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Implications of tree management on poplar and willow pasture-tree systems

A thesis presented in partial fulfilment of the
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To Paty, Lily and Pau.

Abstract

Willow and poplar trees planted at wide spacing have proved their effectiveness as a biological method to control soil erosion in pastoral hill country. Due to lack of management, many trees aged 30⁺ years have grown very large (>60 cm diameter at breast height), resulting in excessive shading of understorey pasture. The large trees are also prone to breakage of branches and toppling during strong winds, potentially damaging farm infrastructure or injuring livestock.

Management of tree size can coincide with providing edible poplar and willow foliage as a source of supplementary fodder in summer droughts. Trees can be pollarded, involving total canopy removal, but the effects of pollarding on tree root dynamics are poorly understood.

This thesis evaluated the effect of the tree canopy removal on the root dynamics and root non-structural carbohydrate dynamics of pollarded mature willow and poplar trees and decapitated young willow and poplar trees grown from cuttings. Impacts of tree canopy removal when trees were at different phenological stages were also studied in pollarded mature willow trees and decapitated young willow and poplar trees. Finally, herbage accumulation under pollarded trees was contrasted with herbage accumulated under unpollarded (UP) trees and in open pasture sites (OP) away from direct tree influence.

Pollarding did not impose a unique impact on the root structure of mature willow and poplar trees. However some similarities were found in both species. For instance, pollarding had its main impact in the roots closest to the trunk and above 300 mm soil depth. In these root sections disrupted by pollarding, fine root length and mass of pollarded (P) trees were, one year after above-ground removal, from 2× to 4× less than equivalent unpollarded (UP) trees. However, one year after pollarding, pollarded trees recovered or maintained the initial fine root densities recorded in the same trees prior to pollarding.

The study conducted with young willow and poplar trees grown from cuttings showed that willow trees had a greater ability to recover from damage in the root structure after decapitation. Nine months after decapitation in early autumn, root mass of young willow decapitated trees was 57% greater than prior to decapitation and 64% less than non-decapitated (ND) trees. In contrast, within the same time frame, root mass of young poplar trees decapitated in early autumn was 80% less than ND trees and 52% less than the initial root mass recorded prior to decapitation. Greater resprouting ability of willow trees than poplar trees after decapitation was proposed as the cause for the greater resilience to decapitation observed in willow trees than in poplar ones.

Further evidence for a greater resilience to pollarding of willow trees was found in the root starch dynamics evaluated after tree canopy removal. Pollarded or decapitated willow trees (mature or grown from cuttings) were able to replenish their root starch concentrations similarly to UP or ND trees in the growing season following tree canopy removal. In contrast, both pollarded and

decapitated poplar trees (mature or grown from cuttings) had lesser root starch concentrations than intact trees one year after tree canopy removal.

Pollarding (P) or decapitation (D) at dormancy (DP or DD trees) showed no clear advantages in terms of the tree root structure maintenance or recovery after above-ground removal, over pollarding or decapitating the trees towards the end of the growing season in early autumn (AP or AD trees), when trees still had leaves. With mature willow trees, annual average fine root density (fRD) recovery of DP trees relative to pre-pollarding density was greater than annual average fRD recovery of AP trees. However, this difference was attributed to record moisture restrictions that disrupted the root growth of both AP and UP trees during the growing season following early autumn pollarding. Similarly, young DD and AD willow and poplar trees showed that four and a half months after decapitation, both treatment trees were able to recover or maintain initial root mass recorded prior to decapitation.

The study on herbage accumulation beneath pollarded trees, suggests that 4 years after being pollarded, P willow trees shaded pasture in a similar way to UP trees, as annual net herbage accumulation (NHA) attained in these two environments was statistically not different. Annual NHA under P and UP environments, were, respectively, 30 and 43% less than annual net herbage accumulation recorded in open pasture sites ($4.9 \text{ t DM ha}^{-1} \text{ yr}^{-1}$).

Ability of willow trees to recover, within the first year after pollarding or decapitation, initial root densities recorded prior to canopy removal, and to replenish root starch concentration similar to intact trees, suggests these trees could have pollarding cycles of 2 to 3 years. Short pollarding cycles could lessen herbage accumulation reductions on a pasture-tree stand level as more trees or more frequent repollarding is practised. However, results derived in this thesis from willow trees, need to be confirmed in at least two year lasting studies before recommending shorter pollarding cycles than currently advised of 3 or 4 years.

In contrast, poplar trees require longer pollarding cycles or higher tree stand densities if a pollarding program is instituted, as these trees were not able to recover within the first year after canopy removal, the root values recorded prior to pollarding and/or to replenish the root starch reserves

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Glossary and abbreviations

ANOVA: analysis of variance

Canopy: part of a tree above the trunk consisting of branches and foliage

Coarse roots (cR): roots with a diameter greater than 2 mm

Complete or total pruning: removal of all branches leaving intact the main stem single leader (mostly practiced in alley tree-crop systems)

Coppicing: cutting a mature tree at the base of the trunk at a height of 10-30 cm

DBH: tree diameter at breast height (1.40 m) over the bark

DM : dry matter

Fine roots (fR): roots with a diameter less than 2 mm

GLM: general lineal model

ha: hectare

Hill country: any land with slopes exceeding 15⁰ and located below 1000 metres above sea level

kg: kilogram

LSD: least significant difference

m: metre

m⁻³: per cubic meter

Mass movement: erosion of soil or rock occurs when stresses (downslope component of gravity pulling soil down the slope, pore water pressure, loading by vegetation, seismic waves propagating through the soil) exceed resistances (in-slope component of gravity holding soil to the slope, friction and cohesion of soil particles, reinforcement by vegetation roots)

mm: millimetre

Mudstone: a sedimentary rock composed of silt and clay particles and weakly cemented together by a small quantity of lime.

N/A: not applicable

N/Av: not available

NHA: net herbage accumulation

NSC: non-structural carbohydrates

Open pasture (OP) hill country pastureland where trees were far away.

PAR: photosynthetically active radiation.

Partial Pruning: removal of branches at a particular height.

Pasture-tree system (PT): pastureland located on a steep slope in hill country where willow or poplar trees have been planted 10 to 15 m apart to each other as a way of biological control shallow landslides.

Pollarding: complete removal of tree canopy at a 1.8 to 2.0 meter height above-ground

Pruning: removal of selected parts of the tree (as otherwise indicated, it was used for branches).

Root length density (RLD): length of the roots per unit volume of soil.

Root mass density (RMD): dry mass of the roots per unit volume of soil.

Sandstone: a sedimentary rock composed of sand grains, compacted and weakly cemented by a small quantity of lime.

SAS: statistical analysis system.

Thinning: the removal of some of the trees within a stand at some time after being planted with purposes of reducing tree stand density.

Wide-spaced tree planting: Trees that are planted 10 to 15 m spaced apart to each other.

Chapter 1. General Introduction

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1.1 Background

Poplar and willow trees have been used for more than 50 years in the pastoral hill country of New Zealand as a biological method to control mass movement soil erosion (Wilkinson, 1999, Benavides et al., 2009). A predominantly mountainous landscape, intense geological activity (tectonic, volcanic), young and weakly developed soil structure, and the influence of strong climatic events (storms, cyclones) are key factors conferring high natural erodibility in hill country (Blaschke et al., 1992, Basher et al., 2008). Replacement of original forest vegetation by pasture swards by the late 19th century, and poor pasture grazing management practices, increased the erosion incidence and severity (Page and Trustrum, 1997, Glade, 1998, Glade, 2003). Shallow landslides (soil slips) are a widespread soil erosion process affecting hill pastoral land and they have significant on-site and off-site impacts (Eyles, 1983, Hicks, 1995). On-site impacts are immediate and long-term reductions in soil and pasture productivity and damage to farm infrastructure including tracks, fences, and buildings (Jones et al., 2008). Off-site impacts are mainly sedimentation of waterways, flooding in urban areas, and the blocking of roads (Jones et al., 2008, McIvor et al., 2011).

Established poplar and willow trees (10⁺ years; >30 cm DBH) planted at wide spacings from 10 x 10 m to 18 x 18 m on pastoral hill slopes are effective in reducing the occurrence and extent of shallow landsliding during and after erosion-inducing storms by around 70% (Hawley and Dymond, 1988) to 95% (Douglas et al., 2013). Effectiveness in stabilising slopes relies mainly on the ability of poplar and willow trees to rapidly develop an extensive lateral and vertical root network, and for roots of neighbouring trees to interlock to form a root venation across susceptible areas of slopes. Frictional and adhesive properties of coarse (>2 mm diameter) and fine (<2mm diameter) roots, and tensile strength of coarse roots spreading sideways and downwards from lateral roots, provides horizontal and vertical stability to the slopes (Reubens et al., 2007, Stokes et al., 2009)

Despite the significant contribution of poplar and willow trees in stabilising slopes, their presence in pastures can decrease understorey herbage accumulation up to 40 to 50% that recorded in open

pasture sites away from direct tree influence (Guevara-Escobar et al., 2007, Wall et al., 2010). Success and adoption by farm owners of these pasture-tree (PT) systems depends on the profitability of the pastoral component and other factors including environmental benefits and personal preferences. Canopy closure, defined as the proportion of the sky hemisphere obscured by vegetation when viewed from an understorey single point (Jennings et al., 1999), relates inversely with the photosynthetically active radiation (PAR) transmitted through the canopy (R^2 0.97) (Wall et al., 2010) and with understorey pasture production (R^2 0.77) (McElwee and Knowles, 2000, Wall et al., 2010). Light transmission through the canopy is often the limiting factor for pasture production in PT systems in New Zealand (Guevara-Escobar et al., 2000, Guevara-Escobar et al., 2007).

In alley tree-crop agroforestry systems, partial or total removal of above-ground parts of trees is a common practice conducted at the beginning of the growing season at sowing time (Chesney, 2012). Reduction in canopy size increases the light reaching the crop and temporarily increases crop productivity to values greater than unpruned tree-crop plots and similar or greater than monocrop systems (Nair, 1993, Sande, 2003). Severely pruned alder trees in a silvopastoral system in New Zealand resulted in understorey herbage accumulation 40% greater than recorded under trees pruned leniently (Devkota et al., 2009).

Poplar and willow trees space-planted 10-15 m apart, on steep erodible slopes are typically not managed. Trees older than 30 years have reached such dimensions (>60 cm diameter at breast height (DBH)) that they are regarded by some farmers as a liability to their farming practice (National Poplar and Willow Users Group, 2007). Additional to shading pastures, large trees are also prone to breakage of branches and toppling during strong winds, damaging fences, blocking roads and harming livestock (National Poplar and Willow Users Group, 2007). The challenges with oversized trees discourage adoption or maintenance by farmers of PT systems. Conversely, logistical problems associated with tree management such as disposal of pruned material and safety concerns with management operations, deter farmers from conducting management approaches like periodic pruning or pollarding, as found beneficial for crops in alley tree-crop

agroforestry systems (Sande, 2003, Thevathasan et al., 2004, Ogunlana et al., 2006, Reynolds et al., 2007).

Management to reduce tree size can be conducted during summer droughts, with the removed edible poplar and willow foliage being useful as supplementary fodder for livestock (Wilkinson, 1999, Kemp et al., 2001, Benavides et al., 2009). With climate change, summer droughts are predicted to become more frequent, longer and more intense (Basher et al., 2012).

Management of tree size can be conducted by pollarding or by pruning. Pollarding comprises the removal of the entire tree canopy by cutting at 1.8 m to 2 m height above the ground, whereas pruning is a partial and conformational removal of the canopy, usually for timber production purposes or to increase light to understorey pasture. While benefits are expected from regular tree canopy management, impacts on the root structure are poorly understood and maintenance of the root structure is crucial for soil conservation, the primary purpose for which the trees are planted. Studies on related forestry (short rotation forestry systems) and agroforestry systems (tree-crop) where canopy removal is practised regularly have focused on tree shoot biomass production (Dickmann and Pregitzer, 1992) or on the associated crop productivity (Nair, 1993, Thevathasan and Gordon, 2004); the impact on the tree root structure after above-ground intervention has received scant attention. In New Zealand, published information on the impact of pollarding on the root structure of poplar and willow trees is very limited.

The main objective of this thesis is to provide understanding of the implications of tree size management by pollarding on root structure dynamics and secondarily to evaluate the impact of pollarding trees in the surrounding pasture production. Research reported in Chapters 3 to 5 focuses on the effects of pollarding on root responses and root reserve carbohydrate dynamics, and Chapter 6 deals with the implications of pollarding on understorey pasture accumulation. Pollarding is a risky and laborious task, and is usually conducted in summer or early autumn when there is a need for additional stock fodder because pasture has decreased yield and is of low nutritive value. However, in terms of the energy reserve status of the tree, pollarding in summer

imposes potentially high developmental constraints to the tree root structure, whereas pollarding conducted when the trees are dormant could have less impact on the root structure. In Chapter 3, root responses and root non-structural carbohydrate dynamics were determined after pollarding mature willow trees at two phenological stages, in late winter when the trees were dormant and in early autumn close to the end of the growing season. In Chapter 4, root responses and root non-structural carbohydrate dynamics after pollarding mature poplar trees in early-autumn are described and discussed. Chapter 5 reports the findings of a glasshouse study conducted with young trees of willow and poplar established from cuttings. In this study, above- and below-ground biomass and root non-structural carbohydrate dynamics after decapitating the plants at dormancy and in early autumn were determined.

Chapter 6 describes a study on a farm where willow trees are pollarded regularly by the landowner in summer and autumn for supplementary stock fodder. As one of the main collateral benefits of tree size management, pasture production under pollarded trees was compared with that under unpollarded trees and at nearby sites away from direct influence by the trees. A general outline of this thesis is presented in Table 1.1

1.2 Objectives

The objectives of this thesis were to determine:

- The impacts of pollarding on the root dynamics of mature willow trees pollarded at two phenological stages.
- The root non-structural carbohydrate dynamics of mature willow trees pollarded at two phenological stages.
- The impacts of pollarding on the root dynamics of mature poplar trees pollarded in early autumn.
- The root non-structural carbohydrate dynamics of mature poplar trees pollarded in early autumn.

-
- The impacts of decapitation on the above- and below-ground dynamics of young willow and poplar trees grown from cuttings and decapitated at two phenological phases.
 - The root non-structural carbohydrate dynamics of young willow and poplar trees grown from cuttings after decapitation at two phenological phases; and
 - Pasture accumulation in three environments (beneath pollarded and unpollarded willow trees, and beyond trees).

1.3 Thesis Outline

Table 1.1 General thesis outline

Chapter	Content
1) General Introduction.	This chapter outlines the contribution of poplar and willow trees for soil conservation in New Zealand pastoral hill country, and highlights the need for tree size management by pollarding or pruning.
2) Literature review.	The series of events and circumstances that led to widespread mass movement soil erosion in pastoral hill country and how the root structure of poplar and willow trees contributes to counteract mass movement erosion, are reviewed. Literature on the implications of canopy removal on tree root structure and understorey pasture production is also reviewed.
3) Root response and carbohydrate dynamics of willow trees pollarded at different phenological stages.	Root and non-structural carbohydrate dynamics were determined in mature willow trees pollarded at dormancy and at the end of the growing season.
4) Fine root response and carbohydrate dynamics of poplar trees pollarded in early autumn, at the end of the growing season.	Mature poplar trees grown in a flat terrain were evaluated in their root response and root non-structural carbohydrate dynamics after being pollarded in early autumn, when trees were still in leaf stage.
5) Above-, below-ground and root non-structural carbohydrate dynamics of willow and poplar plants decapitated at different phenological stages	Young trees grown from cuttings were decapitated at dormancy and in early autumn, and the effects on above- and below-ground dynamics determined. Trees decapitated in early autumn received limited water supply to simulate summer drought conditions when pollarding on farms is most commonly conducted.
6) Pasture production beneath pollarded and unpollarded willow trees.	A study was conducted on a commercial farm where willow trees are pollarded routinely to provide supplementary stock fodder during periods of reduced pasture growth and quality. In a pasture-tree system, herbage accumulation was determined beneath pollarded and unpollarded trees and in nearby open pasture areas.
7) General Discussion and Conclusions.	Practical implications from Chapters 3 to 6 are integrated and conclusions and proposals for future research presented.

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Chapter 2. Literature review

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2.1 Pastoral hill country in New Zealand

The land area of New Zealand known as ‘hill country’ has a significant and strategic importance for the country, not only geographically and scenically, but also economically. Hill country refers to any land with slopes exceeding 15° and located below 1000 metres above sea level (Ministry for the Environment, 2007). Under this definition 37% of the total area of New Zealand, about 10 million hectares, is classified as hill country, with the majority (6.3 million hectares) located in the North Island and the rest in the South Island (Basher et al., 2008).

Hill country covered with pastures (5.2 million ha) comprises about half of the total pastoral land in New Zealand, and pastoral agriculture covers around 39% of the country’s total land area (LCDB v4.0, 2014)

Sheep and beef cattle are the predominant livestock enterprises in North and South Island pastoral hill country. Meat and wool products derived from these hill country enterprises contribute around 30% of exports derived from pastoral industries, which in turn account for more than 40% of the New Zealand’s total exports value (Statistics New Zealand, 2015).

2.2 Soil erosion in pastoral hill country

Sustainability of pastoral hill country has been threatened almost since pasture establishment. Hill country farmers have had to deal with on-going soil erosion represented principally by mass movement erosion processes, that have directly impacted pasture productivity through losses of soil productive and water holding capacity, and caused off-site impacts on water quality, river aggradation, and damage to urban sites,

roads and associated infrastructure (Mackay, 2008, Basher et al., 2008, Jones et al., 2008, McIvor et al., 2011a).

Hill country has a history of ancient and profound natural and also anthropogenic landscape transformations. Mountainous and steep topography, high tectonic activity, large areas of young soils developed over soft sedimentary and crushed rocks, and the influence of strong climatic events (storms, cyclones), are among the main factors that have driven together the New Zealand's hill country natural landscape transformations (Blaschke et al., 1992, Wilkinson, 1999, Basher et al., 2008). Anthropogenic transformations have dramatically accelerated the rate of soil erosion to levels of 1.6× to 18× the rates recorded before pasture establishment (Dregne, 1995, Glade, 2003, Dotterweich, 2013). Studies have found greater incidence and/or severity of shallow landslides on land covered in pasture compared with native forest or scrub land (Blaschke et al., 1992, Glade, 1998). In comparison to hillslopes covered in pasture, the proportion of uneroded hillslopes increased from 10% beneath pine plantation, to 21 and 27% on scrub and indigenous forest, respectively (Hicks, 1991). After Cyclone Bola struck the East Coast of New Zealand in 1988, shallow landslide density (number of landslides per hectare) increased 5 times more on land covered by pasture than by indigenous forest (Marden and Rowan, 1993). Paleolimnology has provided strong evidence of associations between charcoal, sediments and pollen differential and sequential lake depositions, with the timing of the human-induced forest disturbances, and the vegetation changes exerted during either the Maori colonization or European settlement (Page et al., 1994, Wilmshurst et al., 1997, Wilmshurst et al., 2004, McWethy et al., 2009). Lake sediment analysis has shown that historic sedimentation rates are around ten times greater on land under pasture than under indigenous forest (Wilmshurst, 1997, Page and Trustrum, 1997, Wilmshurst et al., 1999). Landslide records were matched with periods of high human-

induced disturbances in forests (Glade, 1998). As proposed by Taylor (1938) the natural drivers for soil erosion like earthquakes or heavy storms are just the trigger action of a “*gun loaded*” with deforestation, inappropriate farming practices and denuded erosion-prone soils. The next sections will describe the series of factors and circumstances that contributed to “*load the gun*” and make trees one of the most suitable strategies to control erosion in pastoral hill country.

2.2.1 Pastoral farming and soil erosion in hill country

The establishment of pastoral farming in hill country involved replacing the original vegetation cover comprising mainly dense temperate forest and scrub, which was estimated to have covered at least 75% of New Zealand’s land area (Wards, 1976, Daly, 1990). Transformation of the original vegetation cover started around A.D. 800 with the first human colonisation, when Polynesian settlers practised forest burning associated with cropping and hunting activities (Cumberland, 1981, McKinnon et al., 1997, Wilmshurst et al., 2004). However, the most dramatic and rapid transformation of the vegetation cover occurred with European settlement, especially from 1840 to the early 20th century, when felling the woody native vegetation, clearing the remnant debris by burning and then oversowing pasture seeds, reduced the forested area to 18% of New Zealand’s total land area (Molloy and Forde, 1980).

Early in the pasture development phases, either because of lack of technical knowledge or encouraged by the expanding wool, lamb and beef growing industries, or both, overstocking over huge open areas led to depletion of soil nutrients and significant reduction in pasture cover (Hodgson et al., 2005, Moot et al., 2009). Depleted and exposed land was rapidly invaded by weeds and secondary growth of native vegetation. Fire and overgrazing were the most recurrent methods to counteract native vegetation reversion, which in turn increased land degradation (Taylor, 1938, Cumberland, 1941, Gibbs, 1945, Campbell, 1945c).

Soon after pasture establishment, a series of erosive events occurred on the treated hill country in various parts of New Zealand. The denuded condition of the soil left the hill country very vulnerable to various forms of surficial erosion and shallow mass movements. Heavy rainfall on exposed soils devoid of vegetation made sheet erosion and shallow landslide (soil slips) the predominant forms of soil damage on the hill lands (Campbell, 1945c, Campbell, 1945a, Cumberland, 1947). As described by Cumberland (1947), “deposition, rather than the erosion, of sheet washed soil is often the more evident. Throughout this region sheep and cattle tracks are filled with fine silt after rain and foot treads obscured; lakes at the foot of eroding slopes change colour in a few minutes (from a clear peat-brown to a milky yellow: slump-dammed lakes filled up rapidly and soon disappear; clover-swarded flats are mantled with coarse waste; and willow fringed, narrow thalwegs are choked with sand and silt”.

Off-farm impacts caused from sheet and mass movement erosion were also widespread with substantial economic damage. Several devastating floods with large loads of silt and sediment occurred since the 1890s in different hill country regions. The recurrent nature of the events increased awareness within the public and official circles, reaching a critical point in the late 1930s East Coast floods in the Gisborne and Hawke’s Bay regions, when deaths occurred, and unprecedented damage on hill farms was observed with many slips and washouts (McCaskill, 1973). In the valleys and on the flats, hundreds of farms and urban sites were buried under up to 1.8 m of silt, sand and gravel (Hill, 1938, Cumberland, 1947, Mather, 1982). In response to the severity of the damage the government created in 1941 the Soil Conservation and Rivers Control Act (McCaskill, 1973, Mather, 1982, Roche, 1997), which, as stated in the Act, was created to “make provision for the conservation of soil resources and for the prevention of damage by erosion and to make better provision with respect to the protection of property from damage by floods”.

Sheet and mass movement erosion were recognized by the 1920s and 1930s as the predominant forms of erosion affecting New Zealand's hill country (Taylor, 1938, DSIR, 1939, Campbell, 1945b, Cumberland, 1947). Sheet erosion was considered at least a partial cause of mass movement erosion. The moisture content of the exposed soil was thought to vary more widely than on the forested slopes; topsoil removed by sheet washing after repeated burning and overgrazing exposed subsoil which dried out in dry summers and induced ground cracks; rain water flowing through the cracks eventually reached an impervious horizon and lubricated the subsoil above causing mass movement (Taylor, 1938, Lamont, 1939, Campbell, 1945c, Cumberland, 1947).

The first soil surveyors and conservationists in the 1930s acknowledged the value of the forest cover in preventing erosion. However, most of the protective role of the forest was attributed to their above-ground features (Taylor, 1938, Campbell, 1945b). "Forest is the controller of erosion *per excellence*. No matter how severe the storm, rain must filter through the forest canopy, through the shrubs and ferns of the undergrowth, and through the forest litter of leaves and twigs before reaching the soil proper. Large quantities are absorbed *en route*, and even when all is saturated and running water commences to move over the forest floor the trunks of trees and shrubs and each projecting leaf and twig of the litter, obstructs its path with *ten billions little dams*, each checking its rate of flow, and hence its power to erode" (Taylor, 1938).

The importance given to the above-ground plant structure in controlling erosion, the predominance and significance given to sheet erosion and its causes and consequences, and the importance of pastoral land to the growing economy in the mid 20th century, were among the main circumstances that led to defining an initial set of strategies to control hill country soil erosion. Strategies applied focused on establishing, or recovering and maintaining a close-matted turf of grasses and herbaceous legumes over the steep land

(DSIR, 1939, Campbell, 1945c, Gibbs, 1945). Replenishing the soil fertility by judicious topdressings with phosphate-based fertilizers, oversowing with improved grasses and legumes, pasture spelling, and better stock grazing control by increasing subdivision of paddocks, were deemed key activities underpinning the soil erosion control strategy (DSIR, 1939, Lamont, 1939, Moot et al., 2009).

The soil conservation strategies implemented soon showed their effectiveness. Run-off and sheet erosion were reduced significantly, slip scars started to revegetate, and pasture dry matter and stock carrying capacity increased dramatically (Campbell and Anaru, 1964, Campbell, 1965, Wilkie and Dixie, 1965, Campbell, 1966). However, shallow mass movements kept occurring in spite of the development of a dense herbaceous turf, especially in hill land soils overlying soft rocks like mudstone and sandstone (Van Kraayenoord, 1966). Herbaceous cover alone proved insufficient to prevent shallow landslides on the hill slopes, with additional measures required on a large scale for use in the presence of grazing livestock (Hicks et al., 2001, McIvor et al., 2011a).

2.2.2 Trees used in hill country erosion control schemes.

Poplar (*Populus* spp.) and willow (*Salix* spp.) trees were introduced to New Zealand almost as early as the European settlers arrived. Initially they were planted mainly for shelter and amenity, but were soon included in basic soil conservation measures, with widespread planting for riverbank protection (Wilkinson, 1999, National Poplar and Willow Users Group, 2007). Occasionally the trees were planted randomly on erodible slopes and observations showed their value for slope stabilisation (Campbell, 1945c, Campbell, 1946, McCaskill, 1973). The ability to propagate them vegetatively with minimum protection in the presence of grazing livestock, using poles that could be grown on a large scale in nurseries, made them ideal for reinforcing the soil conservation

strategies that were being implemented by the 1940s and 1950s (Van Kraayenoord, 1966, Van Kraayenoord and Hathaway, 1986, McIvor et al., 2011a).

In the early stages of using poplar and willow for soil conservation, much of the work was based on the views of practitioners, without experimental evidence. Little was known about which poplar or willow varieties were suitable for specific environments, and survival and growth rates with close- or wide-spaced-planted trees ranged from very high to low or zero. In 1956 a specific program started to identify and evaluate the poplar and willow germplasm to produce new varieties and clones. By the 1960s and 1970s over two million poplars and willows were planted in government-subsidised erosion control schemes (McCaskill, 1973, Wilkinson, 1999). Since then, considerable information about the role of different tree species included poplar and willow in slope stabilisation has been generated within New Zealand (O'Loughlin, 1974a, O'Loughlin, 1974b, Marden and Rowan, 1993, Watson et al., 1995, Watson et al., 1999, Marden, 2004, O'Loughlin, 2005, Knowles, 2006) and worldwide (Wu et al., 1979, Gray and Sotir, 1996, Keim and Skaugset, 2003, Reubens et al., 2007, Stokes et al., 2009, Ghestem et al., 2014). In New Zealand, research has determined the effectiveness of wide-spaced trees in reducing mass movement erosion (Hawley and Dymond, 1988, Hicks, 1992a, Hicks, 1992b, Hicks et al., 1993, Douglas et al., 2013a), quantified the effects of tree size and stand density on root development (McIvor et al., 2008, McIvor et al., 2009, Douglas et al., 2010), defined how wide-spaced trees interact with understorey pasture, (Wall et al., 2006, Douglas et al., 2006a, Douglas et al., 2006b, Guevara-Escobar et al., 2007, Devkota et al., 2009) and described the fodder value of the trees (Oppong et al., 2002). More recently, studies have commenced to determine the implications of tree management on below-ground tree development and pasture understorey responses.

2.3 Role of trees in slope stabilisation

2.3.1 Basic engineering of shallow soil mass movement

In order to understand how trees contribute to slope stabilisation, it is important to describe key aspects of the process of shallow soil mass movement.

Mass movement of soil or rock occurs when stresses (downslope component of gravity pulling soil down the slope, pore water pressure, loading by vegetation, seismic waves propagating through the soil) exceed resistances (in-slope component of gravity holding soil to the slope, friction and cohesion of soil particles, reinforcement by vegetation roots) (Hicks, 1995, Gray and Sotir, 1996, Hicks et al., 2001).

Movement is initially by sliding or a combination of sliding and flowing, but where the failed mass becomes saturated with water, it forms a chaotic mix of debris which can flow down slope for a considerable distance (10s to 100s of metres, or >10 times the scar length) (Lynn et al., 2009).

Shallow landslides, more commonly known in New Zealand as ‘soil slips’ or just ‘slips’, are the most common form of shallow mass movement recorded in hill country (Eyles et al., 1985, Basher et al., 2008). Soil slips are a shallow and rapid sliding about 0.5-5 m/s or flowing movement of the soil and subsoil, exposing a slip surface which is approximately parallel to the slope normally located less than 1 m, but in a few cases up to 2 m, below the original surface (Hicks et al., 2001, Lynn et al., 2009).

In New Zealand, shallow mass movement occurs on a wide variety of terrains and rock types. Mudstone and sandstone hill country are especially susceptible, but loess and tephra covered hills, greywacke hills and ranges, and volcanic mountains and other terrains are also susceptible (Eyles et al., 1985, Lynn et al., 2009).

2.3.2 Tree hydromechanical mechanisms for slope protection.

Trees contribute to soil stability on steep slopes by hydrological and mechanical means. There are a number of mechanisms used by trees to reduce soil pore water pressure. Canopy rain fall

interception and then evaporation together with canopy transpiration are the main mechanisms through which woody vegetation can reduce water content in hillslopes (Greenway, 1987, Gray and Sotir, 1996, Keim and Skaugset, 2003).

Trees provide mechanical protection through above-ground buttressing and arching abutment of the embedded stems, root stumps and large structural roots that counteract downslope shear forces (O'Loughlin, 2005), but mostly, by mechanical reinforcement of the below-ground root structure. The frictional and adhesive properties and the tensile strength exerted by the coarse ($> 2\text{mm}$ diameter) and fine ($\leq 2\text{mm}$ diameter) roots spreading sideways and downward from lateral roots, provides horizontal and vertical stability to the slopes, particularly when the vertical roots penetrate deeply and anchor to more stable material beneath (Reubens et al., 2007, Stokes et al., 2009). The contribution of roots to slope stability can be seen in the increase in shear strength of root-permeated soils (Ekanayake et al., 1997, Ekanayake and Phillips, 1999, Ekanayake and Phillips, 2002, Watson et al., 2007, De Baets et al., 2008) and how soil shear strength decreases after timber harvesting or clearfelling of forested areas (O'Loughlin, 1974a, Watson et al., 1997, Watson et al., 1999). Additionally soil shear strength decreases after timber harvesting or clearfelling of forested areas has been associated in turn with an increase in the frequency of shallow landsliding (O'Loughlin, 1974b, Wu et al., 1979, Sidle et al., 1985, Watson et al., 1999, O'Loughlin, 2005).

The relative contributions of the hydrological and mechanical effects of trees on slope stabilisation are not known precisely. From data collected on a forest stand, Keim and Skaugset (2003) questioned the “overvalue” of roots towards slope stabilisation and highlighted the role of canopy rainfall interception to increasing modelled slope stability relative to areas with no canopy. In contrast, among wide-spaced poplar tree stands Guevara-Escobar et al. (2000) showed that soil water content at 0-300 mm depth was greater than, or similar to, that of neighbouring pastoral areas without trees. It is possible that above-ground mechanical mechanisms contribute more to slope stabilisation at high tree stand densities (> 900 trees ha^{-1}), as in forests, whereas slope protection in pasture-tree systems (30-70 trees ha^{-1}) relies more on tree root extension. On

pastoral hill country, where significant reductions in annual herbage accumulation of up to 40 or 50% have been recorded in poplar and willow pasture-tree systems (Wall et al., 2006, Guevara-Escobar et al., 2007), large roots extending well beyond the canopy radius and connecting with adjacent tree roots could help to reduce the need for high tree stand densities, and reduce the risk of canopy closure, thus increasing light transmission to the pasture understorey.

2.3.3 Root interlocking and the ideal tree stand density

Soil reinforcement by roots is analogous to the reinforcing role of steel mesh in concrete; roots of neighbouring trees must therefore interconnect or interlock within the soil on the slope in order to protect the entire area. The rate at which a planted site is occupied by roots depends on the lateral root growth rate and the tree planting density (Watson et al., 1999). However, as proposed by Phillips et al. (2011) maximum or even mean maximum lateral root spread cannot be considered as an indicator of root connectivity between neighbouring trees. In most field situations lateral roots spread in an asymmetrical pattern around the stem and a few individual long roots may over-represent the value of lateral root site occupancy, and thus, soil reinforcement (Phillips et al., 2011). Root lateral asymmetry distribution has been found by McIvor et al. (2008) and McIvor et al. (2009) in a series of root excavations of poplar clone ‘Veronese’ trees aged from 5 to 11.5 years, located at different slope positions (lower, middle and upper slope). According to McIvor et al. (2008) lateral root distribution of a single tree is not as important in stabilising soil and reducing landsliding as the evenness and density distribution of roots across a slope. On a 10 m × 10 m simulated tree spacing of trees aged 9.5 years, McIvor et al. (2008) showed how the hypothetical adjacent trees could increase more than twice the root mass and length density around the stem of an isolated 9.5-year-old tree. McIvor et al. (2008) concluded that with poplar ‘Veronese’ trees bigger than 30 cm DBH, neighbouring trees contribute to create a more even spatial distribution of roots, and that root density across a slope is largely a function of spacing

The first recommendations published by Hathaway (1986) on the general management of plant materials for slope stabilisation, proposed a wide range of tree spacings from 5 m × 5 m to 20 m

× 20 m depending on the position on the slope, and the extent and severity of slope instability. Hathaway (1986), stated that many of the recommendations were based mainly on experience. More recent research on the effectiveness of wide-spaced trees for erosion control and their root morphology, has provided evidence and tree spacing recommendations (8 to 15 m apart) (Hawley and Dymond, 1988, McIvor et al., 2008, Douglas et al., 2013a) that are within the range proposed by Hathaway (1986).

The first insights into the development of the tree root network were from studies to determine the effectiveness of spaced-planted poplar and willow trees for controlling erosion on hillslopes in regions or districts devastated by cyclones or intense storms.

Based on aerial images of wide-spaced 15-year-old poplars on hillslopes damaged with severe soil slipping after intense storms in 1985 in Gisborne, New Zealand, Hawley and Dymond (1988) estimated that if the trees had been planted at 10 m × 10 m spacing rather than the original 20 m × 20 m, the reduction in ground area in landslide scars would have been 70%, instead of the 13.8% observed. Using the same 10 m × 10 m spacing criterion for classifying unstable hillslopes as “adequately treated” before Cyclone Bola that struck the East Coast of New Zealand in 1988, Hicks (1992b) concluded that, had all the erosion-prone slopes been “adequately treated”, a 74% reduction in shallow mass movement erosion could have been expected compared with no implementation of conservation measures.

Tree stand density recommendations published in 1986 (Hathaway, 1986) were later supported by Hicks (1995) who proposed a tree spacing of 12 m × 12 m which was within the range suggested earlier.

Root morphology studies have strengthened tree spacing management guidelines. Excavations by Puri et al. (1994) of *Populus deltoides* trees found that root asymmetry disappeared with increasing tree spacing from 2 m × 2 m to 6 m × 6 m, and mean length and spread of the primary lateral roots increased from 4.0 m and 3.1 m at the 2 m × 2 m spacing to 5.9 m and 5.2 m at the 6 m × 6 m spacing. In New Zealand, McIvor *et al.* (2008) excavated the whole root structure of *Populus deltoides* × *nigra* ‘Veronese’ trees aged 5, 7 and 9.5 years growing on the lower part of

a hillslope (angle 17°), and planted originally at 8 m × 8 m spacing. The total structural root length (roots >2 mm diameter) of the 9.5- year-old tree was 8.4 times greater than for the youngest tree. Root length density of the oldest tree was more uniform as the distance from the trunk increased than younger trees. Root length density at 8-10 m from the trunk of the tree aged 9.5 years was just 35% less than at 0-2 m from the trunk, compared with 76–80% less root length density between the same two distances for both younger trees. The results of excavations conducted by McIvor *et al.* (2008) suggested when a poplar tree developed a root system capable interconnecting with adjacent trees.

When sampling by trenching, digging to a quarter (0.25) and half (0.5) the distance between adjacent poplar trees aged 9-11 years at spacings ranging from 11 m × 11 m to 3.6 m × 3.6 m, Douglas *et al.* (2010) found that trees at spacings of 8 m × 8 m, 7 m × 7 m and 6.5 m × 6.5 m had moderate to high root occupancy of soil layers, and root numbers and root area ratio (RAR: the fraction of a plane of soil occupied by roots) likely to benefit soil stabilisation. Douglas *et al.* (2010) suggested that savings on planting material and labour could ensue by using the 8 m × 8 m tree spacing instead of the closer spacings, as differences between these three tree spacings were not statistically significant, with the wider spacing would also provide potential increases in pasture accumulation.

Douglas *et al.* (2013a) compared the impact of severe rainstorms on shallow landslide occurrence on pasture sites with spaced-planted trees and pasture sites without trees. Based on the results of the excavations of McIvor *et al.* (2008, 2009) and observations of uprooted trees, Douglas *et al.* (2013a) assumed that trees had a soil protective influence of 10 m radius around tree stems. Using this assumption Douglas *et al.* (2013a) found that trees spaced as wide as 18 m × 18 m reduced shallow landslide occurrence by 95% compared with nearby pasture control sites without trees. This reduction was greater than reported in previous studies (Hawley and Dymond, 1988, Hicks, 1992b). Apart from methodological, scale or tree stand differences between the studies, discussed by Douglas *et al.* (2013a), site and meteorological conditions might explain the discrepancies. Of all regions of New Zealand, the East Coast of the North Island where Hawley and Dymond (1988)

conducted their evaluation, has been subject to the worst damage by shallow mass movement erosion. The area has unconsolidated mudstones which are considered the most prone to soil slipping. Rainstorm intensities recorded in the area damaged by Cyclone Bola and evaluated by Hicks (1992b) were 1 to 9 times more intense than fell in the areas of the Douglas et al. (2013a) study. Therefore, higher tree stand densities could have been required for slope stabilisation in the Hawley and Dymond (1988) and Hicks (1992b) studies.

2.3.4 The soil shear line and tree root architecture.

The soil slip surface shows a shear line with two main regions where soil failure occurs (Fig 2.1 and 2.2). Perpendicular to the soil surface, the shear line (perpendicular shear line) exerts a high tension downslope, and parallel to the soil surface (parallel shear surface), the potential shear surface is located at significant depth, more often 0.5-1m, but sometimes up to 2 m (Fig 2.1) (Hicks, 1995, Reubens et al., 2007, Danjon et al., 2008). Danjon et al. (2008) and Reubens et al. (2007) proposed that different root categories and traits exert different roles according to their position in the soil shear line

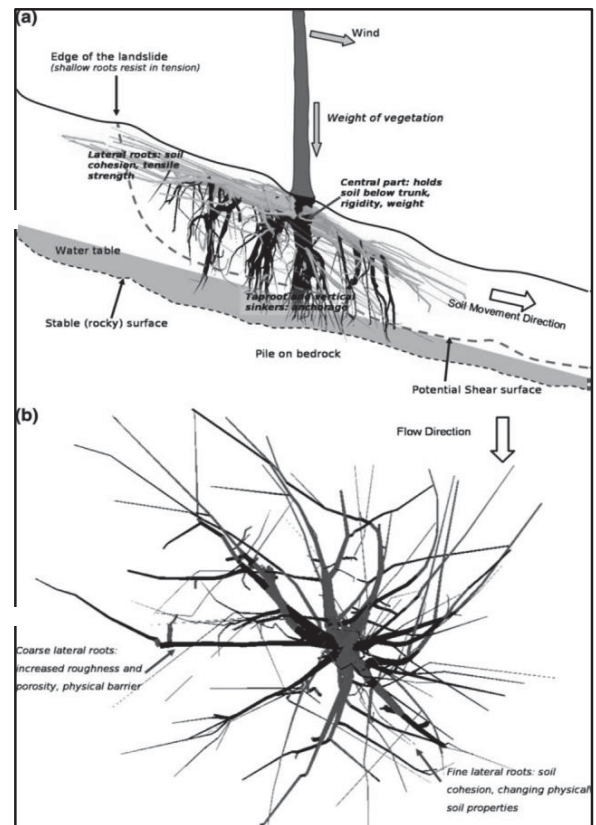


Figure 2.1 Soil slip shear lines (Reubens et al., 2007)

2.3.4.1 Poplar and willow root reinforcement of the perpendicular shear line in shallow mass movements.

Trenching is a suitable technique to collect data to describe how plant roots reinforce the soil potential perpendicular failure zone (Böhm, 1979). Trenches dug at certain distances from the tree, usually from 1 m away from the tree trunk create a soil profile that more likely cuts across or about the diametrical plane of lateral and oblique roots that run parallel to the soil surface and

in angles greater than for about 45° from the taproot (Douglas et al., 2010). Trenching enables measurement of root traits such as number, diameter or distribution and root presence in the soil, from which can be calculated parameters such as root area ratio and root thickness, which are highly associated with soil shear strength (Reubens et al., 2007, Stokes et al., 2009).

Trenching studies involving poplar and willow show that more than 75% of the roots occur in the topsoil and of these more than 70% are roots less than 2 mm diameter (Crow and Houston, 2004, Douglas et al., 2010). There is a pronounced decrease in the number of roots with increasing depth, below 0-30 or 0-45 cm.

Similar distribution patterns have been reported for the below-ground biomass of *Populus deltoides* and other *Populus* clones using coring and full excavation techniques. More than 70% of the fine root (<2 mm diameter) biomass was present in the top 15 cm of soil (Puri et al., 1994, Al Afas et al., 2008), and on average, soil at 0-30 cm depth contained 65.5 % of the coarse root (>2 mm) diameter) biomass of *P. deltoides* planted at densities from 208 sph to 2250 sph (Puri et al., 1994).

From the results of previous trenching, it can be concluded that poplar and willow trees have many thin roots occurring within 0-45 cm soil depth. Several reports have shown that root tensile strength increased with decreasing root diameter (O'Loughlin and Watson, 1979, Bischetti et al., 2005, Genet et al., 2005). This suggests that, in the potential shear line perpendicular to the soil, where tension is one of the main forces promoting soil failure, a greater number of thin roots would be more resistant to soil shear than a few thick roots (Reubens et al., 2007, Danjon et al., 2008, Stokes et al., 2009).

2.3.4.2 Poplar and willow root reinforcement of the potential parallel shear surface in shallow mass movements.

The parallel shear surface is subject not only to tension but also bending as the main stress factors promoting soil slips (Reubens et al., 2007, Stokes et al., 2009). The protection of this line seems to rely more on coarse vertical roots (> 5 mm) like sinker or tap roots that grow within the soil profile and cross the slip shear surface perpendicularly. Under certain circumstances vertical roots

can anchor in firm strata like fissures or cracks in the fragipans or in bedrock, fixing shallow soil layers to firm strata.

The depth of the roots has been determined almost exclusively by time consuming techniques such as excavation of the entire tree root system.

On a semi-arid irrigated plain in India, Puri et al. (1994) recorded the average depth of coarse roots (> 2 mm) at 130 cm in a 9-year-old *P. deltooides* plantation comprising trees spaced at $6\text{ m} \times 6\text{ m}$. Sinker roots were more frequent in the $6\text{ m} \times 6\text{ m}$ spacing than in the $4\text{ m} \times 4\text{ m}$ or $2\text{ m} \times 2\text{ m}$ spacings. In New Zealand, McIvor et al. (2008) found that sinker roots of *P deltooides* \times *nigra* ‘Veronese’ trees aged 5, 7 and 9.5 years extended to depths of 20 to 90 cm. The vertical roots (proximal diameters > 10 mm) penetrated the soil to a maximum depth of about 1.0 m where the fragipan restricted root penetration and promoted the horizontal growth over its surface in a net-like manner to an extent of 40-60 cm.

The position of a tree on a slope can influence root architecture and development. McIvor et al. (2009) observed that vertical roots of 12-year-old *P deltooides* \times *nigra* ‘Veronese’ trees located in shallow soils (0.4-0.8 m depth) in the middle and upper part of a slope penetrated a fragipan. In contrast, roots of trees located lower on the same slope, and those of trees located on the toe of the same slope changed direction horizontally when reaching the fragipan and did not penetrate it (McIvor et al., 2008). According to Danjon et al. (2008), anchorage on firm strata from a slope protection viewpoint seems to be more relevant for trees located in the middle of the slope where the potential parallel shear surface is deeper than in the top or the toe of the slope (Fig 2.2).

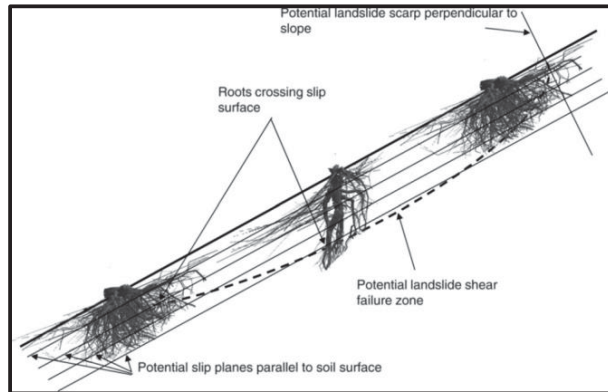


Figure 2.2. Tree root mechanical strength and position on the slope (Danjon et al., 2008)

Conversely, Stokes et al. (2009) suggest that the ability of vertical roots to grow into the bedrock could have an undesirable side effect from a slope protection perspective. While roots generally enhance fixation of soil on slopes, some plant roots anchored and growing into cracks in the bedrock could enlarge them, destabilising the rock and promoting fractures and therefore slope failure (Stokes et al., 2009).

2.4 Implications of management on tree root structure

The ability to grow a fast and extensive root network is one of the main reasons for poplars and willows being used to control soil erosion in the pastoral hill country of New Zealand (Wilkinson, 1999, McIvor et al., 2011a). However, ability to develop a fast and extensive below ground structure is also reflected in the ability to grow and extensive above-ground fraction. Exponential relationship has been found between root mass (R^2 0.95) and root length (R^2 0.96) and DBH of poplar trees aged up to 11 years (McIvor et al., 2009). If the above-ground growth of the trees is not controlled, they can become a nuisance. Irregular multi-branched canopies or large trees are prone to wind damage and their shading of the understorey pasture reduces herbage accumulation (National Poplar and Willow Users Group, 2007). Poplar and willow trees older than 40 to 50 years on steep slopes have reached such dimensions that there is increased risk of their large limbs falling and damaging fences, blocking accesses or water courses, and hurting animals or even humans (National Poplar and Willow Users Group, 2007, McIvor et al., 2011b). There are

additional circumstances, such as current environmental constraints and tree attributes that indirectly favour the practice of regularly managing canopy size. With climate change, extreme climatic events like summer droughts are becoming more frequent and intense (Mackay, 2008, Basher et al., 2012, Porteous and Mullan, 2013). The need for supplementary stock fodder during periods of pasture shortages can be partially overcome with the leaves and thin stems of poplar and willows trees (Wilkinson, 1999, Oppong et al., 2001, Jones and McIvor, 2013). High palatability of poplar and willow foliage for livestock is well known and leaves can provide nutrients above the maintenance requirements for cattle (Kemp et al., 2001, Oppong et al., 2001). Protein content has been found to be in an average of about 13.4% and 16.2% of DM for different willow and poplar species, respectively, (Kemp et al., 2001, Oppong et al., 2001, Kemp et al., 2003). Likewise, dry matter digestibility has been reported to be around 67.5% and 68.3% for different willow and poplar species (Kemp et al., 2001, Oppong et al., 2001, Kemp et al., 2003)

Management of the above-ground part of wide-spaced poplar and willow trees in pastoral systems in New Zealand is conducted mostly by pollarding or pruning (Fig 2.3) (National Poplar and Willow Users Group, 2007). Pollarding is recommended after trees have reached a trunk diameter greater than 30 cm at 1.40m height, which is usually around 8 to 10 years tree age. Standard practice is to remove the total tree canopy above 1.8-2.0 m tree height to prevent cattle reaching the new regrowth shoots (McIvor, 2015). Pruning for conformational or timber purposes implies partial canopy removal and is recommended more for poplar trees, which develop a more natural leader-dominant growing habit than willow trees (National Poplar and Willow Users Group, 2007). Tree age for first pruning varies from 2 to 5 years depending on the site conditions, growth rate of the trees, and the purpose of pruning. First pruning aims to develop a single leader canopy. Subsequent pruning carried out every two years targets a stem clear of branches up to about 50% of the height of the tree, or leaving three years of green canopy. Usually this practice removes a third of the total foliage.

There are only two reports known describing how canopy removal affects root structure of wide-spaced trees on steep erodible slopes in New Zealand hill country. One report is for poplar

(Douglas et al unpublished) and the other for willow (McIvor et al., 2011b). From New Zealand and overseas reports, several factors can be highlighted as modulators of the root response after above-ground intervention, with the most influential being inherent differences between species, time of the year when above-ground disruption occurs, extent of the canopy removal, and soil conditions. These are reviewed henceforth.

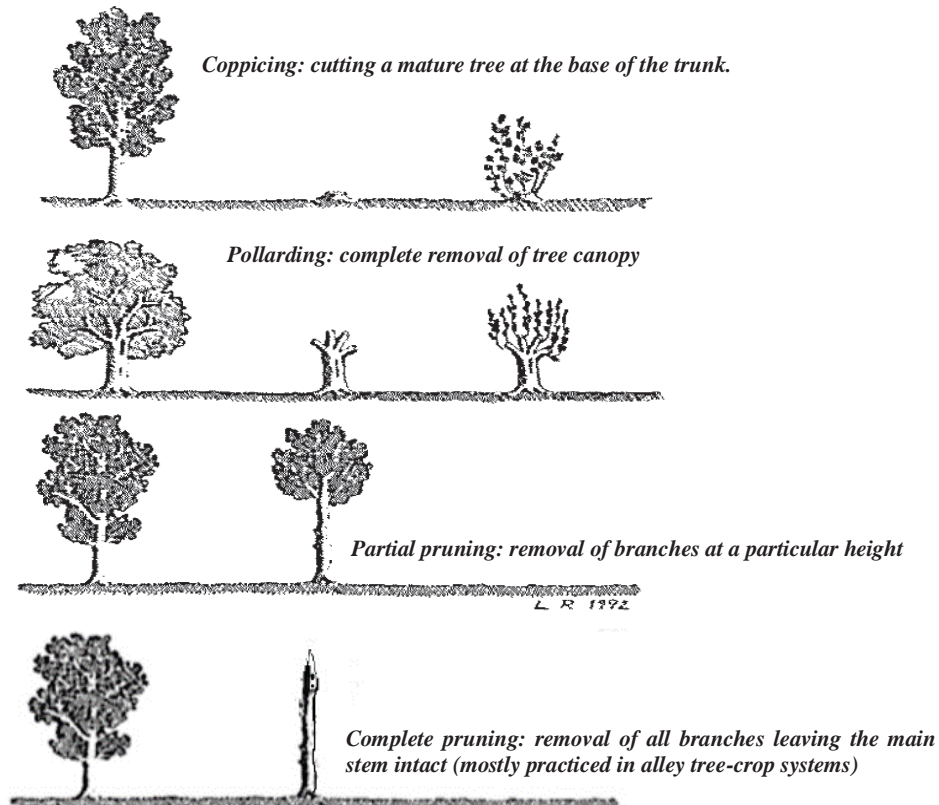


Figure 2.3 Management practices conducted on multipurpose trees. Adapted from Sennerby-Forsse et al. (1992)

2.4.1 Differences between species

Different root responses after total photosynthetic tissue removal have been found between species or clones. Jones et al. (1998) found differences in the root response 60 days after conducting pruning in *Acacia nilotica* and *Prosopis juliflora*. Fine root length density of *A. nilotica* had increased by around 46% whereas that of *P. juliflora* showed a 45% reduction (estimated from figures). One year after coppicing (Fig 2.3) different clones of *Populus × euramericana*, Lee (1994) found that one of the clones (5327) had an increase in root biomass in

the furthest stratum away from tree stem and also in the deepest soil stratum, two clones had increases only in the deepest stratum and one clone had reductions in root biomass in all of the soil strata analysed. Differences between species in root response after above-ground removal have been associated with different strategies and abilities of plant species to restore the root/shoot ratio. Fownes and Anderson (1991) found that coppicing of the slower growing species *Leucaena leucocephala* had a lower impact on root system reduction than on the faster growing *Sesbania sesban*. The differences in the regular growth rate of the seedlings and in the root response after coppicing were attributed to a greater C allocation pattern of *L. leucocephala* to its below-ground fraction, especially the coarse roots, and particularly the tap root (possibly a storage organ). Potentially lower allocation to below-ground storage tissue may explain the greater sensitivity of *S. sesban* to coppicing. Richards (1984) reported different C allocation strategies after herbivory of bunchgrasses with different grazing tolerances. The grazing-tolerant bunchgrass *Agropyron desertorum* allocated more C to shoot restoration immediately after herbivory than the grazing-sensitive species of *A. spicatum*. Grazing-tolerant species had a greater reduction in root length after severe defoliation than *A. spicatum*. However, in the next growing season *A. desertorum* maintained a larger root system than the lower grazing-tolerant species (Richards, 1984). Preferential allocation of C for root growth after defoliation instead of for development of photosynthetic tissue could reduce accumulation of carbohydrates by the end of the growing season, resulting in greater root mortality in the following season.

Differences between species in the organ C source for shoot restoration have also been reported. After partial and complete pruning (Fig 2.3), *E. poeppigiana* mobilised starch preferentially from stems rather than from roots (Chesney and Vasquez, 2007). In contrast, both stems and roots of *Gliricidia sepium* provided energy for shoot restoration (Chesney and Vasquez, 2007). Additional factors must influence the organ C source after above-ground disruption because Erdmann et al. (1993) observed stem starch mobilisation but not root starch mobilisation in *Gliricidia sepium* trees that were coppiced four times at 3-weekly intervals.

2.4.2 Extent of the above-ground disruption.

Following complete canopy removal, regrowth of new shoots and leaves relies on energy reserves stored in the remnant structures. According to Landhäusser and Loeffers (2003), during usual environmental growing conditions, roots are the last organ to replenish C reserves behind canopy tissues such as twigs and branches. The latter is particularly critical when trees experience prolonged conditions of low C assimilation such as during shading, drought or defoliation (Marshall and Waring, 1985, Landhäusser and Loeffers, 2012). If low C assimilation conditions persist and root reserves fall below a critical threshold, loss of fine roots is expected (Landhäusser and Loeffers, 2012).

Although there is a lack of direct evidence on the impact of different intensities of canopy removal on root responses, some insights can be drawn from non-structural carbohydrates (NSC) dynamics observed in plants defoliated to varying extents.

In short rotation forestry systems where coppicing is conducted, resprouting depends on the C reserves stored in the remnant stump and root structure. Ten days after decapitation, remnant stems of *Populus maximowiczii* × *nigra* L. ‘MN9’ plants reduced starch concentrations to about half of those found in intact plants (Tschaplinski and Blake, 1994), whereas 50% defoliation of similarly developed plants did not reduce stem starch concentration in comparison with intact plants (Tschaplinski and Blake, 1994). However, stem sucrose concentration was reduced in all treatments and a decline of 75% in root sucrose concentration was accompanied by an increase in concentration of glucose and fructose (Tschaplinski and Blake, 1994). Tschaplinski and Blake (1989) observed that decapitation increased net photosynthetic rate of remaining leaves (6% of total leaf area) in *Populus maximowiczii* × *nigra* L. ‘MN9’ plants. Chesney and Vasquez (2007) found during the dry season that complete pruned *Gliricidia sepium* trees mobilised greater root starch reserves than partial or unpruned trees. The lowest stem starch concentrations and lowest fine root lengths were observed in partial and complete pruned *Erythrina poeppigiana* trees, in comparison to unpruned trees (Chesney and Vasquez, 2007).

2.4.3 Above-ground removal and time of the year

A number of reports describe similar seasonal trends for non-structural carbohydrates stored and mobilised from organs such as branches, stems and roots of temperate, deciduous trees.

Before bud break there are several processes such as fine root appearance, bud swelling, and flowering or fruit development in some species that are enabled because of the non-structural carbohydrates mobilised from reserves accumulated at the end of the previous growing season (McCamant and Loescher, 1988, Loescher et al., 1990, Kozlowski, 1992). Mobilisation of NSC in late winter and early spring has been shown when starch concentration decreases at bud swelling from canopy and root phloem and xylem cells, and soluble sugar concentrations increase in the xylem sapwood and developing tissues such as sprouting buds and leaves unfolding (Essiamah and Eschrich, 1985, Sennerby-Forsse and von Fircks, 1987, Von Fircks and Sennerby-Forsse, 1998). Once the first leaves produced become photosynthate exporters, starch reserves begin gradually replenishing (Bonicelet al., 1987, Von Fircks and Sennerby-Forsse, 1998). The end of shoot elongation and bud set are the phenomena commonly reported when starch reserves increase sharply and reach a maximum by mid to late fall (Dickson and Nelson, 1982, Isebrands and Nelson, 1983, Nguyen et al., 1990, Dickmann and Pregitzer, 1992). During winter, as a mechanism for frost tissue protection, some species show starch dissolution and a build-up of sugar concentrations (Essiamah and Eschrich, 1985, Marshall and Waring, 1985, Kozlowski, 1992).

The regular seasonal NSC dynamics in deciduous tree storage organs was the focus of special attention 30 to 40 years ago in short rotation forestry systems (SRFS) (Strong and Zavitkovski, 1983, Dickmann and Pregitzer, 1992). Within SRFS, where coppicing is the harvesting method, there was interest in knowing the best time for harvesting without compromising resprouting and following harvests. Studies showed that greater shoot biomass was produced when coppiced plants were harvested during the dormant phase than during early spring (Strong and Zavitkovski, 1983, Blake, 1983, Fitzgerald and Hoddinott, 1983). This was because of the greater C reserves

status of the plants during dormancy than at any other time during the growing season (Dickmann and Pregitzer, 1992).

Pollarding mature trees located on steep slopes is a difficult and expensive task and there are risks to safety. Pollarding of wide-space planted poplar and willow trees is confined mostly to summer droughts when providing livestock fodder justifies the labour and cost involved. There is some evidence that root and shoot regrowth could benefit from total canopy removal when trees are dormant. Dickmann et al. (1996) observed increases in fine root length immediately after coppicing when poplar clones *Populus × euramericana* cv. 'Eugenei' and *Populus tristis* Fisch × *Populus balsamifera* L. cv. 'Tristis1' were still dormant. Trees of the 'Eugenei' clone showed sustained increases in fine root length during the first year after coppicing. Dickmann et al. (1996) proposed that increases in fine root length might have been because dormant poplar roots contained high concentrations of stored carbohydrates and nitrogen necessary to fuel early season root growth, and an initial growth of coppice shoots.

Studies conducted in New Zealand pastoral hill country have shown a negative impact on root structure when willow trees were pollarded in summer (McIvor et al., 2011b) and when poplar trees were pollarded when they were dormant (Douglas et al. unpublished data). After willow trees were pollarded, McIvor et al. (2011b) observed about 50% immediate reduction in fine root (< 2 mm diameter) length density when compared with before pollarding. It took 3 years for fine root length density to attain that of unpollarded trees (McIvor et al., 2011b).

Four years after pollarding 8-year-old poplar trees when they were dormant, Douglas et al (unpublished data) found that mean root mass of coarse roots (> 2mm diameter) of pollarded trees was less than half that of unpollarded control trees but was similar to mass before pollarding. Coarse root length of pollarded trees was also less than half that observed in unpollarded trees and slightly less (8%) than pre-pollarding coarse root length 4 years earlier (Douglas et al unpublished). Data from Dickmann et al. (1996), McIvor et al. (2011b) and unpublished data of Douglas et al. suggest that there must be factors additional to phenological status of trees at canopy removal, that influence root responses.

2.4.4 Soil fertility and moisture conditions where trees resprout after above-ground disruption.

Different cultural practices and soil moisture conditions have been found to influence root responses after total canopy removal. Trees of *P. trichocarpa* × *deltoides* clone ‘Beaupre’ under a 1- and 3-year rotation of coppicing and intensive cultural practice (plastic mulch, weeding between rows, fertilization) showed increases around 23 and 33%, respectively, in fine root production one year after coppicing, whereas trees under extensive cultivation (no weed control, no fertilization) had a 20% decrease in fine root production (Bedenau and Pages, 1984).

Greater water inputs were recommended by Lee (1994) when a set of *Populus* × *euramericana* clones growing under frequent irrigation increases their root dry mass in a 38% one year after coppicing in comparison to trees growing under less frequent irrigation which showed a 35% decrease in their root dry mass.

The influence of slope position on root growth and development of hybrid poplar (*Populus deltoides* × *P. nigra* L.) clone ‘Veronese’ trees aged 11.5 years was shown by McIvor et al. (2009). A tree growing on a lower position on a slope with an angle of 21.8° (accumulation zone for soil that has slipped off a higher position on the slope (upper slope)) had a coarse root mass of 81.35 kg, 10 times greater than that of a tree at the upper slope (32.0°) and twice that for a tree at a mid-slope position on the same slope (28.6°). The proportional difference in root length was smaller, with the tree at the lower slope having 5.9 and 1.5 times greater root length than the trees at the upper and mid-slope positions, respectively (McIvor et al., 2009).

The influence of soil conditions on root development was shown by McIvor and Arnold (2013) for a 3-year-old *Salix matsudana* × *alba* ‘Tangoio’ tree planted as a pole growing in a free-draining, sandy brown soil on a flat site in the Gisborne region. McIvor and Arnold (2013) found that values for above- and below-ground attributes of stump diameter (36 cm), diameter at breast height (33 cm), length of roots >1 mm diameter (2689 m) and dry root mass (14.99 kg) were similar to those reached for willow trees established from poles on pastoral hill slopes after 12-15 years of growth.

2.5 Implications of tree management on responses of the pasture understorey.

Research on the nature and magnitude of the pasture-tree relationship has shown that the presence of trees within paddocks reduces understorey pasture accumulation (Miller et al., 1996, Douglas et al., 2006a, Guevara-Escobar et al., 2007, Devkota et al., 2009, Wall et al., 2010). Reduced light transmission because of interception by the tree canopy is one of the main factors limiting herbage accumulation (Guevara-Escobar et al., 2000, McElwee and Knowles, 2000, Wall et al., 2006, Guevara-Escobar et al., 2007). Decreases in pasture production beneath trees relative to those at sites away from direct tree influence, are within a wide range from non-significant reductions (Gilchrist et al., 1993, Douglas et al., 2001, Guevara-Escobar et al., 2007) to decreases of 40-50% (Wall, 2006, Wall et al., 2006, Guevara-Escobar et al., 2007). This wide range reflects variation in experimental methodology but mainly differences in tree size or age and tree stand densities evaluated. Canopy closure, defined as the percentage of shaded points under a canopy, represents a measure that can account for both tree size and tree stand density (Benavides et al., 2009). One of the main findings in the pasture-tree systems is the acknowledgement that within a theoretical evenly spaced arrangement of trees, there are two main overstorey environments creating in turn two main microenvironments where the understorey herbage component responds with different growth rates (Devkota et al., 2001, Wall, 2006). With trees arranged in a square pattern, the two main overstorey environments are the area directly beneath the vertical projection of the trees' canopy at each of the four corners of the square, and the canopy gap between the tree canopies of the four trees (Fig 2.3).

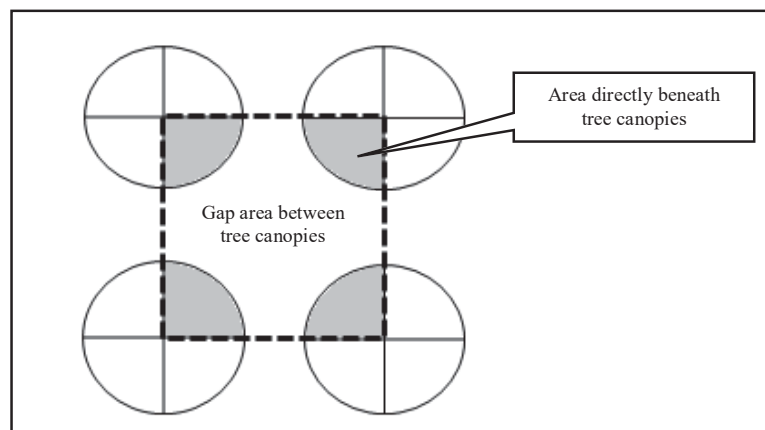


Figure 2.4 The two main overstorey environments in a theoretical arrangement of trees in a square grid pattern.

Devkota et al. (2001) and Wall (2006) found that pasture production beneath the vertical tree canopy projection rapidly decreases to half that produced in open pasture sites, when canopy closure increases from 0% (open pasture sites) to low canopy closure percentages of around 20%. Reductions in pasture production directly beneath the tree canopy remains relatively constant despite of canopy closure increases beyond 20% (Wall, 2006). In contrast, pasture production in the canopy gap between four trees shows a slower and more linear decrease at a reduction of 6.6% in pasture production for each 10% increase in canopy closure (Wall, 2006). Practical implications of the findings of Devkota et al. (2001) and Wall (2006) are that whereas little can be done to reduce the impact of overstorey shade directly below the tree canopy, the area of the gap between the tree canopies can be managed to increase accumulation of understorey herbage growing within this zone (Fig 2.3). Thinning, pruning or pollarding represent strategies to maintain or widen the gap area between adjacent tree canopies trees (Douglas et al., 2013b). Whereas thinning is conducted mostly in the early stages of establishment of the wide-spaced trees, pruning and pollarding can be conducted to maintain the pasture-tree system in the long-term (National Poplar and Willow Users Group, 2007, McIvor, 2015). Some hill country farmers in New Zealand report that they have pollarded some trees every 3 or 4 years for more than 20 years without any apparent detriment to resprouting ability or soil protective function (Olsen and Charlton, 2003, National Poplar and Willow Users Group, 2007). Partial or total tree canopy removal is a common practice in alley tree-crop systems (Nair, 1993, Reynolds et al., 2007). Immediate and temporary production increases in the accompanying crops have been reported after pruning or pollarding the trees (Sande, 2003, Thevathasan and Gordon, 2004). Production of beans grown in combination with trees of *Grevillea robusta* increased 189% and 178% in the first and second seasons, respectively, after the trees were pollarded, compared to bean crops grown with unpollarded trees (Sande, 2003). Two to five weeks after pruning and incorporating the mulch of *Erythrina poeppigiana* trees to alley-cropped beans, bean yield was 15-50% greater than in bean

crops without trees (Henriksen et al., 2002). Whereas benefits to pasture production are expected from increasing the gap size between tree canopies, pruning and pollarding are periodical management practices and fluctuations in pasture production and botanical composition are to be expected within the rotation timeframe.

2.6 Conclusions

The literature review showed the role of the structural and fine roots extending across the soil for the maintenance of the slope stability.

It was determined that pressure on the root system will be greater as above-ground removal is more intense or destructive.

After coppicing, pollarding represents the second most destructive practice in terms of the above-ground fraction removed (Fig 2.3).

There are reports showing that even after coppicing, remnants of the tree can keep elongating and producing more roots than observed before intervention. However, it was shown in the review, that most of the studies reporting no disruption of the root structure after severe above-ground removal, argued favourable environmental conditions (soil moisture and fertility) before, during and after the removal of the above-ground part. Irrigation, weeding, fertilising and plastic mulch have been some of the practices associated with increases in the root structure after coppicing.

Strong influence of soil environmental conditions (fertility and moisture holding capacity) on root development of poplar trees were described in Section 2.4.4.

Coppicing is mostly practiced in short rotation forestry systems where high levels of woody biomass production are aimed for the high valued pulp, board or energy industry. For these industries high input cultural practices are in general, cost permissive. However, in practical pastoral hill country conditions, farmers are unlikely to implement any cultural management aimed specifically to promote tree development. Therefore, research on the impact of pollarding in the root structure of mature wide-space planted willow and poplar trees, is limited to characterising the direction and magnitude in time and space of the changes in the root structure after above-ground removal.

Notwithstanding the limitations, literature review also show there are some low-input strategies that may be successful in the pasture-tree systems in New Zealand, such as pollarding the trees in the dormant stage, instead of mid summer/early autumn droughts as it is commonly practiced

when trees are at a challenging time in terms of C stored reserves. In any case, precise knowledge of the root response after pollarding is necessary to define a canopy management program able to address issues like how many trees pollard at a time, or how often repollard a tree, all aspects aimed to ensure the stability of the slope.

From review done in the implications of above-ground tree removal on understorey herbage accumulation, seems obvious that immediate to and during the first year after pollarding, understorey herbage accumulation around the trees would increase rapidly and attain a level similar to that of open pasture. However it is important to establish how pollarding might impact pasture production on a stand level and how the herbage accumulation dynamics behave, as pollarded trees start recovering above-ground features similar to same age unpollarded trees.

2.7 References

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Chapter 3. Root response and carbohydrate dynamics of willow trees pollarded at different phenological stages.

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3.1 Summary

Pollarding space-planted willow trees in hill pastoral land of New Zealand is mainly conducted during summer or early autumn when pastures decline in quantity and quality because of low soil moisture conditions. Providing edible foliage for stock and diminishing the risk for tree fungal infections are among the main reasons favouring pollarding during or towards the end of the growing season. However, evidence derived from short rotation forestry systems suggests pollarding at the end of the dormancy stage might have a less impact on the remaining structures (stem and roots) as these would be in a better physiological status to provide photosynthates required at early resprouting. This study tested the null hypothesis that fine root length density (fRLD) and fine root mass density (fRMD) dynamics of dormant pollarded trees (DP) were not different to trees pollarded at the end of the growing season in early autumn (AP). Fine root density (fRD) dynamics of pollarded trees (DP and AP) were also contrasted with the dynamics observed in unpollarded (UP) or control trees. Fine root dynamics after pollarding were evaluated using the sequential soil coring technique. Root non-structural carbohydrate dynamics for pollarded and UP trees were also compared. In comparison to UP trees, dormant pollarding had the main impact in the fR located close to the tree trunks and above 300 mm soil depth. One year after pollarding at those soil sections, fRD of DP trees was around half that in UP trees and similar to the fRD recorded immediately before pollarding. Within the time frame evaluated, fRD dynamics following dormant pollarding did not show substantial differences to the fRD dynamics following late summer pollarding of wide-spaced mature willow trees reported in a previous study. It is recommended to evaluate in a longer-term the recovery potential of the roots located above 300 mm soil depth, where the root structure following dormant pollarding was most disrupted. Root non-structural carbohydrates changes observed suggest root energy reserves of DP trees were supporting above- and below-ground synthesis processes related to shoot resprouting and new root production. Replenishment of root starch concentrations of DP trees that occurred within the first growing season after pollarding was similar to that for UP trees.

The main impact in the roots following early autumn pollarding was located in the top 150 mm of soil where annual average fRD recovery of AP was greater than annual average fRD recorded in UP trees. In contrast to UP and data reported from late summer pollarded willow trees in pastoral hill country, AP trees in this study above 150 mm soil depth maintained through dormancy, the maximum fRD reached during the growing season immediate before pollarding. Soil temperature and moisture conditions and pollarding timing differences during the year were adduced as the most likely reasons influencing root response observed in AP trees. During the 2012-2013 growing season, from late winter to early autumn, UP and AP trees showed decreasing fRD values which were attributed to a significant drought experienced in that year. Root starch significantly lower concentrations in AP trees than in the roots of UP and DP trees observed during the 2012-2013 growing season, suggest roots of AP trees were under a greater demand for supplying photosynthates than roots of UP and DP trees.

Apart from the root sections where dormant pollarding showed the main impact (40 cm from the tree trunk above 300 mm soil depth), annual average fRD recovery observed in DP trees at all other soil depths and distances from the tree trunk, was consistently greater than fRD recovery recorded for AP trees. However, differences observed in fRD recovery between DP and AP trees were mostly attributed to record moisture restrictions during the remainder of the growing season following early autumn pollarding, rather than the effect of pollarding at early autumn.

3.2 Introduction

Research and management of willow and poplar pasture-tree systems in New Zealand is being currently driven by the convergence of the following three main considerations: 1) the need to control the size of the trees. 2) adaptation to climate change and, 3) the nutritive value of fodder of poplar and willow trees.

With climate change an increase in the frequency, intensity and length of summer droughts is predicted, with farmers struggling to feed their stock during late summer and autumn (Basher et al., 2012, Porteous and Mullan, 2013). The need for supplementary fodder can be partially overcome with the foliage of willow and poplar trees which have been shown to provide energy and nutrients above maintenance requirements for sheep and beef cattle (Oppong et al., 2001, Kemp et al., 2001). Willow foliage can be harvested by pollarding and fed *in situ* at some point during summer or early autumn (Olsen and Charlton, 2003, National Poplar and Willow Users Group, 2007, McIvor, 2015). Regular pollarding to provide fodder can be used to control the size of the trees. Willow and poplar pasture-tree systems in New Zealand are a particular system where the main contribution or most important functional resource of the trees is found below-ground (Wilkinson, 1999, Douglas et al., 2013). Fine and structural roots of willow and poplar trees extending laterally and vertically into the soil structurally reinforces the soil in a similar way as the steel mesh in concrete, allowing the soil to resist forces causing shallow landslides (Gray and Sotir, 1996, Hicks et al., 2001). Pollarding, the total removal of the tree canopy at a 1.8 to 2.0 meter height above-ground is expected to affect the remaining structures (trunk and roots), as these supply photosynthates for the initial shoot regrowth (Dickmann and Pregitzer, 1992, Luostarinen and Kauppi, 2005, Chesney, 2012). Any management practice conducted on the trees must aim for the long-term sustainability of the root structure. For practical reasons pollarding of willows in the pasture-tree systems in New Zealand is conducted mostly from late summer to early autumn (National Poplar and Willow Users Group, 2007, McIvor, 2015). However, there are evidences suggesting that from the perspective of tree physiology, pollarding late in the growing season might not be the best time for above-ground disruption. At this stage the trunk

and roots (remaining structures after pollarding) are replenishing carbohydrate reserves after the depletion resulting from bud swelling, flowering, leaf flush and general related growing processes during spring and summer (McCamant and Loescher, 1988, Nguyen et al., 1990, Loescher et al., 1990). There is some evidence showing that pollarding could have a much lesser impact on the remaining structures if canopy removal is practiced when plants are dormant. At dormancy tree stem and roots have, under regular conditions, their highest levels of non-structural carbohydrate reserves to support the initial resprouting activity (Nguyen et al., 1990, Dickmann and Pregitzer, 1992, Dickmann et al., 1996).

Pollarding at dormancy should show clear advantages over pollarding in summer in terms of sustaining root structure integrity. Based on the fine root structure recovery observed in mature willow trees after summer pollarding, Beeden and McIvor (2010), and McIvor et al. (2011) proposed pollarding cycles of 3 to 4 years. By reducing the impact on the tree root structure integrity dormancy pollarding could shorten the pollarding rotations. Shorter pollarding cycles than 3 to 4 years might be reflected in increases in light transmission through tree canopy gaps and thus in increases in understorey herbage accumulation.

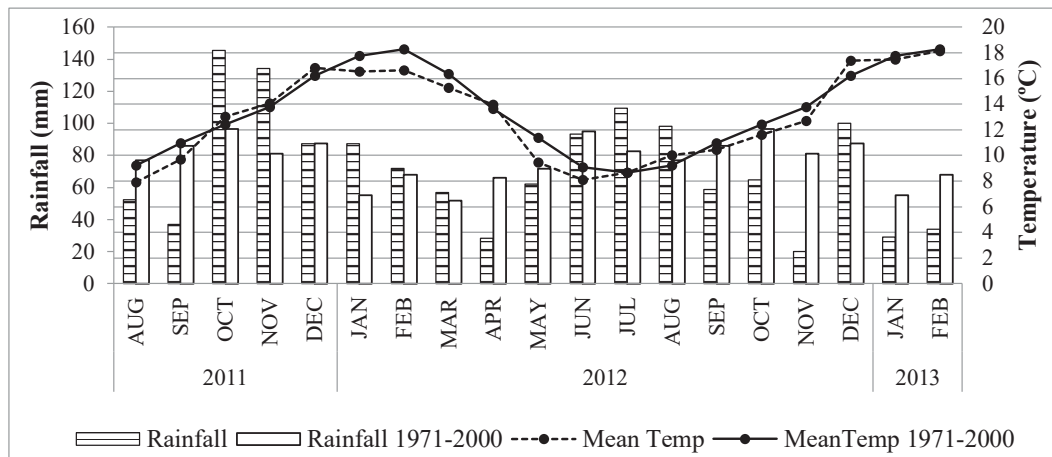
With all the above in mind, the main objective in this study was to determine the impact in the root structure of willow trees pollarded at the two different phenological stages, dormancy and towards the end of the growing season, and to gain understanding of the physiological changes in the root system following pollarding, root non-structural carbohydrate dynamics were also studied.

3.3 Materials and Methods

3.3.1 Site description

This study was carried out at Moginie Pasture and Crop Research Unit at Massey University, Palmerston North (40.4°S, 175.6°E). The soil type is a Tokomaru silt loam. The experiment was conducted from late winter 2011 to late summer 2013. Rainfall and temperature data for the study area were obtained from the AgResearch Palmerston North weather station located no further than 5 km from the study area, and long-term averages from meteorological records supplied by NIWA (National Institute of Water and Atmospheric Research) (Fig 3.1).

Figure 3.1 Temperature and rainfall data for Moginie site during the study



The willow plantation was established in 2004 from unrooted stakes of *Salix matsudana* Koidz. x *alba* L. ‘Tangoio’, and the trees were divided into three separated plots surrounded by open pasture and/or poplar stands (Fig 3.3). The stakes were planted in a square grid pattern (1.2 m × 1.2 m spacing) in six rows of ten stakes each. At the beginning of the study in late August 2011 trees were on average 9.2 m tall and 10.2 cm diameter at breast height (DBH measured at 1.4 m from the ground).

3.3.2 Experimental design and treatments

In order to compare the effect on root structures and on root non-structural carbohydrates dynamics of pollarding at two different phenological stages, a randomized complete block design (Fig 3.3) was set with three blocks and three treatments replicated three times. The treatments were: trees pollarded at the end of the dormancy season (DP) in late winter (28 August 2011), trees pollarded towards the end of the growing season in early autumn (AP) (7 March 2012), and or unpollarded control trees (UP). The trees were pollarded with a chainsaw at 2 m height (Fig 3.2), as usually practised by farmers to prevent cattle reaching new regrowth shoots (Wilkinson, 1999, National Poplar and Willow Users Group, 2007).



Figure 3.2 Unpollarded and pollarded willow trees

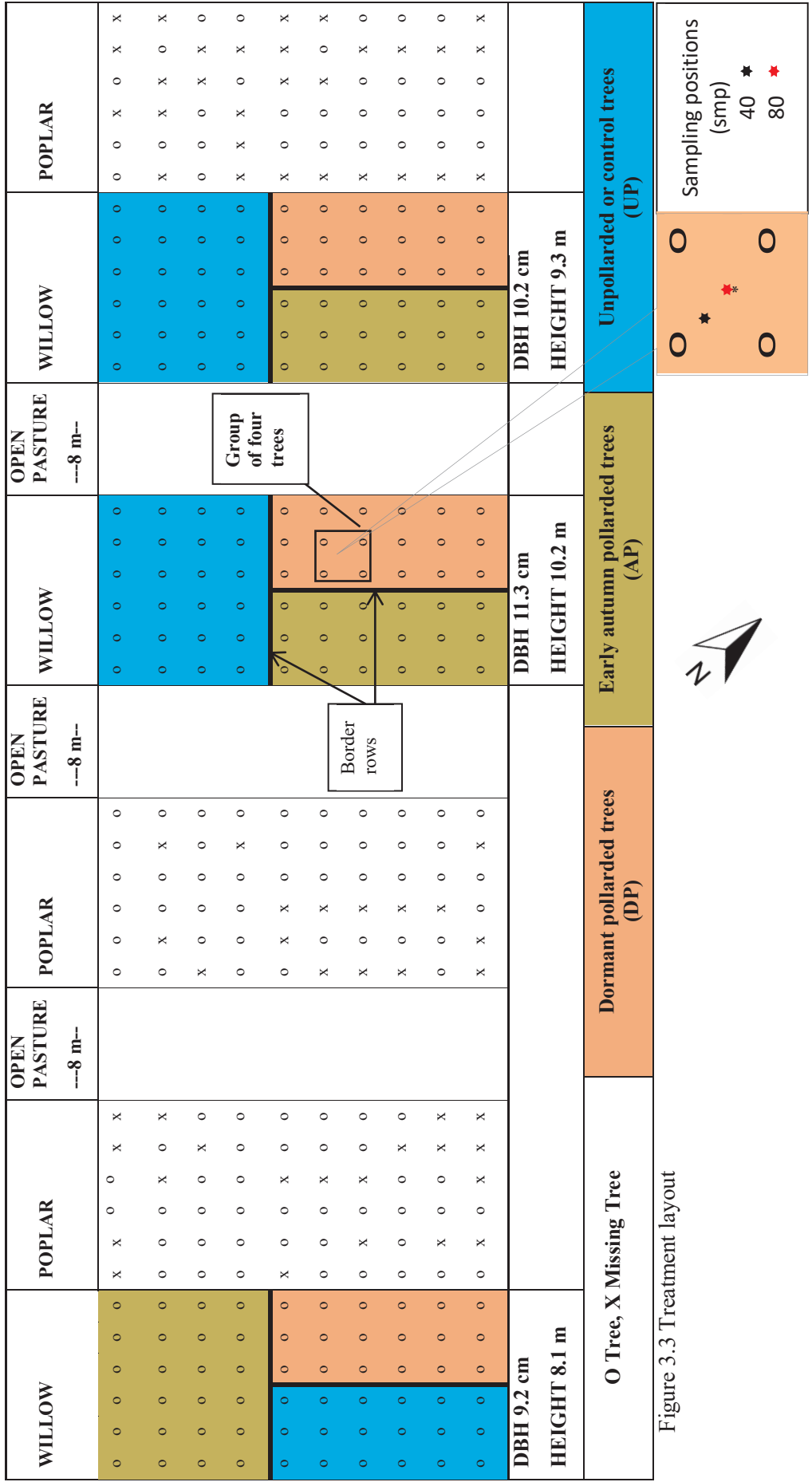


Figure 3.3 Treatment layout

3.3.3 Variables analysed

3.3.3.1 Root density (RD) dynamics

Root response after pollarding at different phenological phases was measured through changes over the time in root length density (m m^{-3}) and root mass density (kg m^{-3}).

Roots of the DP treatment were sampled 3 to 2 days before pollarding, and approximately 1, 3, 6, 8 and 12 months after dormant pollarding (maDP) (Table 3.1). Apart for the 3rd month after early autumn pollarding (maAP), AP trees were monitored approximately within the same periodicity as DP ones. AP were not sampled 3 maAP as this would have fallen within the same season (winter) as the 6th maAP sampling and no great changes were expected.

Several reports show minimum changes in fRD during dormancy (Hendrick and Pregitzer, 1993, Rytter and Hansson, 1996, Kern et al., 2004). During that time, fRD of both AP and DP trees showed relatively steady trends (Fig 3.10a, d and 3.11 a, d). Based on those trends, it was decided to take the average of the sampling periods 1 (autumn 2012) and 6 months (late winter 2012) after early autumn pollarding to fill the missed sampling period of the 3rd maAP (Fig 3.5A-C). UP trees were sampled at the same dates as DP and AP. Season and exact dates for sampling times are shown in Table 3.2.

Coring was employed to obtain root samples using a steel corer of 8 cm internal diameter (Böhm, 1979). For each sampling time at each replicate, two sampling positions (smp) were bored within a randomly chosen group of four trees (Fig 3.3). One sample was collected at the point where the diagonal transects between the four trees intersected, approximately 85 cm from tree stems. The other sample was taken at half the distance between location of the first sample and any randomly chosen stem in the group of four trees, approximately 43 cm from the chosen stem. Henceforth, and for ease of reading, smp at 85 cm from any tree trunk and at 43 cm from a particular tree trunk, will be referred to as 80 smp and 40 smp, respectively (Fig 3.3). There was a border row between treatment plots where root sampling was not carried out (Fig 3.3).

Table 3.1 Sampling periods after pollarding

Year	2011			2012					2013
Season	Late Winter (LW) (28 Aug)	Early Spring (ESp) (22 Sep)	Late Spring (LSp) (15 Nov)	Late Summer (LSm) (24 Feb)	Early Autumn (EA) (7 Mar)	Mid Autumn (MA) (18 Apr)	Late Winter (LW) (24 Aug)	Late Spring (LSp) (19 Nov)	Late Summer (LSm) (26 Feb)
Treatments									
DP	Pollarding 0 ^a	1	3	6		8	12		
AP					Pollarding 10 ^b	<i>/1</i>	<i>/6</i>	<i>/8</i>	<i>/12</i>
UP	0	1	3	6/0		8/1	12/6	/8	/12

Treatments: DP Dormant pollarded trees. AP Early autumn pollarded trees. UP Unpollarded or control trees

a) Numbers indicate approximate months after dormant pollarding (maDP)

b) Numbers in bold italic style after slash indicate approximate months after early autumn pollarding (maAP)

To determine the sampling depth for coring, a trench was excavated next to two trees in the left upper border of each plot (Fig 3.4). The trenches were dug 0.60 m away from the trees to 1 m depth and extended 0.60 m either side of tree trunks. Willow roots were counted using a 120 long x 90 cm deep steel mesh comprising 6 rows, each 15 cm deep (Fig 3.4).

Average root distribution from trenching is shown in Table 3.2. More than 95% of the roots were found in the top 450 mm of soil depth and no roots were found below 750 mm. Fine roots (roots with a diameter ≤ 2 mm) comprised the greatest percentage of counted roots representing more than 80% of the total root count.

The trenching data coincided with trends previously reported for willow (Crow and Houston, 2004) and poplar (Douglas et al., 2010, Bouttier et al., 2014) trees, where more than 75% of the roots were found in the topsoil, with fine roots contributing more than 70% of the total counted roots.

Table 3.2 Willow root vertical profile distribution obtained by trenching (average of six trees)

Section depth (mm)	Number of roots m ² at each diameter category and soil depth						Total	% Total
	Very fine (0 \leq 1mm)	Fine (>1 \leq 2mm)	Small (>2 \leq 5mm)	Medium (>5 \leq 10mm)	Large (>10 \leq 20mm)	Very large (>20mm)		
0-150	120	6	7	4	3	1	142	67
0-300	159	9	9	6	4	1	189	89
0-450	171	9	11*	7*	5*	2*	205	97
0-600	175	9	11	7	5	2	210	99
0-750	176*	10*	11	7	5	2	212	100
0-900	176	10	11	7	5	2	212	100
% Total	83	5	5	4	2	1		

*No additional roots observed in deeper sections

Based on the trenching data it was decided to set the sampling depth to 450 mm. At every sampling time and smp a subsample was taken in 150 mm increments to 450 mm depth. Notations such as 40/150-300 and 80/0-150 will be used henceforth to indicate subsampling positions. 40/150-300 means the subsampling position in the 40 smp at 150-300 mm depth.

After sampling, soil cores were placed in sealed plastic bags, labelled, and stored at 4°C until washing. The samples were washed under a jet water tap and the roots were recovered using a 1 mm sieve. Dead roots (black colour and/or snapping when bent) were discarded. After recovery the roots were squeezed by hand and preserved in 70% ethanol in plastic tubes until measurement for length and mass.

WILLOW	POPLAR	OPEN PASTURE ---8 m---	POPLAR	OPEN PASTURE ---8 m---	WILLOW	OPEN PASTURE ---8 m---	WILLOW	OPEN PASTURE ---8 m---	WILLOW	POPLAR	OPEN PASTURE ---8 m---	WILLOW	POPLAR	WILLOW	POPLAR
O O O O O	X X O O X		O O O O O		O O O O O		O O O O O		O O O O O	O O O O X		O O O O O	O O O O X	O O O O O	O O O O X
O O O O O	O O O X O		O X O O X		O O O O O		O O O O O		O O O O O	O O O O X		O O O O O	O O O O X	O O O O O	O O O O X
O O O O O	O O O O X		X O O O O		O O O O O		O O O O O		O O O O O	O O O O O		O O O O O	O O O O O	O O O O O	O O O O X
O O O O O	O O O O O		O O O O X		O O O O O		O O O O O		O O O O O	O O O O O		O O O O O	O O O O O	O O O O O	O O O O X
O O O O O	X O O X O		O X X O O		O O O O O		O O O O O		O O O O O	O O O O O		O O O O O	O O O O O	O O O O O	O O O O X
O O O O O	O O O O O		X O X O O		O O O O O		O O O O O		O O O O O	O O O O O		O O O O O	O O O O O	O O O O O	O O O O X
O O O O O	O O O X O		X O X O O		O O O O O		O O O O O		O O O O O	O O O O O		O O O O O	O O O O O	O O O O O	O O O O X
O O O O O	O O O O X		O O X O O		O O O O O		O O O O O		O O O O O	O O O O O		O O O O O	O O O O O	O O O O O	O O O O X
O O O O O	O O O O O		X X O O X		O O O O O		O O O O O		O O O O O	O O O O O		O O O O O	O O O O O	O O O O O	O O O O X

O Tree, X Missing Tree

DP trees					AP trees					UP or control trees									
O	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X
O	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X
O	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X
O	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X
O	O	O	O	X	O	O	O	O	O	O	O	O	O	O	O	O	O	O	X

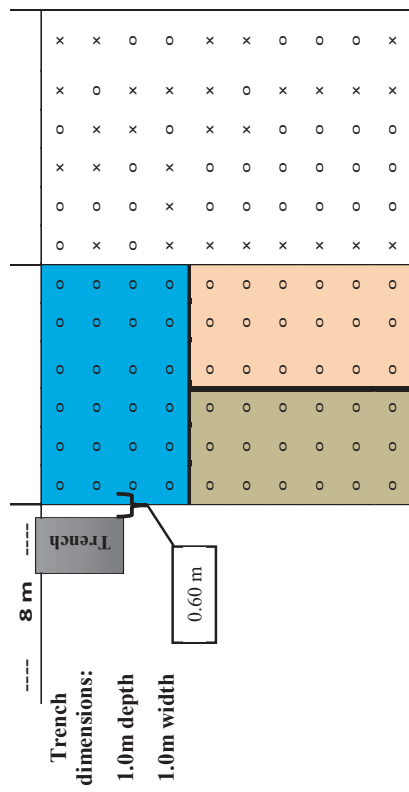
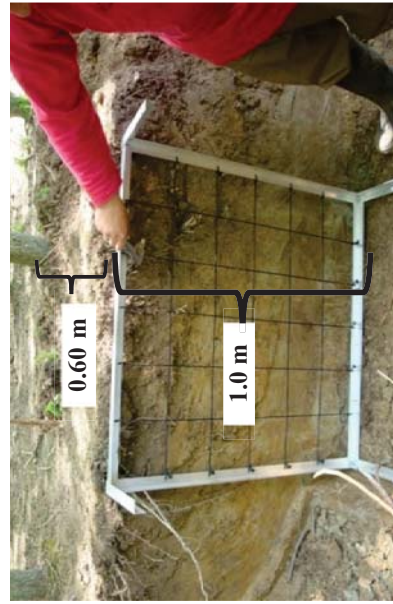


Figure 3.4 Trenching work carried out to determine the coring depth

3.3.3.1.1 Root length density (RLD m m^{-3}) dynamics.

Preserved roots were rinsed, dried with paper towel, trimmed and spread on a crystal tray for scanning with a scanner (EPSON STD4800) equipped with a special dual scan light system.

With large samples, mostly those from the 0-150 mm soil depth, a subsampling process was carried out. All roots thicker than 1 mm diameter were scanned, whereas for roots thinner than 1 mm diameter about 20% of the sample was scanned. The remaining 80% was kept, dried for 48 hrs at 75°C and weighed. After scanning, the 20% subsample was dried and weighed. Total root length was then calculated on a weight-length proportion basis between the 20% subsample and the dry mass of the 80% remainder.

For the measurement of root length, images of the roots were analysed with WinRHIZO software (Regent Instruments Inc, 2012). The software was set up to sort root length into two main root diameter categories, fine roots (fR) (≤ 2 mm) and coarse roots (cR) (> 2 mm).

3.3.3.1.2 Root mass density (RMD kg m^{-3}) dynamics.

Once roots were scanned they were kept in paper bags according to their diameter category and oven dried at 75°C until constant weight, to determine their root mass.

3.3.3.2 Root carbohydrate dynamics.

Concentrations of non-structural root carbohydrates at different phenological stages were measured, and changes resulting from pollarding were determined.

The roots were sampled 60 cm from any tree trunk within the group of four trees sampled for RLD and RMD analysis, with the same sampling technique and depth (0-450mm) as described in Section 3.3.3.1. Only fine roots < 2 mm diameter were included in the analysis

Sampling times for the DP treatment were 3 days before pollarding, and 1, 6, 8, 12 and 15 months after pollarding. Apart for the 12th and 15th month after pollarding, roots in the AP treatment were sampled within the same time periodicity as the DP treatment. Root samples for UP trees were also collected at the same sampling times as those in the DP and AP treatments.

At sampling, after removing the monolith from the corer, the samples were placed in plastic bags, labelled and stored on ice for later washing and root recovery. After washing soil off the roots, they were hand squeezed and placed in plastic air-tight bags for storage at -20°C until laboratory analysis. The time between sampling and placement in the freezer was about 8 hrs.

Before laboratory analysis the frozen roots were freeze-dried (drum freeze dryer, Cuddon Ltd, New Zealand) and ground sufficiently with a Wiley mill to pass through a 1 mm sieve.

Concentrations of non-structural carbohydrates starch, sucrose, glucose and fructose were analyzed. Starch was analysed based on McCleary et al. (1997) in a two-step enzymatic process with amyloglucosidase and α -amylase (AOAC Method 996.11 and AACC Method 76.13) (AOAC International, 2005) using a Megazyme total starch assay kit.

Sucrose and fructose were determined by enzymatic methods and glucose by hexokinase method (R-Biopharm, 2016)

3.3.3.3 Above ground growth

Above ground parameters DBH and height were measured for all trees undergoing the three treatments (DP, AP and UP) at the beginning of the study in late winter 2011, early autumn 2012 and autumn 2013.

Height of pollarded trees, number of resprouted shoots >2 mm basal diameter, and basal diameter of resprouted shoots were measured in autumn (April) 2012 and autumn (April) 2013 for DP and AP trees, respectively, and comparisons in these parameters were conducted between these two treatments.

3.3.4 Data analysis

3.3.4.1 Root density (RD) dynamics

For the age, DBH, height and tree stand density characteristics recovery of coarse roots was very irregular being absent in many subsampling positions at different sampling times (Appendix 3.1 and Fig A.1), therefore analysis was limited to fine root data.

The data were analysed as a randomized complete block design with a split-plot structure, where the main plots were the UP, DP and AP treatments and the sub-plots were the two sampling positions (40 and 80), the three soil depths (0-150 mm, 150-300 mm, 300-450 mm) and the five sampling times after pollarding (1, 3, 6, 8 and 12 months after pollarding).

Data from the same UP trees were compared with both dormant and early autumn pollarded trees. In order to run the analysis data from UP trees were divided into two control 'groups' or two control set of data (Fig 3.5A-B). Fine root density data of UP trees sampled from late winter 2011 (dormant pollarding time) to late winter 2012 were used as the control data for dormant pollarded trees (UP maDP), and fine root density data obtained from the same UP trees from early autumn 2012 (early autumn pollarding time) to late summer 2013 were the control data for AP trees (UP maAP) (Fig 3.5B-C), providing the model with three degrees of freedom for treatments (Fig 3.5C and Table 3.3).

DP and AP trees were pollarded at different ages (6-7 months difference), at different phenological stage (Dormant and In leaf) and at different seasons of the year (Late Winter vs Early Autumn). To take into account these differences, a ratio analysis was conducted using the changes in fine root density after pollarding (Post-Pollarding PP) relative to the initial or Pre-Pollarding (PrP) root densities recorded 2-3 days before pollarding (Post-pollarding : Pre-pollarding ratio) (Fig 3.5 C-D).

Pre-pollarding (PrP) fine root densities applies for both pollarded (DP and AP trees) and UP trees. PrP densities for pollarded trees are the fine root densities recorded a couple of days before the trees were pollarded, either in late winter 2011 for DP trees, or early autumn 2012 for AP trees. PrP densities for UP trees are the root densities recorded in trees that were UP a couple of days before selected trees were pollarded, and that were kept UP after pollarding the selected trees.

In order to help meet assumptions of normality and variance homogeneity, Post-pollarding to Pre-pollarding ratios were natural logarithm transformed. Figures in results section show data back transformed. The ratio analysis was used for analysing differences in fine root density dynamics

between DP and AP trees and between these treatments with the fine root density dynamics of the UP trees (Fig 3.5C-D). Fine root density dynamics after pollarding relative to pre-pollarding densities, were analysed by soil depths under a mixed model using PROC MIXED of SAS software 9.4 (SAS, 2012), that included the fixed effects of the main plots (pollarding treatments) the sub-plots (sampling positions and sampling times) and their interactions, as well as the random effect of the blocks.

Although four sets of data (DP, AP, UP maDP, UP maAP) (Fig 3.5C) were analysed altogether in the same model, whenever a fixed factor interaction resulted significant (Table 3.3) mean comparison were limited between the pollarding treatments and their corresponding UP data (Fig 3.5C) and between the matched in time data (approximate months after pollarding) of the pollarded treatments (DP and AP). Therefore, data were described and discussed in three subsets of data: a) Dormant pollarding evaluation where comparisons were made between DP and UP trees (Section 3.4.1, 3.5.1 and 3.6.1), b) Early autumn pollarding evaluation comparing AP and UP trees (Section 3.4.2, 3.5.2 and 3.6.2) and c) Pollarding treatments evaluation (DP vs AP) (Section 3.4.3, 3.5.3 and 3.6.3).

3.3.4.2 Root non-structural carbohydrates dynamics

Root non-structural carbohydrates dynamics were also analysed using the PROC MIXED of SAS software 9.4 (SAS, 2012), as a split-plot in time design in a model that included the fixed effects of the pollarding treatments (UP, DP and AP) the sampling times and their interactions. Blocks, likewise the fine root density dynamics analyses were also included as a random effect. As indicated in the corresponding figures natural logarithm transformation was conducted when required to help fulfil underlying model assumptions.

A) Treatments and sampling times									
Year	2011			2012					2013
Season	Late Winter (LW) (28 Aug)	Early Spring (ESp) (22 Sep)	Late Spring (LSp) (15Nov)	Late Summer (LSm) (24 Feb)	Early Autumn (EA) (7 Mar)	Mid Autumn (MA) (18 Apr)	Late Winter (LW) (14Aug)	Late Spring (LSp) (11Nov)	Late Summer (LSm) (26 Feb)
DP	Pre-Pollarding 0 ^a	1	3	6		8	12		
AP					<i>Pre-Pollarding 0^b</i>	<i>1</i>	<i>6</i>	<i>8</i>	<i>12</i>
UP	0	1	3	6-0		8-1	12-6	8	12

B) Unpollarded trees data were split up in two sets of data: approximate months after dormant pollarding (maDP) and approximate months after early autumn pollarding (maAP)									
Year	2011			2012					2013
Season	Late Winter (LW) (28 Aug)	Early Spring (ESp) (22Sep)	Late Spring (LSp) (15Nov)	Late Summer (LSm) (24 Feb)	Early Autumn (EA) (7 Mar)	Mid Autumn (MA) (18 Apr)	Late Winter (LW) (14Aug)	Late Spring (LSp) (11Nov)	Late Summer (LSm) (26 Feb)
DP	Pre-Pollarding 0 ^a	1	3	6		8	12		
UP (maDP)	0	1	3	6		8	12		
AP					<i>Pre-Pollarding 0^b</i>	<i>1</i>	<i>6</i>	<i>8</i>	<i>12</i>
UP (maAP)					<i>0</i>	<i>1</i>	<i>6</i>	<i>8</i>	<i>12</i>

C) The four set of data were matched in approximate similar months after pollarding						
Months after pollarding						
2011						
Season	Late Winter (LW) (28 Aug)	Early Spring (ESp) (22 Sep)	Late Spring (LSp) (15 Nov)	Late Summer (LSm) (24 Feb)	Mid Autumn (MA) (18 Apr)	Late Winter (LW) (14 Aug)
DP	Pre-Pollarding 0 ^a	1	3	6	8	12
UP (maDP)	0	1	3	6	8	12
2012						
Season	Early Autumn (EAu) (7 Mar)	Mid Autumn (MAu) (18 Apr)	Early Winter (EW)*	Late Winter (LW) (14 Aug)	Late Spring (LSp) (11 Nov)	Late Summer (LSm) (26 Feb)
AP	<i>Pre-Pollarding 0^b</i>	<i>1</i>	<i>3*</i>	<i>6</i>	<i>8</i>	<i>12</i>
UP (maAP)	<i>0</i>	<i>1</i>	<i>3*</i>	<i>6</i>	<i>8</i>	<i>12</i>

Treatments: DP Dormant pollarded. AP Early autumn Pollarded UP Unpollarded or control trees

a) Numbers indicate approximate months after dormant pollarding (maDP)

b) Numbers in bold italic style indicate approximate months after early autumn pollarding (maAP)

* Fine root densities at early winter 2012 were estimated from the average of the 1st maAP and the 6th maAP (see Section 3.3.3.1 for further details)

Figure 3.5 Data processing for statistical analysis. continues next page

D) A ratio analysis was conducted using the changes in fine root density after pollarding (Post-Pollarding) relative to the initial or Pre-Pollarding (PrP)^c root densities (Post-pollarding : Pre-pollarding ratio). Statistical analysis were then run with 3 degrees of freedom for treatments. Whenever a fixed factor interaction resulted to be significant, mean separations were limited between the pollarded treatments and their respective matched UP data and between DP and AP trees.

Post-Pollarding : Pre-Pollarding Fine root density ratios						
2011						
2012						
Season	Late Winter (LW) (28 Aug)	Early Spring (ESp) (22 Sep)	Late Spring (LSp) (15 Nov)	Late Summer (LSm) (24 Feb)	Mid Autumn (MA) (18 Apr)	Late Winter (LW) (14 Aug)
Treatments						
DP	Pre-Pollarding 0 ^a	1/0	3/0	6/0	8/0	12/0
UP (maDP)						
2012						2013
Season	Early Autumn (EAu) (7 Mar)	Mid Autumn (MAu) (18 Apr)	Early Winter (EW)*	Late Winter (LW) (14 Aug)	Late Spring (LSp) (11 Nov)	Late Summer (LSm) (26 Feb)
Treatments						
AP	<i>Pre-Pollarding 0^b</i>	<i>1/0</i>	<i>3*/0</i>	<i>6/0</i>	<i>8/0</i>	<i>12/0</i>
UP (maAP)						

Treatments: DP Dormant pollarded. AP Early autumn Pollarded UP Unpollarded or control trees

a) Numbers indicate approximate months after dormant pollarding (maDP)

b) Numbers in bold italic style indicate approximate months after early autumn pollarding (maAP)

c) Pre-pollarding densities applies for both pollarded and UP trees. PrP data for pollarded trees are the root densities recorded a couple of days before the trees were pollarded, whereas PrP data for UP trees are the root densities recorded in trees that were UP a couple of days before selected trees were pollarded, and were kept UP after pollarding the selected trees

* Fine root densities at early winter 2012 were estimated from the average of the 1st maAP and the 6th maAP (see Section 3.3.3.1 for further details)

Figure 3.5 Data processing for statistical analysis. continued

3.4 Results

3.4.1 Dormant pollarding evaluation

3.4.1.1 Fine root length density (fRLD) dynamics of unpollarded trees (UP) during the dormant pollarding evaluation.

From early spring 2011 (September), one month after the beginning of the dormant evaluation in late winter (28th August), UP trees at the 0-150 mm soil depth showed increases in fRLD values reaching their maximum around late spring-late summer 2012 at the 40 smp and around late summer 2012 in the 80 smp (Fig 3.6a,d). After reaching their maximum, fRLD of UP trees decreased. fRLD of UP trees below 150 mm soil depth showed similar trends to those observed in their respective smp above 150 mm soil depth (Fig 3.6b-c,e-f). In late winter 2012, one year after the beginning of the dormant pollarding evaluation, fRLD of UP trees was similar or up to 4× greater than recorded in winter, one year before, at the 80 smp (Fig 3.6d-f) and 40 smp (Fig 3.6a-c), respectively,

3.4.1.2 Fine root length density (fRLD) dynamics of dormant pollarded (DP) trees.

At the 0-150 mm soil depth DP trees showed different ($P<0.05$) annual average fRLD values at the different coring positions (Table 3.3 and Fig 3.7B). At this soil depth (0-150 mm) at 40 smp annual average fRLD of DP trees (0.85) was less ($P<0.05$) than determined for UP trees (1.90) and also less ($P<0.05$) than the annual average fRLD changes recorded for DP trees (1.51) at the 80 smp (Fig 3.7B).

Immediately after pollarding, at 0-150 mm soil depth at 40 smp DP trees showed decreases in fRLD around half the pre-pollarding recorded density (Fig 3.6a). In contrast, at this soil depth (0-150 mm) at 80 smp, one month after late winter pollarding, DP trees showed an increase more than 2× the initial fine root length density observed before pollarding (Fig 3.6d).

Table 3.3 F values of the effects of treatments, sampling positions, soil depths, and sampling times on fRLD and fRMD using a mixed model where blocks were random factor

Fixed Factors	DF	Soil depth (mm) & F values					
		0-150		150-300		300-450	
		fRLD	fRMD	fRLD	fRMD	fRLD	fRMD
Treatment	3	19.04***	21.47***	21.83***	10.42***	36.31***	14.62***
Sampling position	1	1.55 ^{NS}	3.89 ^{NS}	0.06 ^{NS}	0.36 ^{NS}	10.59**	9.05**
Treatment*Sampling position	3	4.81**	2.82*	4.06**	7.47***	1.84 ^{NS}	1.14 ^{NS}
Sampling time	4	4.14**	1.51 ^{NS}	2.11 ^{NS}	0.93 ^{NS}	0.64 ^{NS}	0.97 ^{NS}
Treatment*Sampling time	12	0.94 ^{NS}	1.73 ^{NS}	1.26 ^{NS}	1.06 ^{NS}	0.98 ^{NS}	0.89 ^{NS}
Sampling position*Sampling time	4	1.31 ^{NS}	0.59 ^{NS}	0.08 ^{NS}	0.18 ^{NS}	0.96 ^{NS}	1.11 ^{NS}
Treatment*Sampling position*Sampling time	12	0.33 ^{NS}	0.15 ^{NS}	0.56 ^{NS}	1.59 ^{NS}	0.95 ^{NS}	0.98 ^{NS}

fRLD fine root length density. fRMD fine root mass density. Significance level: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS not significant. DF degrees of freedom.

Maximum fRLD of DP trees at the 0-150 mm soil depth at both sampling positions (40 and 80) were observed around late spring 2011 in November, 3 months after dormant pollarding (maDP)(Fig 3.6a,d). This increase relative to pre-pollarding (PrP) values was greater at the 80 smp (150%) (Fig 3.6d) than at 40 smp (50%) (Fig 3.6a). After reaching maximum fRLD, DP trees at both coring positions had a decrease in late summer 2012, which coincided with the maximum fRLD increase reported in the previous section for UP trees (Fig 3.6a, d). At this stage, 6 maDP in late summer in February, fRLD values of DP trees decreased below pre-pollarding densities at the 40 smp (Fig 3.6a), whereas at the 80 smp fRLD decreased to similar densities recorded 2-3 days before dormant pollarding (Fig 3.6d). Later in autumn and winter, fRLD at 80 smp did not show major changes, finishing with a fRLD 0.90× the initial pre-pollarding densities (Fig 3.6d). At 40 smp from late summer in February to late winter in August fRLD increased to a level of 0.92× the initial pre-pollarding densities (Fig 3.6a).

fRLD dynamics observed in DP trees at 80 smp at 150-300 mm soil depth, showed in general the main features of the fRLD dynamics observed in DP trees above 150 mm soil depth (Fig 3.6d-e). The time of the year (late spring in November) when maximum root densities were reached by DP trees, followed by a decrease which coincided with the maximum increases in fRLD recorded in UP trees were dynamics both observed at the 0-150 and 150-300 mm soil depth at the 80 smp (Fig 3.6d-e). Likewise as described at the 80 smp, fRLD dynamics observed in DP trees at 40 smp at 150- 300 mm soil depth followed in general the fRLD dynamics observed above 150 mm soil depth (Fig 3.6a-b).

In contrast to that observed above 300 mm soil depth, fRLD dynamics of DP trees recorded at the 300-450 mm soil depth at both smp showed similar dynamics to that observed in UP trees in that fRLD continuously increased from late winter to late summer, when maximum densities were recorded (Fig 3.6c,f).

3.4.1.3 Fine root mass density (fRMD) dynamics of unpollarded (UP) trees during the dormant pollarding evaluation.

In general fRMD dynamics observed in UP trees (Fig 3.8a-f) agreed with dynamics described for fRLD for the same treatment (Fig 3.6a-f). At the 0-150 mm soil depth at both smp from early spring 2011 fRMD values increased from late spring (November) 2011 to late summer (February) 2012, when fRMD of UP trees showed the maximum increases (Fig3.8a,d). Afterwards, at the 0-150 mm soil depth at both smp decreasing values were observed. fRMD of UP trees at 40 smp at 0-150 mm soil depth finished one year after the beginning of the study with a 90% increase (Fig 3.8a), whereas at the 80 smp fRMD of UP trees ended up with values similar that recorded one year before in the previous late winter season at the beginning of the study (Fig 3.8d). As observed with fRLD, fRMD of UP trees below 150 mm soil depth showed similar dynamics as those registered above 150 mm soil depth, particularly at 80 smp (Fig 3.8b-c,e-f).

3.4.1.4 Fine root mass density dynamics (fRMD) of dormant pollarded (DP) trees.

Significant differences ($P < 0.05$) were detected between DP and UP treatments at the 0-150 and 150-300 mm soil depth at 40 smp (Table 3.3 and Fig 3.9A-B). At these sections of the soil, average fRMD recovery over the annual cycle, was less ($P < 0.05$) in the DP trees (0.86 and 0.65) than the

UP trees (1.73 and 1.89) at both the 0-150 and 150-300 mm soil depth, respectively. (Fig 3.9B). At the 150-300 mm soil depth, annual average fRMD recovery of DP trees was also less ($P < 0.05$) at 40 smp (0.65) than at 80 smp (1.89) (Fig 3.9B). fRMD dynamics observed at 40 smp from 0 to 300 mm soil depth showed that at all of the sampling times, changes in fRMD of DP trees relative to PrP values were less than those recorded in UP trees (Fig 3.8a-b). In contrast, at the 80 smp within 0-300 mm soil depth, from pollarding in late winter 2011 to 3 maDP in late spring 2011, fRMD relative to pre-pollarding densities were greater in DP trees (1.08-2.39) than in UP trees (0.82-0.99) (Fig 3.8d-e).

At the 6th maDP (late summer 2012) at 80 smp from 0 to 300 mm soil depth, DP trees had decreases in fRMD ($0.90 \times \text{PrP fRMD}$) that coincided with the maximum increase recorded in UP trees ($2.13 \times \text{PrP fRMD}$). From mid-autumn 2012 to late winter 2012 (8th to the 12th maDP) DP and UP treatments at the 80 smp at 0-300 mm soil depth showed similar changes relative to pre-pollarding fRMD (Fig 3.8d-e).

Below 300 mm soil depth, apart from the differences observed between DP and UP at 80 smp in the 6th maDP (Fig 3.8f), both treatments showed similar fRMD dynamics at 40 and 80 smp (Fig 3.8c, f).

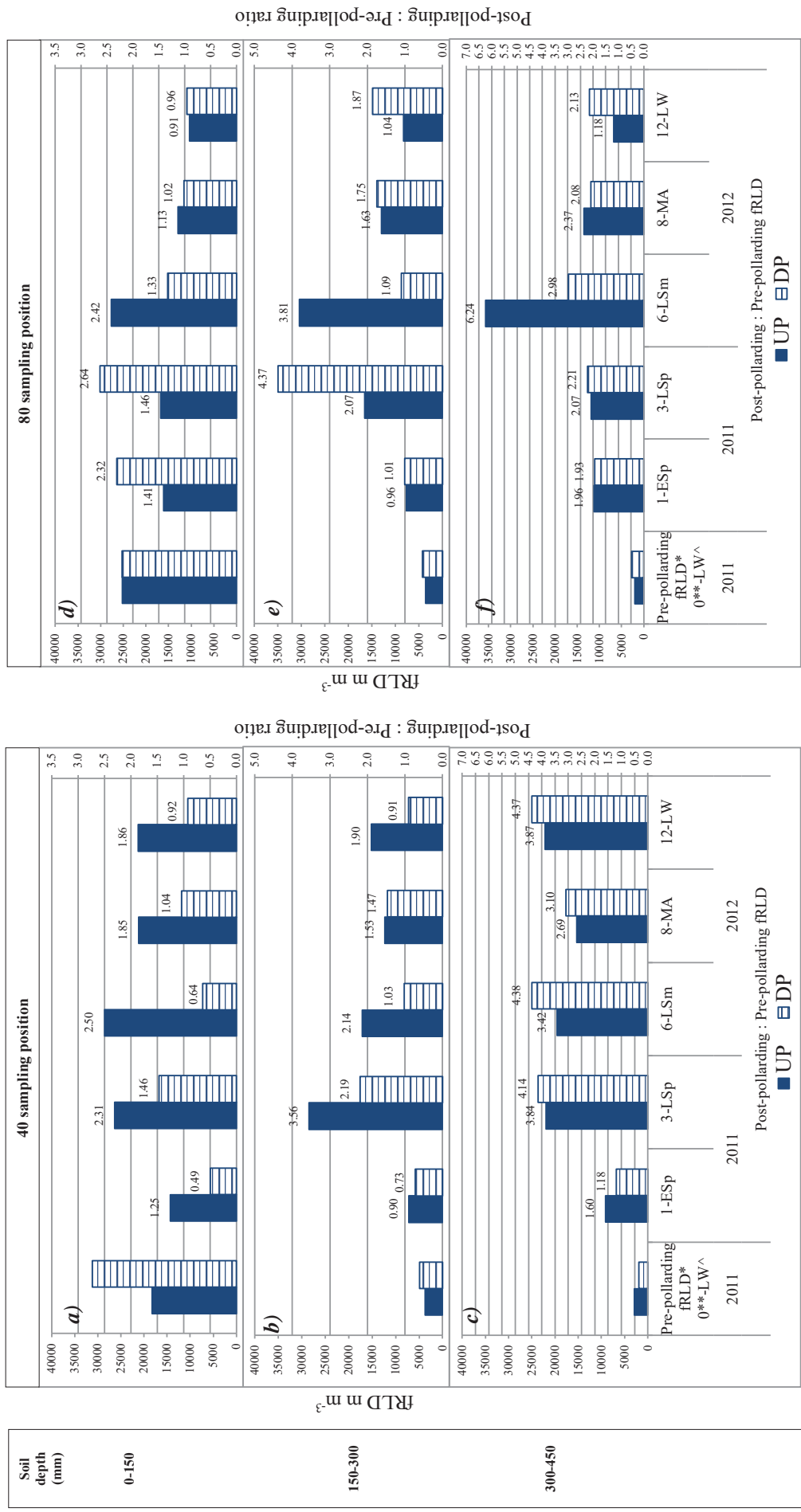


Figure 3.6 Fine root length density (fRLD) dynamics of unpollarded (UP) and dormant pollarded (DP) trees, relative to *pre-pollarding densities recorded in late winter 2011. **numbers indicate approximate months after dormant pollarding. ^ means seasons of the year: LW-late winter ESp-early spring, LSp-late spring, LSm-late summer, MA-mid autumn. a,b,c,d,e & f correspond to different soil depths at 40 and 80 sampling positions

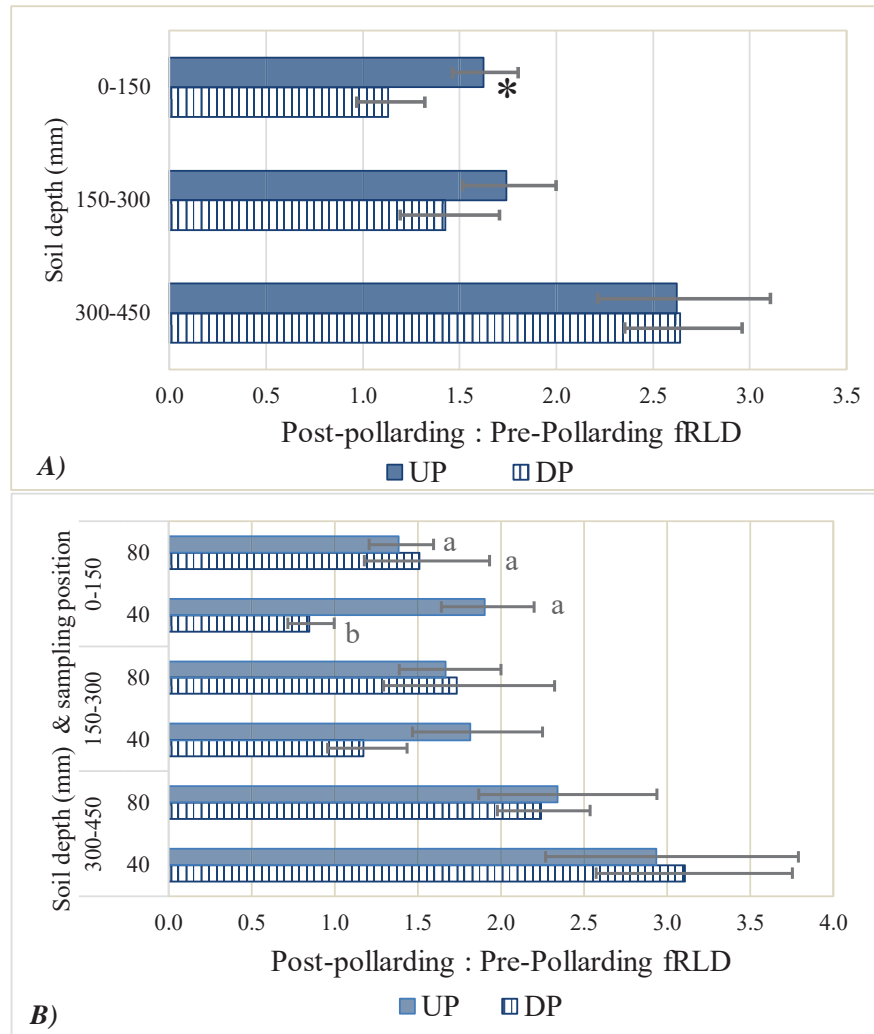


Figure 3.7 Fixed effects interactions on annual average fine root length density (fRLD) dynamics (means and error standard bars) of unpollarded (UP) and dormant pollarded (DP) trees, relative to pre-pollarding densities recorded in late winter 2011.

A) Treatment by soil depth interaction. *indicates significant differences ($P < 0.05$) between treatments at the same depth. B) Treatment by sampling position (smp) interaction at each soil depth. Different letters means significant differences ($P < 0.05$) within and between treatments, within and between smp at each soil depth.

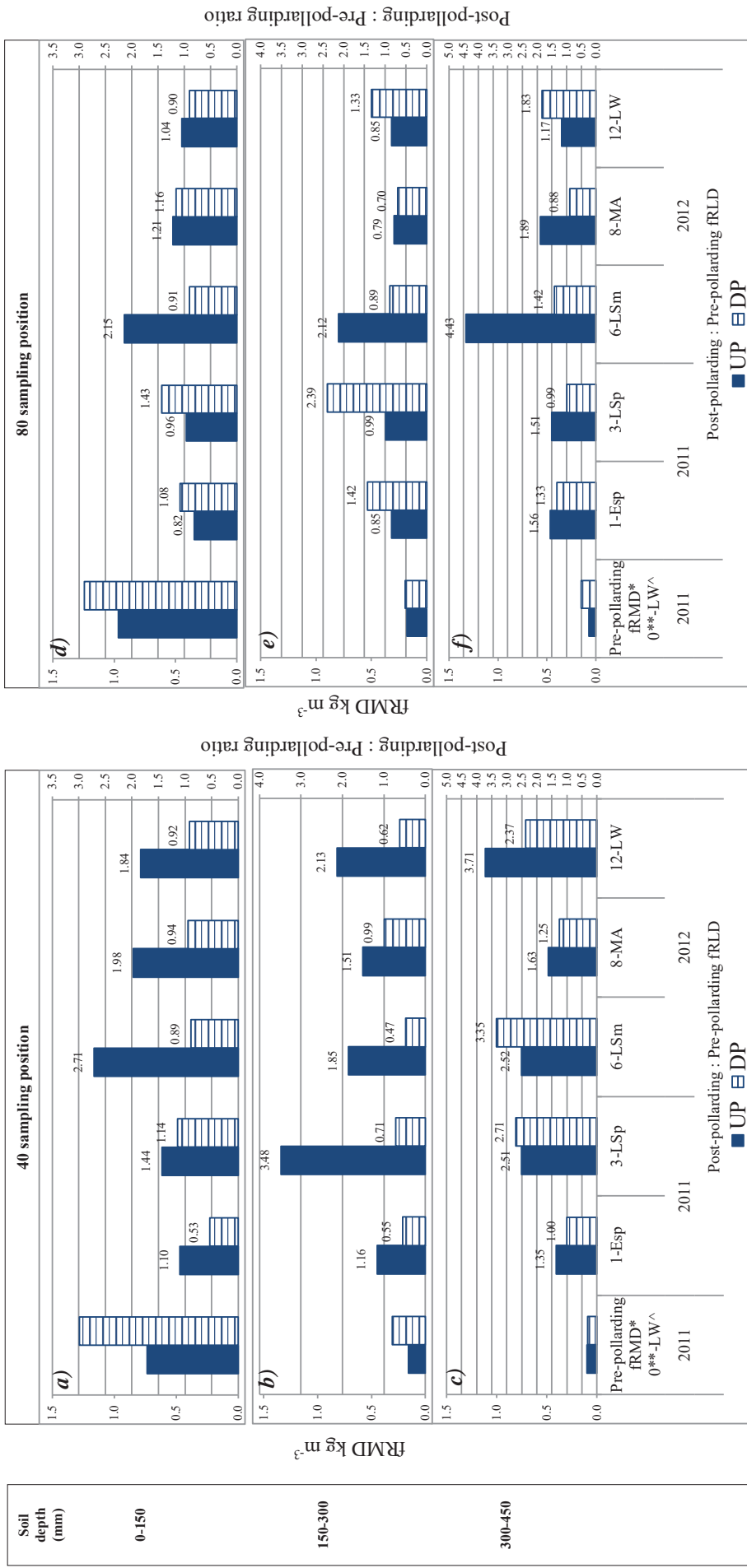


Figure 3.8 Fine root mass density (fRMD) dynamics of unpollarded (UP) and dormant pollarded (DP) trees, relative to *pre-pollarding densities recorded in late winter 2011. **numbers indicate approximate months after dormant pollarding. ^ means seasons of the year: LW-late winter ESp-early spring, LSp-late spring, LSm-late summer, MA-mid autumn. a,b,c,d,e & f correspond to different soil depths at 40 and 80 sampling positions

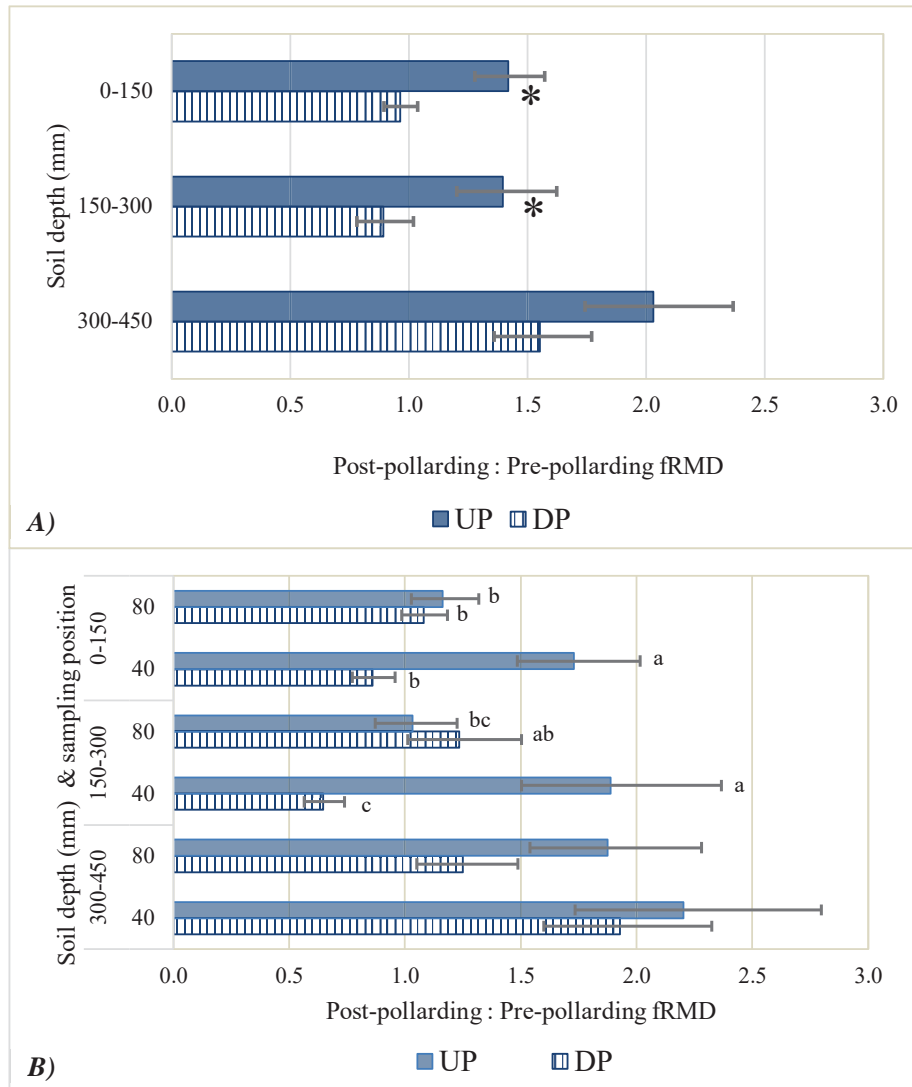


Figure 3.9 Fixed effects interactions on annual average fine root mass density (fRMD) dynamics (means and error standard bars) of unpollarded (UP) and dormant pollarded (DP) trees, relative to pre-pollarding densities recorded in late winter 2011. A) Treatment by soil depth interaction. *indicates significant differences ($P < 0.05$) between treatments at the same depth. B) Treatment by sampling position (smp) interaction at each soil depth. Different letters means significant differences ($P < 0.05$) within and between treatments, within and between smp at each soil depth.

3.4.2 Early Autumn pollarding evaluation

3.4.2.1 Fine root length density (fRLD) dynamics of unpollarded (UP) trees during the early autumn pollarding evaluation.

At 0-150 and 150-300 mm soil depth, significant differences ($P < 0.05$) were detected in UP trees between smp in the annual average fRLD dynamics (Fig 3.11B). At both sampling positions at the 0-150 mm soil depth, UP trees showed decreases in fRLD from early autumn to mid-autumn (Fig 3.10a,d). Decreases relative to pre-pollarding densities were greater at the 80 smp (50%) than at the 40 smp (30%). fRLD decreases recorded in mid-autumn in UP trees at the 0-150 mm soil depth at both smp were maintained through dormancy (Fig 3.10a, d). During spring 2012 and late summer 2013 UP trees showed further decreases in fRLD at the 0-150 mm soil depth at both smp. Below 150 mm soil depth, decreases in fRLD were recorded at both smp in UP trees one month after selected trees were pollarded in early autumn 2012 (Fig 3.10b-c,e-f). As observed above 150 mm soil depth, decreases in fRMD at 150-300 mm soil depth of UP trees were greater at the 80 smp than decreases observed in fRMD in the 40 smp.

Below 300 mm soil depth, at 80 smp, UP trees showed similar fRLD dynamics that observed at the 150-300 mm soil depth (Fig 3.10e-f). In late summer 2013, about one year after the beginning of the early autumn pollarding evaluation, increases greater than the initial fRLD were not recorded in UP trees at any of the subsampling positions, with values ranging from $0.21\times$ (Fig 3.10d) to $0.99\times$ (Fig 3.10b) the pre-pollarding fRLD.

3.4.2.2 Fine root length density (fRLD) dynamics of early autumn pollarded (AP) trees.

Significant differences ($P < 0.05$) were detected in the annual average fRLD recovery between AP and UP trees at the 0-150 mm soil depth and at the 80 smp of this soil depth. (Table 3.3 and Fig 3.11A-B) At this soil depth AP trees showed a greater annual average fRLD recovery at 40 smp (0.80) and at 80 smp (0.66) than observed in UP trees at the 80 smp (0.35).

In contrast to that observed with UP trees from early autumn 2012 to late winter 2012, AP trees at 0-150 mm soil depth, at both smp (40 and 80) did not to show major changes in fRLD after pollarding and through dormancy (Fig 3.10a,d). Decreases in fRLD of AP trees were not seen at

0-150 mm soil depth but until late spring 2012 particularly at the 40 smp where fRLD was about 50% the pre-pollarding densities. fRLD of AP trees continued decreasing by late summer 2013 (Fig 3.13a,d). At this point both UP and AP trees decreased to levels around half and 20% the pre-pollarding densities at the 40 smp and 80 smp, respectively (Fig 3.10a,d)

At the 150-300 mm soil depth, comparing fRLD of AP and UP trees at 80 smp, the pattern was similar to that observed above 150 mm soil depth. At 40 smp in contrast, the relationship between AP and UP trees at 150-300 mm soil depth was inverse to what was recorded at 0-150 mm soil depth (Fig 3.10a-b). At this soil section (150-300 mm) and smp (40), average fRLD dynamics over the annual cycle decreased more ($P < 0.05$) in AP (0.33) than UP trees (0.77) (Table 3.3, Fig 3.10 b and Fig 3.11B). At 150-300 mm soil depth and at 40 smp, one month after selected trees were pollarded in early autumn, UP trees showed a 30% decrease in fRLD, whereas AP trees decreased more than half the pre-pollarding density (Fig 3.10b). At this soil depth (150-300) and smp (40) UP trees showed increasing values during winter, finishing one year after the beginning of the early autumn pollarding evaluation with similar fRLD than the initial pre-pollarding densities (Fig 3.10b). AP in contrast, maintained through dormancy the values observed in mid-autumn (1 maAP), showing a further decrease in late summer 2013 to end up with around 10% the fRLD recorded 1-2 days before pollarding the trees in early autumn 2012 (Fig 3.10b).

Below 300 mm soil depth fRLD relationships between AP and UP at the 80 smp were similar to that found in the next upper soil section (150-300 mm), whereas at the 40 smp fRLD of AP and UP trees followed similar dynamics between both treatments (Fig 3.10c, e-f).

3.4.2.3 Fine root mass density (fRMD) dynamics of unpollarded (UP) trees during the early autumn pollarding evaluation.

As recorded for fRLD of UP trees, in mid-autumn at the 0-150 mm soil depth at both smp there were decreases in fRMD around 30% and 50% at 40 and 80 smp, respectively. Decreases observed in fRMD were maintained relatively unchanged through dormancy, to show then further decreases during the following spring and summer season (Fig 3.12a,d).

Below 150 mm soil depth, decreases in fRMD were also recorded in UP trees at both smp one month after selected trees were pollarded in early autumn 2012 (Fig 3.12b-c,e-f). Annual average fRMD dynamics of UP trees at 150-300 mm soil depth at the 80 smp (0.47) was lower ($P<0.05$) than observed in UP trees at the same soil depth at 40 smp (0.92) (Fig 3.13B). Differences in the fRMD dynamics of UP trees between the 150-300 and 0-150 mm soil depth were particularly evident at the 40 smp (Fig 3.12a-b). In contrast to the steady fRMD values observed in UP trees at the uppermost soil section (0-150 mm), fRMD dynamics at the 150-300 mm soil depth at 40 smp showed increasing values being this, the only subsampling position that showed in late summer 2013, one year after the trial beginning, an increase (around 80%) in fRMD (Fig 3.12b). Below 300 mm soil depth, at the 80 smp, UP trees showed similar fRMD dynamics that observed in the 150-300 mm soil depth (Fig 3.12f).

3.4.2.4 Fine root mass density (fRMD) dynamics of early autumn (AP) pollarded trees.

At the 0-150 mm soil depth, fRMD relationship between AP and UP trees was similar that observed in fRLD dynamics between AP and UP trees (Fig 3.12a, d). Similarly to that observed for fRLD dynamics between AP and UP trees, annual average fRMD decreases at the 0-150 mm soil depth were greater ($P<0.05$) in UP trees (0.57) than observed in AP trees (0.79) (Fig 3.13A). In late summer 2013 one year after pollarding the trees in early autumn 2012, both AP and UP trees showed at 0-150 mm soil depth fRMD around half the initial pre-pollarding densities (Fig 3.12a,d).

Additional similarities between fRLD and fRMD dynamics were found at the 150-300 mm soil depth at 40 smp. At this soil depth and smp UP trees also showed greater ($P<0.05$) annual average recovery in fRMD (0.92) than AP trees (0.49) (Fig 3.12b and Fig 3.13B).

Below 150 mm soil depth at 80 smp, apart from some differences in the magnitude of the fRMD decreases observed, dynamics and relationship in fRMD between AP and UP were similar to that observed above 150 mm soil depth (Fig 3.12d-f). In contrast to the similarities observed at 80 smp at all soil sections evaluated, at the 40 smp below 300 mm soil depth, fRMD recovery of AP

and UP trees showed closer values between each other treatment than observed at 150-300 and at 0-150 mm soil depth (Fig 3.12a-c).

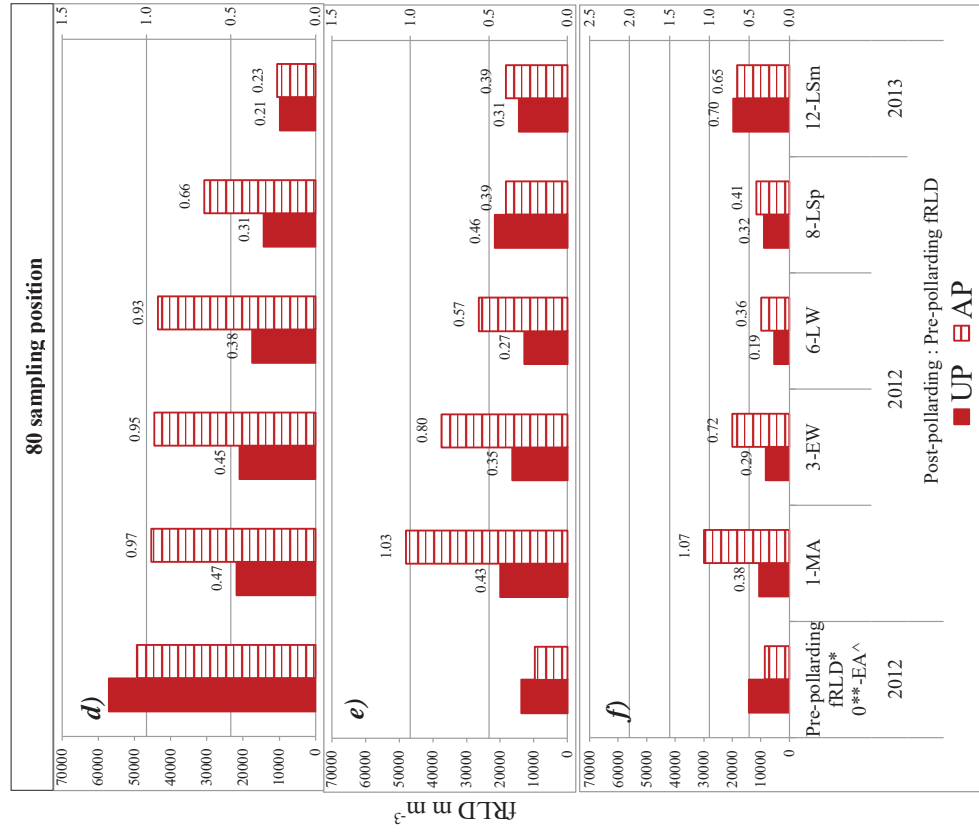
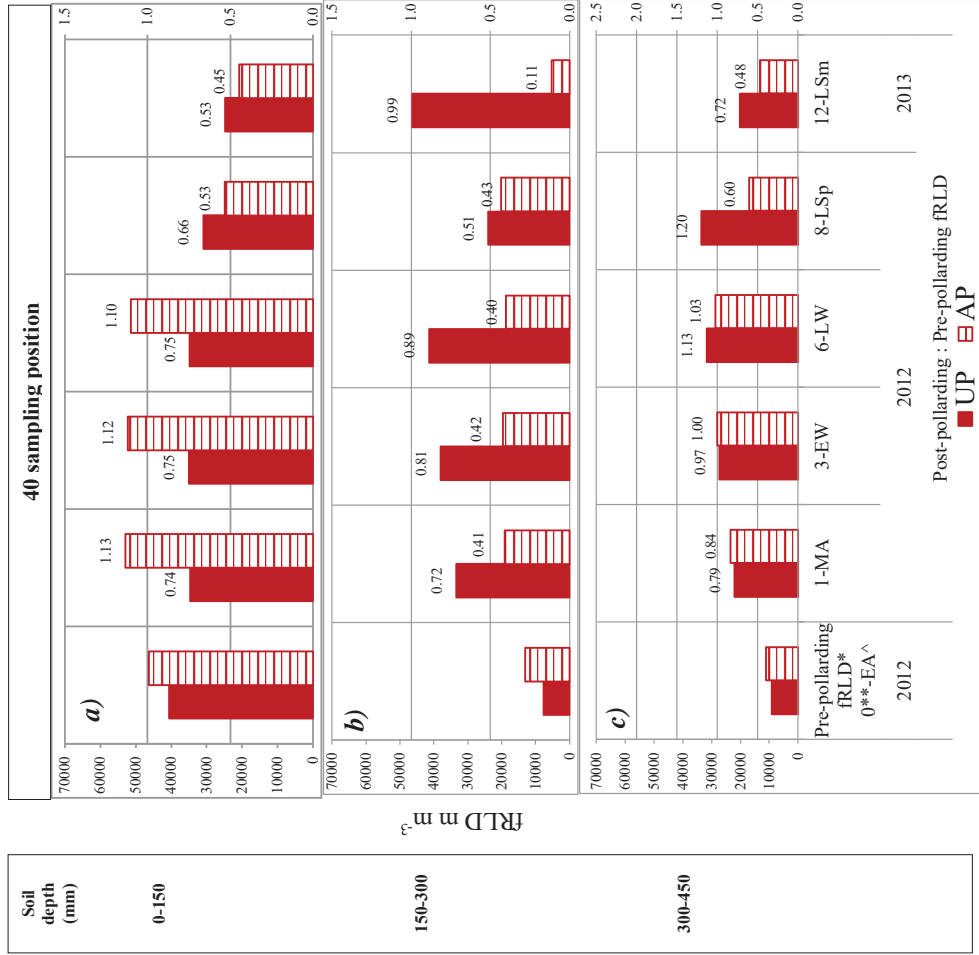


Figure 3.10 Fine root length density (fRLD) dynamics of unpollarded (UP) and early autumn pollarded (AP) trees, relative to *pre-pollarding densities recorded in early autumn 2012. **numbers indicate approximate months after early autumn pollarding. ^ means seasons of the year: EA-early autumn MA-mid autumn, EW-early winter, LW-late winter, LSp-late spring, LSm-late summer. a,b,c,d,e & f correspond to different soil depths at 40 and 80 sampling positions

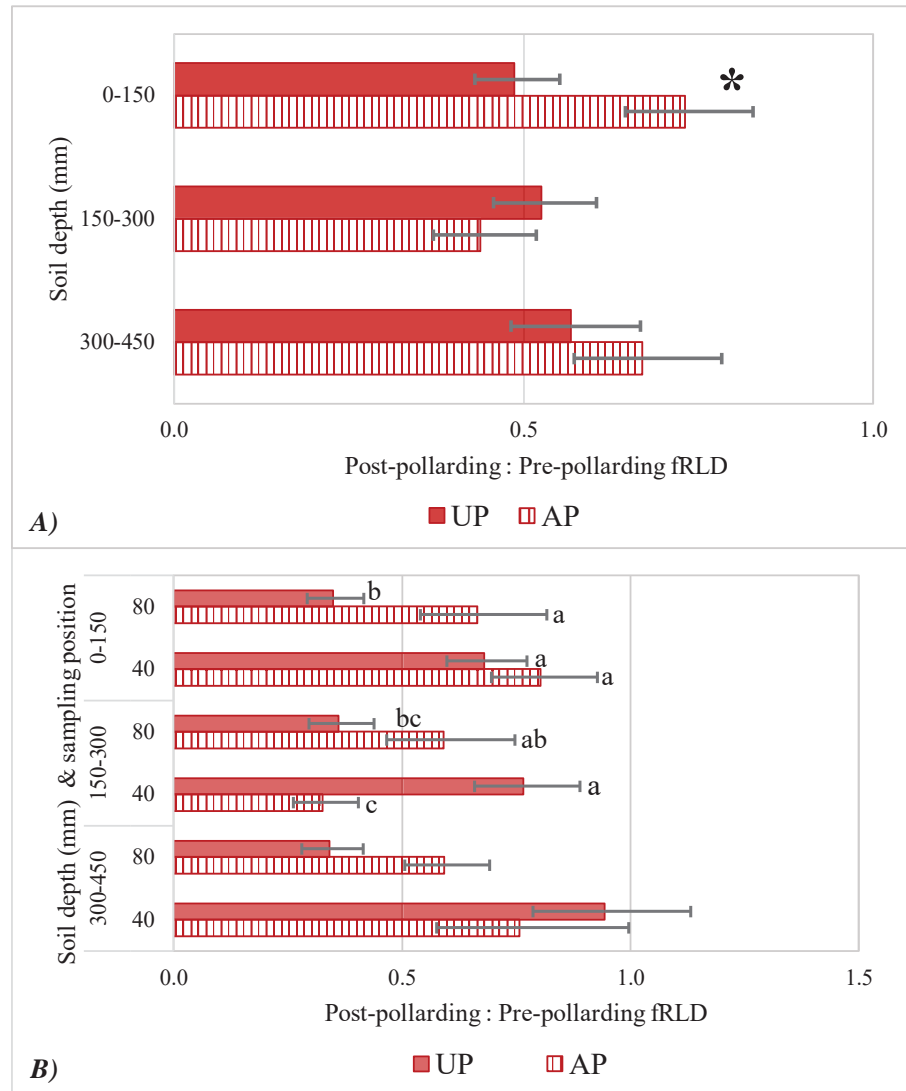


Figure 3.11 Fixed effects interactions on annual average fine root length density (fRLD) dynamics (means and error standard bars) of unpollarded (UP) and early autumn pollarded (AP) trees, relative to pre-pollarding densities recorded in early autumn 2012. A) Treatment by soil depth interaction. *indicates significant differences ($P < 0.05$) between treatments at the same soil depth. B) Treatment by soil depth by sampling position (smp) interaction. Different letters means significant differences ($P < 0.05$) within and between treatments within and between smp at each soil depth.

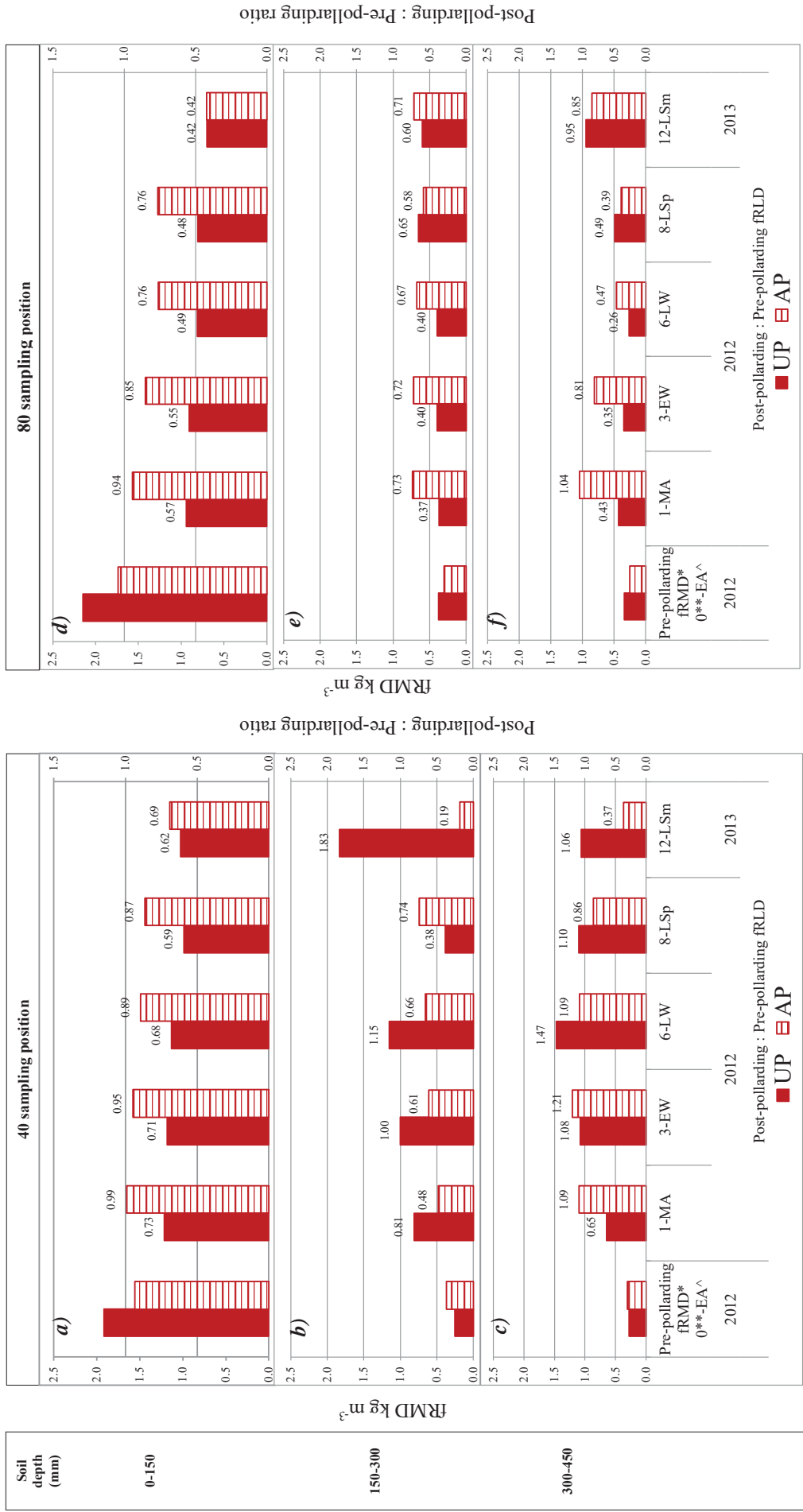


Figure 3.12 Fine root mass density (fRMD) dynamics of unpollarded (UP) and early autumn pollarded (AP) trees, relative to *pre-pollarding densities recorded in early autumn 2012. **numbers indicate approximate months after early autumn pollarding. ^ means seasons of the year: EA-early autumn MA-mid autumn, EW-early winter, LW-late winter, LSp-late spring, LSm-late summer. a,b,c,d,e & f correspond to different soil depths at 40 and 80 sampling positions.

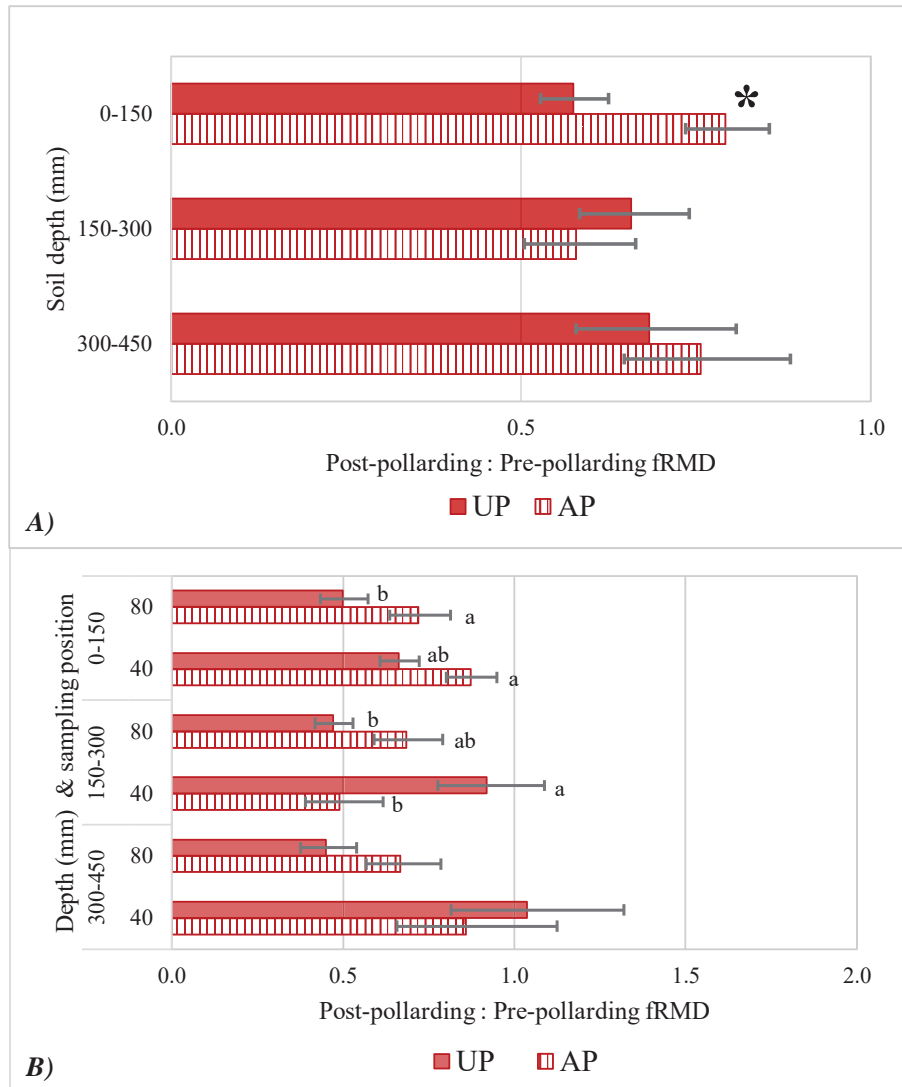


Figure 3.13 Fixed effect interactions on annual average fine root mass density (fRMD) dynamics (means and error standard bars) of unpollarded (UP) and early autumn pollarded (AP) trees, relative to pre-pollarding densities recorded in early autumn 2012. A) Treatment by soil depth interaction. *indicates significant differences ($P < 0.05$) between treatments at the same soil depth. B) Treatment by soil depth by sampling position (smp) interaction. Different letters means significant differences ($P < 0.05$) within and between treatments within and between smp at each soil depth.

3.4.3 Pollarding treatments evaluation (DP and AP)

3.4.3.1 Fine root length density (fRLD) dynamics of dormant (DP) and early autumn pollarded (AP) trees.

Differences in annual average fRLD recovery between DP and AP trees were statistically different ($P < 0.05$) at the three soil depths, at both smp at the 150-300 mm soil depth and at the 80 smp at 0-150 mm soil depth (Fig 3.15A-B). Apart from the 40 smp at the 0-150 mm soil depth, fRLD of DP trees at all other sampling positions and soil depths showed annual average fRLD changes above the pre-pollarding densities recorded 2-3 days before late winter pollarding (Fig 3.15B). AP trees in contrast, showed decreases in the annual average fRLD dynamics at both smp at all depths (Fig 3.15B).

The fRLD recovery observed in DP trees at 40 smp at the 0-150 mm soil depth was the only subsampling position where annual average fRLD recovery was significantly less than found in the UP trees (Fig 3.7B). fRLD densities in DP trees at all other subsampling positions were in general characterized by immediate fRLD responses (1 maDP) that maintained or increased pre-pollarding fRLD. Subsequent sampling times showed that fRLD were kept above or no less than 90% the pre-pollarding densities (Fig 3.14b-c,d-f).

fRLD dynamics observed in AP were characterized in general 1 maAP by the maintenance or small decreases of pre-pollarding fRLD, minimal changes or decreasing values through dormancy, and further decreases during spring and summer particularly at the 0-150 mm soil depth at both sampling positions. One year after early autumn pollarding fRLD of AP trees decreased to densities from 11 to 45% that recorded prior to pollarding (Fig 3.14a-f).

3.4.3.2 Fine root mass density dynamics of dormant (DP) and early autumn pollarded trees (AP)

fRMD dynamics between DP and AP showed in general a similar relationship as it was described for fRLD dynamics between these two treatments (Fig 3.14 and 3.16).

At 80 smp, above 300 mm soil depth, where annual average fRMD recovery of DP trees was similar to UP trees (Fig 3.7B), annual average fRMD recovery of DP trees (1.23 and 1.08) were greater ($P<0.05$) than annual average recovery of AP trees (0.68 and 0.72) (Fig 3.17B). Greater ($P<0.05$) annual average fRMD recovery of DP trees over fRMD recovery of AP trees was also detected at the 150-300 and at the 300-450 mm soil depth as was reported for fRLD recovery between DP and AP trees (Fig 3.17A).

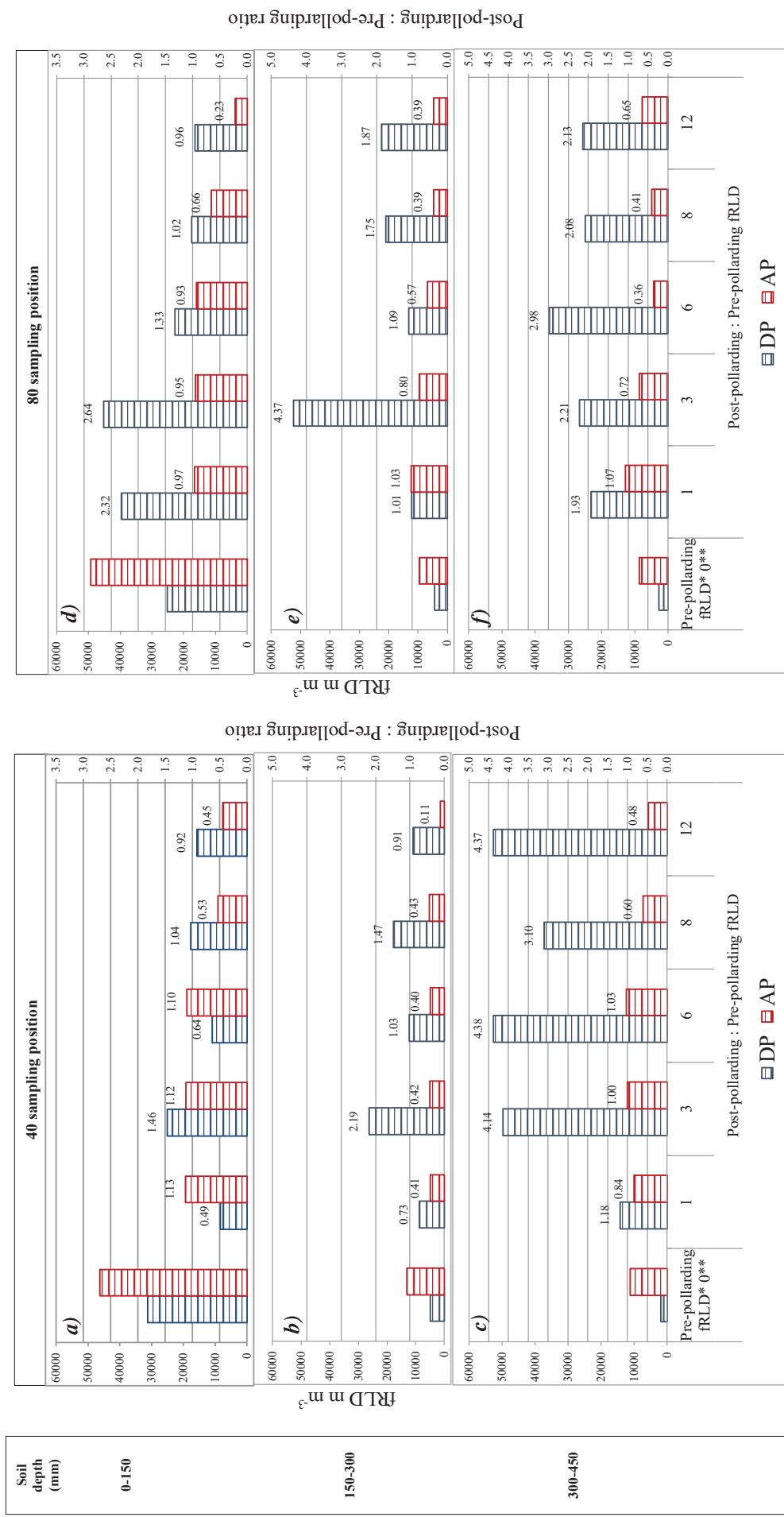


Figure 3.14 Fine root length density (fRLD) dynamics of dormant pollarded (DP) and early autumn pollarded (AP) trees, relative to *pre-pollarding densities recorded in late winter 2011 and early autumn 2012 for DP and AP trees, respectively. **numbers indicate approximate months after pollarding. a, b, c, d, e & f correspond to different soil depths at 40 and 80 sampling positions

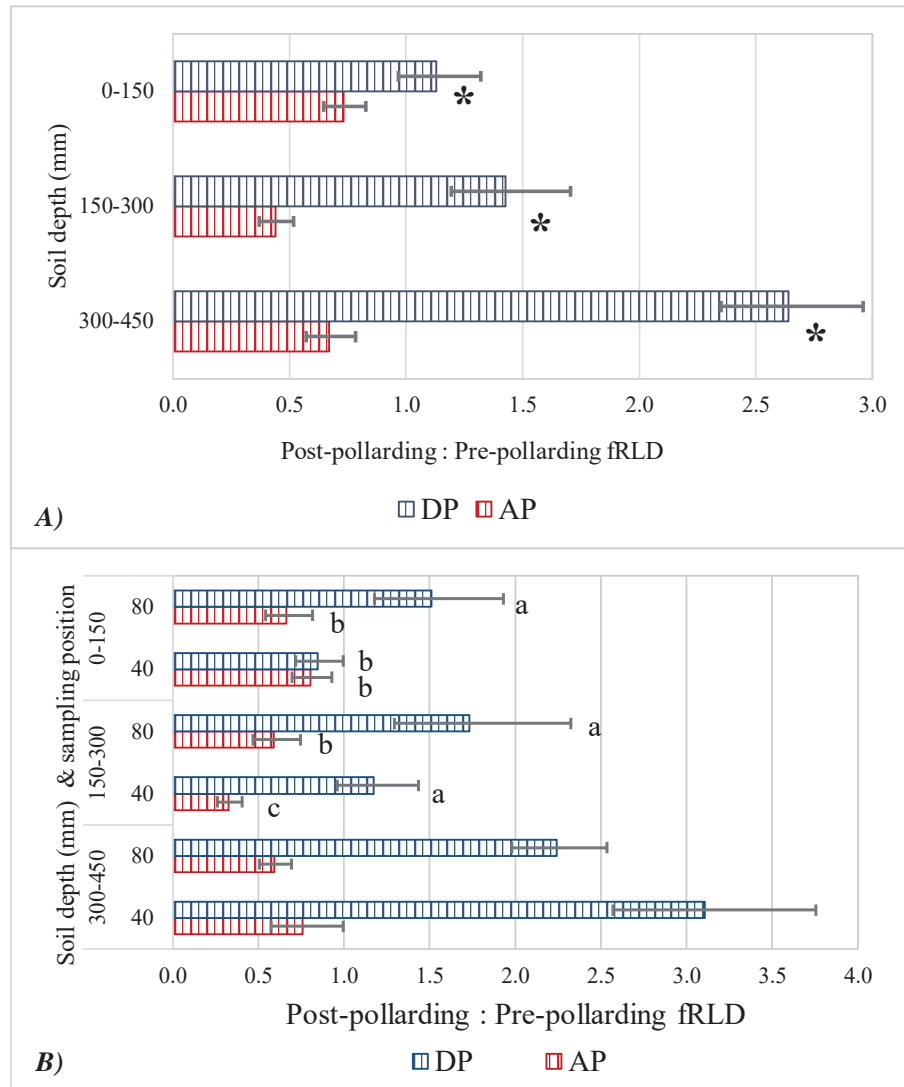


Figure 3.15 Fixed effect interactions on annual average fine root length density (fRLD) dynamics (means and error standard bars) of dormant pollarded (DP) and early autumn pollarded (AP) trees, relative to pre-pollarding densities recorded in late winter 2011 and early autumn 2012 for DP and AP trees, respectively. A) Treatment by soil depth interaction. *indicates significant differences ($P < 0.05$) between treatments at the same depth. B) Treatment by soil depth by sampling position (smp) interaction. Different letters means significant differences ($P < 0.05$) within and between treatments within and between smp at each soil depth.

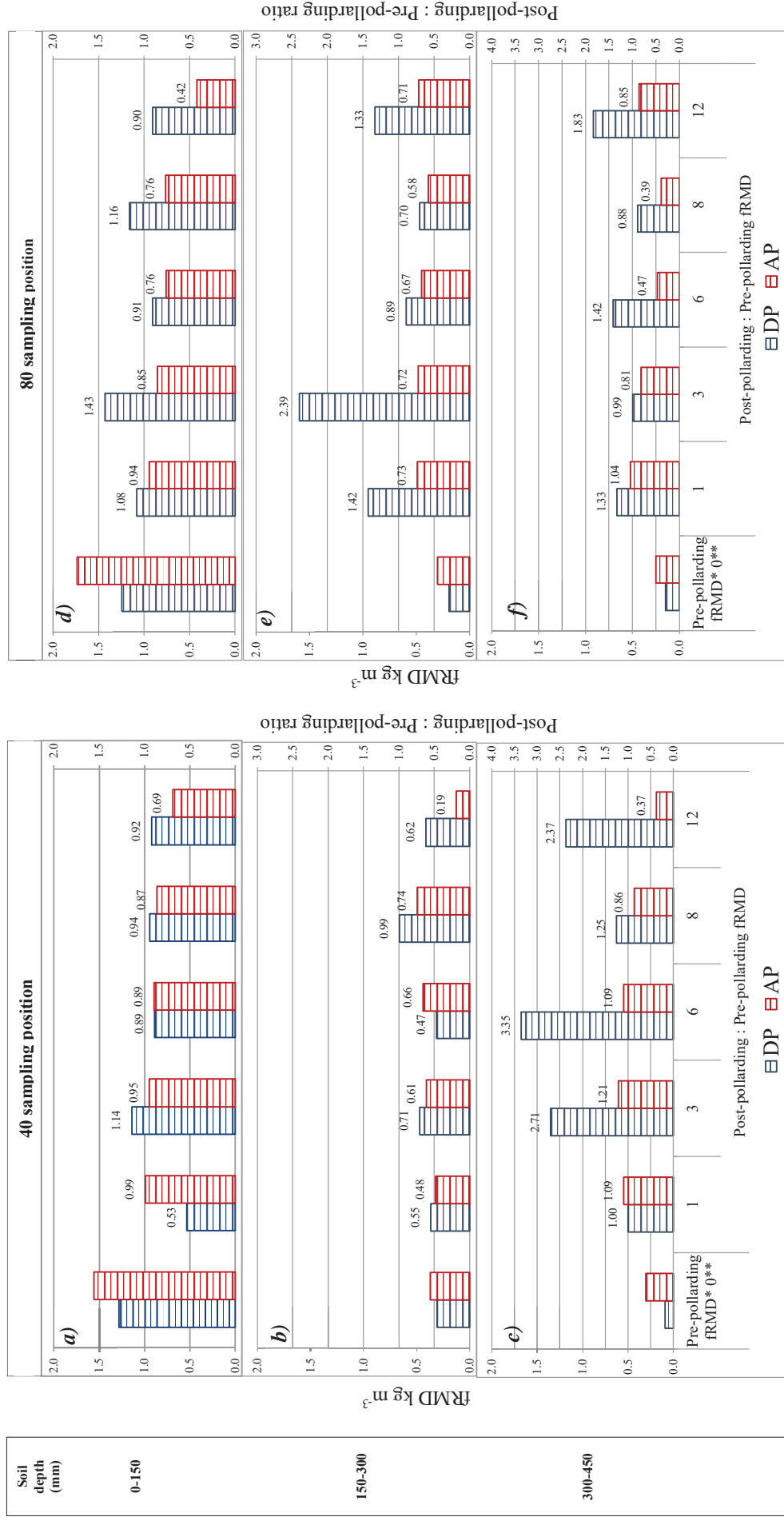


Figure 3.16 Fine root mass density (fRMD) dynamics of dormant pollarded (DP) and early autumn pollarded (AP) trees, relative to *pre-pollarding densities recorded in late winter 2011 and early autumn 2012 for DP and AP trees, respectively. **numbers indicate approximate months after pollarding. a,b,c,d,e & f correspond to different soil depths at 40 and 80 sampling positions

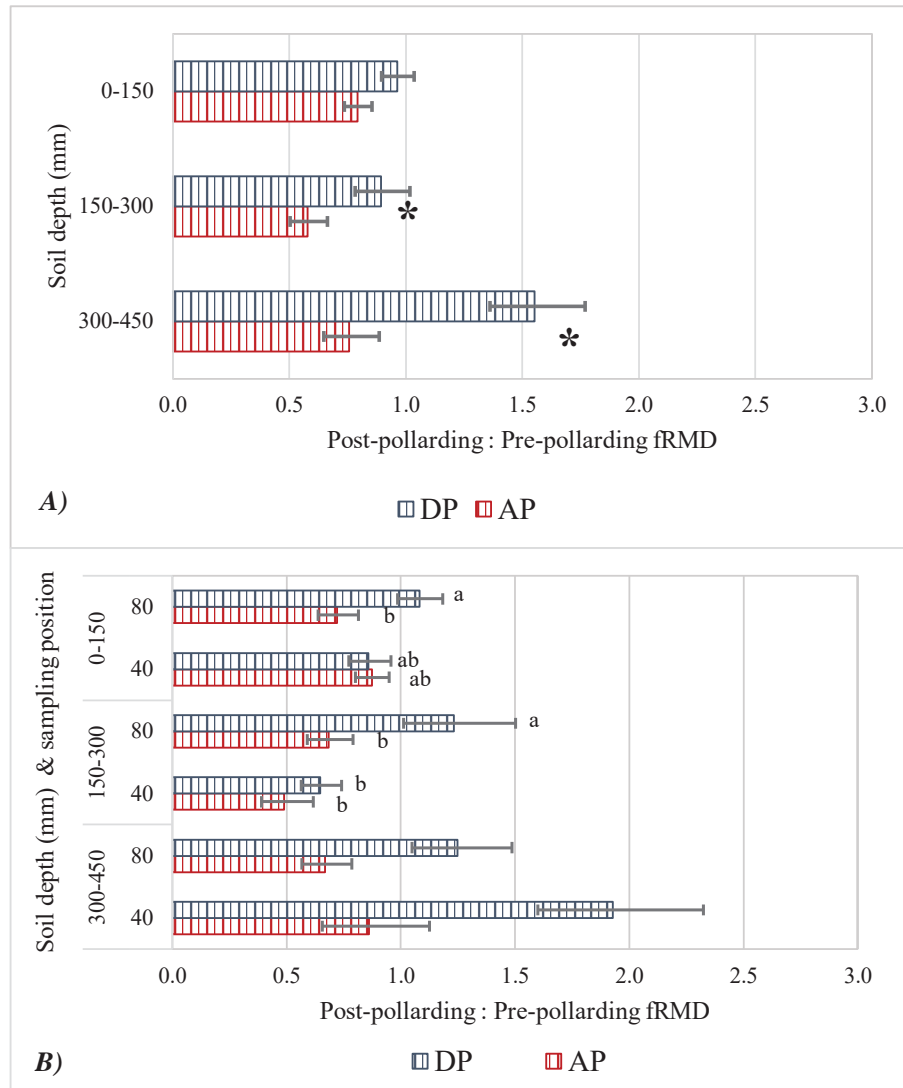


Figure 3.17 Fixed effect interactions on annual average fine root mass density (fRMD) dynamics (means and error standard bars) of dormant pollarded (DP) and early autumn pollarded (AP) trees, relative to pre-pollarding densities recorded in late winter 2011 and early autumn 2012 for DP and AP trees, respectively. A) Treatment by soil depth interaction. *indicates significant differences ($P < 0.05$) between treatments at the same depth. B) Treatment by soil depth by sampling position (smp) interaction. Different letters means significant differences ($P < 0.05$) within and between treatments within and between smp at each soil depth.

3.4.4 Root non-structural carbohydrates (NSC) dynamics after pollarding the trees at different phenological phases

3.4.4.1 Root starch dynamics after pollarding the trees at the end of the dormant stage

At the beginning of the growing season in early spring 2011 (September), starch concentration in roots of UP and DP trees declined (Fig 3.18a). UP tree roots showed a recovery in starch concentration after early spring 2011 (September), whereas roots of DP trees continued to decline in starch concentration, reaching their lowest values by late summer 2012 (February) (Fig 3.18a). At this time, their root starch concentration was significantly lower ($P < 0.05$) than in roots of UP and AP trees, days before the AP trees were pollarded in early autumn 2012 (March) (Fig 3.18a). Replenishment of root starch concentration of DP trees resumed from late summer 2012 (February). Thereafter roots of DP trees experienced a sharp increase in starch concentration, with roots of both UP and DP trees reaching their similar highest concentrations in mid-autumn 2012 (April). In the last two sampling times in late winter (August) and spring 2012 (November) starch concentrations of roots of UP and DP trees had decreased, from around 20 mg/g to around 10 mg/g of dry root biomass (Fig 3.18a).

3.4.4.2 Root sucrose dynamics after pollarding the trees at the end of the dormant stage.

No significant differences were detected in root sucrose concentration between DP and UP trees at any of the sampling times (Fig 3.18b). Both treatments showed declining values from pollarding in late winter 2011 to the 6th maDP. From this time sucrose concentration in roots of DP and UP trees showed increases which were seen first in the DP treatment (Fig 3.18b).

3.4.4.3 Root glucose and fructose dynamics after pollarding the trees at the end of the dormant stage

1 maDP glucose and fructose concentrations in roots of UP and DP trees decreased (Fig 3.18c-d). From the 1st to the 6th maDP, roots of UP trees showed an increase in glucose and fructose concentration, whereas DP continued the decreasing trend (Fig 3.18c-d). No significant differences were detected between UP and DP treatments in root glucose and fructose

concentrations 6 maDP. However, significant differences in root glucose concentrations were detected between DP trees and AP trees when the latter were still unpollarded in early autumn 2012 at the moment of the root sampling. At this moment (6 maDP) significant differences between AP and UP trees were not significant (Fig 3.18c-d).

From the 8th maDP, decreases in glucose and fructose root concentrations of DP trees were recorded (Fig 3.18c-d). The same was observed for the glucose root concentration of UP trees, whereas an increase in root fructose concentration of UP trees one year after dormant pollarding showed significant differences in comparison of root fructose concentration of DP trees (Fig 3.18c-d).

3.4.4.4 Root starch dynamics after pollarding the trees towards the end of the growing season in early autumn.

In mid-autumn 2012, 1 maAP, there was an increase in root starch concentration of both AP and the corresponding UP trees (Fig 3.18a). From this point to late spring 2013 (8 maAP) roots of AP and UP trees had declining starch concentrations which were significantly greater for AP than for UP and DP trees (Fig 3.18a).

3.4.4.5 Root sucrose dynamics after pollarding trees towards the end of the growing season in early autumn.

Significance was not detected in the interaction of the fixed factors Treatment \times sampling time for the root sucrose concentration (Fig 3.18b).

There were no significant differences in root sucrose concentrations between treatments after pollarding in spite of a seemingly higher concentration in UP trees by the end of the sampling period (Fig 3.18b).

3.4.4.6 Root glucose and fructose dynamics after pollarding trees at the end of the growing season in early autumn.

Glucose and fructose root concentrations of AP trees continuously declined following pollarding in autumn 2012 to late spring 2012 (Fig 3.18c-d). Root monosaccharide concentrations in UP trees in contrast, showed minimal changes 1 maAP and increases in root fructose concentration

were observed by the 6th maAP, followed finally by decreases in late spring 2012 (Fig 3.18c-d). Root glucose concentrations in AP trees were significantly lower than UP concentration only by the 1st maAP in late winter 2012, whereas significant differences in root fructose concentration between AP and UP trees were observed in the 6th (late winter 2012) and 8th maAP (late spring 2012) (Fig 3.18c-d).

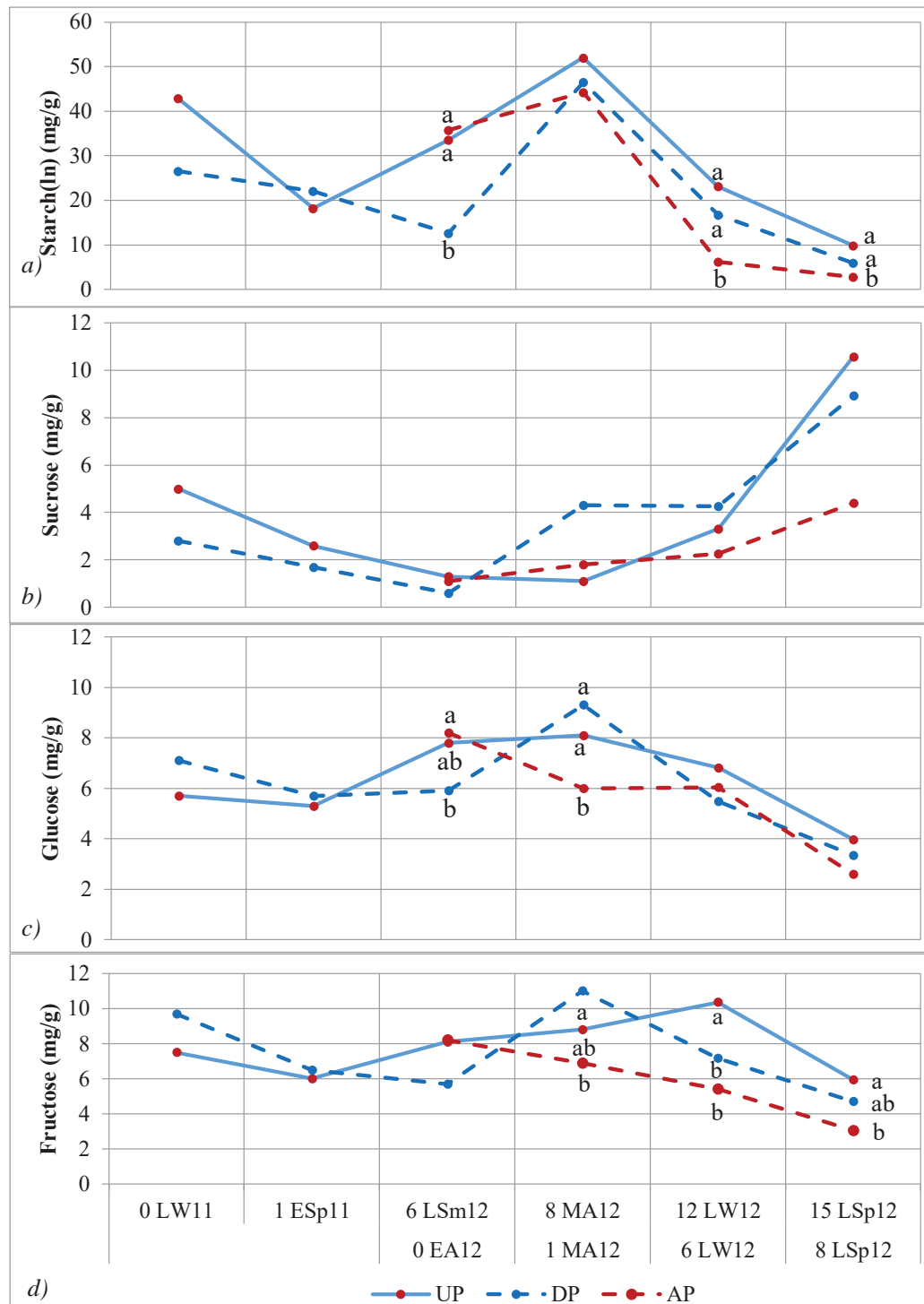


Figure 3.18 Root non-structural carbohydrate dynamics after pollarding willow trees at different phenological phases. (ln)natural logarithm back transformed. UP: unpollarded trees, DP: trees pollarded at the end of the dormancy stage on late winter 2011, AP: trees pollarded at the end of the growing season on early autumn 2012. Sampling times: 11 (2011), 12 (2012). Late winter (LW), Early spring (ESp), Late summer (LSm), Early autumn (EA), Mid autumn (MA), Late spring (LSp). Months after pollarding: 0, 1, 6, 8, 12, 15. Dormant pollarded trees were sampled from late winter 2011 to late spring 2012. Early autumn pollarded trees were sampled from early autumn 12 to late spring 2012. For each carbohydrate and sampling time, different letters indicate significant differences at $p < 0.05$.

3.4.5 Above-ground growth of pollarded trees.

One growing season after pollarding there were no differences in height, number of shoots or average basal diameter of shoots thicker than 2 mm, between trees pollarded at the end of the dormant stage (DP) and trees pollarded at the end of the growing season (AP) (Table 3.4).

Table 3.4 Resprouting vigour one growing season after trees were pollarded at different phenological phases.

Treatments	Resprouting vigour		
	Height (m)	Number of shoots (>2 mm basal diameter)	Basal diameter of shoots (mm)
DP	4.7 ± 0.2	43.7 ± 5.2	39.7 ± 6.5
AP	4.8 ± 0.2	35.3 ± 4.0	32.7 ± 4.4

DP: Trees pollarded at the end of the dormant stage in late winter 2011 were measured on April 2012 AP: Trees pollarded at the end of the growing season in early autumn 2012 were measured on April 2013

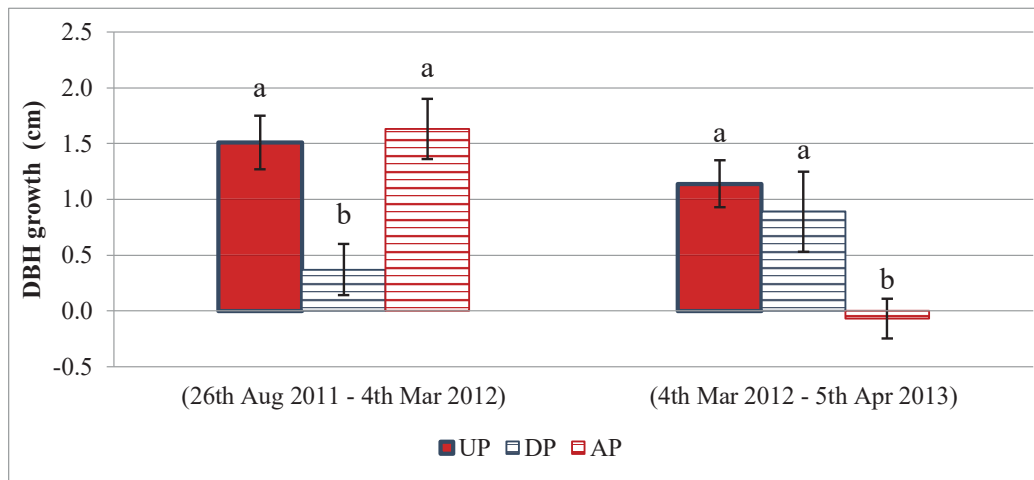


Figure 3.19 Diameter at breast height (DBH) measured in unpollarded trees (UP), dormant pollarded trees (DP) and early autumn pollarded trees AP. DP trees were pollarded on the 28th of August 2011 and AP trees were pollarded on the 7th of March 2012

Six months after pollarding in late winter 2011, dormant pollarded trees had less than a third ($P < 0.05$) the growth observed in unpollarded trees (Fig 3.19). Impact of dormant pollarding in DBH growth was not observed during the second growing season evaluated from early autumn 2012 to autumn 2013 when DP trees showed non-significant differences to UP trees in DBH growth (Fig 3.19).

Pollarding in early autumn had also a significant impact in DBH growth when negative growth was recorded in AP trees which was significantly less than growth observed in UP and DP trees (Fig 3.19).

3.5 Discussion.

3.5.1 Dormant pollarding evaluation

3.5.1.1 Fine root density (fRD) dynamics of unpollarded (UP) trees during the dormant pollarding evaluation.

Fine roots of UP trees in both smp (40 and 80) at all soil depths (0-150, 150-300 and 300-450 mm) followed the regular seasonal patterns commonly reported for intact deciduous trees (Fig 3.6 and 3.8) (Hendrick and Pregitzer, 1993, Pregitzer et al., 2000) *Salix* spp. and *Populus* spp. grown in plantations show a rapid increase in root production at the beginning of the growing season and during spring, peaking during the summer and then declining slightly by late summer or early autumn (Rytter and Hansson, 1996, Rytter, 1999, Coleman et al., 2000, Kern et al., 2004). The maximum fRD observed in unpollarded trees at 40 smp and 80 smp and at all depths was observed in spring and summer (Fig 3.6 and 3.8). Seasonal trends for fine root standing crop are explained by seasonal fluctuations in mortality and fine root production. Mortality of fine roots shows a steady rate during the growing season, increases late in the growing season, and peaks in mid-autumn (Rytter and Hansson, 1996, Kern et al., 2004). In mid-autumn, root production nearly ceases (Kern et al., 2004). Fine root mortality and production in a *Salix viminalis* plantation were low during winter (Rytter and Hansson, 1996). Trends of decreasing fine root length and mass density of UP trees were observed in this study during autumn and winter (Fig 3.6 and 3.8).

3.5.1.2 Fine root density dynamics of dormant pollarded (DP) trees.

The main impact of dormant pollarding was detected in the fine roots located closer to the tree trunks (40 smp) and above 300 mm soil depth (Fig 3.6a-b, 3.7A-B, 3.8a-b, 3.9A-B). At these soil sections UP trees had annual average fRD recovery up to 50% greater than DP trees. Similarly, above 300 mm soil depth at 80 smp, DP trees had annual average fRD recovery around 50% greater than at 40 smp (Fig 3.7B and 3.9B).

Higher labile or dynamic response of roots closer to tree stems has been reported previously for willow and closely related deciduous tree species. The greatest decrease (30-50%) in fine root length density after pollarding mature isolated willow trees occurred closer to trees (3m), whereas

negligible decrease was observed at 5 m and beyond in comparison to unpollarded trees (Beeden and McIvor, 2010). Likewise, Lee (1994) observed one year after coppicing increases in root dry weight at the furthest sampling positions to the tree stems (41 to 71 cm), whereas decreases were recorded at the closest sampling positions to tree stems (14 to 24 cm) in poplar plantations with densities of 5000, 10000 and 15000 tree/ha.

Twelve maDP at the 40/0-150 and 40/15-300 sampling positions, fine root length growth of UP trees relative to pre-pollarding densities was about twice that found in DP trees (Fig 3.6a-b). One year after dormant pollarding, fine root mass growth of UP trees was around two and three and a half times greater than DP trees at 40/0-150 and at 40/150-300 smp, respectively (Fig 3.8a-b). Assuming exactly the same fine root length densities at the beginning of the study between DP and UP trees, fine root length density of DP trees above 300 mm soil depth and closer to the tree trunk (40 smp) would have been 50% that of UP trees (Fig 3.6a-b). Under the same assumption, at 40 smp fine root mass density of DP trees would have been 50% and 33% that of UP trees at 0-150 and 150-300 mm soil depth, respectively (Fig 3.8a-b).

Similar data to these observed in this study were found by McIvor et al. (2011) with mature willow trees pollarded in a summer drought at a hill country site in New Zealand. One year after being pollarded, willow trees evaluated by McIvor et al. (2011) had fine root length densities 57% that observed in unpollarded trees (McIvor et al., 2011).

Greater labile or dynamic response following above-ground plant removal has also been found previously for shallow roots. Significant differences in fRLD were detected to 300 mm soil depth between pollarded and unpollarded willow trees 1 year after canopy removal (McIvor et al., 2011). Lee (1994) found 1 year after coppicing poplar clones that root biomass (fine and coarse roots) decreased within 0-15 and 15-30 cm soil depths, but increased at 30-45 cm depth. Changes in root length density (fine and coarse), either increases or decreases observed in *Alnus nilotica* and *Prosopis juliflora*, respectively, 60 days after pruning, were more pronounced in the first 40 cm than from 40 to 100 cm below soil surface (Jones et al., 1998)

Why do roots closer to the trunk and to the soil surface seem to be the most disrupted at canopy removal? Sink hierarchy phloem translocation model offers a partial, tentative but plausible explanation. In its simplest form, this model suggests that photosynthate translocation in the phloem follows a sink path where structures closer (twigs, branches and upper bole) to the source will be the first to have access to the carbohydrates synthesized by the leaves, and that structures like roots located at the end of the path will be the last (Minchin et al., 1993, Minchin and Lacoite, 2005, Thompson, 2006). Evidence supporting the model in *Populus tremuloides* trees was provided by Landhäusser and Lieffers (2003) and Landhäusser and Lieffers (2012).

Based on seasonal changes in carbohydrate reserves of *Populus tremuloides* clones, Landhäusser and Lieffers (2003) concluded that leaf flush can be entirely fuelled by carbohydrate reserves stored in the closest structures to the buds bursting like twigs, branches and stem. On the other hand, in defoliated *Populus tremuloides* clones, Landhäusser and Lieffers (2012) reported that structures closer to the leaves like twigs and branches, were the first to decrease and the first to replenish carbohydrates at the end of the 1st growing season after defoliation, whereas roots took up to 2 growing seasons after defoliation to replenish their carbohydrate reserves. In this study it is hypothesised that with pollarded trees, non-structural carbohydrates to support new shoot growth came from the remaining closest structures (stems and roots) to the resprouting sink. Carbohydrate reserves of fine roots closest to the stem and soil surface, which are indeed the greatest proportion of the total fine roots, would decrease to minimum levels to cause the death and abscission of fine roots.

At 300-450 mm soil depth at the 40 and 80 smp, results for fRLD of DP trees were in agreement with those found previously for unpollarded trees (Fig 3.6c,f) (Hendrick and Pregitzer, 1993, Rytter, 1999, Kern et al., 2004). fRLD of DP trees at 40/300-450 and at 80 smp below 150 mm soil depth finished 12 maDP 1.87 and 4.37× greater than pre-pollarding root densities (Fig 3.6c,e-f). fRMD dynamics typical of intact trees were also seen for DP trees at 40/300-450 smp, whereas a similar more discrete trend was observed at 80/300-450 smp (Fig 3.8c,f). At 40/300-450 smp

and at 80 smp below 150 mm depth, fine root mass densities of DP trees were one year after pollarding 10% to 128% greater than pre-pollarding densities (Fig 3.8c,e-f).

If the radial and vertical differential root response observed in this study would be indicative of what might happen in the root structure of mature space-planted willow trees; very important insights may be drawn when comparing results of this study and the data reported by McIvor et al. (2011) in late summer pollarded wide-spaced willow trees planted in steep slopes ($>16^\circ$) in pastoral hill country. Within the short term evaluated after pollarding (12 months) it seemed that dormant pollarding in this study did not exert a different impact in the fine root response to that reported by McIvor et al. (2011) for AP willows. Both studies showed that one year after pollarding the main impact was seen above 300 mm soil depth and at the coring positions closest to the stems, 2-3 m in the McIvor's study and 40 cm in this study. At those coring positions, differences in fRD growth between pollarded and unpollarded trees in both studies were around the order of 50%. McIvor et al. (2011) reported that it took around 4 years for fine roots disturbed by late summer pollarding to recover similar densities than similar aged unpollarded trees. It is as yet unknown how long it takes for the fine roots disrupted by dormant pollarding to recover similar fine root densities as unpollarded trees.

When compared with their corresponding pre-pollarding densities, both this study and mature willow trees pollarded in late summer evaluated by McIvor et al. (2011), show that any decreases observed in fRD after pollarding were temporary in nature, and that following pollarding pollarded trees recovered by or before the end of the first year the initial fRD recorded prior to pollarding.

Apart from the fRMD at 40 smp at 150-300 mm soil depth, fine root density of DP trees (length and mass) at this sampling position (40 cm from the trunk) above 300 mm soil depth, resulted one year after pollarding, with values at least 91% the pre-pollarding fine root densities (Fig 3.7a-b, 3.8a). One year after pollarding, fRD of DP trees at 80 smp above 300 mm soil depth ranged from 10% less to 86% more than the fRD recorded prior to pollarding.

3.5.2 Early autumn pollarding evaluation.

3.5.2.1 Fine root density (fRD) dynamics of unpollarded (UP) trees during the early autumn pollarding evaluation.

From the end of the growing season in early autumn 2012 and through dormancy (autumn and winter), fRD of UP trees exhibited similar trends to those previously reported in the literature (Hendrick and Pregitzer, 1993, Rytter and Hansson, 1996, Kern et al., 2004). From early to mid-autumn the magnitude of decreases in fRD of UP trees varied with sampling position. Decreases in fRD of UP trees were greater at 80 smp than at 40 smp (Fig 3.11B and 3.13B). At 0-150 mm soil depth, UP trees showed immediate decreases in fine root densities (length and mass) of about 30% and 50% at 40 smp (Fig 3.10a and 3.12a) and at 80 smp (Fig 3.10d and 3.12d), respectively. After immediate decreases, UP trees maintained fRD with minimum changes through dormancy. However, atypically to trends for intact trees, the following growing season at the 0-150 mm soil depth, fRD of UP trees were characterized by further value decreases in fRLD (Fig 3.10a,d) and fRMD (Fig 3.12a,d). At both smp (40 and 80) at all soil depths sampled, fRLD of UP finished in late summer 2013 with lower values than one year before (Fig 3.10a-f). fRMD of UP trees was only higher one year after pollarding than pre-pollarding values at 40/150-300 smp (Fig 3.12b). One year before, during the dormant pollarding evaluation, within the same phenological phases from late winter 2011 to the end of the growing season in late summer 2012, UP trees showed fine root length growth from twice at 40/150-300 (Fig 3.6b) to even 6 times at 80/300-450 (Fig 3.6f). Within the same timeframe (late winter 2011 to late summer 2012) fine root mass growth of UP trees oscillated from the double to 4.8 times the values recorded at 80/150-300 and 80/300-450 smp, respectively, when selected trees were pollarded at dormancy (Fig 3.8e-f).

Growing season 2012-2013, when UP were evaluated, New Zealand experienced a record drought (Porteous and Mullan, 2013). Mild drought conditions have been observed to stimulate fine root production and elongation in Norway spruce (*Picea abies* (L.) Karst.) (Gaul et al., 2008) or European Turkey-oak (*Quercus cerris* L.) (Montagnoli et al., 2012). However other studies report both increases in fine root mortality and fine roots production declining when soil moisture decreases at suboptimal levels (Pregitzer et al., 2000, LuShuang et al., 2015)

3.5.2.2 Fine root density (fRD) dynamics of early autumn pollarded trees (AP).

In contrast to fRD changes observed in UP trees, at 0-150 mm soil depth, AP trees did not show major changes in fRD immediately after pollarding (1 maAP) and fine root densities observed in mid-autumn 2012 (1 maAP), were maintained in general with minimum changes through dormancy (Fig 3.10a,d and 3.12a,d). It is thought that these fRD dynamic peculiarities observed in AP trees led to the significant differences found in fRD between AP and UP trees at 0-150 mm soil depth, particularly at 80 smp (Fig 3.10a,d and 3.12 a,d).

The maintenance of root densities after pollarding the trees in early autumn contrasts with the findings of McIvor et al. (2011), who reported that willow trees lost 48% of the total root (fine and coarse) length density 90 days after being pollarded in a summer drought. Ninety days after being pollarded, fine root length density of late summer pollarded willow trees was 52% that of unpollarded trees (McIvor et al., 2011). Several factors could have influenced the root responses after pollarding in this study and in that of McIvor et al. (2011). First, the McIvor et al. (2011) study was conducted on scattered, mature willow trees on moderately steep ($>16^\circ$) pastoral hill country in Hawke's Bay in the eastern North Island. Willow trees in this study were planted at a high density in a low steep ($<5^\circ$) on a Tokomaru silt-loam soil. Soil fertility and moisture properties between sites might have been influential in the root response observed after pollarding. In McIvor's et al. (2011) study, pollarding the trees was conducted because of the need for stock fodder under the intense, dry conditions experienced in the 2009 summer. In contrast, the 2011 summer conditions during this study were typified by above normal rainfall during the 2011-2012 growing season (Fig 3.1)

Differences in soil moisture content because of irrigation were proposed by Dickmann et al. (1996) and Lee (1994) as a likely reason for the greater fRD responses observed in their respective experiments. Dickmann et al. (1996) observed that irrigated *Populus* \times *euramericana* cv. "Eugenei" had greater increases in root number and length after coppicing than material not irrigated. When comparing two different locations with the same set of *Populus* \times *euramericana* clones, Lee (1994) found that in the location irrigated more frequently, trees showed an increment

of 38% in root dry mass one year after dormant coppicing, while the location with less frequent irrigation had a 35% decrease in root dry mass. More favourable environmental conditions were proposed by Bedenau and Pages (1984) in contributing to increased root production after coppicing poplar trees (*P. trichocarpa* × *deltoides*, clone Beaupre). One and two years after coppicing, trees in an “intensive” cultural treatment (plastic mulch, weeding between rows, fertilization) had greater root production, regardless of rotation coppice length (1 or 3 years), than trees in an “extensive” treatment (no weed control, no fertilization) and under 3 years rotation coppice length (Bedenau and Pages, 1984).

High soil temperatures have been shown to increase fine root mortality, particularly when the increase in soil temperature occurs along with a decrease in soil moisture (Pregitzer et al., 2000). After pruning alder trees with lowest branches at 7.0 m height from ground, Devkota et al. (2009) recorded significant increases in soil temperature up to 3.4° during the spring. Clear cutting of *Quercus variabilis* forest stands caused micro-environmental changes, increasing soil temperature and reducing soil moisture around the stumps below the removed canopies of the cut trees (Ma et al., 2013). Soil temperature and moisture were positively and negatively correlated, respectively, with fine root mortality of control and clear cutting stands of *Q. variabilis* trees (Ma et al., 2013).

Increases in soil temperature and reductions in soil moisture around the trees might have been greater and lasted for longer around the wide-spaced trees monitored by McIvor et al. (2011) under dry summer conditions than in the dense willow block evaluated during the wetter summer conditions in this study. Refoliation of pollarded trees and closer presence of unpollarded trees to pollarded trees in this study might have cooled the microenvironment earlier than where trees were spaced more widely as in the McIvor et al. (2011) study.

Variation in the time of pollarding may also help explain the differences in root response between this study and that of McIvor et al. (2011). Willow trees in the McIvor et al. (2011) study were pollarded in summer (mid-February), whereas those in this study were pollarded in early autumn (7th of March). Autumn environmental conditions (light and temperature) in this study might not

have stimulated vigorous regrowth, and root carbohydrate reserves were potentially more available to supply any carbon (C) demand. A number of reports show that after an initial decline driven by budbreak and leaf flush, root non-structural carbohydrates of woody plants start replenishing when the plants are fully refoliated (Singh and Srivastava, 1986, Kozlowski, 1992, Johansson, 1993), reaching maximum levels around bud set and leaf abscission (Isebrands and Nelson, 1983, Nguyen et al., 1990, Loescher et al., 1990, Landhausser and Lieffers, 2003). Root carbohydrates, as seen in starch concentrations in the AP and UP trees in this study (Fig 3.18a), might have had greater concentrations at the time of pollarding than in the trees in the McIvor et al. (2011) study. Govindarajan et al. (1996) also found that pruning had less impact on the root structure of *Leucaena* when it was conducted at the end of the dry season, when the root system was less active, than when it was conducted at the end of the rainy season when the root system was more active.

Fine root production and mortality have been linked to above-ground canopy processes, such as leaf expansion in spring and senescence in autumn, respectively. It has been suggested that communicative mechanisms at the whole-plant biomass level could be directing the seasonal patterns in fine root standing biomass (Block et al., 2006).

Leaves of *Populus* and *Salix* spp have been shown to possess an extraordinary complex machinery that is crucial for sensing day light length and temperature, and initiate a cascade of metabolic and transcriptional events for dormancy onset (Johansson et al., 2015). It is assumed that in early autumn these environmental factors had just started to shift for autumnal dormancy driving conditions. It is beyond the scope of this study to go too deep in this matter, but defoliation resulted by pollarding in early autumn might have disrupted the dormancy onset signalling processes. Minimal resprouting activity observed after pollarding might have also disrupted the possibility to initiate or resume any regular dormancy onset process.

Seeming advantage 1 to 6 maAP in fRD response of AP trees in this study in comparison with late summer pollarded willow trees studied by McIvor et al. (2011) vanished as AP trees failed to

show, similarly as UP trees, fRD growth at sampling times recorded during the 2012-13 growing season. One year after late summer pollarding, willow trees evaluated by McIvor et al. (2011) had around 57% the fRD of unpollarded trees. However, in contrast with the AP trees of this study, late summer pollarded trees in McIvor study, had already recovered the pre-pollarding fine root densities recorded one year before, whereas fRD of AP trees were in a range of 10-70% the fRD observed in early autumn 2012 a couple of days before pollarding.

Historical dry environmental conditions were attributed as one of the most influential factors driving for the low root performance observed in AP and UP trees during the 2012-2013 growing season. As this poor root development was observed in both UP and AP trees, it is difficult to assess how much early autumn pollarding could have contributed for the low fRD observed in AP trees during times of the year expected (spring-summer) for high root tissue development.

3.5.3 Evaluation of fine root density (fRD) dynamics for the two pollarding treatments (DP and AP).

Pollarding in this study was conducted at two contrasting phenological phases, at the end of dormancy and at the end of the growing season. During the dormant pollarding evaluation, UP trees showed fRD dynamics in agreement with reports in Salicaceae temperate species, showing a consistent fRD growth from early spring to late summer and then slowing down the growth during autumn and winter. Dormant pollarding had major impact in fRD recovery of DP trees above 300 mm soil depth at the closest sampling position to the tree stems (40 smp). These sampling positions (above 300 mm soil depth at 40 cm from tree trunk) were the only where AP trees had annual average fRD recovery greater than DP trees (Fig 3.14d-e, 3.15A-B, 3.16d-e and 3.17A-B). As going deeper in the soil, fRD dynamics of DP trees showed dynamics closer that observed in UP trees, meanwhile AP trees below 150 mm soil depth did not showed, as observed above 150 mm soil depth, the maintenance through dormancy of the pre-pollarding fRD. As a result, differences in annual average fRD recovery between DP and AP trees got greater as going deeper in the soil (Fig 3.14c, f, 3.15A-B, 3.16c, f and 3.17A-B).

As explained at the end of Section 3.5.2.2, part of the differences between DP and AP trees can be explained by the failure of AP trees to show fRD growth during the 2012-2013 growing season when they were evaluated. It is difficult to determine if this failure can be attributed to the influence of early autumn pollarding, as UP trees also showed similar magnitude decreases in the same growing season as recorded for AP trees.

One of the main objectives of this chapter was to determine the differences in root response dynamics of trees pollarded at two phenological phases (dormant and end of the growing season), building on findings obtained 20 to 30 years earlier in short rotation forestry systems. Those findings identified the best time of the year to harvest trees in order to promote vigorous resprouting and thus high biomass production in the following harvesting season. There was empirical and scientific evidence that trees coppiced during dormancy would yield greater biomass than trees cut during the growing season (Strong and Zavitkovski, 1983, Blake, 1983). Greater shoot and mass production of trees coppiced during the dormant stage were associated with high concentrations of non-structural carbohydrates stored in the remaining plant structures (Schier and Zasada, 1973, Fitzgerald and Hoddinott, 1983, Blake, 1983). A key aim in this study was to determine if trees pollarded when dormant would show greater below-ground response or at least, a lower reduction in root density than trees pollarded at the end of the growing season. Literature supports both responses occurring. Dickmann et al. (1996) found that poplar clones increased root number and length immediately and 2 years after being coppiced at the end of the dormant season. They proposed that these increases might be because dormant poplar roots, both coarse and fine, contained high concentrations of stored carbohydrates and nitrogen necessary to facilitate early season root growth, and initial growth of coppices shoots. In contrast, McIvor et al. (2011) reported that initial reductions in fRLD and fRMD of willow trees pollarded during the growing season were about half that of intact trees. Fine root densities of pollarded willow trees did not recover values similar to unpollarded trees until three or four years after being pollarded (McIvor et al., 2011).

Results from this study vary from the inconsistent results reported previously (Dickmann et al., 1996, McIvor et al., 2011). A series of circumstances are proposed to explain the discrepancies.

From the Dickmann et al. (1996) perspective, poplar roots contained high concentrations of carbohydrate reserves at the moment of being pollarded. Differences in root non-structural carbohydrate seasonal dynamics have been reported between poplar clones (Nguyen et al., 1990). Trees in this and the Dickmann et al. (1996) study both had canopy removal just before or at the very beginning of the growing season. Tree root starch concentrations in this study suggest that by late winter - early spring, root energy reserves had already started to decline because greater starch concentrations were observed by early autumn (Fig 3.18a). Findings from Dickmann et al. (1996) resemble more those found in this study at 0-150 and 150-300 mm soil depths at 80 smp than at 40 smp. It is noteworthy that Dickmann et al. (1996) monitored only at one position 1 m from trees using minirhizotrons 1.8 m long, buried with 45° inclination. Similar to Dickmann observations, in this study initial fRD response (1 to 3 maDP) at the 80 smp had increased up to 3.5 times that recorded before above-ground removal (Fig 3.6d-f). One year after pollarding, fRD of DP trees at the 80 smp showed a declining trend, with fRD being slightly less than pre-pollarding values as observed by Dickmann et al. (1996) for non-irrigated 'Eugenei' poplar and irrigated 'Tristis' poplar.

Early autumn pollarded trees (AP) in this study had a greater initial fRD response at 0-150 mm soil depth (Fig 3.10a,d and Fig 3.10a,d) than late summer pollarded trees in the study by McIvor et al. (2011). AP trees in this study may have had a lower energy demand during early autumn in a moment of higher energy reserve status than pollarded willow trees in the McIvor et al. (2011) study. The seasonal trend for starch in AP trees in this study (Fig 3.18a) suggests that stored energy levels were greater in early autumn than earlier during the last stage of the growing season.

Different environmental conditions were discussed in Section 3.5.2.2, also being likely causes of different root responses after trees were pollarded in late summer and early autumn.

3.5.4 Root non-structural carbohydrate dynamics after pollarding the trees at different phenological phases.

3.5.4.1 Predominant forms of root non-structural carbohydrates.

The order of concentration of the assayed carbohydrates was starch > fructose and glucose > sucrose (Fig 3.189a-d). Species influence the prevalence of root carbohydrate reserve forms (Loescher et al., 1990, Kozlowski, 1992). Substantial variation has been found in woody plants in the carbohydrate type that is the predominant non-structural carbohydrate energy reserve. Loescher et al. (1990) reviewed, for instance, that fructose and glucose are more commonly present at higher concentrations than sucrose. Cranswick et al. (1987) reported for both coarse and fine roots of *Pinus radiata* concentrations in the order of starch > sucrose > monosaccharides as storage carbohydrates.

Differences in the prevalent form and concentration of the root carbohydrate reserves have been reported in the same species at different phase of development. Oppong et al. (2002), for instance, evaluated the carbohydrate dynamics of the same clone (*S. matsudana* X *alba* “Tangoio”) evaluated in this study, under similar soil conditions (silt loam) and planting density, but 5 years younger than the ‘Tangoio’ willow trees (7 years old) here. In their study Oppong et al. (2002) reported different predominant carbohydrate reserve forms, but mainly large differences in carbohydrate concentrations in comparison to those found in this study. They found that sucrose was the most abundant form of carbohydrate in the roots. Sucrose values reported by Oppong et al. (2002) were of the order of ten times greater than the next most abundant root carbohydrate in their study. In this study, sucrose concentration was lower than that for starch, fructose, and glucose (Fig 3.18a-d). Supporting Oppong et al. (2002), Bonicel et al. (1987) found in one year-old cuttings of *P. trichocarpa* × *deltoides* that root sucrose was the main root carbohydrate reserve followed by the monosaccharides glucose and fructose and then starch. As observed by Oppong et al. (2002), the concentration of root sucrose reported by Bonicel et al. (1987) was about ten times that of starch concentration. As seen with the mature willow trees in this study (Fig 3.18a), starch was the predominant root non-structural carbohydrate in 60 year-old trees of *P. tremuloides* clones evaluated by Landhausser and Lieffers (2003). Fine root non-structural

carbohydrate concentrations were 12% higher in a 19 year old *Tectona grandis* L.f. plantation than in a 10 year older plantation. (Singh and Srivastava, 1986).

Dynamics of root non-structural carbohydrates such as starch, sucrose, glucose and fructose are highly interconnected and seasonal increases or decreases of some of these are associated between each other.

At the beginning of bud set, for instance, sucrose downward translocation is associated with a sudden increase in the root starch concentrations (Bonicel et al., 1987, Nguyen et al., 1990). Tissue cold hardiness in winter is characterised by a dissolution of root starch associated with an increase in root monosaccharides (Sennerby-Forsse and von Fircks, 1987, Von Fircks and Sennerby-Forsse, 1998). Root starch re-synthesis has been found in canopy tissues at late winter when days lengthen and intermittent periods of frosty days activate bud swelling (Essiamah and Eschrich, 1985). In this study, late spring 2012 was the sampling time when root starch concentration of UP trees showed their lowest concentration of 10 mg g^{-1} and root sucrose concentration of UP trees its maximum (10.5 mg g^{-1}) (Fig 3.18a-b). At all other sampling times root starch concentration ranged in the order of 7 to 50 times that of root sucrose concentration (Fig 3.18a-b). Reports cited in this section (Cranswick et al., 1987, Bonicel et al., 1987, Opong et al., 2002, Landhäuser and Lieffers, 2003) were obtained from sampling periods of at least 6 months, where contrasting seasonal dynamics in root NSC were observed. Predominant form of root NSC reported in those studies showed consistency through time.

3.5.4.2 Root non-structural carbohydrate dynamics of unpollarded (UP) trees

In UP trees, root starch, glucose and fructose concentrations showed in general similar dynamics during the study. Root starch of UP trees followed the regular pattern for root carbohydrate seasonal mobilisation reported in the literature for temperate, deciduous trees (Isebrands and Nelson, 1983, Loescher et al., 1990, Nguyen et al., 1990, Johansson, 1993, Von Fircks and Sennerby-Forsse, 1998, Landhäuser and Lieffers, 2003).

The concentrations of root starch and monosaccharides of UP trees in this study showed a fast initial decline at bud burst and leaf flush (Fig 3.18a,c-d) as reported previously for *Populus* spp. (Bonicel et al., 1987, Landhausser and Lieffers, 2003) and *Salix* spp. (Von Fircks and Sennerby-Forsse, 1998). Replenishment of root starch in temperate deciduous trees has been reported to start soon after refoiliation begins (Von Fircks and Sennerby-Forsse, 1998). Under the sampling protocol in this study, it is difficult to identify exactly when replenishment occurred in the willow tree roots. There was a gap of 5 months between the lowest root starch and monosaccharide concentrations observed in early spring 2011, and the next sampling time in late summer 2012 (Fig 3.18a,c-d), when an increase in non-structural carbohydrates occurred. The greatest increase in root starch, glucose and fructose concentrations in roots was recorded in mid-autumn 2012. (Fig 3.18a, b-c). Several reports on deciduous trees, including willows, show that after shoot elongation ceases, the beginning of bud set is the triggering factor for the translocation of non-structural carbohydrates downwards to the roots, when the fastest replenishment and the maximum root starch concentrations are recorded (Dickson and Nelson, 1982, Isebrands and Nelson, 1983, Nguyen et al., 1990, Von Fircks and Sennerby-Forsse, 1998).

From the peak of root starch concentrations observed in early autumn 2012, root starch concentrations of UP trees declined considerably by late winter 2012 (Fig 3.18a). Decreasing root starch concentrations during dormancy have been widely documented in literature. Reasons for this include conversion of starch to sugars because of cold hardiness, respiration maintenance, consumption and mobilisation of root starch to sustain root extension itself or blossoming before leaf appearance (Marshall and Waring, 1985, Sennerby-Forsse and von Fircks, 1987, Von Fircks and Sennerby-Forsse, 1998, Landhausser and Lieffers, 2003).

During the next growing season, by late spring 2012, a further decline in concentrations of root starch and monosaccharides of DP and UP trees was recorded (Fig 3.18a,c-d). This suggests beginning of replenishment of root non-structural carbohydrates might starts well into the growing season after late spring, which was not detected during the previous year because the

wider gap in sampling times within the growing season between early spring and late summer (Fig 3.18a-d).

3.5.4.3 Root non-structural carbohydrate dynamics of trees pollarded at the end of the dormant stage.

After a complete removal of photosynthate sources, either by complete pruning, pollarding or coppicing, the regenerating structures, coppice shoots or new branches rely, at least during the initial phases of regrowth, on the energy reserves stored in the remaining plant structures (Kozłowski, 1992, Dickmann and Pregitzer, 1992, Von Fircks and Sennerby-Forsse, 1998, Garcia et al., 2001, Crow and Houston, 2004, Luostarinen and Kauppi, 2005, Chesney and Vasquez, 2007).

Faster depletion of root starch concentration was observed in decapitated *Salix viminalis* plants than in intact ones (Von Fircks and Sennerby-Forsse, 1998). In this study root starch concentrations of UP and DP trees declining to similar level from late winter 2011 to early spring 2011 (Fig 3.18a). Afterwards root starch concentrations of UP trees showed an increase by late summer 2012, while by the same time, root starch of DP trees continued decreasing (Fig 3-18a). Likewise replenishment of root monosacharide (glucose and fructose) concentrations started earlier in the growing season in UP trees than in DP trees (Fig 3.18c-d). Later replenishment of root starch and monosacharides in DP trees, resulted by mid-autumn, in similar starch and greater fructose concentrations in DP trees than in UP trees (Fig 3.18a,c-d).

The stage of plant development might influence carbohydrate reserve mobilization. After canopy removal, a contrasting root non-structural carbohydrate mobilization trend to that recorded in this study was observed by Oppong et al. (2002) in younger trees of willow clone ‘Tangoio’, cultivated under similar environmental, soil and planting density conditions as in this study. After coppicing the trees in winter, Oppong et al. (2002) reported that root starch concentration had a high increase until spring when, contrary to findings in the literature, it decreased and reached its lowest value by autumn. In contrast to the findings of Oppong et al. (2002), root starch concentration in this

study showed replenishment from the end of the growing season, reaching its highest value by mid-autumn (Fig 3.18a).

After reaching their maximum concentration in mid-autumn, decreases in root starch and monosaccharides concentration were recorded in DP and UP trees by late winter and late spring (Fig 3.18a,c-d). As discussed for UP trees in previous section (3.5.4.2), the declining trends in root starch concentrations during dormancy have been related with processes such as cold hardiness or maintenance respiration (Marshall and Waring, 1985, Sennerby-Forsse and von Fircks, 1987, Landhausser and Lieffers, 2003), and during the growing season with supporting leaf flush and blossoming and root self-growth appearance and elongation processes (Von Fircks and Sennerby-Forsse, 1998).

The response of root sucrose concentration to late winter pollarding of the 7 year-old ‘Tangoio’ willow trees evaluated in this study is also in contrast to that found by Oppong et al. (2002) in younger (2 year-old) coppiced ‘Tangoio’ trees. Sucrose concentration dynamics in DP and intact tree roots followed a pattern different to that observed with concentrations of starch and monosaccharides (Fig 3.18a-d). While root sucrose concentration of DP trees followed the same trend seen for root starch and monosaccharides from pollarding to mid-autumn, root sucrose concentration of UP trees began to increase later than in DP trees (Fig 3.18a-d). Contrary to what was recorded from mid-autumn with root starch and monosaccharide concentrations of both UP and DP trees, root sucrose concentration of UP and DP trees showed similar increasing values (Fig 3.18a-d).

Root sucrose dynamics after above-ground disturbance have been generally evaluated within an immediate period after canopy removal. Tschapinski and Blake (1994) monitored root sucrose and monosaccharide dynamics within the first 36 days after decapitation of *Populus maximowiczii* x *nigra* L. ‘MN9’ plants. In their experiment it was highlighted that a decrease in sucrose concentration was associated with large increases in concentration of the monosaccharides glucose and fructose 4 days after shoot decapitation. Thirty-six days after decapitation, root

sucrose concentration was still 70% less than before decapitation and root glucose and fructose concentrations had already decreased to values only slightly greater than before decapitation. In this study, in a similar timeframe (1 maDP), root sucrose concentration was 40% less than pre-pollarding values, whereas fructose and glucose concentrations were 33% and 20%, respectively, less than their pre-pollarding values (Fig 3.18b-d).

It is noteworthy that the disaccharide, sucrose, was the only carbohydrate assayed that showed an increasing trend in both intact and pollarded trees from early autumn 2012 to late spring 2012 (Fig 3.18a-d). It is important to note again that the 2012-2013 growing season was characterized by a significant drought (Porteous and Mullan, 2013).

Under severe drought conditions, roots of *Salix nigra* plants increased concentrations of starch and ethanol-soluble carbohydrates 13 days after harvesting, whereas well-watered harvested plants showed a high carbohydrate mobilization (Carpenter et al., 2008). Root solute accumulation via glucose and fructose increase was associated with a decrease in root sucrose concentration as was reported by Tschaplinski and Blake (1994) 4 days after decapitation of one year-old plants of *Populus maximowiczii x nigra L.* Both Carpenter et al. (2008) and Tschaplinski and Blake (1994) proposed that root solute accumulation is a mechanism of the plants for osmotic adjustment to maintain root turgor, which is important for the maintenance of root function and as a mechanism to re-establish the water column halted by shoot removal.

3.5.4.4 Root non-structural carbohydrate dynamics of trees pollarded at the end of the growing season in early autumn.

Pollarding the trees in early autumn did not produce an immediate change (1 maAP) on root starch concentration (Fig 3.18a), which similarly to UP trees showed an increase in the concentration from early to mid-autumn. Root starch concentration increase in AP trees aligned with the maintenance of pre-pollarding fRD within the first 6 to 8 months after early autumn pollarding (Fig 3.10a,d and Fig 3.12a,d). In Section 3.5.2.2 it was proposed that environmental conditions after early autumn were unfavourable for resprouting, which created low sink strength by the meristematic growing points and thus a low demand for the carbohydrates stored at pollarding.

Sequential defoliation studies from the middle to the end of the growing season show that if high concentrations of carbohydrate reserves are desired, defoliation should be conducted before or very close to the end of the growing season (McCamant, 1988, Kwack et al., 2014). Defoliation long before the end of the growing season allows refoliation, and more importantly, provides time for those leaves to mature and become net exporters of photosynthates. After mid-autumn, in late winter and late spring, AP and UP trees showed decreases in root starch concentrations which were greater for AP than for UP and DP trees (Fig 3.18a). After defoliation events in *Populus tremuloides* Michx. Landhäusser and Lieffers (2012) observed that roots are the structures that take more time to replenish starch concentrations (up to 2 growing seasons) than canopy tissue like branches (1 growing season). When defoliation and refoliation occurs during dry periods root starch replenishment could take longer than during wetter years (Landhäusser and Lieffers, 2012).

Decreases in root monosaccharide concentrations in AP trees suggest mobilization or consumption after pollarding (Fig 3.18c-d). Root fructose and glucose concentrations of AP trees showed a consistent declining trend after pollarding, whereas an increasing trend was observed particularly in root fructose concentration of UP trees, from early autumn to 6 months after early autumn pollarding in late winter 2012 (Fig 3.18c-d). During this period of time root monosaccharide concentrations were different between UP than AP trees, with glucose and fructose being greater in UP than AP trees in the 1st and 6th maAP for glucose and fructose, respectively (Fig 3.18c-d). From the 6th maAP (late winter 2012) decreases in root monosaccharide concentrations were recorded in UP and AP trees, with root fructose concentrations of DP trees still being significantly less than UP trees by the 8th maAP (late spring 2012).

Root sucrose concentrations of AP and UP followed similar dynamics from early autumn pollarding (Fig 3.18b). Although UP trees seemed to have a greater increase in root sucrose concentration by the 8th maAP, significant differences were not found between AP and UP treatments. Evidence of lower root soluble carbohydrates was reported by Carpenter et al. (2008) in complete pruned and moisture restricted *Salix nigra* plants than in complete pruned but

periodically flooded plants. Root ethanol-soluble carbohydrates (ESC) were decreased 5% in complete-pruned *Salix nigra* plants maintained under periodic flooding, whereas similarly treated plants under drought conditions decreased ESC by 47% (Carpenter et al., 2008). Differences in ESC mobilization were interpreted by Carpenter et al. (2008) as an ability of *Salix nigra* to maintain root function under combined stresses of flooding and complete shoot removal. However, it seems that *Salix nigra* was more susceptible to drought injury in roots, when the additional stress of complete shoot removal was applied, as occurred in this study during the dry growing season of spring 2012- summer 2013.

Lack of significance in the root sucrose concentrations between early autumn pollarded trees and UP trees at particular sampling times, was also evident between trees pollarded in late winter and UP trees. Variation within treatments in the root sucrose concentrations seems to be the reason for this lack of significance. Without ruling out any sampling or laboratory artefact, intra-treatment variation might be due to the particular sucrose dynamics per se. It has been shown in many woody species that sucrose is the main photosynthate produced and translocated from sources to sinks and, under particular circumstances, from sinks to sources (Kozłowski, 1992, Loescher et al., 1990). Studies on decapitated plants have also shown that this metabolite is particularly sensitive to restricted conditions of C assimilation like above-ground removal or drought (Tschaplinski and Blake, 1994 and Carpenter et al., 2008). Plants idiosyncrasy can play a role for the time it takes to individual plants to adjust to low C assimilation circumstances and therefore individual variation might occur.

3.6 Conclusions

Dormant pollarding of tree willow *Salix matsudana* had the main impact in the fine root structure above 300 mm soil depth and in the closest coring position (40 smp) to the tree trunks.

At these soil sections (40 smp, above 300 mm depth) annual average fRD of dormant pollarded (DP) trees (0.65-0.86) relative to pre-pollarding (PrP) densities were less than observed in UP trees (1.73-1.90) and less than observed in the same DP trees (1.23-1.51) at 80 smp.

One year after pollarding at these soil depths (40 smp, above 300 mm depth) fRD of DP trees were around half the fRD recorded in UP trees.

One year after pollarding, at different soil depths, DP trees maintained, recovered or increased the initial pre-pollarding fRD.

DP trees replenished their root starch concentrations similar to UP trees within the first growing season after pollarding.

Within the short-term evaluated in this study, if the radial and vertical impact of dormant pollarding are indicative of what might happen in the root structure of mature (30⁺ cm DBH) space-planted willow trees in pastoral hill country, then results of this study do not differ substantially of what has been reported for similar referenced willow trees pollarded in summer drought conditions.

Decreases in annual average fRD relative to PrP densities, were lower in AP trees (0.73-0.79) than UP trees (0.48-0.57) at the 0-150 mm soil depth. In contrast to that observed in UP trees, AP trees maintained after pollarding and through dormancy the maximum fRD reached at the growing season.

Maintenance of fRD after early autumn pollarding is also in contrast to reports in space-planted willow trees pollarded in late summer.

Maintenance of fRD in AP trees after pollarding during autumn and dormancy were attributed to a series of factors prevalent at the moment and after pollarding, among which the following were considered the most influential: a) Minimal resprouting observed in AP trees after pollarding from early autumn to dormancy onset. b) Minimal resprouting activity of AP trees after pollarding was reflected in the lack of root starch mobilisation immediate to pollarding, when AP trees had similar root starch concentration than UP trees. c) Defoliation resulted by pollarding in early autumn might have disrupted the signalling dormancy onset processes and events that have been associated with decreases in fine root densities, as was observed in UP trees. The following growing season after early autumn pollarding, both AP and UP trees showed decreases below the pre-pollarding densities. Such atypical behaviour particularly in UP trees was attributed to historical summer drought conditions that did not allow to discriminate between moisture restriction and pollarding impact in AP trees.

Annual average fRD dynamics relative to PrP densities, were greater in DP trees (0.89-2.63) than AP trees (0.43-0.79) at all soil depths evaluated.

In root sections where impact of dormant pollarding in the fine root integrity diminished away from the tree stems and deeper from the soil surface, differences in fRD recovery between DP and AP trees got greater as was recorded in the following root sections: a) at all soil depths, annual average fRLD recovery of DP trees (1.13, 1.42 and 2.63 at 0-150, 150-300 and 300-450 mm soil depth, respectively), relative to PrP densities, were greater than those recorded in AP trees (0.73, 0.43 and 0.66 at 0-150, 150-300 and 300-450 mm soil depth, respectively. b) at all soil depths, annual average fRMD dynamics of DP trees relative to PrP densities (0.96, 0.89 and 1.55) at 0-150, 150-300 and 300-450 mm soil depth, respectively, were greater than those recorded in AP trees (0.79, 0.57 and 0.75 at 0-150, 150-300 and 300-450 mm soil depth, respectively) and c) at 0-150 and 150-300 mm soil depth annual average fRMD dynamics of DP trees were significantly greater to those recorded in AP trees only at the 80 smp.

Impact of pollarding in the root structure was less in DP trees than in AP trees. However, it is proposed that differences between DP and AP trees were mostly as a result of the failure of AP trees to show fine root growth in the growing season following pollarding. Failure to show fine root growth were observed in both AP and UP trees during record moisture restrictions, which suggests environmental factors might have influenced differences between DP and AP trees. Fine root recovery of DP observed in this study do not differ substantially from observations done in mature willow trees wide-space planted in pastoral hill country that were pollarded in late summer in the mid of a summer drought. Therefore it is concluded that pollarding the trees while dormant does not offer advantages in terms of root structure integrity maintenance over what has been observed after pollarding the trees at the end of the growing season.

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Chapter 4. Fine root response and carbohydrate dynamics of poplar trees pollarded in early autumn, at the end of the growing season.

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4.1 Summary

The effectiveness of wide-spaced-planted poplar trees for reducing shallow landslide occurrence relies mainly on the extensive root development of individual trees and root interlocking between neighbouring trees. Practices conducted to control the size of the trees require assessment of their impact on the root structure of the managed trees. The objective of this study was to determine the impact of pollarding at the end of the growing season on the root structure of poplar trees aged 11 years. One group of three trees were pollarded (P) in early autumn 2012, and were compared with another group of three unpollarded (UP) trees. Changes in root dynamics after pollarding were evaluated by the soil core method at different times during one year. In contrast to other studies, significant differences in fine root length and mass density between P and UP trees were not found except during late spring and early autumn, and then only at 0-150 mm soil depth. One year after pollarding, fine root density of P trees was similar to pre-pollarding values. It is thought that soil and environmental conditions typical in hill pastoral landscapes might have a greater and longer negative impact on the root structure of pollarded trees than recorded in this study.

4.2 Introduction

Poplar trees were introduced into New Zealand by European settlers during the 19th century (Van Kraayenoord and Hathaway, 1986, Wilkinson, 1999). They were evaluated and incorporated into soil conservation programmes in 1956, after the Water and Soil Conservation Act was passed in 1941 by the New Zealand Government (Van Kraayenoord and Hathaway, 1986, McIvor et al., 2003). Thereafter, regardless of structural and organizational changes in legislation and entities in charge of soil conservation, a national poplar improvement programme has released a series of clones with specific traits for particular environments (dry, wet sites), purposes (timber, shelter) and also with herbivory and disease resistance (*e.g.* poplar leaf rust) properties (McIvor, 2011, Douglas et al., 2013). From the late 1950s to 1990 around six million poplar trees were established for soil conservation and wind breaks on New Zealand farms (New Zealand Poplar Commission, 1995) with many, particularly those planted for slope stabilization, receiving negligible or no above-ground management (National Poplar and Willow Users Group, 2007, McIvor, 2015). Managing poplars for tree size can be achieved by pruning or pollarding (National Poplar and Willow Users Group, 2007, McIvor, 2015). Both practices are recommended to be conducted late in the growing season from February to March and initiated at an early stage in the life of the tree (3-10 years depending on the growth rate and management purpose). Trees pruned from late summer to early autumn have fewer chances to develop unwanted epicormic shoot regrowth, avoid the peak of the flight season of wood boring beetles, and drier weather at that time reduces the potential for fungus wound infection (New Zealand Poplar Commission, 1995, National Poplar and Willow Users Group, 2007, McIvor, 2015). Pruning or pollarding in late summer or early autumn can provide valuable nutritious livestock fodder as a supplement to low quality pasture. Despite the benefits derived from managing tree size (timber, fodder, increase in light transmission to understorey pasture), canopy removal can cause intense changes in the tree photosynthate source-sink balance (Kozlowski, 1992, Chesney, 2012). Depending on the magnitude of the imbalance, structures remaining after pollarding, particularly the most labile,

like fine roots (<2mm diameter), might die (Chesney and Vasquez, 2007, Landhüsser and Lieffers, 2012).

The contribution of fine roots to slope stabilization is substantial because they can comprise more than 90% of the total root length of poplar trees (Coleman et al., 2000, McIvor et al., 2008). Root tensile strength measured as force per root cross-sectional area is greater in fine than in coarse roots (>2 mm diameter), and therefore in soil shear planes perpendicular to the soil surface, more fine roots can withstand greater tension stresses than a few coarse roots (Stokes et al., 2009). Studies on the impact of total canopy removal on root structure are required to answer questions like how many trees in a paddock should be pollarded at a time, or how frequently a tree should be repollarded. In this study the objective was to determine the immediate and short-term impact of pollarding at the end of the growing season on the fine root structure of mature poplar trees; and simultaneously, to gain understanding of changes in the root non-structural carbohydrate dynamics resulting from pollarding.

4.3 Materials and Methods

4.3.1 Site description

The study was at the Massey University Equestrian Facility, formerly known as Frewen's Farm, which is near the Turitea Stream, Palmerston North (40.4°S, 175.6°E). The site comprised flat terrain at the edge of a small valley bordered by slopes of 25° and 35° at the southern and western sides, respectively (Fig 4.1 and 4.2). At the bottom of the slopes there was a swampy zone between 2 and 3 m wide that provided moisture to the surrounding area. Parts of the study paddock were rush (*Juncus* spp.)-infested with waterlogging a recurrent phenomenon after periods of heavy or prolonged rainfall (Fig 4.2). The soil is a Manawatu fine sandy loam, classified as a weathered fluvial recent soil (Hewitt, 2010).

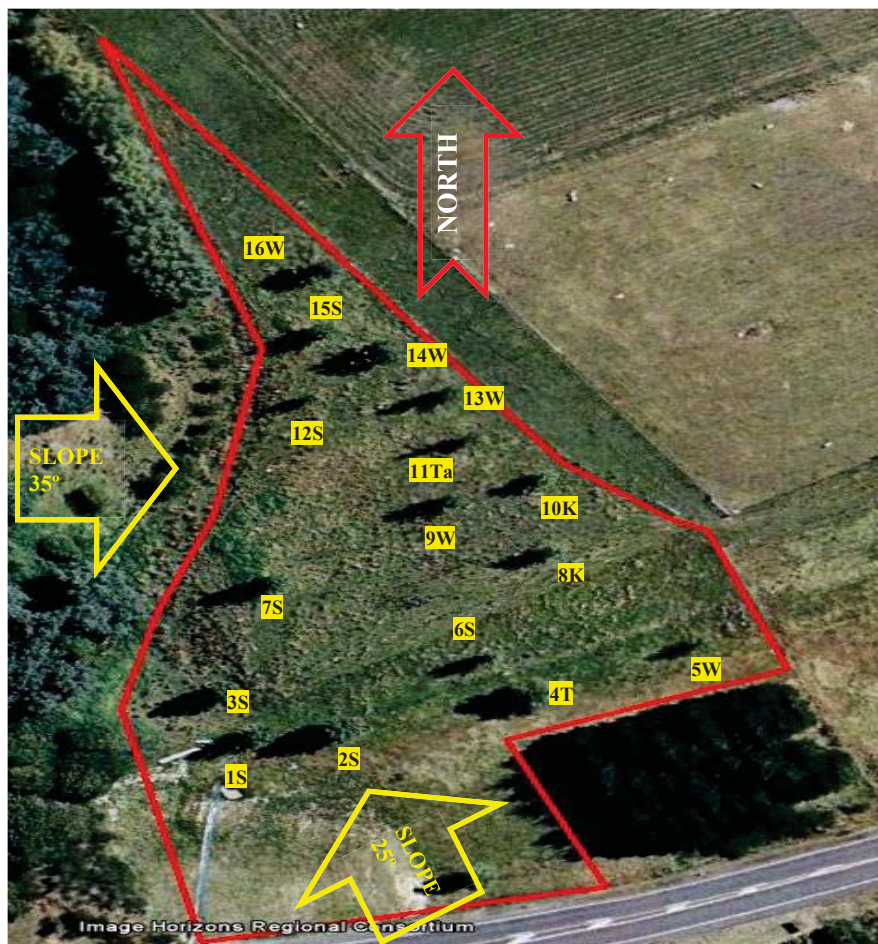


Figure 4.1 Layout of the poplar study, including orientation and surrounding topography. Id tree number and clones are highlighted in yellow: K ('Kawa'), S ('Shinsei'), T ('Toa'), Ta ('Tasman'), W ('Weraiti').



Figure 4.2 View of poplar trees in the study.

The poplar trees were established in 2001 from vegetative poles of 2.5 m height, with 30-50 mm diameter at the base and planted to 60-80 cm soil depth. Poplar clones planted were ‘Kawa’ (K) (*Populus deltoides* Marsh. × *yunnanensis* Dode), ‘Shinsei’ (S) (*P. nigra* L. × *maximowiczii* Henry.), ‘Tasman’ (Ta) (*P. deltoides* Marsh. × *nigra* L.), ‘Toa’ (T) (*P. euramericana* Dode (Guinier) × *yunnanensis* Dode) and ‘Weraiti’ (W) (*P. deltoides* Marsh. × *nigra* L.). Out of 16 trees present in the paddock ‘Shinsei’ and ‘Weraiti’ were the predominant clones with 6 and 5 individuals, respectively.

Weather conditions during the study are shown in Fig 4.3. Rainfall in the 2011-2012 growing season exceeded the long-term (1981-2010) average whereas in the 2012-2013 growing-season, rainfall was about 45% less than the long-term average. The period from spring 2012 to summer 2013 was one of the driest in 30 to 40 years (Porteous and Mullan, 2013).

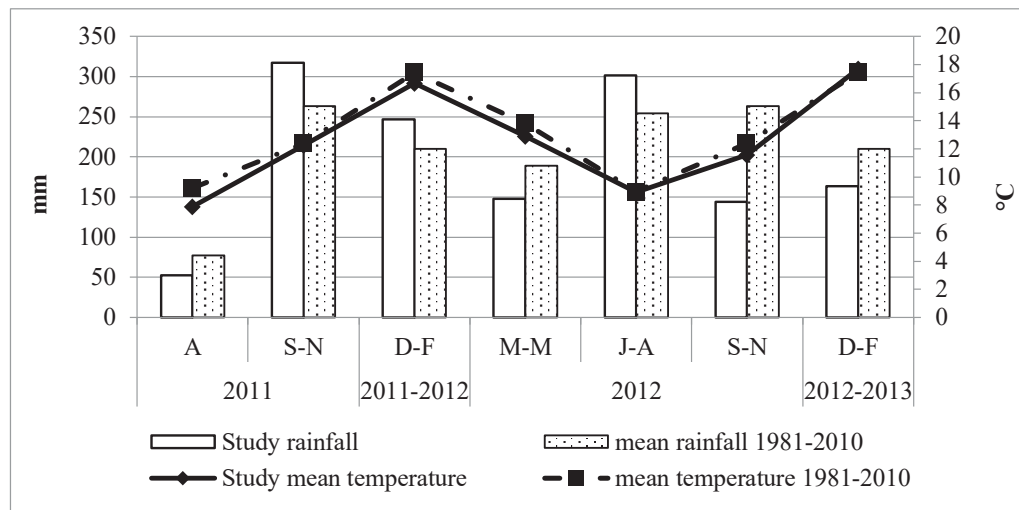


Figure 4.3 Rainfall and mean air temperature during the study compared with mean long-term (1981-2010) records.

4.3.2 Experimental design and treatments

The diversity in clones and micro-environmental variation at the study site precluded using all 16 available trees in the study. Avoiding trees on excessively wet or sloping land and the desire to minimise the range of clones involved in the study resulted in the selection of six trees, which were divided into two groups (Table 4.1). Both groups of trees had similar trunk diameter at breast height (1.40 m; DBH) and height (Table 4.1). Each group had a representative tree of the same three clones. Trees in one of the groups were pollarded (P) in early autumn 2012 (March 25th) when all clones were still in-leaf and there were no signs of dormancy. Phenology of the trees was also observed and recorded in transition points at autumn-winter and winter-spring. Trees in the other group were unpollarded (UP). The UP trees were used as a control to compare the changes in the root system following pollarding. Initial differences in height and DBH between the two groups of trees (Table 4.1) were not significant. Trees were pollarded with a chainsaw at 1.8m height, as practised regularly by farmers to prevent cattle browsing new shoots (Wilkinson, 1999, National Poplar and Willow Users Group, 2007).

Table 4.1 Tree height and diameter at breast height (DBH) at the beginning of the study (mean \pm standard error)

Parameters	Treatments	
	Pollarded trees (P)	Unpollarded trees (UP)
	12S 'Shinsei'	15S 'Shinsei'
	14W 'Weraiti'	9W 'Weraiti'
	10K 'Kawa'	8K 'Kawa'
DBH (cm)	31.8 \pm 5.9	34.4 \pm 0.9
Height (m)	18.1 \pm 1.8	16.9 \pm 3.1

4.3.3 Variables analysed.

4.3.3.1 Tree parameters.

4.3.3.1.1 Height and diameter at breast height (DBH).

Height of the six trees was measured with a clinometer and DBH was measured with a diametric tape at 1.4 m height. Height and DBH of all trees were measured before pollarding in early March 2012, and one year after pollarding.

4.3.3.1.2 Resprouting.

Number of shoots and percentage of shoots greater than 2 mm basal diameter were recorded one year after pollarding. The length of the longest shoot was also estimated one year after pollarding by subtracting the pollarding height from the total height.

4.3.3.1.3 Above pollarding woody biomass.

The total woody (non-leafy) dry biomass of P trees above pollarding height was measured. Twigs and branches were classified in to four diameter categories (twigs and branches less than 10 mm, and branches 10 to 50 mm, 50 to 100 mm and greater than 100 mm), and weighed fresh in the field. Twig and branch samples from the different diameter categories were taken to the laboratory for dry matter estimation. They were dried at 70°C until constant weight which took 24 to 48 hrs. Dry biomass of twigs and branches was calculated by multiplying the fresh mass determined in the field by the dry matter percentage of the different branch diameter categories as determined from the dried samples.

The above-pollarding dry biomass of the main stem was estimated by summing the dry biomass of three log sections cut from the main stem. Estimation of dry biomass of the individual logs of each tree was calculated by multiplying the volume of the logs by their dry mass density.

The volume (m³) of the logs was calculated using Smalian's formula (Fonseca, 2005):

$$V = \pi \times \frac{(Dx)^2}{4} \times L$$

where:

V = volume of the log (m³)

$\pi = 3.1416$

(Dx) = average diameter of the log (m) ((Diameter at the base + Diameter at the top) / 2)

L = length of the log (m)

Dry mass density (kg m⁻³) of the logs was calculated by taking a 50 mm cylinder sample at the mid-point of each log. Cylinders were taken to the laboratory and dried at 70°C until constant weight, which was attained after 48 to 72 hrs. Dry mass density of the cylinders was obtained by dividing their dry mass by their volume.

4.3.3.2 Root density dynamics after pollarding

In order to describe and understand the dynamics of root length density (m m⁻³) and root mass density (kg m⁻³) of poplar trees after being pollarded in late summer, roots were recovered by the soil core sampling technique (Böhm, 1979, Oliveira et al., 2000). A steel corer (8 cm internal diameter) was used to collect roots to 450 mm soil depth. In order to determine the most appropriate coring depth, trenches were excavated in March 2012 to observe root distribution. Around two trees (7S and 16W), three trenches (1.5 m length × 1.0 m depth × 1.2 m width) perpendicular to transects 120° apart from each other were dug at 2 m from the trunk (Fig. 4.4). Roots protruding from the smoothed wall of each trench were counted over a 90 cm × 90 cm steel frame comprising six rows of six adjacent 150 mm × 150 mm squares (0.135 m² per row). Based on the root distribution observed in the trenches (Section 4.4.3) it was decided to sample at 150 mm increments down to 450 mm soil depth.

Core samples were collected in early autumn 2012 (March 23rd), late autumn (May 15th), late winter (August 27th), late spring (November 19th) and in early autumn 2013 (March 4th). At each sampling, to account for potential variability in root distribution around the tree, three sampling positions were located 120° apart from each other around the tree trunk (Fig 4.5). To reduce the

likelihood of encountering large roots (>20 mm diameter), core samples were excavated 2 m away from the tree stem. Subsequent samplings were conducted 20° away from the previous position.

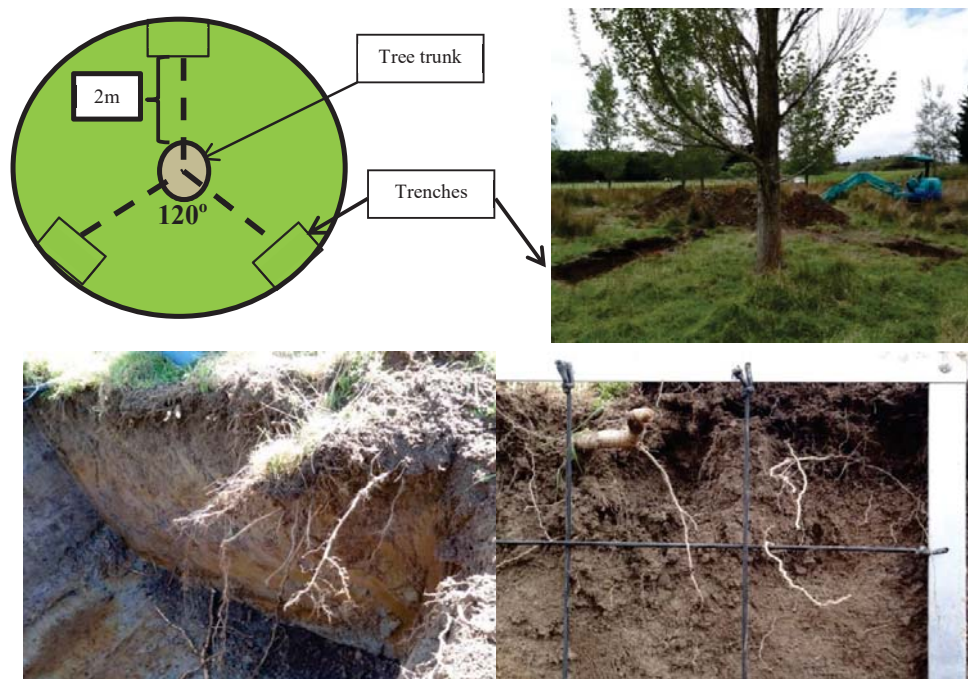


Figure 4.4 Trenching work to determine root distribution of poplar trees and sample coring

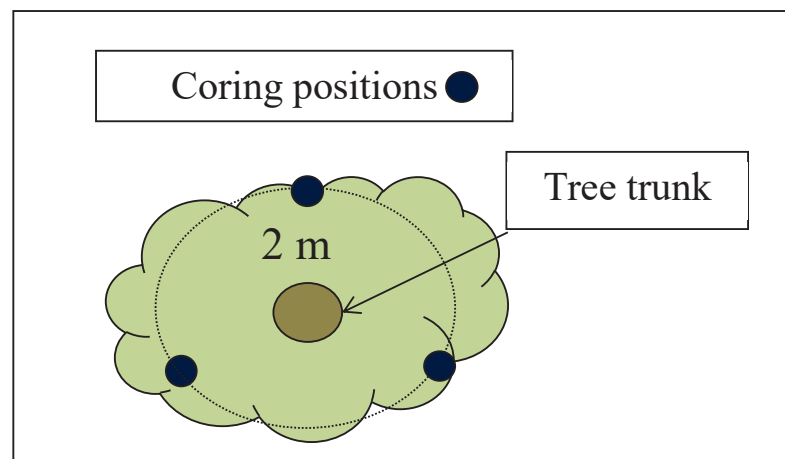


Figure 4.5 Sample coring positions around the trees for determining changes in root dynamics after early autumn pollarding.

Recovery of roots from soil cores and measurement of root length and root mass density followed the same procedures described for willow tree roots in Sections from 3.3.3.1. to 3.3.3.1.2.

4.3.3.3 Root non-structural carbohydrates (NSC) dynamics

For analysing root NSC soil cores were taken down to 450 mm depth. Samples were taken in early autumn (20th March), late autumn (20th May), early spring (18th September) and late spring (21st November). Starch and the soluble sugars sucrose, glucose and fructose were analysed using the techniques described in Section 3.3.3.2.

4.3.4 Statistical analysis.

At each sampling, root density data for the three sampling positions around individual trees were averaged and expressed as per m³ of soil. All data were analysed as a repeated measures design over the trees as subjects. The MIXED procedure of the SAS software 9.4 (SAS, 2012), was used with an autoregressive correlation structure to take account of the repeated measures. For root density dynamics, treatments (UP and P), root sampling time (early autumn, late autumn, late winter, late spring and early autumn) and their interactions were considered in the model as fixed effects and separate analyses were run for each depth (0-150 mm, 150-300 mm and 300-450 mm). Similarly, for root NSC dynamics after pollarding, treatments and sampling times (early autumn, late autumn, early spring and late spring) and their interactions were considered as fixed effects. Since coarse roots were frequently absent from soil core samples (Appendix 4.1 and Fig A.1), transformation of the data including the zero values plus a constant was conducted to help meet the underlying model assumptions. Likewise, root non-structural carbohydrates data that required transformation are identified in their corresponding figures.

4.4 Results

4.4.1 Above-ground tree responses

The range of DBH at the beginning of the study was wider for P trees than for UP trees and there was initial clonal variation in the biomass above pollarding height (Table 4.3). There was considerable variation between pollarded clones/trees in their shoot regrowth characteristics (Table 4.3). The largest tree at pollarding ('Weraiti') had the lowest increment height growth one year after pollarding, whereas the was the smallest clone ('Shinsei') at the beginning of the study, had, along with 'Kawa' tree, the greatest increments in height growth. (Table 4.3).

One year after pollarding, P trees had significantly lower increase in DBH and greater increase in height growth than UP trees (Table 4.2). Unpollarded trees showed a DBH increment of 3.9 cm whereas P trees had a much reduced increment of 0.6 cm. These increments in DBH represented a 4 and 24% increase in the trunk biomass at a pollarding height for P and UP trees, respectively.

Table 4.2 Tree parameters (mean \pm s.e.) at the beginning of the study and after one year for unpollarded (UP) and pollarded (P) trees.

Treatment	Initial			One year increment	
	DBH (cm)	HEIGHT (m)	Biomass above pollarding height (kg DM/tree)	DBH (cm)	HEIGHT (m)
UP	34.4 \pm 0.9a	16.9 \pm 3.1a	N/A	3.9 \pm 0.9a	0.9 \pm 0.5a
P	31.8 \pm 5.9a	18.1 \pm 1.8a	258.3 \pm 58.3	0.6 \pm 0.8b	2.8 \pm 0.8b

Means in the same column followed by different letters are significantly different ($P < 0.05$). NA not applicable

Table 4.3 Differences in tree parameters at pollarding and one year after pollarding.

Parameter	Trees pollarded		
	'Shinsei'	'Weraiti'	'Kawa'
Biomass above pollarding height (kg DM/tree)	143	331	301
One year growth			
Number of shoots	44	33	64
Shoots >2 mm basal diameter (% of all shoots)	52	3	16
Total basal diameter (mm) (of shoots >2 mm basal diameter)	656	64	460
Longest shoot (m)	3.2	1.9	3.2

4.4.2 Phenology of the trees

4.4.2.1 Autumn-Winter transition

In the Autumn-Winter transition with UP trees, senescence and dormancy occurred in the sequential order of 'Weraiti', 'Shinsei' and 'Kawa' clones. By late April 2012 trees of the first clone showing senescent leaves were those of 'Weraiti'. By mid May 2012 'Weraiti' trees had shed almost all their leaves, and 'Shinsei' trees showed early senescence, having started to lose their leaves. Meanwhile 'Kawa' trees were still in leaf and showed signs of senescence in most of the foliage. By June 2012 trees of 'Weraiti' were in a complete (no leaves) dormant stage whereas those of 'Kawa' and particularly 'Shinsei' were in pre-dormancy stage shedding leaves actively. By early-mid July, trees of all three clones were leafless.

4.4.2.2 Winter-Spring transition

In September 2012 'Weraiti' and 'Shinsei' UP trees were the first to burst bud. 'Weraiti' trees had flowers on the branches of the upper third of the canopy whereas branches in the mid and lower third of the canopy had started leaf flushing. Branches of the 'Shinsei' tree were already growing shoots and leaves in almost the whole canopy but preferentially from the mid to the lowest part of the canopy. The 'Kawa' UP tree (tree number 8) had flowers on the branches of the upper third of the canopy. By late October/early November all three clones were in leaf.

Pollarded trees followed a resprouting sequence similar to that observed for UP trees. In September 2012 all clones were showing the tip of a few buds emerging, with the 'Shinsei' P tree

already extending a few small leaves. By late October all P trees showed growing leaves with ‘Shinsei’ having a more advanced growth than the other clones.

4.4.3 Vertical root distribution of poplar trees

Trenching work carried out at the beginning of the study showed that 97% and 98% of the roots were within 0 to 450 mm soil depth for the ‘Weraiti’ and ‘Shinsei’ clones, respectively, with very fine (<1 mm diameter) and fine (1<2 mm diameter) roots together representing 90% and 93% of the total roots counted for the ‘Weraiti’ and ‘Shinsei’ clones, respectively (Tables 4.4 and 4.5).

Table 4.4 Vertical root distribution of one ‘Weraiti’ poplar tree in autumn 2012 (total number of roots within a frame 90 cm × 90 cm in each of three trenches around the tree)

Soil depth (mm)	Number of roots m ⁻² at each diameter category and soil depth						Total	% of Total
	Very fine (0 ≤ 1 mm)	Fine (> 1 ≤ 2 mm)	Small (>2 ≤ 5 mm)	Medium (>5 ≤ 10 mm)	Large (>10 ≤ 20 mm)	Very large (>20 mm)		
0-150	104	28	7	1	1	1*	142	67
0-300	137	42	11	2	1	1	194	91
0-450	141	47	14	3	2*	1	207	97
0-600	142	47	14*	3*	2	1	209	98
0-750	142	49	14	3	2	1	211	99
0-900	143	50	14	3	2	1	213	100
% of Total	67.2	23.4	6.6	1.5	0.8	0.5		

*No additional roots observed in deeper sections

Table 4.5 Vertical root distribution of one ‘Shinsei’ poplar tree in autumn 2012 (total number of roots within a frame 90 cm × 90 cm in each of three trenches around the tree)

Soil depth (mm)	Number of roots m ⁻² at each diameter category and soil depth						Total	% of Total
	Very fine (0 ≤ 1 mm)	Fine (> 1 ≤ 2 mm)	Small (>2 ≤ 5 mm)	Medium (>5 ≤ 10 mm)	Large (>10 ≤ 20 mm)	Very large (>20 mm)		
0-150	93	28	4	2	2*	1*	130	80
0-300	111	33	5*	2*	2	1	154	95
0-450	115	34	5	2	2	1	159	98
0-600	115	34	5	2	2	1	159	98
0-750	116	34	5	2	2	1	161	99
0-900	117	35	5	2	2	1	163	100
% of Total	72.1	21.3	3.0	1.5	1.3	0.8		

*No additional roots observed in deeper sections

4.4.4 Fine root density dynamics

4.4.4.1 Fine root density (fRD) dynamics of unpollarded (UP) trees.

At 0-150 mm soil depth, from early autumn (March 2012) to late autumn (May 2012), fine root length (fRLD) and mass (fRMD) densities of UP trees increased by more than 2-fold ($P < 0.01$) (Fig 4.6). These were followed by decreases in both attributes in winter and then attainment of maximum fine root densities, both fRLD and fRMD, in late spring (November 2012). At the last sampling in early autumn in March 2013, fRLD was less than half ($P < 0.05$) that in November 2012 and was not significantly different ($P > 0.05$) to that recorded in the same UP trees in the previous year at the beginning of autumn 2012. In contrast, fRMD in autumn 2013 was similar to that in spring 2012 and about 2.4-fold greater ($P < 0.05$) than observed in early autumn 2012 (Fig 4.6).

The significant increases in fRLD and fRMD observed in autumn (May 2012) at 0-150 mm depth were not observed deeper in the soil profiles. At 150-300 mm and 300-450 mm soil depth no significant changes in densities were detected between sampling times, although the highest fine root densities were recorded in November at 150-300 mm depth, as also found at 0-150 mm soil depth (Fig 4.6).

4.4.4.2 Fine root length density (fRLD) dynamics after pollarding the trees in early autumn.

Early trends in fRLD for P trees were similar to those observed for UP trees. At 0-150 mm soil depth, between time of pollarding and late autumn (May 2012), fRLD increased by about 3-fold (Fig 4.6). In late autumn, there were no significant differences in fRLD between P and UP trees. As found for UP trees, fRLD of P trees decreased in late winter, but in contrast to UP trees, late spring was the time when the lowest fine root length densities were observed for the P trees. In late spring 2012, P trees had significantly less fRLD ($P < 0.05$) than UP trees (Fig 4.6).

From late spring in November to early autumn 2013, one year after the trees were pollarded, a decrease in fRLD of UP trees and a slight increase in fRLD of P trees resulted in similar densities ($P > 0.05$) between both treatments. Both treatments also showed one year after the beginning of

the study similar fRLD compared with the initial densities recorded 2-3 days before selected trees were pollarded (Fig 4.6).

Below 150 mm soil depth, major differences in fRLD of P trees were not detected between sampling times and there were no significant differences in fRLD between P and UP treatments. However, in November 2012 at 150-300 mm soil depth, the greatest difference in fRLD between UP and P treatments was found, which supported the findings at 0-150 mm depth (Fig 4.6).

4.4.4.3 Coarse root length density (cRLD) dynamics after pollarding the trees in early autumn.

Coarse roots (>2 mm diameter) contributed less than 10% to total root length density, with the maximum treatment \times time combination being less than 350 m m⁻³ (Fig 4.7) compared with a minimum of 2,000 m m⁻³ for fine roots (Fig. 4.6). High variability in coarse root length density was recorded, with coarse roots being frequently absent from soil cores at different depth increments and sampling times (Appendix 4.1 and Fig A.1). There were no significant differences in coarse root length density between sampling times within treatments or between treatments at any of the sampling times.

4.4.4.4 Fine root mass density (fRMD) dynamics after pollarding the trees in early autumn.

Except in early autumn 2013 (March), at 0-150 mm soil depth, where significant differences in fRMD were detected between UP and P trees, at all other samplings, fRMD showed similar responses to pollarding as found for fine root length density. Immediately after pollarding, fRMD of P trees increased ($P < 0.05$) by about 3-fold and trees in P and UP treatments had similar densities ($P > 0.05$) (Fig 4.6). fRMD had decreased by late winter (August 2012) in both treatments, although values were not significantly less than in autumn. In late spring (November 2012) fRMD of trees in the P treatment averaged about 75% less ($P < 0.05$) than for trees in the UP treatment.

By early autumn 2013, P trees still had significantly less ($P < 0.05$) fRMD than UP trees but the difference between the treatments was smaller (50% less). This was because of reduced fRMD of UP trees and increased fRMD of trees in the P treatment (Fig 4.6).

In soil from 150 mm to 450 mm depth, fRMD was not significantly different between treatments at any of the sampling times (Fig 4.6).

As observed for fRLD, fRMD of pollarded trees was one year after pollarding, similar to that recorded 2-3 days before pollarding. (Fig 4.6)

4.4.4.5 Coarse root mass density (cRMD) dynamics after pollarding the trees in early autumn.

In contrast to trends observed for coarse root length density, coarse roots contributed a significant proportion of the total root mass density, with mass densities about twice those for fine roots (Fig 4.7). However, data for coarse root mass density were also highly variable and no significant differences were detected between treatments at any of the sampling times. Model assumptions of normality and variance homogeneity were improved by natural logarithm transformation (Section 4.3.4), however the transformed outcome did not differ from the *F* test outcome of analyses carried out on the original measurement scale.

Soil depth (mm)

0-150

150-300

300-450

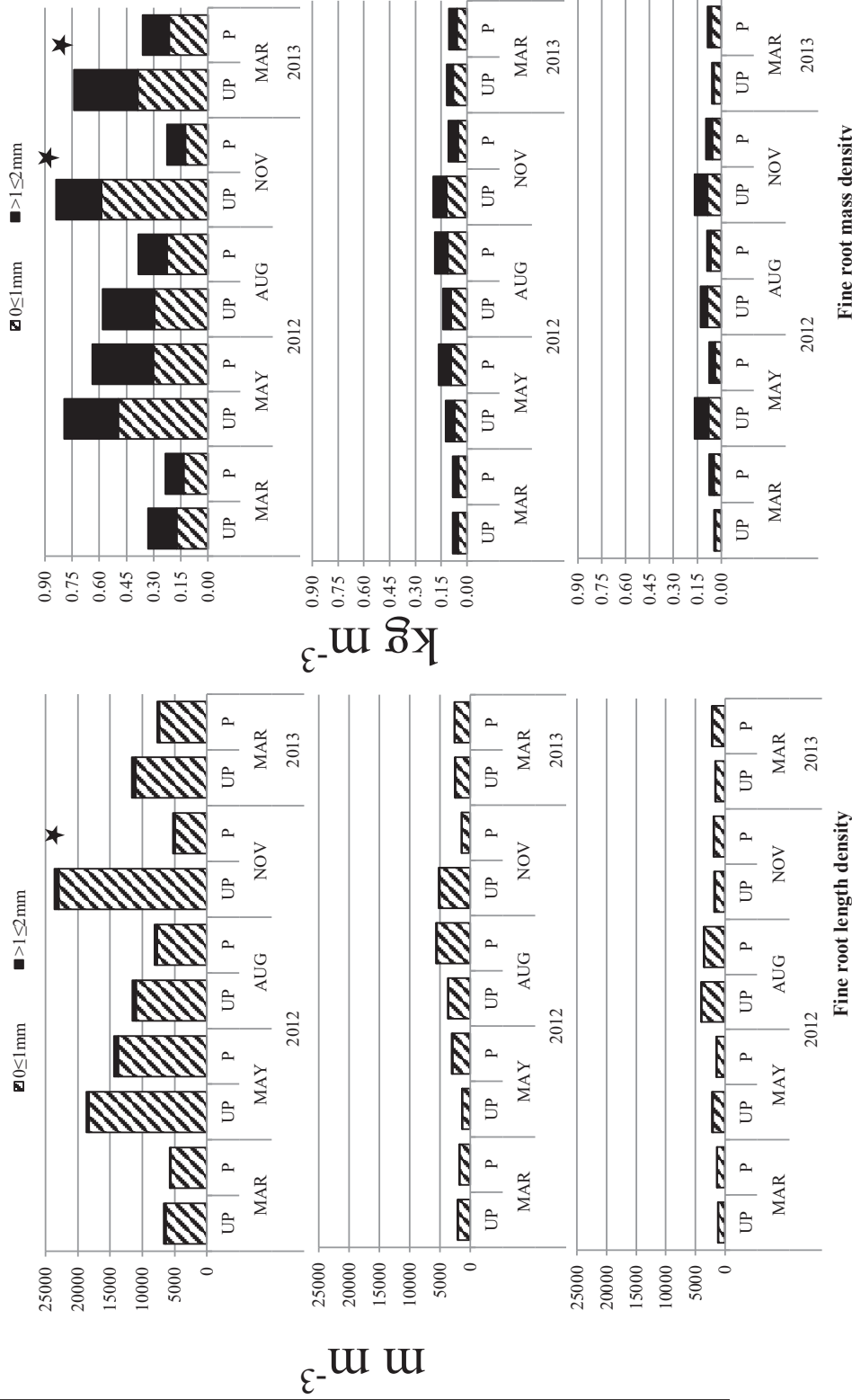


Figure 4.6 Fine root length and root mass density dynamics of poplar trees unpollarded (UP) and pollarded (P) in early autumn 2012. soil sample volume= 754 cm³ * indicates significant differences between treatments in overall fine roots (0 ≤ 2 mm) at individual sampling times (P < 0.05); root diameter categories: 0 ≤ 1 mm and > 1 ≤ 2 mm

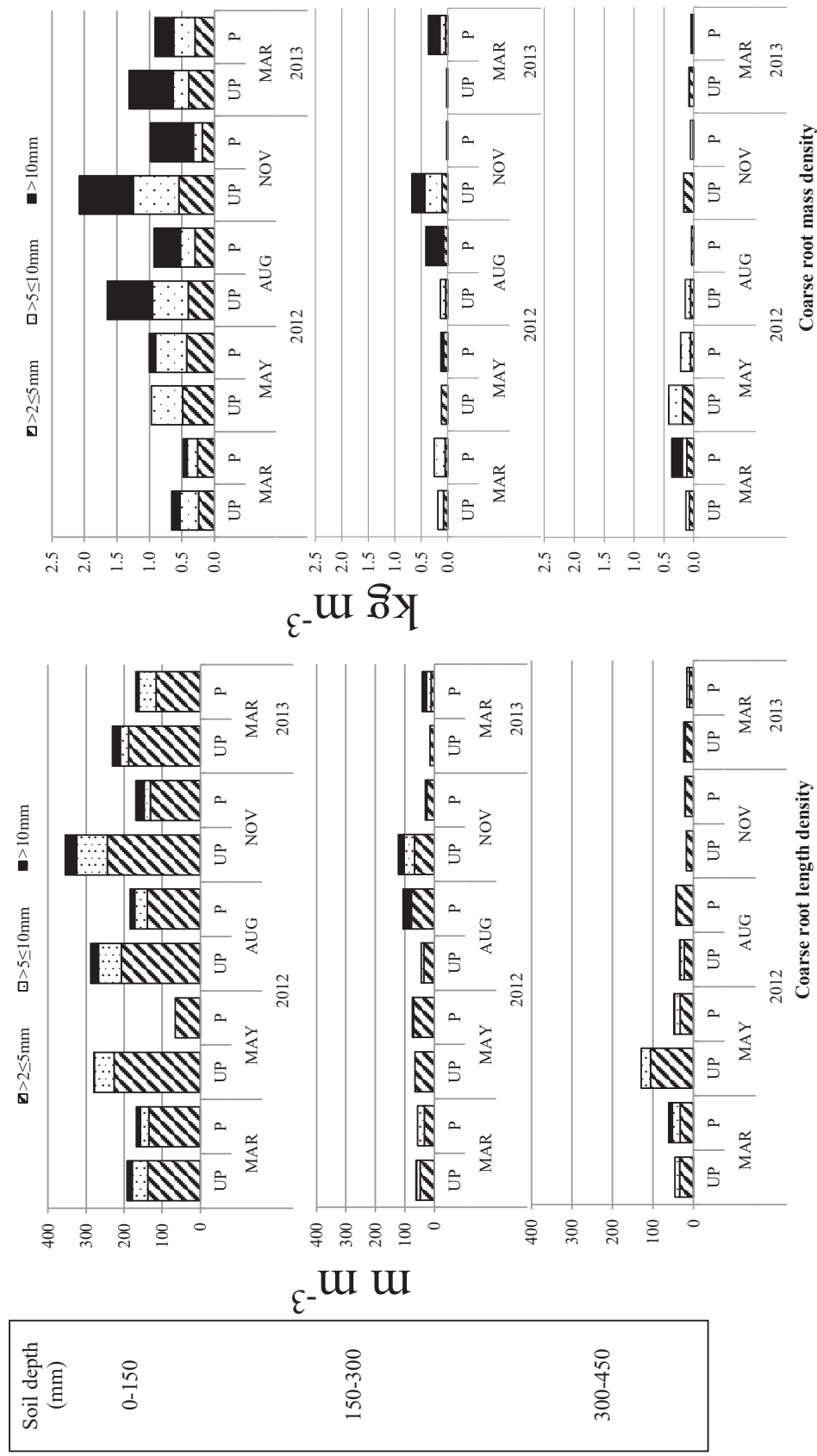


Figure 4.7. Coarse root length and root mass density dynamics of poplar trees uncollared (UP) and collared (P) in early autumn 2012. soil sample volume= 754 cm³. Root diameter categories: >2≤5 mm, >5≤10 mm and >10 mm. In, natural logarithm back transformed data

4.4.5 Root non-structural carbohydrate dynamics of poplar trees pollarded in early autumn.

Root starch concentrations found in the P and UP treatments decreased from early autumn 2012 to late spring 2012 (Fig 4.8). A slightly greater decrease occurred in trees in the P treatment, which had lower concentrations than UP trees in late spring 2012 ($P < 0.05$).

Root sucrose concentrations of trees in P and UP trees showed a similar trend across all sampling times and there were no significant differences in concentration between times or between treatments within times (Fig 4.8). At the last sampling in late spring 2012, treatments had similar concentrations of root sucrose (Fig 4.8).

Within UP and P treatments, root glucose and fructose concentrations followed similar patterns from time of pollarding, in autumn, until early spring. During this period, for each monosaccharide there were no significant decreases in concentration in the P treatment whereas in the UP treatment, there was a greater decrease ($P < 0.05$) in concentration of glucose and fructose between early autumn 2012 and early spring 2012 (Fig 4.8). Afterwards, root glucose and fructose concentrations of P trees followed different and opposite trends with fructose concentration increasing to that similar before pollarding and glucose concentration decreasing below ($P < 0.05$) that in early autumn 2012 (Fig 4.8).

In contrast to P trees, root concentrations of glucose and fructose of UP trees decreased from pollarding to late spring 2012 (Fig 4.8). At the end of the study, in late spring 2012, both glucose and fructose root concentrations of UP trees were less ($P < 0.05$) than those of P trees.

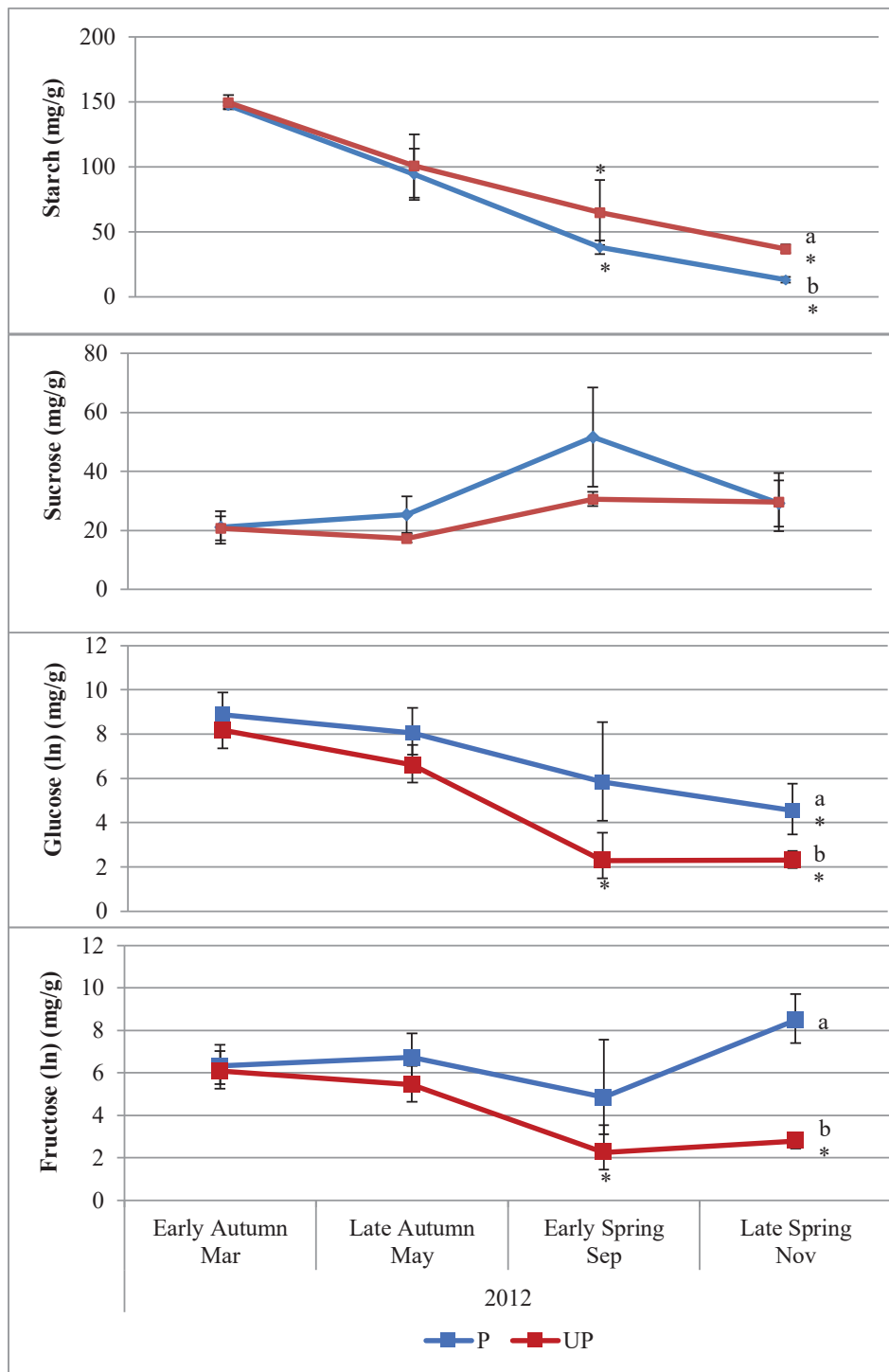


Figure 4.8 Mean (n=3) and standard error bars of root non-structural carbohydrate dynamics of unpollarded (UP) and poplar trees pollarded (P) in early autumn 2012. In late spring, treatment means with different letters are significantly different ($P < 0.05$). *indicates less than concentration in early autumn ($P < 0.05$). (ln) indicates natural logarithm back transformed data.

4.5 Discussion

4.5.1 Fine root density (fRD) dynamics of unpollarded (UP) poplar trees.

Vertical root distributions observed in the trenches dug at the beginning of the study (Tables 4.4 and 4.5) concurred with findings of Douglas et al. (2010) and Bouttier et al. (2014). Over a range of poplar (*Populus deltoides* Marshall × *P. nigra* L. clone ‘Tasman’) densities from 84 to 770 stems per hectare, with trenches dug half and a quarter the distance between adjacent trees, Douglas et al. (2010) found that 86% of the total roots identified on trench faces were located within 0-450 mm soil depth. Bouttier et al. (2014) reported for two hybrid poplars (*P. deltoides* Marshall × *P. nigra* L.) that 95% of the fine root length density within 0-1000 mm soil depth was located above 450 mm.

Major changes in fine root density of UP trees were observed for roots located within 0-150 mm soil depth (Fig 4.6).

In general terms, at the 0-150 mm soil depth, from late winter 2012 (August) to early autumn 2013 (March), fine roots of UP trees showed the regular seasonal trend most commonly found for deciduous trees, including *Populus* and *Salix* species growing in temperate environments. Appearance of new fine roots starts and peaks before bud break (Rytter and Hansson, 1996, Rytter, 1999, McCormack et al., 2015). After bud break, fine roots continue appearing and elongating during leaf flush and through the growing season (Hendrick and Pregitzer, 1993). Fine root biomass reaches a peak during summer or autumn depending mostly on the inherent attributes of the tree species and on weather conditions during the growing season (Hendrick and Pregitzer, 1993, Coleman et al., 2000, Kern et al., 2004). Shortly before or after shoot growth ceases, production and growth of fine roots decrease, and root mortality, which is maintained at relatively stable low levels during the growing season, increases. At the end of the growing season, depending on the magnitude of the decreases in fine root production and increases in fine root mortality, fine root biomass levels off or has different degrees of decrease (Rytter and Hansson, 1996, Coleman et al., 2000, Kern et al., 2004, Berhongaray et al., 2013).

At the study commencement, UP trees showed an initial trend that differed from the most commonly observed seasonal trends (Fig 4.6) (Hendrick and Pregitzer, 1993, Rytter and Hansson, 1996, Rytter, 1999, Coleman et al., 2000, Kern et al., 2004, Block et al., 2006, Berhongaray et al., 2013). From early (March) to late (May) autumn 2012, fine root length and mass density of UP trees increased by more than 2-fold (Fig 4.6). Fine root densities recorded in the growing season from late winter 2012 to late summer 2013 suggest that in the previous season (from winter 2011 to late summer 2012), either fine root production was delayed and reached its maximum in autumn 2012 or it was because of a bimodal pattern of growth. Both circumstances have been reported previously and have been attributed to environmental conditions constraining above- and below-ground growth (Rytter and Hansson, 1996, Landhäusser and Lieffers, 2003). Bimodal growth patterns with two peaks in root biomass during the year were observed by Singh and Srivastava (1986) in a *Tectona grandis* plantation growing in a tropical region of India, characterised by recurrent and well defined dry summers. Similarly, two peaks in fine root biomass in Douglas fir (*Pseudotsuga menziesii*) trees were observed in spring and autumn, and were associated with dry summers (Santantonio and Hermann, 1985).

Under the hypothesis of a shift in the period of maximum fine root growth, Landhäusser and Lieffers (2003) observed that under boreal forest conditions, *Populus tremuloides* clones had maximum fine root production after the end of the shoot growth period in late autumn. Landhäusser and Lieffers (2003) proposed that microclimatic soil conditions characteristic of boreal ecosystems, like prolonged time for top soil warming, could have been responsible for the shift in the root growth period.

Weather conditions during this study (Fig 4.3) precluded dry or soil freezing conditions as factors influencing the root growth pattern observed. However, the growing season in 2011-2012 in this study was particularly wet. Records during the study showed rainfall from September 2011 to February 2012 was above historical records (Fig 4.3). The study site was located in a seasonally wet area, where waterlogging is a recurrent phenomenon after periods of heavy or prolonged rainfall. This could have limited below-ground growth during the early and middle stages of the

wet 2011-2012 growing season and also might have resulted in mortality of some fine roots. Reduction of 60% in root growth were recorded in the few *Populus nigra* plants surviving (survivorship rate of 30%) inundation conditions in fine textured substratum in a glasshouse experiment (Francis et al., 2005). Flooded and completely submerged treatments applied to different clones of *Populus deltoides* plants reduced the root biomass to less than half that observed in regular watered plants (Cao and Conner, 1999). According to the records taken by Cao and Conner (1999), reductions in root biomass were caused primarily by root death and decay and secondly by root growth inhibition. However, differences between the *Populus deltoides* clones to withstand flooded conditions were also observed by Cao and Conner (1999).

The increase in fine root density observed in 2012 from early autumn to late autumn occurred simultaneously with an atypical decrease in root starch concentration during the same period (Fig 4.8). Reports on root starch dynamics in poplar trees show that after an initial decline in root starch concentrations associated with bud burst and leaf flush, root starch concentrations start replenishing when first leaves are fully expanded (Bonicel et al., 1987, Fitzgerald and Hoddinott, 1983, Loescher et al., 1990, Kozłowski, 1992, Von Fircks and Sennerby-Forsse, 1998). However, the fastest replenishment and highest root starch concentrations are not observed until shoot growth has ceased and after bud set in autumn (Von Fircks and Sennerby-Forsse, 1998, Nguyen et al., 1990, Isebrands and Nelson, 1983, Dickson and Nelson, 1982). Landhäusser and Lieffers (2003) reported that the high root growth observed in late autumn in *Populus tremuloides* trees occurred simultaneously and was associated with a decrease in the root total non-structural carbohydrates. In the current study, it is possible that the decrease in root starch concentration observed in autumn in the UP trees was associated with supporting the fine root growth observed during the same period. Indirect evidence for this was found for UP willow trees (Chapter 3) that showed an increase in root starch concentration commonly reported in autumn (Von Fircks and Sennerby-Forsse, 1998, Nguyen et al., 1990, Isebrands and Nelson, 1983, Dickson and Nelson, 1982) (Fig 3.9). In contrast to the UP poplar trees in this study, the UP willow trees reported in Chapter 3 had decreased fine root length and mass densities from early to mid autumn (Figs 3.6 and 3.7).

4.5.2 Fine root density (fRD) dynamics of poplar trees pollarded (P) in early autumn.

Compared with UP trees, the impact of pollarding trees in early autumn on the fine root system can be described as concentrated within 0-150 mm soil depth and being of short duration. This conclusion is based on the following three main findings: a) the greatest impact of pollarding was limited to the fine roots located at 0-150 mm soil depth, with no major changes observed in fine root densities below 150 mm depth; b) at 0-150 mm soil depth, root response was characterised by an immediate increase in fine root density after pollarding, and c) significant differences in fine root density between P and UP trees were limited to the peak of the growing season (late spring and early autumn) when fRD of P trees were around 50 to 75% less than UP trees (Fig 4.6).

4.5.2.1 Early autumn pollarding had the greatest impact on the shallowest fine roots.

Differences in fine root density between P and UP trees at individual sampling times were detected only at 0-150 mm soil depth (Fig 4.6).

A series of reports on tree root responses to canopy removal have shown that the main impacts have occurred in the shallow soil layers. One year after coppicing poplar clones, Lee (1994) recorded decreases in root number in the 0-150 mm and 150-300 mm soil depths and increases at 300-450 mm soil depth. One year after pollarding mature willow trees (36.3 cm DBH), McIvor et al. (2011) found that fine root length density of P trees was 49% that of unpollarded trees at 0-300 mm depth, but was unaffected deeper in the soil profile. One year after pollarding, pollarded willow trees studied by McIvor et al. (2011) had recovered to pre-pollarding fRLD levels. Jones et al. (1998) reported that the main changes in fine root length density of *Prosopis juliflora* and *Acacia nilotica*, either increases or decreases, occurred in the top 400 mm of soil 60 days after trees were pruned.

4.5.2.2 An immediate increase in fine root density after trees were pollarded in early autumn.

Within the overall root response, it is important to highlight the increase in fine root density 1.5 months after pollarding (Fig 4.6). This was also shown and discussed for UP trees in Section 4.5.1.

Immediate increases in fine root length and mass densities following canopy removal have been reported previously. Jones et al. (1998) found differences between species in root responses after pruning of *Acacia nilotica* and *Prosopis juliflora* growing in the same plot and pruned at the same time. Sixty days after being pruned at the end of the rainy season in drylands of Nigeria, *Prosopis juliflora* showed a reduction of 45% in fine root length density while *Acacia nilotica* had a 46% increase (estimated from figures).

Dickmann et al. (1996) found an immediate and sustained increase in root number and length one year after poplar clones (*Populus × euramericana* cv. 'Eugenei' and *Populus tristis × Populus balsamifera* cv. 'Tristis 1') were coppiced a few days before commencement of spring growth. They proposed that at the moment of coppicing, the root system of the trees contained carbon and nitrogen reserves able to fuel a spring flush of fine-root growth, even though the canopies were severed during the dormant season. Based on the root starch dynamics of UP trees in this study during the 2012-2013 growing season (Fig 4.8), it is hypothesised that roots of poplar trees at the moment of pollarding, in early autumn 2012, had already started replenishing energy reserves at levels that supported a moderate carbon demand either for resprouting or for root growth processes. As was seen for UP trees in this study, the increase in fine root density in P trees from pollarding in early autumn to late autumn happened simultaneously with an atypical decrease in root starch concentrations. Most commonly late autumn after bud set has been reported as the time for a relatively sudden downward carbon translocation and the greatest increases in root starch accumulation were observed during this period (Isebrands and Nelson, 1983, Nguyen et al., 1990, Von Fircks and Sennerby-Forsse, 1998, Dickson and Nelson, 1982)

Re-sprouting of P trees was not observed during the period from pollarding to late autumn. However re-sprouting occurred at the beginning of the following growing season in spring when

all pollarded clones were already flushing leaves around late October early November. It is suggested that the relatively high root starch concentrations at the time of pollarding were used preferentially for the fine root growth. This phenomenon was also reported by Landhäusser and Loeffers (2003) in *Populus tremuloides* clones grown in a boreal forest when a delayed late autumn root growth was associated with a decrease in root starch concentration. It is noteworthy that the willow trees pollarded in early autumn (Chapter 3) showed an increase in root starch concentration, which is commonly found in autumn (Fig 3.18). The number and growth of sprouts observed from early autumn pollarding and dormancy onset of willow trees reported in Chapter 3 was minimal (estimated visually). However, in contrast to the poplar trees pollarded in early autumn in this study, willow trees pollarded in early autumn (Chapter 3) showed no change in fine root density within the same period.

4.5.2.3 Temporary impact of pollarding poplar trees in early autumn on the fine root system.

Immediate reductions in fRLD after early autumn pollarding, observed during dormancy between P and UP willow trees, were maintained in the following spring and summer season one year after pollarding (McIvor et al., 2011). In this study, the main impact detected of pollarding on the fine root system occurred during the following growing season after pollarding, mainly in spring, when UP trees reached their greatest fine root length and mass densities and P trees, their lowest. Ma et al. (2013) also found that differences in fine root biomass between a stand of clear cut *Quercus* trees and a stand of uncut trees was mainly seen at the peak of the growing season. These patterns coincide with those reported in Sections 3.4.1.2. and 3.4.1.4. when during the peak of the growing season (spring to late summer), the greatest fine root densities were observed in UP willow trees, and fine roots of dormant pollarded willow trees failed to show the regular peak growth commonly reported at that time. This particular finding in Chapter 3 and this study strongly suggest that regardless of the immediate root response of different tree species pollarded at different phenological phases, pollarded trees fail to show root growth at the moment when regularly it is expected to see the maximum growth.

Under the hypothesis of hierarchy carbon (C) phloem sink depletion, Landhäusser and Lieffers (2012) proposed that after severe defoliation of *Populus tremuloides* trees, canopy and bole tissues, nearer to the renewed sources, are the first to restore non-structural carbohydrate reserves; and roots, which are the C sinks at the end of a proposed “C phloem stream”, would be the last. Landhäusser and Lieffers (2012) proposed that the phenomenon would be more obvious during the first part of the growing season when leaf area is developing and cambial activity along the large branches in the canopy and particularly in the long bole is high. After shoot growth ceases and diameter growth slows, most of the phloem stream bypasses those proximate sinks and C is available to replenish the more distal sinks such as the root system. If root reserves fall below a critical threshold, loss of fine roots is expected (Landhäusser and Lieffers, 2012). Ma et al. (2013) observed after three years of an oak forest clear cutting that mass of fine roots deeper in the soil decreased more than in the 0-10 cm soil depth. Similarly to the ‘C phloem stream’ principle proposed by Landhäusser and Lieffers (2012), Ma et al. (2013) suggested that the first fine roots to regrow are those in the shallowest soil layers because they may obtain carbohydrates from resprouting sources ahead of those deeper in the soil. In this study it is proposed that around the peak of the growing season, pollarded poplar trees, which were restoring shoot:root ratio, preferentially allocated available resources for shoot extension.

Immediate increases or transient reductions in fine root density observed in this study and in dormant and early autumn pollarded willow trees reported in Chapter 3, contrast with the findings of McIvor et al. (2011). They observed an immediate and sustained significant reduction in the fine root density of wide-spaced-planted willow trees growing on steep hill pastures, which were pollarded during a summer drought. Fine root reductions observed by McIvor et al. (2011) were maintained during the 1st year after pollarding and from the beginning of the 2nd year to before or at the end of the 3rd year after pollarding. Several factors were proposed in Section 3.5.2.2. to explain the differences in root response between early autumn pollarded willow trees and those in the McIvor et al. (2011) study. The factors that also might have had an influence on the fine root density dynamics found for poplar trees in this study are: 1) root energy reserves at the time of pollarding, 2) resprouting intensity between time of pollarding and the onset of dormancy, and

3) soil properties as they influence the extent and rate at which shoot to root ratios are restored. The factors proposed provide hypotheses feasible to be tested in field and glasshouse studies.

1). Based on the root starch dynamics of UP trees in this study and of the UP willow trees reported earlier (Fig 3.9), it is suggested that root starch concentrations started replenishing in spring and reached maximum levels in autumn. The trees in this study were pollarded later in the year in early-mid autumn (day of the year DOY 80) than the willow trees pollarded by McIvor et al. (2011) in late summer (DOY 45). This may have resulted in the poplar trees of this study and willow trees of Chapter 3 (pollarded DOY 67) at the time of pollarding having higher energy reserves than the willow trees studied by McIvor et al. (2011), thereby enabling greater responses to the C demands exerted by resprouting or fine root growth processes.

2.) Based on the time of pollarding, willow trees in the McIvor et al. (2011) study had a longer opportunity for resprouting than the pollarded poplar trees in this study, because the latter were pollarded closer to dormancy. Trees in the McIvor et al. (2011) study could have had a greater immediate demand for energy reserves stored in the remnant organs for resprouting purposes, than those involved here, because no resprouting response was observed from pollarding in early autumn until dormancy. The time for resprouting of willow trees in the McIvor et al. (2011) study might have been too short before dormancy to develop a canopy able to replenish carbohydrate reserves for both above- and below-ground growth in the following growing season. Defoliation of kiwifruit vines (*Actinidia chinensis*) (Kwack et al., 2014) and sweet cherry trees (*Prunus avium* L) (McCamant, 1988) towards the end of the growing season resulted in the lowest tissue starch accumulation measured after natural leaf abscission, in comparison with defoliations conducted either earlier in the growing season, or closer to dormancy (Kwack et al., 2014). Defoliations conducted near the end of the growing season resulted in small, yellow leaves and poor sweet cherry fruit set in the following year (McCamant, 1988).

3) Soil environmental conditions, principally soil fertility and water holding capacity, may have limited resprouting potential of willows on drought-prone hill country (McIvor et al., 2011) compared with that of trees on the Manawatu soil types in this study and the earlier willow study

(Chapter 3). Research conducted with poplar trees (Bedenau and Pages, 1984, Lee, 1994, Dickmann et al., 1996) found increased fine root densities after above-ground intervention for trees growing under improved soil fertility or soil moisture conditions.

4.5.3 Coarse root density dynamics of poplar trees pollarded in early autumn.

Lateral distribution of coarse roots around a tree can be asymmetrical, particularly on sloping land. With hybrid poplar trees (*Populus deltoides* Marshall \times *P. nigra* L.) clone ‘Veronese’, McIvor et al. (2008) found asymmetry in the radial coarse root (≥ 2 mm diameter) distribution around individual trees aged 5, 7 and 9.5 years, located near the accumulation zone on the lower part (17° slope angle) of a hillslope. Over a range of slope angles on the same hillslope, McIvor et al. (2009) found increasing symmetry in the radial coarse root distribution of Veronese poplar trees aged 11.5 years, with decreasing slope angle. An increase in the symmetry of radial root distribution was also observed by Puri et al. (1994) in *Populus deltoides* plantations, when the tree stand density decreased from 2250 to 208 stems per hectare (sph). In a *Eucalyptus* plantation with 800 sph, Levillain et al. (2011) concluded that the auger core method was reliable for estimating fine root biomass but not coarse root biomass. Asymmetric coarse root distribution was proposed by Levillain et al. (2011) as the most likely cause for the differences in accuracy and precision of the estimations.

In this study soil cores collected for different trees at different sampling times had no coarse root presence (Appendix 4.1 and Fig A.1). High variability was observed in the coarse root length and mass densities of the poplar trees and no significant differences between treatments were detected. Nonetheless, for the pollarded poplars coarse root density dynamics still showed some of the distinctive features observed for the fine root density dynamics, like spring being the season where the greatest differences in coarse root density were recorded between P and UP trees.

4.5.4 Root non-structural carbohydrate dynamics of poplar trees pollarded in early autumn.

From pollarding in early autumn to late autumn, P and UP trees showed similar fRD and root starch concentration dynamics. As proposed in Section 4.5.1 there were environmental conditions

that might have shifted or delayed the peak of root growth from late summer to late in autumn. The decline in starch concentrations measured at that time in both P and UP trees suggest that starch was used to support the fine root growth observed. Meanwhile soluble sugars of P and UP trees showed similar trends.

By the beginning of the next growing season in late August 2012, roots of both P and UP trees had similar starch concentrations to support leaf flush or resprouting in UP and P trees, respectively (Fig 4.8). Some species of willows and poplars which develop flowers before leaf expansion rely initially to a great extent on non-structural carbohydrate reserves (Loescher et al., 1990). Observations in early September 2012 revealed that reserve resources demanding processes were occurring in all UP trees, like unfolding new leaves in the ‘Weraiti’ tree and blossoming in trees of ‘Shinsei’ and ‘Kawa’. Pollarded trees in turn in September, were observed with breaking buds with ‘Shinsei’ trees resprouting a little earlier than trees of the other clones as ‘Shinsei’ had already a few small leaves unfolding. During the 2012 growing season root starch concentrations in P and UP trees continued decreasing, reaching their lowest values in spring, when starch concentration in the roots of P trees was less than that of UP trees (Fig 4.8). Trends of decreasing root starch concentration in intact deciduous trees at leaf flush and during spring have been reported (Kozłowski, 1992, Loescher et al., 1990, Johansson, 1993, Dickmann and Pregitzer, 1992). Partial or complete canopy removal can result in faster decreases in root starch concentration than in intact trees. Von Fircks and Sennerby-Forsse (1998) found a decline in root starch concentration in intact and coppiced *Salix viminalis* plants during shoot extension. Decline in starch concentration was faster in coppiced than in intact plants (Von Fircks and Sennerby-Forsse, 1998).

Among different poplar tree species, starch and sucrose (Bonicel et al., 1987, Nguyen et al., 1990) are the non-structural carbohydrates (NSC) with more regular and defined seasonal trends in intact trees than monosaccharides like glucose or fructose (Cranswick et al., 1987). Similarly, for different temperate deciduous (Luostarinen and Kauppi, 2005, Von Fircks and Sennerby-Forsse, 1998) and tropical tree species (Chesney and Vasquez, 2007, Erdmann et al., 1993), after

complete canopy removal starch has been found as the NSC more labile and more commonly mobilised from storage organs like stems and roots, than soluble sugars.

Responses of soluble carbohydrates to above-ground biomass removal vary more between tree species than responses of starch, which makes drawing conclusions about the patterns observed more difficult. Chesney and Vasquez (2007) observed that while root soluble sugars increased in *Gliricidia sepium* after total pruning, no changes were recorded in *Erythrina poeppigiana*. After coppicing, root glucose and fructose concentrations were reduced more in *Betula pendula* than in *B. pubescens* (Luostarinen and Kauppi, 2005).

In this study, root sucrose concentration of P trees followed a similar response to that of UP trees. Sucrose concentrations in both treatments were maintained and showed similar concentrations from the beginning in early autumn to the last sampling in late spring.

In intact and above-ground managed trees over a range of species, root glucose and root fructose dynamics are often very similar (Bonice et al., 1987, Cranswick et al., 1987, Luostarinen and Kauppi, 2005). The concentrations of glucose and fructose found in this study, supported these earlier findings, except for the spring sampling when concentrations of glucose and fructose of P trees showed opposite trends (Fig 4.8).

Overall, in this study, concentrations of root soluble sugars (sucrose, glucose and fructose) of P trees were greater than for UP trees. Greater sucrose concentrations were found when *Salix matsudana* × *alba* clone ‘Tangoio’ trees were coppiced four times per year compared with twice per year, which implied greater sucrose mobilisation to support carbon demand in the regrowth shoots (Oppong et al., 2002).

Based on the starch and soluble sugar dynamics observed weeks before bud break in stem branches, current shoots and buds of intact *Populus tremuloides* mature trees, Landhäuser and Lieffers (2003) concluded that stem and branches have sufficient NSC to support leaf flush. At leaf flush unpollarded trees must have had a greater starch pool available from canopy structures for resprouting than P trees where those canopy structures had been removed. Resprouting in P trees would have imposed higher reserve mobilisation in the trunk and roots than leaf flush might

have imposed to the same structures of UP trees. A series of reports on different deciduous tree species show that in winter, hydrolysis of part of the starch accumulated in reserve organs during autumn results in an increase of soluble sugars that are later readily mobilised during bud break and leaf flush (Lacointe et al., 1993, Sauter and van Cleve, 1994, Essiamah and Eschrich, 1985). It is possible that mobilisation of energy root reserves at bud break requires starch dissolution which might increase at least momentarily concentrations of a series of soluble sugars before they are incorporated into the sapwood. In early Spring 2012 with different degrees of development, both UP and P trees were showing new tissue synthesis activity that required non-structural carbohydrate reserve mobilisation, like blossoming or leaf flushing in UP trees or appearance and swelling of re-sprouting buds in P trees (Hansen, 1971, Loescher et al., 1990, Landhäusser and Lieffers, 2003).

Accumulation of solutes in roots has been proposed as a mechanism to adjust osmotic pressure and maintain or re-establish the water column halted by shoot removal (Tschaplinski and Blake, 1994) or drought conditions (Carpenter et al., 2008). The phenomenon has been shown as a result of starch and soluble carbohydrate immobilisation (Carpenter et al., 2008) or through accumulation of monosaccharides via sucrose degradation (Tschaplinski and Blake, 1994). The “root accumulation solutes phenomena” was evaluated by Tschaplinski and Blake (1994) and Carpenter et al. (2008) within the first 4-13 days after removal of above-ground components. In the short to medium term, at conditions causing low C assimilation, like drought, defoliation or shading, Marshall and Waring (1985) and Landhäusser and Lieffers (2012) found that root soluble sugars were maintained over root starch depletion. It has been suggested that under prolonged low C assimilation conditions, root starch reserves may be mobilized to such a level that root soluble sugars will no longer be available for growth or respiration, and require being maintained at a minimum level to sustain basic cell functions, like osmotic balance (McDowell and Sevanto, 2010). Root starch and soluble sugar dynamics observed in this study might be in agreement with the root solute accumulation hypothesis under situations when root starch is supporting high C demand. The results showed that root starch concentrations of P poplar trees decreased to close

to undetectable levels (Fig 4.8), whereas root soluble sugars of the P trees remained in general, greater than root soluble sugars of UP trees.

4.6 Conclusions

Pollarding did not cause an immediate decrease in the fine root length and mass density of the poplar trees. After pollarding in early autumn both UP and P trees showed a peak in fine root length and mass density late in autumn. Soil environmental constraints were argued as a likely cause for shifting the period of maximum root density from late summer-early autumn to late autumn. Changes in root starch concentration suggest that this reserve was mobilised to support fine root growth processes, and one year after pollarding root starch concentration of P trees was less than UP trees. The impact of pollarding on the roots occurred mainly in shallow soil and was temporary, because only the roots at 0-150 mm soil depth had around 50 to 75% less root densities than UP trees and only around the peak of the growing season.

4.7 References

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Chapter 5. Above-, below-ground and root non-structural carbohydrate dynamics of willow and poplar plants decapitated at different phenological stages.

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5.1 Summary

With the aim to make a closer monitoring between the above- (ABG), below-ground (BG) and root non-structural carbohydrate (NSC) dynamics of willow and poplar plants after decapitation at different phenological phases, in this study, a total destructive plant sequential sampling was conducted. Plants were decapitated close to the end of the growing season at early autumn and in winter when plants were dormant. At each sampling time resprouting vigour (number of shoots, basal diameter of shoots, above-ground mass), changes in root dry mass and root NSC (starch, sucrose, glucose and fructose) were evaluated.

Immediate response of willow plants to early autumn decapitation (AD) was characterised by high resprouting activity and decreases in root mass and in root non-structural carbohydrates. Number of shoots increased by 3.5 \times , root dry mass decreased by 37% and represented half the non-decapitated (ND) willow root mass plants. Period from autumn (one month after early autumn decapitation) to early summer (9 months after early autumn decapitation) represented a period for root mass and root starch recovering. Root mass of early autumn decapitated (AD) willow plants finished 57% greater than initial root mass before decapitation. However, it represented only 36% the root mass of ND willow plants, which from the beginning (early autumn) to the end of the study (early summer) showed a 4.0 \times root mass growth.

Spring growth of dormant decapitated (DD) willow plants was characterised by a low resprouting activity in terms of the number of shoots produced and the total shoot basal diameter grown. During spring, DD willow plants maintained or recovered the root mass recorded at dormant decapitation and represented 56% the root mass of ND willow plants.

Similarly that observed in AD willow plants, AD poplar plants had 4 months after decapitation similar root mass that recorded at early autumn decapitation. In comparison to ND poplar plants which grew vigorously from early autumn to winter, root mass of AD poplar plants was 40% that of ND poplar plants. Number of shoots recorded in AD poplar plants in winter was similar that found in ND poplar plants.

During spring AD poplar plants continued producing new shoots finishing by early summer with more shoots (5.7) than ND poplar plants (2.0). Spring sprouting activity of AD poplar plants was accompanied with a reduction in root mass which finished with 52% less mass than the initial root mass recorded when poplar plants were decapitated 9 months earlier in early autumn. It is proposed that moderate above-ground resprouting activity recorded in poplar plants during the first 4 months after early autumn decapitation, might have compromised the root development observed in the short term at the beginning of the following growing season.

Resprouting activity of DD poplar plants during spring was as moderate as observed in plants after early autumn decapitation. In comparison to the root mass recorded at dormant decapitation, ABG removal did not reduce root mass and by early summer it was similar to the root mass recorded in ND poplar plants. However, in contrast to the vigorous growth observed in ND poplar plants from early autumn to winter, root mass of ND poplar plants increased only 9% during spring. Pot volume constraints were proposed as a likely cause for the limited growth observed during spring in ND poplar plants.

Results suggest that willow and poplar plants might be applying different strategies after early autumn decapitation for the immediate root structure restoration resulting in a greater negative impact in the short term root mass recovery in AD poplar plants.

5.2 Introduction

Generate information from mature trees is always challenging. This time frame from seedlings or cuttings to maturation is practically beyond pre-planned experiments possibilities. Most of the times, experimental designs need to be adjusted to what it is found in the field with mature trees, otherwise time and labour costing activities like thinning or pruning must be carried out to adjust tree arrangement to particular designs (Wall, 2006).

Information derived from pot studies has been used strategically in early tree genotype selection for specific productive, contaminant remediation or environmental conditions, and thus reducing time and costs associated when working with mature trees (McIvor et al., 2014).

Pot studies offer on the other hand the possibility to conduct total plant destructive sequential samplings which allow to study how the dynamics in different plant structures are related to each other. Studies on carbon (C) plant pattern allocation (Pregitzer et al., 1990) or root carbohydrate seasonal dynamics in the entire plant (Isebrands and Nelson, 1983, Nguyen et al., 1990, Von Fircks and Sennerby-Forsse, 1998) have been possible thanks to versatility pot studies offer

The main aim of this study was basically to gain finer understanding between resprouting activity, root structure and root non-structural carbohydrate reserve dynamics after decapitation at different phenological phases of the tree species (willow and poplar) most commonly used for soil conservation in steep slopes under pastoral management in New Zealand.

5.3 Materials and Methods

5.3.1 Site description.

The present experiment was carried out at the Massey's University Plant Growth Unit (PGU) at Palmerston North. Fifty cuttings of willow (*Salix matsudana* Koidz. *x alba* L. 'Tangoio') and poplar (*Populus deltoides* Marsh. *X P. nigra* L. 'Dudley') of 15-20 cm long and 2-4 cm basal diameter were planted in late October 2012 in 8 lt pots with a 50:50 mix of topsoil and sand. Soil mix was enriched with a slow release long term fertilizer (15N-9P-11K). Two months after planting, willow plants had a 96% survivorship rate in contrast with the 40% rate observed in poplar plants

5.3.2 Experimental design

Pots were arranged in a randomized block design, and three blocks were aligned on a south-north direction of the glasshouse. Willow and poplar had two and one pot-plant per block, respectively.

Temperature inside the glasshouse was semi-controlled with automatic fans regulated by a thermostat set to 25°C. Environmental conditions inside and outside the glasshouse are shown in Figure 5.1. Temperature inside the glasshouse was in average 4° higher than environmental temperature.

Both plant species were subject to the same decapitation schemes, which were carried out at two different phenological phases: Early autumn decapitation (AD) in mid March (day of the year DOY 75), when plants were still in leaf and decapitation in winter (DOY 210), when plants were at the dormant stage (DD) (Table 5.1 and 5.2). A group of plants were left intact (non-decapitated ND) and used as a control group. Decapitations were carried out with secateurs, cutting the stems with a diagonal sharp cut, leaving three and ten buds on the stems of willow and poplar plants, respectively.

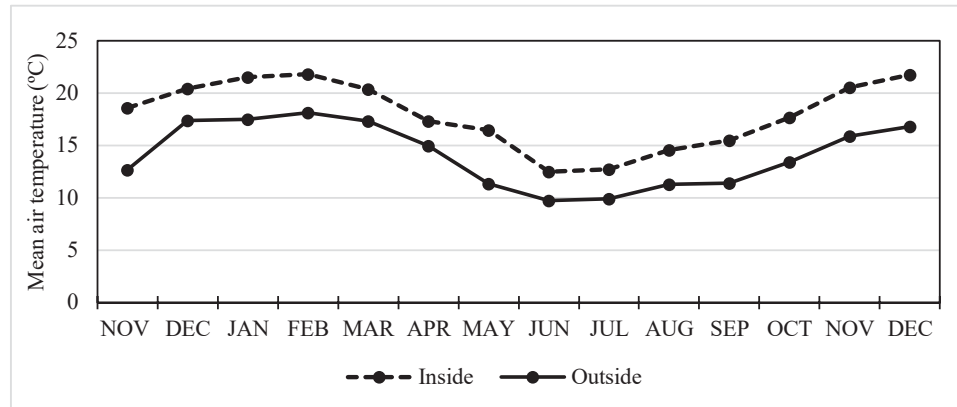


Figure 5.1 Mean air temperature inside and outside the glasshouse.

With the aim to simulate similar drought conditions to those typically experienced in summer-early autumn on hill country farms, the soil moisture regime in the pots was adjusted in such a way that from mid-January 2013 until late April 2013, gravimetric water content was in average 39% of field capacity, ranging from 25% to 48%. During the rest of the study pot soil moisture content was set up to oscillate between 80 and 90% field capacity.

To analyse the impact of decapitation on above- and below-ground growth and root non-structural carbohydrates of the plants, sequential destructive samplings were carried out on decapitated and non-decapitated plants. Willow plants were destructively sampled at four intervals, whereas poplar plants were destructively sampled at three intervals only, because of the lower number of plants available (lower survival rate) The general sampling scheme for willow and poplar plants is shown in Table 5.1 and Table 5.2, respectively.

Table 5.1 Treatments, sampling sequence and number of willow plants decapitated and sampled at each sampling time.

Treatments	2013 Sampling sequence and number of plants decapitated and sampled				
	EARLY AUTUMN (DOY 75)	AUTUMN (DOY106)	WINTER (DOY 210)	EARLY SUMMER (DOY 354)	TOTAL PLANTS SAMPLED
Non-decapitated (ND)	6	6	6	6	24
Early Autumn Decapitated plants (AD)	18 plants decapitated	6	6	6	18
Dormant Decapitated plants (DD)			6 plants decapitated	6	6

Table 5.2 Treatments, sampling sequence and number of poplar plants decapitated and sampled at each sampling time.

Treatments	2013 Sampling sequence and number of plants decapitated and sampled			
	EARLY AUTUMN (DOY 75)	WINTER (DOY 210)	EARLY SUMMER (DOY 354)	TOTAL PLANTS SAMPLED
Non-decapitated (ND)	3	3	3	9
Early Autumn Decapitation (AD)	6 plants decapitated	3	3	6
Dormant Decapitation (DD)		3 plants decapitated	3	3

5.3.3 Variables analysed.

5.3.3.1 Above-ground growth.

At each sampling time, above-ground plant material was separated in leafy and non-leafy components (shoots + branches), oven dried at 70°C until constant weight and weighed.

After decapitation at each sampling time, resprouting vigour was evaluated by counting the number of shoots and measuring the basal diameter of the shoots with a calliper.

During the study, different resprouting origin was seen in willow plants, and shoots were distinguished and named as 1st, 2nd and 3rd shoots according to their source and time of origin (Fig 5.2). The 1st shoots were those that sprouted from the original cutting, 2nd shoots resprouted from the remnants of the 1st shoots after those were harvested in early autumn, and 3rd shoots were the shoots sprouting in spring from buds located in the underground part of the original cutting (Fig 5.2). Any other shoot emerging from 1st 2nd or 3rd shoots were considered as branches.

5.3.3.2 Root mass dynamics.

Recovery of the roots was carried out by washing the root structure directly with water from a hose, and a sieve with a screen of 1.0 mm was used to collect the roots detaching from the main structure. After washing, roots were separated from original cutting and the latter was weighed separately. Roots were then oven dried and weighed as described in previous subsection for above-ground part components. High amount of root mass found since the 1st sampling made impractical a thorough live from dead roots separation process. Only the most external or roots detaching at washing underwent a more meticulous live to dead sorting process. Black opaque colour, snapping at bending, or the loss of the peridermis were all considered as a criteria for labelling roots as dead when those features were present together or individually. Roots considered dead were discarded.

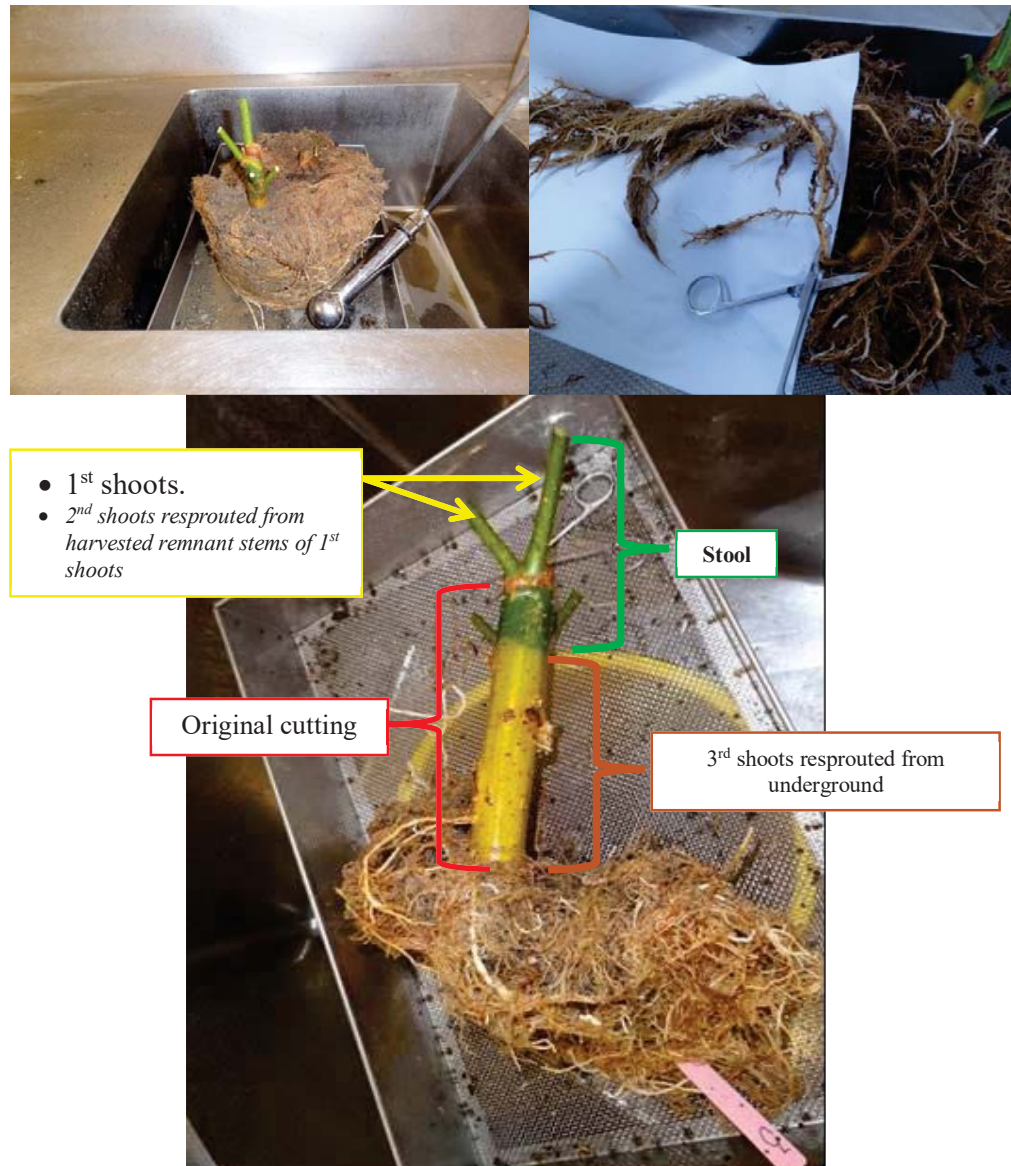


Figure 5.2 Root recovery process and origin points of 1st, 2nd and 3rd shoots

5.3.3.3 Root non-structural carbohydrate (NSC) dynamics.

A subsample of the washed roots was taken for NSC analysis. Starch and the soluble sugars sucrose, glucose and fructose were analysed. For willow and poplar plants NSC were determined in fine roots (≤ 2 mm diameter). In poplar plants starch dynamics were also analysed for coarse roots ($> 2 \leq 10$ mm diameter). NSC were determined according to the procedures and techniques described in Chapter 3 Section 3.3.3.2.

5.3.4 Statistical analysis.

All data were analysed as a randomised block design with an Analysis of Variance (ANOVA) using the general lineal model (GLM) procedure of SAS software 9.4 (SAS, 2012). Willow and poplar plants were analysed separately, and variables measured were contrasted with their corresponding ND plants and with their initial values recorded prior to decapitation.

Mean separation of the variables analysed was carried out by the by least significant difference (LSD) test using SAS software 9.4 (SAS, 2012).

5.4 Results

5.4.1 Above- and below-ground dynamics of non-decapitated (ND) willow plants.

Total above-ground growth (dry mass of leaves and non-leafy mass (stems plus branches)) of ND plants during the study (early autumn-early summer) was 130%. Number of shoots increased significantly ($P<0.05$) from 4.3 to 6 and total basal diameter of shoots showed a growth of 79% ($P<0.05$) (Table 5.3).

Root mass had from early autumn (DOY 75) to early summer (DOY 354) an increase ($P<0.05$) of 324% from which 110% occurred from early autumn to winter and the 214% was during spring (winter to early summer). During the study shoot to root ratio decreased from 2.9 to 1.7 and cuttings grew 1.9 times (Table 5.3).

5.4.2 Above- and below-ground dynamics of willow plants after early autumn decapitation

One month after being decapitated in early autumn (DOY 106), root mass of willow decapitated plants were 47% less ($P<0.05$) than non-decapitated (ND) plants and 37% less ($P<0.05$) than the original root mass observed before decapitation (Table 5.3). Root recovery in the laboratory did not imply an exhaustive sorting live from dead roots process (Section 5.3.1.1.2). Early autumn decapitation must have caused an extensive fine root detachment and partial to total decomposition of decaying roots that were either not observed or discarded after washing the soil off in a 1.0 mm sieve.

The reduction in root mass of the early autumn decapitated (AD) plants occurred together with a vigorous resprouting. Number of shoots of AD plants increased 2.7 times the initial shoot number recorded before decapitation and were one month after decapitation 3.8× greater ($P<0.05$) than number of shoots in ND willow plants. Total shoot basal diameter of AD willow plants was similar ($P>0.05$) that of the ND willow plants one month after decapitation (Table 5.3). During the same period of time (DOY 75 – DOY106) cutting maintained the initial mass recorded at early autumn (Table 5.3).

Above-ground growth of AD plants was sustained after autumn. The increase in non-leafy above-ground biomass from autumn (DOY 106) to winter (DOY 210) was 4.7 times, and total shoot basal diameter was similar ($P>0.05$) that of ND plants (Table 5.3). Root mass started showing a recovery compared to root biomass recorded before decapitation, yet, the difference between ND and AD plants increased ($P<0.05$) by an additional 10% (Table 5.3). Shoot:root ratio of AD plants (0.3) was in winter (DOY 210) significantly less ($P<0.05$) than shoot:root ratio of ND plants (1.4). In contrast to the maintenance of cutting mass observed in AD plants from early autumn (DOY 75) to autumn (DOY 106), from autumn (DOY 106) to winter (DOY 210) cutting mass showed a significant ($P<0.05$) decrease. The cutting mass observed in AD plants in winter was also significantly less ($P<0.05$) than the cutting mass recorded in winter for ND plants.

The period from winter (DOY 210) to early summer (DOY 354) was characterised by an intense growing period for ND and AD plants (Table 5.3). Root mass of ND plants increased 2.0 times, whereas within the same period, AD plants had a root mass increase of 1.7 times that recorded in winter (Table 5.3). In early summer, AD plants had a root mass 57% greater ($P<0.05$) than observed at decapitation 9 months before, but the difference from ND plants continued increasing, and root mass of AD plants decreased to less than 40% ($P<0.05$) the root mass in non-decapitated plants (Table 5.3).

During spring 2013, above-ground growth of early autumn decapitated plants was mostly produced by new shoots classified as 3rd shoots (see section 5.3.1.1.1), that sprouted from the underground part of the original cutting. The 3rd shoots accounted for around 60% of the total above-ground dry mass recorded in early summer (DOY 354) (Table 5.3). The number of shoots on AD plants ended up being 3 times higher ($P<0.05$) than in ND plants, and the total shoot basal diameter of AD plants was 40% higher ($P<0.05$) than ND plants (Table 5.3). 3rd shoots of AD plants originating from the original cutting produced 90% of the increase in shoot basal diameter observed from winter (DOY 210) to early summer (DOY 354). During this period, winter to early summer, shoot:root ratio of AD willow plants increased from 0.3 to 1.3 (Table 5.3).

5.4.3 Above- and below-ground dynamics of willow plants after dormant decapitation

Five months after decapitation of willow plants while they were dormant, did not reduce the root mass. In comparison with the ND plants, in early summer (DOY 354), plants decapitated when dormant (DD) had approximately 64% less ($P < 0.05$) root mass (Table 5.3). Mass of the cuttings of DD plants did not show significant changes during spring either.

In early summer the number of shoots of the DD plants was 38% less than ND plants, and the total shoot basal diameter was significantly less ($P < 0.05$) than that recorded for ND and AD plants (Table 5.3).

5.4.4 Root non-structural carbohydrate (NSC) dynamics of willow plants after decapitation.

5.4.4.1 Early autumn decapitation.

Immediate reduction in root mass, and the intense resprouting of early autumn decapitated plants were accompanied with a decline in root starch and sucrose concentrations (Fig 5.3). In autumn, one month after decapitation, root starch of AD willow plants (23.7 mg g^{-1}) were less than ND willow plants (113.7 mg g^{-1}). The decrease in root starch concentrations in AD plants one month after decapitation, contrasted with the sharp increases observed in the root starch and sucrose concentrations of ND plants. Root monosaccharide concentrations (glucose and fructose) of AD plants, also showed decreases that were one month after decapitation, significantly ($P < 0.05$) lower than root monosaccharide concentrations in ND plants (Fig 5.3).

The period of time from autumn (one month after decapitation, DOY 106) to late July in winter (DOY 210), was a period of above- and below-ground plant growth in both ND and AD plants. During this period, sucrose was the only root NSC in AD plants that maintained decreasing values which were in winter (DOY 210) significantly less ($P < 0.05$) than root sucrose concentrations of ND plants (Fig 5.3). In winter (DOY 210) root starch levels in AD plants were still lower ($P < 0.05$) than ND plants (Fig 5.3), but contrary to root sucrose, root starch concentrations of AD plants started showing an increase from autumn (DOY 106) to winter (DOY 210) (Fig 5.3). Similarly to

starch, root monosaccharide concentrations of AD plants showed increasing values from autumn (DOY 106), but in contrast to root starch and sucrose, these did not show in winter (DOY 210) significant differences with root glucose and fructose concentrations of ND plant roots (Fig 5.3).

During spring (DOY 210 to DOY 354), roots of ND plants showed a decrease in starch and sucrose concentrations (Fig 5.3), whereas root starch of AD plants sustained the increasing concentrations observed from autumn (DOY 106) and by early summer (DOY 354) significant difference was not observed with the root starch concentration of ND plants (Fig 5.3).

Root sucrose concentrations of AD plants showed a slight recovery from the decreasing values observed since the beginning of the study, but the values were still significantly ($P < 0.05$) below the root sucrose levels of ND plants (Fig 5.3).

Monosaccharide concentrations in the roots of AD plants maintained the increasing values observed from autumn (DOY 106). In the last sampling time in early summer (DOY 354) root fructose and glucose concentrations of AD plants were similar and significantly higher than root fructose and glucose concentration of ND plants, respectively, which were maintained with minimal changes since the beginning of the study (Fig 5.3).

5.4.4.2 Dormant decapitation

Similarly to ND plants, from winter (DOY 210) to early summer (DOY 354), root starch and sucrose concentrations of DD plants showed a decrease which ended with sucrose values significantly less ($P < 0.05$) in DD plants than in the ND ones (Fig 5.3). Root glucose and fructose of DD plants did not show significant differences with the root monosaccharide concentration of ND plants (Fig 5.3).

Table 5.3 Resprouting vigour, above-ground growth and root mass dynamics of willow (*Salix matsudana x alba* “Tangoio”) plants decapitated at different phenological phases

Parameters	Early Autumn (DOY 75)		Autumn (DOY 106)		Winter (DOY 210)		Early Summer (DOY 354)	
	ND	AD	ND	AD	ND	AD	ND	AD
Resprouting vigour (No and basal diameter of shoots)								
1 st shoots	4.3	4.4	4.2		4.5		3.8	6.0
2 nd shoots				15.8		12.0		10.7
3 rd shoots								9.0
Total shoots (no per plant)	4.3a	4.4a	4.2b	15.8^{^a}	4.5b	12.0^{^a}	3.8b	6.0^{^b}
Basal diameter (mm)								
1 st shoots	30.8	31.9	32.8		37.4		31.2	55.0
2 nd shoots				32.0		36.7		40.8
3 rd shoots								38.5
Total basal diameter (mm per plant)	30.8a	31.9a	32.8a	32.0a	37.4^{^a}	36.7a	31.2b	55.0^{^b}
Above-ground dried Mass (gr)								
1 st shoots (stems + branches)	73.8	69.6	97.2		103.7		97.5	180.4
1 st shoots (leaves)	37.5	35.8	36.9		0.0		0.0	76.0
2 nd shoots (stems + branches)				1.9		8.6		16.4
2 nd shoots (leaves)				3.6		0.0		11.2
3 rd shoots (stems + branches)								28.1
3 rd shoots (leaves)								16.8
Total above-ground dried mass (gr)	111.4a	105.4a	134.2a	5.5b	103.7a	8.6b	97.5a	256.4a
Cutting mass (gr)	49.6	46.8*	61.3a	48.4b	62.4a	36.5b	58.7*	95.9a
Root mass (gr)	36.5	35.1**	43.5a	22.9^{^b}	76.8^{^a}	32.6b	72.2**	155.0^{^a}
Shoot/Root	3.0	3.0**	3.1a	0.2b	1.4a	0.3b	1.4**	1.3a

ND non-decapitated plants AD early autumn decapitated plants. 1st shoots) sprouted from original cutting. 2nd shoots) sprouted from the 1st shoots remnants after early autumn decapitation. 3rd shoots) sprouted in spring from buds located in the underground part of the original cutting. Origin of shoots (Section 5.3.1.1.1 and Fig 5.2). *Estimated from above-ground:cutting mass ratio of ND plants ** Estimated from above-ground :root mass ratio of ND plants. At each sampling time and parameter, different letters mean significant differences (P < 0.05). ^ indicates significant differences (P < 0.05) compared to the initial values recorded at decapitation.

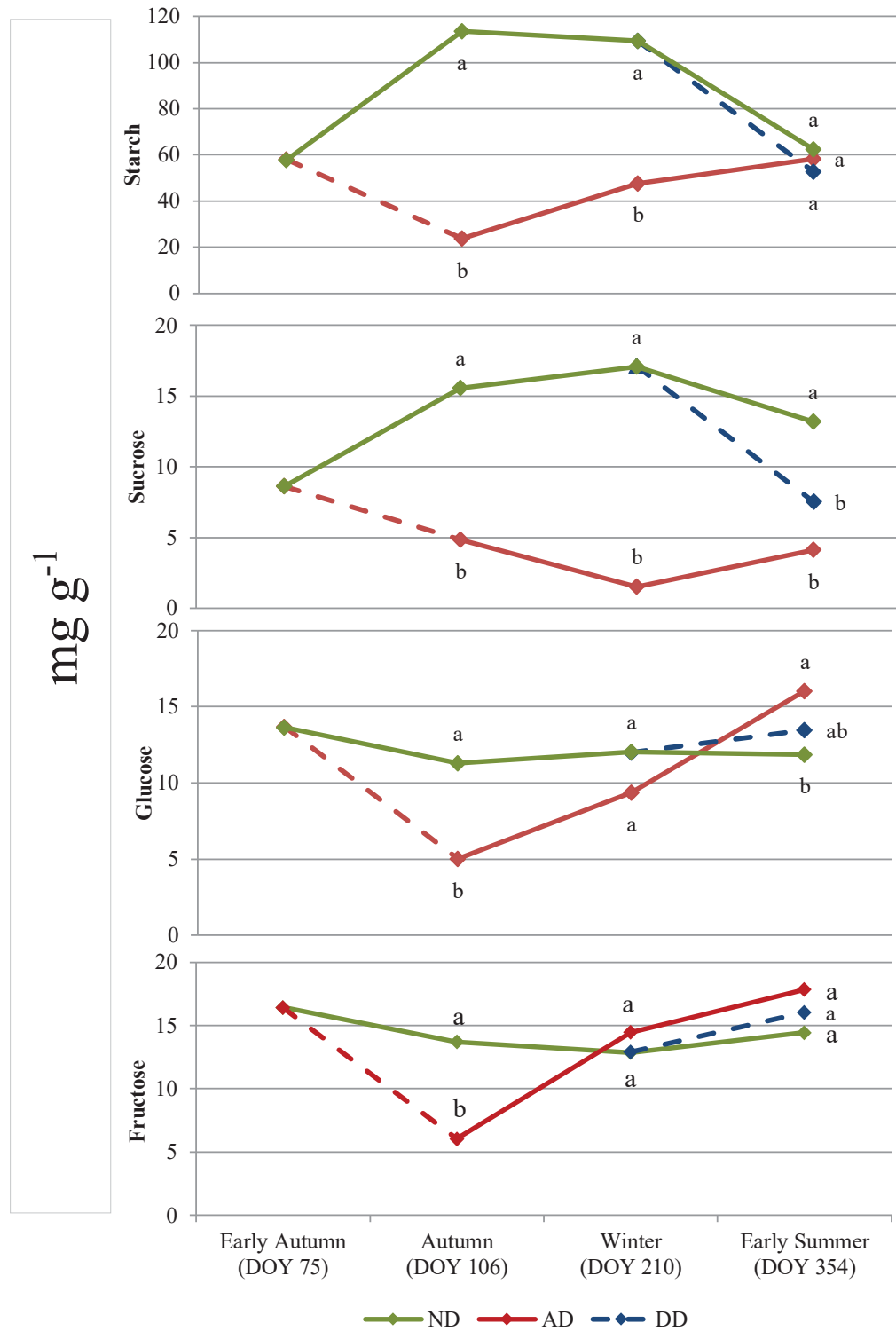


Figure 5.3 Fine root non-structural carbohydrate dynamics of willow (*Salix matsudana* x *alba* ‘Tangoio’) plants decapitated at different phenological phases. ND non-decapitated plants AD early autumn decapitated plants. DD dormant decapitated plants.. Dashed lines: assumed trends as from non-decapitated plants values. Different letters at each sampling period mean significant differences between treatments ($P < 0.05$).

5.4.5 Above- and below-ground dynamics of non-decapitated (ND) poplar plants.

From the beginning of the study in early autumn (DOY 75) to early summer (DOY 354) mean number of shoots and mean total basal diameter of shoots significantly ($P<0.05$) increased both 100% passing from 1 to 2 shoots and from 11.4 to 22.4 mm, respectively (Table 5.4).

Within the same time frame total above-ground biomass (stems, branches and leaves) increased 28% and root mass increased ($P<0.05$) 92%. More than 90% of the root mass growth in ND plants occurred from early autumn (DOY 75) to winter (DOY 210) and the rest from winter (DOY 210) to early summer (DOY 354) (Table 5.4). During the lapse of the study cutting mass grew ($P<0.05$) 140% and as occurred with root mass, most of the growth observed, around 100%, happened from early autumn to winter. From early autumn to early summer shoot to root ratio changed from 1.7 to 1.2 (Table 5.4).

5.4.6 Above- and below-ground dynamics of poplar plants after early autumn decapitation.

In winter (DOY 210), four and a half months after early autumn decapitation, root mass of AD plants was 40% ($P<0.05$) that of ND plants and similar to the root mass prior decapitation (Table 5.4). Within that period, resprouting of AD plants yielded a similar number of shoots compared to ND plants and total basal diameter of shoots of AD plants was not significantly different than ND plants, even though it was 43% less than observed in the latter plants (Table 5.4). Low number of available plants and variability in this parameter within treatments might have both contributed for the lack of significance.

Above-ground dry mass production of AD poplar plants from early autumn decapitation (DOY 75) to winter (DOY 210) was minimal (1.1 gr) (Table 5.4). Cutting mass of AD plants followed a similar dynamic to ND plants since cutting biomass between treatments was similar in winter four months after decapitation (Table 5.4).

During the following spring season differences in root mass between AD poplar plants and either ND poplar plants or initial root mass before decapitation, increased (Table 5.4). In early summer (DOY 354) root mass of poplar plants decapitated in early autumn was 20% ($P<0.05$) that of non-

decapitated plants and approximately half ($P < 0.05$) the root mass recorded in early autumn at decapitation (Table 5.4). Cuttings of AD plants also showed a decrease during spring that reduced their mass to levels recorded in early autumn before decapitation and that was by early summer (DOY 354) significantly less than cutting mass of ND plants (Table 5.4).

From winter (DOY 210) to early summer (DOY 354), the number of shoots of AD plants increased from 3.3 to 5.7 shoots per plant, which was significantly greater ($P < 0.05$) than the number of shoots found in ND plants (2.0) and greater than the recently produced new shoots of the plants decapitated in winter (3.0) (Table 5.4). Total basal diameter of shoots was not significantly different between treatments. However, in both winter and early summer, total basal diameter of shoots of AD plants was at least 20% less than recorded in ND plants (Table 5.4).

Above-ground dry mass was lower ($P < 0.05$) in AD plants than in the other two treatments (ND and DD plants) (Table 5.4).

5.4.7 Above- and below-ground dynamics of poplar plants after dormant decapitation

Above-ground dry mass recorded in DD plants in early summer (DOY 354) was 48% less ($P < 0.05$) than that observed in ND plants (Table 5.4), and root mass was similar that of ND plants. In early summer (DOY 354), both non-leafy above-ground dry mass (33.2 gr) and root dry mass (95.8 gr) of DD plants, were similar that recorded in winter (DOY 210) prior decapitation (Table 5.4).

Table 5.4 Resprouting vigour, above-ground growth and root mass dynamics of poplar (*Populus deltoides* x *nigra* 'Dudley') plants decapitated at different phenological phases

Parameters	Early Autumn (DOY 75)		Winter (DOY 210)			Early Summer (DOY 354)		
	ND	AD	ND	AD	DD	ND	AD	DD
Resprouting vigour (No and basal diameter of shoots)								
1 st shoots	1.0	1.3	2.0		1.3	2.0		
2 nd shoots				3.3			5.7	3.0
Total shoots (no per plant)	1.0a	1.3a	2.0a	3.3^{^a}	1.3a	2.0b	5.7^{^a}	3.0b
Basal diameter (mm)								
1 st shoots	11.4	12.4	18.5		16.2	22.4		
2 nd shoots				10.6			17.4	20.1
Total basal diameter (mm per plant)	11.4a	12.4a	18.5a	10.6a	16.2a	22.4^{^a}	17.4^{^a}	20.1a
Above-ground dried Mass (gr)								
1 st shoots (stems + branches)	38.3	32.6	43.3		38.6	61.4		
1 st shoots (leaves)	57.2	49.8	0.0		0.0	61.3		
2 nd shoots (stems + branches)				1.1			8.8	33.2
2 nd shoots (leaves)				0.0			12.7	31.0
Total above-ground dried mass (gr)	95.4a	82.5b	43.3a	1.1b	38.6a	122.7a	21.6c	64.2b
Cutting mass (gr)	23.3	20.1[*]	49.5a	46.4a	44.7[*]	56.4a	30.8b	47.3a
Root mass (gr)	55.3	47.7^{**}	96.9^{^a}	38.6b	86.5^{**}	106.4^{^a}	22.8^{^b}	95.8a
Shoot/Root	1.7	1.7^{**}	0.4a	0.03b	0.4^{**}	1.2a	0.9a	0.7a

ND non-decapitated plants AD early autumn decapitated plants. 1st shoots) sprouted from original cutting, 2nd shoots) sprouted from the 1st shoots remnants after early autumn decapitation. Origin of shoots (Section 5.3.1.1.1 and Fig 5.2) * Estimated from above-ground:cutting mass ratio of ND plants ** Estimated from above-ground :root mass ratio of ND plants. At each sampling time and parameter, different letters mean significant differences (P< 0.05). [^]indicates significant differences (P< 0.05) compared to the initial values recorded at decapitation

5.4.8 Root non-structural carbohydrate dynamics of poplar plants after decapitation.

5.4.8.1 Early autumn decapitation.

Whether by the total of the observations, by season or by treatment analysis, starch concentrations were higher ($P < 0.05$) in coarse roots than in fine roots (Fig 5.4).

Early autumn decapitation reduced starch concentrations only in the coarse roots ($> 2 \leq 10$ mm diameter), as was seen in the winter sampling. ND plants increased root starch concentrations in fine roots, and coarse roots maintained starch concentrations recorded in early autumn (Fig 5.4).

In winter coarse root starch concentration of AD plants was less ($P < 0.05$) than ND plants.

During spring, starch concentrations declined in both fine and coarse roots of ND and AD plants (Fig 5.4). By early summer, concentrations of starch in fine and coarse roots of the AD plants were significantly lower ($P < 0.05$) than in ND plants (Fig 5.4).

Root soluble sugars of AD plants did not show different values ($P > 0.05$) than the ND plants after decapitation (Fig 5.5). Sucrose and monosaccharides, glucose and fructose, followed opposite patterns in ND and AD plants. When sucrose levels increased, glucose and fructose decreased and vice versa (Fig 5.5).

5.4.8.2 After dormant decapitation.

Following dormant decapitation starch concentrations in fine roots reduced similar to ND and AD plants (Fig 5.4). In contrast, starch concentration in coarse roots of AD plants maintained the high concentrations assumed from the starch levels observed in winter (DOY 210) in coarse roots of ND plants (Fig 5.4).

All root soluble sugars but sucrose of DD plants showed concentrations significantly lower ($P < 0.05$) than in ND plants 5 months after dormant decapitation (Fig 5.5).

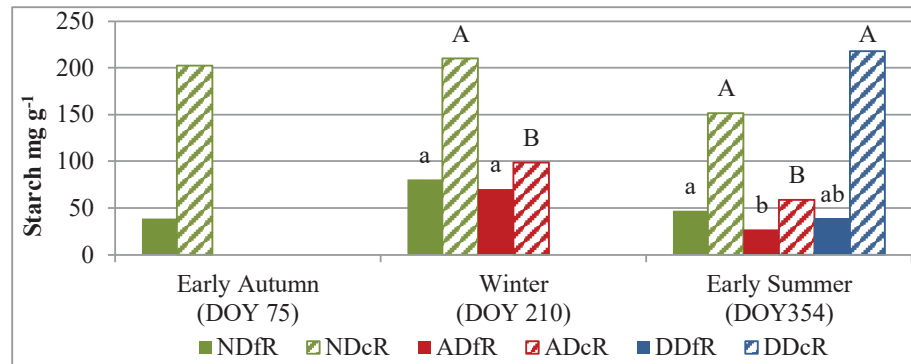


Figure 5.4 Root starch concentration in fine (fR) and coarse (cR) roots of poplar (*Populus deltoides* x *nigra* 'Dudley') plants decapitated at different phenological phases. non-decapitated (ND), early autumn decapitated (AD) and dormant decapitated (DD). Different letters at each season and root category means significant differences ($P < 0.05$)

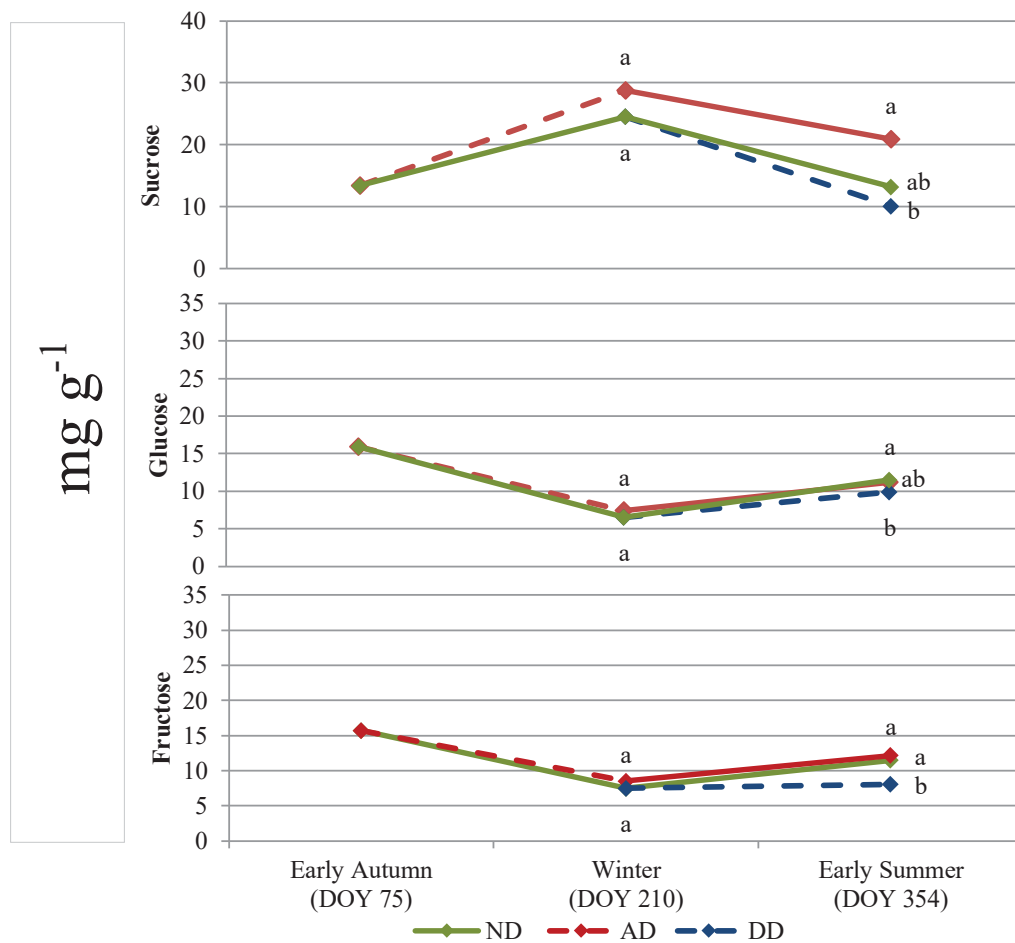


Figure 5.5 Root non-structural carbohydrate dynamics of poplar (*Populus deltoides* x *nigra* 'Dudley') plants decapitated at different phenological phases. ND non-decapitated plants AD early autumn decapitated plants. DD dormant decapitated plants. Dashed lines: assumed trends as from non-decapitated plants values. Different letters at each sampling period mean significant differences between treatments ($P < 0.05$).

5.5 Discussion

5.5.1 Above-, below-ground and root non-structural carbohydrate (NSC) dynamics of willow plants decapitated in early autumn

After removal of above-ground plant parts, the recovery of the canopy must be supported, at least initially, by the resources available in the remaining structures (Loescher et al., 1990, Kozlowski, 1992, Dickmann and Pregitzer, 1992). The amount and source of resources mobilised seems to be plant species specific. Chesney and Vasquez (2007) observed that complete pruning had a greater impact in the starch mobilization of stems than in the roots of *Erythrina poeppigiana*. The contrary was reported by Chesney and Vasquez (2007) for complete pruned *Gliricidia sepium* trees where greater mobilisation was observed in roots than in stems. Plant provenance or site conditions might be additional factors influencing the organ carbohydrate reserve donor after above-ground removal as Erdmann et al. (1993) observed that *Gliricidia sepium* coppiced every 3 weeks mobilised more starch from stems than from roots.

Immediate C demand intensity after above-ground intervention seems to be highly influenced by the number of meristematic growing points that are activated. Tschaplinski and Blake (1994) suggested that defoliated plants could have a greater assimilate demand than decapitated ones, as respiratory demands would be greater in the former plants, because they maintain both active apical and lateral meristems. Defoliated plants have however, a greater carbohydrate pool reserve from remaining structures (branches, stem) than decapitated ones. (Tschaplinski and Blake, 1995, Chesney, 2012)

It is considered that not long after the beginning of resprouting, that the first leaves produced, become net photosynthate exporters, (Dickmann and Pregitzer, 1992, Sennerby-Forsse et al., 1992, Tschaplinski and Blake, 1995). Thus, it might be that the highest C cost for the plant after above-ground disruption, mostly relies on how much the plant invests in the immediate shoot restoration.

In general, for the period of time evaluated, the response of willow plants decapitated in early autumn, can be described as follow, and points are discussed thereafter:

- A) An immediate (one month after decapitation) vigorous resprouting response, accompanied with a significant reduction in root mass and root starch concentration (Table 5.3 and Fig 5.3).
- B) In winter, four months after early autumn decapitation, a slight recovery of both root mass and root starch was seen (Table 5.3 and Fig 5.3) in comparison to pre-coppicing values. From resprouting to winter, the decapitated plants sustained the vigorous growth observed initially in the new shoots.
- C) During spring, plants decapitated in early autumn recovered the initial, pre-decapitation root mass (Table 5.3). However, an unexpected new sprouting response was observed, when the tertiary (3rd) shoots, (section 5.3.1.1.1) grew from buds located in the underground part of the original cutting. Also during this season an irregular, gradual and delayed bud burst and leaf flush was observed in all the willow plant treatments (ND, AD and DD). Causes of this both unexpected phenomenon are discussed.

Immediately after early autumn decapitation (one month after), willow plants must have mobilised a high amount of resources as they produced around 4 times more shoots than those found in non-decapitated plants, and restored the total shoot basal diameter to that observed in non-decapitated plants. The vigorous resprouting observed in willow plants after early autumn decapitation was accompanied with a 37% decrease in the root mass and a high mobilisation of all the NSC evaluated (Table 5.3 and Fig 5.3). Meanwhile, non-decapitated willow plants followed the well-known above- and below-ground mass changes and root starch dynamics associated with the end of the growing season and bud set (Table 5.3 and Fig 5.3). By the end of shoot growth and bud set, reported research on non-decapitated plants shows a shift in the photosynthate translocation downwards the lower stem and roots, which is reflected by increased root starch (Dickson and Nelson, 1982, Isebrands and Nelson, 1983, Nguyen et al., 1990). Also, similarly to what has been reported here in the non-decapitated willow plants (Fig 5.3), Nguyen et al. (1990) observed increased root mass in poplar plants due to C translocation to roots after bud set.

From autumn (DOY 106) to winter (DOY 210), willow plants decapitated in early autumn showed a recovery of root mass similar to that seen at the beginning of the study (Table 5.3), and at the same time there were a series of NSC dynamics that deserve further attention (Fig 5.3).

It is well-known that sucrose is the main photosynthate translocated to the sink tissues, either in intact plants or after decapitation when new leaves start exporting C (Kozlowski, 1992, Salisbury and Ross, 1992, Kozlowski et al., 1997). ^{14}C labelled studies conducted by Isebrands and Nelson (1983) with *Populus* clones (*P. tristis* × *P. balsamifera* cv. ‘Tristis’ and *P.* × *euramericana* cv. ‘Eugenei’) showed at bud set the down-ward C translocation from upper mature leaves to the stem, hardwood cutting, and roots. Root starch accumulation after bud set has been documented in *Populus* and *Salix* spp by Nguyen et al. (1990) and Von Fircks and Sennerby-Forsse (1998), respectively.

In this study out of all the NSC evaluated, sucrose was the only one which maintained the decreasing values observed one month after early autumn decapitation (Fig 5.3). The decrease in root sucrose can be interpreted as linked to the observed increase in root starch. As can be inferred from the reports cited (Isebrands and Nelson, 1983, Nguyen et al., 1990, Von Fircks and Sennerby-Forsse, 1998), leaves grown in this study, from resprouting willow plants until bud set, must have translocated C after bud set. Once in the roots, sucrose then provides the monomeric units for starch biosynthesis (Salisbury and Ross, 1992, Kozlowski, 1992).

The increase in the glucose and fructose concentrations (Fig 5.3) is less obviously explained given that theoretically they would also be used for starch synthesis. It may be that plants had just started to develop cold hardiness with the dissolution of starch into sugars during dormancy (Marshall and Waring, 1985, Essiamah and Eschrich, 1985, Von Fircks and Sennerby-Forsse, 1998), however this phenomena should have also been observed in non-decapitated plants. The alternative explanation might be as follows. Under conditions of low C assimilation, like drought, shading, or as in this experiment, above-ground defoliation, root starch is readily mobilised to support the shoot:root reestablishment (Sala et al., 2010, McDowell and Sevanto, 2010). Observations show that after immediate intense (Tschaplinski and Blake, 1994) or sustained

starch mobilisation (Landhäusser and Lieffers, 2012), plant tissues, in this case roots, require a minimum of soluble sugars to sustain basic cell functions, and that below a critical threshold it is likely that sugars are no longer available for growth or respiration (Tschaplinski and Blake, 1994, Sala et al., 2010, Landhäusser and Lieffers, 2012). Inside the plant cells there are different forms of monosaccharides. While some predominate in the free state, for example, glucose and fructose, others are components of more complex polymers, like galactose and mannose (Salisbury and Ross, 1992). Interconversion between these monosaccharides has been shown (McCready and Hassid, 1941). In this study it is hypothesised that under a situation where monosaccharides released by sucrose were being intensively used for starch synthesis, a series of monosaccharide interconversion might have been occurring in order to maintain a minimum concentration of glucose and fructose in the root tissues.

By the final stage evaluated, from winter (DOY 210) to early summer (DOY 354), willow plants decapitated in early autumn recovered the pre-decapitation root mass; however, differences with non-decapitated plants became greater as the latter showed a vigorous above- and below-ground growth, with root mass of non-decapitated plants increasing two times the root mass recorded in winter (DOY 210) (Table 5.3). Recovery of pre-decapitation root mass has significant practical implications for questions like how long does it take for the trees to recover the pre-pollarding root-structure, and what is the immediate and short term impact on the root structure after above-ground intervention? These questions have profound implications for issues like to what extent, and how long for, does the land under the protective influence of the tree roots, remain at risk to being eroded after tree above-ground intervention and before the root structure starts recovering? These and additional questions are discussed in the Chapter 7 “General Discussion and Conclusions”.

From winter (DOY 210) to early summer (DOY 354), AD plants maintained their sprouting vigour as more shoots sprouted (Table 5.3). However, these new shoots, named 3rd shoots (see section 5.3.1.1.1.), originated from the shallowest underground part of the original cutting. Tertiary shoots produced during spring accounted for 60% of the above-ground dry mass recorded

in early summer (Table 5.3). There are a couple of insights that suggest underground resprouting was as a result of damage to the buds in the 2nd shoots (see section 5.3.1.1.1.). From early autumn to early winter, plants were struck by an aphid infestation, which was difficult to control. Similarly, shoots developing from underground parts of the stool of basket willow plants (*Salix viminalis*), were attributed to frost damage of the above-ground parts of the stool (Sennerby-Forsse et al., 1992). It is likely that aphid infestation could have contributed to the unexpected underground resprouting origin response observed during spring.

Additional evidence supporting the idea of some kind of damage in the buds of the plants it was an irregular and delayed bud bursting during spring in all the willow treatments (ND, AD and DD) with a rather slow and gradual leaf flush that delayed the full on-leaf presentation until late October-early November.

Root NSC dynamics observed from winter to early summer also showed their own singularities. Any energy root reserve replenishment observed from autumn to winter, in early autumn decapitated plants, seems to have been at a minimum, as starch concentrations only recovered to values similar to those observed in early autumn before decapitation (Fig 5.3). Reports usually show that root starch concentrations observed during late spring - early summer are one of the lowest found during the year (Singh and Srivastava, 1986, Johansson, 1993, Von Fircks and Sennerby-Forsse, 1998). From post-dormancy to early spring root energy reserves have to support different processes before leaves able to be net photosynthate exporters have been created (Loescher et al., 1990, Kozłowski, 1992, McCormack et al., 2015). Initial root appearance and flowering are processes that require C support before net photosynthate leaf exporters are produced (Loescher et al., 1990). After leaf flush, mature leaves support the appearance of new leaves and growth of internodes (Isebrands and Nelson, 1983, Loescher et al., 1990, Kozłowski, 1992). It is very likely that root reserves support root growing processes (McCormack et al., 2015). In this experiment, at the beginning of the spring, root energy reserves of early autumn decapitated plants, were too low as to have been the main C source supporting the resprouting activity observed (Table 5.3 and Fig 5.3). Even more interestingly, during spring, root reserves

(starch and sucrose) of the early autumn decapitated plants, in contrast to non-decapitated or dormant decapitated plants, not only did not decrease but increased, yet, the increasing trend, was only enough to equate with the root starch concentrations of non-decapitated and dormant decapitated plants (Fig 5.3). The question is then, if root energy reserves did not support the spring associated growing processes of the willow plants decapitated in early autumn, where did the energy come from? A possible answer can be drawn from an integrative analysis derived from the findings of Isebrands and Nelson (1983), Tschaplinski and Blake (1995), Landhüsser and Lieffers (2003) and Landhüsser and Lieffers (2012).

Isebrands and Nelson (1983) showed that in the establishment year, during the period of active shoot elongation, that the upper mature leaves of intact *Populus* plants, exported C basipetally to the stems and also large quantities were translocated to the hardwood cutting. After bud set, mature leaves of *Populus* plants shifted C allocation drastically and preferentially to the roots (Isebrands and Nelson, 1983).

In an Tschaplinski and Blake (1995) experiment where one year old *Populus* plants were decapitated, stems of resprouted secondary shoots (all shoots but the tallest) were attributed with a storage role, as they had five times more starch than the tissues from which they originated (lower stem of dominant shoot). Together with upper leaves, lower stem (stem below ^{14}C labelled leaves) of the dominant shoot was the structure that most imported ^{14}C for starch synthesis (Tschaplinski and Blake, 1995).

Based on the amount and mobilisation of soluble sugars and starch dynamics observed in canopy tissues (stem branches, current shoots and buds) of intact *Populus tremuloides* mature trees just before bud break, Landhüsser and Lieffers (2003) concluded that stem and branches have sufficient NSC to support the leaf flush. When the same trees were insect defoliated, Landhüsser and Lieffers (2012) observed that branches recovered NSC reserves within the same season, while it took up to two years for the roots to replenish to levels similar to that of the control trees. Landhüsser and Lieffers (2012) proposed the C sink hierarchy model to explain the differences in the time frame for C replenishment of the proximal and distal plant structures from C sources.

Integrating the findings of the last four experiments described above, it can be proposed in this study that apart from supporting their own growing process, dominant and secondary shoots that sprouted after early autumn decapitation, were actively translocating and replenishing C to the structures below, such as stems or hardwood cutting. After bud set in winter, a slight starch replenishment was seen in the roots. In agreement with the C sink hierarchy model proposed by Landhäusser and Lieffers (2012), we can speculate that 2nd shoots (secondary and dominant) growing after early autumn decapitation to dormancy onset, were only able to replenish C reserves in the lower stem of dominant shoots, stems of secondary shoots and the original cutting. After bud set, when roots gained sink strength, there were only minimum photosynthates left for replenishment of the root starch reserves. In the following growing season, because of the low C reserves in the roots and the breaking failure of the buds in the 2nd shoots, C reserves stored in the 2nd shoots (secondary and dominant) and the original cutting, might have been mobilised to support the new underground resprouting observed during spring (Table 5.3 and Fig 5.3).

5.5.2 Above-, below-ground and root NSC dynamics of willow plants decapitated in the dormant stage.

Contrary to what was observed in early autumn decapitated willow plants, dormant decapitated plants did not show a reduction in root mass in comparison to the pre-decapitation values (Table 5.3). Dickmann et al. (1996) observed an increase in fine root number and length of roots in *Populus* plants decapitated at the end of the dormancy period. An increase in fine roots was attributed by Dickmann et al. (1996) to the high levels of root starch and soluble sugars of poplar plants at the moment of decapitation. In this study at the moment of decapitation when the plants were dormant, root reserve carbohydrates (starch and sucrose) were indeed at the highest levels recorded during the experiment (Fig 5.3). It is proposed that growing environmental conditions (degree days, length of the day and soil moisture) inside the glasshouse, were, from dormancy decapitation to early summer, if not optimum, at least better than those from early autumn decapitation to dormancy onset. However, unexpectedly, resprouting activity (number of shoots and total basal diameter) from dormancy to early summer, was far less that observed from early autumn decapitation to dormancy onset (Table 5.3). The question is then: why early autumn

decapitated plants had a higher resprouting response than dormant decapitated plants. When it is considered that, the former plants had at coppicing lower energy reserve status (Fig 5.3), and rather depressive growing environmental conditions typical of an early autumn-winter period, than the dormant decapitated plants had? Part of the answer can be found when comparing the above and below ground dynamics, observed from winter to early summer (Table 5.3) between early autumn decapitated plants and dormant decapitated ones. In previous Section it was mentioned that early autumn decapitated plants showed an unexpected vigorous underground sprouting. In contrast, in dormant decapitated such sprouting response was negligible. Reasons for such underground sprouting in early autumn decapitated plants were attributed tentatively to damage in the buds of the 2nd shoots during winter by either aphid infestation, frost damage, or both. The proposal is then that, for an unknown reason, dormant decapitated plants were not able to activate the underground buds, and that the buds in the above-ground stool were equally affected as those in the 2nd shoots of early autumn decapitated plants.

The suppressed resprouting activity proposed for dormant decapitated plants, exerted a low C demand to the remnants sources (roots and stool), which were enough to support the moderate resprouting observed and to keep the pre-decapitation root mass (Table 5.3).

Both non-decapitated and dormant decapitated plants showed similar NSC dynamics during spring (Fig 5.3). The only phenomena suggesting that dormant decapitated plants could have been mobilising or using higher photosynthates than non-decapitated plants for shoot:root restoration, was observed in the root sucrose concentration, which by early summer, was less in dormant decapitated plants than in the non-decapitated ones (Fig 5.3).

Though reduction in root mass was not observed after dormant decapitation, above-ground removal caused growth constraints, as root mass of dormant decapitated plants was by early autumn, about half the root mass of non-decapitated plants (Table 5.3).

5.5.3 Above-, below-ground and root NSC dynamics of poplar plants decapitated in early autumn (AD)

The resprouting ability of plants after decapitation has been associated with a series of factors, among which, the following are highlighted. Position, abundance and activity of the remaining shoot-producing buds after above-ground intervention are considered as the essential structures for resprouting (Sennerby-Forsse et al., 1992). The ability of the plants to store large amounts of non-structural carbohydrates (Chesney and Vasquez, 2007), is important, but it is the ability of the plants to mobilise those carbohydrates in order to support synthesis and growing activity in the shoot producing buds that is of greatest importance (Dickmann and Pregitzer, 1992, Tschaplinski and Blake, 1994, Von Fircks and Sennerby-Forsse, 1998, Chesney, 2012).

Particular high resprouting activity in willow species has been reported (Sennerby-Forsse et al., 1992, Sennerby-Forsse and Zsuffa, 1995) and resprouting differences between willow and poplar cuttings were evident from the beginning of this study, when willow cuttings showed a survivorship rate more than 90% in comparison to the 40% observed in poplar cuttings. Similarly, Hussain et al. (2009) reported that 2 years after the establishment of unrooted willow (*Salix matsudana* × *alba* ‘Tangoio’) and poplar (*Populus deltoides* × *P. nigra* ‘Dudley’) stakes, willow plants had a greater above-ground growth, being higher (1.90 vs 1.35 m), thicker in stem diameter (43.5 vs 32.6 mm), wider in canopy diameter (69 vs 34 cm) and with more number of shoots (8.7 vs 2.3) than poplar plants.

In early summer 9 months after the early autumn decapitation, and in comparison with their corresponding ND plants, poplar plants had a lower resprouting ability and poorer root mass recovery (Table 5.4) than willow plants decapitated in early autumn (Table 5.3).

Commonly in New Zealand willow species used in this study starts bud bursting and leaf flush before the poplar species in spring (McIvor per. comm. 2015). However, this was not the case in this study, since it was observed for willow plants (Section 5.5.1) these showed an irregular and gradual bud burst and leaf flush that delayed the in-leaf stage until late October. In fact poplar plants showed an earlier establishment of the in-leaf stage than willow plants.

Above-, below-ground and root NSC dynamics observed in poplar plants from early autumn decapitation to early summer (Table 5.4, Fig 5.4 and Fig 5.5) might explain some of the differences observed with the performance of willow plants decapitated in early autumn.

In winter, 4 months after early autumn decapitation, both the number of shoots and the total basal diameter of poplar plants decapitated in early autumn were not significantly different than recorded in poplar non-decapitated plants (Table 5.4). The initial moderate resprouting response of poplar plants, was observed together with what might be considered a conservative mobilisation of root reserve carbohydrates (Fig 5.4).

In poplar plants it was possible to evaluate the starch dynamics in both fine (≤ 2 mm) and coarse roots ($> 2 \leq 10$ mm) (Fig 5.4). Reports show that both root categories show regular seasonal NSC dynamics, like the decreasing concentrations trends associated with the leaf flush and early spring root growth (Singh and Srivastava, 1986), or the root starch accumulation observed after bud set (Isebrands and Nelson, 1983, Nguyen et al., 1990). Mobilisation of root NSC has also been observed in both root categories after different forms of above-ground disturbance (decapitation or defoliation) (Tschaplinski and Blake, 1994, Von Fircks and Sennerby-Forsse, 1998, Kosola et al., 2002). In winter (DOY 210), four and a half months after early autumn decapitation in DOY 75, it seems that either poplar decapitated plants did not use the root starch of fine roots, or that, after bud set, there was only enough C available to replenish fine roots but not the coarse ones (Fig 5.4). In willow plants decapitated in early autumn (DOY 75), where the number of shoots was greater than that of non-decapitated willow plants in winter, root starch of fine roots, as well as root sucrose, were less than the root concentrations of both NSC in non-decapitated willow plants (Fig 5.3). In the early autumn decapitated poplar plants where numbers of new shoots after decapitation were not significantly different in winter to non-decapitated plants, root sucrose also showed similar values to those of the non-decapitated plants (Fig 5.5). The latter finding suggests that the moderate resprouting activity observed in poplar plants decapitated in early autumn, did not compromise additional NSC, as seems to have been the case in early autumn decapitated willow plants.

In winter (DOY 210) four and a half months after early autumn decapitation, shoot:root ratio of early autumn decapitated (AD) poplar plants and AD willow plants was significantly less than shoot:root ratio of their corresponding non-decapitated (ND) plants (Table 5.3 and 5.4). However, the shoot:root ratio of AD willow plants was 78% less than ND willow plants, whereas the shoot:root ratio of poplar plants was 95% less than the shoot:root ratio ND poplar plants (Table 5.3 and 5.4).

In the next growing season, during spring, AD poplar and willow plants continue showing sprouting activity (Table 5.3 and 5.4). Spring sprouting activity of AD poplar plants made them to have in early summer (DOY 354) a greater number of shoots than ND poplar plants.

Spring sprouting activity of AD poplar plants occurred along with decreases in root mass and root starch concentration in fine and coarse roots. AD poplar plants finished 9 months after decapitation with a root mass 52% lighter. In contrast, AD willow plants showed a root mass 57% higher than the initial root mass recorded in early autumn at the moment of decapitation (Table 5.3 and 5.4).

Moderate resprouting activity observed in AD poplar plants from decapitation to winter, was associated to a suggested low C energy reserves demand, as only coarse, but not fine root starch concentration in AD poplar plants was less, four and a half months after early autumn decapitation, than starch concentration in coarse roots of ND poplar plants (Fig 5.4). In contrast, high sprouting activity observed during spring in AD poplar plants was associated to a less starch concentration in both coarse and fine roots than roots (coarse and fine) of ND poplar plants (fig 5.4).

Working with different bunch grasses species known to have different grazing tolerances (tolerant or low tolerant), Richards (1984) observed different C allocation strategies after herbivory. According to Richards (1984), grazing tolerant species allocated more C for shoot regrowth immediately after defoliation than less grazing tolerant species. Immediately after defoliation, grazing tolerant species had higher root mortality. In the long term, during the following growing season, the less tolerant species had more root mortality than grazing tolerant species. Richards

(1984) proposed that after defoliation, more tolerant grazing species invest more resources for shoot regrowth in order to restore faster the root:shoot balance, as a long term survivorship strategy in ecosystems where herbivory is important.

In tropical tree legumes, Fownes and Anderson (1991) also argued that different C allocation strategies enable species to respond differently to coppicing. In their study Fownes and Anderson (1991) observed that from establishment to before coppicing, in comparison to *Sesbania sesban*, *Leucaena leucocephala* allocated more resources to the below-ground part, particularly to coarse roots and tap root. Fownes and Anderson (1991) argued that species with a more developed root structure at the moment of severe above-ground removal will also show more resilience in the long term under programs of frequent coppicing during the year.

Richards (1984) and Fownes and Anderson (1991) studies show differences respect to when the different C allocation strategies are used (before or after decapitation). Regardless these differences both studies coincide in the importance of the maintenance or recovery of the root system in species known for greater resilience at periodical above-ground removal management sustained in the long term.

Based on the above-ground, below-ground, and root NSC dynamics observed after early autumn decapitation in poplar and willow plants, it is possible to suggest, that the plants might have been using different strategies to restore the shoot:root ratio.

5.5.4 Above, belowground and root NSC dynamics of poplar plants decapitated while dormant

At the moment of dormant decapitation, poplar plants showed the highest values of root starch and sucrose recorded during the study (Fig 5.4 and 5.5). However, resprouting response during spring was as moderate as that observed in early autumn decapitated plants from early autumn to winter, when the number of resprouted shoots was not different to those recorded in non-decapitated plants (Table 5.4). During spring, poplar plants decapitated in winter showed once again a seemingly conservative use of C as starch was only mobilised, contrary of that seen in plants decapitated in early autumn, in the fine, but not in the coarse roots (Fig 5.4). In spite of the

low resprouting activity, dormant decapitated plants, recovered the non-leafy shoot dry mass structure observed in winter at the moment of decapitation (Table 5.4). Above-ground growth observed during spring in dormant decapitated plants did not cause a reduction in the root mass structure (Table 5.4). Again, as proposed by Dickmann et al. (1996), high energy reserve status at the moment of dormant decapitation might have contributed to the maintenance of the root structure.

Non-decapitated and dormant decapitated plants showed a thick mat of roots coming out from the drainage holes at the bottom of the pots. Pot volume constraints could have been one of the causes of the minimum below-ground growth observed in non-decapitated poplar plants during spring. This low growth in non-decapitated poplar plants might also explain the similar root mass values observed in early summer between these and dormant decapitated plants (Table 5.4).

Differences in resprouting vigour and below-ground performance between poplar and willow plants decapitated in early autumn were not evident after the poplar and willow plants were decapitated while dormant (Table 5.3 and 5.4). Proposed bud damage in willow plants decapitated in winter, and possibly volume constraints in poplar plants could have limited the regular growing intensity typical of the spring.

5.6 Conclusions

Results in this study suggest that after early autumn decapitation willow and poplar plants might be using different strategies for the root structure restoration, that make willow plants more resilient to decapitation than poplar plants.

Four months after early autumn decapitation, willow and poplar plants had maintained or recovered the initial root mass recorded at decapitation. However, poplar plants reduced the root mass during the following spring after decapitation.

Nine months after early autumn decapitation, root mass of willow plants was 57% greater than initial root mass, whereas root mass of poplar plants was 52% less than their initial root mass. Differences in the immediate resprouting vigour after early autumn decapitation between willow and poplar plants are proposed as a likely cause for the differences in the short term root mass dynamics observed in these two species.

Additional elements supporting the proposal that willow trees are more resilient to decapitation than poplar plants, can be found in the root starch dynamics observed.

Willow plants decapitated in early autumn replenished the root starch reserves similar to ND willow plants within the first growing season after decapitation, whereas nine months after early autumn decapitation, poplar plants had less coarse and fine root starch concentrations than ND poplar plants.

In comparison to initial root mass prior to above-ground removal, dormant decapitation did not reduce root mass, neither in willow nor in poplar plants.

Root mass of DD poplar plants in early summer was similar that recorded for ND poplar plants, whereas root mass of DD willow plants was 56% that of ND willow plants. However, it is proposed that pot volume constraints might have considerably limited the root mass growth during spring of ND poplar plants which from winter to early summer showed a 9% increase, in contrast to the 75% increase observed in root mass from early autumn to winter.

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Chapter 6. Pasture production beneath pollarded and unpollarded willow trees.

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6.1 Summary

Herbage accumulation beneath a recently pollarded tree is expected to quickly increase to a level similar to that at an adjacent open pasture (OP) site. However, it is important to establish the accumulation dynamics within a pollarding cycle of about 3 or 4 years, when regrowing pollarded trees develop a more branched, bushy canopy than before pollarding.

This study determined net herbage accumulation (NHA) under mature (aged 11⁺ years) willow (*Salix matsudana* × *S. alba*) trees 4 years after they were pollarded. The trees were established to control shallow mass movement erosion in a paddock with an average slope of 16°. They had been pollarded to provide supplementary stock fodder during a drought period when pasture productivity and quality were low. Pasture NHA beneath pollarded (P) trees was compared with that beneath unpollarded (UP) trees and with NHA of nearby OP away from the direct influence of trees.

Herbage accumulation measurements were taken on the south, shady side of P trees. Four years after being pollarded, annual NHA beneath P and UP trees was respectively 30% and 47% less than at an OP site. It is proposed that 4 years after pollarding, values of above-ground attributes of P trees had attained values similar to those of UP trees, which was reflected in similar NHA recorded beneath P and UP trees. Annual NHA in OP sites (4.9 t DM ha⁻¹) was below that commonly reported for pastoral hill country. Average grass matter percentage in the sward was also particularly lower (30%) than values frequently reported in pastoral hill country.

On a seasonal basis, NHA of OP sites was greater than in understorey environments only in spring.

It is suggested that particularly dry conditions experienced during the study might have been the determinant for the NHA accumulation pattern and botanical composition observed. Therefore, results need to be interpreted with caution due to the prevalent climatic conditions in this study.

6.2 Introduction

Pasture production on hill country has been determined for three situations: a) on stable slopes, b) on unstable erodible slopes, and c) beneath and between wide-spaced willow and poplar trees established to control shallow mass movement erosion. In pasture-tree (PT) systems, the impact on pasture production of reducing canopy size of trees, such as by pollarding at one or multiple times, has received very little attention. Such practices may enhance understorey pasture production and quality, and provide additional options for sustainable management of PT systems involving poplars and willows.

Where erosion has occurred following severe storms, there is an immediate loss in the area of pasture cover on hillslopes, either because of landslide scars or debris deposition (Hawley and Dymond, 1988). While zones of debris accumulation could benefit in the short- and mid-term from nutrient deposition, exposed subsoil or bedrock on landslides scars requires a longer time frame to revegetate (Lambert et al., 1984, Douglas et al., 1986). Landslide scars usually revegetate relatively quickly during the first 20 years after soil loss. During that time, pasture production of revegetated scars recovers to between 60% and 80% of that on uneroded sites; further recoveries have not been observed thereafter (Lambert et al., 1984, Douglas et al., 1986, Derosé et al., 1995, Blaschke et al., 2000, Rosser and Ross, 2011). When integrating the percentage of a slope with landslide scars, revegetation rate of the scars, and the likelihood of further erosion events, Derosé et al. (1993) estimated that on unstable slopes steeper than 28°, without the presence of wide-spaced trees, pasture production would be reduced at a rate of around 1-3% per decade. In the Wairarapa hill country, it was estimated that since forest clearing around 1880, pasture productivity has declined 18% because of the impact of shallow landslide erosion (Trustum et al., 1984). Conversely, it has been estimated that the presence of wide-space trees reduced the area of bare ground from landsliding after an erosion-inducing storm by 70% (Hawley and Dymond, 1988) to 95% (Douglas et al., 2013).

The presence of trees on hillslopes reduces pasture production beneath and adjacent to the canopy. Estimates of reductions in annual pasture production relative to open pasture sites have ranged from 20% beneath individual poplar trees aged 11 years (Douglas et al., 2006), to 40% under

mature (29 to 40 years) poplar trees (Guevara-Escobar et al., 2007). A series of studies have shown strong relationships between canopy closure (proportion of the sky hemisphere obscured by vegetation when viewed from a single understorey point (Jennings et al., 1999)), light transmission, and the influence of these factors on pasture productivity (McElwee and Knowles, 2000, Wall et al., 2010). Canopy closure has been reported to explain more than 90% the variation in photosynthetically active radiation (PAR) reaching understorey (Wall, 2006) and PAR in turn has been reported to explain more than 80% the variation in pasture NHA (Wall et al., 2010)

It is expected that pasture production will increase around wide-spaced trees in the immediate and short term after pollarding, but it is important to establish the dynamics in herbage accumulation as pollarded trees start regrowing their canopy. Based on the recovery of fine root structure after pollarding, McIvor et al. (2011) proposed a pollarding cycle of three or four years. This study, conducted on a hill country farm where pollarding has been practised during the last 10 years, aimed to determine herbage accumulation rates around trees pollarded 4 years earlier, and compare them with those around UP trees and in adjacent OP, away from the direct influence of trees.

6.3 Materials and methods

6.3.1 Site description

This study was conducted on a hill country sheep and beef farm (40.1°S, 176.4°E) located approximately 10 km SW of Waipukurau in central Hawke's Bay. The region typically experiences dry summers with daytime air temperatures ranging from 20°C to 28°C, and occasionally exceeding 30°C. High temperatures in summer may be accompanied by strong, dry winds from the northwest. Parts of a pasture-tree system in a paddock located on a south-facing slope averaging 16°, with a silt loam soil (Purimu soil: NZ Soils Database) (Hewitt, 2010) overlaying a sandstone bedrock, were used in this study.

Weather conditions during the study are shown in Fig 6.1. Rainfall during the study was recorded *in situ*, whereas long term (1981-2010) rainfall was obtained from a climate station located 6 km away from the site (40.17°S, 176.45°E). Study and long-term (1981-2010) mean air temperature data were obtained from a climate station 18 km from the experimental site (40.043°S, 176.268°E). Summer 2012-13 was dry, with rainfall around the region ranging from 39% to 69% of mean, long-term rainfall from September 2012 to March 2013, respectively. Soil moisture deficit in March 2013 (more than 130 mm) was considered extreme for that period in much of the region, where long-term normal conditions for the same time of the year are between 90 and 110 mm of soil moisture deficit (Chapell, 2013). Based on the potential evapotranspiration deficit, the 2012-13 drought was the worst drought experienced in central Hawke's Bay region since 1945-46 (Chapell, 2013, Porteous and Mullan, 2013). On the farm, additional fodder was provided by pollarding trees.

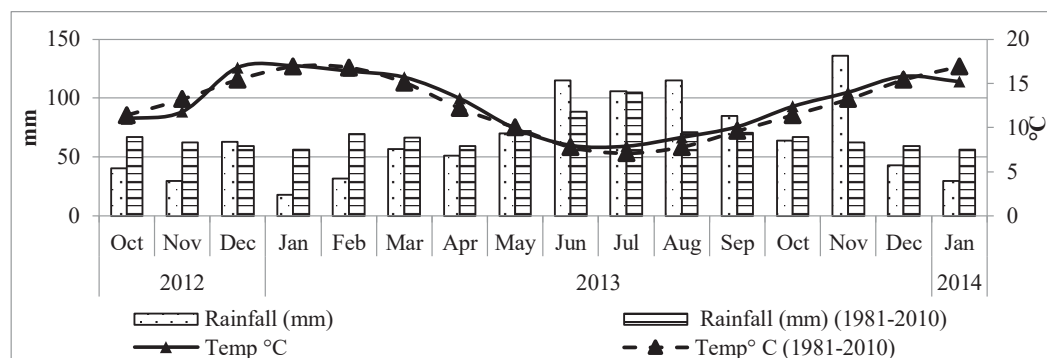


Figure 6.1 Rainfall and mean air temperature during the trial compared with mean long-term (1981-2010) records.

Over the past 16 years, an extensive willow (*Salix matsudana* Koidz. x *alba* L. ‘Tangoio’) tree planting programme has been conducted on the farm and those in this study were aged 12 to 14 yrs. Tree stand density in the paddock (1.7 ha) was 49 stems per hectare.

Remnants of several old shallow landslide scars were observed in the paddock where the study was conducted and the bedrock was exposed on the scars. The study paddock was grazed regularly by both sheep and cattle.

In the study paddock over the past 10 years, some of the willow trees have been pollarded once or twice, while a group of trees remains unpollarded (UP). The first pollarding was undertaken to supply additional stock fodder in February 2006 and some of those trees were repollarded in February 2009 when another drought occurred.

At this site, McIvor et al. (2011) determined the effect of pollarding on tree fine root dynamics. They proposed a pollarding frequency of three or four years, to enable fine root densities of pollarded trees (P) to attain values similar to those of UP trees. Based on the McIvor et al. (2011) work, for this study beginning in 2013, the trees repollarded in February 2009 were considered as being at the end of a pollarding cycle, and were therefore considered P trees to distinguish them from the UP trees.

6.3.2 Experimental Design

In the slope UP trees predominated in the steeper upper section of the slope, whereas pollarded trees were most abundant in the easiest of access toe-section of the slope. In the mid-section of the slope, available P and UP trees were randomly and unevenly distributed. Such a condition precluded the possibility to have a defined sampling area dominated by either pollarded or unpollarded trees.

Understorey herbage accumulation beneath tree canopies has been observed to decrease fast and remains relatively steady at levels around 50% of the open pasture regardless the tree stand canopy closure (CC), when this decline beyond 20% (Wall et al., 2006).

Therefore with the aim to isolate as much as possible, the influence of a pollarded and unpollarded environment, the area for herbage accumulation evaluation was situated beneath the canopies on

the south shady side of six trees (3 each for P and UP trees) and extended along a transect where shade of the trees is cast at noon at the end of spring. On average this area extended from the base of the trunk 6.8 m for P trees and 9.3 m for UP trees (Fig 6.2).

Understorey herbage accumulation of the P and UP environments was compared with herbage accumulation in sites located in the same mid-section of the slope and situated at least at 11 m away from any surrounding tree trunk.

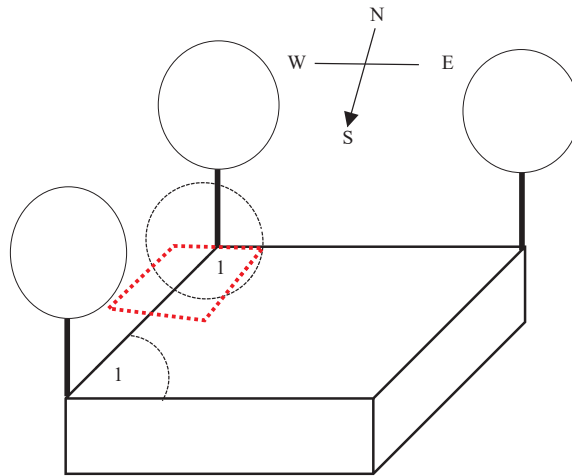


Figure 6.2 Herbage accumulation sampling area (red dashed rectangle). Sampling area comprised the area beneath the horizontally projected tree canopy on the south shady side of the trees and extended southerly from the trunk 6.8 m and 9.3 m for pollarded and unpollarded trees, respectively. 1: area directly below the vertical projection of the tree canopies (Adapted from Wall (2006))

6.3.3 Measurements

6.3.3.1 The trees

Stem diameter at breast height (DBH), height (H), canopy length (CL), mean canopy diameter (MCD), horizontal cross sectional area (HCA) and canopy ellipsoidal volume (CEV) of the trees were recorded at the beginning of the study.

DBH was taken at 1.4 m above-ground level with a diameter tape on the upslope side of trees. H was measured from ground level to the top of the canopy with a digital hypsometer (Vertex III and transponder T3, Haglof Sweden AB). CL was calculated as H minus canopy base height from

ground level. The base of the canopy was considered from the point on the stem when foliage occupied at least three of the four quadrants around the stem (Canham et al., 1999). MCD was estimated from two perpendicular measurements taken north to south and east to west beneath the canopy of the trees. Measurement limits were taken from the outermost edges of the canopy vertically projected to the ground (Schreuder et al., 1993). HCA was calculated from MCD applying the formula:

$$\text{HCA} = \pi \text{MCD}^2 / 4 \text{ (units: m}^2/\text{stem)}$$

For CEV a solid vertical ellipse tree canopy with perfect symmetry was assumed, and was calculated from measurements of MCD and CL using the formula:

$$\text{CEV/tree} = 3/4 \pi R^2 h \text{ (units: m}^3\text{)}$$

Where R = horizontally projected green canopy radius per tree (half of MCD)

h = half the vertical green CL per tree

6.3.3.2 Herbage accumulation measurements and botanical composition

Herbage accumulation was determined from December 2012 to November 2013 using a standard pre-trimming technique (Radcliffe, 1974) involving 1.20 m × 0.50 m grazing exclusion cages. One exclusion cage was located around each of the three P and three UP trees selected. An exclusion cage was also located at each at three different OP sites.

For each sampling period, pasture inside the nine exclusion cages was trimmed with a portable shearing hand piece to a uniform height of 25 mm above-ground. After trimming, a 0.1 m² (200 mm × 500 mm quadrat) herbage sample from ground level was taken to quantify the residual herbage mass below the trimming height. Depending on herbage growth, 4 to 6 weeks after the trimming cut, pasture accumulated was harvested to ground level from a 0.1 m² pre-trimmed subsection.

Residual herbage mass and herbage mass accumulated above pre-trimmed height were taken to the laboratory where tree material (leaves, twigs and bark) not removed in the field was discarded. Samples were then washed with fresh water to remove soil contamination or any other material

different from herbage sample. After washing, the clean samples were dried in a forced draught oven at 80°C for 48 hours. Dried samples were finally weighed on electronic scale to two decimal places (d.p.)

Net herbage accumulation (NHA) ($\text{kg dry matter (DM) ha}^{-1} \text{ day}^{-1}$) was then calculated by subtracting residual herbage mass below the pre-trimming height from the herbage mass harvested to ground level, multiplied by 100 and divided by the number of days between pre-trimming and harvesting date. After each sampling, exclusion cages around trees were moved clockwise within the pasture sampling areas. (Fig 6.2). NHA of individual cuts in each environment were pooled to provide seasonal mean daily growth and annual total.

Within the exclusion cages installed for determining herbage accumulation, additional 0.1 m² herbage subsamples were taken to ground level on 11/02/13, 06/06/13, 26/08/13 and 06/11/13 to assess botanical composition. Herbage was dissected into categories of grass, legume, dead matter, weed, moss and plantain.

6.3.4 Data analysis

Differences between tree parameters and annual mean NHA were analysed by Analysis of Variance (ANOVA), with the general lineal model procedure of the SAS software 9.4 (SAS, 2012).

Repeated measures ANOVA was conducted on monthly and seasonal (NHA) and botanical composition data. For herbage accumulation, the model included, between subjects effect, 2 degrees of freedom (d.f.) for treatment. For within subjects effect, the model included 11 and 22 d.f. for monthly sampling time and the interaction between monthly sampling time and treatment, respectively. Mean separations were analysed with the Least Significance Difference (LSD) test at the 5% level.

6.4 Results

6.4.1 The trees

DBH, H and CL of trees were not significantly different between the P and UP treatments. Means of tree parameters based on assumptions of perfect tree canopy forms, like MCD, HCA and CEV were all statistically different between both treatments (Table 6.1) with MCD, HCA and CEV of UP trees being 20, 36 and 47% greater, respectively, than observed for P trees.

Table 6.1 Means of tree parameters measured on pollarded and unpollarded trees \pm SE. Within columns, means with different letters in parentheses are significantly different ($P < 0.05$)

Trees	N	Parameters					
		DBH (cm)	Height (m)	canopy length (m)	Mean canopy Diameter (m)	Horizontal cross sectional area (m ²)	canopy ellipsoidal volume (m ³)
Unpollarded	3	36.9 \pm 2.3	14.1 \pm 0.4	11.70 \pm 0.4	9.14 \pm 0.39(a)	65.71 \pm 4.4(a)	513.0 \pm 50.0(a)
Pollarded	3	39.4 \pm 1.7	12.1 \pm 0.7	9.7 \pm 0.7	7.32 \pm 0.1(b)	42.1 \pm 0.7(b)	272.2 \pm 19.5(b)

6.4.2 Net herbage accumulation

Net herbage accumulation (NHA) in both tree understorey environments, averaged over a year, was significantly less ($P < 0.05$) than in the OP environment (4.9 ± 0.7 t DM ha⁻¹ yr⁻¹), being 30% less beneath P trees (3.4 ± 0.6 t DM ha⁻¹ yr⁻¹) and 47% less beneath UP trees (2.6 ± 0.4 t DM ha⁻¹ yr⁻¹). There were no significant differences in NHA between the understorey environments.

On a monthly basis, significant differences ($P < 0.05$) in NHA between treatments were detected in autumn and spring (Fig 6.2). In autumn (March-May), April was the only month when differences were observed, with mean NHA in the P environment being approximately 80% less than in the OP environment; NHA in the UP environment was intermediate between that in the other environments and not significantly different from either (Fig 6.3). During spring, in October and November, NHA in the UP and P environments were significantly less ($P < 0.05$) than in the OP environment. For example, in November, when the greatest mean NHA was recorded in the OP environment (52.2 ± 2.6 kg DM ha⁻¹ day⁻¹), NHA in the P (29.7 ± 0.8 kg DM ha⁻¹ day⁻¹) and UP (29.3 ± 3.6 kg DM ha⁻¹ day⁻¹) environments was about 43% less (Fig 6.3).

On a seasonal basis, differences in NHA between environments were detected only in spring when NHA in the P ($20.9 \pm 1.9 \text{ kg DM ha}^{-1} \text{ day}^{-1}$) and UP ($18.6 \pm 1.44 \text{ kg DM ha}^{-1} \text{ day}^{-1}$) environments was significantly less than in the OP environment ($36.6 \pm 2.8 \text{ kg DM ha}^{-1} \text{ day}^{-1}$) (Table 6.2).

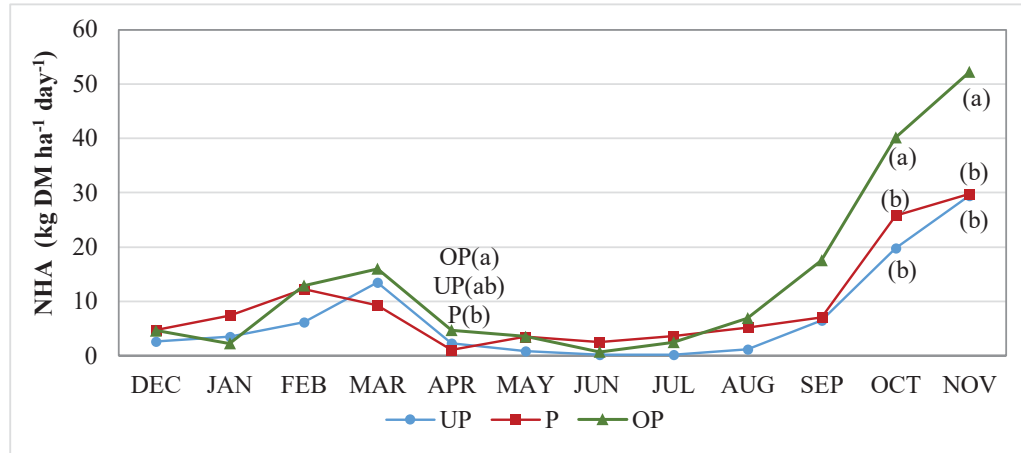


Figure 6.3 Mean net herbage accumulation (NHA) ($\text{kg DM ha}^{-1} \text{ day}^{-1}$) on a monthly basis, beneath unpollarded (UP) and pollarded (P) environments and in open pasture (OP). Different letters at monthly sampling times indicate significant differences ($P < 0.05$) between treatments.

Table 6.2 Mean \pm SE net herbage accumulation ($\text{kg DM ha}^{-1} \text{ day}^{-1}$) on a seasonal basis, beneath unpollarded (UP) and pollarded (P) trees and in open pasture (OP).

Environment	SUMMER (DEC-FEB)	AUTUMN (MAR-MAY)	WINTER (JUN-AUG)	SPRING (SEP-NOV)
OP	6.6 ± 1.5	8.1 ± 0.6	3.4 ± 1.9	$36.6 \pm 2.8 \text{ a}$
P	8.1 ± 3.8	4.6 ± 1.8	3.8 ± 2.1	$20.9 \pm 1.9 \text{ b}$
UP	4.1 ± 1.3	5.6 ± 2.3	0.6 ± 0.3	$18.6 \pm 1.4 \text{ b}$

Botanical composition

Differences between treatments in any of the botanical components in any particular season were not significantly different (Fig 6.4).

Averaged across the 4 sampling seasons dead matter content in samples from the P environment was about 10 percentage units less than in those from the UP and OP environments (Fig 6.4).

There were no other significant differences in botanical composition.

Grasses in samples were predominantly *Agrostis capillaris*, *Anthoxanthum odoratum*, *Lolium perenne* and *Poa trivialis*.

Average grass content was approximately 40% of sward DM in all environments. The lowest grass content was found in summer 2013 (8-16% of DM) and coincided with the greatest dead matter content observed (71-87% of DM) (Fig 6.4). Thereafter, grass content increased to a maximum in spring 2013 (68-71% of DM) when the lowest dead matter content was observed (8-18% of DM). The greatest legume content in any season (4% of DM) was observed in spring in the P environment (Fig 6.4).

Wild plantain recorded in spring represented 5% in all the treatments. Moss was present all year round with its highest values in August representing 15, 21 and 30% of the components in UP, OP and P environments respectively

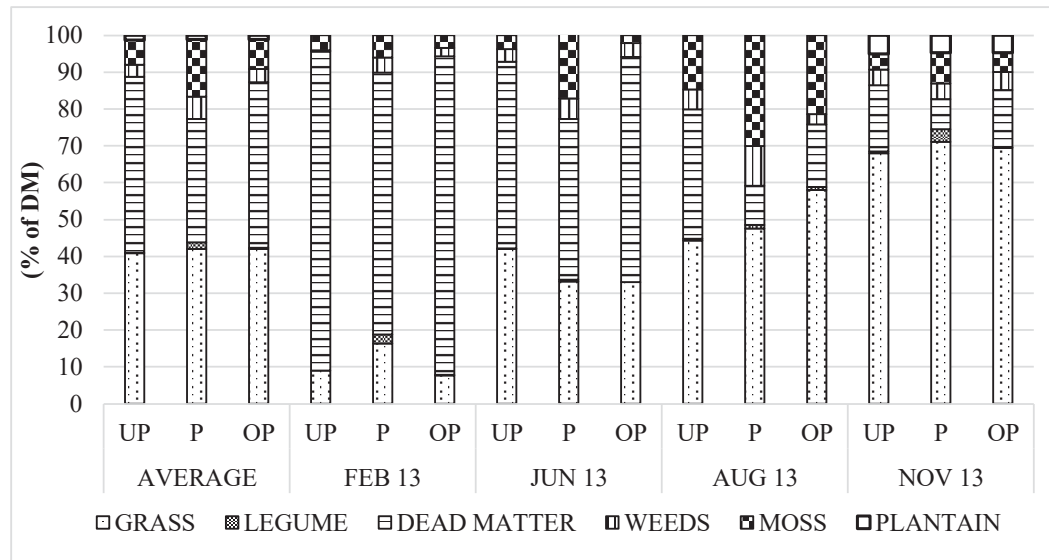


Figure 6.4 Mean botanical composition (% of DM) of swards beneath unpollarded (UP) and pollarded (P) trees and in open pasture (OP).

6.5 Discussion

6.5.1 The trees

When used as independent variables, Wall et al. (2010) showed that the tree parameters measured in this study (Table 6.1) were highly influential (R^2 0.91-0.95) for estimating PAR transmission between and through the canopy of poplar tree stands of different size. However, significant differences were found in the slope of the relationship and in the estimated PAR transmission across different sites. Differences between sites were attributed by Wall et al. (2010) to the inability of such tree parameters to account for variation in tree leaf area caused mainly by intensive silvicultural practices such as pruning (Devkota et al., 2009), or as in this study, by pollarding.

Pollarding, the complete removal of the tree canopy, by releasing apical dominance, promotes vigorous sprouting which results in a distinctive thick, bushy, appearance of the trees (Sennerby-Forse et al., 1992, de Figueiroa et al., 2006, Islam et al., 2008). Branching pattern and leaf area changes following pollarding are not accounted for within the tree parameters measured in this study. Measurements of P trees in this study showed that their canopies were indeed smaller and narrower than those of UP trees (Table 6.1), and visual estimations suggested that the canopies of P trees were more branched and leafy than UP trees.

6.5.2 Net herbage accumulation

Most reports show that pasture production beneath willow and poplar trees is less than in adjacent OP sites away from the influence of trees (Guevara-Escobar et al., 1997, Douglas et al., 2006, Wall, 2006, Guevara-Escobar et al., 2007). Yet reductions in pasture growth beneath trees relative to that at OP sites are highly variable. Differences reported depend mostly on the approach used, sampling strategies, age-size of the trees, stand density and site characteristics where studies have been conducted. Thus, Guevara-Escobar et al. (2007) did not find significant differences in pasture production between OP sites and beneath 5 year-old poplar trees in a stand of 50 to 100 stems ha^{-1} . In contrast, Miller et al. (1996) estimated a 40% reduction in pasture accumulation

beneath willow trees aged 6 -10 years at a density of 400 stems/ha, compared with that of swards on a stable open site.

In this study, NHA on an annual basis beneath P trees was 30% less than at OP sites, and that beneath UP trees was 47% less. These reductions beneath trees were in agreement with a series of studies conducted in pasture-tree systems in hill country where the herbage sampling area included (Douglas et al., 2006) or was exclusively situated beneath the tree canopy area (Guevara-Escobar et al., 2007). A reduction of 40% in herbage accumulation relative to open pasture was reported by Guevara-Escobar et al. (2007) in a pasture-tree system comprising poplar trees aged 29⁺ years at a density of 40 stems per hectare (sph). Douglas et al. (2006) reported a 36% reduction in annual pasture production compared to an OP site at a pasture-poplar site with trees aged 11 years at a density of 25-400 sph.

Reductions in NHA of about 10-15% have been reported around isolated trees compared with at OP sites (Gilchrist et al., 1993, Douglas et al., 2001). It was suggested that environmental conditions constrained herbage accumulation in both OP and understorey sites.

In order to obtain a more reliable estimation of stand level NHA in a pasture-tree system, Devkota et al. (2001) and Wall (2006) showed that herbage sampling should be conducted in at least two main environments, namely, directly below the tree canopy, and in the vertical canopy gap formed between the canopies of adjacent trees (Fig 6.5). Using that sampling strategy, Devkota et al. (2001) found that NHA directly below a poplar canopy was around 65% less than at OP sites, and it varied little with tree stand density ranging from 31 to 89 sph. In contrast, NHA in the canopy gap increased from 37% to 74% of that at OP sites when stand density declined from 89 to 31 sph.

In this study, as described in Section 6.3.2, herbage sampling was conducted mostly below the tree canopies and extending to a total length where the shade of the canopy was cast at noon in the middle of the spring (Figs 6.2 and 6.5). This sampling area aligned with that described by Wall (2006) as Zone 1 (directly below the tree canopy) and transitional Zone 2 (area midway between the centre of the vertically projected canopy gap (Zone 3) and its respective limits at the

edges of the tree canopies) (Fig 6.5). Wall (2006) found that annual NHA in Zone 1 declined rapidly and was maintained at approximately half that of open pasture when going from open pasture to canopy closures (CC) of around 20%. In Zone 3, rate of decline in NHA was estimated to be 6.6% for each 10% CC increment. In a pasture-tree system with poplar trees aged 30⁺ years, measured herbage accumulation was 63% of OP site at 50 % CC and decreased to 50% of OP site at 70% of CC (Wall, 2006).

Based on Devkota et al. (2009) and Wall (2006) reports, it is suggested that reductions in annual pasture production recorded in this study of 30% beneath P trees and 47% beneath UP trees would have been smaller if canopy gap zones had been included in the sampling scheme.

6.5.2.1 NHA on a pasture-tree stand level.

With the aim to estimate in this study how gap areas between canopy trees influence the herbage accumulation on a pasture-tree stand level, and how herbage accumulation might change within a 4 year pollarding cycle, a series of estimations were developed based on the following series of facts and assumptions.

First of all it is proposed a scenario of 1 ha pasture-tree stand, with a tree density, as measured in this study site, of 49 sph. It is assumed that 33% of the trees (16) were pollarded in time 0, and 33% of the left UP trees were pollarded (11 trees) 4 years after the first 16 trees were pollarded. The trees are evenly distributed in a square grid pattern of 16.6 m × 16.6 m (Fig 6.5).

The ground area influenced by the P or UP environment was assumed to have an ellipsoidal form (Fig 6.5). The ellipsoidal ground area influenced by the P or UP trees on the south shady side of the trees (A) was then estimated with the ellipse area formula:

$$A = \pi \times B \times C$$

Where: $\pi = 3.1416$

B = Semi-major axis of the ellipse (average of half the length beneath the canopy of the P and UP trees, respectively, taken east to west from the outermost edges of the canopy vertically projected to the ground (Section 6.3.3.1)

C = Semi-minor axis of the ellipse was considered half the length of the herbage sampling transect set at the beginning of the study (Section 6.3.2, Fig 6.2)

It is assumed that the annual NHA obtained from the sampling area in this study for P (3.4 t DM ha⁻¹) and UP (2.6 t DM ha⁻¹) trees is representative of the resulted ellipsoidal areas cast for the canopy of the P and UP trees (Fig 6.5).

Differences in NHA have been found at different aspects around the trees, and it has been reported that these differences have a strong seasonal influence (Douglas et al., 2006). In a pasture-poplar tree stand, herbage accumulation on the north side of the trees during spring (September and October) was significantly greater than on south side, whereas in summer (January and February) the contrary was reported (Douglas et al., 2006). It may be because of these different seasonal responses in herbage accumulation at different aspects around the tree that no annual NHA differences were reported by Douglas et al. (2006) between the north and the south side of the poplar trees.

Similarly Wall (2006) did not find differences in annual NHA between the shade-facing or sun-facing side of the trees on a North aspect slope when evaluating herbage accumulation below poplar tree canopies.

Based on the Douglas et al. (2006) and Wall (2006) observations it was assumed that the annual NHA in the ellipse area located in the south shady side of the trees was the same in a similar ellipsoidal area cast from the trunk towards the north side of the trees (Fig 6.5). Therefore, the total ground area influenced by the canopy of the P and UP trees was twice the ellipsoidal assumed ground area influenced by the canopy of the trees on the south shady side of the trees.

The rest of the area outside from the P and UP trees influence in a 1 ha proposed paddock, was considered to have the same annual NHA that recorded in OP sites (4.9 t DM ha⁻¹) and was named as the gap area.

With this general framework annual NHA was evaluated under 4 situations (Table 6.3): A) the current situation 4 years after 33% of the trees were pollarded, B) the current situation with none

of the trees pollarded, C) during the first year of a 4 year pollarding cycle, after pollarding 33% of the trees, and D) the current situation, four years after the first trees were pollarded, plus 11 more trees pollarded in the 4th year. Results of these situations are shown in Table 6.3.

6.5.2.1.1 Situation A and B.

Results in Table 6.3 show that reduction in annual NHA would increase 6% if there would not have been any pollarded tree (situation B) in comparison to the current scenario (situation A) 4 years after 33% of the trees were pollarded. A couple of factors might be contributing to this low impact in herbage accumulation at the end of the pollarding cycle by pollarding only 33% of the trees. Herbage accumulation under trees pollarded 4 years earlier in this study was not significantly different than accumulation recorded under UP trees. The influence of the pollarded environment on the total area (12%), four years after only 33% of the trees were pollarded is low for it to make a considerable contribution in diminishing the reductions in herbage accumulation imposed by the presence of UP trees.

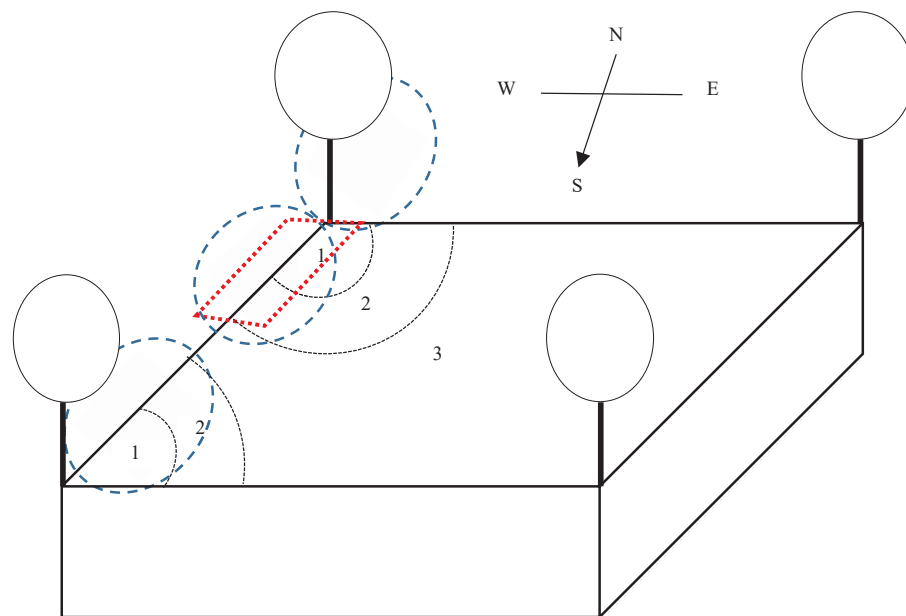


Figure 6.5 Sampling area in the present study (red dashed rectangle) and in previous studies with intensive sampling strategies. Zone 1: area directly below the vertical projection of the tree canopies. Zone 2: (area midway between the centre of the vertically projected canopy gap (Zone 3) and its respective limits at the vertically projected edges of the tree canopies. Zone 3: at the centre of the vertically projected canopy gap. (Adapted from Wall (2006)) Ellipses (dashed outline) are the assumed area under the influence of either pollarded or unpollarded trees, derived from the mean canopy diameter of the trees and the length of the sampling transect (red rectangle). Annual NHA on the ellipsoidal area of tree influence on the south-shady side was assumed to be the same for the same ellipse area extension on the north side of the trees.

Table 6.3 Influence of pollarding in the annual net herbage accumulation (NHA) on pasture-free stand level under different situations within a 4 year pollarding cycle.

Situation A) 1 ha, 49 sph, 33% of the trees (16) were pollarded 4 years before						
Environment	Area under the influence of an individual tree (m ²) ^a	No of trees	Area under the influence of the trees and gap area (m ²)	Annual NHA under the sampling area (t DM ha ⁻¹)	Annual NHA within the area influenced by (t DM ha ⁻¹)	NHA reduction ^b (%)
P trees	78.15	16	1250.4	3.4	0.43	24
UP trees	129.4	33	4270.2	2.6	1.11	
Gap			4479.4	4.9	2.19	
total			10000.00		3.73	
Situation B) 1 ha, 49 sph, none of the trees were pollarded						
P trees	0.00	0	0.00	3.4	0.00	30
UP trees	129.43	49	6342.07	2.6	1.65	
Gap			3657.93	4.9	1.79	
total			10000.00		3.44	
Situation C) 1 ha, 49 sph, 1st year after pollarding 33% of the trees						
P trees ^c	7.82	16	125.12	4.9	0.06	20
UP trees ^e	129.4	33	4270.2	2.6	1.11	
Gap			5604.68	4.9	2.75	
total			10000.00		3.92	
Situation D) 1 ha, 49 sph, 33% of the trees were pollarded 4 years before, 33% of the left UP trees were pollarded this year						
P trees 4 yr before	78.15	16	1250.4	3.4	0.43	17
P trees-this year	7.82	11	86.02	4.9	0.04	
UP trees	129.4	22	2846.8	2.6	0.74	
Gap			5816.78	4.9	2.85	
total			10000.00		4.06	

a) See section 6.5.2.1

b) (Open pasture NHA - NHA yield beneath trees) × 100/(Open pasture NHA). NHA (4.9 t DM ha⁻¹ yr⁻¹) measured in the Open pasture was assumed to be the same in the gap area between the assumed ellipsoidal areas under the tree influence

c). It was assumed that in the first year of a 4 year pollarding cycle, the ellipsoidal area cast by the tree canopies was 5% smaller than 4 years later.

6.5.2.1.2 Situation C.

A series of reports show the inverse relationship between canopy closure (CC) and photosynthetically active radiation (PAR) transmission through the tree canopy and in turn, the direct relationship between PAR and understorey pasture production. Regression analysis shows that CC explains >90% of the variation in PAR (Wall, 2006) and that PAR in turn relates directly ($R^2 = 0.84$) to pasture production (Wall et al., 2010). Canopy closure of mature poplar trees has also been shown to explain a high proportion (77%) of the variation in pasture production (McElwee and Knowles, 2000).

Based on reports, it is hypothesised that immediately after pollarding, NHA of understorey pasture would increase rapidly and attain a level similar to that of open pasture. If a regular pollarding regime is not imposed, pollarded trees could develop a shoot:root ratio approaching that before pollarding, resulting in NHA decreasing to levels beneath UP trees.

In an alley tree-crop system after one and a half year after total pruning *Alnus acuminata* trees, bean production (kg/ha) in the tree-crop system was not different that of sole bean crop yield (Sande, 2003).

Over ten months after pollarding, pastures in the open and around recently pollarded poplar trees accumulated 14.3 t DM/ha and 15.7 t DM/ha, respectively, which were not significantly different from each other. Swards beneath UP trees accumulated 9.8 t DM/ha over the same period, which was an average reduction of 34% compared with that in the open and pollarded treatments (Douglas et al., 2009).

Based on Sande (2003) and Douglas et al. (2009) reports, it was assumed that within the first year after pollarding, herbage accumulation around pollarded willow trees is similar that of the annual NHA recorded in this study in OP sites (4.9 t DM ha⁻¹). Table 6.3 show that within the first year after pollarding 33% of the trees, herbage accumulation reductions would be 4% less than reductions observed at the 4th year after pollarding, if no additional UP trees are incorporated into the pollarding program.

6.5.2.1.3 Situation D

Situation D in Table 6.3 shows that by pollarding 11 new UP trees in the 4th year of the pollarding cycle when 16 trees have already been pollarded 4 years before, NHA reductions relative to OP sites would diminish by 7% in comparison to situation A (only 16 trees pollarded 4 years before), and by 13% in comparison to situation B where none of the trees have been pollarded.

Estimations developed on Table 6.3 show that if pollarding is going to be used as a systematic strategy to increase herbage accumulation in pasture-tree stands, more new unpollarded trees should be incorporated within the pollarding cycle in order to increase the area under the influence of pollarded trees. However, incorporation of additional trees into a pollarding scheme is contingent on the presence of undesirable pasture shortage conditions like summer/autumn droughts.

In this study, annual NHA beneath P trees suggests that four years after being pollarded their canopies had developed a leaf area and architecture sufficient to decrease NHA to less than that of open pasture and similar to that beneath UP trees.

McIvor et al. (2011) found that after pollarding, trees take about three or four years to recover fine root densities similar to those of UP trees. Al Afas et al. (2008) found a positive, high correlation ($r=0.91$) between fine root area index (fRAI) and leaf area index (LAI) in five different poplar clones. If the findings of Al Afas et al. (2008) are applicable to *Salix* spp., and based on the McIvor et al. (2011) findings, it is hypothesised that 4 years after pollarding, the P trees had increased their levels of fRAI and LAI to levels similar to those of UP trees. This redevelopment of above- and below-ground attributes of P trees may explain the similarity in NHA beneath P and UP trees after 4 years.

6.5.2.2 Seasonal net herbage accumulation

Differences in NHA between tree and OP sites are influenced strongly by season and are in turn highly related to the presence or absence of leaves on the trees (Douglas et al., 2006, Wall, 2006, Guevara-Escobar et al., 2007).

Differences in NHA have mostly been found during spring, summer and early autumn, whereas in late autumn and winter, when trees are without leaves, NHA of understorey and OP sites is often similar. However the extent of this similarity has differed from year to year and between sites, and studies have shown variation in the timing when understorey NHA temporarily recovers to levels similar to those in OP sites (Douglas et al., 2006, Wall, 2006, Guevara-Escobar et al., 2007).

In this study differences in seasonal NHA between environments were only detected in spring 2013 when accumulation in the OP environment was 44% greater than recorded in both understorey environments (P and UP) (Table 6.2). Conditions from spring 2012 to summer 2013 were particularly dry (Fig 6.1). Based on rainfall and potential evapotranspiration deficit records, the 2012-2013 drought was considered one of the worst droughts in the previous 30 to 40 years (Porteous and Mullan, 2013, Chapell, 2013).

The annual NHA estimated in the OP environment in this study (4.9 ± 0.7 t DM ha⁻¹ yr⁻¹) was less than the average (7.0 t DM ha⁻¹ yr⁻¹) (Bryant and Sheath, 1987) and close to the minimum value (5.0 t DM ha⁻¹ yr⁻¹) (Valentine and Kemp, 2007) commonly reported for herbage accumulation in pastoral hill country during dry summers.

Reports of minimal or non-significant differences in NHA between understorey and OP environments have generally been found where site or environmental conditions constrained pasture production in both the understorey and the OP sites.

Douglas et al. (2001) found that in comparison to OP plots, annual NHA at a site with larger trees (Pohangina, southern North Island) was reduced 10.5% compared with a reduction of 27% at a site with smaller trees (Lawrence, southern South Island). The site at Pohangina had greater variation in soil water content with a drier late spring and summer than at Lawrence. The authors suggested that the lower soil water contents at Pohangina may have limited pasture growth more than solar irradiance in both the tree understorey and OP plots. Herbage production in the OP plots reported by Douglas et al. (2001) averaged 5.2 t DM ha⁻¹ less at Pohangina than at Lawrence. Douglas et al. (2001) proposed that under conditions where pasture growth is more limited by

factors other than solar irradiance, variation in pasture growth owing to the presence of trees is reduced.

In pasture-tree systems involving poplar and willow (Gilchrist et al. (1993), annual NHA (6.3 t DM/ha/year) in OP plots was near the lowest usually recorded on hill country (Bryant and Sheath, 1987, Valentine and Kemp, 2007). Similar to that observed by Douglas et al. (2001), Gilchrist et al. (1993) found no significant differences in annual pasture production between OP sites and beneath the canopies of poplar (16-19 yrs) or willow (11-14 yrs) trees. In general, Gilchrist et al. (1993) also reported that soil moisture deficits were present at the study site.

Negligible or even positive effects on pasture production below tree canopies relative to OP sites are commonly reported in pasture-tree systems in environments with harsh climates, with well-defined and recurrent drought periods like the rangelands in California (Frost and McDougald, 1989), grass production under *Quercus* forest in Mediterranean climates in the region of Middle Atlas in Morocco (Qarro and Montard, 1992), or the Oak Dehesas in Spain (Moreno et al., 2007).

6.5.3 Botanical composition

Significant differences between environments were only found in the average dead matter content across the four seasons evaluated, where sward under the P environment had 10% less dead matter than the UP and OP environment. Lack of significance between understorey and open pasture in different sward components on an annual basis has been previously reported (Guevara-Escobar et al., 1997, Douglas et al., 2001, Douglas et al., 2006). However, in contrast to this study, where differences between treatments in any of the botanical components in any of the seasons evaluated were not found, Guevara-Escobar et al. (1997), Douglas et al. (2006) and Guevara-Escobar et al. (2007) do report interactions between sampling time and environments (tree understorey and OP sites) in different components of the sward.

Douglas et al. (2006) for instance, reported that grass content was significantly higher beneath trees than in OP sites in all seasons except winter, when pasture growth was lowest, and no differences were detected between environments. In contrast Guevara-Escobar et al. (1997)

showed that apart from autumn in one of a two year evaluation, grass content was lower in the understorey than in the OP sites.

Legume, dead matter and weed content were also reported by Guevara-Escobar et al. (1997) and Douglas et al. (2006) as showing differences between environments within different seasons of the year.

Part of the explanation in the discrepancies of this study and those reported by Guevara-Escobar et al. (1997), Douglas et al. (2006) and Guevara-Escobar et al. (2007) might be found in the contrasting differences observed between this study and cited reports in the grass and dead matter content.

The average grass content of this study was around 40% of sward DM in all environments, with minimum values of 8-16% during summer and maximum of 68-71% in spring. In contrast, Guevara-Escobar et al. (1997), reported annual average grass content in swards of 65% and 75% of DM under mature poplar trees and in OP sites, respectively. Douglas et al. (2001) found that grass content at two different sites with mid-aged poplar trees exceeded 75% of DM at all times and was frequently more than 85% of DM. Likewise, average content of grass in the swards assessed by Wall (2006) at three different sites was at a minimum of 60% of DM with seasonal values exceeding 75% of DM.

It has been explained in Section 6.3.1 of the harsh historical dry conditions experienced in the spring 2012-summer 2013 which very likely caused the death of many plants in the sward, which in turn might have caused balance disruptions in sward composition.

An additional element that might help in explaining differences observed in the sward composition between this study and those reported might be because of the differences in the herbage sampling technique used.

In this study, herbage for botanical composition was collected to ground level and, at least, as specified by Wall et al. (2006) and Douglas et al. (2001), herbage samples in their studies were collected at a height of 2.5 cm above the ground. Greater dead matter content in the herbage mass

below 2.5 cm trimming height has been documented (Keogh, 1973a, Keogh, 1973b). Additionally, herbage in this study was sampled on the south (shady) side of the trees. Douglas et al. (2001) observed on a slope of similar aspect to that in this study that swards on the south side of trees had greater dead matter content than those on the north side of trees and those in OP plots. Douglas et al. (2001) suggested that greater dead matter content on the south side of trees was because of leaf tissue senescence in response to shade, and cooler temperatures slowing the rate of decomposition of plant debris. On the same south-facing slope, Douglas et al. (2001) found that swards on the north side of trees had up to eight percentage units greater grass content than those on the south side and in the open, in all seasons. In this study, average dead matter content, on an annual basis, was less in P than in OP and UP environments (Fig 6.4).

Regardless of the differences in the contents of grass and dead matter compared to previous reports, these herbage components showed similar seasonal fluctuations to those reported previously. For example, the greatest grass and lowest dead matter contents in spring were also observed by Guevara-Escobar et al. (1997) and Guevara-Escobar et al. (2007) under mature poplar trees. Similarly, this study and that by Guevara-Escobar et al. (1997) found that grass content decreased and dead matter content increased during the late summer–autumn period.

Legume content in this study was greatest in spring in the P environment where it attained about 4% of DM, and legume content averaged over the period February to November 2013 was less than 1% of DM in OP swards (Fig 6.4). The latter value was below that normally found in pastoral hill country, ranging from 7% of DM (Wall, 2006), through 11% of DM (Guevara-Escobar et al., 1997) to 15.4% of DM at its peak in spring (Douglas et al., 2006).

6.6 Conclusions

Four years after pollarding, annual net herbage accumulation beneath the south (shady) side of P and UP trees was reduced, respectively, by 30% and 43% of that at nearby OP sites. It is suggested that 4 years after pollarding P trees had attained values of above-ground attributes similar to those of UP trees, resulting in swards having similar NHA in these two environments.

Annual NHA in OP sites (4.9 t DM ha^{-1}) was below the average and close below the minimum value commonly reported for the pastoral hill country.

Differences in NHA on seasonal basis were only detected in spring when understorey herbage accumulation was 43% less than accumulation recorded in OP sites.

No significant differences between environments in any botanical component in any season evaluated were detected. Average, minimum and maximum grass matter content in this study were around 30, 48 and 10% less, respectively, than the contents reported in previous studies.

Estimations of the influence of pollarding in NHA on a pasture-tree stand level suggest that within a 4 year pollarding cycle new trees must be incorporated each year into the pollarding program if considerable increases in herbage accumulation relative to OP sites are aimed by pollarding.

This study was conducted during the worst drought experienced in the region and New Zealand in the last 30 to 40 years, and results may be applicable only under this particular climate condition.

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Chapter 7 General Discussion and Conclusions

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7.1 Introduction

Poplar and willow trees wide-space planted (10 to 15 m apart) in pastoral hill country of New Zealand have proved their effectiveness in reducing incidence and extent of shallow landslides after erosion-inducing storms by 70% to 95% (Hawley and Dymond, 1988, Douglas et al., 2013a). Fodder of the trees provide sheep and cattle with the necessary maintenance nutrition at times when pasture reduces in quantity and quality (Kemp et al., 2001, Oppong et al., 2001). Amenity value and vista enhancement are additional benefits the presence of trees add to the farm's landscape (Wilkinson, 1999, National Poplar and Willow Users Group, 2007).

Despite all the benefits the presence of the trees offer to the pastoral hill country, the lack of a regular tree canopy size management can exacerbate one of their main disadvantages, the reduction in understorey herbage accumulation. Excessive shading by overlapping canopies of mature trees of 29⁺ years old can reduce by up to 40-50% the understorey herbage accumulation compared with that produced in open pasture sites (Wall, 2006, Guevara-Escobar et al., 2007). Oversized trees are also prone to limb breakage and toppling under wet, windy conditions, potentially damaging farm infrastructure (tracks, fences, buildings etc.), injuring livestock or even humans and creating debris that can hinder livestock mustering and smother pasture growth (McIvor et al., 2011a, Douglas et al., 2013b). Problems associated with large trees are deterring farmers from continuing or adopting tree planting programs for soil conservation.

Pollarding by removing the tree canopy, represents an alternative that when repeated periodically, could help to control the size of trees, provide fodder for stock during summer/autumn droughts, and increase, temporarily, sun light reaching the understorey (National Poplar and Willow Users Group, 2007, Douglas et al., 2013b).

Removal of above-ground structure from trees is expected to have an impact on the below-ground structure. Understanding the nature and magnitude of this impact is crucial in order to design a regular canopy management program able to address questions like how many trees to pollard at

any one time, what is the immediate risk to slope stability after pollarding or how regularly to repollard the same trees?

In this Chapter, the general discussion is focused and designed to explain how the results obtained within the short term time frame of this thesis, help to find or refine the answers needed to define a regular tree canopy size management program.

How tree root structure could benefit from pollarding trees when they are dormant rather than the most common practice of pollarding in summer/autumn droughts when trees are still in leaf, was an important question evaluated in Chapter 3 and Chapter 5. The findings of those chapters are also discussed in this chapter.

Pollarding, by suddenly increasing light reaching understorey to similar levels to that of open pasture sites is expected to add new elements to the herbage accumulation patterns in pasture-tree systems. This aspect was evaluated in Chapter 6 and the main practical implications are discussed.

7.2 When to start pollarding.

Even though this issue was not explored in the studies conducted, this initial section is presented as fundamental for the topics and issues discussed in the following sections.

At the early stages of a pasture-tree system establishment, the main aim is to colonize the soil as soon as possible with a protective vertical and horizontal root network, in a concept defined by Watson et al. (1999) and Phillips et al. (2000) as the root site occupancy.

In order to promote an early root interlocking between neighbouring trees, at the beginnings of the pasture-tree system establishment, tree spacings are recommended to be between 8×8 m to 10×10 m (Hathaway, 1986, Hicks et al., 2001). As trees start expanding their canopies and extending their root structure around the tree's trunk, thinning operations are recommended to set final tree spacings between 12×12 m or 15×15 m (Hicks, 1995, National Poplar and Willow Users Group, 2007).

Thinning operations should start once individual trees have developed a root structure long enough to ensure with the contribution of neighbouring tree roots, a regular root density distribution in a radius of about 8-10 m around the tree.

Based on a series of total tree root structure excavations conducted by McIvor et al. (2008) and McIvor et al. (2009) on poplar trees (*Populus deltoides* × *nigra* ‘Veronese’) aged 5 to 11.5 years and located at different positions on the slope, it was concluded that thinning operations might start when trees have reached an age between 8-10 years and a diameter at breast height (DBH) of at least 30 cm.

If the pasture-tree system has recommended tree stand densities (10 to 15 m apart) and trees are big enough (DBH ≥ 30 cm), it is considered that roots of the trees are already interlocking between each other and creating a root network that provides a sufficient stability to the slope to resist slippage. The main question at this stage is then, whether in order to sustain the slope stability the trees within the pasture-tree system require to keep growing according to their potential and prevalent environmental conditions. Larger trees mean a larger and a stronger root network across the slope. However, larger trees also mean the landowner has to deal with the problems associated with oversized trees. The proposal of this thesis is that if pollarding is initiated when the trees are large enough (DBH ≥ 30 cm), and separated to each other no further than 10 to 15, stability of the slope will be maintained, as long as the root structure of pollarded trees remains as it was prior to pollarding.

Based on fine root density recovery observed in pollarded mature willow trees, McIvor et al. (2011b) and McIvor (2015) proposed that no more than 33% of the trees present in the paddock be pollarded at a time, and that these be scattered between unpollarded trees. Trees that are left intact will keep extending their root structure to counteract, at a certain point, disruptions caused in the root structure of pollarded trees.

7.3 What is the immediate risk for slope stability after pollarding.

Farmers who have practiced pollarding for more than 20 years, repollarding every 2 or 3 years, have reported that trees that underwent pollarding have kept growing vigorously and no signs of

erosion problems directly associated with pollarding have been observed near those trees (Olsen and Charlton, 2003, National Poplar and Willow Users Group, 2007).

Explanation for farming pollarding experiences can be found tentatively in results of this thesis, published and unpublished material generated in New Zealand (Table 7.1), and can be summarized as follow:

- Major impact is observed in roots closer to the trunk and above 300 mm soil depth. It is proposed that decreases in fRD at these soil sections would be more than compensated by the presence of large structural roots that contribute significantly to the soil stabilisation.
- In those root depths disrupted by pollarding, decreases in fine root density in comparison to initial pre-pollarding densities are temporary in nature, and by the end of the first year after pollarding, trees had already recovered fine root densities similar or greater than densities recorded prior to pollarding.

In Chapter 3, Section 3.4.1. it was shown that fine root density of pollarded willow trees at 40 cm from the trunk and from 0 to 300 mm soil depth temporarily decreased down to half the initial pre-pollarding densities. However, one year after pollarding fine root densities (length and mass) were similar to pre-pollarding values, but with half the fRD recorded in UP trees. In contrast, fine root densities of the same pollarded willow trees below 300 mm soil depth at 40 cm from the trunk, and at 80 cm from the trunk from 0-450 mm soil depth, stayed the same or increased during the 1st year after pollarding, from the densities recorded prior to pollarding.

Working with mature pollarded willow trees, McIvor et al. (2011b) and Beeden and McIvor (2010) also observed that root sections disrupted by pollarding were those located no further than 3 m from the trunk and above 150 mm soil depth. Willow trees grown in pastoral hill country conditions evaluated by McIvor et al. (2011b) and Beeden and McIvor (2010) also showed temporary decreases in fRLD in comparison to densities recorded prior to pollarding which were eventually recovered within the first year after pollarding. However, it took between 3 to 4 years for the pollarded trees to recover fRLD similar to UP trees (Table 7.1).

Similar root dynamics followed the young willow trees decapitated in Chapter 6, which also showed reductions in root mass 1 month after decapitation, but one year after decapitation had a root mass 57% greater than root mass recorded prior decapitation (Table 7.1).

The study of the root responses following pollarding in poplar trees was more contrasting. In Chapter 4, Section 4.4.4. it was described that mature poplar trees located in flat terrain in high fertility sandy loam soil, did not show decreases in fRD in comparison to pre-pollarding densities, and reductions in comparison to UP trees were only observed in spring and early autumn in roots located no deeper than 150 mm (Table 7.1).

Root response after above-ground removal in young (1 year old, Chapter 5) and mature poplar trees (Douglas et al. unpublished) show poplar trees might be more sensitive to pollarding than reported for pollarded poplar trees studied in Chapter 4 and in reports on pollarded willow trees.

Four years after pollarding at age 12 years, pollarded poplar trees had less than half the coarse RM and RL of UP trees aged 12 years, and 8% less in coarse root length and statistically not different in coarse root mass than UP trees measured four years previously at age eight years (at the time of pollarding) (Douglas et al. unpublished) (Table 7.1).

Increases in root mass or root production following coppicing of poplars, have been associated with favourable environmental conditions, notably irrigation, fertilizing and regular weeding (Bedenau and Pages, 1984, Lee, 1994, Dickmann et al., 1996).

It is likely that poplar trees evaluated in Chapter 4, grown on flat terrain in soil with high fertility experienced better environmental conditions before and after pollarding than the poplar trees grown in pastoral hill country in a north facing slope (15-20° steepness) (Douglas et al. unpublished) and the young poplar trees evaluated in Chapter 5, where plants were intentionally moisture restricted 2 months before and 1 month after decapitation.

Pollarded poplar trees evaluated in the pastoral hill country by Douglas et al. (unpublished) were around 21 cm DBH, 10 cm smaller than the pollarded poplar trees evaluated in Chapter 4. This

might have meant a large difference in the amount of nutrient reserves available in the remaining structures (trunk and roots) for resprouting processes and for the shoot-to-root ratio recovery. Pollarded mature poplar trees evaluated in the pastoral hill country (Douglas et al unpublished) were also 15 cm smaller in DBH than mature pollarded willow trees evaluated by McIvor et al. (2011b). Root responses after pollarding between these two studies contrast. McIvor et al. (2011b) reported that pollarded willow trees recovered 3 years after pollarding the fine root density recorded in same age UP trees, whereas coarse root length and mass of poplar trees 4 years after pollarding were less than half the coarse roots of UP trees. These data become more significant when it is taken into account that coarse roots naturally are expected to be more resilient to pollarding than the more labile fraction of the root system, the fine roots.

Experiments with young poplar and willow trees grown from cuttings (Chapter 5), also showed that willow trees might have a greater inherent ability to recover their root structure after pollarding than poplar trees. In that study the root mass of decapitated poplar trees 9 months after decapitation was 52% less than the root mass prior to decapitation, whereas within the same time frame willow trees finished one year after decapitation with 57% greater root mass than recorded prior to decapitation. Different resprouting ability and C allocation strategies after pollarding between willow and poplar trees were proposed in Section 5.5.3 as a likely explanation for the differences observed in root response between these two species.

Table 7.1 Summary of findings of the impact of above-ground removal on the root structure of willow and poplar trees wide spaced planted for soil erosion control in pastoral hill country of New Zealand

Source	Species	Trees & Sampling method	Parameter	In comparison to pre-pollarding root values					In comparison to root values of unpollarded trees
				Impact of pollarding is observed in the roots closest to the trunk and above 300 mm soil depth	Temporary decreases	Recovery within the 1st year after pollarding	No decreases observed	Decreases at the end of the 1 st yr after pollarding	
Chapter 3	Willow (<i>Salix matsudana</i> Koidz × <i>S. alba</i> L. 'Tangoio')	Mature trees 7 yr old / soil cores	fRLD & fRMD	✓	✓	✓	×	×	<ul style="list-style-type: none"> 1 yr after pollarding, roots above 300 mm soil depth and closest (40 cm) to the trunk were 50% to 70% less than UP trees. Furthest roots to trunk (80 cm) from 0 to 450 m soil depth were similar or greater to UP trees
Chapter 5	Willow (<i>Salix matsudana</i> Koidz × <i>S. alba</i> L. 'Tangoio')	Young trees grown from cuttings / recovery of the total root structure.	RM	N/A	✓	✓	×	×	<ul style="list-style-type: none"> 9 months after early autumn decapitation, RM of decapitated plants was 64% less than ND willow plants
(McIvor et al. unpublished data)	Willow (<i>Salix matsudana</i> Koidz × <i>S. alba</i> L. 'Tangoio')	Mature trees 12-14 yr old / soil cores	RLD	N/A	✓	✓	×	×	<ul style="list-style-type: none"> 1 yr after pollarding, RLD of P trees 2 m from the trunk above 150 mm soil depth was 43% less than UP trees. 1 yr after pollarding, RLD of P trees 2 m from the trunk below 150 mm soil depth was similar to UP trees.
(McIvor et al., 2011b)	Willow (<i>Salix matsudana</i> Koidz × <i>S. alba</i> L. 'Tangoio')	Mature trees 12-14 yr old / soil cores	RLD	N/A	N/A	N/A	N/A	N/A	<ul style="list-style-type: none"> 1 yr after pollarding, decreases (45%) were only observed in roots above 150 mm soil depth 3 years after pollarding, RLD of P trees was similar to UP trees
(Beeden and McIvor, 2010)	Willow (<i>Salix matsudana</i> Koidz × <i>S. alba</i> L. 'Tangoio')	Mature trees 12-14 yr old / soil cores	RLD and RMD	N/A	N/A	N/A	N/A	N/A	<ul style="list-style-type: none"> 1 yr after pollarding, RLD and RMD of DP trees 5⁺ m from the trunk were similar to UP trees
Chapter 4	Poplar (<i>Populus</i> spp)	Mature trees 11 yr old / soil cores	fRLD & fRMD	N/A	×	N/A	✓	N/A	<ul style="list-style-type: none"> Temporary decreases within the 1st yr after pollarding in roots located 2 m from the trunk and above 150 mm soil depth
Chapter 5	Poplar (<i>P. deltoides</i> Marsh x <i>nigra</i> L. 'Dudley')	Young trees grown from cuttings / recovery of the total root structure.	RM	N/A	✓	N/A	×	✓	<ul style="list-style-type: none"> 9 months after early autumn decapitation RM of decapitated plants was 80% less than ND poplar plants
(Douglas et al. unpublished data)	Poplar (<i>P. deltoides</i> Marsh x <i>nigra</i> L. 'Veronese')	Mature trees 8-13 yr old / total tree root structure excavation.	cRL	8% decrease 4 years after pollarding					<ul style="list-style-type: none"> 4 years after pollarding cRL & cRM of P trees were about 60% less the cRL and cRM of UP trees
			cRM	similar 4 years after pollarding					

R roots, f fine, c coarse, L length, M mass, D density. UP unpollarded, RL or RM includes both coarse and fine roots, N/A not applicable, N/Av: not available. ✓ response observed, × response not observed

In summary, if the slope stability immediate following pollarding is sought the following conditions must be met: 1) pollarding should start once the trees have reached dimensions greater than 30 cm DBH, 2) the trees should not be spaced apart further than 15 m, and 3) at least 60 to 70 % of the trees within a pasture-tree stand should be left intact at any particular time pollarding is practiced. Root structure growth of trees that are left unpollarded contribute to counteracting the disruptions in the root structure of the neighbouring pollarded trees.

7.4 How often to repollard trees

Based on fine root density recovery observed in pollarded mature willow trees, where 3 years after being pollarded the willows recovered similar fine root densities to unpollarded trees, McIvor et al. (2011b) suggested pollarding cycles between 3 to 4 years (McIvor, 2015). However, the ability of pollarded trees to maintain or recover in the short-term the root structure recorded prior to pollarding, raises the question whether the pollarding cycle could be shortened.

Shortening the pollarding cycle might ease the practice and diminish the associated safety risks by handling smaller canopies. Herbage accumulation would also benefit from smaller canopies letting more sun light to reach the understorey.

On-farm observations of no erosion problems associated with pollarded trees have been made on shorter pollarding cycles (2 or 3 years) (Olsen and Charlton, 2003, National Poplar and Willow Users Group, 2007) than the cautious cycle of 3 or 4 years proposed by McIvor et al. (2011b) and McIvor (2015)

Information that might help to explore the possibility of shortening pollarding cycles come from the root starch dynamics observed in Chapters 3, 4 and 5, similar published reports and the bulk of literature dealing with the regular non-structural carbohydrate dynamics of poplar, willow and different woody species (Isebrands and Nelson, 1983, Loescher et al., 1990, Nguyen et al., 1990, Von Fircks and Sennerby-Forsse, 1998).

Starch has been considered as one of the most important reserve carbohydrates in woody species, because it acts as an indicator of the carbohydrate status (Kozłowski, 1992) and has been used as

a more sensitive indicator of sprouting ability than any other non-structural carbohydrate (Von Fircks and Sennerby-Forsse, 1998). Tropical tree species managed in alley tree-cropping systems, that show faster starch reserves replenishment, have also shown greater resilience for periodical above-ground removal sustained in the long term (Chesney, 2012).

Additional to recovering pre-pollarding fine root density, mature willow trees of Chapter 3 and young willow trees of Chapter 5 showed, within the first year after pollarding, similar root starch concentration to that recorded prior to above-ground removal and similar root starch concentrations of unpollarded or non-decapitated trees.

Sink hierarchy theory proposed and studied by different authors (Wardlaw, 1990, Minchin et al., 1993, Minchin and Lacoite, 2005) states that the furthest sinks (roots) from the sources (new resprouting shoots), would be the last to replenish energy reserves. Under this principle it is assumed that organs other than roots (trunk and branches) had also replenished energy reserves in case these would have been mobilized to support resprouting activities.

Root starch dynamics observed in mature poplar trees in Chapter 4 and in young poplar trees in Chapter 5, suggest once again, that poplar trees may be more sensitive to pollarding than willow trees and that these might require longer pollarding cycles.

Even though mature pollarded poplar trees did not show reductions in pre-pollarding root densities after pollarding, root starch concentrations of fine roots of mature pollarded poplar trees (Chapter 4) twelve months after pollarding were less than fine root starch concentrations of mature unpollarded poplar trees. Similarly, starch concentration of coarse and fine roots of young poplar trees (Chapter 5) nine months after decapitation, were less than root starch concentrations young non-decapitated poplar trees. The latter suggests poplar trees could take longer to replenish carbohydrate reserves, and there are reports indicating that during dry years, such as those when pollarding is more commonly practiced in pastoral hill country, replenishment of carbohydrates of defoliated aspen trees (*Populus tremuloides* Michx.) takes longer than in non-restricted moisture growing seasons (Landhäuser and Lieffers, 2012).

The question is that if restoration of root structure prior to pollarding and replenishment of organ starch reserves could be used as criteria to repollard a tree, would these trees be able to show a similar root dynamic as the one observed within the previous pollarding cycle? Answering these questions is not simple and these issues are proposed as elements for future research.

7.5 Dormant pollarding or early autumn pollarding.

This issue was evaluated with mature willow trees in Chapter 3 and young willow and poplar trees grown from cuttings in Chapter 5.

Pollarding mature trees is a time consuming, laborious and potentially risky operation. It is usually confined to pasture-tree systems in the hill country in summer/autumn droughts when pasture reduces in yield and quality, and there is a need to provide supplementary fodder for stock. However, summer is the season of the year when energy reserves in perennial organs are either close to minimum or have only started to replenish, as these have been used for bud swelling, flowering, leaf flush and general related growing processes involved with spring and summer season (McCaman and Loescher, 1988, Nguyen et al., 1990, Loescher et al., 1990). Soil moisture restrictions imposed by summer/autumn dry conditions constrain even more the carbon plant assimilation process. On the contrary, there is some evidence suggesting that the impact of above-ground removal could have minimal impact on the tree root structure if pollarding is practiced when the trees are dormant, as they have replenished to maximum the energy reserves and can respond better to the energy resprouting demands (Dickmann et al., 1996).

Pollarding at any time, other than summer/autumn droughts, must show clear benefits in terms of root structure integrity maintenance such that giving up the trees' fodder reserve would be worth it.

Results from Chapter 3 and 5 did not show clear advantages of dormant pollarding over pollarding in early autumn.

In Chapter 3 dormant pollarded willow trees showed greater annual average fRD recovery than early autumn pollarded trees. However, these differences were attributed to historical dry conditions prevalent in New Zealand during the period (spring-summer 2013) that early autumn willow pollarded trees were evaluated from the 6th to the 12th month after pollarding. During this period, decreases in fRD below pre-pollarding fRD were observed in both unpollarded and early autumn pollarded trees and significant differences were not detected between these treatments at any of the sampling positions evaluated. Therefore, decreases in fRD of early autumn pollarded willow trees were attributed to moisture constraints rather than to the effect of pollarding.

When comparing the data of DP willow trees of Chapter 3 with mature willow trees pollarded in a late summer drought in pastoral hill country in Central Hawke's Bay, New Zealand (McIvor et al., 2011b), it is possible to state, in general terms, that root response of dormant pollarded willow trees of Chapter 5 did not show any particular advantage over the mature willow trees pollarded in late summer.

In terms of the horizontal and vertical impact of pollarding in the root structure, both studies showed that the major impact was located in the shallowest roots (above 300 mm depth) and in the roots closest to the trunk (Table 7.1)

In both studies, reductions in root density in comparison to root densities recorded prior to pollarding were temporary and by the end of the first year after pollarding, trees had recovered root densities similar to those recorded prior to pollarding.

Also, studies conducted on young willow and poplar trees in Chapter 5 did not show either, that dormant decapitation had clear advantages over decapitating the plants in early autumn.

Young willow trees decapitated either in early autumn or at the dormant stage, showed 5 months after decapitation that their root mass was similar to the root mass recorded prior to decapitation. Root mass of early autumn and dormant decapitated willow trees when measured four and a half months after decapitation were 57 and 44% less, respectively, than their corresponding non-decapitated plants.

Similarly with young willow trees, early autumn and dormant decapitated young poplar trees recovered 5 months after pollarding a similar root mass to that recorded at the moment of decapitation. Five months after decapitation, root mass of early autumn decapitated poplar plants was 60% less than root mass of non-decapitated poplar plants, whereas root mass of dormant decapitated poplar plants when measured 5 months after decapitation, was similar to root mass observed in non-decapitated poplar plants. However, similarities in root mass between dormant decapitated poplar trees and non-decapitated poplar trees were attributed to pot volume constraints as root mass of non-decapitated poplar plants increased only 9% from winter to spring in comparison to the 75% root mass growth recorded from early autumn to winter.

7.6 Impact of pollarding in the herbage accumulation of pasture-tree systems in New Zealand.

Partial or total pruning is a systematic strategy used in agroforestry alley tree-cropping systems. Apart from providing nutrient rich, fast-decomposing leafy mulch to the soil and crops, and improving wood quality, pruning of trees is mainly aimed at minimizing shading of associated crops (Thevathasan et al., 2012, Maathai, 2012).

During the first year after pollarding, herbage accumulation around pollarded trees is similar to that recorded in open pasture plots (Douglas et al., 2009).

Canopy removal in alley tree-crop systems usually involves all the trees in the plot. Fine roots dieback has been reported immediately after total pruning (Chesney and Vasquez, 2007, Chesney, 2012). As long as this does not compromise the above- and below-ground recovery and survivorship of the tree, above-ground removal has been sometimes practiced 3 or even 4 times a year.

Such a practice is unfeasible for pasture-tree systems in New Zealand, where the most valuable functional resource and the primary purpose for which trees are planted is found below-ground. Based on the fine root responses of pollarded willow trees, it has been recommended to pollard at any one time no more than 33% of the trees present in a paddock. Root responses after above-

ground removal observed in willow and poplar trees within the short term evaluated in this thesis, do not provide information that could considerably counteract this recommendation.

Pollarding or high intensity pruning of the hedgerows in tree-cropping systems gives a time window between 3-4 months, where light competition between crops and recent pruned trees is close to zero (Chesney, 2012). Greater crop yields than non-pruned plots and similar crop yields to monocrop plots have been reported in time frames, as long as one and a half years after above-ground removal (Sande, 2003).

Results from Chapter 6 suggest 4 years after being pollarded, willow trees had already recovered a canopy big enough, as to yield similar herbage accumulation to that recorded adjacent to unpollarded trees. Thus, the impact of pollarding in herbage accumulation depends on how much sward area is under the influence of the canopy shade of the trees, how many trees are pollarded at a time, how frequently the trees are repollarded and how often unpollarded trees are incorporated into the pollarding program. However, much of pollarding in the pasture-tree systems in hill country is contingent on the need for supplementary fodder for stock, at times when summer/autumn drought reduces pasture production and its nutritive value decreases.

According to the recommendations, within the tree stand density (49 sph) of the study site described in Chapter 6, 16 trees would be pollarded at time 0. In Section 6.5.2.1. it was assumed and estimated that 4 years after being pollarded, an individual tree would be modifying herbage accumulation over a sward area of 78.15 m². In a 1 ha paddock, 16 pollarded trees would be then determining the herbage accumulation in 12% of the total area. On a stand level, under the annual herbage accumulation recorded for P trees, this would have meant a herbage accumulation 24% less than in an open pasture (OP) sward and it would represent a herbage accumulation 9% greater than in a pasture-tree system where none of the trees had been pollarded.

Had 11 UP trees (33% of the left UP trees) been pollarded 4 years after the first trees were pollarded, herbage accumulation would have been 17% less than OP sites and it would have meant a herbage accumulation 15% greater than in a pasture-tree stand conformed exclusively by unpollarded trees.

Under the previous scenario, the possibility to shorten the pollarding cycles becomes particularly important as more frequent repollarding or more frequent incorporation of UP trees into the pollarding program, could considerably enhance the herbage accumulation in comparison of what would be obtained under a pasture-tree stand conformed exclusively by unpollarded trees.

7.7 Future research needs

7.7.1 Root dynamics on pollarded trees

In Section 7.3, the possibility of shortening the pollarding cycles from current recommendations of 3 to 4 years was proposed.

Such a proposal is the result of the root recovery observed particularly in willow trees, that within the first year after pollarding or decapitation have recovered the root structure prior to above-ground removal and replenished a root starch concentration similar to unpollarded trees or decapitated trees at the time of decapitation. However, it is important to verify if these root recoveries are sustained or increased within at least the first two years after above-ground removal, before recommending pollarding cycles shorter than 3 or 4 years.

7.7.2 Herbage accumulation on pasture-tree stand where pollarding is regularly practiced

Significant research has been conducted in pasture-tree systems in hill country of New Zealand, on establishing the relationship between different tree stand parameters and herbage accumulation. However, these studies have been conducted exclusively on non-disturbed young or mature poplar trees (McElwee and Knowles, 2000, Wall, 2006, Wall et al., 2010).

Tree stand parameters where regular canopy shapes are assumed (*v.gr.* green canopy length, vertical projected canopy coverage, canopy ellipsoidal volume) do not account for canopy foliage anatomical differences between clonal or poplar tree species or for changes in the canopy structure imposed by management practices like pruning or pollarding (Wall, 2006).

Tree stand canopy closure has been shown to have a simple linear (straight-line) relationship with herbage accumulation, and the slope of the line did not vary significantly between tree stands located at different sites, composed of different poplar clones or species under different canopy removal practices (pruning or pollarding) (Wall et al., 2010).

In pasture-poplar tree stands, canopy closure has been found to explain more than 90% the variation on photosynthetically active radiation (PAR) reaching the understorey. PAR in turn has been found to account for more than 80% of the variation observed in herbage accumulation. However, it has also been shown that with different tree genus or families at similar canopy closures, different herbage accumulation estimations can result. (Wall et al., 2010).

Estimations on herbage accumulation on a pasture-tree stand level developed in Chapter 6 in a pasture-willow tree system where pollarding has been practiced for several years, were based on a series of facts and assumptions that would have been strengthened or at least contrasted with herbage accumulation prediction equations specific for willow tree stand parameters.

Therefore, there is an opportunity to find out how different tree stand parameters, particularly canopy closure would relate with herbage accumulation in pasture-trees systems composed for willow trees that have been pollarded at different times.

7.8 Conclusions

Willow trees show that in comparison with values recorded prior to pollarding or decapitation, reduction in root densities are temporary in nature and are recovered by the end of the first year after pollarding or decapitation.

Pollarded or decapitated willow trees also have the ability to replenish root starch concentration within the first growing season after above-ground removal.

Recovery of the initial pre-pollarding fine root density and replenishment of root starch reserves in willow trees requires to be verified in at least two year lasting studies after pollarding, before recommending shorter pollarding cycles of 2 or 3 years.

Poplar trees which have less resprouting ability than willow trees, are not able to recover the root values recorded prior to pollarding and/or to replenish the root starch reserves within the first year after above-ground removal, either by decapitation or pollarding.

Poplar trees need longer pollarding cycles than willow trees or greater tree stand densities would be required if a pollarding program is instituted.

Impact magnitude of pollarding on herbage accumulation on a pasture-tree stand level depends on the number of trees that are pollarded at a time, how often trees are repollarded, and how many new unpollarded trees could be incorporated periodically to the pollarding programme.

On a 3 to 4 year pollarding cycle and with incorporation of new pollarded trees contingent on the need for supplementary fodder stock, increases in herbage accumulation would be minimal in comparison to pasture-tree systems conformed entirely by unpollarded trees.

The possibility of shortening the pollarding cycles could impact significantly in reducing the herbage accumulation differences observed between pasture-tree systems and open pasture sites.

7.9 References

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APPENDICES

Appendix 3.1 Coarse root length and mass density recorded in willow trees (pollarded and un-pollarded) after being pollarded at different phenological stages.

Treatment	Coarse root length density (cRLD) m m ⁻³										Coarse root mass density (cRMD) kg m ⁻³									
	2011					2012					2011					2012				
	Sampling position	Soil Depth	Late Winter (LW) (28 Aug)	Early Spring (ESp) (22 Sep)	Late Spring (LSp) (15 Nov)	Late Summer (LSm) (24 Feb)	Mid Autumn (MAU) (18 Apr)	Late Winter (LW) (24 Aug)	Sampling position	Soil Depth	Late Winter (LW) (28 Aug)	Early Spring (ESp) (22 Sep)	Late Spring (LSp) (15 Nov)	Late Summer (LSm) (24 Feb)	Mid Autumn (MAU) (18 Apr)	Late Winter (LW) (24 Aug)				
UPmaDP ^b	40	0-15	286.89	140.05	292.74	442.18	141.51	498.73	40	0-15	0.8900	0.1921	1.5520	2.0165	0.9961	1.2875				
UPmaDP	40	0-15	52.37	394.48	265.23	241.72	438.60	320.95	40	0-15	0.0103	1.1331	0.9579	2.8199	0.8353	1.3828				
UPmaDP	40	0-15	436.04	290.86	127.42	597.47	857.74	429.26	40	0-15	1.3853	0.6472	0.5245	5.4928	12.5275	3.3968				
UPmaDP	40	15-30	147.64	15.96	628.57	0.00	315.65	139.78	40	15-30	0.0959	0.0000	10.8839	0.0000	1.0924	0.1523				
UPmaDP	40	15-30	11.92	556.42	88.07	195.10	20.57	324.89	40	15-30	0.0000	5.7991	0.0608	1.8709	0.0000	2.4984				
UPmaDP	40	15-30	13.71	0.00	23.63	113.90	0.00	355.55	40	15-30	0.0048	0.0000	0.0000	0.2721	0.0000	0.1150				
UPmaDP	40	30-45	170.44	61.72	29.11	0.00	32.57	50.36	40	30-45	0.5879	0.1277	0.0000	0.0000	0.0000	0.0469				
UPmaDP	40	30-45	0.00	97.12	29.80	173.00	0.00	297.06	40	30-45	0.0000	0.0465	0.0071	0.7403	0.0000	0.7715				
UPmaDP	40	30-45	40.15	0.00	292.98	125.59	120.35	636.10	40	30-45	0.0100	0.0000	0.5585	12.1469	0.1847	4.7299				
UPmaDP	80	0-15	245.60	99.45	170.09	549.52	67.99	112.36	80	0-15	0.2327	0.0000	0.3464	2.3805	0.2213	0.6057				
UPmaDP	80	0-15	404.86	322.55	99.63	305.30	173.51	236.28	80	0-15	1.2571	4.1240	0.1936	1.6831	0.2443	0.7899				
UPmaDP	80	0-15	145.74	283.10	11.11	194.10	241.94	207.69	80	0-15	0.2801	0.4156	0.0000	0.2677	0.4036	1.1535				
UPmaDP	80	15-30	6.71	0.00	38.86	151.09	0.77	57.79	80	15-30	0.0000	0.0000	0.0156	0.3924	0.0000	0.0763				
UPmaDP	80	15-30	103.08	1.59	89.45	428.69	1.15	9.56	80	15-30	0.3179	0.0000	0.0219	7.2376	0.0000	0.0000				
UPmaDP	80	15-30	1.58	23.14	0.00	101.05	0.00	107.71	80	15-30	0.0000	0.0000	0.0000	0.0403	0.0000	0.0607				
UPmaDP	80	30-45	28.27	22.46	1.75	91.78	0.46	94.30	80	30-45	0.0219	0.0000	0.0000	0.0667	0.0000	0.1061				
UPmaDP	80	30-45	0.00	0.00	82.09	149.45	2.15	0.00	80	30-45	0.0000	0.0000	0.2093	0.2744	0.0000	0.0000				
UPmaDP	80	30-45	0.00	102.63	0.58	1.17	48.59	0.00	80	30-45	0.0000	0.2412	0.0000	0.0000	0.1020	0.0000				

a) approximate months after selected trees were pollarded when they were dormant in late winter.

b) UP: un-pollarded trees.

c) DP: trees pollarded when they were dormant in late winter.

d) approximate months after selected trees were pollarded when they were still in-leaf stage in early autumn.

e) AP: trees pollarded when they were still in-leaf in early autumn.

* root densities at early winter 2012 were estimated from the average of the 1st ma.AP and the 6th ma.AP (see Section 3.3.3.1 for further details)

Appendix 3.1 (continued)

		Coarse root length density (cRLD) m ³						Coarse root mass density (cRMD) kg m ⁻³									
Treatment	Sampling position	Soil Depth	2011			2012			Treatment	Sampling position	Soil Depth	2011			2012		
			Late Winter (LW) (28 Aug)	Early Spring (ESp) (22 Sep)	Late Spring (LSp) (15 Nov)	Late Summer (LSm) (24 Feb)	Mid Autumn (MAu) (18 Apr)	Late Winter (LW) (24 Aug)				Late Winter (LW) (28 Aug)	Early Spring (ESp) (22 Sep)	Late Spring (LSp) (15 Nov)	Late Summer (LSm) (24 Feb)	Mid Autumn (MAu) (18 Apr)	Late Winter (LW) (24 Aug)
			0 ^a	1	3	6	8	12				0	1	3	6	8	12
DP ^c	40	0-15	181.98	231.07	382.69	38.47	123.81	307.13	DP	40	0-15	0.3368	1.0200	0.9127	0.0000	0.5480	0.6657
DP	40	0-15	254.06	456.48	155.82	376.70	74.51	56.87	DP	40	0-15	1.7952	1.3744	0.0796	12.3500	0.0000	0.0000
DP	40	0-15	130.93	161.24	157.55	400.40	118.68	403.10	DP	40	0-15	0.1753	0.3397	0.6452	1.9363	0.1217	0.8452
DP	40	15-30	63.01	0.00	7.93	62.59	4.29	82.74	DP	40	15-30	0.0524	0.0000	0.0087	0.5847	0.0000	0.0212
DP	40	15-30	201.38	0.48	25.14	321.04	26.79	287.46	DP	40	15-30	0.7212	0.0000	0.0000	0.3191	0.0000	0.8937
DP	40	15-30	47.14	4.91	0.00	9.95	104.61	2.65	DP	40	15-30	0.0175	0.0000	0.0000	0.0000	0.8389	0.0000
DP	40	30-45	111.29	0.00	110.22	3.75	72.72	72.60	DP	40	30-45	0.2803	0.0000	0.3292	0.0000	0.0381	0.0207
DP	40	30-45	0.00	6.23	70.37	52.34	28.08	430.53	DP	40	30-45	0.0000	0.0000	0.0315	0.0037	0.2957	2.3096
DP	40	30-45	15.21	80.25	123.44	16.98	96.62	111.58	DP	40	30-45	0.0057	0.1764	0.5524	0.0000	0.5128	0.1015
DP	80	0-15	113.08	260.79	69.16	975.79	244.91	331.89	DP	80	0-15	1.3832	0.4096	0.0852	1.3521	0.4937	0.9513
DP	80	0-15	258.51	200.82	122.55	281.88	230.44	300.02	DP	80	0-15	0.6289	0.9367	0.2099	0.6377	1.0789	0.9339
DP	80	0-15	244.35	44.25	553.83	102.67	553.47	260.53	DP	80	0-15	0.5333	0.0675	0.0972	0.1616	1.0105	0.6672
DP	80	15-30	597.36	176.33	209.08	3.33	1.34	0.00	DP	80	15-30	1.0383	0.2387	0.5911	0.0000	0.0000	0.0000
DP	80	15-30	84.27	202.45	28.29	2.56	0.00	2.31	DP	80	15-30	0.0311	0.1773	0.0112	0.0000	0.0000	0.0000
DP	80	15-30	0.00	6.55	102.36	106.53	0.00	80.33	DP	80	15-30	0.0000	0.0000	0.0639	0.3821	0.0000	0.0857
DP	80	30-45	14.71	96.60	18.15	12.66	72.87	168.32	DP	80	30-45	0.0000	0.3352	0.0000	0.0000	0.1228	0.5447
DP	80	30-45	0.00	122.43	0.00	30.41	0.00	42.02	DP	80	30-45	0.0000	0.1619	0.0000	0.0036	0.0000	0.0192
DP	80	30-45	13.15	47.42	108.08	1.70	105.99	76.05	DP	80	30-45	0.0000	0.0456	0.9464	0.0000	0.1791	0.1139

a) approximate months after selected trees were pollarded when they were dormant in late winter.

b) UP: unpollarded trees.

c) DP: trees pollarded when they were dormant in late winter.

d) approximate months after selected trees were pollarded when they were still in-leaf stage in early autumn.

e) AP: trees pollarded when they were still in-leaf in early autumn.

* root densities at early winter 2012 were estimated from the average of the 1st maAP and the 6th maAP (see Section 3.3.3.1 for further details)

Appendix 3.1 (continued)

		Coarse root length density (cRLD) m ⁻³						Coarse root mass density (cRMD) kg m ⁻³						
Treatment	Sampling position	Soil Depth	2012			2013			2012			2013		
			Early Autumn (E:Aut) (7 Mar)	Mid Autumn (M:Aut) (18 Apr)	Early Winter (E:W)*	Late Winter (L:W) (14 Aug)	Late Spring (L:Sp) (11 Nov)	Late Summer (L:Sm) (26 Feb)	Early Autumn (E:Aut) (7 Mar)	Mid Autumn (M:Aut) (18 Apr)	Early Winter (E:W)*	Late Winter (L:W) (14 Aug)	Late Spring (L:Sp) (11 Nov)	Late Summer (L:Sm) (26 Feb)
			0 ^d	1	3	6	8	12	0	1	3	6	8	12
UPmaAP ^b	40	0-15	442.18	141.51	320.12	498.73	217.30	347.00	2.0165	0.9961	1.1418	1.2875	0.4079	0.3065
UPmaAP	40	0-15	241.72	438.60	379.77	320.95	359.02	293.89	2.8199	0.8353	1.1091	1.3828	0.5853	0.4416
UPmaAP	40	0-15	597.47	857.74	643.50	429.26	204.22	20.08	5.4928	12.5275	7.9621	3.3968	0.3995	0.0000
UPmaAP	40	15-30	0.00	315.65	227.72	139.78	0.00	321.97	0.0000	1.0924	0.6223	0.1523	0.0000	1.6548
UPmaAP	40	15-30	195.10	20.57	172.73	324.89	0.00	119.29	1.8709	0.0000	1.2492	2.4984	0.0000	1.6087
UPmaAP	40	15-30	113.90	0.00	177.78	355.55	17.69	89.19	0.2721	0.0000	0.0575	0.1150	0.0013	0.0304
UPmaAP	40	30-45	0.00	32.57	41.46	50.36	0.00	145.32	0.0000	0.0000	0.0235	0.0469	0.0000	0.0952
UPmaAP	40	30-45	173.00	0.00	148.53	297.06	145.33	2.79	0.7403	0.0000	0.3857	0.7715	0.0547	0.0000
UPmaAP	40	30-45	125.59	120.35	378.23	636.10	463.39	172.17	12.1469	0.1847	2.4573	4.7299	1.6824	1.1865
UPmaAP	80	0-15	549.52	67.99	90.18	112.36	159.08	324.82	2.3805	0.2213	0.4135	0.6057	0.2720	0.6215
UPmaAP	80	0-15	305.30	173.51	204.89	236.28	474.02	352.18	1.6831	0.2443	0.5171	0.7899	1.7435	0.8528
UPmaAP	80	0-15	194.10	241.94	224.81	207.69	305.04	594.03	0.2677	0.4036	0.7785	1.1535	0.5139	1.4425
UPmaAP	80	15-30	151.09	0.77	29.28	57.79	128.96	161.36	0.3924	0.0000	0.0381	0.0763	0.1051	0.2509
UPmaAP	80	15-30	428.69	1.15	5.36	9.56	145.82	39.21	7.2376	0.0000	0.0000	0.0000	0.5452	0.0183
UPmaAP	80	15-30	101.05	0.00	53.85	107.71	61.45	75.23	0.0403	0.0000	0.0303	0.0607	0.0663	0.0832
UPmaAP	80	30-45	91.78	0.46	47.38	94.30	0.00	230.19	0.0667	0.0000	0.0531	0.1061	0.0000	0.9948
UPmaAP	80	30-45	149.45	2.15	1.08	0.00	9.33	43.04	0.2744	0.0000	0.0000	0.0000	0.0000	0.0101
UPmaAP	80	30-45	1.17	48.59	24.30	0.00	96.14	109.05	0.0000	0.1020	0.0510	0.0000	0.3461	0.3069

a) approximate months after selected trees were pollarded when they were dormant in late winter.

b) UP: unpollarded trees.

c) DP: trees pollarded when they were dormant in late winter.

d) approximate months after selected trees were pollarded when they were still in-leaf stage in early autumn.

e) AP: trees pollarded when they were still in-leaf in early autumn.

* root densities at early winter 2012 were estimated from the average of the 1st maAP and the 6th maAP (see Section 3.3.3.1 for further details)

Appendix 3.1 (continued)

		Coarse root length density (cRLD) m m ⁻³						Coarse root mass density (cRMD) kg m ⁻³						
Treatment	Sampling position	Depth	2012			2013			2012			2013		
			Early Autumn (EAu) (7 Mar)	Mid Autumn (MAu) (18 Apr)	Early Winter (EW)*	Late Winter (LW) (14 Aug)	Late Spring (LSp) (11 Nov)	Late Summer (LSm) (26 Feb)	Early Autumn (EAu) (7 Mar)	Mid Autumn (MAu) (18 Apr)	Early Winter (EW)*	Late Winter (LW) (14 Aug)	Late Spring (LSp) (11 Nov)	Late Summer (LSm) (26 Feb)
			0 ^d	1	3	6	8	12	0	1	3	6	8	12
AP ^e	40	0-15	163.25	230.23	395.40	560.56	462.96	519.15	0.1853	0.2433	0.4947	0.7460	1.6571	1.4741
AP	40	0-15	232.60	310.46	299.76	289.07	307.13	340.49	0.5013	1.6367	1.5328	1.4289	0.4593	1.1752
AP	40	0-15	183.39	361.96	344.47	326.99	37.25	0.08	0.3268	1.4196	2.0881	2.7565	0.0524	0.0000
AP	40	15-30	62.60	0.00	5.39	10.79	52.73	190.45	0.2327	0.0000	0.0000	0.0000	0.0932	1.8109
AP	40	15-30	20.98	273.97	158.13	42.29	224.36	243.05	0.0000	0.5067	0.2680	0.0293	0.7285	1.9247
AP	40	15-30	0.00	59.13	126.52	193.92	92.93	0.00	0.1064	0.1056	0.1048	0.6149	0.0000	0.0000
AP	40	30-45	9.32	3.99	293.33	582.67	0.53	4.77	0.0000	0.0000	0.7580	1.5160	0.0000	0.0000
AP	40	30-45	51.72	0.00	0.84	1.68	4.32	0.46	0.0215	0.0000	0.0000	0.0000	0.0000	0.0000
AP	40	30-45	128.84	103.65	120.67	137.70	190.97	0.00	1.7407	0.0651	0.1851	0.3051	0.0825	0.0000
AP	80	0-15	455.21	216.00	368.38	520.76	155.84	187.35	1.6769	3.1247	2.7804	2.4361	0.0913	0.3196
AP	80	0-15	441.13	391.09	572.40	753.70	373.97	250.61	0.5979	0.8629	1.3833	1.9036	0.9620	0.6105
AP	80	0-15	305.44	99.82	122.81	145.80	314.13	348.65	4.4169	0.1329	0.1574	0.1819	1.8913	2.7588
AP	80	15-30	83.99	2.53	19.10	35.67	20.07	22.56	0.3680	0.0000	0.0262	0.0524	0.0000	0.0059
AP	80	15-30	1.97	128.47	79.03	29.59	9.05	66.83	0.0000	0.1901	0.0951	0.0000	0.0000	0.0391
AP	80	15-30	40.07	85.80	58.63	31.46	57.19	136.05	0.0000	0.1299	0.0789	0.0279	0.1677	0.2255
AP	80	30-45	11.02	163.17	81.58	0.00	0.00	4.22	0.0000	0.4844	0.2422	0.0000	0.0000	0.0000
AP	80	30-45	0.00	163.19	96.39	29.59	100.71	27.16	0.0000	0.7027	0.3513	0.0000	0.1825	0.0061
AP	80	30-45	179.69	2.79	4.25	5.72	72.11	30.56	0.8623	0.0000	0.0000	0.0000	0.0296	0.0000

a) approximate months after selected trees were pollarded when they were dormant in late winter.

b) UP: unpollarded trees.

c) DP: trees pollarded when they were dormant in late winter.

d) approximate months after selected trees were pollarded when they were still in-leaf stage in early autumn.

e) AP: trees pollarded when they were still in-leaf in early autumn.

* root densities at early winter 2012 were estimated from the average of the 1st maAP and the 6th maAP (see Section 3.3.3.1 for further details)

Appendix 4.1 Coarse root densities of unpollarded and pollarded poplar trees from pollarding in March 2012 to March 2013

Coarse root length density (cRLD) m m ⁻³										Coarse root mass density (cRMD) kg m ⁻³						
Treatment	Soil Depth	2012				2013		Treatment	Soil Depth	2012				2013		
		MAR	MAY	AUG	NOV	MAR	MAR			MAR	MAY	AUG	NOV	MAR	MAR	
UP ^a	0-15	228.70	275.88	286.45	307.69	317.90	UP	0-15	0.7992	0.5746	0.8845	1.3546	1.8992			
UP	0-15	101.48	226.59	148.74	242.98	238.72	UP	0-15	0.2982	0.8946	0.3437	2.1913	0.6956			
UP	0-15	248.71	334.60	430.06	514.47	136.45	UP	0-15	0.8688	1.4468	3.7060	2.6848	1.3458			
UP	15-30	40.38	105.66	40.89	195.77	38.97	UP	15-30	0.0432	0.2384	0.3251	1.3278	0.0560			
UP	15-30	12.50	60.88	25.19	3.92	0.00	UP	15-30	0.0012	0.0648	0.0034	0.0000	0.0000			
UP	15-30	126.35	29.25	66.26	163.79	5.56	UP	15-30	0.5055	0.0505	0.1017	0.7181	0.0111			
UP	30-45	72.94	28.49	29.87	0.00	0.00	UP	30-45	0.2389	0.0361	0.1392	0.0000	0.0000			
UP	30-45	14.86	6.63	8.62	0.12	7.84	UP	30-45	0.0458	0.0000	0.0000	0.0000	0.0183			
UP	30-45	49.52	349.62	64.47	51.57	63.63	UP	30-45	0.1200	1.2243	0.2783	0.5042	0.2014			
P ^b	0-15	205.34	320.91	233.72	159.32	317.68	P	0-15	0.5262	0.7367	2.0769	1.7739	1.9319			
P	0-15	198.05	314.71	179.00	299.08	47.49	P	0-15	0.5787	1.5753	0.3404	1.1149	0.5511			
P	0-15	98.88	153.56	139.57	49.46	142.48	P	0-15	0.3471	0.6926	0.3799	0.0683	0.2523			
P	15-30	166.97	0.00	160.82	49.75	28.75	P	15-30	0.7644	0.0000	1.0719	0.0560	0.1316			
P	15-30	0.94	219.59	117.08	5.63	7.67	P	15-30	0.0000	0.3908	0.1113	0.0000	0.0000			
P	15-30	0.06	5.31	38.81	34.28	84.54	P	15-30	0.0000	0.0000	0.0533	0.0000	0.9724			
P	30-45	46.46	8.19	6.92	25.40	36.82	P	30-45	0.1669	0.0091	0.0040	0.0276	0.1271			
P	30-45	12.39	25.14	0.16	0.00	11.00	P	30-45	0.0119	0.0228	0.0000	0.0000	0.0053			
P	30-45	122.17	111.24	120.43	37.12	0.57	P	30-45	0.9075	0.6136	0.1112	0.1275	0.0000			

a) unpollarded tree.

b) pollarded tree.



Figure A.1 Image analysis software WinRHIZO (Regent Instruments, Inc 2012, Canada) where there are small segments of both fine (b) (< 2 mm diameter- delineated in red and yellow) and coarse (a) roots (> 2 mm diameter, delineated in green) that for practical reasons were not possible to dissect from the main root either a coarse or a fine root.

In Appendix 3.1 and 4.2 there are some cases (v. gr. Appendix 3.1, UPmaDP, 15-30, 2011, early spring, 22 Sep.) where there was a record for cRL (15.96 m m⁻³) but not for cRM. This occurred when there was a root where the image analysis software detected small segments of coarse roots (>2 mm diameter) that for practical reasons were not possible to dissect from the fine roots and thus there was not a weight record (Fig A.1a). The opposite also occurred (Fig A.1b).