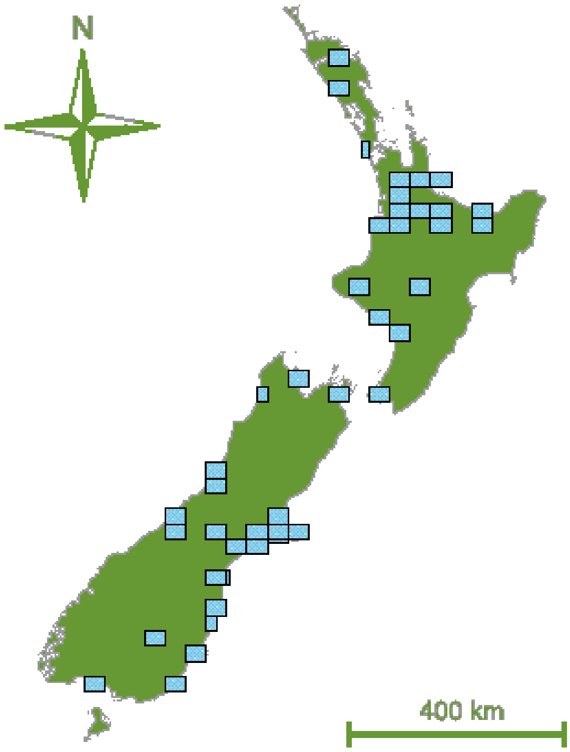

Figure 6 The geographical distribution of Salix cinerea within New Zealand (each rectangle represents a New Zealand 260 Map Series (1:50,000) Map Sheet; URN: LSID:landcareresearch.co.nz:Names:C902E6B1-E225-418B-B867-B991233EE555).

of kahikatea timber per year (Clifton 1994). Burns et al. (2000) sampled various population fragments through-out the Waikato and found the average age was 75-125 years, coinciding with European land clearance activity. They concluded the majority of kahikatea swamp forests in the Waikato and Manawatu consist of small fragments, formed by kahikatea acting opportunely to colonise disturbed sites after anthropogenic vegetation clearance, primarily for agriculture (Wardle 1974).Today the best remaining kahikatea forests likely survived harvest due to their remote location in South Westland (Wardle 1974) and Lake Whangape, Awaroa Scenic Reserve in South Waikato (Champion 1988).

Grey willow was first recorded as naturalized in New Zealand in 1925 but likely invaded much earlier (Webb et al. 1988). In New Zealand grey and crack willow species are the most abundant exotics after *Pinus radiata* (NWASCA 1987). There are few wetland areas left in the country which have not been colonized by grey willow (de Winton & Champion 1993). The regions of highest density include the Bay of Plenty, the eastern South Island and the Waikato (Webb et al. 1988), shown in Figure 6. The species was first identified in the Waikato in 1957 on the margin of Lake Ngaroto (Champion 1994). Between the years 1989 to 1993 a survey taken of 38 lakes in the South Waikato found grey willow present at all the lakes and the dominant species in the marginal vegetation at most, while kahikatea was rarely found as an associate in the canopy (Champion et al. 1993; de Winton & Champion 1993). At present grey willow is found at almost all of the 50 Waikato lakes and surrounding the peat bogs of the Kopuatai and Whangamarino swamps (de Winton & Champion 1993).

Niche preferences

In New Zealand grey willow and kahikatea populations overlap in moderate to highly fertile wet areas such as river and lake margins and wetland sites (Clarkson et al. 2002). This habitat frequently undergoes high levels of disturbance in the form of flooding. Any resident species needs to be able to tolerate temporary to permanent inundation by water, anaerobic conditions and take root in sometimes unstable substrate (Champion 1994). Until colonisation by exotic species, like grey willow, kahikatea has historically had few native competitors in wetland areas.

Both species tolerate temporary inundation, but are excluded in areas where water levels rise permanently above ca. 0.5 metres (Champion 1994). The production of adventitious roots is an adaptation shared by both species (small, numerous roots found close to the surface), which have a number of uses including the uptake of oxygen, to assist in tolerating silt burial (Wardle (1974) observed kahikatea covered at depths of up to 60cm), feeding and the release of metabolic toxins such as ethanol (Champion 1994). At wetter sites kahikatea produces buttressed roots to provide stability and to trap organic sediment for adventitious roots to feed on (Wardle 1974; Beveridge 1983; Champion 1988) and grey willow develops cracks in its bark called ‘lenticels’ which act as entry points for oxygen (Champion 1994). Both species also utilise metabolic adaptations to tolerate flooding. Kahikatea reduces its metabolic rate to prevent toxin build-up from prolonged anaerobic respiration (Crawford 1982). Champion (1988) noted this is illustrated in the shorter trees (of similar age) found in permanently flooded sites vs. temporary inundated sites. Grey willow produces malic acid to bind toxins such as ethanol and lactic acid which are formed during anaerobic respiration (Champion 1994).

Kahikatea prefers soils with relatively high levels of organic content and moisture (Entrican 1949; Salmon 1980). The species contains mycorrhizal symbionts in nodules on its root system, which may provide a competitive edge in phosphate uptake in less fertile soils (Yeates 1924; Russell et al. 2002). Grey willow is more tolerant of reduced fertility than kahikatea (illustrated in Figure 7), which is shown by its ability to invade manuka scrub vegetation. Both species tolerate carboxylic acid release involved in peat accumulation. Kahikatea is found in pH values as low as 3.8-5 in boggy sites to 5.7-6 in more swampy sites (often lake, river or lagoon margins), however the crowns are misshapen and smaller when found in lower pH environments (Wardle 1974). At a site in Aokautere, near Palmerston North, van Kraayenoord & Hathaway (1986) observed grey willow tolerating pH levels of 3.0, though de Winton & Champion (1993) noted grey willow is excluded by conditions in the interior of peat bogs.

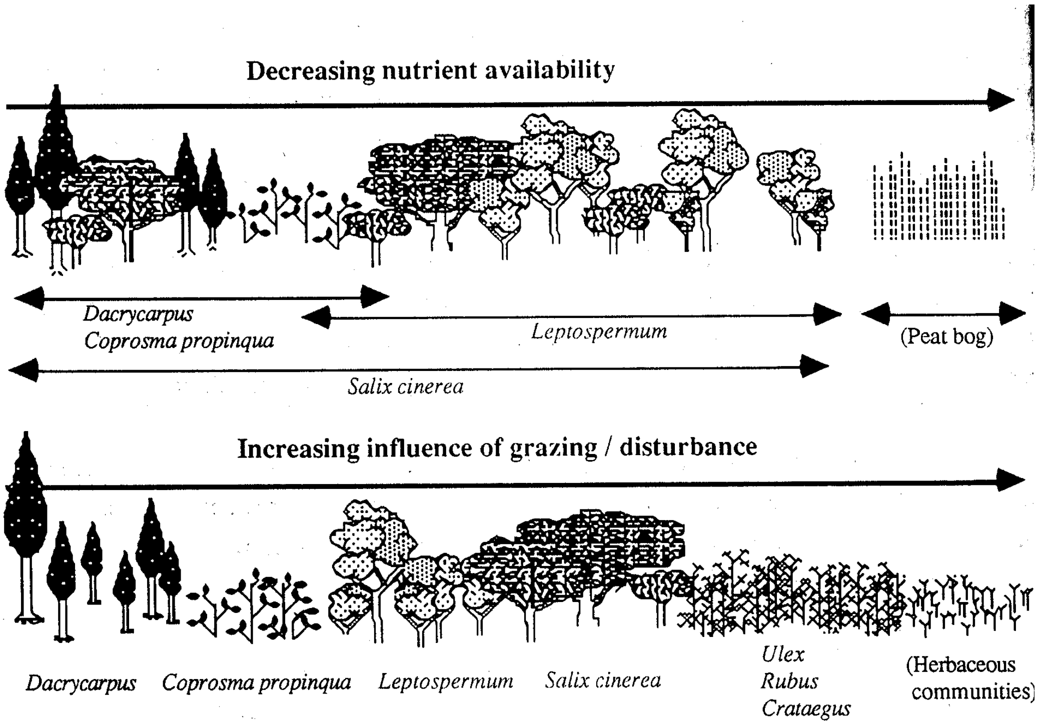

Figure 7 Factors influencing the distribution of woody wetland vegetation types in 38 Waikato Lakes (de Winton & Champion 1993). Note the overlap of *Dacrycarpus* and *Salix cinerea* vegetation types in moderate nutrient availability.

Kahikatea seedlings show good tolerance to the regular inversion frosts that occur on the large open surfaces they prefer to colonise (Leathwick 1995). Grey willow is deciduous and avoids exposure to cold temperatures, frost and the high energetic costs associated with frost tolerance. Leaves are shed in autumn and resprout from dormant buds the following spring. Optimum temperatures for growth are daily temperatures of 27°C for kahikatea (Hawkins & Sweet 1989) and between 18 - 28 °C for grey willow (Koncalova & Jacinska 1985).

Both species are sensitive to drought stress. Stephens (1997) observed reduced growth in kahikatea at lower soil moistures and increased stomatal sensitivity to atmospheric drought. Atkinson & Greenwood (1972) observed large numbers of kahikatea killed in two Manawatu stands after the summer drought of 1969-1970. Niinements & Valladares (2006) found grey willow is extremely intolerant of drought. They indexed grey willow tolerance values to a scale of 0 to 5 (0 = no tolerance, 5 = max tolerance) at 1.9 for shade tolerance, 4.1 for waterlogging tolerance and 0.1 for drought tolerance. Shade intolerance is also characteristic of kahikatea. Kahikatea stands are usually even-aged 'cohorts' (Duncan 1993), of similar height because they die if overtopped, but at times varying substantially in diameter (Whitmore 1988; Veblen 1992). The regeneration strategies of these two species are strongly influenced by their intolerance of shade.

Regeneration strategies

Both species complete their entire reproduction cycle within one year. Kahikatea produces both male and female cones (on separate trees) around October, which are wind pollinated. Fertilization usually occurs in January and the seeds are ripe from March to May. Kahikatea seed is produced in large numbers and is dispersed widely by birds (Beveridge 1964; Burke 1974). Beveridge (1964) recorded a yield of 4,500,000 seeds from a single tree in the Pureora forest park. Grey willow is also dioecious and produces catkins from September to October. These are insect pollinated (usually bees) and produce copious amounts of tiny seed which is attached to cotton-like hairs that aid in wind dispersal (Meikle 1984).

Kahikatea conforms to the catastrophic mode of regeneration (Veblen & Stewart 1980; Veblen 1992; Ogden & Stewart 1995). Optimum regeneration conditions are large, wet sites recently exposed to some form of catastrophic disturbance, usually in the form of flooding. Dense canopy vegetation, including mature kahikatea, will inhibit shade intolerant seedlings (Smale 1984; Duncan 1993). The species will often colonise in extremely high densities in level to slightly raised areas (Wardle 1974; Duncan 1991; Ogden & Stewart 1995). Like most podocarps, kahikatea is relatively slow growing, but may dominate the canopy for 400 - 700 years. Bond (1989) described this form of regeneration as the tortoise and the faster growing, shorter-lived angiosperm as the hare. He went on to state that in steady state environments the slow regenerative capabilities of podocarps restrict them to less productive habitats with higher levels of disturbance. Duncan (1993) suggested the reason for the maintenance of the vast kahikatea swamp forests in South Westland is due to the continued influence of flooding, which is preventing succession to an angiosperm dominant forest type. For kahikatea to achieve dominance in the canopy, it requires maintained sufficient light conditions caused by a prolonged, large gap in the canopy. Kahikatea’s growth rate is fast for a podocarp, but slow in comparison to angiosperms (Table 1). In comparison *Salix* species can attain growth rates of up to 0.5 – 1.5 metres in height, in their first growing season (Stromberg 1997; Glenn *et al.* 1998; Klimkowska *et al.* 2009).

Grime & Hunt (1975) recorded a relative growth rate of 1-1.4 week-1, and concluded it had the highest growth rate of all *Salix* species they tested. This allows it to overtake and suppress seedlings of kahikatea and many other canopy species. Once grey willow has reached the canopy, it is able to aggressively spread via both vegetative and sexual means, until often it forms a monospecific community. Like kahikatea, grey willow is also described as a pioneer and its regeneration is facilitated at cleared and grazed sites as this species is also intolerant of high shade conditions present under a dense canopy (Champion 1988; de Winton & Champion 1993; Niinemets & Valladares 2006). Grey willows rapid spread in New Zealand has likely been facilitated by agricultural vegetation clearance of waterways, which opened up large areas of wetland habitat (Champion 1995).

Table 1 Published kahikatea growth rates (note the Stephens data is not annual but over 180 days).

	Kahikatea annual diameter and height growth rates		
Study	Diameter (mm.yr^{-1})	Height (cm.yr^{-1})	Sample size
Champion (1988)	2.05		32
Duncan (1989)	0.67		70
Ebbett & Ogden (1998)	0.60 - 2.40	2.5 - 44.8	30
Beveridge (1973)		30	
Stephens (1997) 180 days	6.30 - 13.50	63.5 - 129.2	24

Both sexes of grey willow are found in New Zealand and Australia and are not clonal like most other willow populations (Partridge 1994). This suggests grey willow reproduces sexually rather than vegetatively when colonizing new areas. However Champion (1988, 1994) noted the presence of around 10 individuals of grey willow at the forest edge bordering Lake Whangape (Awaroa Scenic Reserve), but no seedlings within the forest and a lack of seedling colonization at Koupuatai wetland, which indicates propagation within these areas after grey willow has achieved dominance is predominantly vegetative. In addition once grey willow establishes, it often modifies water flow regimes through damming caused by prolific stem and root growth (Cremer 2001, 2003), causing flooding which inhibits further colonization of many native species. This makes it extremely difficult for forest succession to move beyond a grey willow dominated canopy via lack of gap creation (Whitmore 1988) and a raised water table.

Karrenberg *et al.* (2002) outlined many of the members of the family Salicaceae use mast seeding in spring as an adaptation to capitalize on the open wet areas created after flooding. However seedling establishment appears to be the 'Achilles heel' of grey willows regenerative capabilities. Seedlings are vulnerable to desiccation and overheating as root growth is extremely slow at the onset of development (1mm per day; Cremer 2003). During establishment seedlings require an absence of grazing, drought and prolonged flooding (Cremer 2001, 2003). They prefer waterlogged soils, high light levels and optimum temperatures from 18 to 28ºC (Koncalova & Jicinska 1985). In addition grey willow seed is only viable within a period of seven weeks. Kahikatea seed is much more robust, remaining viable for over 2 years in the soil (Moles et al. 2000). Although kahikatea seeds are sensitive to desiccation, this is reduced by the presence of the fleshy receptacle (Fountain et al. 1989).

Previous research

Champion (1988) outlined five factors he believed to be the most important influences on kahikatea regeneration. These included; light intensity, soil moisture, siltation disturbance, the presence of a tree root mat and allelopathy. His conclusions were based on previous studies and observations at a number of kahikatea regeneration sites in the Waikato including Kopuatai bog, Awaroa Wildlife management reserve, Whewells Bush, Barrett Bush Meads Bush and other similar stands. Champion's observations included the lack of kahikatea regeneration under its own canopy, and rarely under a broadleaf canopy, but present on 'willow islands' or in forest gaps and edges and the common occurrence of kahikatea saplings in wet and open conditions. Champion supported the conclusions reached by Wardle (1974) and later Burns *et al.* (2000) that continued flooding and siltation coupled with impeded drainage were essential for the regeneration of kahikatea forest as this excludes faster growing but flooding intolerant broadleaf species.

Champion used water table averages to classify willow forest, wet kahikatea forest and dry kahikatea forest (Table 2) and noted willow forest is capable of tolerating a higher water table. He also compared photosynthetic photon flux densities (PPFD) under a kahikatea canopy to those present under grey willow and found light intensity was 0.3% of full sunlight under kahikatea and 1% under grey willow in summer and 26% in winter (leaf fall). Champion suggested the light intensity present under a kahikatea canopy may be below the light compensation point for seedling regeneration, but not under willow, as kahikatea seedling densities under a willow canopy were similar to those in clearings or under *Coprosma* (1625 and 1500 saplings per hectare respectively).

Table 2 Water table heights for willow forest vs. kahikatea forest (Champion 1988)

Forest type	Water table height (mm ± SEM)
willow	35 ± 9 above ground
wet kahikatea	21 ± 8 below ground
dry kahikatea	380 ± 16 below ground

Champion noted the deciduous nature of grey willow likely permitted the establishment of a number of other native species including *Coprosma tenuicaulis* and *Coprosma propinqua* and that it may act as a nursery species for kahikatea. Later Champion (1994) observed that species assemblages present under grey willow depend on the age of the stand, the amount of prior disturbance and the proximity of the stand to indigenous vegetation (acting as a seed source). He noted older willow stands with low levels of disturbance have similar understorey species to kahikatea forest, or herbaceous native swamp vegetation similar to that found before willow establishment but not as dense.

Champion (1988) conducted a dendrochronological analysis of kahikatea at Kopuatai wetland. He found kahikatea ages ranged from 50 to 250 years (n=32) and that the relationship between diameter and age gave a correlation coefficient of 0.770 (corrected to 0.828 by the exclusion of three mature ‘stag headed’ trees), which indicated diameter was a reliable indication of age, provided the tree was of ‘pyramidal’ growth form. He calculated a mean annual diameter growth increment of 2.05 ± 0.26 mm, which is fast for a podocarp (see Norton *et al.* 1987). Additional dendrochronological data was collected on kahikatea by Duncan (1991) who also found a strong correlation between age and diameter ($r^2 = 0.69$, n=70, $P < 0.001$), Burns *et al.* (2000) and Whaley *et al.* (1997).

Molloy et al. (1978) demonstrated kahikatea displays autotoxicity (an allelopathic effect on its own growth). They measured the effects on growth and survival of kahikatea seedlings after they were sprayed repetitively with adult root, green leaf, litter, bark and soil extracts. They found kahikatea did display autotoxicity and that 50% of seedlings were killed when sprayed with litter extract. These findings were summarized by Champion (1988) to illustrate the importance of allelopathy as a factor affecting the regeneration of kahikatea.

Research objectives

Is grey willow dominant due to its ability to inhibit other species, including kahikatea, or the fact it tolerates the environmental conditions better? Previous studies have suggested grey willow acts as a nursery species for kahikatea and other natives to regenerate (Champion 1988; Meurk 1991). However the data presented was not unequivocal and observation suggested further data is required to determine whether this regeneration is sufficient (without active management) for kahikatea to achieve dominance in the stand. Champion (1988) suggests while there are areas where the ‘do nothing’ management approach will work, such as South Westland National Park, which maintains a flooding regime and is large enough to sustain all successional stages of kahikatea forest development (exposed silt, shrub seral communities and kahikatea forest), the long-term viability of kahikatea in Waikato fragments is likely to require active management.

The eradication of grey willow has become too expensive to consider due to its wide distribution and ease of dispersal. The Department of Conservation classes grey willow as one of the top 10 invasive weeds in 7 out of the 13 conservancies (Froude 2002). However it is possible to locally control the species if the exact extent of its impact is understood. By quantifying some of these impacts on kahikatea, we can establish whether it is a priority to control grey willow to achieve restoration of kahikatea dominance at these sites.
This research aims to answer the following questions:

- What is the developmental history of grey willow and kahikatea at six stands in the Waikato Ecological Region?
- What is the frequency of kahikatea regeneration?
- Is kahikatea’s population structure affected by the presence of grey willow?

- Is diameter a reliable estimate for age for these species?
- What effect does the disturbance history of a site have on kahikatea and grey willow population dynamics?
- Does a grey willow canopy affect the growth of kahikatea saplings?
- Is there an allelopathic interaction between kahikatea and grey willow?
- What recommendations can be made for other swamps with these species?

References

Antonovics J, Levin D A 1980. The Ecological and Genetic Consequences of Density-Dependent Regulation in Plants. Annual Review of Ecology and Systematics 11: 411-452.

Argus G W 1997. Infrageneric Classification of Salix (Salicaceae) in the New World. Systematic Botany Monographs 52: 1-121.

Atkinson I A E, Greenwood R M 1972. Effects of the 1969-70 drought on two remnants of indigenous lowland forest in the Manawatu district. Proceedings of the New Zealand Ecological Society 19: 34-42.

Azuma T, Kajita T, Yokoyama J, Ohashi H 2000. Phylogenetic relationships of *Salix* (Salicaceae) based on rbcL sequence data. American Journal of Botany 87(1): 67-75.

Beveridge A E 1964. Dispersal and Destruction of Seed in the Central North Island Podocarp Forests. Proceedings of the New Zealand Ecological Society 46: 378-384

Beveridge A E 1983. Regeneration of podocarp forests and maintenance of productivity. In: Lowland forests in New Zealand (Eds. K Thompson, A P H Hodder, A S Edmonds), pp. 93-112. University of Waikato, Hamilton.

Bond W J 1989. The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. Biological Journal of the Linnean Society 36: 227-249.

Brunsfeld S J, Soltis D E, Soltis P S 1992. Evolutionary Patterns and Processes in *Salix* sect. *Longifoliae*: Evidence from Chloroplast DNA. Systematic Botany 17(2): 239-256.

Burke W D 1974. Regeneration of Podocarps on Mt Tarawera, Rotorua. New Zealand Journal of Botany 12: 219-226.

Burns B R, Barker G M, Harris R, Innes J 2000. Conifers and cows: forest survival in a New Zealand dairy landscape. Pp 81-89. In: Nature conservation 5: Conservation in production environments. Managing the matrix (Eds. J L Craig, N D Mitchell, D A Saunders). Surrey Beatty and Sons. Chipping Norton, Australia. 712pp.

Champion P D 1988. The Ecology and Management of kahikatea *Dacrycarpus dacrydioides* (A. Rich.) de Laubenfels in the Waikato, North Island, New Zealand. University of Waikato Masters Thesis (unpub.).

Champion P D, de Winton M D, de Lange P J 1993. The vegetation of the lower Waikato lakes. Volume 2. NIWA Ecosystems Publication No. 8.

Champion P D 1994. Extent of willow invasion – the threats. Chp 6 In: Wild willows in New Zealand (Eds. C J West). Proceedings of a Willow Control Workshop, Department of Conservation, Hamilton. Pp. 43-49.

Clarkson B D, Merrett M, Downs T 2002. Botany of the Waikato. Waikato Botanical Society Inc., c/o University of Waikato, Hamilton.

Clarkson B R, Schipper L A, Silvester W B 2009. Nutritional niche separation in coexisting bog species demonstrated by ^{15}N-enriched simulated rainfall. Austral Ecology 34: 377-385.

Clifton N C 1994. New Zealand Timbers: The complete guide to exotic and indigenous woods. GP Publications, Wellington.

Cockayne L, Phillips-Turner E 1967. The Trees of New Zealand. Govt. Printer, Wellington, New Zealand.

Connell J H 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302-1310.

Crawford R M M 1982. Physiological Responses to Flooding. In: Physiological Plant Ecology III (Eds. O L Lange, P S Nobel, C B Osmond, H Zeigler). Springer-Verlag.

Cremer K W 2001. Exterminate Wild Pussy Willows and its most invasive relatives. CSIRO Forestry and Forest Products, Kingston ACT.

Cremer K W 2003. Introduced willows can become invasive pests in Australia. Biodiversity 4 (4): 17-24.

de Laubenfels D J 1969. A revision of the Malesian and Pacific rainforest conifers, 1 Podocarpaceae, in part. Journal of the Arnold Arboretum 50: 274-314.

de Winton M D, Champion P D 1993. The vegetation of the lower Waikato lakes. Volume 1. NIWA Ecosystems Publication No. 7.

Duncan R P 1989. An Evaluation of Errors in Tree Age Estimates based on Increment Cores in Kahikatea (*Dacrycarpus dacrydioides*). New Zealand Natural Sciences 16: 31 – 37.

Duncan R P 1991. Competition and the Coexistence of Species in a Mixed Podocarp Stand. The Journal of Ecology 79(4): 1073-1084.

Duncan R P 1993. Flood Disturbance and the Coexistence of Species in a Lowland Podocarp Forest, South Westland, New Zealand. The Journal of Ecology 81(3): 403-416.

Entrican A R 1949. The properties and uses of Kahikatea or White Pine (*Podocarpus dacrydioides*). Revised by Reid J S. New Zealand Forest Service Information Series No. 5, Wellington.

Fang C 1987. On the distribution and origin of *Salix* in the World. Chinese Acta Phytotax. Sin. 25: 307-312.

Fountain D W, Holdsworth J M, Outred H A 1989. The dispersal unit of *Dacrycarpus dacrydioides* (A. Rich.) de Laubenfels (Podocarpaceae) and the significance of the fleshy receptacle. Botanical Journal of the Linnean Society 99(3): 197-207.

Foweraker C E 1929. The podocarp rain forests of Westland, New Zealand. Te kura Ngahere 11(4): 7pp.

Fowler N 1988. The effects of environmental heterogeneity in space and time on the regulation of populations and communities. Chp 13 In: Plant Population Ecology (Eds. A J Davy, M J Hutchings, A R Watkinson). Blackwell Scientific Publications.

Foy C L, Inderjit 2001. Understanding the Role of Allelopathy in Weed Interference and Declining Plant Diversity. Weed Technology 15: 873-878.

Froude V A 2002. Biological control options for invasive weeds of New Zealand protected areas. Science for Conservation 199. Department of Conservation, Wellington.

Glenn E, Tanner R, Mendez S, Kehrer T, Moore D, Garcia J, Valdez C 1998. Growth rates, salt tolerance and water use characteristics of native and invasive riparian plants from the delta of the Colorado River, Mexico. Journal of Arid Environments 40: 281-294.

Grime J P, Hunt R 1975. Relative growth-rate; its range and adaptive significance in a local flora. Journal of Ecology 63: 393-422.

Harding M 1997. Forest Heritage Fund: Waikato Protection Strategy. Forest Heritage Fund, Wellington.

Hardin G 1960. The Competitive Exclusion Principal. Science 131 (3409): 1292-1297.

Harper J L 1961. Approaches to the study of plant competition. Mechanisms in biological competition. Symposium of the Society for Experimental Biology 15: 1-39.

Hawkins B J, Sweet G B 1989. Evolutionary interpretation of a high temperature growth response in five New Zealand forest tree species. New Zealand Journal of Botany 27: 101-107.

Hurlbert S H 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Hutchinson G E 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22: 415-427.

Karrenberg S, Edwards P J, Kollmann J 2002. The life history of Salicaceae living in the active zone of floodplains. Freshwater Biology 47: 733-748.

Keddy P A, Shipley B 1989. Competitive hierarchies in herbaceous plant communities. Oikos 54: 234-241.

Kelch D 1998. Phylogeny of Podocarpaceae: comparison of evidence from morphology and 18S rDNA. American Journal of Botany 85(7): 986-996.

Kershaw A P, McGlone M S 1995. The Quaternary History of the Southern Conifers. In: Ecology of the Southern Conifers (Eds. N J Enright, R S Hill). Melbourne University Press, Victoria.

Klimkowska A, Dzierża P, Kotowski W, Brzezińska K 2009. Methods of limiting willow shrub re-growth after initial removal on fen meadows. Journal of Nature Conservation, doi:10.1016/j.jnc.2009.01.002.

Končalová M N, Jičínská D 1985. Differences between Ecological Niches in juvenile Salix cinerea and S. pentandra. Folia Geobotanica & Phytotaxonomica 20 (3): 319-321.

Leathwick J R 1995. Climatic relationships of some New Zealand forest tree species. Journal of Vegetation Science 6 (2): 237-248.

Leathwick J R, Clarkson B D, Whaley P T 1995. Vegetation of the Waikato Region: current and historical perspectives. Landcare Research Contract Report: LC9596/022. Landcare Research, Hamilton.

Margalef R 1963. On Certain Unifying Principles in Ecology. The American Naturalist 97 (897): 357-374.

McEwen W M 1988. Cone and Seed Phenology in Several New Zealand Conifer Tree Species. Tuatara 30(1).

Meikle R D 1984. Willows and Poplars of Great Britain and Ireland. BSBI Handbook no. 4. ISBN 0-901158-07-0.

Menninger H L, Palmer M A 2006. Restoring Ecological Communities: From Theory to Practice. Chp 5 In: Foundations of restoration ecology (Eds. D A Falk, M A Palmer, J B Zedler). Island Press.

Metcalf L J 2002. Trees of New Zealand. New Holland, Auckland.

Meurk C D 1991. Assessment and management options for several wetland patches along the Christchurch-Akaroa Highway. DSIR Land Resources contract report No. 91/24.

Moen J, Meurk C D 2001. Competition abilities of three indigenous New Zealand plant species in relation to the introduced plant *Hieracium pilosella*. Basic and Applied Ecology 2: 243-250.

Moles A T, Hodson D W, Webb C J 2000. Seed size and shape and persistence in the soil in the New Zealand flora. OIKOS 89: 541-545.

Molloy B P J, Ferguson J D, Fletcher P J 1978. The Allelopathic Potential of Kahikatea. A Progress Report. New Zealand Journal of Ecology 1: 183-184.

Muller C H 1966. The role of chemical inhibition (allelopathy) in vegetational composition. Bulletin of the Torrey Botanical Club 93 (5): 332-351.

Muller C H 1969. Allelopathy as a factor in ecological process. Vegetation 18: 348-357.

Niinemets Ü, Valladares F 2006. Tolerance to shade, drought and waterlogging of temperate, Northern hemisphere trees and shrubs. Ecological Monographs 76: 521-547.

Nilsson M-C 1994. Separation of allelopathy and resource competition by the boreal dwarf shrub *Empetrum hermaphroditum* Hagerup. Oecologia 98: 1-7.

Norton D A, Herbert J W, Beveridge A E 1988. The ecology of *Dacrydium cupressinum*: A review. New Zealand Journal of Botany 26: 37-62.

Norton D A, Palmer J G, Ogden J 1987. Dendroecological studies in New Zealand 1. An evaluation of tree age estimates based on increment cores. New Zealand Journal of Botany 25: 373-383.

NWASCA 1987. Willows for the future. Streamland 53.

Ogden J, Stewart G H 1995. Community Dynamics of the New Zealand Conifers. In: Ecology of the Southern Conifers (Eds. N J Enright, R S Hill). Melbourne University Press, Melbourne.

Ogden J, Wardle G M, Ahmed M 1987. Population dynamics of the emergent conifer *Agathis australis* (D. Don) Lindl. (kauri) in New Zealand. 2. Seedling population sizes and gap-phase regeneration. New Zealand Journal of Botany 25: 231-242.

Partridge T R 1994. Ecological impacts of willows in wetlands. Chp 3 In: Wild Willows in New Zealand (Eds. C J West). Proceedings of a Willow Control Workshop, Department of Conservation, Hamilton. Pp. 43-49.

Philipson W R, Molloy B P J 1990. Seedling, shoot, and adult morphology of New Zealand conifers The genera *Dacrycarpus, Podocarpus, Dacrydium* and *Prumnopitys*. New Zealand Journal of Botany 28: 73-84.

Pickett S T A 1980. Non-equilibrium coexistence of plants. Bulletin of the Torrey Botanical Club 107: 238-248.

Pocknall D T 1981. Pollen morphology of the New Zealand species of *Dacrydium* Solander, *Podocarpus* L'Heritier, and *Dacrycarpus* Endlicher (Podocarpaceae). New Zealand Journal of Botany 19: 67-95.

Poole A L, Adams N M 1963. Trees and Shrubs of New Zealand. Govt. Printer, Wellington.

Putwain P D, Harper J L 1970. Studies in the dynamics of plant populations III. The influence of associated species on populations of *Rumex acetosa* L. and *R. acetosella* L. in grassland. Journal of Ecology 58: 251-264.

Rees M, Condit R, Crawley M, Pacala S, Tilman D 2001. Long-term studies of vegetation dynamics. Science 293: 650-655.

Rice E L 1984. Allelopathy 2nd Edition. Academic Press, New York

Rich. A 1832. Essai d´une Flore de la Nouvelle Zéland, 358. t. 39.

Russell A J, Bidartondo M I, Butterfield B 2002. The Root Nodules of the Podocarpaceae Habour Arbuscular Mycorrhizal Fungi. New Phytologist 156(2): 283-295.

Salmon J T 1980. The Native Trees of New Zealand. Reed Publishing (NZ) Ltd, Auckland.

Seabloom E W, Harpole W S, Reichman O J, Tilman D 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proceedings of the National Academy of Sciences 100 (23): 13384-13389.

Shmida A, Ellner S 1984. Coexistence of plant species with similar niches. Vegetation 58: 29-55.

Skvortsov A K 1986b. Willows of the USSR. A taxonomic and geographic revision. Moscow: Publishing Office “Nauka”.

Slobodkin L B 1961a. Growth and regulation of animal populations. Holt, Rinehart & Winston, New York. 184 p.

Smale M C 1984. White Pine Bush – an alluvial kahikatea (*Dacrycarpus dacrydioides*) forest remnant, eastern Bay of Plenty, New Zealand. New Zealand Journal of Botany 22: 201-206.

Smale M C, Ross C W, Arnold G C 2005. Vegetation recovery in rural kahikatea (*Dacrycarpus dacrydioides*) forest fragments in the Waikato region, New Zealand, following retirement from grazing. New Zealand Journal of Ecology 29(2): 261-269.

Stephens D W 1997. Influences of Soil and Atmospheric Water Environments on the Establishment Site Preferences of Kauri and Kahikatea. University of Waikato Masters thesis (unpub.).

Stromberg J C 1997. Growth and survivorship of Fremont Cottonwood, Gooding willow, and Salt Cedar seedlings after large floods in central Arizona. Great Basin Naturalist 57: 198-208.

Tilman D 1997. Mechanisms of Plant Competition. Chp 8 In: Plant Ecology 2nd Edition (Ed. M J Crawley). Blackwell Publishing.

van Kraayenoord C W S, Hathaway R L 1986. Plant Materials Handbook for Soil Conservation, Volume 2: Introduced Plants. Water and Soil miscellaneous publication No. 94, NWASCO, Wellington.

Veblen T T 1992. Regeneration dynamics. Chp 4 In: Plant Succession: Theory and prediction (Eds. D C Glenn-Lewin, R K Peet, T T Veblen). Chapman & Hall, London.

Veblen T T, Stewart G H 1980. Comparison of forest structure and regeneration on Bench and Stewart Islands, New Zealand. New Zealand Journal of Ecology 3: 50-68.

Wardle P 1963. The Regeneration gap of New Zealand gymnosperms. New Zealand Journal of Botany 1: 301-315.

Wardle P 1974. The Kahikatea (*Dacrycarpus dacrydioides*) Forest of South Westland. Proceedings of the New Zealand Ecological Society 21: 62-71.

Wardle P 1977. Plant communities of Westland National Park (New Zealand) and neighbouring coastal areas. New Zealand Journal of Botany 15: 323-398.

Wardle P 1991. Vegetation of New Zealand. Cambridge University Press, Cambridge.

Watt A S 1947. Pattern and process in the plant community. Journal of Ecology 35: 1-22.

Webb C J, Sykes W R, Garnock-Jones P J 1988. Flora of New Zealand Volume IV – Naturalised Pteridophytes, Gymnosperms, Dicotyledons. Botany Division, D. S. I. R., Christchurch, New Zealand. 1365p.

Weiner J 1984. Neighbourhood interference amongst *Pinus rigida* individuals. Journal of Ecology 72: 183-195.

Whaley P T, Clarkson B D, Smale M C 1997. Claudelands Bush: Ecology of an Urban Kahikatea (*Dacrycarpus dacrydioides*) Forest Remnant in Hamilton, New Zealand. Tane 36: 131-155.

Whitmore T C 1988. The influence of tree population dynamics on forest species composition. Chp 14 In: Plant Population Ecology (Eds. A J Davy, M J Hutchings, A R Watkinson). Blackwell Scientific Publications.

Wilson A D 1980. Soils of Piako County, North Island, New Zealand. NZ Soil Bureau.

Wilson J B 1990. Mechanisms of species coexistence: Twelve explanations for Hutchinson’s ‘paradox of the plankton’: Evidence from New Zealand plant communities. New Zealand Journal of Ecology 13: 17-42.

Yeats J S 1924. The root nodules of the New Zealand pines. New Zealand Journal of Science and Technology 7: 121-124.

Zimdahl R L 1999. Fundamentals of Weed Science, 2nd Edition. San Diego Academic Press.

CHAPTER 2: POPULATION DYNAMICS OF KAHIKATEA AND GREY WILLOW ALONG A DISTURBANCE GRADIENT

Introduction

To determine whether interference is important in structuring populations is an important goal of ecologists (Antonovics & Levin 1980). Weiner (1984) suggested if competition influences plant performance, individuals with fewer, smaller neighbours should perform better than those with many or larger neighbours. Competition may also cause population clumping due to crowding of seedlings in forest gaps (Pielou 1960). However, spatial distribution of populations is complicated by habitat heterogeneity, created during physical disturbance, which can cancel out the effects of competition through provision of refuge environments (Fowler 1988). Gathering information on a sites disturbance history is vital to understanding its present population structure, and to assessing the relative importance of interference on this structure.

The native podocarp kahikatea (*Dacrycarpus dacrydioides*) has lost dominance in wetland margin and floodplain habitat throughout the Waikato due to forest clearance and the loss of regular flooding disturbance which promotes mass regeneration of the species (Wardle 1974; Duncan 1991; Duncan 1993). Adding to this decline is the invasion of the highly competitive exotic species grey willow (*Salix cinerea*), which occupies a similar environmental niche to shade intolerant kahikatea, but likely reaches the canopy faster. In environments where these species coexist, their population structures have been shaped by their history of disturbance as well as possible effects from interference, although the relative importance of each factor is unknown.

Tree-ring dating, or dendrochronology, of kahikatea has been successfully applied by multiple studies to reconstruct disturbance histories of forest fragments in the Waikato because the species has clear rings, is fast growing and has a low incidence of juvenile lobate growth (Duncan 1993; Whaley *et al.* 1997; Burns *et al.* 2000). Burns *et al.* (2000) concluded the population structures of kahikatea in the middle Waikato comprises two cohorts, the first contains individuals aged two to five hundred years old (one to two metres in diameter) that are survivors of initial forest clearance and the second cohort, aged eighty to one hundred and twenty years old (thirty to ninety centimetres in diameter), opportunely established after mass forest clearance for agriculture during European colonization.

Dendrochronology also enables performance assessment of individuals and populations in response to abiotic and biotic factors through variations in ring width (Fritts 1970). Using this method it is possible to detect and date individual suppression and release events and on occasion cross-date these events between samples if growth limiting factors, such as climate are shared (Scott 1972; Buckley *et al.* 2000). There is evidence cross-dating methods are difficult to apply in New Zealand in this manner due to inconsistent ring patterning between trees, probably because trees are not experiencing the same underlying factors limiting their growth, or if they are this factor is not distributed homogeneously (Cameron 1960; Scott 1964; Bell 1958; Bell & Bell 1959). This seems to suggest dendrochronological analysis of New Zealand trees, such as kahikatea, may be more useful when applied at the level of the individual.

So far no published dendrochronological studies of the exotic invader, grey willow (*Salix cinerea*) have been recorded in New Zealand, and would provide valuable information on the population history in New Zealand. Gill (1974) conducted a dendrochronological analysis of 300 grey willow on a reservoir margin in Montgomeryshire, England to determine the effect of flooding on radial growth increment. Gill found highly significant negative correlations with age and duration of flooding on growth increment, but concluded grey willow was ill suited to dendrochronological analysis due to the tendency for ring clarity to decrease in rings more than five years old.

The present study uses vegetation sampling and dendrochronological methods to measure the population structures of kahikatea and grey willow at six Waikato sites dominated by these species, along an urban, peri-urban to rural gradient. This information is then used to reconstruct species population age structures and the disturbance histories at each site, to ascertain whether grey willow is inhibiting the regeneration of kahikatea populations. In addition, the growth rates of both species are compared to quantify the competitive advantage grey willow has over kahikatea in reaching the canopy in these populations.

Methods

Study sites

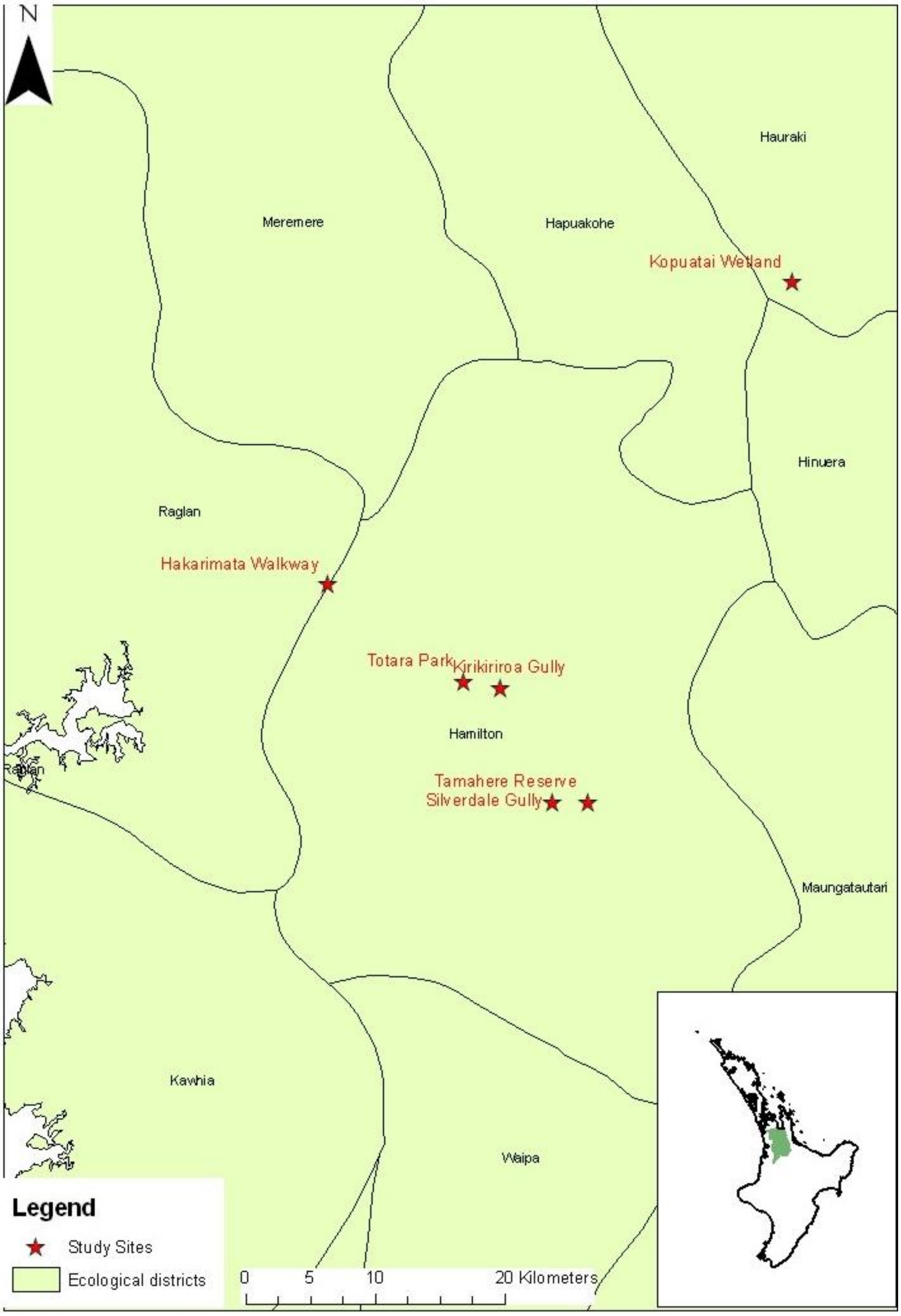

Figure 1 Location of study sites within the Hamilton, Raglan and Hauraki Ecological Districts.

The sites included in this research were selected based on the following criteria; they belong to the Waikato Ecological Region with comparable climates and alluvial soils, they contain regenerating kahikatea and a dominant canopy of grey willow, a flooding regime and they are located in an urban, peri-urban or rural setting (Figure 1). The urban to peri-urban to rural gradient was sampled to determine whether a sites disturbance history has any affect on the population structures of kahikatea and grey willow, either through changing species assemblages or changes in the physical site attributes. The urban sites generally were the most disturbed due to high levels of vegetation and physical disturbance, altered nutrient and flooding regimes and increased exotic species pools (Table 1). All the sites are excluding the Kirikiriroa gully are unmanaged.

Table 1 Site characteristics summary (Climate information courtesy of Clifflo NIWA database and New Zealand Meteorological Service 1985; soil information obtained from Newsome *et al.* 2000)

Summary of site characteristics

	study site					
	Totara Park	Silverdale	Kirikiriroa	Tamahere	Hakarimata	Kopuatai
Average rainfall (mm)	1207	1207	1207	1207	1433	1146
Average temperature (°C)	13.5	13.5	13.5	13.5	14.0	11.1
Soil type	Esk	Esk	Horotiu	Horotiu	Kaawa clay loam	Elstow clay
Landform	gully	gully	gully	stream terrace	stream terrace	floodplain terrace
landtype	urban	urban	urban	peri-urban	peri-urban	rural
Disturbance history	high	high	high	high	medium	low

Urban sites

Totara Park is a 3.76 hectare inner-city park in the suburb of St Andrews, Hamilton City (Figures 1 and 2). The site was mined for sand by Taupo Totara Timber Company around 1969 and nearly completely devegetated (Pudney 2009). Later, the Hamilton City Council constructed a field at the northern end of the park with a few small drainage pipes beneath draining to the Waikato River, which enabled a swampy wetland to develop. Silverdale gully is located in the southeastern outskirts of Hamilton City (Figures 1 and 3). The water sources at the site include a natural spring, gully seepages and stormwater that discharge to the Mangaonua stream, then to the Waikato River. The Kirikiriroa gully is located in the suburb of Chedworth Park, Hamilton City (Figures 1 and 4) and is part of an extensive gully network that eventually drains into the Waikato River. Most of the kahikatea at this site were planted, although there are a few seedlings or saplings which may be considered natural regeneration. The gully was sampled to obtain valuable dendrochronological data on three kahikatea, planted in 1994, that were growing in different drainage regimes and five kahikatea, planted in the early 1990’s, and released in 2003 -04 from a grey willow canopy.

Peri-urban sites

The Tamahere Reserve is located just south of Hamilton City (Figures 1 and 4). The Mangaone Stream runs through the gully, until it meets the Mangaonua Stream further north. The primary water sources include a spring and gully water seepages and a water uptake is located within the reserve (Porter *et al.* 2009). The site is currently being considered for habitat restoration purposes due to its size, the fact it contains an underrepresented indigenous wetland habitat (kahikatea dominant swamp forest) and that it displays promising regenerative capacity (Porter *et al.* 2009). The Hakarimata Walkway site lies a few minutes south of Ngaruawahia. The main water sources include seepages and rain which drain slowly to a tributary of Firewood creek that discharges to the Waipa River. The site borders protected native bush known as the Hakarimata Scenic Reserve (Figure 5), which is administered by the Department of Conservation.

Rural site

In 1989 the 10, 201 hectare Kopuatai Wetland was listed as an internationally important site under the Ramsar Convention (1971). The sample area consists of 14 hectares of kahikatea forest surrounded by grey willow, situated on the mineralized soils at the western edge of the Kopuatai Peat dome. Sampling was undertaken between the main kahikatea stand and the Waitoa canal (Figure 6). Soils have an average pH of 5.6 and a medium to high nutrient status (influenced by nutrient influx from the Waitoa canal; Champion 1988). This site is the only kahikatea swamp forest remaining in the Hauraki floodplains that still has a natural flooding regime and as a consequence is highly ecologically significant.

Field work dates

Thirty five grey willow increment cores were collected at Totara Park between the 15th and 27th of January, 2009. Thirty five kahikatea cores were obtained at Totara Park between the 21st of April and the 19th of May, 2009 and population surveys for both species were completed on the 10th of September. Tamahere Reserve, Silverdale gully, Hakarimata walkway, Kirikiriroa gully and Kopuatai wetland sites were surveyed and sampled between the 7th of September and the 26th of November.

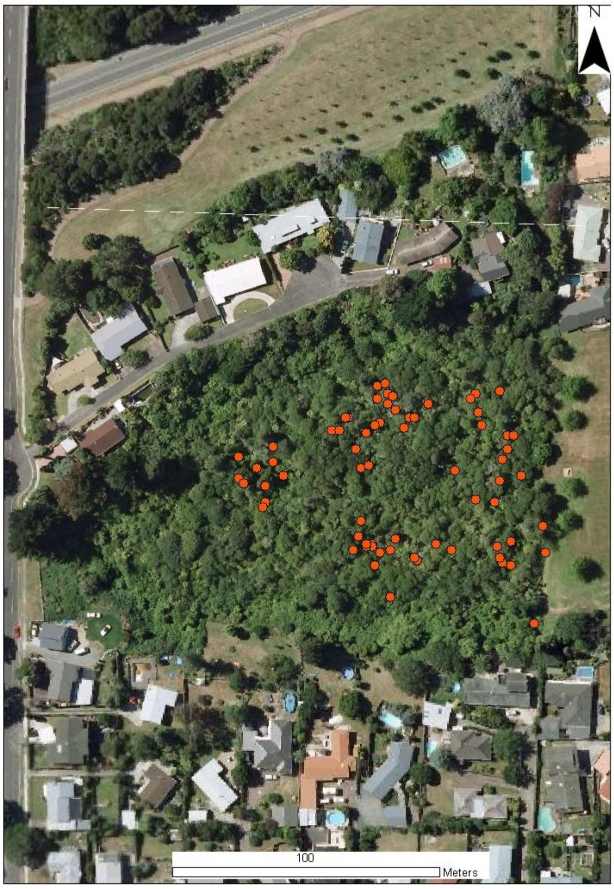

Figure 2 Totara Park study site, Hamilton Ecological District (dots represent cored trees).

Figure 3 Silverdale Gully study site, Hamilton Ecological District (dots represent plot locations).

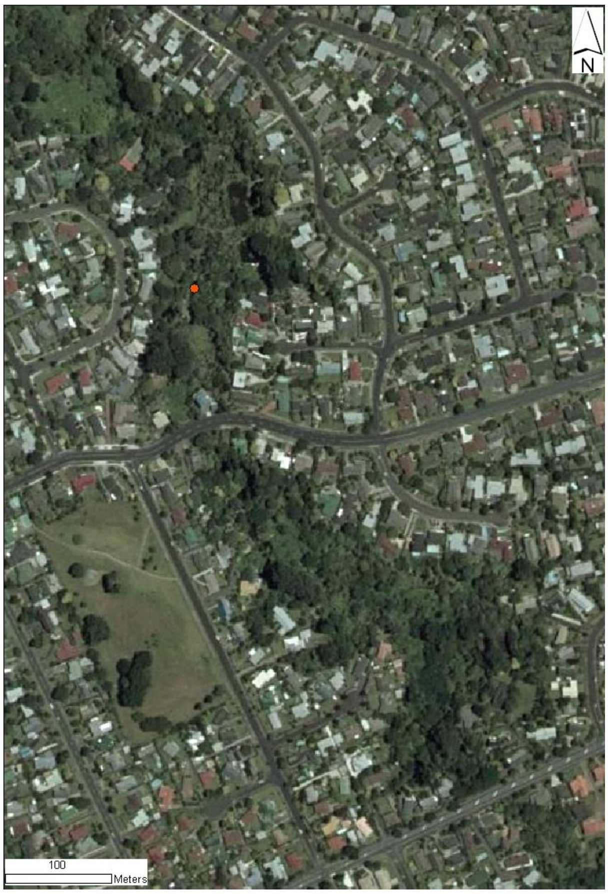

Figure 4 Kirikiriroa gully site, Hamilton Ecological District (dot represents coring location).

Figure 5 Tamahere Reserve study site, Hamilton Ecological District (dots represent plot locations).

Figure 6 Hakarimata Walkway study site, Raglan Ecological District (dots represent plot locations).

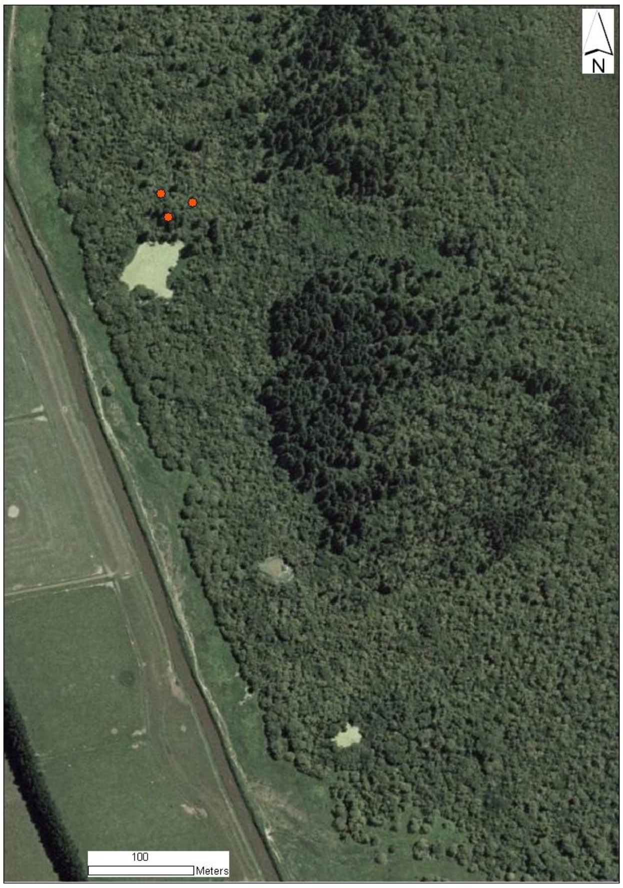

Figure 7 Kopuatai Wetland study site, Hauraki Ecological District (dots represent plot locations).

Increment core collection

Sample selection varied depending on the size of the site, the diameter distributions of kahikatea and grey willow and the available population size to be cored. At all sites the largest individuals were cored (where possible) to get a maximum age estimate. At Totara park individuals were randomly selected by pacing west along the grassed area of the park, and then into the park for a predisposed randomly generated number of steps. Specimens were selected based on their proximity to the end point. Further discrimination of samples was exercised to ensure adequate representation for each diameter size class. Sample selection at Silverdale gully, Tamahere Reserve and Hakarimata walkway involved sampling individuals within the main kahikatea clumps to get a range of diameters and within grey willow control plots (excluding Hakarimata). Sampling at Kirikiriroa gully was restricted to any available individual above 5cm in diameter (limit for all the sites to avoid excessive damage to juveniles by the borer). Individuals sampled in Kopuatai were selected randomly in the plot selection area. As shown in Table 2, fewer individuals were cored at Silverdale gully due to the lack of suitable kahikatea present (four mature individuals), two of which could not be cored due to heart rot and extensive buttressing.

Table 2 Number of grey willow and kahikatea cored at each site

	Sample size	
Site	Grey willow	Kahikatea
Totara Park	33	35
Silverdale gully	5	2
Kirikiriroa gully	5	9
Tamahere Reserve	10	10
Hakarimata Walkway	10	10
Kopuatai wetland	10	10

For multi-stemmed individuals the largest stem was selected to core to ensure the most accurate age estimate. At Totara Park eleven grey willow individuals needed a repeat core taken due to rot, and of these eleven, three trees were replaced with a core from the closest individual and two individuals were cored again for a third time and excluded from the study. Increment coring was done at 1.35m above ground for most individuals excluding those that needed to be higher due to the presence of buttressing, higher or lower due to rot and in some cases lower to avoid multi stemming. Coring height was recorded and later used in age estimate analysis. A Suunto increment borer (Forestry Suppliers Inc., MS, USA) with a 5mm diameter and 350mm long bit was used to core all the trees. Care was taken when starting the borer to avoid damaging the core. Cores were removed from the borer and stored in milkshake straws, labeled with the tree id and diameter, and stapled at both ends to avoid losing plugs or sections of the core if the core had been broken.

Increment core analyses

Increment cores were left in the straws for up to a week to dry out. They were then glued in to a 39 × 1.9 × 0.9 cm MDF block with a 5mm saw cut groove down the centre. Once mounted the core was sanded using an electric rotary sander and on occasion oiled if this assisted in clarifying annual growth rings. The initial seventy cores obtained from Totara Park were analysed using a zoom microscope (63x magnification, 0.8 zoom setting with a built in camera) and photographed. Radial lengths were counted and measured from the photographs using a program called AxioVision AC. Once it was established the cores at Totara Park did not cross-date, the remaining cores were analysed using an Olympus S2H10 Research Stereo Microscope at 0.7x magnification. Annual growth rings were counted but radial lengths were not measured. Mean annual diameter growth was calculated by dividing the length of the core by the number of rings. Periods of inhibition and release were noted and dated. These were defined as being rings over 2 times smaller or larger than the previous ring respectively and were required to last longer than 4 rings (Henry & Swan 1974).

For the few cores that directly hit the centre the only modification made to the age estimate was to include the time taken (in years) for the tree to reach coring height. This can be done in two ways, either taking another core at ground level or estimating time taken to reach this height using seedlings. Both of these methods have limitations. In the case of kahikatea there is often extensive buttressing especially of mature individuals at ground level. Also estimates of seedling growth rates do not uniformly apply to all individuals, especially those heavily suppressed. The present study estimated the time taken to reach coring height at 7 years for all kahikatea samples. This was based on data in Chapter 3 (8.1 ± 0.9 years taken to reach 1.35m of forty kahikatea seedlings used in the seedling experiments) averaged with Champion’s results (1988) of 5.8 ± 2.8 years (he extrapolated back from his diameter age regression). For trees that underwent early suppression this average would be an underestimate, however suppressed kahikatea tend to show more variation in height than diameter (Whitmore 1988), so it should be accurate enough for our purposes.

Cores that did not hit the centre (pith) did so for a number of reasons. Firstly the tree was too large in diameter for the borer. In this case there was no curve in radial increments to apply a geometric model to estimate age, so the average radial length for the increment core was calculated and extrapolated to the estimated radius of the tree. The first assumption with this method is that the dendrochronological centre of the tree is the same as the geometric centre, which ignores eccentric growth. Another important assumption was made that average radial growth was consistent throughout the life of the tree. Often as a tree ages it produces smaller growth increments, however ontogenic growth curves in kahikatea that established under a canopy are complicated by regular occurrence of early suppression. The trees aged in this way were mature and any age estimate made was likely to contain high margins of error, so I avoided adjustment of the data to include uncertain levels of ontogenic growth variation. The second reason the centre was not visible was due to heart rot, which was only found in grey willow individuals. I used the same method as above to gain the age estimate in cases where the centre arc could not be seen but was visible in the outer rings. The final reason cores did not reach the centre was the orientation of the borer. Because a trees dendrochronological centre is often not in the geometric centre it is often ‘guesswork’ to hit the centre, especially in larger individuals. In these instances I applied a geometric model developed by Clayton-Greene (1977) based on the Pythagoras theorem that uses the central arc to decipher length of the missing radius and then the number of missing rings.

Population surveys

The variable area radial plot method was used to sample kahikatea and grey willow populations at all sites, which is adapted from the constant count plot method (Jane 1982), however instead of counting stems the plot was extended until a range of diameters for each species was included. This technique is a good way to sample species with clumped distribution, such as kahikatea, and each plot was extended until a representative diameter range of grey willow samples was collected. At Totara Park, plots were selected by randomly assigning previously cored individuals as the centre of the plot. For the remaining sites, plots were selected based on the inclusion of representative populations of kahikatea and grey willow. The total number of plots sampled at each site depended on the size of the site and also the range of diameters (and hence ages) of both species present. At each site, excluding the Hakarimata walkway where no suitable area was found, an additional plot was selected containing only grey willow to act as a control for any possible influence on growth and density caused through the presence of kahikatea, and to ensure all grey willow size classes were represented. Plots were further categorized into dominant vegetation types using the method of Atkinson (1962). Population surveying methods included counting the numbers of kahikatea seedlings (< 50cm) in the total plot, randomly selected half of the plot, or for very large plots, randomly placed $1m^2$ subplots. Seedlings and saplings over 50cm were counted and height was measured using a 2m tape. Saplings were defined as over 1.35 m in height and under 4 cm in diameter (Champion 1988). For any stems over 2cm in diameter a 2m diameter tape was used to measure the diameter at breast height (d.b.h.) and the height was estimated by eye or using an inclinometer if the tree was very large. Canopy openness was estimated by randomly orientating a transect across the plot and recording whether the canopy was open or closed at each meter.

Data analyses

Kahikatea and grey willow average growth rates were calculated for each site and Statistica box and whisker plots were used to display mean ring growth ± standard deviation for each year and for each ring number for the Totara Park samples. Relationships between diameter and age, and height and age for both species were tested using multiple linear regression. Site frequency distribution histograms for each diameter size class were created using excel column charts. Plot frequency distributions were then combined for each site and displayed with age data. One way analysis of variance (ANOVA) was used to test for a significant difference ($p < 0.05$) between mean sapling frequency for all plots. Kahikatea and grey willow total densities, basal area and % multileadered stems and kahikatea sapling and seedling densities were calculated for each plot. These attributes were tested for correlations using multiple regression.

Results

Grey willow and kahikatea mean diameter growth rates for all sites were 2.96 ± 1.37 mm yr^{-1} (n = 68) and 2.45 ± 1.37 mm yr^{-1} (n = 75) respectively. Mean diameter growth rates showed high levels of variation between samples for both kahikatea and grey willow at each site (Table 3). Grey willow mean diameter growth rates were faster at Silverdale, Tamahere, Hakarimata and Kopuatai sites, while kahikatea diameter growth rates were faster at Totara Park and Kirikiriroa. Kahikatea recorded a maximum diameter growth increment of 12.76 mm and grey willow of 8.95 mm (Figures 8 and 9).

Table 3 Average annual diameter growth (mm yr^{-1}) for both species at each site.

	Average annual diameter growth rates (mm yr^{-1} ± SD)					
	Site					
	Totara Park	Silverdale gully	Kirikiriroa gully	Tamahere Reserve	Hakarimata Walkway	Kopuatai Wetland
Kahikatea	2.67 ± 1.07	1.27 ± 0.41	2.97 ± 1.29	2.92 ± 1.73	1.44 ± 0.71	2.08 ± 0.98
Grey willow	2.43 ± 1.20	5.37 ± 2.10	2.57 ± 1.05	3.27 ± 0.91	2.87 ± 0.78	3.73 ± 1.29

The dendrochronological record for Totara Park extends back to 1957 through a grey willow individual. An attempt was made to cross-date the thirty five kahikatea and thirty three grey willow core samples obtained from Totara Park. However results were similar to that of Cameron (1960), and after the percentage deviation from the mean ring growth rate was calculated for each ring (per individual) no patterns, or ‘marker rings’ that unified the samples were found. Figures 10 and 11 display mean ring width at the park from 1964 to 2009 for rings measured using the microscope and do not include rings calculated based on missing radial lengths. Kahikatea mean diameter increments appeared to be increasing over the population’s history at the park, but this was not seen in grey willow samples.

Next we plotted mean diameter growth rates against the ring number to see if there was any ontogenic growth processes occurring in the early years of growth for either species (Figures 12 and 13). Kahikatea diameter growth appears to be increasing throughout the ring history. Grey willow appears to reach maximum diameter growth rates early and maintains these for 20 years after which they drop off. Kahikatea mean diameter growth rates are faster at Totara Park.

Figure 8 Largest kahikatea diameter increment.

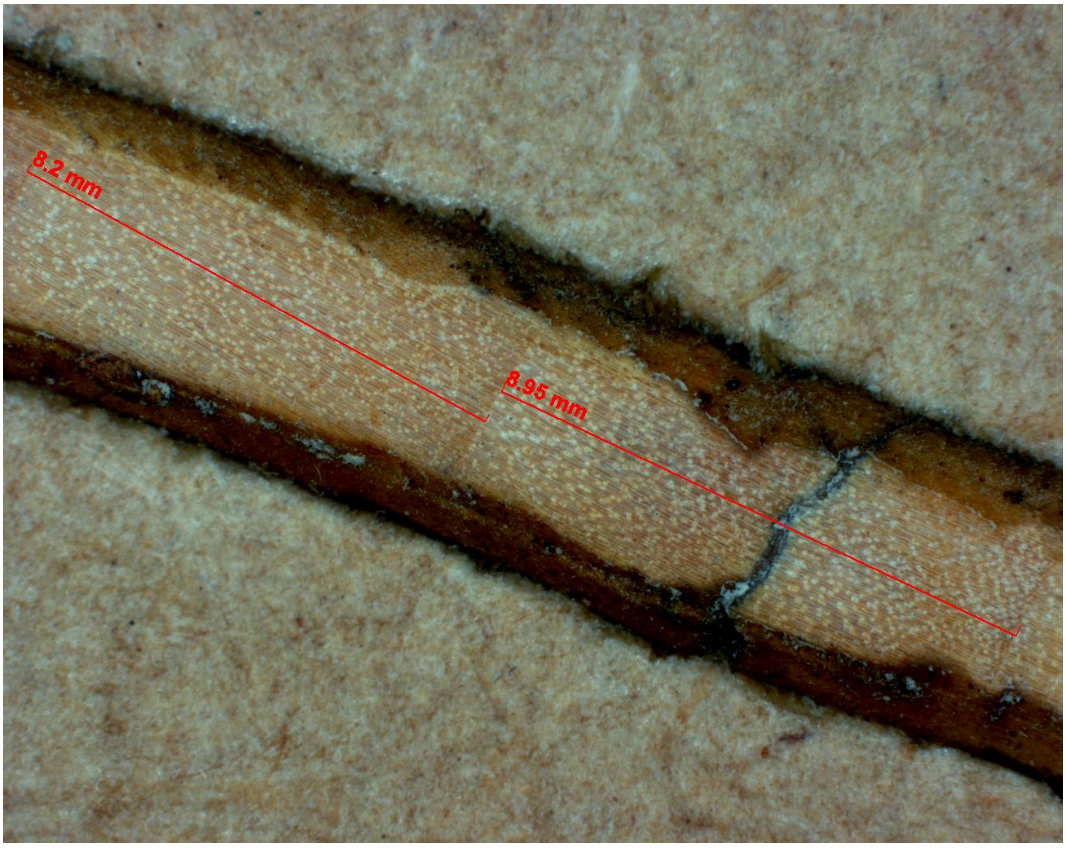

Figure 9 Largest grey willow diameter increment.

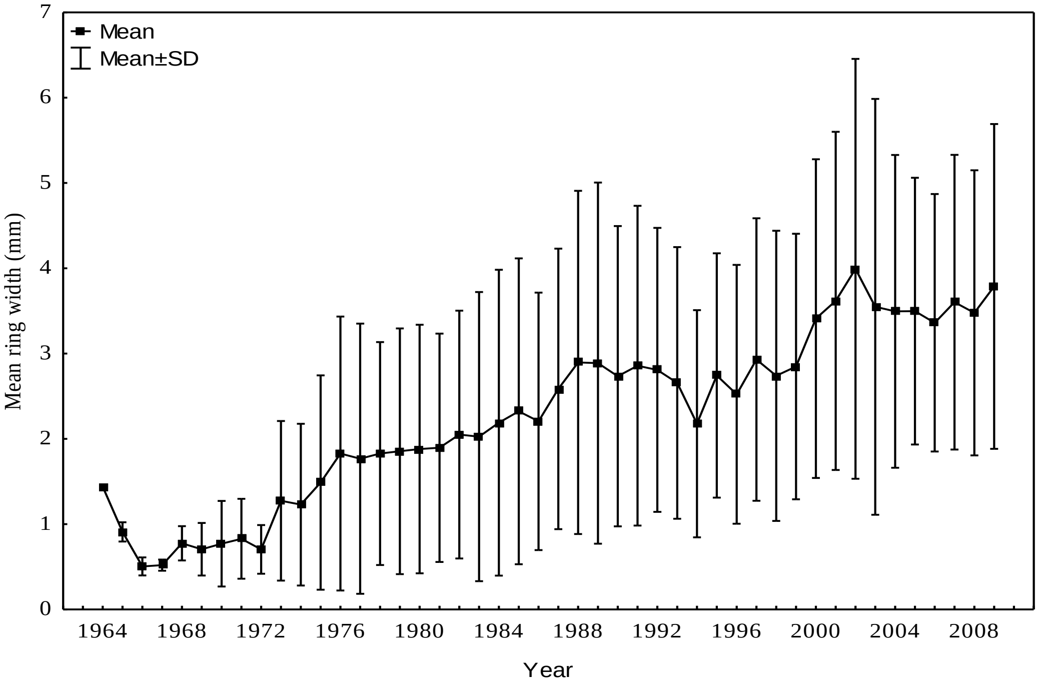

Figure 10 Totara Park kahikatea average diameter growth from 1964 to 2009.

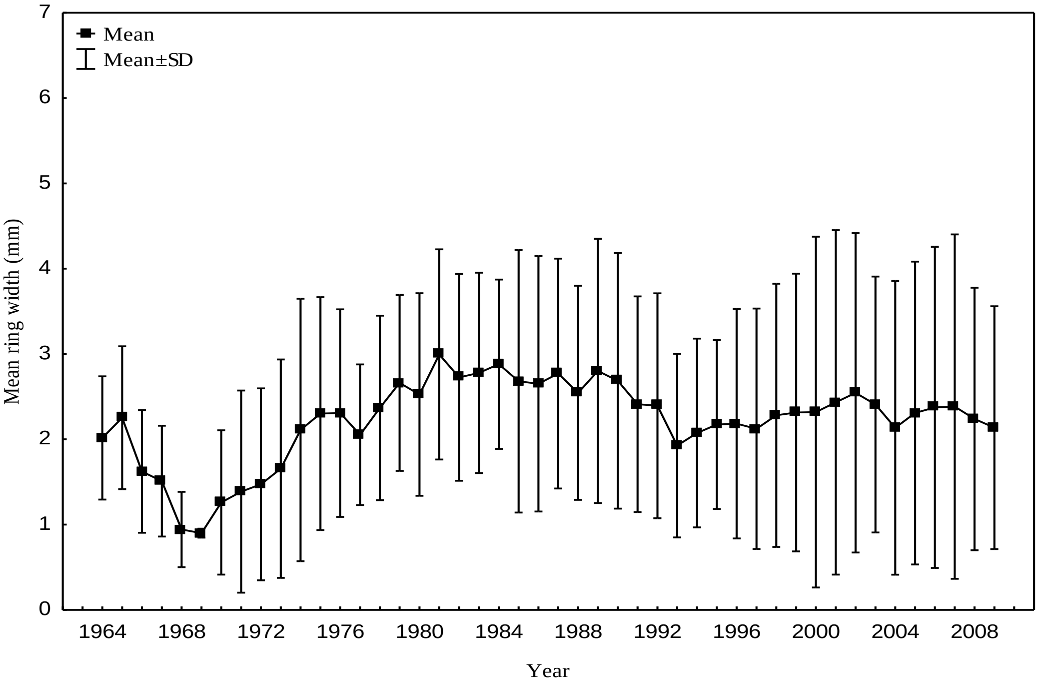

Figure 11 Totara Park grey willow average diameter growth from 1964 to 2009.

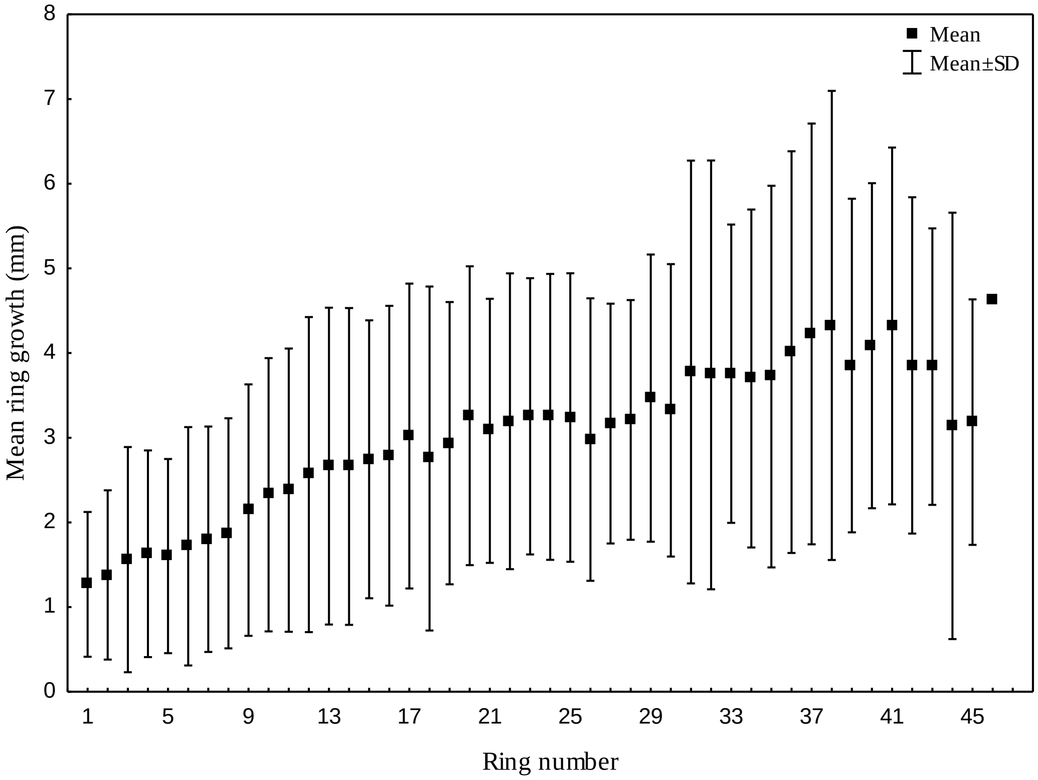

Figure 12 Totara Park kahikatea average diameter growth vs. age.

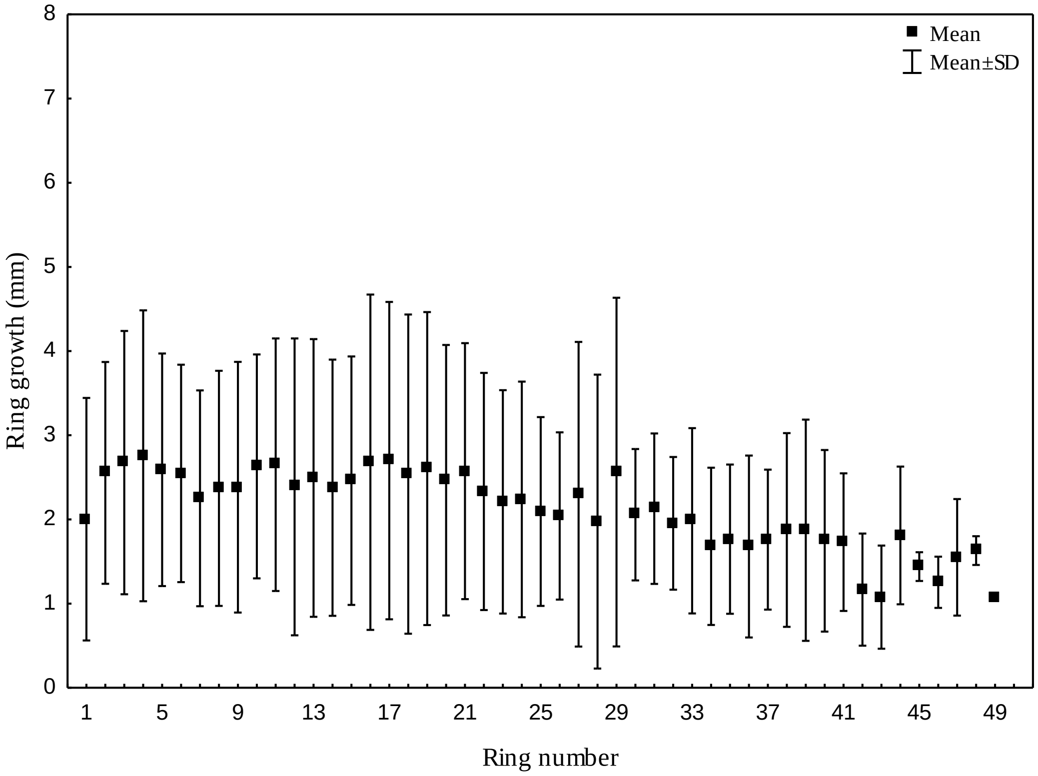

Figure 11 Totara Park grey willow average diameter growth vs. age.

Diameter explained 50% of the variation in age for kahikatea and 43% of the variation in age for grey willow (Figures 14 and 15). A positive linear relationship existed for estimated height and age regressions of kahikatea (r = 0.71), and height explained 50% of the variation in age of kahikatea individuals (Figure 16). Age and height were not as positively related for grey willow (r = 0.28), but displayed lower variance and height explained 76% of the variation in age (Figure 17).

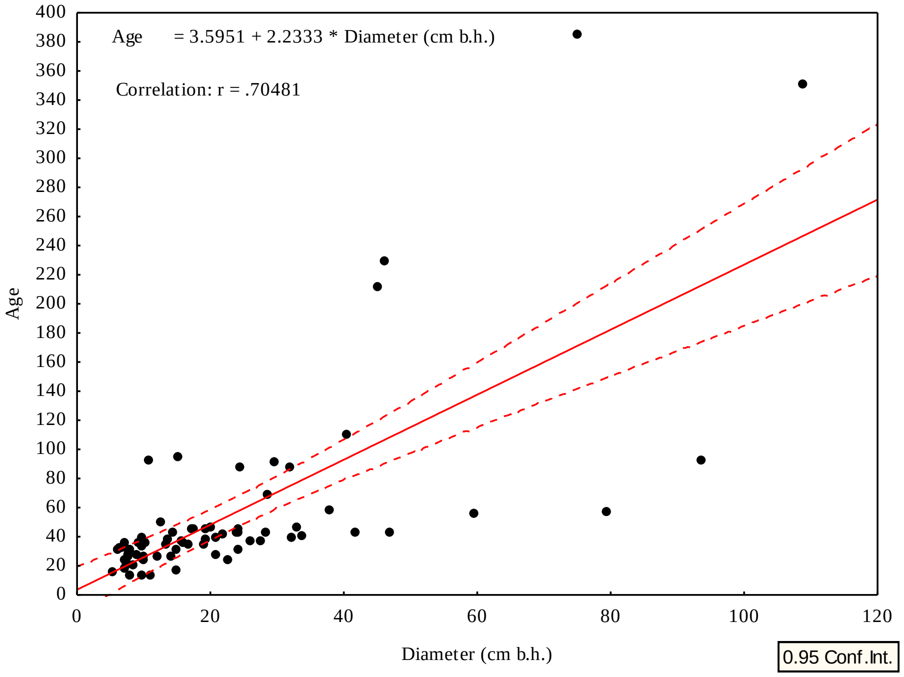

Figure 14 Kahikatea age vs. diameter regression for all sites (n=74; r^2=0.50; F(1,68)=71.1; *P* < 0.000).

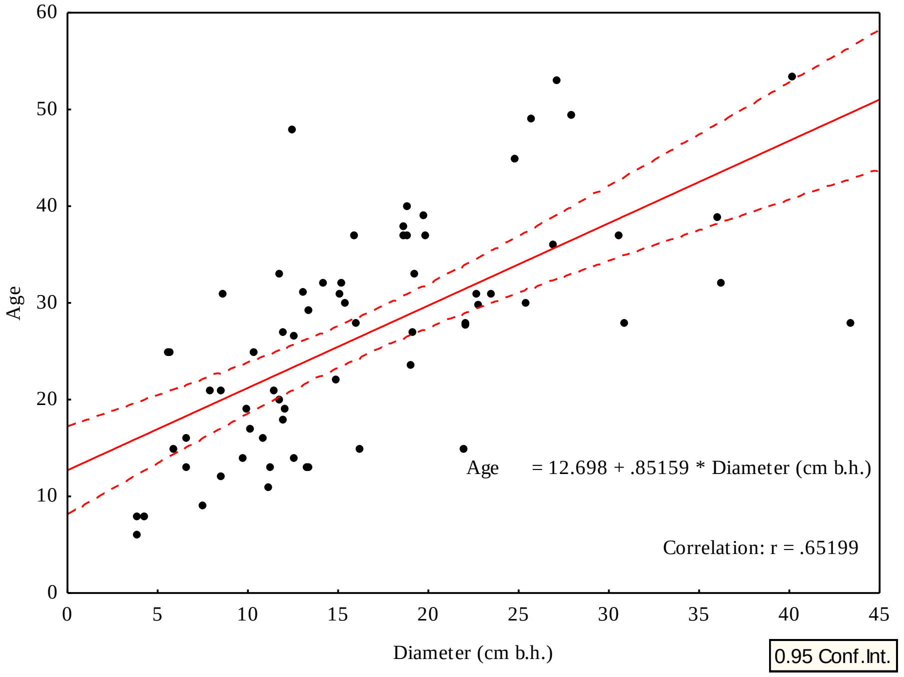

Figure 15 Grey willow age vs. diameter regression for all sites (n=68; r^2=0.43; F(1,66)=48.8; *P* < 0.000).

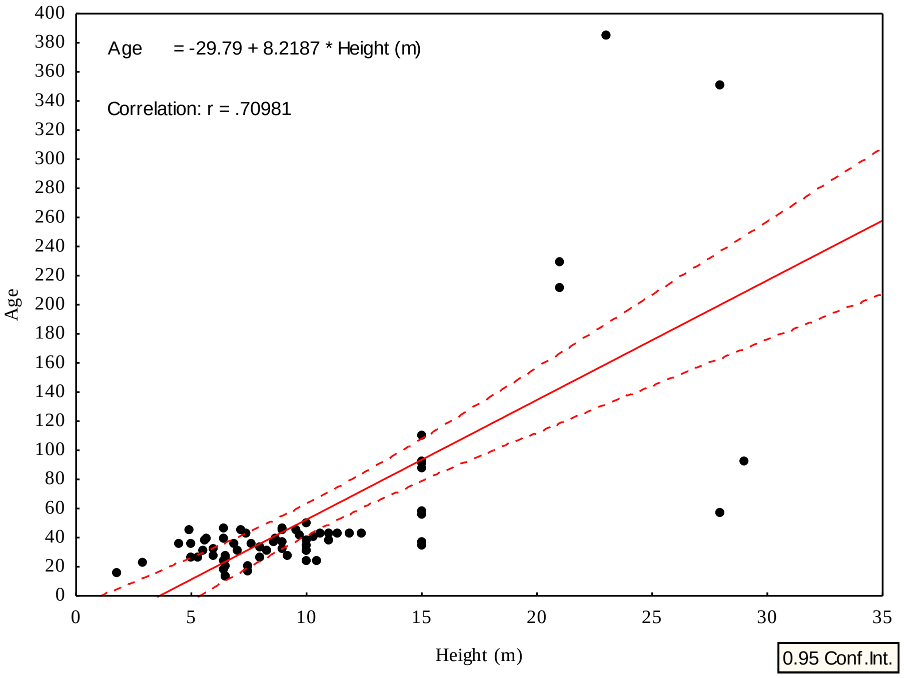

Figure 16 Kahikatea age vs. estimated height regression for all sites (n=70; r^2=0.50; F(1,68)=69.1; *P* < 0.000).

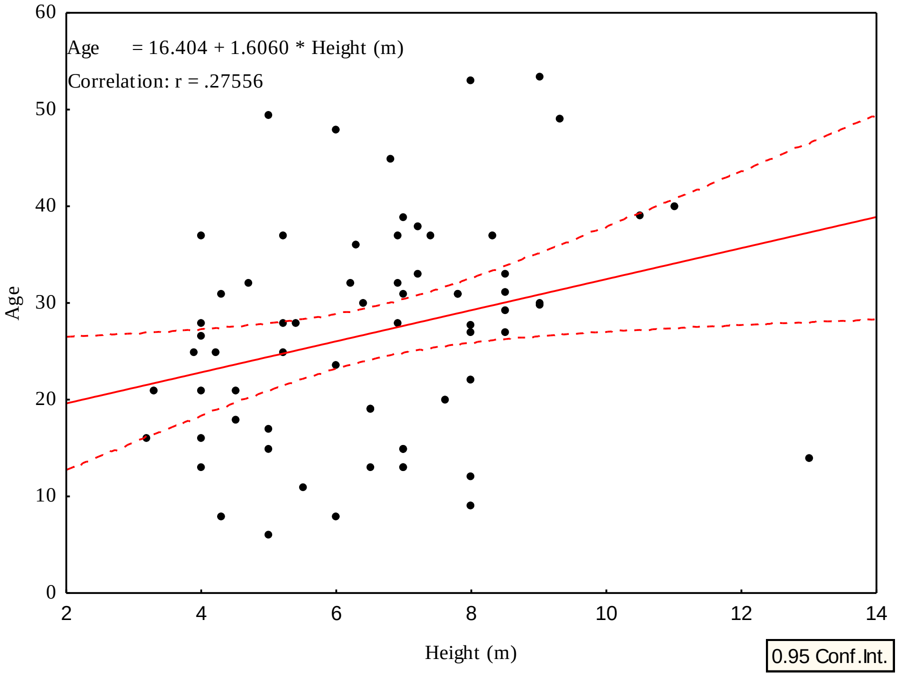

Figure 17 Grey willow age vs. estimated height regression for all sites (n=68; r^2=0.76; F(1,65)=5.3; *P* < 0.024).

Kahikatea seedlings were present at all plots at Totara Park (Table 4). Plot 1 contained few seedlings, probably due to dense *Baumea rubiginosa* mats, plot 2 contained seedlings over a meter in height but not sapling height. Plots 3 and 4 had high seedling densities, which probably reflected the higher light levels at these sites (Table 5).

Table 4 Kahikatea seedling tally for each site (% values indicate area searched if not entire plot).

	Seedling tally				
	Plot				
Site	1	2	3	4	5
Totara	3	45	142 (50%)	97 (1%)	
Silverdale	132 (50%)	5	414	1	
Tamahere	2	244 (11%)	2	0	16
Hakarimata	3	22			
Kopuatai	362	4			

Table 5 Site physical characteristics and dominant vegetation.

		Plot summary				
		Plot				
Site		1	2	3	4	5
Totara	Area (m^2)	366	50	302	380	
	% canopy openess	14	13	21	32	
	Vegetation class	kahikatea/willow forest	kahikatea forest	kahikatea/willow forest	kahikatea forest	
	Water table	below	below	surface	below	
Silverdale	Area (m^2)	254	20	254	20	
	% canopy openess	16	0	21	0	
	Vegetation class	(kahikatea)/willow forest	willow forest	(kahikatea)/willow-wheki forest	willow forest	
	Water table	surface	surface	surface	below	
Tamahere	Area (m^2)	290	314	302	1064	79
	% canopy openess	10	5	30	10	30
	Vegetation class	pate shrubland	willow forest	kahikatea/willow forest	kahikatea/willow forest	willow forest
	Water table	below	surface	below	below	above
Hakarimata	Area (m^2)	154	79			
	% canopy openess	29	20			
	Vegetation class	kahikatea/willow forest	kahikatea/willow forest			
	Water table	surface	below			
Kopuatai	Area (m^2)	616	346	95		
	Vegetation class	kahikatea/willow forest	kahikatea/willow forest	willow forest		
	Water table	above	surface	above		

Totara Park plots 1 and 4 had the highest recruitment of kahikatea into the sapling size classes, with the remaining two plots showing little or none (Figure 18). Plot 4 had a number of kahikatea under 4cm in diameter but of similar height (4 metres) to their neighbours, indicating they may have been suppressed and could be similar in age, however we were unable to confirm their ages due to increased risks in coring individuals that small. Higher frequencies of grey willow in plots do not appear to coincide with lower frequencies of kahikatea saplings. Kahikatea diplays lower age spread overall and lower age variation between diameter size classes than grey willow (Figure 19). Both species have similar maximum ages of 45 to 50 years old. The youngest kahikatea were aged around 15 years old compared to 8 for grey willow. Both species appear to have established around the same time at Totara Park.

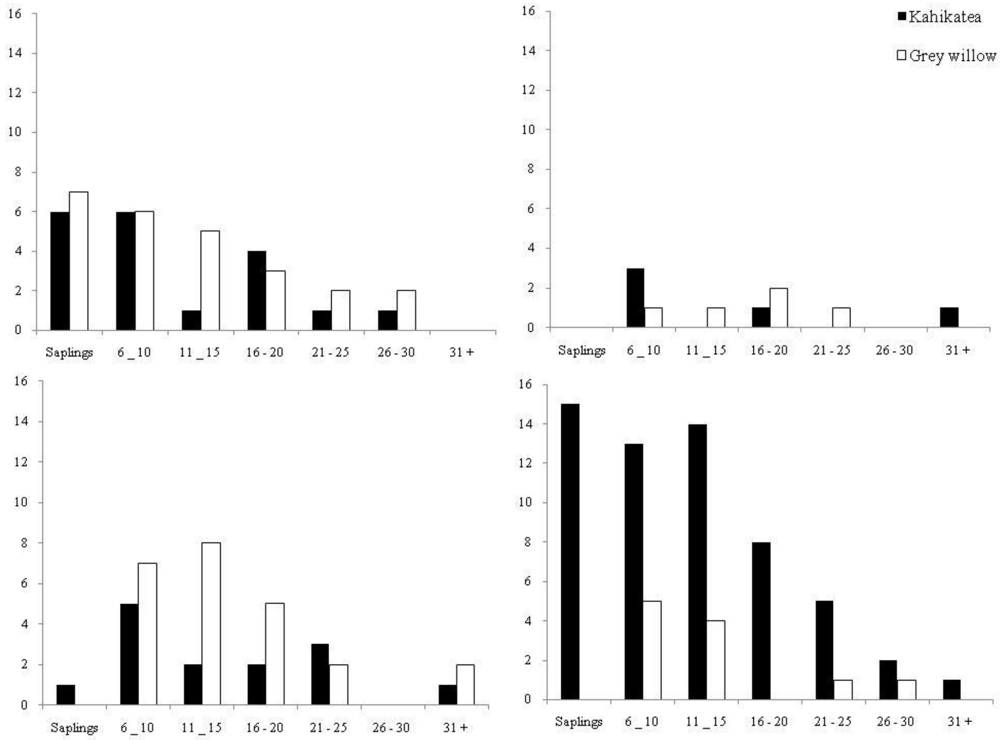

Figure 18 Totara Park diameter size class (x axis, cm at breast height) frequency distributions (plot 1 = top left, 2 = top right, 3 = bottom left, 4 = bottom right). Note: grey willow in the sapling class are present as resprouts or branching.

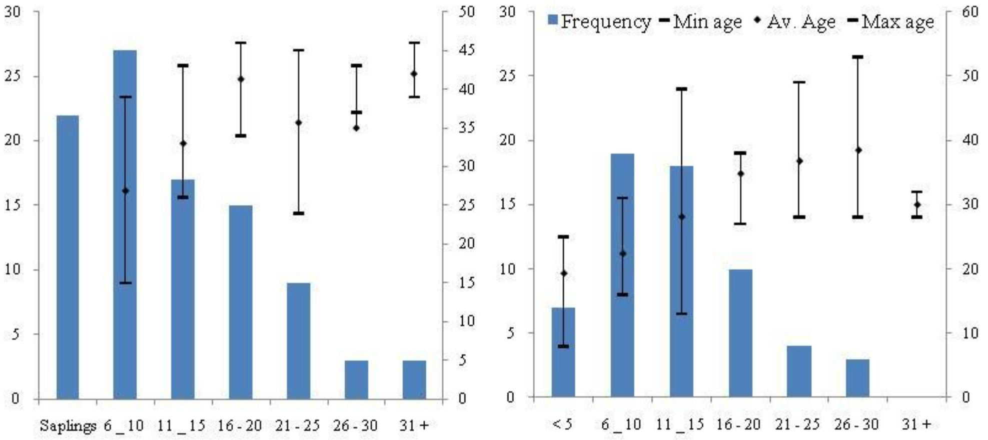

Figure 19 Totara Park kahikatea (left) and grey willow diameter size class (cm dbh; x axis) frequency distributions for all plots and the age range (years; right y axis) of cored individuals within these size classes.

Dendrochronologies for grey willow and kahikatea extend back to 1961 and 1964 respectively. Five cored kahikatea and three grey willow had histories dating prior to 1969, when it is likely mining started and vegetation clearance began. After this year frequencies of grey willow and kahikatea in our sample clearly increased (Figure 20).

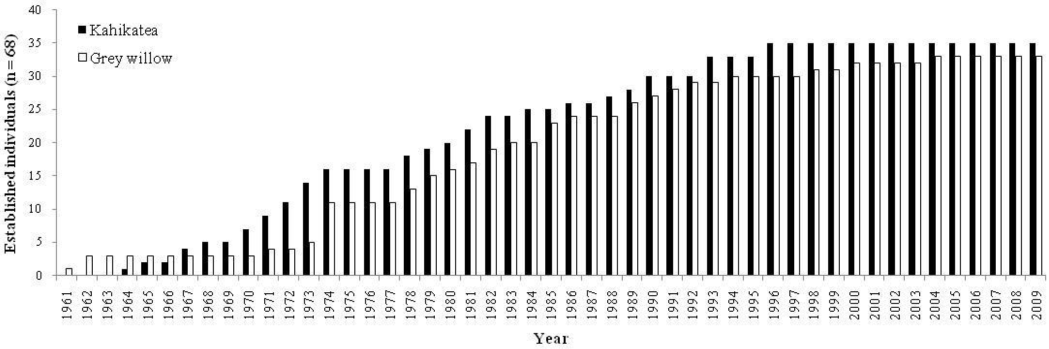

Figure 20 Establishment history of cored kahikatea and grey willow at Totara Park.

The Silverdale gully site contained lower densities of grey willow and kahikatea than any other site (Figure 21), and much of the site was regularly flooded. The kahikatea population consists of four mature individuals and only plot 2 plot had recruitment into the sapling size class. Seedling densities were highest in plots 1 and 3 (Table 5), but seedlings were mostly those that had established that year.

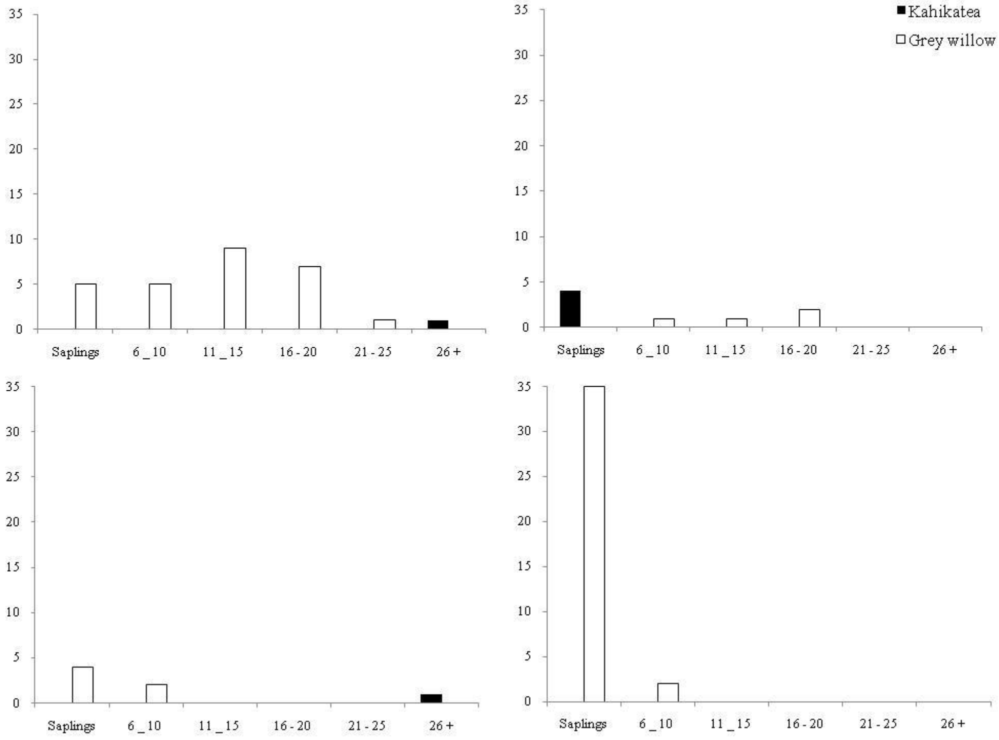

Figure 21 Silverdale gully diameter size class (x axis, cm at breast height) frequency distributions (note the differential scales for plots 1 & 3 and 2 & 4; plot 1 = top left, 2 = top right, 3 = bottom left, 4 = bottom right). Note: grey willow in the sapling class are present as resprouts or branching.

Figure 22 shows kahikatea trees aged at Silverdale gully were remnants of pre-european forest, over 70 cm in diameter and aged over three hundred and fifty years, these individuals were the oldest cored in the study. The oldest grey willow cored at the site was aged at 22 years old and the youngest was six. The grey willow control plot was situated on a footslope on the western side of the gully and contained the highest grey willow densities of the study (18.5 grey willow per 10 m^2), which were mostly in the under 5 cm size class, indicating recent colonization. This plot was excluded from later regression correlations with kahikatea sapling density because of its unusual outlier density of grey willow.

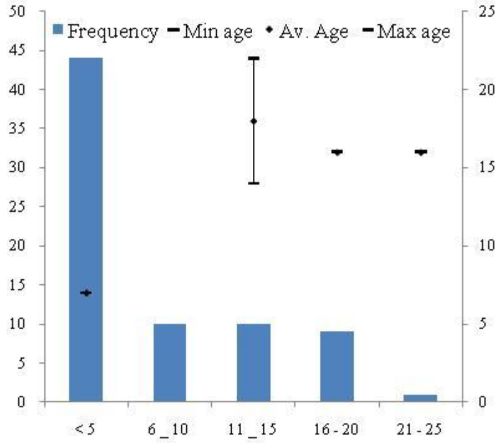

Figure 22 Silverdale gully grey willow diameter size class (x axis, cm at breast height) frequency distribution for all plots and the age range (right y axis) of cored individuals within these size classes.

The sampling undertaken at Kirikiriroa gully found variation in diameter of 4.2 to 5.4 cm (b.h.) between the even aged individuals (19 years old), planted in 1996, were exposed to different drainage regimes. One individual was located closest to the stream with the poorest drainage, but with the water table still below the surface, one individual was intermediate and one was located on the upper slope. In addition the five individuals cored downstream clearly showed increased growth rates following removal of the grey willow canopy in 2003 – 04.

At Tamahere Reserve, plot 2 was the only plot showing significant colonisation of kahikatea seedlings (Table 5). This was reflected in recruitment of saplings and again sapling presence did not appear to be influenced by grey willow frequencies (Figure 23). Kahikatea individuals were present in most diameter sizes, but the majority of stems occurred in the under 9 cm class. Grey willow stem frequencies were relatively consistent between sites with most occurring in the 10 to 19 cm size class, excluding the grey willow control plot, which contained high numbers under 9 cm in diameter and a plot density of 5.2 per 10 m^2.

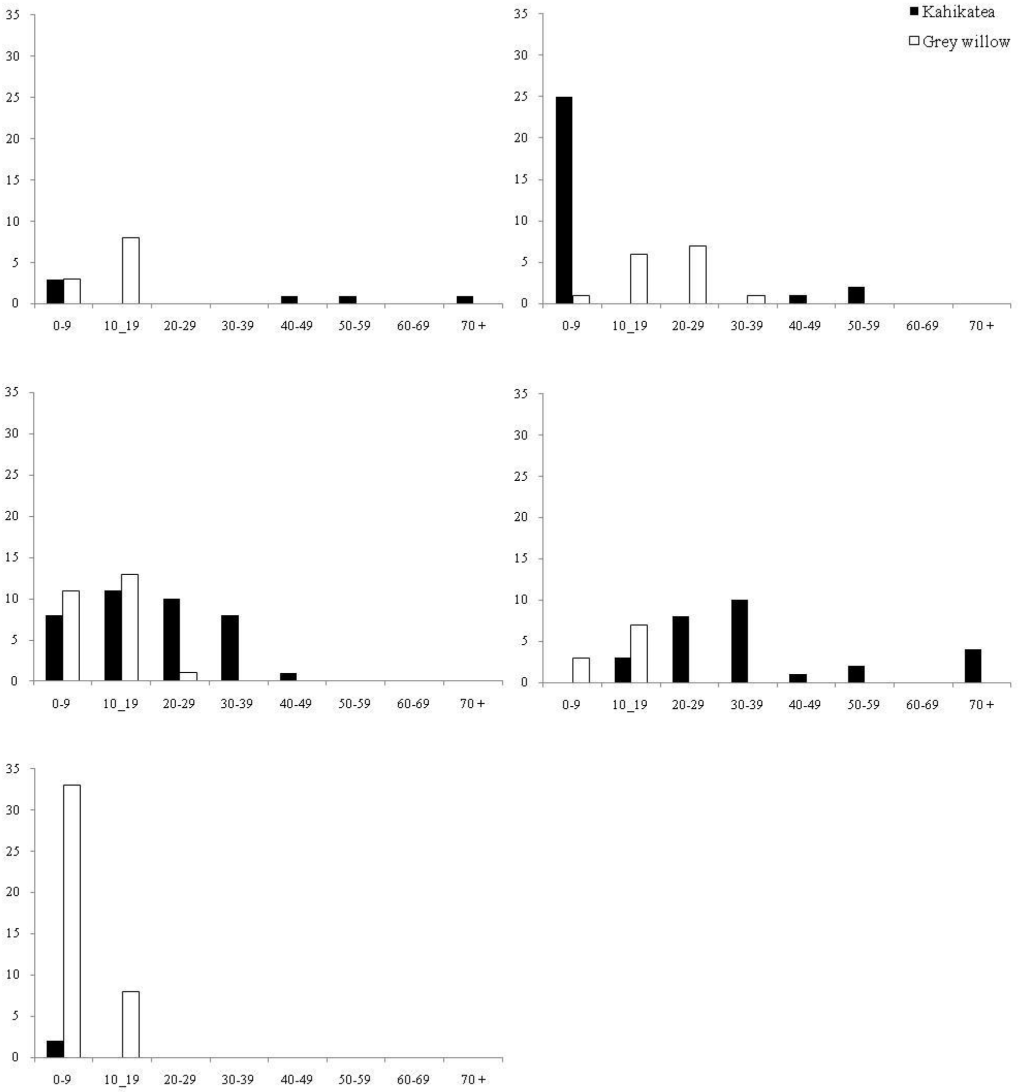

Figure 23 Tamahere Reserve diameter size class (x axis, cm at breast height) frequency distributions (plot 1 = top left, 2 = top right, 3 = middle left, 4 = middle right, 5 = bottom left). Note: all graphs exclude seedlings.

Tamahere Reserve age structures (Figure 24) were between 55 and 109 for kahikatea and 12 and 50 years old for grey willow, indicating the kahikatea population established before grey willow colonisation at this site. Kahikatea populations were likely recruiting well from 1900 to 1954, but after this period there seems to be a shortage of recruits, until the unknown aged population of saplings. Grey willow looks to be regenerating well at the site since its establishment, probably in the 1950's (the oldest grey willow cored was 51). However from our cored sample we found no individuals aged under 12 years old, which could indicate no recent regeneration at the site.

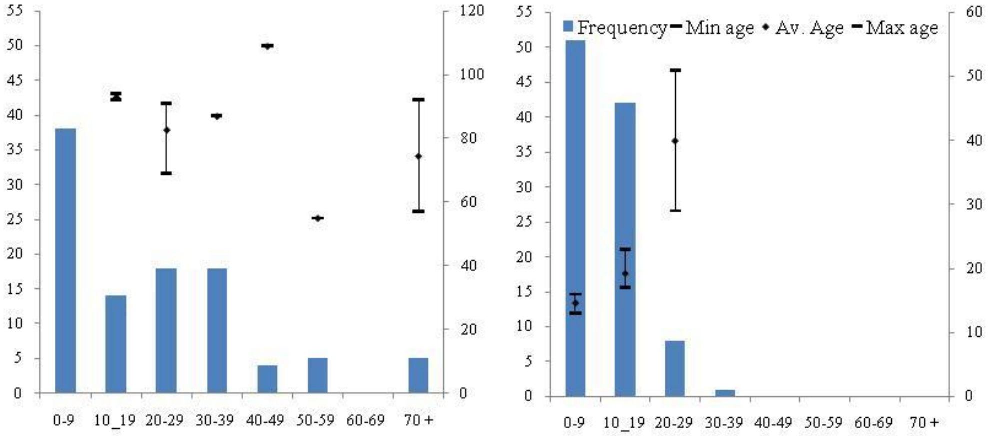

Figure 24 Tamahere Reserve kahikatea (left) and grey willow diameter size class (x axis, cm at breast height) frequency distributions for all plots and the age range in years (right y axis) of cored individuals within these size classes.

The Hakarimata walkway site contained the smallest grey willow populations and the greatest regeneration of kahikatea of all the sites (Figure 25). Kahikatea were not present above the 11 to 15cm diameter size class, and occurred in greatest frequencies in the sapling size class. A large grey willow measuring 40.1 cm in diameter was present, but the highest stem frequencies occurred in the 11 - 15 cm size class.

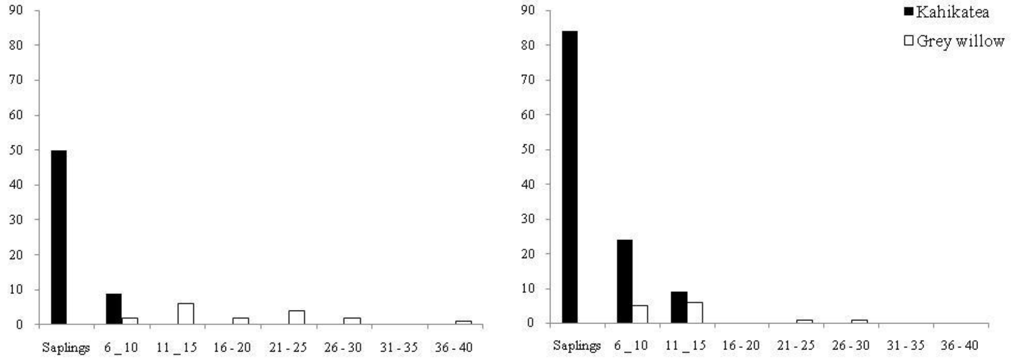

Figure 25 Hakarimata walkway diameter size class (x axis, cm at breast height) frequency distributions (plot 1 = left, 2 = right).

It appears both species colonised the Hakarimata walkway site around the same time in 1953 to 1955 (Figure 26). The kahikatea population appears to be a relatively even aged cohort of individuals between 30 and 40 (with one individual 56 years old) and a group of saplings of unknown age. A number of kahikatea in the sapling diameter size class are possibly suppressed older individuals in the 30 + age class, due to their presence in the canopy, however there is also many saplings between 1.35 and 5 metres in height that are likely younger. Most cored grey willow were aged under 30 years old, but one individual was aged 54. Similar to Tamahere Reserve, no cored grey willow were aged under 10 years.

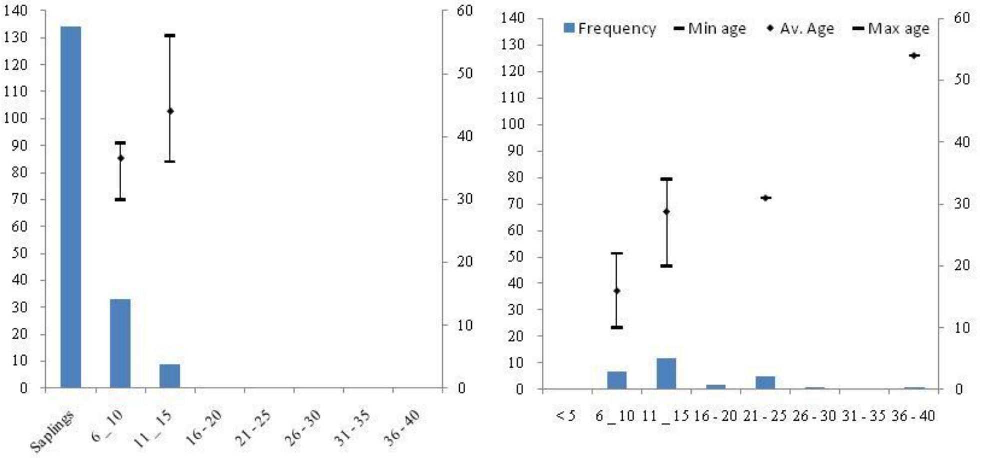

Figure 26 Hakarimata walkway kahikatea (left) and grey willow diameter size class (x axis, cm at breast height) frequency distributions and the age range (right y axis) of cored individuals within these size classes.

Kopuatai wetland kahikatea diameter frequencies were highest in the sapling and over 36 cm size classes (Figure 27). Maximum frequencies were 20 stems per plot for kahikatea and 50 for grey willow.

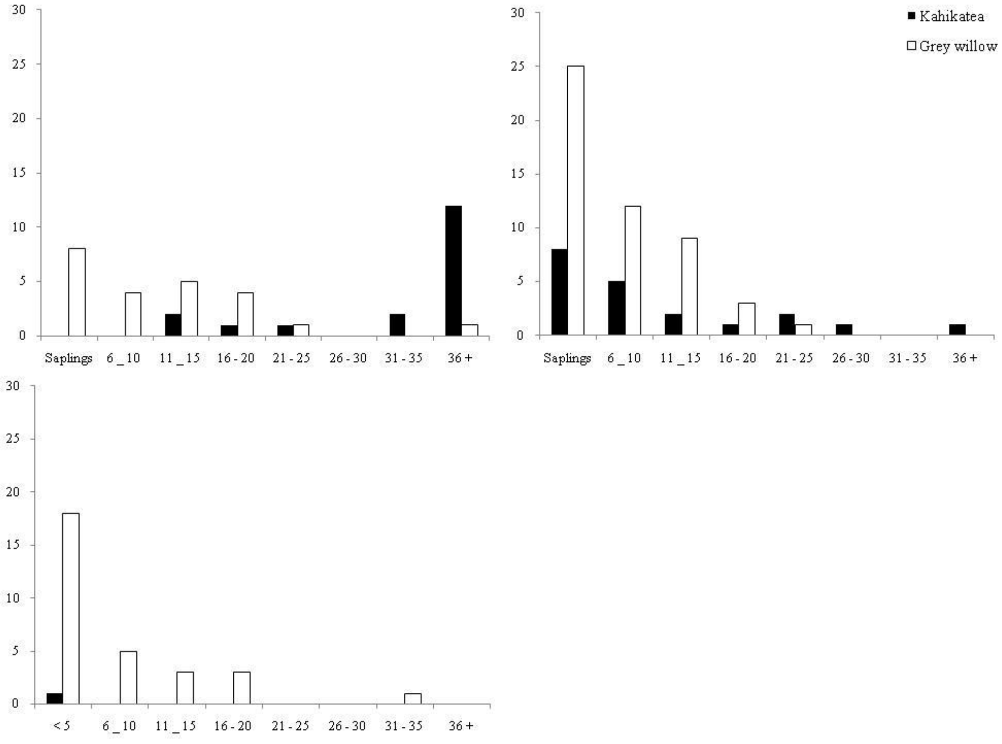

Figure 27 Kopuatai wetland diameter size class (x axis, cm at breast height) frequency distributions (plot 1 = top left, 2 = top right, 3 = bottom left). Note: grey willow in the sapling class are present as resprouts or branching.

Most seedlings were found in plot one (Table 5), but were not recruiting into the sapling size class. Significant sapling regeneration was only seen in plot 2. The grey willow control plot (3) displayed grey willow frequencies intermediate to the other two plots. Kahikatea age structures consisted of two 200 + year olds in plot 1 and another group aged between 30 and 65 in plot 2. Grey willow displayed ages between 9 and 30, with one individual 40 years old (Figure 28).

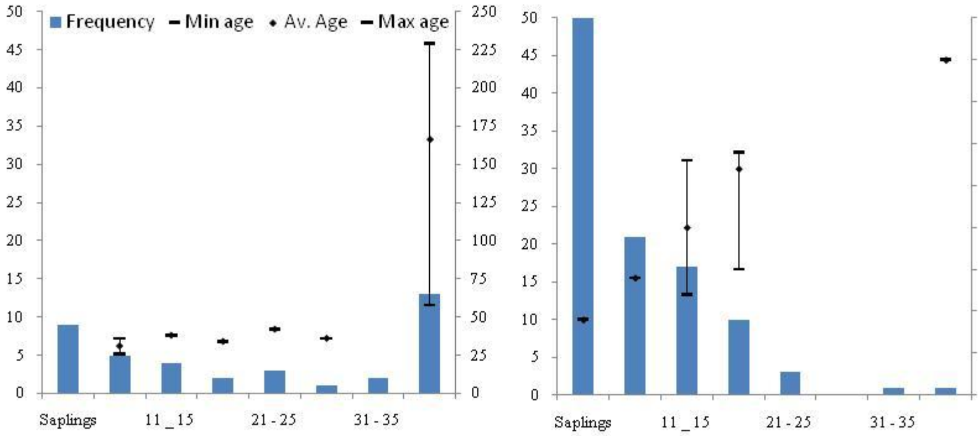

Figure 28 Kopuatai wetland kahikatea (left) and grey willow diameter size class (x axis, cm at breast height) frequency distributions and the age range (right y axis) of cored individuals within these size classes. NB: Kahikatea seedlings number closer to 400, but for the sake of scaling have halved this.

Regression correlations between kahikatea sapling frequency and grey willow plot total basal area (Figure 29) and plot density (Figure 30) were not related (r^2 = 0.01 & 0.003, F(1,15) = 0.2 & 0.05, $P < 0.66$ & $P < 0.83$ respectively). Kahikatea saplings occurred in all grey willow basal area volumes but only in densities under 2 grey willow per 10 m^2. Figure 31 shows kahikatea sapling frequency did relate strongly to kahikatea plot density over all sites, due to the Hakarimata site ($r^2 = 0.9$, F (1,16)= 137.8, $P < 0.00$). However once this site was removed so was the relationship (r = 0.31, $r^2 = 0.09$, F (1,14) = 1.45, $P < 0.25$). Though it is important to note the Hakarimata site was the only site sampled with kahikatea densities exceeding 2 per 10 m^2. Kahikatea sapling frequency was then correlated with grey willow plot density, basal area and kahikatea plot density using only the sites containing saplings but no improvements on correlations strength were noted (r^2 = 0.002, 0.001 and 0.938 respectively).

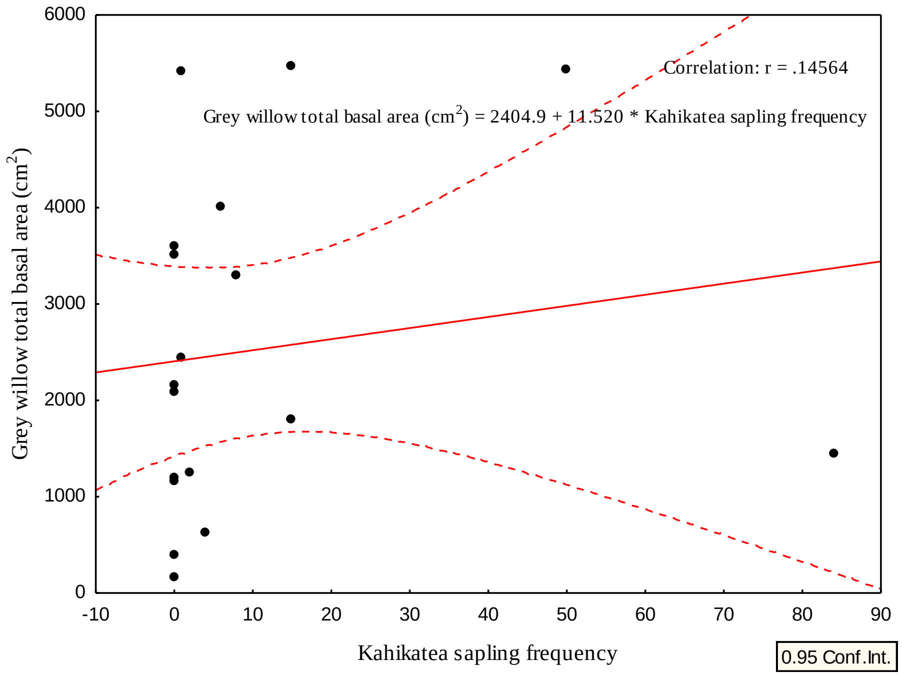

Figure 29 Kahikatea sapling frequency vs. grey willow total basal area.

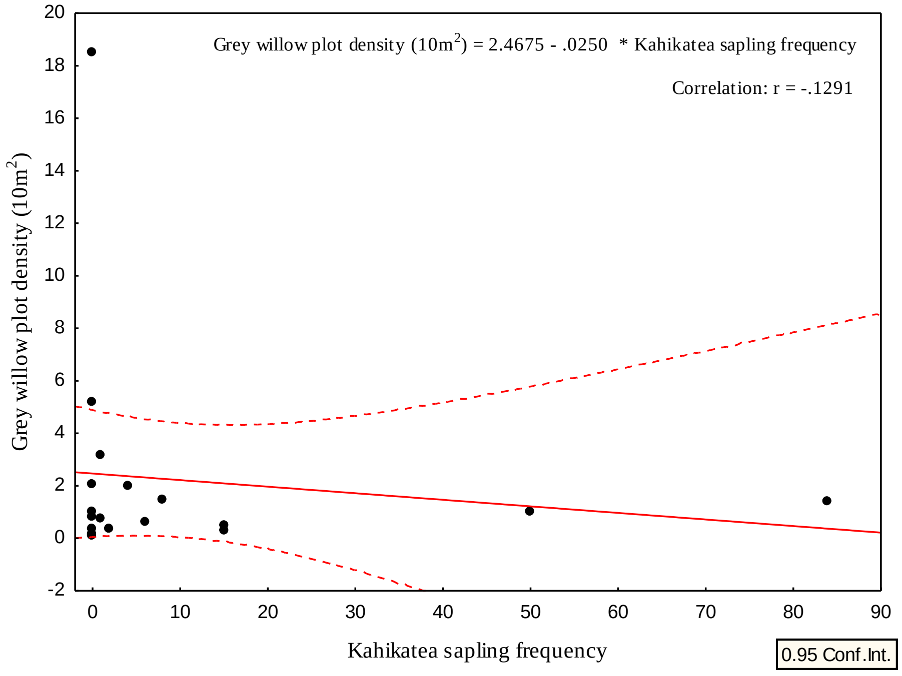

Figure 30 Kahikatea sapling frequency vs. grey willow plot density.

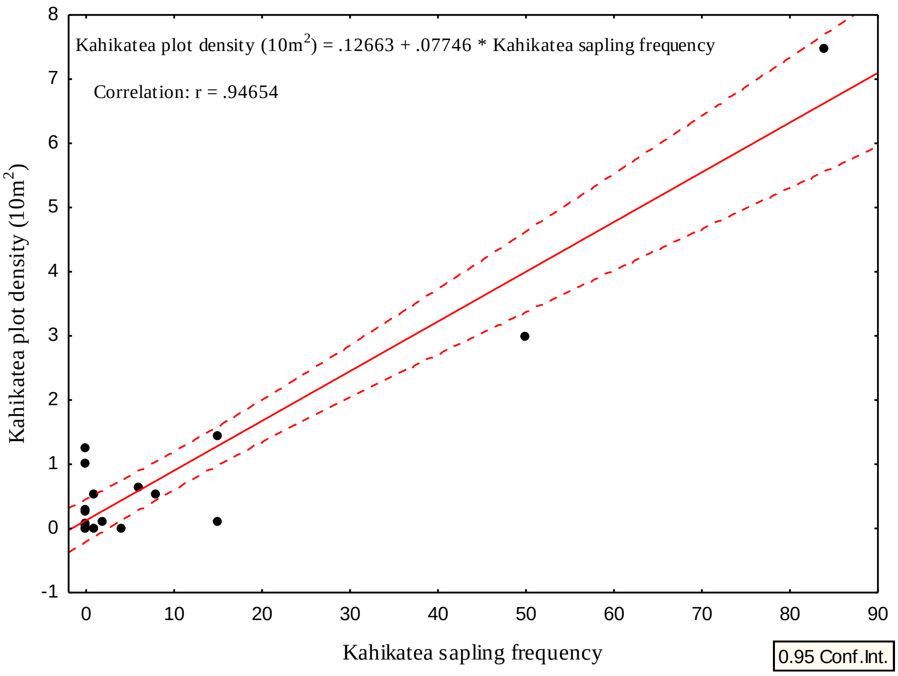

Figure 31 Kahikatea sapling frequency vs. kahikatea plot density.

ANOVA comparisons of mean sapling frequency between sites were significantly different. The Hakarimata site contained the most saplings and the remaining sites averaged under 10 saplings per plot (Figure 32).

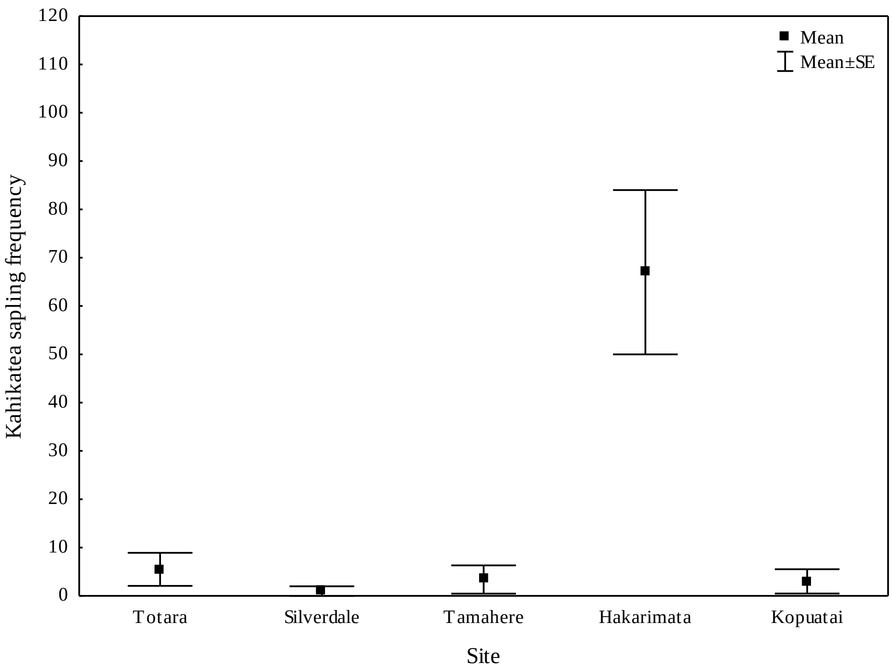

Figure 32 ANOVA boxplot displaying variation between sites in mean plot sapling frequency for kahikatea (*P* < 0.000).

Correlation results in Table 6 were all insignificant. Scatterplots of grey willow density and basal area against kahikatea density and basal area were not linearly, logarithmically, polynomially or exponentially related, but we did note in plots with high densities of kahikatea or grey willow the other species was present in low densities. Plot canopy openess did not relate to kahikatea seedling or sapling density. However the methodology for estimating canopy openess was insufficient to represent all seedling and sapling environments.

Table 6 Plot regression results.

Regression correlations for plot totals				
Relationship	r	r^2	F value	P value
Kahikatea vs. grey willow basal area	0.01	0	0	0.97
Kahikatea basal area vs. grey willow density	0.28	0.08	1.4	0.25
Kahikatea density vs. kahikatea seedling density	0.04	0	0.03	0.87
Grey willow density vs. kahikatea seedling density	0.18	0.03	0.56	0.47
Grey willow basal area vs. kahikatea seedling density	0.13	0.02	0.26	0.62
Kahikatea basal area vs. kahikatea seedling density	0.04	0	0.03	0.86
Plot canopy openess vs. kahikatea sapling density	0.24	0.06	0.78	0.39
Plot canopy openess vs. kahikatea seedling density	0.22	0.05	0.67	0.43
Kahikatea density vs. % kahikatea multileaders	0.07	0	0.07	0.79
Kahikatea density vs. % grey willow multileaders	0.35	0.12	2.27	0.151
Grey willow density vs. % grey willow multileaders	0.18	0.03	0.53	0.47

Discussion

Grey willow is marginally faster growing in diameter than kahikatea. Kahikatea diameter growth rates were relatively consistent with other studies (Duncan 1989; Champion 1988; Ebbett & Ogden 1998). However, the present study found significant variation between sites for diameter growth in both species. Likely reasons for this were variance in population ages and distributions, which emphasized the effect of ontogenic processes and competitive influences on diameter growth. Kahikatea growth rates were reduced at the Silverdale site because only large mature individuals were sampled, which due to ontogenic processes naturally have smaller diameter increments. Slower growth at Hakarimata was likely due to intraspecific competition as the highest kahikatea densities were found at this site. Grey willow displayed greatest diameter growth at the Silverdale and Kopuatai sites, which had the youngest populations. Ontogenic diameter growth in grey willow appeared to slow after 20 years. Kahikatea did not show this trend and continued to increase throughout the sampled history at Totara Park. Increased diameter growth rates may be explained by enhanced light levels after canopy penetration, but cannot be confirmed due to high variability in mean annual growth rates.

This study confirms there are other factors influencing the diameter growth of both grey willow and kahikatea than simply age, and as a result diameter may not be a wholly reliable indicator of age. Our diameter age regressions for kahikatea were not as strongly related as previous studies (Champion 1988; Duncan 1991), which may be due to the fact our study incorporated data from more than one site. Height was also not a strong indicator of age for kahikatea, but is relatively reliable for grey willow ages. This implies grey willow allocates more resources to height over diameter growth than kahikatea, an advantage in reaching canopy height which has been noted in early successional trees (King 1981). Maximum age estimates for grey willow are just over 50 years (Totara Park and Hakarimata sites), which are higher than those previously reported in the literature of 18 to 25 years (Gill 1974; Alliende & Harper 1989) and at odds to the general trend that patches dominated by members of the Salicaceae family are usually under 20 years old (Bayard & Schweingruber 1991). Whitmore (1988) noted vegetative reproduction can perpetuate the same species composition, and has the potential to halt successional processes. Add to this a reduced late succession angiosperm species pool in New Zealand, capable of tolerating the environmental conditions under grey willow (in particular high water tables and anoxic soils) and there is a good chance grey willow is slowing or preventing successional processes of vegetation change in the Waikato. Like Gill (1974), this study found grey willow was much harder to age due to decreasing ring clarity and conclude the age estimates of the grey willow samples are likely less accurate than kahikatea.

Kahikatea and grey willow were determined unsuitable species for cross dating as ring patterns were inconsistent between trees at each site (Dunwiddie 1978). This indicates factors limiting growth were different for individuals and the underlying climate signal was perhaps not as important as microclimate influences.
Pudney (2009) recorded soils at Totara Park are rich in all the required plant nutrients with the exception of phosphorus which is present in amounts unlikely to be limiting. He also recorded reduced pH values (from the mean of 5.7) in areas in the park with higher water tables. Factors most likely to characterize habitat heterogeneity at Totara Park are light levels, water table levels (and resultant pH values) and biotic interactions. It is likely one or all of these factors are involved in limiting kahikatea and grey willow growth rates rather than climatic influences. This is reflected in many New Zealand tree species (Cameron 1960; Scott 1972;

Dunwiddie 1979). Scott (1972) found only 9 – 37% of total variation in *Podocarpus halii, Phylocladus alpinus, Pinus contorta, Pinus nigra, Discaria toumatou* and *Nothofagus solandri* ring indices were attributed to changes in monthly mean temperature and rainfall. Therefore quantifying how interference affects growth and survival of kahikatea at Totara Park may only be possible through measuring these at the level of the individual and will require in depth historical knowledge of microclimate conditions.

Historic trends in population structure across all sites seem to indicate kahikatea and grey willow are able to establish at the same time in the successional sequence. Both species colonised Totara Park around the same time after vegetation clearance, but appear to have been present at the site before sand mining activities (prior to 1969), which equalized the dispersal factor. Grey willow came later than kahikatea at the remaining sites because kahikatea populations did not undergo as much disturbance. Once grey willow reaches the canopy, it appears kahikatea recruitment suffers. At Tamahere Reserve, results suggest grey willow colonised around 50 years ago which coincides with the youngest age of our cored kahikatea (55 years old). This is also true of the Hakarimata and Kopuatai sites except occurred at Kopuatai around 30 years ago. Champion’s (1988) suggestion kahikatea is spreading into grey willow forest at Kopuatai, may be correct in the seedling and sapling size classes, but is not evident in the larger size classes.

Extensive seedling mortality and disproportionately lower recruitment into the sapling size class has regularly been observed for kahikatea trying to regenerate under a canopy (Beveridge 1973; McSweeney 1982; Smale 1984; Duncan 1991, 1993), which suggests seedling regeneration alone is not an indicator of sustainable kahikatea recruitment and the sapling size class is of greater relevance. Because I could not age the saplings their history can only be estimated, either by extrapolating back from diameter and height growth regressions (Champion 1988), or by comparing individual growth responses to suppression events. Kahikatea stems in the sapling size class that are present in the canopy are likely to be of similar age to their neighbours because it is common for pioneer species such as kahikatea to gain height at the expense of girth if competing for light in a stand (Antonovics & Levin 1980; Weiner 1984; Whitmore 1988; Duncan 1991).

For saplings that have not reached the canopy, their age could vary substantially. These saplings have potential to be much older than expected, and extrapolation of our age diameter regressions indicate some may be up to 20 years old.
The data from Kirikiriroa gully confirms the powerful effect suppression from a grey willow canopy can have on kahikatea diameter growth rate by illustrating high variance in diameter growth between even aged individuals, planted at the same time.

Kahikatea sapling frequency across sites was not linearly related to grey willow density or basal area, however the observation that saplings do not occur in environments with grey willow densities over 2 per 10 m^2 should be further analysed (we only had three plots with grey willow densities exceeding this). Kahikatea sapling frequency was positively linearly related to kahikatea plot density, but only once we included the high density site at Hakarimata which has kahikatea plot densities above 2 per 10 m^2. The length of time a site has been colonised by kahikatea does not seem to impact on sapling frequencies as the oldest kahikatea population at the Kopuatai site has fewer saplings than all the sites with the exception of Silverdale gully. The time since the last major disturbance and the distance to the nearest seed source are probably more important factors influencing sapling frequencies, as the highest sapling frequencies were found at the site bordering the Hakarimata scenic reserve and the younger, more recently disturbed sites.

Conclusion

It appears grey willow density or basal area has no effect on kahikatea seedling or sapling plot frequencies unless it is at extremely high densities. However the presence of seedlings and saplings does not always equal recruitment into the canopy. Because kahikatea diameter is not always a good indicator of age, it is difficult to confirm the age of saplings. They may be older individuals that have been suppressed for decades. Age structures at all sites seem to suggest cessation of kahikatea canopy cohort development once grey willow has entered the stand, and that interference from grey willow is negatively affecting kahikatea recruitment into the canopy.

References

Alliende M C, Harper J L 1989. Demographic Studies of a Dioecious Tree. I. Colonisation, Sex and Age Structure of a Population of Salix Cinerea. The Journal of Ecology 77 (4): 1029-1047.

Antonovics J, Levin D A 1980. The Ecological and Genetic Consequences of Density-Dependent Regulation in Plants. Annual Review of Ecology and Systematics 11: 411-452.

Atkinson I A E 1962. Semi quantitative measurements of canopy composition as a basis for mapping vegetation. Proceedings of the New Zealand Ecological Society 9: 1-8.

Bayard M, Schweingruber F H 1991. Trees at their limit on the riverbed of the Maggia in the Canton of Tessin, Switzerland: a dendroecological study. Botanica Helvetica 101: 9-28.

Bell R E 1958. Dendrochronology. Proceedings of the First Annual Conference, N. Z. Archaeological Assoiciation. New Zealand Science Review 16 (1): 13-17.

Bell V, Bell R E 1958. Dendroecological studies in New Zealand. Tree-Ring Bulletin 22 (1): 7-11.

Beveridge A E 1973. Regeneration of podocarps in a central North Island forest. New Zealand journal of forestry 18: 23-35.

Buckley B, Ogden J, Palmer J, Fowler A, Salinger J 2000. Dendroclimatic interpretation of tree-rings in *Agathis australis* (kauri). 1. Climate correlation functions and master chronology. Journal of the Royal Society of New Zealand 30 (3): 263-275.

Burns B R, Barker G M, Harris R, Innes J 2000. Conifers and cows: forest survival in a New Zealand dairy landscape. Pp 81-89. In: Nature conservation 5: Conservation in production environments. Managing the matrix (Eds. J L Craig, N D Mitchell, D A Saunders). Surrey Beatty and Sons. Chipping Norton, Australia. 712pp.

Cameron R J 1960. Dendrochronology in New Zealand. Journal of the Polynesian Society 69: 37-38.

Champion P D 1988. The Ecology and Management of kahikatea *Dacrycarpus dacrydioides* (A. Rich.) de Laubenfels in the Waikato, North Island, New Zealand. University of Waikato Masters Thesis (unpub.).

Clayton-Greene K A 1977. Structure and origin of *Libocedrus bidwillii* stands in the Waikato District, New Zealand. New Zealand Journal of Botany 15: 19-28.

Duncan R P 1991. Competition and the Coexistence of Species in a Mixed Podocarp Stand. The Journal of Ecology 79(4): 1073-1084.

Duncan R P 1993. Flood Disturbance and the Coexistence of Species in a Lowland Podocarp Forest, South Westland, New Zealand. The Journal of Ecology 81(3): 403-416.

Dunwiddie P W 1978. Recent dendrochronological sampling in New Zealand: a preliminary note. New Zealand Journal of Botany 16: 409-410.

Fowler N 1988. The effects of environmental heterogeneity in space and time on the regulation of populations and communities. Chp 13 In: Plant Population Ecology (Eds. A J Davy, M J Hutchings, A R Watkinson). Blackwell Scientific Publications.

Fritts H C 1970. Tree-ring analyses and reconstruction of past environments. In: Tree-ring analysis with special reference to Northwest America (Eds. J H G Smith, J Worrall). University of British Columbia, Faculty of Forest, Bulletin No. 7: 92-98.

Gill C J 1974. Studies of Radial Stem Growth in Salix cinerea L. on a Reservoir Margin. The Journal of Applied Ecology 11 (1): 215-221.

Henry J D, Swan J M A 1974. Reconstructing Forest History from Live and Dead Plant Material – An Approach to the Study of Forest Succession in Southwest New Hampshire. Ecology 55(4): 772-783.

King D A 1981. Tree dimensions: maximizing the rate of height growth in dense stands. Oecologia 51: 351-356.

McSweeney G D 1982. Matai/Totara floodplain forests in south Westland. New Zealand Journal of Ecology 5: 121-128.

Newsome P F J, Wilde R H, Willoughby E J 2000. Land Resource Information System Spatial Data Layers. Volume 1: ‘Label Format’. Landcare Research New Zealand Ltd, Palmerston North.

New Zealand Meteorological Service 1985. Annual rain-fall climatic map. Part 6. Ministry of Transport, Wellington.

Pielou E C 1960. A single mechanism to account for regular, random and aggregated populations. Journal of Ecology 48: 575-584.

Porter S, Aldridge B, Wilcox F 2009. Ecological Effects Assessment of the Proposed Titoki Sands Ltd Quarry Access Road and Culvert on the Mangaone Stream. Prepared for Titoki Sands Ltd by Kessels & Associates Ltd.

Pudney K J 2009. The autecology of *Lonicera japonica* in a restoration context. The University of Waikato Masters Thesis (unpub.).

Scott D 1972. Correlation between tree-ring width and climate in two areas in New Zealand. Journal of the Royal Society of New Zealand 2(4): 545-560.

Scott S D 1964. Notes on archaeological tree-ring dating in New Zealand. New Zealand Archaeological Association Newsletter 7(1): 34-35.

Smale M C 1984. White Pine Bush – an alluvial kahikatea (*Dacrycarpus dacrydioides*) forest remnant, eastern Bay of Plenty, New Zealand. New Zealand Journal of Botany 22: 201-206.

Weiner J 1984. Neighbourhood interference amongst *Pinus rigida* individuals. Journal of Ecology 72: 183-195.

Wardle P 1974. The Kahikatea (*Dacrycarpus dacrydioides*) Forest of South Westland. Proceedings of the New Zealand Ecological Society 21: 62-71.

Whaley P T, Clarkson B D, Smale M C 1997. Claudelands Bush: Ecology of an Urban Kahikatea (*Dacrycarpus dacrydioides*) Forest Remnant in Hamilton, New Zealand. Tane 36: 131-155.

Whitmore T C 1988. The influence of tree population dynamics on forest species composition. Chp 14 In: Plant Population Ecology (Eds. A J Davy, M J Hutchings, A R Watkinson). Blackwell Scientific Publications.

CHAPTER 3: TESTING FOR GREY WILLOW CANOPY INTERFERENCE ON KAHIKATEA SEEDLING GROWTH AND SURVIVAL

Introduction

Interference between species has been demonstrated by measuring changes in plant performance during coexistence, or after one species is added or removed. Many studies have successfully used the release technique (e.g. Sagar & Harper 1961; Putwain & Harper 1970) despite its limitations, which can involve compensatory effects of non target species obscuring target species responses (Lewis 1973; Foster 1984) and insufficient experimental length to measure slow species response times (Allen & Forman 1976). Interference effects between shade intolerant species that occupy relatively fertile sites, such as floodplain terraces, are likely to be expressed in the struggle for light resources (Keddy *et al.*1997; Dehlin *et al.* 2008). Kahikatea (*Dacrycarpus dacrydioides*) and grey willow (*Salix cinerea*) occupy similar environmental and regeneration niches in the Waikato floodplains. Both are shade intolerant pioneer species, however the native kahikatea is at a growth rate disadvantage in reaching the canopy, where grey willow often almost monospecifically dominates (Champion 1994).

Studies undertaken on the shade tolerance of New Zealand podocarp seedlings suggest light-compensation points of between 1 and 4%, which is similar to that of native angiosperm seedlings (Wardle 1991; Lusk *et al.* 2009). However, the prevalence of discontinuous population structures in podocarp recruitment, or regeneration gaps, suggests podocarps may become more light demanding at the sapling stage (Beveridge 1973; Duncan 1993; Lusk *et al.* 2009), when carbohydrate reserves that support seedlings in low light environments become depleted, saplings either perish or persist until a canopy gap opens (Kobe 1997). Various studies have found kahikatea seedlings display one of the strongest growth responses of the podocarps to increased light (Beveridge 1973; Bartlett 1984; Ebbett & Ogden 1998). Kahikatea regeneration does not occur under its own canopy and Champion (1988) advised this is likely because the photosynthetic flux density (0.3% reduction of full sunlight) is below the light compensation point. In contrast, a deciduous grey willow canopy supports kahikatea seedling regeneration, and on occasion, saplings. Champion (1988) recorded a winter and summer photosynthetic flux density of 26% and 1% respectively in this ground layer environment.

The deciduous nature of grey willow may facilitate kahikatea recruitment by allowing exploitation of the higher light levels available in winter leaf fall (Champion 1988). Although, whether seedling regeneration opportunities result in sapling emergence through the canopy, and a general return to kahikatea dominant swamp forest is uncertain. This study aims to determine if a grey willow canopy has any interference effect on kahikatea seedling growth and survival. I hypothesise canopy interference reduces the growth and survival rates of kahikatea seedlings, thus reducing the likelihood of kahikatea growing past the sapling stage, due to light resource limitations exerted by a grey willow canopy.

Methods

Study site

All field work was conducted at Totara Park which is located in the northwestern suburb of St Andrews, Hamilton city. The park is an unmanaged gully, 1.7 hectares in size (one of the largest urban populations of kahikatea and grey willow), which historically drained into the Waikato River. Urban development meant the gully drainage was reduced to a few drainage pipes, which created the wetland conditions, suitable for kahikatea and grey willow, found in the park today. The parent soil is water deposited (alluvium) from sandstone and/or greywacke which is often found on floodplain or river terraces and consists of deposition of sand over older permeable deposits, often stones (Newsome *et al.* 2000). This soil is highly permeable and susceptible to erosion if dried. The climate at Totara Park is warm to humid in summer and cool to mild in winter with a reliable average rainfall of 1186mm yr^{-1} and average summer and winter maximum temperatures of 23.8 °C and 13.6 °C respectively (courtesy of the NIWA Clifflo online database). The most recent catastrophic disturbance event occurred in the form of sand mining in 1969 and 1970, when the site was almost completely devegetated (Pudney 2009). This was followed by subsequent colonization of the pioneers grey willow and occasional kahikatea. The mature kahikatea population is concentrated into three main clumps but regeneration is more widely distributed. Grey willow is only vegetatively regenerating but is the

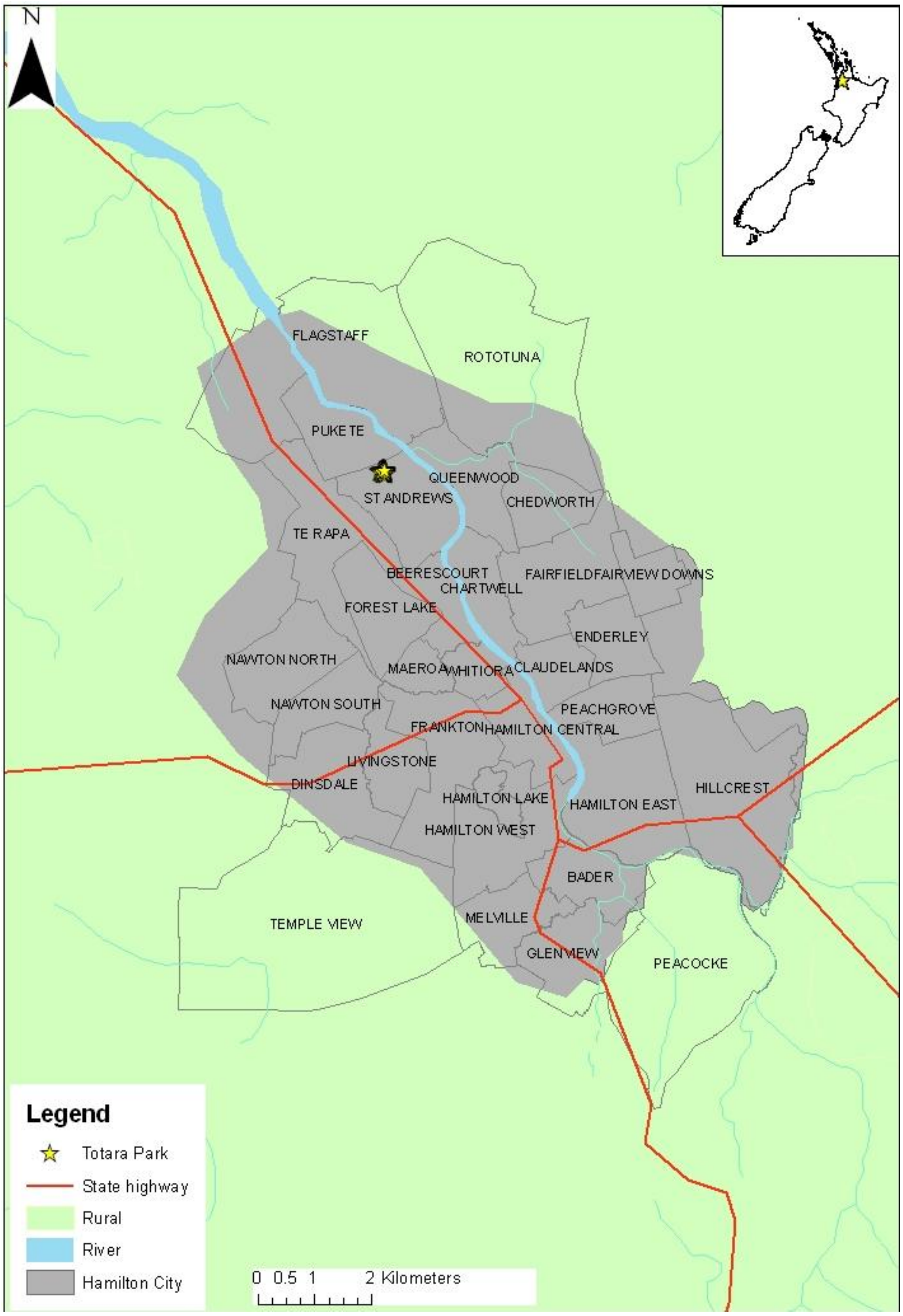

Figure 1 Totara Park, Hamilton city.

canopy dominant in the gully basin. Other dominant exotic and native swamp loving species present at the park include cabbage tree (*Cordyline australis*), wheki (*Dicksonia squarrosa*), arum lily (*Zantedeschia aethiopica),* wandering jew (*Tradescantia fluminensis*), karamu (*Coprosma robusta*), kio kio (*Blechnum novae-zealandiae*), pate (*Schefflera digitata*), chinese privet (*Ligustrum sinense*), mahoe (*Melicytus ramiflorus*), *Baumea rubiginosa* and the climber japanese honeysuckle (*Lonicera japonica*).

Field work dates

The kahikatea seedlings used in the grey willow canopy experiments were placed in Totara Park on the 10th, 11th and 15th of December, 2008. The kahikatea seedlings used in the release experiments were measured and released on the 9th of January, 2009. Additional fieldwork was undertaken monitoring seedlings once or twice a month throughout 2009, depending on rainfall and evaporation levels. Water table heights and hemispherical photographs were undertaken at all seedling locations in August 2009 and December 2009. All seedlings were re-measured on the 7th of December, 2009 and the 26th of January, 2010.

Canopy experiment

Forty kahikatea seedlings, five years in age, were obtained from Peter Morris in December, 2008. These were grown from seed sourced at the Masters Ave stand of kahikatea, southeastern Hamilton city. All seedlings were transplanted to PB 6.5 bags containing Dalton's potting mix and left to acclimatize for a month. In December 2008, height and diameter measurements were recorded for all seedlings (Table 1) and twenty were placed at random locations in the park using the random pace technique across the mid section of the park (grassed area) and into the park. From that point a decision was made where to dig in the seedling (still in its bag) depending on whether it was to be located under or free of a grey willow canopy. Each bag has six 5mm holes at the base and eight on the sides, which equalised water table levels with those surrounding the bag. Another ten seedlings were emplaced next to naturally established seedlings at the park, which were either under a grey willow canopy or free of it, to compare seedling growth rates between naturally established seedlings and introduced seedlings. Another ten naturally established kahikatea seedlings were selected to be released from their grey willow canopy, based on whether they stood above 40 cm and their surrounding neighbours to encourage maximum growth responses after release. If the selected seedlings were in a clump, the tallest seedlings were chosen to minimize interspecific competition (Duncan 1991). A total of four release sites were set up, with varying numbers of seedlings present at each (see Table 2). Each seedling was measured for height, diameter (Table 1) and labeled prior to the removal of the grey willow canopy (using a pruning saw). The remaining ten seedlings were used as a control group and kept out of the park in open, sheltered conditions in Te Awamutu (10th of December 2008 to the 6th of September 2009) and later Beerescourt, Hamilton City (from the 6th of September 2009 until cessation of the experiment). Table 1 shows the summary of seedling attributes for each treatment. Through-out the year seedlings were monitored for hydration and on occasion released from arum lily, Japanese honeysuckle and Chinese privet. Seedlings were re-measured the following December and collected and measured again late January 2010. Water table heights were measured (using a spade) and hemispherical photographs were taken at each seedling location in Totara Park in August and December 2009.

Table 1 Seedling attributes for each treatment (includes the release treatment in the following methods section).

Seedling attributes					
	Treatment				
	control	open introduced	closed introduced	closed natural	release natural
Sample size	10	11	19	9	10
Initial mean height (cm)	91.0	93.5	94.9	76.9	91.0
Initial mean diameter (cm)	1.17	1.10	0.98	0.67	0.82
Conditions	Open site away from park	At park, no canopy	At park, under canopy	At park, under canopy	At park, no canopy
Source	Masters Ave	Masters Ave	Masters Ave	Totara Park	Totara Park

Table 2 Release sites at Totara Park

Release site	GPS location	Seedling number
1	E2708540, N6381541	1
2	E2708484, N6381563	1
3	E2708479, N6381557	6
4	E2708473, N6381545	2

Hemispherical photography

Photographs of the canopy were taken with a Nikon coolpix 995 with an FC-E8 fisheye adapter for all saplings used in the canopy and release experiments. Photographs were taken in overcast, dusk or dawn conditions and underexposed by 1 stop, to increase the contrast between the leaves and sky for improved percent canopy openness estimates. The exposure was standardized by setting it in the open (canopy gaps or the grass field next to the park) excluding canopy influences and repeated as the light changed (every fifteen minutes in the dawn and dusk photographs). The camera was positioned level and directly above the seedling using a tripod and orientated toward north using a compass, to allow for the inclusion of solar tracking information in photo analysis.

Photographs were analysed using Gap Light Analyzer, Version 2.0 which uses information on the image orientation, projection distortion, site location, growing season length, sky-region brightness and atmospheric conditions to calculate canopy and site openness, leaf area index, sunfleck frequency distribution and the amount of above and below direct, diffuse and total solar radiation (Frazer *et al.* 1999). The image was registered to set the circle parameters to those of the camera in use, then the configuration file was loaded which contained the input data required to run the model suited to our canopy openness analysis (Frazer *et al.* 1999). The blue colour plane was removed when viewing the photographs to allow improved colour contrast. The image was then classified into canopy and sky components using the threshold function. This was somewhat subjective but kept as consistent throughout as possible by selecting an area close to the centre as a reference for each photograph to avoid over emphasizing the influence of underexposed vegetation on the horizons. The final step was to generate the output results for canopy structure and gap light transmission data. All the results represent the output % total transmitted light which is the amount (mol m^{-2} day^{-1}) of monthly direct and diffuse radiation recorded below the canopy.

Data analyses

Average seedling growth rates for height and diameter ± standard deviation were calculated for each treatment. One way analysis of variance (ANOVA) was used to test for a significant difference ($p < 0.05$) in mean annual height and diameter growth between treatments using Statistica. Statistica was also used to undertake regression analyses to test whether annual seedling height growth was correlated with % total transmitted light and water table height, and whether annual seedling diameter growth was related to % total transmitted light.

Results

The mean annual height and diameter growth of all kahikatea seedlings for each treatment were significantly different from one another ($p = 0.000$; Figures 2 and 3). The greatest seedling height growth occurred in the introduced bagged seedlings placed free of a grey willow canopy, followed by the control group and then the release treatment. The introduced and naturally established kahikatea seedlings under a grey willow canopy showed the lowest height growth (Table 3).

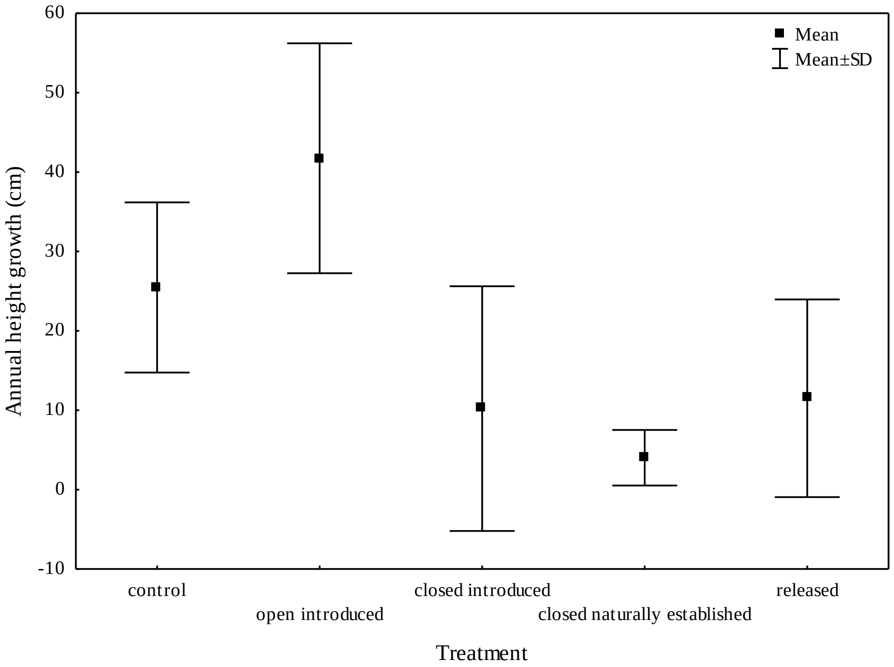

Figure 2 ANOVA boxplot showing the variation in means for annual height growth between each treatment.

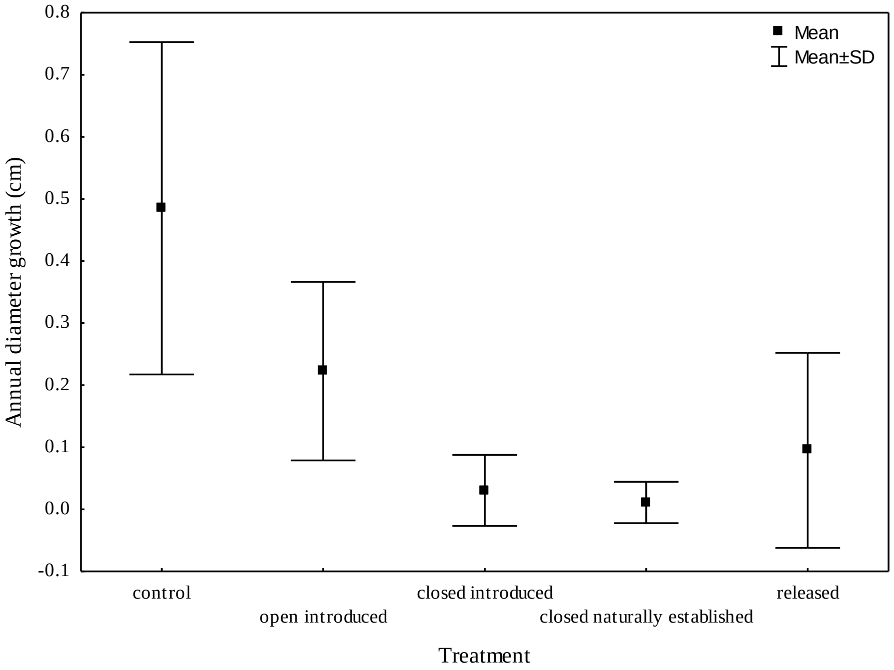

Figure 3 ANOVA boxplot showing the variation in means for annual diameter growth between each treatment.

A similar pattern was shown for diameter growth except the largest response was seen in the control group this time, followed by the open introduced treatment, then the release treatment and the remaining closed canopy treatments were similar in diameter growth (Table 3). Both height and diameter seedling growth responses showed high variance within treatments. In the introduced and naturally established seedlings located adjacent to each other in the same environmental conditions (n=10), the introduced seedlings had a much greater mean annual growth rate of 7.8 cm yr^{-1}, compared to just 3.6 cm yr^{-1} for the naturally established individuals.

Table 3 Kahikatea seedling mean growth rates for each treatment.

	Seedling growth rates (cm yr^{-1} ± SD)				
	Treatment				
	control	open introduced	closed introduced	closed natural	release natural
Height	25.5 ± 10.7	41.7 ± 14.5	8.0 ± 17.8	4.0 ± 3.5	11.5 ± 12.4
Diameter	0.49 ± 0.27	0.22 ± 0.14	0.02 ± 0.06	0.01 ± 0.03	0.10 ± 0.16

Not all seedlings displayed optimum or positive annual increases in height. There were a number of reasons for this (see Table 4), but the most commonly occurring factor negatively affecting seedling growth was damage to photosynthetic structures (chlorophyll bleaching) caused by high light conditions. This did not cause negative annual height growth measurements (all the other factors did), but affected the linear relationship of annual seedling height growth to percentage transmitted light. All the seedlings affected by this (n = 14) were growing in average winter and summer total transmitted light conditions exceeding 40% and did not show the height growth responses expected.

Table 4 Causes of seedling damage affecting height and diameter growth in kahikatea seedlings. Both apical stem deaths recorded for the open introduced treatment were due to smothering by invasive lianes, all other incidences were due to shading. Other damage refers to damage caused by vandalism, wind and branch fall.

	Seedling damage (%)				
	Treatment				
Damage	control	open introduced	closed introduced	closed natural	release natural
PS pigment bleaching	100	36			
Apical stem death (shading/parasitism)		18	22	11	
Other	10		11		
Death			11		

Winter light environments were more intense and less varied between treatments than summer, due to the loss of grey willow leaves in the canopy (Figures 4 and 5). In both seasons the greatest light intensity occurred in the open introduced treatment and the lowest in the closed introduced and naturally established treatments (Table 5). The release treatment was comparable to the closed canopy treatments in winter due to leaf fall, but showed greater light intensity in the summer, after canopy recovery.

Figure 4 Hemispherical photograph quantifying the summer light environment above a seedling in the introduced closed canopy treatment (KL3).

Figure 5 Hemispherical photograph quantifying the winter light environment above a seedling in the introduced closed canopy treatment (KL3).

Table 5 Mean % total transmitted light (mol m^{-2} day^{-1} SD) for each treatment.

	Mean % total transmitted light (mol m^{-2} day^{-1} ± SD)			
	treatment			
Season	open introduced	closed introduced	closed natural	released natural
winter	39.2 ± 12.9	16.8 ± 5.7	14.6 ± 5.0	16.0 ± 3.3
summer	29.3 ± 13.5	3.1 ± 2.9	2.7 ± 2.8	9.5 ± 6.3

Regression analyses for annual height growth against winter transmitted light percentages were positively but not strongly related ($r = 0.54$, $r^2 = 0.29$, $P < 0.00008$). The data was log transformed, as often seedling growth curves fit this model better, however this was not the case here ($r = 0.50$, $P < 0.006$). The annual height growth responses were then separated into introduced and naturally established seedling groups. Initially this did not have a positive effect on the regression ($r = 0.49$), but after examining outliers, it was noted four individuals in the open introduced treatment displayed yellow brown foliage due to the destruction of photosynthetic pigments and did not show the expected height growth response. Once these individuals were removed the linear regression fit improved ($r^2 = 0.37$, $P < 0.001$; Figure 6). Negative height growth (seedling apical stem death or seedling death) measurements were only found below winter transmitted light levels of 25%. The regression analyses for annual height growth against percentage summer transmitted light were very similar to winter results ($r = 0.61$, $r^2 = 0.38$, $P < 0.001$; Figure 7), with summer transmitted light levels explaining 38% of the variation in introduced seedling annual height growth. Negative height growth was found only under summer transmitted light levels of 5%, which was much more compressed than the winter transmitted light results.

Water table height had a slightly less important but still positive effect on seedling annual height growth ($r = 0.51$ and $r = 0.45$ for winter and summer water table heights respectively), however only explained 26% and 20% of variation in annual height growth (Figures 8 and 9). Regression results for naturally established seedlings were barely positively correlated with any of the environmental parameters (correlation coefficients ranged close to zero apart from against % summer transmitted light, $r = 0.31$). Annual seedling diameter growth correlated with winter and summer percentage transmitted light but not seasonal water table heights (Figures 10 and 11).

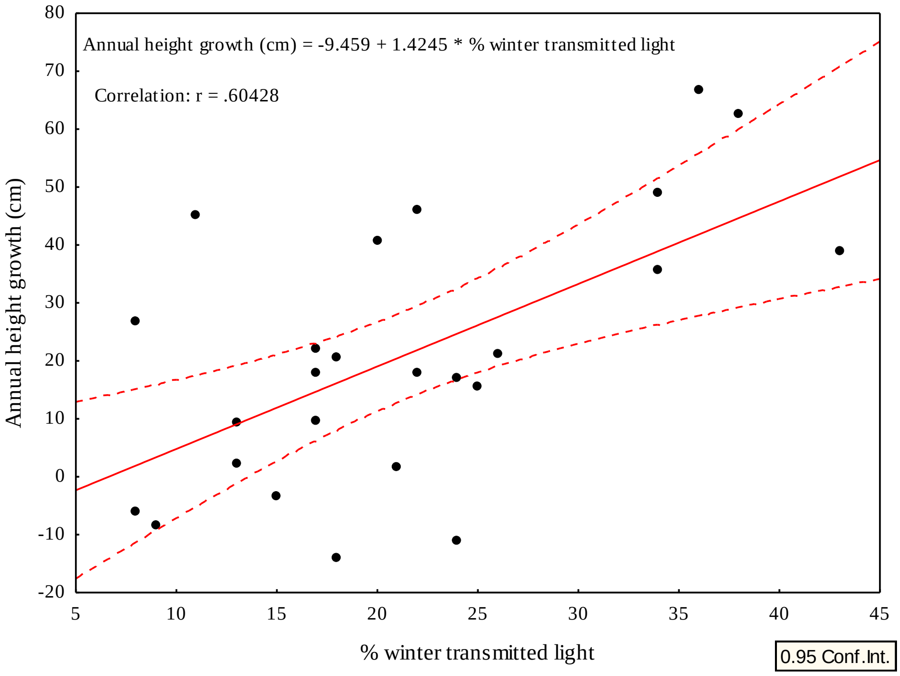

Figure 6 Linear regression of annual height growth against % winter transmitted light.

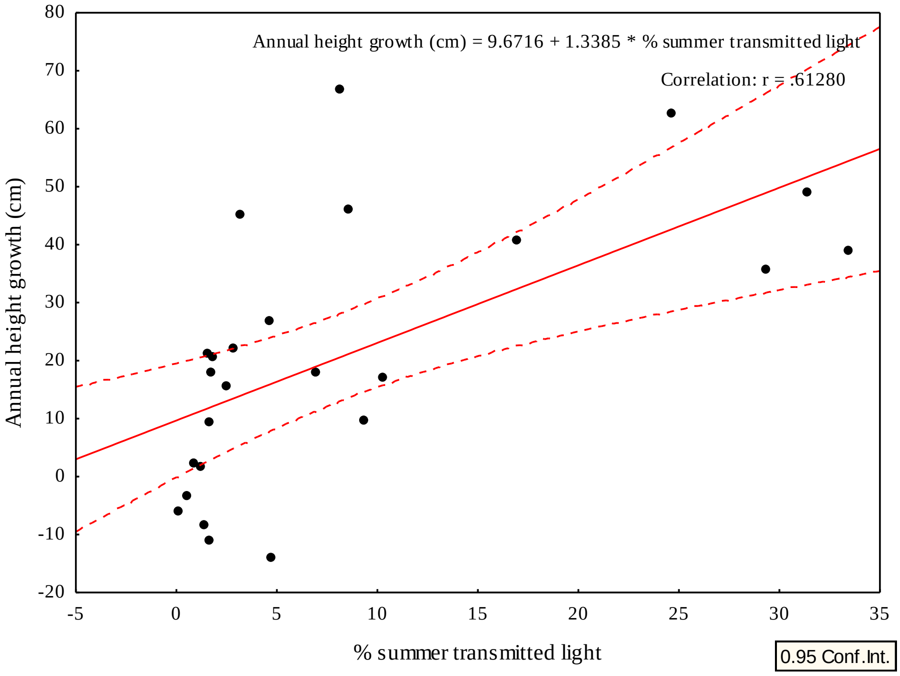

Figure 7 Linear regression of annual height growth against % summer transmitted light.

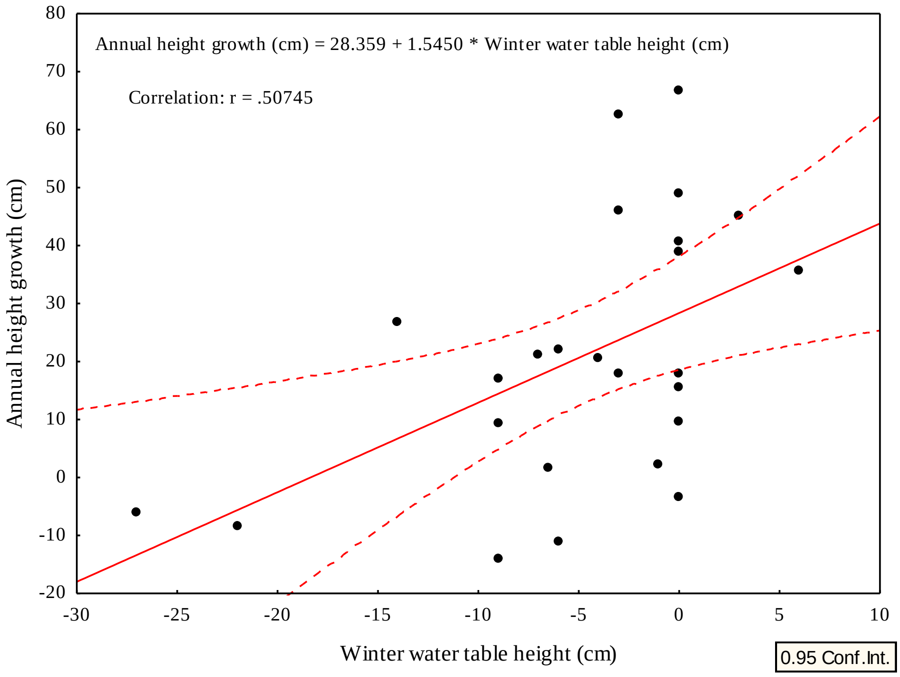

Figure 8 Linear regression of annual height growth against winter water table.

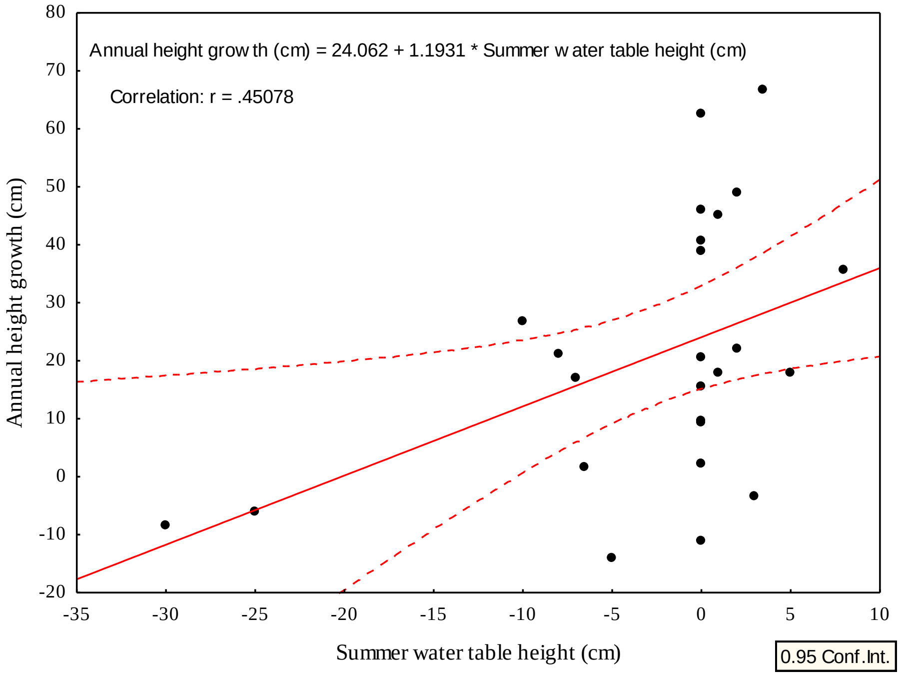

Figure 9 Linear regression of annual height growth against summer water table height.

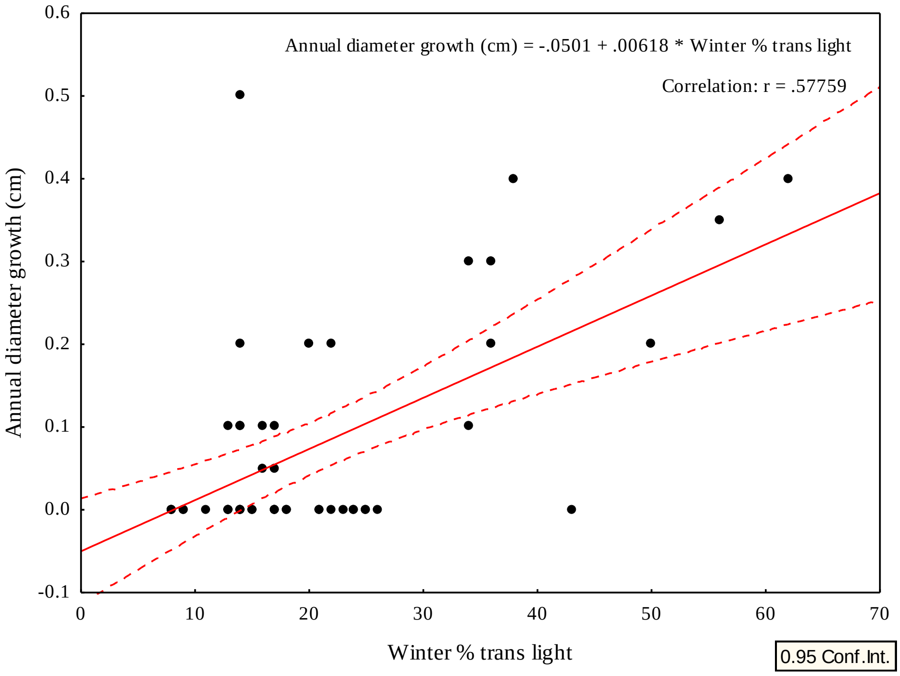

Figure 10 Annual seedling diameter growth vs. percent winter transmitted light ($r^2 = 0.33$, $P < 0.00002$)

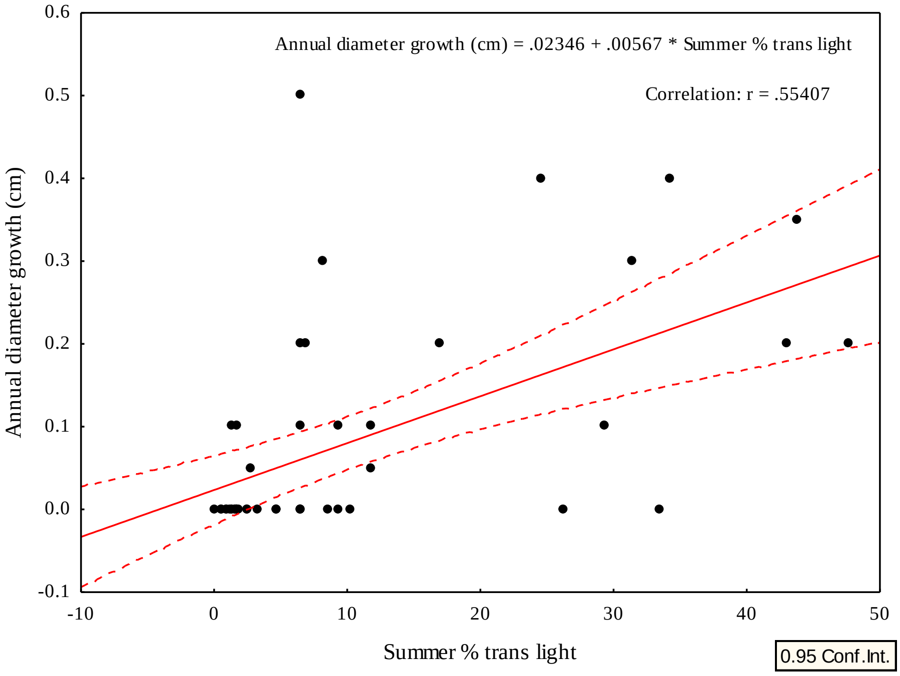

Figure 11 Annual diameter growth vs. percent summer transmitted light ($r^2 = 0.31$, $P < 0.00004$).

The expected increase in height growth over the summer months was not significantly different from annual growth rates but was higher than the expected values for the control, open introduced seedlings and release seedling groups. Of all the treatments the release treatment showed the greatest increase over expected ($x^2 = 1.6$). An analysis of whether initial seedling height affected height growth response in naturally established seedlings found in seedling groups, found no relationship (r = -0.05), indicating height variation driven by intra-specific competition for light was unlikely, although this phenomenon is common in dense mature kahikatea stands (Weiner 1988; Duncan 1991).

Discussion

Seedling height and diameter growth rates recorded in this study were similar to those of previous studies (Beveridge 1973; Champion 1988; Duncan 1989; Ebbett & Ogden 1998). Beveridge (1973) also documented podocarp annual height growth rate data after canopy release within submontane second growth forest on the Mamaku Plateau (Bay of Plenty Ecological District), where the control group recorded a mean growth of 3cm yr^{-1} and the release group grew between 8 and 10 cm yr^{-1}. Combined results indicate kahikatea responds well to canopy release and subsequent increases in light levels. Seedling height growth varied substantially within the treatments. In the case of the control group, one damaged seedling disrupted otherwise closely distributed results. The closed canopy treatment included both introduced and naturally established seedlings, which exhibited high growth rate variation likely due to increased carbohydrate reserves present in the introduced over the naturally established seedlings, which were at a metabolic disadvantage. It is acknowledged that the possibility measurement error may have contributed to variation in our height growth responses, as ground levels fluctuated due to flooding, which made it difficult to ensure height was measured from the same point. Seedling diameter growth was also significantly different between treatments and followed a similar order to height growth except the control group showed the greatest response. Again there was high variation in diameter responses. The results of the present study and the results of other studies suggest kahikatea naturally presents high diameter and height growth variation within similar treatments or populations (Cameron 1960; Ebbett and Ogden 1998).

Of all the seedlings, 100% of the controls and 40% of the open introduced seedlings (free of a grey willow canopy) displayed yellow foliage discolouration. Those seedlings in the open introduced treatment were in environments with a seasonal average of above 40% transmitted light and the control group was certain to exceed this amount. Ebbett and Odgen (1998) also noticed yellow brown foliage was displayed in their kahikatea seedling experiments. They recorded it in the highest light treatment of their glasshouse seedlings (25% of full sun), but not the forest site (30% of full sun), and concluded this effect may be produced by not only radiation stress but also temperature stress. Whether this effect is displayed by seedlings is likely to be related to their germination and early growth light environment. The kahikatea seedlings used in this experiment were raised in partial shade and once exposed to transmitted light conditions above 40% they were damaged.

The early environmental conditions of the nursery seedlings influenced their responses to low light conditions as well. Negative seedling height growth due to apical stem death or seedling mortality was recorded in seedlings with winter and summer transmitted light levels of 25 and 5% respectively. The summer values likely represent the light compensation points for these seedlings as this is after canopy recovery. For naturally established seedlings there was only one individual that displayed light related damage (growing in summer transmitted light levels of 0.9 %), compared to 22 introduced individuals, indicating transplant shock probably increased the likelihood of introduced seedling damage. The two seedlings that died had summer transmitted light environments of 1.4 and 0.6%, and both were in the introduced closed treatment. This study suggests the light compensation point for kahikatea is less than 1.4% transmitted light, which is close to Champion’s (1988) results, between 0.3 and 1% PPFD. The only seedling that did not record a negative height growth under this light range recorded a low height growth of 2.3 cm yr^{-1} in light levels of 0.9%.

Water table measurements did not correlate well with seedling height and diameter growth. It is likely the method of estimating water table was not effective at capturing the representative level, as there were only two measurements made over the year. However, the instantaneous measurements obtained showed a weakly positive relationship with introduced seedling height growth ($r^2 = 0.26$) and there was virtually no relationship with diameter or with the naturally established individuals. Previous studies on kahikatea growth response to water levels focused on drought rather than flooding tolerance (Stephens 1997) and no seedlings involved in this experiment were exposed to drought stress. Both the seedlings that died had water table heights within the range of other healthy individuals.

The present study found a positive relationship for both height and diameter growth with increased light levels, which is consistent with other studies (Beveridge 1973; Bartlett 1984; Ebbett & Ogden 1998). However, these results did not show particularly strong correlations due to high variation in growth responses within treatments and possible limitations in the methodology. Machado & Reich (1999) found hemispherical photography explained 67% of the variation in PPFD, and our closed canopy % transmitted light levels were comparable to their canopy estimates of between 1 and 3%. These results indicate a grey willow canopy negatively effects kahikatea height and diameter growth to the point of suppression at transmitted light levels below 5% in summer. A grey willow canopy also significantly reduces kahikatea seedling growth at percent transmitted light levels above 5% and it is likely a grey willow canopy is not a nursery environment. Releasing seedlings is a viable management practice to promote kahikatea seedling growth and the maximum seedling growth rates are found above 25% transmitted light in winter and 5% in summer.

Conclusion

The light compensation point for kahikatea seedling growth lies below 1.4 % transmitted light. The presence of a grey willow canopy clearly negatively affects kahikatea seedling survival and growth at summer transmitted light levels below 5 %, thus reducing the likelihood of seedlings reaching the sapling stage and eventually emerging above the canopy. The presence of a grey willow canopy at light transmission levels above this can significantly reduce seedling growth, but does not appear to prevent it. Due to high variation in the diameter and height growth responses in kahikatea seedlings within and between treatments, variation in summer percent transmitted light levels only explained 38% of variation in seedling height growth and 31% of variation in diameter growth and water table heights is not a reliable indicator of seedling growth responses. However, it is acknowledged water table data was not comprehensive and the method of hemispherical photography has limitations. In conclusion, early environmental conditions prevailing during kahikatea seedling development stages and carbohydrate reserves are critical in determining a seedlings growth response to later introduced shading (overtopping by a grey willow canopy).

References

Allen E B, Forman R T T 1976. Plant Species Removals and Old-Field Community Structure and Stability. Ecology 57 (6): 1233-1243.

Bartlett R M 1984. Canopy gap microclimate and seedling growth. Unpublished MSc thesis, The University of Auckland, New Zealand.

Beveridge A E 1973. Regeneration of podocarps in a central North Island forest. New Zealand journal of forestry 18: 23-35.

Cameron R J 1960. Dendrochronology in New Zealand. Journal of the Polynesian Society 69: 37-38.

Champion P D 1988. The Ecology and Management of kahikatea *Dacrycarpus dacrydioides* (A. Rich.) de Laubenfels in the Waikato, North Island, New Zealand. University of Waikato Masters Thesis (unpub.).

Champion P D 1994. Extent of willow invasion – the threats. Chp 6 In: Wild willows in New Zealand (Eds. C J West). Proceedings of a Willow Control Workshop, Department of Conservation, Hamilton. Pp. 43-49.

Dehlin H, Peltzer D A, Allison V J, Yeates G W, Nilsson C, Wardle D A 2008. Tree seedling performance and below-ground properties in stands of invasive and native tree species. New Zealand Journal of Ecology 32 (1): 67-79.

Duncan R P 1989. An Evaluation of Errors in Tree Age Estimates based on Increment Cores in Kahikatea (*Dacrycarpus dacrydioides*). New Zealand Natural Sciences 16: 31 – 37.

Duncan R P 1991. Competition and the Coexistence of Species in a Mixed Podocarp Stand. The Journal of Ecology 79(4): 1073-1084.

Duncan R P 1993. Flood Disturbance and the Coexistence of Species in a Lowland Podocarp Forest, South Westland, New Zealand. The Journal of Ecology 81(3): 403-416.

Ebbett R L, Ogden J 1998. Comparative seedling growth of five endemic New Zealand podocarp species under different light regimes. New Zealand Journal of Botany 36: 189-201.

Foster J R 1984. Causes of tree mortality in wave-regenerated balsam fir forests. PhD thesis, Dartmouth College, Hanover, New Hampshire.

Frazer G W, Canham C D, Lertzman K P 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, British Columbia, and the Institute of Ecosystem Studies, New York.

Keddy P A, Twolan-Strutt L, Shipley B 1997. Experimental evidence that interspecific competitive asymmetry increases with soil productivity. Oikos 80: 253-256.

Kobe R K 1997. Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. Oikos 80: 226-233.

Lewis A J 1973. Ragweed control techniques: Effect on old-field plant populations. Bulletin of the Torrey Botanical Club 6: 333-338.

Lusk C H, Duncan R P, Bellingham P J 2009. Light environments occupied by conifer and angiosperm seedlings in a New Zealand podocarp-broadleaved forest. New Zealand Journal of Ecology 33(1): 83-89.

Machado J-L, Reich P B 1999. Evaluation of several measures of canopy openess as predictors of photosynthetic flux density in deeply shaded conifer-dominated forest understorey. Canadian Journal of Forest Research 29: 1438-1444.

Putwain P D, Harper J L 1970. Studies in the dynamics of plant populations III. The influence of associated species on populations of *Rumex acetosa* L. and *R. acetosella* L. in grassland. Journal of Ecology 58: 251-264.

Sagar G R, Harper J L 1961. Controlled interference with natural populations of *Plantago lanceolata*, *P. major* and *P. media*. Weed Research 1: 163-176.

Stephens D 1997. Influences of Soil and Atmospheric Water Environments on the Establishment Site Preferences of Kauri and Kahikatea. The University of Waikato MSc thesis (unpub.).

Wardle P 1991. Vegetation of New Zealand. Cambridge University Press.

Weiner J 1988. Variation in the performance of individuals in plant populations. Chp 5 In: Plant Population Ecology (Eds. A J Davy, M J Hutchings, A R Watkinson). Blackwell Scientific Publications.

CHAPTER 4: ASSESSING THE ALLELOPATHIC POTENTIAL OF KAHIKATEA ON GREY WILLOW SURVIVAL

Introduction

Production of biochemicals by a plant that are not necessary for its metabolism and which are released into the environment exerting an effect on the growth or survival of neighbouring plants, is termed allelopathy (Rice 1984). The Greek origins of the word, 'allelo' meaning mutual harm and 'pathy' meaning suffering, suggest the effects of allelopathy are negative and multiple studies have defined it as such (Lambers *et al.* 1998; Foy & Inderjit 2001). The original definition includes both inhibitory and stimulatory effects (Rice 1984). Allelopathy is a form of interference, but is not grouped under the general term of competition, as it does not involve one plant competing with another for access to a resource, rather adding biochemicals to the environment which may affect this interaction (Rice 1984).

Allelochemical production is often increased when a plant is exposed to stressors. Rice (1984) provides a review of studies completed that test which factors increase the levels of allelochemical production. These factors included; increased light quality, UV and daylength, limiting nutrients (eg. nitrogen and phosphorus), drought, chilling, youth, genetics and increased pathogen and predator attack. Muller (1966) hypothesized that allelochemical production in plants is often for excretionary purposes and inhibitory effects on neighbours is secondary, but advantageous. It is still unclear how important allelopathic interference is in structuring natural plant communities. Future studies need to experimentally separate plant responses to allelopathic effects from competitive effects involving the struggle for resources, other soil interactions or the influence of pathogens and herbivores (Harper 1975).

Nilsson (1994) provides an assessment of the relative importance of allelopathic and resource competition effects of crowberry (*Empetrum hermaphroditum*) on Scots pine (*Pinus sylvestris* L.).The experiment contained four treatments; Scots pine in PVC tubes to reduce the effect of below ground competition from crowberry, spreading activated carbon on the soil around Scots pine seedlings to absorb toxins leached from crowberry litter, a control where both conditions were left untreated and a treatment including both PVC tubes and activated carbon. Results indicated Scots pine dry weight and shoot length was greatest in the dual treatment, lowest in the control and intermediate when PVC and activated carbon was applied separately (the PVC tube treatment showed greater growth than the activated carbon). This study concluded both forms of interference were important influences on growth of Scots pine seedlings.

Molloy et al. (1978) demonstrated kahikatea displays autotoxicity (a negative allelopathic effect on its own growth), after observing the lack of first year seedlings under mature kahikatea forest. They measured the effects on growth and survival of kahikatea seedlings after they were sprayed repetitively with 600ml of 500 gL^{-1} extracts of adult root, green leaf, litter, bark and soil and controls of nutrient solution and distilled water. Their results showed 100% of seedlings were killed when sprayed with green leaf extract and almost 50% of seedlings were killed when sprayed with litter extract within 30 days. They found activity of the allelochemical did not diminish after cold storage and suggested phenolic substances were likely involved. These findings were summarized by Champion (1988) who believed allelopathy may be an important factor influencing regeneration patterns of kahikatea.

This study focuses on whether kahikatea has the potential for allelopathic interference with survival of grey willow and the sensitive indicator species, white mustard (*Sinapis alba*), and excludes any competition interference via potting seedlings separately. If kahikatea does contain an allelochemical in its litter, is this effective on other species and is it present in great enough concentrations to inhibit seedling survival? If allelopathy is involved this could provide an important factor for distribution patterns of kahikatea and grey willow in co-existing situations.

Methods

Field work dates

Forty grey willow cuttings were collected from Totara Park on the 9th of March, 2009 and another fifty cuttings were collected on the 20th of March. Due to 100% mortality, the final collection of one hundred cuttings was taken from Totara Park on the 27th of March, 2009. All grey willow seed was collected from Totara Park on the 2nd of November, 2009.

Glasshouse allelopathy experiment

The grey willow cuttings were stored in a moistened plastic bag in a chilly bin and transported to a misting system (Treeline Native Nursery, Rotorua). From the original one hundred, fourteen cuttings took root and were tubed up in one part Dalton's seed mix to one part Dalton's horticultural pumice. All cuttings were transported to the university glasshouse on the 14th of October. In addition to the grey willow, three hundred white mustard seed (*Sinapus alba*) were sown in a tray of Dalton's seed mix on the 15th of October, 2009. Ninety individuals were then tubed up using Dalton's seed mix to one part Dalton's horticultural pumice and transported to the university glasshouse, where all cuttings and seedlings were then stored at 25° Celsius for the duration of the experiment.

The experiment began on the 5th of November and mustard seedlings and grey willow cuttings were separated equally into two treatments. The first treatment was sprayed daily with distilled water and the second was sprayed daily with $350 gL^{-1}$ kahikatea litter extract until the 28th of November, when the concentration was increased to $500 gL^{-1}$ of litter extract until the cessation of the experiment. Kahikatea litter was collected from Totara Park in the high density stand to ensure the majority of litter was kahikatea foliage; however other material was present including dead fronds of *Dicksonia squarrosa.* The litter extract was made up using the method of Molloy *et al.* (1978), soaked overnight in distilled water, and filtered for use the next day. Spray volumes were kept constant for both treatments and worked out to be on average 1 litre each day. The experiment was undertaken for five weeks and two days, until the 12th of December, 2009. During the experiment regular observation was made of seedlings for the presence of excessive yellowing, wilting or death.

Glasshouse germination experiment

Due to the difficulty encountered propagating grey willow cuttings, a small grey willow germination trial was conducted to ascertain whether grey willow is easier to grow from seed. Seed viability was tested using 10 seeds sown on the 5th of November, 2009 in a tray filled with Yates seed raising mix, wetted and covered in clear plastic and grown at 25º Celsius in the university glasshouse. After seed viability was confirmed 100 grey willow seeds were sown on the 10th of November, in a tray of Yates seed raising mix using the same method above except covered with clear glass. Another 100 seeds were sown in a tray filled with soil collected from a mature kahikatea stand at Totara Park, using the same method. All seed trays were monitored for hydration levels each day.

Results & Discussion

Glasshouse allelopathy experiment

All cuttings and seedlings in both treatments survived excluding two grey willow cuttings in the distilled water treatment, which were already under stress at the beginning of the experiment (roots were under developed). No differences in height or colour were noted in either treatment for grey willow or mustard, including both the 350 and 500gL^{-1} concentrations of litter extract. Figures 1 and 2 show the foliage of *Sinapus alba* in the control and treatment groups after the experiment was completed. No evidence of yellowing, wilting or senescence was visible between the treatment and control group. Figures 3 and 4 show both the treatment and control seedlings for grey willow and mustard after cessation of the experiment when the mustard began to seed and die back. No evidence of variation in height, yellowing, wilting or senescence was visible between the treatment and control group.

Observation in the field indicates kahikatea and grey willow frequently grow adjacent to each other with foliage at times touching. This seems to indicate mature grey willow growth is not influenced by allelochemicals produced by kahikatea. The study results support these field observations and suggest either allelochemicals present in kahikatea litter do not affect species other than itself (Molloy *et al.* 1978), or the experiment conducted here was not able to detect the difference. Molloy *et al.* (1978) did not publish their sample size or the total volume of extract used, which may indicate our volumes and sample size were too reduced to detect an effect. In addition they may have collected 100% pure kahikatea litter, which this study did not because it was not an accurate measure of what seedlings would grow in under natural conditions. Molloy *et al.* (1978) also made observations kahikatea litter was no barrier to seedling germination and only affected growth at later stages.

This may reflect the increased demand for water and nutrients as seedlings mature and hence increased allelochemical uptake rates. In the case of grey willow, root growth is extremely slow (1mm day^{-1}) in the early stages of development (Cremer 2003), which could suggest an increased tolerance to the presence of allelochemicals. White mustard root systems were extremely well developed. If allelochemicals were present that affected white mustard growth, this species was expected to show a response. Our results indicate kahikatea does not affect grey willow and white mustard growth and survival at the concentrations, volume, and composition of the litter used in the experiment. Further experiments using kahikatea green leaf extract sprayed on grey willow and white mustard would be required to assess if at excessive concentrations kahikatea has an allelopathic effect on these species, and the potential to affect the structure of grey willow populations.

Glasshouse germination experiment

In the grey willow germination trial four of the original 10 sown seeds germinated (Figure 5). However the larger experiments were not as successful. The same experiment undertaken using 100 seeds recorded a germination rate of zero in the control and 6 in the kahikatea soil treatment (Figure 6). An algal layer was present in the control and other species germinated in the kahikatea soil treatment. These germination rates are not consistent with Cremer's (1999) willow germination trials, which recorded 90 to 100% germination success (n=100), however he did not specify the willow species he trialed.

Grey willow seed has no dormant stage and requires wet soil or water to germinate (Koncalova & Jacinska 1985). As the soils were well hydrated, it is unlikely the cause of the germination failure was due to water stress. Seed lives for around 20 days after shedding (Cremer 1999) and some of the seed collected was already shed and may have been in stages of decline. This trial indicated the germination rate of grey willow seed is possibly quite low due to increased seed age or unfavourable parentage (Cremer 1999). Low seed longevity, a lack of dormancy period and high light and hydration requirements are likely the major reasons why grey willow seedlings are rarely if ever seen in natural communities in the Waikato, however this needs to be studied further. In addition, any negative effects from inbreeding on seed viability should be assessed in this species.

Figure 1 Foliage of *Sinapus alba* in the distilled water control group, after cessation of the experiment

Figure 2 Foliage of *Sinapus alba* in the litter extract treatment, after cessation of the experiment (dark patches are litter extract residue).

Figure 3 *Sinapus alba* litter extract treatment (left) and control group (right) after completion of the experiment.

Figure 4 Grey willow litter extract treatment (left) and control group (right) after completion of the experiment.

Figure 5 Seed viability trial showing four grey willow seedlings.

Figure 6 Germination trial of 100 grey willow seeds sown in kahikatea soils from Totara Park (six grey willow seedlings are present).

Conclusion

The present study suggests kahikatea litter does not affect grey willow and white mustard growth and survival and therefore distribution. Further experimental evidence is required to determine if this is truly due to a lack of effect from allelochemicals present in kahikatea litter, or whether this experiment was insufficient to show the effect, as greater volumes and composition of kahikatea litter may be required. It is unlikely allelopathy plays a great role in the distribution of grey willow and kahikatea in swamp forests in the Waikato, as the two species are often found together (side by side), and grey willow predominantly reproduces vegetatively rather than sexually, hence the species is not as vulnerable in the early stages of development.

References

Champion P D 1988. The Ecology and Management of kahikatea *Dacrycarpus dacrydioides* (A. Rich.) de Laubenfels in the Waikato, North Island, New Zealand. University of Waikato Masters Thesis (unpub.).

Cremer K W 1999. Willow management for Australian rivers. In: Natural Resource Management. The Australian Association of Natural Resource Management, Special Issue.

Foy C L, Inderjit 2001. Understanding the Role of Allelopathy in Weed Interference and Declining Plant Diversity. Weed Technology 15: 873-878.

Harper J L 1975. Review of ‘Allelopathy’ by E. L. Rice. Quarterly Review of Biology 50: 493-495.

Končalová M N, Jičínská D 1985. Differences between Ecological Niches in juvenile Salix cinerea and S. pentandra. Folia Geobotanica & Phytotaxonomica 20 (3): 319-321.

Lambers H, Chapin III F S, Pons. T L 1998. Plant Physiological Ecology. Springer-Verlag, Berlin.

Molloy B P J, Ferguson J D, Fletcher P J 1978. The Allelopathic Potential of Kahikatea. A Progress Report. New Zealand Journal of Ecology 1: 183-184.

Muller C H 1966. The role of chemical inhibition (allelopathy) in vegetational composition. Bulletin of the Torrey Botanical Club 93 (5): 332-351.

Nilsson M-C 1994. Separation of allelopathy and resource competition by the boreal dwarf shrub *Empetrum hermaphroditum* Hagerup. Oecologia 98: 1-7.

Rice E L 1984. Allelopathy 2nd Edition. Academic Press, New York

CHAPTER 5: FINAL CONCLUSIONS

This study suggests grey willow's dominance is probably a combination of its broader environmental range than kahikatea (tolerates a higher water table and lower pH values and lower nutrient status) and its superior competitive ability. Average growth rates of grey willow and kahikatea are surprisingly comparable for diameter (between 2 and 3mm per year), which indicates the competitive growth advantage grey willow exerts over kahikatea is likely emphasized in height growth. Both species are capable of colonizing similar sites after moderate to large-scale disturbance and kahikatea probably has an advantage in establishment and early growth due to increased drought and temperature extreme tolerance, and carbohydrate reserves in the seed. In general the ecological niches of kahikatea and grey willow overlap, and heterogeneity in microhabitat conditions does not provide a refuge for kahikatea populations. The methods to escape the negative effects of competition outlined by Rees *et al.* (2001) are not available to kahikatea as both species are shade intolerant and kahikatea is overtaken by grey willow in colonization ability and when exploiting regeneration opportunities such as forest gap creation. The mechanisms by which grey willow exerts interference effects on kahikatea revolve largely on grey willows ability to overtake kahikatea in reaching canopy height and greater site densities, and later suppression of kahikatea regeneration. It achieves this through greater allocation of resources to height growth than kahikatea and via its remarkable capacity to vegetatively re-sprout.

Results indicate the light compensation point for kahikatea is under 1.4% transmitted light, and that levels below 5% negatively affect kahikatea seedling growth. Summer transmitted light levels recorded under a grey willow canopy were lower than 5%, but winter levels exceeded this threshold due to the deciduous nature of grey willow. In addition, as seedlings and saplings get larger, it is likely this compensation point decreases and carbohydrate reserves get lower (Beveridge 1973; Duncan 1993; Lusk *et al.* 2009), which explains increasing mortality in the larger sized juveniles not yet at canopy height. Average annual diameter growth for adult kahikatea at Totara Park was 2.67 ± 1.07 mm. Average seedling diameter growth rates were higher than this in the control, similar in the open canopy treatment and lower in the closed canopy treatments in the park, indicating the presence of a grey willow canopy is having a negative effect on kahikatea diameter growth rate.

Kahikatea sapling frequency (as a measure of regeneration) does not correlate with grey willow density or basal area, other than no saplings were found in plots with grey willow densities above 2 per $10m^2$. Dendrochronological histories at the sites were much more informative and indicated kahikatea cohort development ended once grey willow had reached the canopy and grey willow was definitely encroaching on kahikatea populations not the other way around. Because diameter is not always a good indicator of age for kahikatea, we were unable to accurately assess the age of the sapling size class at all sites. However, the frequency of saplings increased in relation to the incidence of recent disturbance and increased proximity to abundant kahikatea seed sources rather than the length of history of the kahikatea population at a site, indicating kahikatea regeneration is not sustaining adult populations under a grey willow canopy, without the presence of catastrophic disturbance.

The present study suggests grey willow and kahikatea are temporarily coexisting due to disproportionate coinciding establishment after catastrophic disturbance. But kahikatea regeneration is not sustained for the duration of the grey willow canopy, which is persisting past the expected lifespan for Salicaceae dominance of 20 years up to 50 years. This highlights a functional gap of limited indigenous shade and flood tolerant species capable of out-competing the willow in New Zealand (Lee 1998). It is possible grey willow will continue to vegetatively propagate until the next major disturbance and is preventing vegetation successional processes from occurring.

The experimentation to ascertain if kahikatea has an advantage over grey willow in terms of allelopathic interference was inconclusive. It appears that the allelochemicals Molloy *et al.* (1978) discovered present in kahikatea leaf, litter, bark and roots do not affect grey willow in the litter concentrations present at Totara Park. Therefore this mechanism of interference is unlikely to be important in structuring kahikatea and grey willow populations at similar sites in the Waikato.

Management recommendations

The present study confirms the need for active management of kahikatea stands in the Waikato to promote ongoing regeneration and dominance of the species. This needs to involve control of grey willow in sites targeted for restoration towards kahikatea dominant swamp forest. Restoration opportunities of this forest type are likely to be highly successful in Waikato urban wetland sites because urban development often provides recent moderate to large-scale disturbance that promotes establishment of kahikatea recruits. The following scientific based recommendations may be useful for organizations or individuals within the Waikato and New Zealand wishing to promote the re-establishment of kahikatea dominance in kahikatea swamp forests. Priority should be given to sites with reduced grey willow densities, or where extermination is still viable (eg. Awaroa Scenic Reserve), sites close to indigenous seed sources (eg. Hakarimata Scenic Reserve) and those with valuable kahikatea populations already present (eg. Kopuatai Wetland, Tamahere Reserve, Totara Park):

- Grey willow is at its most competitive in the early stages of vegetative regeneration (substantial increases in height and diameter), indicating until kahikatea occupies the canopy; regular release will need to be undertaken.
- Grey willow densities must remain below 2 per 10m^2 to allow kahikatea regeneration (sapling growth).
- Areas containing kahikatea sapling and seedling regeneration below a grey willow canopy need to retain transmitted light levels above the 5% threshold, which could be achieved through annual canopy release after spring canopy recovery.
- On occasion it may be advisable to supplement kahikatea populations with ecosourced plantings, such as when seed sources are insufficient or accelerated succession is required.

Sites containing high densities of emergent kahikatea are much more resistant to invasion by grey willow; in these situations willow is restricted to edges. Kahikatea can maintain dominance for hundreds of years, which allows time for trialing and refinement of willow control methods.

Future research

This study confirms grey willow does not act as a nursery for kahikatea regeneration in the Waikato and highlights the need for reliable, cost effective measures for the control of grey willow populations. Previous research into grey willow control methods have so far indicated herbicide use alone is not effective (Klimkowska *et al.* 2009) and should be used in concert with mechanical methods. Eser & Rosen (2000) outlined water table manipulations around Lake Taupo populations are unlikely to succeed and may actually promote further colonization by the willow in areas previously too deep. Harman (2004) recommended further research into the use of biological control agents such as the nematine gall-forming sawflies, which are host specific to grey willow. Grey willow was believed to preferentially reproduce sexually over vegetatively in New Zealand, which is the case in Australia (Adair *et al.* 2006), however the present study indicates this may be the case for initial establishment, but once grey willow occupies the canopy, reproduction is vegetative. Therefore biological control methods that target reproductive organs will be of little use in controlling Waikato grey willow populations.

Long-term monitoring of the sites included in this research involving 10 year surveys of the population structures of the seedlings and saplings would be particularly useful to determine the exact degree of mortality in the smaller size classes. Sampling additional sites in the North and South Islands containing these two species will be needed to determine whether the effects from interference are as pronounced in cooler climates with shorter growing seasons for the deciduous grey willow, and whether it is possible for kahikatea to regenerate under grey willow in these conditions.

References

Adair R, Sagliocco J-L, Bruzzese E 2006. Strategies for the biological control of invasive willows (*Salix* spp.) in Australia. Australian Journal of Entomology 45: 259-267.

Beveridge A E 1973. Regeneration of podocarps in a central North Island forest. New Zealand journal of forestry 18: 23-35.

Duncan R P 1993. Flood Disturbance and the Coexistence of Species in a Lowland Podocarp Forest, South Westland, New Zealand. The Journal of Ecology 81(3): 403-416.

Eser P, Rosen M R 2000. Effects of controlling levels of Lake Taupo on Stump bay wetland. Journal of Marine and Freshwater Research 34: 217-230.

Harman H 2004. Feasibility of biological control of grey willow *Salix cinerea*. DoC Science Internal Series 183. Department of Conservation, Wellington.

Klimkowska A, Dzierża P, Kotowski W, Brzezińska K 2009. Methods of limiting willow shrub re-growth after intial removal on fen meadows. Journal for Nature Conservation: doi:10.1016/j.jnc.2009.01.002.

Lee W G 1998. Vegetation of New Zealand: functional, spatial, and temporal gaps. In: Ecosystems, Entomology & Plants. Proceedings of a retirement symposium held at Lincoln University to mark the retirement of Bryony Macmillan, Brian Molloy, Peter Wardle and John Dugdale. The Royal Society of New Zealand, Miscellaneous series 48: 91-1-1.

Lusk C H, Duncan R P, Bellingham P J 2009. Light environments occupied by conifer and angiosperm seedlings in a New Zealand podocarp-broadleaved forest. New Zealand Journal of Ecology 33(1): 83-89.

Molloy B P J, Ferguson J D, Fletcher P J 1978. The Allelopathic Potential of Kahikatea. A Progress Report. New Zealand Journal of Ecology 1: 183-184.

Rees M, Condit R, Crawley M, Pacala S, Tilman D 2001. Long-term studies of vegetation dynamics. Science 293: 650-655.

APPENDIX A – Totara Park core sample data

Tree ID	Diameter (cm at b.h.)	Total rings	Average GR (mm)	Chord AB	b = AB/2	Height missing radius (c)	Length missing radius (d)	Est. GR (mm yr^{-1})	# of missing rings
K10	16	36	2.898	5.97	2.985	0.81	5.10	1.07	5
K32	28.3	43	3.108	4.44	2.22	0.72	3.06	1.05	3
K27	14.5	43	1.729	8.21	4.105	0.72	11.34	0.75	15
K34	10.45	36	1.253	7.67	3.835	0.79	8.91	2.30	4
K21	24.3	45	3.834	14.8	7.4	1.25	21.28	1.35	16
*K31	17.4	45	1.517						
K23	22	41	2.319	1.78	0.89	0.31	1.12	1.54	1
K2	19.3	38	2.873	17.34	8.67	1.28	28.72	2.13	14
K11	7.25	18	1.926	4.25	2.125	0.29	7.64	1.90	4
K17	14.1	26	1.460	8.35	4.175	1.17	6.86	1.33	5
K33	26	37	3.612	10.96	5.48	0.77	19.12	4.07	5
K29	22.8	24	4.642	11.52	5.76	1.47	10.55	2.86	4
K14	12.1	26	2.499	6.32	3.16	0.47	10.39	1.72	6
K24	19.3	45	2.175	2.73	1.365	0.57	1.35	0.68	2
K35	10.1	24	2.875	3.12	3.12	1.24	3.31	1.59	2
K26	33	46	3.990	4.93	2.465	0.65	4.35	1.07	4
K5	7.5	20	1.801	7.07	3.535	1.37	3.88	1.42	3
K9	8.45	20	2.766	6.01	3.005	0.99	4.07	1.41	3
*K12	7.15	36	1.391						
*K6	15.65	37	2.426						
K22	41.8	43	4.060	16.73	8.365	1.52	22.26	3.19	7
K20	7.4	23	1.728	6.77	3.385	0.71	7.71	1.30	6
K30	47	42	5.889	9.98	4.99	0.95	12.63	3.38	4
K3	9.85	39	1.069	3.91	1.955	0.42	4.34	0.54	8
K8	5.35	15	1.716	1.48	0.74	0.26	0.92	0.96	1
K28	24.35	31	3.821	7.67	3.835	1.43	4.43	2.48	2
K1	33.9	40	3.251	8.98	4.49	1.49	6.02	1.83	3
*K7	21	39	2.186						
*K18	24.3	43	2.626						
*K25	9.7	38	1.327						
K19	17.5	45	2.217	4.11	2.055	0.63	3.04	0.51	6
K13	16.87	34	3.643	4.28	4.28	0.96	9.06	1.63	6
K16	21	27	3.330	5.82	2.91	1.55	1.96	2.14	1
*K4	20.1	46	2.578						
K15	32.35	39	2.813	12.89	6.445	2.73	6.24	3.65	2
*GW2	22	28	3.491						
GW29	5.7	25	0.901	6.26	3.13	1.04	4.03	0.74	5
*GW25	7.9	21	1.628						
*GW5	6.6	16	2.183						
*GW27	10.3	25	1.673						
GW24	8.6	31	1.361	4.16	2.08	0.47	4.37	1.34	3
GW10	13.2	13	4.043	12.89	6.445	2.69	6.38	6.19	1
GW35	30.8	28	3.610	7.34	3.67	1.34	4.36	2.95	1
GW17	19.1	27	1.686	9.58	4.79	1.83	5.35	1.85	3
GW9	15.35	30	1.591	2.31	1.155	0.26	2.44	3.13	1
*GW28	5.6	25	0.995						
*GW7	12.4	48	1.088						
GW30	27.1	53	2.120	18.83	9.415	3.15	12.50	2.45	5
GW33	43.4	28	4.592	20.86	10.43	5.06	8.22	3.03	3
GW19	3.8	8	1.498	3.59	1.795	0.58	2.49	1.38	2
*GW18	25.7	49	2.171						
GW15	15.9	37	1.876	10.59	5.295	2.01	5.97	5.12	1
GW11	11.7	20	2.188	4.14	2.07	1.15	1.29	1.94	1
GW14	30.5	37	3.008	4.53	2.265	1.04	1.95	3.04	1
GW12	15.2	32	2.218	3.02	1.51	1.09	0.50	1.75	0
GW8	9.9	19	1.886	2.43	1.215	0.52	1.16	1.80	1
GW22	19.2	33	1.994	6.53	3.265	0.99	4.89	2.42	2
*GW4	14.2	32	1.875						
GW34	36.25	32	4.394	5.25	5.25	3.33	2.47	2.59	1
GW13	13.4	13	4.167	16.21	8.105	2.93	9.75	3.58	3
GW16	18.6	38	1.713	4.96	2.48	1.01	2.54	3.84	1
GW21	18.8	37	1.904	2.87	1.435	0.69	1.15	1.40	1
GW20	19.8	37	2.339	9.34	4.67	2.82	2.46	2.17	1
GW3	24.8	45	2.343	13.74	6.87	1.85	11.83	2.13	6
GW31	23.5	31	5.212	16.95	8.475	1.46	23.87	2.30	10
GW23	22.7	31	3.119	9.19	4.595	2.7	2.56	4.81	1
GW1	18.6	37	2.433	5.25	2.625	1.38	1.17	1.00	1
*GW26	26.9	36	2.989						

*hit centre

APPENDIX B – Other sites core data

Site order; Tamahere Reserve, Kirikiriroa gully, Silverdale gully, Hakarimata walkway, Kopuatai Wetland (excl. cores unable to age)

Tree ID	Location	Tree Height (m)	Core Height (m)	Diameter (cm at b.h.)	Radius (cm)	Core length (cm)	Visible Ring #	Est. age (+ missing rings + yrs to coring height	GR (core length / visible ring #) mm yr^{-1}
K1	Plot 1	29	1.35	93.6	46.80	30.7	86	98	3.57
K2	Plot 2	15	1.70	59.7	29.85	28.1	54	61	5.20
K3	Plot 3	15	1.35	24.5	12.25	8.9	85	94	1.05
K4	Plot 4	28	2.10	79.5	39.75	27.5	51	63	5.39
K5	Plot 3	15	1.35	29.8	14.90	13	61	97	
K6	Plot 3	15	1.35	10.9	5.45	5.6	59	98	0.95
K7	Plot 3	15	1.35	40.4	20.20	27	107	115	2.52
K8	Plot 4		1.35	15.3	7.65	10.9	85	100	
K9	Plot 4		1.35	28.7	14.35	20	67	75	2.99
K10	Plot 4		1.35	32.0	16.00	14.5	87	93	1.67
GW1	Plot 2	5	1.35	27.9	13.95	9.8	36	51	2.72
GW2*	Plot 1	8	1.35	14.9	7.45	7.9	22	23	3.59
GW3	Plot 2	5	1.35	10.1	5.05	4.6	15	18	3.07
GW4*	Plot 4		1.35	9.7	4.85	5.4	14	15	3.86
GW5*	Plot 4	4.5	1.35	11.9	5.95	5.6	18	19	3.11
GW6*	Plot 3	8	1.35	8.5	4.25	3.2	12	13	2.67
GW7	Plot 3	8	1.35	22.0	11.00	10.6	22	29	4.82
GW8*	Plot 5	4	1.35	10.8	5.40	6.3	16	17	3.94
GW10*	Plot 5	5	1.35	5.9	2.95	2.5	15	16	1.67
K1	Downstream	7.5	1.35	14.9	7.45	7	14	22	5.00
K3*	Downstream	6	1.35	7.7	3.85	4	27	33	1.48
K4*	Downstream	6.5	1.35	10.0	5.00	5.7	26	32	2.19
K5	Downstream	6.5	1.35	9.8	4.90	4.9	25	31	1.96
K6*	Downstream	6.5	1.35	9.1	4.55	4.9	27	33	1.81
K7*	Upstream	6.5	1.35	11.1	5.55	5.4	13	19	4.15
K8*	Upstream	6.5	1.35	9.8	4.90	5.1	13	19	3.92
K9*	Upstream	6.5	1.35	8.1	4.05	4.2	13	19	3.23
GW1	Downstream	10.5	1.35	19.7	9.85	9.3	38	40	2.45
GW2*	Downstream	11	1.35	18.8	9.40	8.3	40	41	2.08
GW3*	Downstream	13	1.35	12.5	6.25	5.7	14	15	4.07
GW5*	Downstream	7	1.35	15.1	7.55	5.2	31	32	1.68
K1	outside plot 1	28	2.60	109.0	54.50	25.7	165	356	1.56
K4	Plot 3	23	2.10	75.2	37.60	21.9	224	391	0.98
GW1*	Plot 1	7	1.35	16.2	8.10	7.3	15	16	4.87
GW2	Plot 1	7	1.35	21.9	10.95	11.4	14	16	8.14
GW3	Plot 1	7	1.35	11.2	5.60	7.6	11	14	6.91
GW4	Plot 2	4.5	1.35	11.4	5.70	6.1	17	22	3.59
GW5*	Plot 4	5	1.35	3.8	1.90	2	6	7	3.33
K1	Plot 1	8	1.35	9.9	4.95	3.4	31	39	1.10
K2	Plot 2	10	1.35	14.9	7.45	9.3	29	36	3.21
K3	Plot 2	10	1.35	7.2	3.60	3	21	30	1.43
K4	Plot 2	10	1.35	12.6	6.30	6.1	50	56	1.22
K5*	Plot 2	10	1.35	7.8	3.90	5.4	31	37	1.74
K6*	Plot 2	10	1.35	13.3	6.65	6.2	34	40	1.82
K7	Plot 2	9	1.35	6.6	3.30	3.4	31	38	1.10
K8*	Plot 1	7	1.35	8.1	4.05	3.7	31	37	1.19
K9*	Plot 1	6	1.35	6.5	3.25	2.1	32	38	0.66
K10	Plot 1	5.5	1.35	6.1	3.05	2.6	28	37	0.93
GW1	Plot 1	8.5	1.35	11.7	5.85	5.3	31	34	1.71
GW2	Plot 1	9	1.35	40.1	20.05	16.9	52	54	3.25
GW3	Plot 2	8	1.35	7.5	3.75	2.1	8	10	2.63
GW4	Plot 2	6.5	1.35	12.0	6.00	5.7	18	20	3.17
GW5	Plot 2	4	1.35	8.5	4.25	4.9	20	22	2.45
GW6	Plot 1	9	1.35	25.4	12.70	11.3	29	31	3.90
GW7	Plot 1	9	1.35	22.8	11.40	12	28	31	4.29
GW8*	Plot 1	8.5	1.35	11.9	5.95	6	27	28	2.22
GW9	Plot 1	8.5	1.35	13.1	6.55	7	29	32	2.41
GW10	Plot 1	8.5	1.35	13.4	6.70	7.2	27	30	2.67
K1	Plot 1	21	2.50	45.2	22.60	17.1	138	217	1.24
K2	Plot 1	21	1.90	46.2	23.10	20.5	203	235	1.01
K3	Plot 2	10	1.35	13.6	6.80	7.6	30	44	2.53
K4	Plot 2	5	1.35	7.7	3.85	2.8	24	32	1.17
K5	Plot 2	11	1.35	24.1	12.05	13.4	38	48	3.53
K6*	Plot 2	5	1.35	9.3	4.65	6.2	36	42	1.72
K7*	Plot 2	15	1.35	19.1	9.55	4.6	34	40	1.35
K8	Plot 2	15	1.35	27.7	13.85	10.4	32	42	3.25
K9	Plot 2	15	1.35	38.0	19.00	15.2	52	64	2.92
GW1*	Plot 1	5.5	1.35	11.1	5.55	7	11	12	6.36
GW2	Plot 1	7	1.35	36.0	18.00	15.2	37	40	4.11
GW3*	Plot 2	4	1.35	6.6	3.30	3.5	13	14	2.69
GW4	Plot 2	4	1.35	16.0	8.00	8.1	26	29	3.12
GW5	Plot 2	4	1.35	12.5	6.25	6.5	25	28	2.60
GW6	Plot 2	2	1.00	4.9	2.45	4.7	20	21	
GW7	Plot 3	6	1.35	19.0	9.50	8.2	21	25	3.90
GW8*	Plot 3	6	1.35	4.3	2.15	2.7	8	9	3.38

Year(s) and duration of suppression	Comments	Model (no centre arc)	Geometric model (centre arc visible)					
		Missing radius × GR	b = AB/2	c	d = (b2 - c2) / 2c	r = c + d	Av. GR (adj. rings)	r / adjusted GR
1935 - 1945		6.44						
NA		1						
estab - 2009			4.9	0.2	2.397	2.6	0.9	3.0
NA		6						
estab - 2009			10	3	86.5	89.5	3.0	29.8
estab - 2009			4	0.3	15.9865	16.3	0.5	32.6
estab - 1979	6 partial rings		2	0.5	3.9375	4.4	2.0	2.2
estab - 2009			4.7	0.8	8.58	9.4	1.0	9.4
estab - 1960			2	1	1.5	2.5	1.3	1.9
estab - 1996			2.5	0.5	1.5	2.0		
?	Stained		5	3	24	27.0	2.0	13.5
NA								
NA			3	1.5	5.0625	6.6	3.3	2.0
NA								
NA								
NA								
NA			5	3.5	22.3125	25.8	4.5	5.7
NA	Distortion of rings							
NA								
1986 - 1999			2	1	1.5	2.5	1.3	1.9
1976 - 2004	False rings excl.							
1977 - 1999	another release after 2004							
1977 - 2003			0.5	0.5		0.5	1.2	0.4
1976 - 2003	False rings excl.							
1990 - 2001	in 14th growing season							
1990 - 2003	in 14th growing season							
1990 - 2004	in 14th growing season							
NA			1.5	0.8	1	1.8	1.7	1.1
NA								
not visible	heavily stained							
not visible								
not visible	no centre arc, mature	184.9027237						
not visible	no centre arc, mature	160.5844749						
NA								
NA	estimated c		3.5	3	0.5	3.5	4.0	0.9
NA	estimated c		8	2.5	11.6	14.1	6.3	2.2
NA			3	0.75	5.6	6.4	1.5	4.3
NA	hard to see							
1970 - 2009	suppressed		2.5	1	2.6	3.6	1.5	2.4
1973 - 1987			3.5	2.5	1.2	3.7	3.0	1.2
1979 - 2009			1.8	1	1.1	2.1	0.8	2.6
1953 - 1987	no arc visible	0.02						
1972 - 2009	suppressed							
1969 - 1992; 1999 - 2009								
1971 - 2009	suppressed		2	1.2	1	2.2	1.7	1.3
1972 - 2009	suppressed							
1971 - 2009	heavily suppressed							
1972 - 2009	suppressed		1.5	1	0.6	1.6	0.5	3.2
	shorter rings		4.5	2	4.1	6.1	3.0	2.0
NA	really hard to see		5	3.5	1.8	5.3	4.0	1.3
	no arc visible	0.51						
1990 - 2009	hard to see		2.5	1	2.6	3.6	3.7	1.0
1997 - 2008	suppressed		2.5	1	2.6	3.6	4.0	0.9
NA	hard to see		2	1	1.5	2.5	2.7	0.9
NA			3	1.5	2.3	3.8	2.0	1.9
	shorter rings, hard to see							
1986 - 2008	shorter radial lengths		3.8	1	6.7	7.7	3.5	2.2
NA			4.5	2.5	2.8	5.3	2.3	2.3
not visible	false rings excl., mature		8.5	0.5	72	72.5	1.0	72.5
not visible	mature	26						
NA			4.5	1	9.6	10.6	1.3	8.0
1977 - 2009			3.5	1.6	3	4.6	2.0	2.3
NA			3.5	1	5.6	6.6	1.5	4.4
1997 - 2008								
1969 - 2009								
NA			11.5	3.3	18.4	21.7	5.0	4.3
NA			3.6	1.2	4.8	6	1.0	6.0
NA								
NA			5	1.5	7.6	9.1	5.0	1.8
NA	rings hard to see							
NA	rings hard to see		5	5	0	5	2.5	2.0
NA	rings hard to see		3.5	1	5.6	6.6	4.0	1.7
NA	rotten in centre							
NA			4.5	2.8	2.2	5	2.0	2.5
NA								

APPENDIX C – Seedling data

Tree	**Treatment**	**Height GR**	**Diameter GR**	**W.t. height (cm)**		**% Trans total light**	
ID		**(cm.yr^{-1})**	**(mm.yr^{-1})**	**winter**	**summer**	**winter**	**summer**
KL1	under GW canopy	-6.1	0.00	-27	-25	8.0	0.1
KL2	under GW canopy	-14.0	0.00	-9	-5	18.0	4.8
KL3	under GW canopy	17.0	0.00	-9	-7	24.0	10.3
KL4	under GW canopy	18.0	0.20	-3	1	22.0	6.9
KL5	under GW canopy	21.9	0.05	-6	2	17.0	2.8
KL6	under GW canopy	-11.2	0.00	-6	0	24.0	1.6
KL7	under GW canopy	1.6	0.00	-6.5	-6.5	21.0	1.2
KL8	under GW canopy	21.1	0.00	-7	-8	26.0	1.6
KL9	under GW canopy	20.6	0.00	-4	0	18.0	1.9
KL10	under GW canopy	45.2	0.00	3	1	11.0	3.2
average		**11.4**	**0.03**	**-7.5**	**-4.8**	**18.9**	**3.4**
KL11	free of GW canopy	46.0	0.00	-3	0	22.0	8.6
KL12	free of GW canopy	66.8	0.30	0	3.5	36.0	8.2
KL13	free of GW canopy	62.5	0.40	-3	0	38.0	24.6
KL14	free of GW canopy	22.6	0.40	-11	-6	62.0	34.3
KL15	free of GW canopy	38.8	0.00	0	0	43.0	33.4
KL16	free of GW canopy	34.3	0.20	-12	-23	50.0	43.1
KL17	free of GW canopy	19.5	0.20	-8	-3	36.0	47.6
KL18	free of GW canopy	35.5	0.10	6	8	34.0	29.4
KL19	free of GW canopy	43.6	0.35	2	2	56.0	43.9
KL20	free of GW canopy	48.8	0.30	0	2	34.0	31.4
average		**41.8**	**0.23**	**-2.9**	**-1.7**	**40.2**	**30.4**
KL1	Control	21.1	0.40				
KL2	Control	22.0	-0.10				
KL3	Control	28.4	0.75				
KL4	Control	26.0	0.40				
KL5	Control	21.6	0.75				
KL6	Control	28.5	0.50				
KL7	Control	37.5	0.45				
KL8	Control	0.0	0.20				
KL9	Control	33.3	0.50				
KL10	Control	36.2	0.90				
average		**25.5**	**0.48**				
KRO1	Naturally established	3.5	0.10	-9	-20	14.0	1.3
KRO2	Naturally established	6.6	0.00	0	4	25.0	2.6
KRO3	Naturally established	11.5	0.00	-6	-8	17.0	9.4
KRO4	Naturally established	-0.7	0.00	-1	0	13.0	0.9
KRO5	Naturally established	3.0	0.00	-9	-16	13.0	1.7
KRO6	Naturally established	4.5	0.00	-14	-30	8.0	4.7
KRO7	Naturally established	0.0	0.00	-3	0	20.0	17.3
KRO8	Naturally established	4.4	0.00	0	0	17.0	1.7
KRO9	Naturally established	2.2	0.00	-7	-10	15.0	0.6
KRO10	Naturally established	1.2	0.00	-27	-30	9.0	1.4
average		**3.6**	**0.01**	**-7.6**	**-11**	**15.1**	**4.2**
KRO11	Introduced bagged	-32.0	0.10	-9	-10	14.0	1.3
KRO12	Introduced bagged	15.5	0.00	0	0	25.0	2.6
KRO13	Introduced bagged	9.7	0.10	0	0	17.0	9.4
KRO14	Introduced bagged	2.3	0.00	-1	0	13.0	0.9
KRO15	Introduced bagged	9.4	0.10	-9	0	13.0	1.7
KRO16	Introduced bagged	26.8	0.00	-14	-10	8.0	4.7
KRO17	Introduced bagged	40.7	0.20	0	0	20.0	17.3
KRO18	Introduced bagged	17.8	0.00	0	5	17.0	1.7
KRO19	Introduced bagged	-3.5	0.00	0	3	15.0	0.6
KRO20	Introduced bagged	-8.4	0.00	-22	-30	9.0	1.4
average		**7.8**	**0.05**	**-5.5**	**-4.2**	**15.1**	**1.3**
KRE1	Released	15.8	0.00	-8	-30	21.0	26.2
KRE2	Released	3.5	0.00	-10	0	23.0	6.5
KRE3	Released	18.7	0.20	-16	-9	14.0	6.5
KRE4	Released	0.7	0.10	-16	-9	14.0	6.5
KRE5	Released	25.6	0.00	-16	-9	14.0	6.5
KRE6	Released	2.2	0.00	-16	-9	14.0	6.5
KRE7	Released	36.7	0.50	-16	-9	14.0	6.5
KRE8	Released	1.3	0.00	-16	-9	14.0	6.5
KRE9	Released	0.7	0.10	-5	-6	16.0	11.8
KRE10	Released	9.9	0.05	-5	-6	16.0	11.8
average		**11.5**	**0.10**	**-12.4**	**-9.6**	**16.0**	**9.5**
negative = water below surface			DEAD				