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The effect of poplar stand density on hill country pastures

A thesis submitted in partial fulfilment
of the requirements for the degree of

Doctor of Philosophy (PhD)

Massey University, Palmerston North
New Zealand

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2006**

Abstract

One-third of the North Island of New Zealand has been identified as requiring increased soil conservation if pastoral farming is to be sustainable. For over 50 years the planting of widely spaced poplar trees (*Populus* spp.) has been one of the main methods used to control soil erosion on hill pastures. Research has shown that these plantings have successfully decreased soil erosion but their impact on the productivity of pastoral farming has received little research attention. The research that has been undertaken has found poplars can suppress understorey pasture production by up to 40%, suggesting that farmers require more research information on the impact of planting conservation trees on the productivity of their farm if the use of conservation trees is to be more widely adopted on erosion prone land.

The objective of this thesis was to provide comprehensive data on the relationship between the range of poplar densities used for soil conservation on the light and soil under poplars, and consequently the effect on understorey pastures. Three field sites on commercial sheep and beef hill farms, in regions with contrasting summer soil moisture availability, Manawatu (one site) and Central Hawke's Bay (two sites), were monitored for two years. Tree stocking rates ranged from 0 to 375 trees/ha. Measurements were based on units of four trees with most measurements either directly below the tree crowns or in the gaps between the trees, but more intensive transect measurements were also made.

Photosynthetically active radiation (PAR) and the ratio of red to far red light (R:FR) were measured under the trees and in open pasture controls. Stand density indices used included all the commonly used measures of tree canopies, including digital photography, and stem diameter at breast height (DBH). PAR transmission was inversely related to all of the stand density indices with canopy closure based on digital photographs being the most robust of the indices used. PAR under the trees, relative to open pasture, was greater in the gaps than below tree crowns. Under a completely closed canopy, PAR transmission was reduced to 15-20% and 50-55% of the open pasture in summer and winter, respectively. The R:FR under the trees, relative to open pasture, decreased markedly at high stand densities (allowing less than 40% PAR transmission) in summer, but was similar in winter. The change in PAR under the trees was shown to be a major factor limiting pasture growth, particularly directly below the tree crowns. For both summer and winter, canopy closure

measured with a standard digital camera was strongly related to stand level PAR transmission ($r^2=0.88-0.97$; $P<0.0001$) and was also a practical method of measuring canopy closure in the field.

The soil measurements confirmed earlier research that soil pH increases under mature poplar trees. There was a 0.2 – 0.7 unit increase in soil pH in the upper 75 mm of soil over both contrasting regions. The soil fertility under the trees in terms of requirements for pasture growth was similar to that of the open pasture with calcium and potassium up to 2.2 and 9.0 quick test units higher in the soil under the trees than in the open pasture, respectively. The direct cause of the increased concentration of some cations under the trees was the annual tree leaf litter. Overall, the soil fertility under the trees had the potential to produce similar pasture production to that of the open pasture with the added advantage of less acid conditions.

Averaged over all sites the respective annual net herbage accumulation (ANHA) under poplar canopy closures of 25, 50 and 75 % was estimated from the equations developed to be 77, 60 and 48% of the open pasture. The greatest decrease was directly below the tree crowns where at canopy closures greater than 20% the ANHA was a relatively constant 50% of open pasture. In the vertically projected gap between trees the ANHA decreased by 6.6% relative to open pasture for each 10 % increase in canopy closure. At approximately 80% canopy closure there was no difference between the ANHA directly below the trees and in the gap. Pasture net herbage accumulation (NHA) under the trees relative to open pasture was at its lowest in summer and autumn (36% of open pasture under a closed canopy), and at its greatest in early spring before tree canopy leafed out (72% of open pasture under a closed canopy). The botanical composition and feed value of the pasture under the trees was broadly similar to that of the open pasture.

The greatest impact of the poplars on the pasture was decreased NHA due to shading. The decrease in NHA directly below mature unpruned poplars is substantial and would decrease farm profitability if the poplar stand density were high over a large area of the farm. The use of poplars for soil conservation is essential but these results show the importance of managing trees through pruning and thinning so that canopy closure is minimised. ANHA under the trees can be maintained at 75% of the open pasture if canopy closure is prevented from exceeding 30-40%.

Acknowledgements

My PhD could not have been completed without the assistance and guidance of so many people, but foremost my supervisors Associate Professor Peter Kemp and Dr Alec Mackay.

I thank Associate Professor Peter Kemp for his great patience, guidance, and encouragement during my studies and for the numerous readings and editing of my PhD manuscript. To Dr Alec Mackay I thank you for your guidance, enthusiasm for the project, and willingness to answer many questions, especially during when I was setting up the field experiments. Associate Professor Peter Kemp and Dr Alec Mackay were instrumental and the catalyst in the development of concepts and understanding of tree-pasture systems enabling this study.

Many thanks must go to all of the farmers involved in this project. Allister Clark and later Darrell Shellard (Kiwitea), John Dunderdale (Hautope), and Martin Meredith (Hautope) thank you for allowing me to use your properties for my fieldwork.

I would like to acknowledge the support of all those people who helped me in so many ways during the course of my PhD thesis. To Yvonne Gray and the ladies in the Herbage Laboratory at AgResearch Grasslands, I thank you for helping me with the pasture composition dissections. Thanks to Ian Power for travelling all the way down from Ruakura to take light measurements at each of the farm sites. Thanks to Aurelio Guevara-Escobar for teaching me how to analyse canopy digital images. Thanks also to Roger Levy for your tireless help with pasture cuts on some pretty rugged terrain and to Phil Budding for helping me with soil sampling and taking tree measurements. To all who helped me in the field, Naba Devkota, Tara Pande, Cameron McKinnon, Lee Matheson, Joanne Wall, Chris Wall, and many others, your assistance was greatly appreciated.

For financial support during my studies, I would like to express my gratitude to AgResearch. Their financial contribution and the scholarship opportunity they provided enabled this study to be undertaken.

My appreciation also goes out to my parents Suzanne and Chris Wall for their tremendous moral support and help over the years.

Finally I wish to thank Leesa Roy my partner, for her love, support, understanding, and extreme patience over the many years of my field research and during the writing up process of this thesis. I will never forget.

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1 Introduction and objectives

1.1 Introduction

The inherent geology and climate of the North Island hill country of New Zealand combine to make a deeply dissected landscape, which is prone to high rates of natural soil erosion (Molloy 1988; Eyles & Newsome 1992; Anonymous 1996). Adding to the land's instability has been the removal of forest and subsequent development of extensive pastoral farming (Trustrum *et al.* 1984; Blaschke *et al.* 1992; Miller *et al.* 1996). Overall, an estimated 3.7 million hectares or 33% of the North Island requires significant soil conservation measures in order for it to be able to physically sustain pastoral based land uses (Eyles & Newsome 1992).

The problems of North Island hill country erosion have long been recognised, however, voluntary and Government subsidised soil conservation programmes have achieved only localised reductions in soil erosion (Glasby 1991; Anonymous 1996; Miller *et al.* 1996). Surveys between 1989 and 1992 indicated that about 80% of North Island hill country farmland needed soil erosion control measures and that 55% had not received adequate treatment (Clough & Hicks 1992). The Ministry for the Environment has identified that hill country soil erosion is a key issue that needs to be addressed within the next 10 to 15 years due to the potential size of the problem, the negative and often irreversible nature of soil erosions impacts, and its economic and social significance. As a key principle it also places the primary responsibility for achieving sustainable land management with individual farmers (Anonymous 1996).

Also identified as an emerging issue, is the perception of New Zealand's extensive agricultural production systems by affluent and well-informed consumers from key international markets (e.g. Europe, North America, and Asia) (William 1995; Mathews 1996; West 1997). Several agencies monitoring world market trends have identified that New Zealand's environmental and animal welfare standards are a matter of increasing strategic significance to our agricultural export industries. The competitive advantage gained from New Zealand's quality image is seen as an essential element required for the optimum positioning of exports in premium markets and enables any threats to trade, in the post-GATT era, to be minimised (Bayvel 1993; West 1997).

Soil conservation on North Island hill country farms has centred on the planting of exotic tree species, which counter the loss of soil strength resulting from pastoralism (Van Kraayenoord & Hathaway 1986; Hicks 1995; Miller *et al.* 1996). Where trees are appropriately planted and maintained for the type of erosion present they can reduce soil erosion by 50 to 80% (Hicks 1992, 1995). This lowers the magnitude of soil erosion close to levels found on stable hill country, even during large storm events (Miller *et al.* 1996). Trees are predominantly used because they are relatively inexpensive in relation to the large areas that require control measures (Van Kraayenoord 1976). The main tree species used for erosion control on pastoral hill land include poplar (*Populus* spp.), willow (*Salix* spp.) and radiata pine (*Pinus radiata* D. Don) (Van Kraayenoord & Hathaway 1986; Thompson & Luckman 1993; Wilkinson 1999).

Since the early 1950s poplars have been extensively planted for soil erosion control on North Island hill country (Van Kraayenoord 1993). However, it has become evident that over the same period, most research on tree-pasture systems has been directed at the more commercial timber species - radiata pine (Hodgson 1997; Wall *et al.* 1997). Agroforestry research based on radiata pine shows that, over time, trees can significantly alter the microclimate, soil properties, and the water balance of farm systems (Fahey & Rowe 1992; Hawke & Wedderburn 1994; Maclaren 1996). These changes, along with trees competitive dominance, usually leads to reduced understorey pasture production in temperate zones (Percival & Hawke 1985; Kellas *et al.* 1995; Scholes & Archer 1997). Predictably, the negative impact of trees on pasture production increases when they are planted at high stocking rates and also as the trees mature and their crowns develop in size (Hawke & Percival 1992).

Animal production in New Zealand's hill country is based on the extensive grazing of open pastures. Therefore, any impact that trees have on pasture production and the microclimate will likely influence animal production. The shelter and shade provided by trees can reduce the exposure of farm animals to climatic extremes and in doing so provide animal welfare benefits (Gregory 1995; Mathews 1996). However, when farm animals are grazed continuously under evergreen trees (e.g. *Pinus radiata* and *Eucalyptus*) their productivity generally declines, relative to farm animals grazed on stable open pastures (Percival *et al.* 1988; Knowles 1991; Bird *et al.* 1995).

Many of the factors limiting pasture and animal production under evergreen trees may also be present under poplars. Nevertheless, there are a number of distinct contrasts between the tree species and their normal management requirements that may have different effects on pastoral hill farms. For example: poplars are deciduous species; depending on hybrid, they can maintain a narrow and less dense crown when planted at low stocking rates; their foliage is nutritious and reasonably palatable to browsing livestock; soil conservation plantings generally establish trees at low planting-to-final-tree-stocking ratios; and the use of individually protected pole planting stock allows trees to be planted into erosion susceptible areas of farms without having to exclude smaller livestock classes, such as sheep (Wall *et al.* 1997).

Poplars have been shown to suppress understorey pastures by 20 to 40%, relative to stable open pastures (Gilchrist *et al.* 1993; Miller *et al.* 1996; Guevara-Escobar *et al.* 1997; Douglas *et al.* 2001). However, these studies are based on a small number of tree stocking rates and tree ages. The interactions between trees and their surrounding environment varies both spatially and temporally, with the extent and intensity of the relationships depending on the particular farm site, planting configuration, tree age, and silvicultural management. This dynamic nature of tree-pasture systems, along with the lack of homogeneity often found between different stands of trees makes inferences from the above studies of limited use for strategic farm planning.

Over the last fifty years poplars have been extensively planted for soil erosion control on North Island hill country farms (Van Kraayenoord 1993; Haslett *et al.* 1995), and today there still remains great potential for further plantings (Clough & Hicks 1992); tree-pasture systems continue to be the most practical technology for sustaining pastoral farming on erosion prone hills. However, the lack of data to support the integration and management of such systems, along with the difficulty in universally applying current information, is a major hindrance to farmers when they consider soil conservation trees as a sustainable land management option.

1.2 Objectives

As a consequence of the above, the general goal of this thesis was to provide farmers with comprehensive, applicable, and user-friendly information on the effects of widely-spaced poplars on the productivity of pastoral hill farms. Thereby, assisting farmers with more optimal integration and management of poplars as a soil conservation option and enabling farmers to make complex sustainable land-use decisions based on sound and robust information.

Specific objectives for this thesis were to:

1. Set up a treatment structure that would allow the dynamic nature of tree-pasture systems to be taken into account.
2. Determine how different densities of poplars alter the quantity and quality of light reaching the understorey and to predict the likely consequences of the changes on pasture production.
3. Determine, based on the tree's effect on light, which stand density index or indices is/are best for characterising poplar stands.
4. Determine how different densities of poplar alter the soil resource status of hill farms, thereby providing farmers with an indication of the effects of poplars on the long-term viability of pastoral hill farm systems.
5. Develop a predictive relationship between poplar stand characteristics and seasonal pasture production that can be used by farmers to gauge the impact of poplars on farm productivity.
6. Determine the forage value of poplar leaves as a potential fodder source for browsing livestock.

1.3 Thesis outline

This thesis is divided into six chapters. Chapter 1 briefly discusses the main use of poplar trees on New Zealand hill country farms and reasons why research into their impacts on pastures is needed. More detailed discussion of previously published literature related to tree-pasture systems is given in each relevant Chapter and a review has been presented in the Proceedings of the New Zealand Grassland Association (Wall *et al.* 1997). Chapter 2 describes the commercial farm sites and main treatment structure used throughout this study. Chapter 3 investigates how poplars affect both the quantity and quality of light reaching the understorey and the likely consequences on pasture production. Different stand density indices are compared for their simplicity, precision, and robustness as predictors of light transmission. The best index was then used in following chapters to characterise/quantify the density of each poplar stand. Chapter 4 examines how changes in poplar stand density affects topsoil fertility in relation to pasture production directly below and in-between the trees. Chapter 5 builds on information gathered from the previous two chapters and integrates it with actual pasture production and pasture quality measurements. The forage value of poplar leaves is also investigated. Chapter six summarises the main conclusions from each previous chapter.

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2 The application of an experimental design to existing stands of poplar trees in New Zealand's North Island hill country.

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2.1 Introduction

Researchers have used a number of different approaches and experimental designs to investigate the impacts of trees on pastoral systems. Many of these studies are based on either systematic tree-spacing designs (Cameron *et al.* 1989; Eastham & Rose 1990; Bird *et al.* 1994), or more classical randomised designs (Anderson & Batini 1983; Percival & Knowles 1988; Pollock *et al.* 1994; Kellas *et al.* 1995). Systematic designs have an advantage in being able to accommodate a far greater number of replicated stand density treatments within a much smaller area than classical randomised designs (Nelder 1962; Bleasdale 1967; Cameron *et al.* 1989; Bird *et al.* 1994). However, as a trade-off, they require very homogenous environmental conditions, and also the statistical methods applicable to them are more restricted (Nelder 1962; Cameron *et al.* 1989; Bird *et al.* 1994).

Irrespective of the type of experimental design, where trees are planted specifically for research purposes a long time frame is required to adequately capture the temporal variation found within the mixed tree-pasture system (Knowles *et al.* 1999). For more short-term experiments, an alternative is to modify the structure of older existing stands of trees through selective thinning and/or pruning (Anderson & Batini 1983; Sibbald *et al.* 1991; Devkota *et al.* 1998). However, this approach has problems in relation to the typical size and structure of poplar soil conservation plantings in the New Zealand landscape. Large areas (or stands) of evenly spaced-apart trees are required. This contrasts with the relatively small pockets of unevenly spaced-apart poplar trees normally seen scattered over the hillsides of New Zealand (Wilkinson 1988; van Kraayenoord 1993). In addition, the time and resources needed for modifying stands of large-sized trees on hill-to-steepland terrain would likely be substantial (Kellas *et al.* 1995).

One way to avoid the limitations of the above approaches is through the application of an experimental design to unmodified stands of mature trees, along with the use of their resident understorey vegetation (Pyke & Zamora 1982; Scanlan & Burrows 1990; Crowe 1993; Gilchrist *et al.* 1993; Guevara-Escobar *et al.* 1997). Nevertheless, the predetermined arrangement of these trees can impede the control of extraneous sources of environmental variation. This in turn may confound the interpretation of any observed treatment (stand

density) effects (Remmenga 1981). Many of the environmental factors governing both the composition and production of hill pastures in New Zealand can vary substantially across a single paddock, as reviewed by Harris (1994) and White (1994).

The short-term nature of the research project, along with the unavailability of large, well-established poplar stands, severely limited the number of approaches available for this thesis. Given the above limitations, the initial objective was to create a broad gradient of poplar overstorey densities based on existing unmodified stands of mature trees, which would form the main treatment structure for this thesis. Careful management of extraneous sources of environmental variation, not pertinent to the main treatment structure, would also be required as part of the experimental design.

2.2 Methodology

2.2.1 Selection of poplar stands in the Manawatu and Hawke's Bay regions

A number of farmer interest groups assisted in finding commercial farm sites with potentially suitable stands of mature poplar trees. In January 1998, the Manawatu/Rangitikei branch of 'Federated Farmers of New Zealand Inc.' helped to find eight prospective sites within the Manawatu region. Each of these sites was subsequently visited and a short reconnaissance taken to assess their general suitability for carrying out field research. The search for prospective sites within the Hawke's Bay region did not start in earnest until November 1998, after an appropriate experimental design had been developed and successfully applied in Manawatu. Between December 1998 and January 1999 fifteen sites were assessed in this region with help from the 'Hawke's Bay Regional Council' and the lower North Island 'New Zealand Landcare Trust'.

The suitability of a site for the planned research depended on several factors. At the broadest scale, both the site's geography and livestock farming system had to be representative of where poplar trees are normally planted for soil erosion control purposes. Trees of similar age, and planted at a wide range of tree stocking rates, including adjacent open pastures areas, was also essential. At a more detailed scale, to increase the precision of the research, there needed to be an opportunity for minimising the extraneous sources of environmental variation found between the different overstorey environments. Hence, the more suitable sites had their stands of poplar trees and adjacent open pasture areas situated on a similar aspect and hillslope, and were subjected to comparable grazing management and fertiliser histories. All of the overstorey environments needed to be well managed and used regularly as part of the farm's overall grazing system.

The logistical aspects of each potential farm site were also considered in relation to the resources available and the practicalities involved with running fieldwork over an extended period of time. Enthusiastic farmers were sought who would take a proactive approach towards the research programme and allow continuous access to the farm sites for a period of one to two years. The distance travelled to the sites each day could not be excessive and on-farm access by four-wheel-drive vehicle had to be available all year around.

2.2.2 Elimination process for simultaneously creating a gradient treatment structure and selecting experimental units

When applying experimental designs to unmodified stands of trees, which are not originally planted for research purposes, the treatments are inherently linked to the experimental units (i.e. they are not actually applied to the experimental units but instead come with them) (Urquhart 1981). Thus, the process for simultaneously creating a structured set of overstorey (stand) density treatments and selecting appropriate experimental units (microsites) on each commercial farm involved three stages: initial identification and basic characterisation of all potential experimental units; grouping of these units into strata with similar overstorey densities; and lastly, the selection of experimental units within each stratum.

2.2.2.1 Stage 1

In June 1998, a field reconnaissance was made to identify and mark all of the potential experimental units with and without trees at the commercial farm selected for the Manawatu region. Experimental units with trees consisted of a nucleus of four trees, arranged approximately in a square grid-pattern that, in turn, were surrounded by buffer trees of similar age and spacing (thus minimising any possible border or edge effects). Experimental units without trees (controls) were adjacent open pasture areas located (>50m) away from the influence of tree shade, drift from leaf fall, and laterally extending tree roots.

The position of the open pasture controls away from any interference by the trees was particularly critical as this could have severely distorted any comparisons made between the overstorey environments, thus introducing a major source of error (Ong 1996). Under such circumstances the overall productivity of experimental units with trees will usually be overestimated relative to that found in the open (Ong et al. 1996).

2.2.2.2 Stage 2

A resource inventory of each potential experimental unit was taken as part of the initial field reconnaissance. This inventory described the general physical characteristics of the units, including their aspect, macro-slope, position on the hillside, homogeneity of the ground surface, and any irregularities. Each experimental unit with trees was also tape surveyed, as described by Studman (1990). Using the stems of the four nuclei trees as corner reference points for the tape survey, the size, shape (based on 1:100 scale drawings), and representative tree stocking rate were determined and this information was then collectively used to group all of the experimental units into strata with similar dimensions.

Experimental units with irregular (non-square) shapes were discarded from the selection process and directly adjacent units of the same size were combined together as a single unit (Urquhart 1981). An approximate square shape was sought to maintain a similar spatial pattern of tree influence within the boundary of the four nuclei trees. The representative tree-stocking rate (on a per hectare basis) of each experimental unit was also calculated assuming the trees were planted on a perfectly square grid pattern. Tree-stocking rate (stems/ha) was calculated using the formula:

$$\text{Stems/ha} = 10,000 \text{ m}^2 / \text{experimental unit area (m}^2\text{)}.$$

The systematic grouping of experimental units served two main functions: firstly, it provided a base for selecting a wide range of representative overstorey densities and secondly, it enabled a reasonably even spread to be chosen in order to obtain well defined relationships between the independent (overstorey density) and dependent variables studied (Steel & Torrie 1980; Myers 1990).

2.2.2.3 Stage 3

The general physical characteristics, included in the resource inventory, helped to determine the final selection of experimental units. Where possible the experimental units within each stratum were randomly selected. However, in order to reduce the effects of recognised causes of variation not pertinent to the required comparisons, the experimental units were also situated, as much as possible, on areas with a similar aspect, macro-slope,

vertical position on the hillside, and away from any irregularities, such as stock camps, large amounts of tree debris, or areas with poor localised drainage (Figure 2.1). This was a form of local error control, where the influence of known experimental heterogeneity was minimised between the experimental units (Steel & Torrie 1980). The open pasture (control) experimental units served as benchmarks (or standards) in the final selection process.

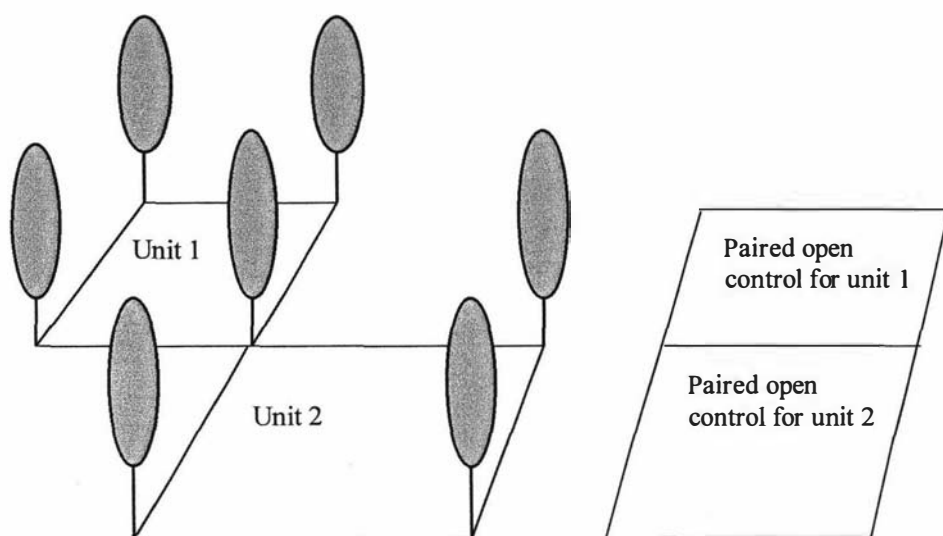


Figure 2.1 Schematic diagram of the pairing of tree and open pasture experimental units.

In February 1999, a similar selection process was used at two neighbouring commercial farms within the Hawke's Bay region. However, as an additional restraint on the selection process, some overlap in overstorey densities between all of the farm sites in both regions was sought.

2.2.3 An index for describing the overstorey density of an experimental unit

The overstorey density of each selected experimental unit was initially described in terms of their representative stand basal area. Usually, this index is strongly related to total stand biomass (Hoffmann & Usoltsev 2002; Johansson 2002), and is commonly used in forestry, and to lesser extent agroforestry, for quantitatively describing the density of a stand (Carron 1968; Percival & Knowles 1988; Scanlan 1991; Reed & Mroz 1997). The basal area of an experimental unit was calculated from circumference (C) measurements taken at 1.4 m above ground level (upslope) on the stems of the four nuclei trees. Assuming a circular cross-sectional area for each stem, the mean diameter (D) and basal area (BA) at

breast height over bark per stem were derived for the selected experimental units using the basic geometric formula:

$$D = C/\pi \text{ (units: m/stem)}$$

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

The representative stand basal area per hectare (m²/ha) for each experimental unit was calculated as the product of the representative tree stocking rate per hectare (refer section 2.2.2.2) and the mean basal area per tree stem.

2.2.4 Data analysis

Simple linear regression analyses, using the REG procedure of SAS[®] (version 8.02 for Windows[®], SAS Institute Inc. 1999), were performed to determine the relationship between stand basal area and tree-stocking rate for each of the selected commercial farm sites. The SAS[®] NOINT option forced all of the regressions through the origin (SAS Institute Inc. 1991).

In general, the small size of the data sets hindered the analysis of the residuals from the regression models. Nevertheless, for the commercial farm site selected in the Manawatu region one potential outlier was detected from the residual plots and more formal test statistics (R-student statistic, $\alpha = 0.05$). Influence diagnostics (Cook's D, HAT DIAG, DFFITS) indicated that this suspect point exerted an appreciable influence on the slope of the regression, thus reducing the performance/precision of the fitted model (Myers 1990). On a closer re-examination of the data, the suspect point was found to be the only experimental unit situated on a south-facing aspect, as opposed to the rest, which were on a north-facing aspect. Given that these two aspects may have different effects on the growth and development of the trees, the single experimental unit on the southern aspect was removed as an outlier.

The simple linear regressions developed for each commercial farm site were compared by analysis of covariance (ANCOVA) using the GLM procedure of SAS[®] (Littell *et al.* 1991; Kleinbaum *et al.* 1998).

2.3 Results & Discussion

2.3.1 General description of the selected commercial hill farms

Selected for this research project were three commercial sheep and beef farms, located within the Southern Hill Country of the North Island. A general description of each farm is given in Table 2.1. The first farm chosen (Kiwitea) was situated within the Kiwitea district of Manawatu, whereas, the second and third farms (Hautope 1 & 2) were two adjacent properties at Hautope in Hawke’s Bay.

Table 2.1 General stand and trial site characteristics

		Kiwitea	Hautope 1	Hautope 2
STAND	Poplar species	<i>Populus x euramericana</i>	<i>P. x euramericana</i>	<i>P. x euramericana</i>
	Age (years)	> 30	> 25	> 25
	Position on hillside	Upper-lower slopes	Upper-lower slopes	Mid-lower slope
SITE	Location (Region)	Manawatu	Hawke’s Bay	Hawke’s Bay
	Latitude Longitude	40.08°S 175.47°E	39.58°S 176.43°E	39.58°S 176.44°E
	Macro-topography	Hill - steep-land (20–36°)	Hill (15–27°)	Hill (23–28°)
	Aspect	North	South-east	North-west
	Altitude a.s.l (m)	320 ¹	160	220
	Annual rainfall (mm)	1062 ²	868 ³	868
		Summer-moist	Summer-dry	Summer-dry

¹Topographic map reference: 260-T23 470153 (Kiwitea), 260-V22 279327 (Hautope 1), and 260-V22 295322 (Hautope 2) (Terralink 1996; Terralink 1997); ²Suckling (1975); ³Rainfall observations from closest meteorological station at Patangata (NZMS 1986). Abbreviation: a.s.l, above sea level.

2.3.1.1 Livestock farming systems

All three farms had sheep and beef cattle production systems that were fairly typical for their respective west and east coast regions of the North Island (MAF 1991). Romney breeding ewe flocks, generally rearing most replacement ewes, and finishing the majority of lambs in prime condition, were common sheep policy features. The cattle policies were more varied. Nevertheless, they included either a traditional beef cow breeding herd or a more flexible dry cattle system, incorporating a mixture of finishing and store strategies. Overall, the Kiwitea farm carried a 60:40 mixture of sheep and cattle at 10.5 stock units

per hectare (SU/ha) (Clark per. comm. 1998). In comparison, both of the Hautope farms ran a slightly higher 64:36 ratio of sheep to cattle, at a lower stocking rate of around 9.2 SU/ha (Meredith per. comm. 2001; Dunderdale per. comm. 2001).

2.3.1.2 Soils

The soils at Kiwitea comprised of Raumai hill soils on the easier slopes and hilltops, and related Pohangina steepland soils for most areas that were steep and broken (Suckling 1975; Rijkse 1977). These sandy loam soils are classed as intergrades between yellow-grey earths and yellow-brown earths; and are formed from unconsolidated (loose) marine sands, sandstones, and siltstones, interbedded with compacted greywacke gravel bands and pumiceous bands (Rijkse 1977). The underlying parent material is unstable, especially on the steeper slopes, and easily erodes in the form of slow healing slips and gullies (Suckling 1950, 1975; Rijkse 1977).

The soils at Hautope consisted of Hatuma-Raukawa soils (Pohlen 1971). These soils are classed as yellow-grey earths, derived from sandy mudstone, calcareous mudstone, and bentonitic and sandy mudstone (Pohlen 1971). Associated with these soils is dense subsoil that impedes deep drainage and in many places forms a hard pan. Under highly saturated soil conditions this subsoil boundary often leads to slip and slump erosion, which usually heals readily, and also tunnel-gully erosion (Pohlen 1971; McCaskill 1973).

2.3.1.3 Climate

The climates of Manawatu and Hawke's Bay are dominated by the main axial mountain ranges that stretch across the North Island in a north-east to south-west direction and the southern hemisphere's mid-latitude westerly airstreams. These mountain ranges act as a barrier to weather systems moving eastwards and consequently, Hawke's Bay on their leeward side is significantly drier and sunnier than Manawatu, which is fully exposed to the predominant rain-bearing westerlies (Burgess 1983; Zwartz 1997). As a result, the mean annual rainfall recorded at the nearest meteorological station to Kiwitea was slightly higher (22%) than for Hautope (Table 2.1) and was also more evenly distributed throughout the year (data not shown). In contrast, with the westerly airstreams being particularly common in late spring and summer, Hautope experiences extremely variable rainfall during this period and often summer evapotranspiration rates are high enough to

cause seasonal drought conditions especially on the sunny northerly aspects (Pohlen 1971; Thompson 1987).

2.3.1.4 Poplar stands

The stands of poplars selected at Kiwitea were a mixture of untended *Populus x euramericana* (Dode) Guinier black hybrid clones (Table 2.1). The hybrids included a small number of 'Flevo' and more predominantly the Italian bred selections I45/51, I214 and I488 (Fung per. comm. 2001). All of the trees were planted before the 1970s, except for the small number of 'Flevo' trees (Clark per. comm. 1998). Adequate soil moisture over the poplar-growing season, along with fertile and free-draining soils, had enabled good tree establishment across the entire hillsides.

The older Italian bred hybrids also made up the poplar stands selected at the Hautope farm sites (Fung per. comm. 2001). Hautope 1 contained I78's and I214's strategically planted in stands to prevent mass movement erosion, with additional paired-plantings also running down the hillsides in main drainage lines. At Hautope 2, only the more drought resistant I214 was present, which was planted further downhill because of the extreme summer-dry nature of the particular northwest-facing hillside. None of the stands had received any silvicultural management (pruning or thinning) and all were planted prior to, or around the time of, the 1973 outbreak of *Melampsora* rust diseases in New Zealand (McGregor per. comm. 2001; Faulknor per. comm. 2001).

2.3.2 General description of selected experimental units

2.3.2.1 Kiwitea

A total of four large open pasture areas and twelve experimental units with trees were selected at this site (Table 2.2). Replication of treatments was limited to the open pasture areas and two tree stocking rates at approximately 30 and 60 stems/ha (Table 2.2).

As a former hill country research farm (Te Awa; 1945-1969) the paddocks were intensively subdivided in relation to aspect (Suckling 1954, 1975). Most experimental units (with and without trees) were located in four adjoining paddocks on a north-facing hillside, with an additional pair situated in two neighbouring paddocks over the hilltop on a southerly aspect (Table 2.2).

The macro-topography varied between hill and steep land (Table 2.2). However, experimental units with higher tree stocking rates (especially >60 stems/ha) were more associated with steep land, which also tended to be more heterogeneous and eroded (Table 2.2). This association was likely a consequence of the normal soil conservation practice of planting high tree stocking rates where erosion is severe and then widening the spacing as the trees extended out into more stable areas (Van Kraayenoord & Hathaway 1986).

All of the experimental units were grazed similarly, with breeding ewes set stocked between lambing and weaning (August – December), and various mobs of sheep and cattle rotated on and off the paddocks, depending on the pasture covers, throughout the rest of the year (Clark per. comm. 1998). In late summer, cattle were often tactically used to remove any rank pasture cover (Clark per. comm. 1998).

The paddocks were topdressed with superphosphate at a rate of 220-240 kg/ha/yr (average rate over the last 50 years) and only a single dressing of lime had been applied at 1 tonne/ha (Suckling 1975; Clark per. comm. 1998).

2.3.2.2 Hautope 1

Two large open pasture areas and ten unreplicated experimental units with trees were selected at this site (Table 2.3). The open and tree overstorey environments were located towards the upper hill slopes in two adjacent paddocks on a south-easterly aspect. The ground surface was generally smooth, but showed signs of previous soil erosion for the experimental units with trees (Table 2.3).

Both of the adjacent paddocks were normally set stocked with breeding ewes just prior to lambing in mid August and remained so until weaning in November/December. Rising two-year-old steers and heifers were normally added to the paddocks during November to help control peak spring pasture growth, and they remained set stocked with weaned lambs until late summer. Through autumn and winter all stock classes were rotated around the farm initially to 'clean up' rank summer pastures and then to maintain adequate pasture covers.

Alternating between years, either sulfur superphosphate or single superphosphate was applied to the paddocks at a rate of 300 kg/ha/yr (Meredith per. comm. 2001).

2.3.2.3 Hautope 2

Two large open pasture areas and four experimental units with trees, located within a single northwest-facing paddock, were selected at this site (Table 2.4). The experimental units were all positioned towards the base of the hillside, and their ground surface was generally terraced with little visual signs of soil erosion, except for at the highest tree-stocking rate (Table 2.4). Shallow gullies separated the selected experimental units.

Compared to Hautope 1, lambing began a month earlier and accordingly breeding ewes were set stocked in late June. After weaning in November/December the paddock was mob stocked with ewes for the rest of the year. Rising two-year-old heifers and steers were also finished on the farm; nevertheless they seldom grazed the selected paddock.

The farm was topdressed with Dicalcic superphosphate at 200 kg/ha/yr (Dunderdale per. comm. 2001).

2.3.3 Overstorey densities

The experimental units selected at each farm site provided a broad gradient of stand basal areas ranging between 0-43 m²/ha (Figure 2.2). The elimination process (refer to section 2.2.2) allowed the increments in stand basal area at each site to be evenly spaced apart within a range typical of soil conservation and agroforestry plantings in New Zealand (Thompson & Luckman 1993; Wilkinson 1996; Knowles *et al.* 1998; McElwee & Knowles 2000). Overall, both the range and spread of stand basal areas (used as an index of overstorey density) should aid in determining the appropriate form (linear or curvilinear) of the relationships to be studied. Considerable overlap in stand basal area was also present between the three commercial farm sites (Figure 2.2), which would help in comparisons between the two regions.

The rate of change in stand basal area per unit increase in tree-stocking rate was significantly different between the three commercial farm sites ($P < 0.001$; Table 2.5). This

most likely reflected differences in tree age, poplar hybrid, and the environmental site attributes for growing trees (Carron 1968; Phillip 1994). It also emphasises the unsuitability of tree stocking rate as an index of overstorey density where the relative size of the trees is not constant (Carron 1968; Phillip 1994).

Table 2.2 Resource inventory for selecting experimental units at Kiwitea

Experimental unit	Paddock	Tree-stocking rate (stems/ha)	Aspect (degrees)	Macro-slope	Vertical position on hillside	Terrain	Homogeneity of ground	Irregularities	Selection
40	6	0	10	3	1	3	3		*
41	4	0	350	2	1	1	1		*
42	2	0	5	2	2	1 & 3	2		*
43	10	0	205	2	1	1 & 3	2		*
39	2	10	350	2	1	1	2	Poor drainage (many rushes)	*
12	4	22	20	2	3	4	3	Tree debris	
36	3	25	5	3	2	1 & 3	2		*
25	3	27	10	2	2	1	2	E.U. shape	
30	3	29	350	2	2	1	2		*
23	3	32	345	3	4	1 & 3	3		*
1	4	34	15	2	1	1	2	Incomplete tree buffer	
8	3	38	335	2	1	1 & 3	1	Many impinging buffer trees	
38	3	39	350	2	1	1 & 3	1		*
10	4	41	50	3	2	4	3		
13	4	45	50	2	1	1 & 3	1	Stock camp	
14	4	47	50	2	2	1 & 3	1		
28	3	47	340	2	2	1	2		*
2	4	48	50	3	1	4	4		
9	3	49	355	3	2	4	3	Incomplete tree buffer	
29	3	51	0	2	1	1	2		*
11	4	56	340	2	2	4	2	Poor drainage, tree debris	
16	4	58	50	3	1	4	4		
33	3	60	310	3	1	1	4	Incomplete tree buffer	
26	3	62	0	2	2	1 & 3	1	Incomplete tree buffer	
7	3	63	355	2	1	1	2		*
3	4	64	350	3	4	4	3	Poor drainage (few rushes)	*
15	3	73	340	3	1	3	4		
5	3	76	340	3	2	3	4		
24	3	77	5	3	2	4	2	Poor drainage (few rushes)	*
27	3	83	350	3	2	3	4		
6	3	88	0	3	2	4	3		*
35	3	105	340	3	1	4	4		
4	5	119	150	3	1	4	4	Poor drainage (few rushes)	*

Rank: Macro-slope, < 12° (1), 12-28° (2), and > 28° (3); Vertical position on hillside, upper slope (1) to lower slope (5); Terrain, smooth ground surface without (1) and with (2) signs of previous soil erosion, to a terraced ground surface without (3) and with (4) signs of previous soil erosion; Ground surface, homogeneous (1) to heterogeneous (5).

Table 2.3 Resource inventory for selecting experimental units at Hautope 1

Experimental unit	Paddock	Tree stocking rate (stems/ha)	Aspect (degrees)	Macro-slope	Vertical position on hillside	Terrain	Homogeneity of ground	Irregularities	Selection
1	3	0	180	2	1	3	1		*
2	3	0	170	2	2	1	2		*
102	2	21	240	2	4	1	2		
196	2	25	355	2	4	1 & 3	3	Incomplete tree buffer	
3	4	29	175	2	1	2 & 4	4		*
72	3	53	130	2	3	4	3		
100	2	58	130	1	5	1	1	Poor drainage (many rushes)	
93	2	61	165	2	4	1	2	Sparse tree buffer	
4	4	63	145	2	2	2	2	Thistles	*
103	2	71	165	1	5	1	2	Poor drainage (many rushes)	
5	4	73	160	2	2	2	3		*
56	2	74	165	1	5	1	1	Thistles	
6	4	74	110	2	1	4	2		*
99	2	76	30	2	5	1	2	Incomplete tree buffer	
46	2	109	215	1	5	1	1	Incomplete tree buffer	
7	4	113	150	2	2	2	3		*
177	2	125	155	1	5	1	1	Few thistles	
69	1	130	155	1	5	1	1	Incomplete tree buffer, thistles	
8	4	153	150	2	1	1	1	Few thistles	*
112	2	174	115	1	5	1	1	Incomplete tree buffer	
9	4	172	140	2	2	2	2		*
175	2	193	135	1	5	1	1	Incomplete tree buffer	
70	4	209	120	2	3	2 & 4	3	Bare ground patches	
192	2	229	120	1	5	1	2	Many thistles	
10	4	222	125	2	2	2	3		*
11	4	232	145	2	2	2	2		*
82	4	267	125	2	4	2	1	Incomplete tree buffer	
189	4	337	135	2	2	2 & 4	2		
12	4	374	150	2	2	2	2		*

Rank: Macro-slope, < 12° (1), 12-28° (2), and > 28° (3); Vertical position on hillside, upper slope (1) to lower slope (5); Terrain, smooth ground surface without (1) and with (2) signs of previous soil erosion, to a terraced ground surface without (3) and with (4) signs of previous soil erosion; Ground surface, homogeneous (1) to heterogeneous (5). After selection, the chosen experimental units were re-numbered 1-12.

Table 2.4 Resource inventory for selecting experimental units at Hautope 2

Experimental unit	Paddock	Tree stocking rate (stems/ha)	Aspect (degrees)	Macro slope	Vertical position on hillside	Terrain	Homogeneity of ground	Irregularities	Selection
1	1	0	330	2	3	3	1		*
2	1	0	275	2	4	1 & 3	1		*
3	1	30	310	2	4	3	3		*
179	2	47	90	2	3	1	3		
131	2	73	20	2	1	1 & 3	3	Incomplete tree buffer	
79	1	79	345	3	4	1 & 3	3	Incomplete tree buffer	
34	1	94	345	3	5	1	3	Very dense tree buffer	
146	2	98	20	2	5	1 & 3	4	Incomplete tree buffer	
87	2	109	20	2	1	1 & 3	4		
103	2	116	20	3	5	1	2	Incomplete tree buffer	
4	1	130	340	2	4	1 & 3	3		*
93	2	152	90	2	2	1 & 3	4	Incomplete tree buffer	
5	1	171	345	2	4	1 & 3	3		*
31	2	178	90	2	5	2	3		
186	1	181	345	2	5	2	3		
194	2	225	90	2	4	1 & 3	4		
100	2	240	90	3	5	1 & 3	4		
6	1	291	345	3	4	4	4		*

Rank: Macro-slope, < 12° (1), 12-28° (2), and > 28° (3); Vertical position on hillside, upper slope (1) to lower slope (5); Terrain, smooth ground surface without (1) and with (2) signs of previous soil erosion, to a terraced ground surface without (3) and with (4) signs of previous soil erosion; Ground surface, homogeneous (1) to heterogeneous (5). After selection, the chosen experimental units were re-numbered 1-6.

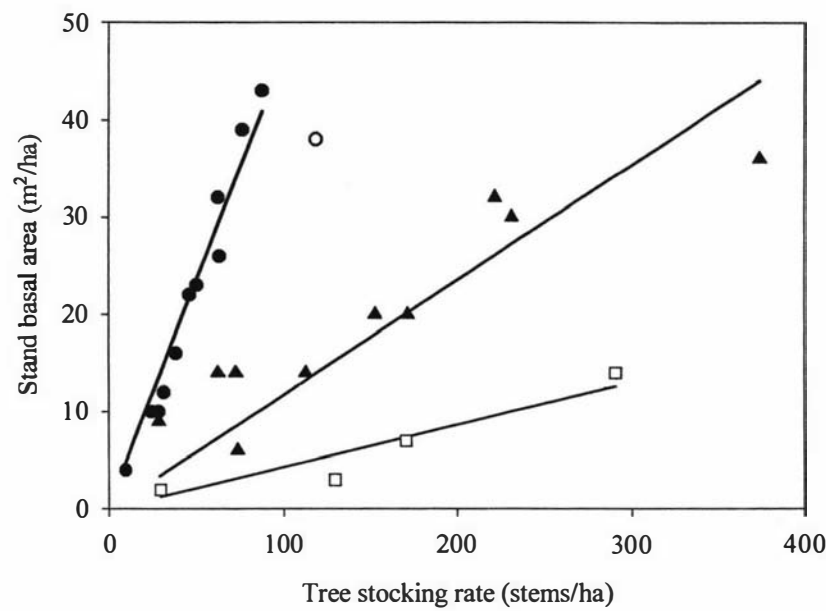


Figure 2.2 The relationship between stand basal area and tree stocking rate at Kiwitea (●), Hautope 1 (▲), and Hautope 2 (□). The open circle (○) represents the south-facing experimental unit at Kiwitea, which was identified as an outlier in the regression analysis.

Table 2.5 Regression parameters for *P. x euramericana* stand basal area (m²/ha) in relation to tree stocking rate (stems/ha), at each commercial farm site, where $Y = bX$ (constrained through origin).

Site	b (SE)	r^2	RMSE	n
Kiwitea	0.465 (0.014)	0.99	2.541	11
Hautope 1	0.118 (0.009)	0.95	4.963	10
Hautope 2	0.043 (0.005)	0.95	1.782	4

All simple linear regressions were significant ($P \leq 0.003$). Abbreviations: b , slope; SE, standard error; r^2 , adjusted coefficient of determination; RMSE, standard error of prediction; n , number of experimental units with trees.

2.4 Conclusion

The short time frame and the unavailability of extensive poplar stands, limited the number of approaches available for investigating the relationships between the overstorey density of a soil conservation poplar stand and its understorey abiotic and biotic components. Nevertheless, the careful selection of relatively small stands of poplar trees, along with the application of a stratified random sampling process, produced an even gradient of overstorey densities (measured as stand basal area) typical of soil conservation and agroforestry plantings in the Southern Hill Country of the North Island, New Zealand. The selection of farm sites in the Manawatu and Hawke's Bay regions provided contrasting summer-moist and summer-dry climates. The selection of stands from these two regions can be considered as broad types of replication with the purpose to increase or broaden the scope of inference for the study. Stage three of the elimination process helped to control extraneous sources of environmental variation found between the experimental units at each site. However, inherent in such soil conservation plantings is that higher tree stocking rates, and thus overstorey densities, tend to be more associated with previously eroded ground. The gradient of overstorey densities developed in this chapter forms the main treatment structure for the experiments in Chapters three, four, and five.

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3 The relationship between poplar stand density and PAR transmission

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3.1 Introduction

A central objective of most silvopastoral systems is to increase, or at least sustain over the long term, the total productive capacity of land through either more efficient utilisation and/or greater conservation of available resources (Wojtkowski 1998). This is normally attempted by mixing trees and understorey pastures that collectively enhance the stability of the environment, while on an interspecies basis impose different demands on the system's available resources (Sinclair *et al.* 2000). However, scope for the latter niche separation in mixed tree-pasture systems is somewhat limited, as both components usually require similar resources (energy, water, mineral nutrients) for growth and development (Ong 1996; Ong *et al.* 1996).

Photosynthetically active radiation (PAR) is one resource where there is usually a strong overlap in requirements from both the overstorey and understorey plant species (Hanan & Bégué 1995; Gendron *et al.* 1998; Lieffers *et al.* 1999). PAR is commonly defined as short-wave radiation in the visible part of the spectrum, ranging between 380 nm to 710 nm in wavelength (Larcher 1980); and a critical determinant of its availability for photosynthesis at different levels within a mixed tree-pasture association is determined by the three-dimensional structure and optical properties of the overstorey canopy (Grace *et al.* 1987; Sibbald & Griffiths 1992; Lieffers *et al.* 1999).

Short-wave solar radiation reaching understorey pasture consists of two forms: direct-beam radiation, emitted relatively unimpeded from the sun to the understorey; and diffuse radiation, circuitously transmitted from all hemispherical directions, owing to scattering in the atmosphere and/or downward reflectance from and transmittance through leaves in the overstorey canopy (Federer & Tanner 1966; Reifsnyder *et al.* 1971; Hutchison & Matt 1976, 1977; Endler 1993). Both forms of short-wave solar radiation passing directly through canopy gaps, without impinging on plant parts, are rich in PAR (Larcher 1980; Barnes *et al.* 1997). This contrasts with the reflected and through-leaf transmitted radiation, which is often depleted in photosynthetically active wavelengths as a result of selective absorption by foliage (Hughes *et al.* 1985; Wilson & Ludlow 1991; Barnes *et al.* 1997). In particular, ultraviolet, blue, and red wavelengths are highly absorbed by foliage compared

with green, and especially far-red wavelengths (Messier & Bellefleur 1988; Wilson & Ludlow 1991; Messier & Puttonen 1995; Barnes *et al.* 1997).

A variety of external and internal factors govern the incidence of PAR transmitted through a canopy (Hutchison & Matt 1977; Lieffers *et al.* 1999). The incidence of short-wave solar radiation reaching the top of a canopy varies regularly with diurnal and seasonal changes in earth-sun geometry (seasonal variations increasing at higher latitudes), and irregularly with changing atmospheric conditions (Hutchison & Matt 1977b; Canham 1988; Sturman & Tapper 1996; Comeau *et al.* 1998; Lieffers *et al.* 1999). The subsequent transmission of this incident radiation to different parts of the understorey depends on its source (diffuse or direct-beam radiation) and the structure and optical properties of the overstorey canopy (Hutchison & Matt 1977b; Barnes *et al.* 1997; Gendron *et al.* 1998).

Typical plantings of soil conservation trees in New Zealand's North Island Hill Country encompass a wide range of overstorey densities. Plantings range from almost single independent trees, with very large inter-tree gaps, to closed-canopy forest (Van Kraayenoord & Hathaway 1986; Thompson & Luckman 1993; Wall *et al.* 1997; Wilkinson 1999). As a result of the trees spatial arrangement complex gradients of PAR transmission within and around adjacent canopy openings can be formed, depending on the size and orientation of the gap, dimensions of the surrounding trees, sun angle, sky conditions, and topography of the ground surface (Canham 1988; Canham *et al.* 1990; Sibbald & Griffiths 1992; Runkle *et al.* 1995; Lieffers *et al.* 1999).

Several methods are available for directly measuring both direct-beam and diffuse PAR transmission through scattered tree canopies (Wünsche *et al.* 1995; Gendron *et al.* 1998; Lieffers *et al.* 1999). To account for the high spatial and temporal variation, caused by the different forms of short-wave radiation, these methods usually involve either integrated arrays of quantum sensors placed simultaneously underneath and outside/above the canopy (Hutchison & Matt 1977a,b; Sibbald & Griffiths 1992), or alternatively fewer sensors moved to various sampling positions with repeated readings taken over time (Chen *et al.* 1997; Hassika & Berbigier 1998).

However, intensive sampling over an extended period, with a large amount of specialised and often expensive equipment, limits the total number of experimental units (microsites) that can be accurately sampled at any one time (Rich *et al.* 1993; Wünsche *et al.* 1995; Comeau *et al.* 1998; Gendron *et al.* 1998; Lieffers *et al.* 1999; Machado & Reich 1999; Englund *et al.* 2000). Thus, alternative instantaneous sampling techniques have been used as a way to indirectly estimate the average fraction of incident PAR transmitted or intercepted by a canopy (Anderson 1964a; Canham 1988; Chen *et al.* 1991; Hanan & Bégue 1995; Parent & Messier 1996; Gendron *et al.* 1998; Lieffers *et al.* 1999). Simulation models based on individual tree or stand architecture provide another alternative (Comeau *et al.* 1998; Gendron *et al.* 1998).

While farmers have no control over the incidence of above-canopy PAR reaching soil conservation stands, they can control its transmission to the understorey pastures by manipulating the density of the overstorey tree canopy (e.g. by thinning, pruning, & pollarding). Given the importance of PAR transmission, as one of the key ecological processes driving understorey pasture production within temperate silvopastoral systems, the objective of this chapter is to define the relationship between the overstorey density of a poplar stand and a simplified estimate of incident PAR reaching the understorey. A number of different stand parameters are commonly used as overstorey density indices in both agroforestry and forestry (Carron 1968; Schreuder *et al.* 1993; Phillip 1994; Reed & Mroz 1997). Thus, in addition to the main objective, a selection of commonly used overstorey density indices will also be evaluated for their simplicity, power, and robustness as predictors of estimated PAR transmission.

3.2 Methodology

3.2.1 Treatments

The broad range of overstorey (stand) densities previously developed in Chapter 2 formed the main treatment structure for this study. An additional 18 experimental units from within a systematic-spacing ‘Nelder’ experimental design (Nelder 1962), planted at AgResearch’s Ballantrae Hill Country Research Station, were also sampled. Measurements were taken from 2 spokes of the fan shaped design. Each spoke contained 9 experimental units, ranging in size from 50 to 750 stems/ha. This extra site further improved the overall spread of the overstorey densities, especially towards the lower density range. The Ballantrae site (Lat. 40.18°S Long. 175.50°E) was planted with ‘Tasman’ poplars (*P. x euramericana*), on a gently sloping northeasterly facing hillside, at 135 m above sea level. When sampled the trees were five years old and their stems had been pruned to $3.65\text{m} \pm 0.05\text{m}$ (mean \pm SEM, $n=72$).

3.2.2 Overstorey (stand) density indices

In Chapter 2, the overstorey density¹ above each experimental unit was initially described in terms of stand basal area (m^2/ha) (refer to Section 2.2.3). This is one of the main stand density indices traditionally used in forest resource inventories, as it is usually strongly related to stand volume or biomass (Carron 1968; Phillip 1994). However, the above relationship does not remain constant under the intensive silvicultural management usually associated with silvopastoral systems. For example, the pruning of lower tree branches can significantly reduce the density of a stand’s overstorey, while at the same time not affecting its overall basal area (Percival & Knowles 1988). Thus, several alternative stand parameters were measured, which potentially could give a more integrated measure of both tree stocking rate (stems/ha) and individual crown size. Measurements were taken from the four nuclei trees of each experimental unit (with trees) and were scaled up to a per unit area basis (or representative stand level) via their respective tree stocking rates (refer to Section 2.2.2.2).

¹ Overstorey density: the amount of tree material in a stand per unit area (Carron 1968).

3.2.2.1 Stand parameters based on the height of the tree crowns

The vertical height from ground level to the top (total height) and base (crown height) of the live tree crowns was measured either directly with a telescopic measuring pole (Senshin Industry Co.) or indirectly with a hypsometer (Suunto Precision Instruments). Ignoring epicormic side shoots, the base of a crown was the point where foliage occupied at least three of the four quadrants around the stem (Canham *et al.* 1999). The green crown length (GCL) per stem, otherwise known as crown depth, was calculated as the difference between the total height and crown height (Carron 1968; Phillip 1994; Ellis & Hayes 1997; Reed & Mroz 1997):

$$\text{GCL/stem} = \text{total height} - \text{crown height (units: m/stem)}.$$

3.2.2.2 Stand parameters based on the horizontal crown diameter

The mean diameter of each tree crown was calculated from two horizontal tape measurements, which were taken at perpendicular angles to each other (the first direction determined at random). Two people were required for this measurement - with one person standing away from the tree, aligning a plumb-line on to its outermost edge, while the other marked the vertically projected point onto the ground (Carron 1968; Schreuder *et al.* 1993). This measurement allowed the horizontal cross-sectional area of the tree crowns (m^2/stem) to be calculated using the same geometrical formula and assumptions used for determining stem basal area (refer to section 2.2.3.1). However, for this calculation, the maximum horizontal crown diameter was limited to within the mean distance between the trees for a particular experimental unit, based on the assumption that adjacent tree crowns do not overlap (Figure 3.1).

When scaled up to a per unit area basis the above stand parameter gives a simple estimate of the canopy closure ratio on a horizontal plane (Schreuder *et al.* 1993). Based on the assumptions of non-overlapping tree crowns with equal circular cross-sectional areas, and the trees planted on a square grid pattern, the theoretical maximum horizontally projected canopy closure ratio (HPCC) for the scaled up stands is 78.5% (Assmann 1970; Phillip 1994).

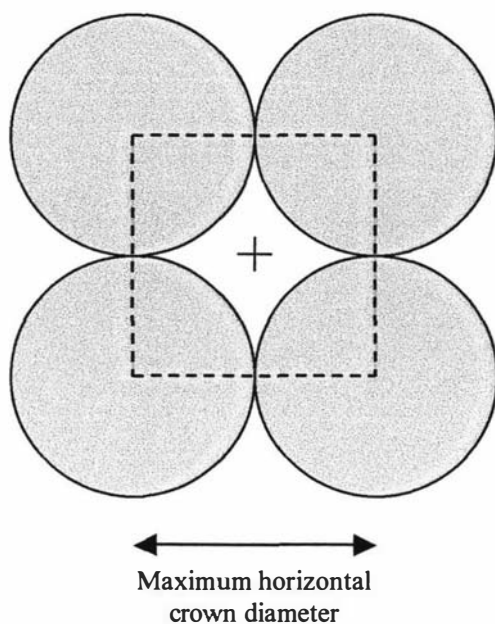


Figure 3.1 A schematic aerial view of four 'nuclei' trees (grey circles) defining the boundary (dashed lines) of an experimental unit. The total area of an experimental unit represents the expanded canopy gap and the non-shaded area within the centre of the experimental unit represents the vertically projected canopy gap (Runkle 1982; Runkle *et al.* 1995).

3.2.2.3 Stand parameter based on the volume of the tree crowns

The ellipsoidal volume of each tree crown (CEV) was calculated from the measurements of crown diameter and green crown length using the formula:

$$\text{CEV/stem} = \frac{4}{3}\pi R^2 H \quad (\text{units: m}^3/\text{stem})$$

where R = horizontally projected green crown radius per stem

H = half the vertical green crown length (depth) per stem

A solid vertical ellipse with perfect symmetry was assumed to represent the shape of the individual tree crowns (Wilkinson 1995; Karlik & Winer 1999; Stadt & Leiffers 2000).

3.2.2.4 Stand parameter based on colour digital images of the overstorey canopy

A series of colour digital images were taken to estimate the degree of canopy closure (CC) above each experimental unit. All of the images were captured with a Sony MVC-FD7 digital camera, set to view vertically upwards with the aid of a spirit-bubble-level, and mounted at 0.7 m above the ground (measured from the top of the lens) on a height adjustable tripod (Becker *et al.* 1989; Bunnell & Vales 1990; Englund *et al.* 2000). At the time of use, the spatial resolution (VGA 640 x 480 pixels²) of the Sony camera's image was not the highest available, compared to other digital cameras, for a sharper definition of the boundary between foreground-canopy and background-sky (Jähne 1997; Wagner 1998; Frazer *et al.* 2001). However, its system of JPEG³ (1:4 compression) image recording directly onto a low-cost 3.5-inch floppy disk effectively provided the camera with an unlimited memory capacity, enabling large numbers of images to be recorded relatively quickly at the remote farm locations (aided by carrying an extra rechargeable battery). All of the images were captured with the camera's standard lens (producing rectangular or non-equidistant images), and were taken preferably under uniformly overcast sky conditions (e.g. Stratus clouds) to maximise image contrast and to minimise interference by direct sunlight (Roxburgh & Kelly 1995; Wünsche *et al.* 1995; Englund *et al.* 2000; Frazer *et al.* 2001).

Field sampling

The spacing between the four 'nuclei' trees, used to define an experimental unit, created an overstorey canopy that was naturally more open towards the plot centre (Figure 3.1). Therefore, estimating the average canopy closure by random sampling was inappropriate, as there was a chance the majority of sampling points could have been concentrated under a dense or open part of the overstorey canopy (Knowles *et al.* 1999). Instead, to provide complete coverage of the canopy above each experimental unit, sampling points were restricted using a systematic star-shaped design developed by Knowles *et al.* (1999)⁴.

² A pixel or picture element is the smallest individual unit of a digital image. Thus, image matrices with greater numbers of pixels have higher image resolution (McKenna 1995).

³ JPEG (Joint Photographic Experts Group) is a standardised compression technique used to reduce the size of a digital image (Frazer *et al.* 2001).

⁴ Messier *et al.* (1998) also used a similar systematic sampling design for light measurements in boreal forests.

Seventeen non-overlapping digital canopy images were taken for each experimental unit: at the centre of the plot, and at distances of 6 m and 12 m, radiating outwards along the eight major compass directions from the central point (Figure 3.2).

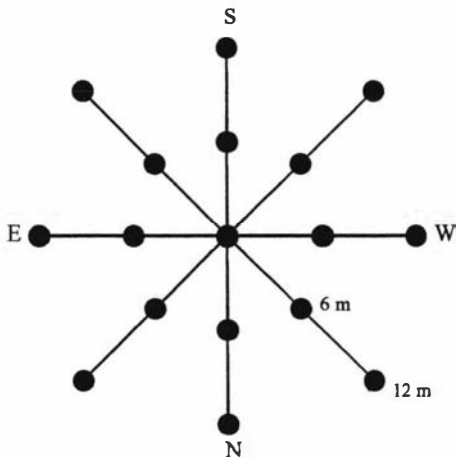


Figure 3.2 Sample grid overlaid and centred on an experimental unit to estimate canopy closure (Knowles *et al.* 1999).

To account for the deciduous nature of poplars, all experimental units were sampled when the trees were fully with (summer) and without (winter) leaves (Table 3.1). No measurements were made through spring and autumn because of the changing phenology of the overstorey canopy and the associated difficulty in determining a single point in time representative of these two seasons.

Table 3.1 Dates when canopy closure was measured in the field.

Site	Date	
	Summer	Winter
Kiwitea	25/01/1999	27/08/1999
Hautope 1	13/02/2000	13/09/2000
Hautope 2	13/02/2001	13/09/2000
Ballantrae	2/03/2001	8/09/2000

Digital image processing and analysis

The colour digital images obtained in the field were analysed using the methods and mainstream software packages described by Guevara-Escobar (1999). Essentially, digital image processing and analysis followed three stages: firstly, identifying and separating the

overstorey canopy and background sky areas of an image through their respective colours (segmentation process); secondly, reducing these two colour-defined areas to purely black and white, respectively; and thirdly, counting the total number of pixels within each simplified category to give an estimate of canopy closure (i.e. the proportion of sky obscured by the poplar overstorey). Overall, the above method shared many similarities with the methodology used by Knowles *et al.* (1999), McElwee & Knowles (2000), and Englund *et al.* (2000).

The sky and canopy pixels of an image were differentiated using a colour filter created for each experimental unit in Corel Photo-Paint® (version 9.0 for Windows®, Corel Corp. 1999). An individual filter consisted of a palette of representative sky colours manually selected directly from an image via the software's colour masking function. A threshold value was set for the selected colours so that each would include 20 of their closest neighbours within the available colour spectrum. This reduced the total number of distinctive colours, and thus time, needed for identifying pixels belonging to the sky portion of an image. The variable-zoom function in Corel Photo-Paint® aided in the investigation of finer image detail, but similar to the results of Englund *et al.* (2000), solely focusing on a small portion of the image often caused inaccuracy in separating other parts of an image. A semitransparent red overlay was added (tagged) to all of the pixels associated with the selected colours to visually check the precision of the segmentation process. Overall, 3 to 10 colours were usually selected for separating the sky and canopy pixels of an image; depending on the degree of contrast between the two elements and also their respective uniformity of colour. Similar to Englund *et al.* (2000) and Frazer *et al.* (2001), images captured on completely overcast days were preferred, as this reduced the negative effects of colour halos and blurring of canopy edges. Once the filter (colour mask) was completed, it was then saved as a standard template for the remaining images of an experimental unit. Nevertheless, the precision of the standard filter was visually rechecked for each image and the original set of base colours were modified where necessary. Potential bias or non-random variation, caused by human error, was minimised by having one-person process and analyse all of the digital images (Canham *et al.* 1990; Gendron *et al.* 1998).

The individually tailored filters (colour masks) protected image pixels that fell within the colour ranges specified, but could also be inverted so protecting either the sky or overstorey

canopy areas of an image. This enabled the entire originally unprotected canopy area to be converted to black, the mask inverted, and the remaining sky area converted to white. These simplified black and white binary images were saved as new files, and the black canopy pixels were identified and counted in SigmaScan® Pro (version 4.0 for Windows®, SPSS Inc. 1998). The counted number of black canopy pixels divided by the total number of pixels within the image matrix (640 x 480 pixels) represented the canopy closure ratio (CC). Overall, the estimated canopy closure ratio (CC) for an entire experimental unit was based on the mean of the seventeen images obtained in the field (Knowles *et al.* 1999; McElwee & Knowles 2000).

3.2.3 Light measurements

3.2.3.1 Photosynthetically active radiation

The percentage of above-canopy photosynthetically active radiation (PAR) transmitted through the tree canopy was estimated from diffuse non-intercepted radiation⁵ (DIFN) measurements taken with paired LAI-2000 Plant Canopy Analysers (LI-COR Inc., Lincoln NE, USA). These sensors measure short-wave radiation of less than 490 nm, simultaneously, from five integrated concentric annuli of the upward hemisphere, covering a 150° field-of-view (Welles & Norman 1991; Hanan & Bêgué 1995; Lieffers *et al.* 1999). Under a wide range of different canopy structures (or light gradients), several researchers have shown that instantaneous readings of understorey DIFN (I_u), relative to simultaneous above-canopy readings (I_o), can be used as a reliable estimate of PAR transmission (Hanan & Bêgué 1995; Comeau *et al.* 1998; Gendron *et al.* 1998; Lieffers *et al.* 1999; Machado & Reich 1999):

$$\text{Estimated PAR transmission (\%DIFN)} = (I_u / I_o) \times 100 \text{ (units: \%)}$$

This measurement is conceptually similar to the diffuse site factor obtained from hemispherical (fisheye) canopy photographs/images and also paired quantum sensor readings, taken simultaneously from above and below a canopy on completely overcast days (Messier & Puttonen 1995; Parent & Messier 1996; Gendron *et al.* 1998; Messier *et al.*

⁵ Diffuse non-intercepted radiation: diffuse short-wave radiation that passes directly through gaps in the canopy and is not scattered by or transmitted through the canopy biomass.

1998; Machado & Reich 1999). However, an important difference is that the latter method accounts for scattered diffuse (transmitted and down-reflected) radiation from the overstorey, whereas the former two methods treat all overstorey elements (e.g. trunks, branches, leaves) effectively as opaque (Becker *et al.* 1989; Rich *et al.* 1993; Hanan & Bégué 1995; Roxburgh & Kelly 1995; Gendron *et al.* 1998; Lieffers *et al.* 1999).

%DIFN measurements were taken using two synchronised and cross-calibrated LAI-2000 Plant Canopy Analyser units; one was moved around the various sampling positions of interest, while the other was positioned permanently in a nearby open paddock, as an above-canopy reference. Both LAI-2000 units had their short-wave radiation sensor fields of view (azimuth) restricted to 180 degrees, and were orientated to the general aspect of the farm site (refer to Table 2.1). The view restriction prevented the LAI-2000 sensors from 'seeing' the operator or direct sunlight (Welles & Norman 1991; Hanan & Bégué 1995; Comeau *et al.* 1998; Gendron *et al.* 1998). At each sampling point 8 %DIFN measurements were taken with the portable LAI-2000 unit levelled horizontally at approximately one metre above the ground (Welles & Norman 1991). All %DIFN measurements were obtained within a month of taking the digital canopy images (refer to Table 3.1), except for the summer %DIFN measurements at Ballantrae, which were obtained in the same month but in the year prior (this exception was due to the unavailability of equipment).

3.2.3.2 Red to Far-red ratio

The red to far-red ratio (R:FR) was measured using a single-point sensor (Skye Instruments LTD., Llandrindod Wells, Powys, U.K.) to determine any changes in the quality of light reaching the understorey. Sampling was carried out at the same time and place as the %DIFN measurements. 3 R:FR readings were taken from each sampling position. No R:FR measurements were taken at Kiwitea in the winter period. Results are presented as the R:FR relative to a reference open pasture (above-canopy) reading, averaged from measurements taken at the beginning and end of sampling at each site.

3.2.3.3 Sampling positions within an experimental unit

As mentioned in Section 3.2.2.4, the canopy of the poplar stands was often not continuous and usually contained a patchwork of tree crowns and inter-tree gaps. For this experiment,

instead of studying a limited number of overstorey density treatments in detail, it was opted to study a much larger range less comprehensively. The sum of the interactions in mixed tree-pasture systems is likely to be minimised mid-way between the trees and, conversely, the most intense within close proximity to the trees (Runkle *et al.* 1995; Ong *et al.* 1996). Therefore, based on this premise, two extreme overstorey environments (or zones of tree influence) were chosen for sampling in each experimental unit. The first overstorey environment (Zone 1) was defined as the area directly below the vertical projection of the tree crown on the northeastern corner of an experimental unit (Figure 3.3). This zone was positioned on the shaded side of the tree and received direct-beam radiation later in the day (compared to the opposite tree on the north-western corner of an experimental unit), when leaf and air temperatures, along with atmospheric humidity were likely to be less conducive for photosynthesis and plant growth (Wayne & Bazzaz 1993). The second overstorey environment (Zone 3) was defined as the vertically projected gap (VPG; Ban *et al.* 1998) between the crowns of the 4 nuclei trees (Figure 3.3). All light measurements were taken at the centre of each overstorey environment (zone of tree influence).

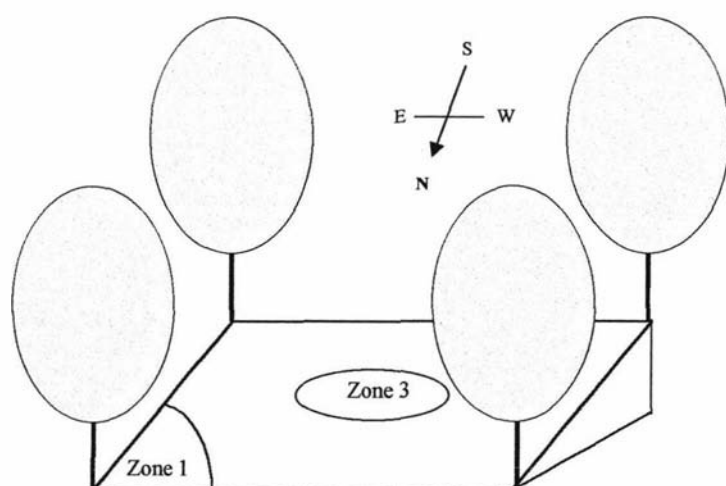


Figure 3.3 Overstorey environments within the boundary of an experimental unit: Zone 1 – area within the expanded canopy gap, directly underneath the crown of the ‘nucleus’ tree located at the north-eastern corner of an experimental unit; and Zone 3 – area at the centre of the vertically projected canopy gap (also refer to Figure 3.1).

3.3 Data analysis

Linear and non-linear regression analyses, using the REG and NLIN procedures of SAS[®] (version 8.02 for Windows[®], SAS Institute, Inc. 1999), were performed to determine relationships between the overstorey (stand) density indices (Table 3.2), as single independent (regressor) variables, and estimated PAR transmission (%DIFN), as the dependent (response) variable. Data from the 4 sites were pooled together, and separate regressions carried out for the 2 zones of tree influence (Zones 1 & 3) and 2 seasons (summer & winter). CurveExpert[®] (version 1.37 for Windows[®], Hyams 2001), scatter plots, and applicable published ecological studies, were used to determine potential regression models for the data.

Table 3.2 Overstorey (stand) density indices

Abbreviation	Units	Definition
DBH	m/ha	Sum of stem diameters over bark at breast height (1.4m) per hectare
BA	m ² /ha	Sum of stem basal areas at breast height (1.4m) per hectare
GCL	m/ha	Sum of vertically projected crown lengths per hectare
HPCD	m/ha	Sum of horizontally projected crown diameters per hectare
HPCC	%	Horizontally projected canopy closure ratio
CEV	'000 m ³ /ha	Sum of stem crown ellipsoidal volumes per hectare
CCL	%	Canopy closure ratio when trees are fully in leaf
CCNL	%	Canopy closure ratio when trees are completely without leaves (no leaf)

For each overstorey density index, the simplest model with the smallest standard error of prediction (RMSE), a high adjusted coefficient of determination⁶, and no trend in the residuals was selected (Vales & Bunnell 1988; Gendron *et al.* 1998). The adequacy (quality of fit) of each regression model was checked through inspection of scatter, residual, and normal probability plots, along with more formal test statistics. Some of the independent variables were either natural logarithm or square root transformed to help meet the underlying model assumptions (as indicated in the appropriate tables). Systematic trends in

⁶ Approximated r^2 for the non-linear models: $1 - \text{SSE}/\text{CSS}$, where SSE is the error sum of squares of the full model and CSS is the corrected total sum of squares. Adjusted $r^2 = 1 - (1 - r^2) * [(n - 1) / (n - m - 1)]$, where n is the total number of observations and m is the number of model parameters.

the residuals for DBH, HPCD, and GCL indicated additional independent or concomitant variables were needed for their regression models.

Analysis of residuals (R-student statistic, $\alpha = 0.05$) detected an outlier for regression models using CCNL, BA, HPCC, and CEV as single regressors of estimated PAR transmission (%DIFN) at the centre of a vertically projected canopy gap (Zone 3) when the trees were completely without leaves (winter). Based on influence diagnostics (Cook's D, HAT DIAG, DFFITS, and DFBETAS) this outlier exerted an appreciable influence on one or more of the regression coefficients and overall reduced the precision of the fitted models (Myers 1990). Nevertheless, after rechecking, the suspect observation was not removed from the data as it was deemed a valid observation.

Relationships between CCL and CCNL, BA, HPCC, and CEV were also investigated using regression analyses. Based on the model developed for CCL vs. HPCC a simplified stand-level estimate of PAR transmission (weighted %DIFN) for each experimental unit was calculated using the equation:

$$\text{Weighted \%DIFN} = (\text{Zone 1 \%DIFN} \times \text{Zone 1 area}^7) + (\text{Zone 3 \%DIFN} \times \text{Zone 3 area})$$

This simplified stand-level estimate of PAR transmission was regressed against the in-leaf canopy closure ratio (CCL) for both summer and winter seasons.

The relationship between the R:FR and estimated PAR transmission (%DIFN) was investigated using a logarithmic function ($Y = a + b \cdot \ln X$). The linear forms of the regressions developed for each season (summer & winter) were compared by analysis of covariance (ANCOVA) using the GLM procedure of SAS® (Littell *et al.* 1991; Kleinbaum *et al.* 1998).

Where appropriate F-tests were used to determine whether the coefficients of simple linear regressions were significantly ($\alpha = 0.05$) different from specified values.

⁷ Calculated as the proportion (fraction) of an experimental unit that the zone covered on a horizontal plane (this was derived from the relationship between HPCC and CCL).

3.4 Results

3.4.1 %DIFN within the vertically projected gap between fully in-leaf poplars

Estimated PAR transmission at the centre of a vertically projected canopy gap (Zone 3 %DIFN) was inversely related to all of the tested stand density indices (Table 3.3). However, there were marked differences in the general form, complexity, and precision of the above relationships (Table 3.3).

CCL measured with a standard digital camera provided the simplest relationship with Zone 3 %DIFN (Table 3.3). Out of the different stand density indices tested, the assigned simple linear model for CCL had one of the lowest standard errors of prediction (RMSE=5.39) and explained 97% of the variation in Zone 3 %DIFN (Table 3.3). In addition, the slope of the relationship was not significantly different from -1 ($P=0.0958$) and the intercept was not significantly different from open pasture %DIFN ($P=0.5226$) (Table 3.3; Figure 3.4a). Overall, Zone 3 %DIFN decreased at a constant rate from open pasture levels to 17% under the highest measured CCL of 82% (Figure 3.4a).

The more complex exponential decay, natural logarithm transformed quadratic, and quadratic regression models, with varying degrees of concave curvature, fitted using BA, HPCC, and CEV as single independent variables, respectively, also showed a very strong relationship with Zone 3 %DIFN (Table 3.3). These relationships each accounted for over 90% of the variation in Zone 3 %DIFN and their standard errors of prediction ($RMSE \leq 8.77$) were similar to that of CCL (Table 3.3). However, there were marked site differences for the relationship between CEV and Zone 3 %DIFN (Figure 3.5). As CEV increased, Zone 3 %DIFN decreased at a much faster rate under the young/small trees at Ballantrae, compared to at the other three sites ($P < 0.05$). In addition, over a common range of CEV sampled in the field (i.e. 30,000-80,000 m^3/ha), Zone 3 %DIFN was consistently around 20% higher at Kiwitea than at Hautope 1 and 2 (Figure 3.5). Overall, Zone 3 %DIFN decreased rapidly up to a BA and CEV of 30 m^2/ha (Figure 3.4b) and 120,000 m^3/ha (Figure 3.5), respectively, thereafter remaining relatively constant at around 20%. In contrast, Zone 3 %DIFN decreased to 26% at the maximum theoretical HPCC of 78.5% (Table 3.3).

The remaining square-root transformed simple linear models, using DBH, HPCD, and GCL, explained less than 65% of the variation in Zone 3 %DIFN and their standard errors of prediction were at least twice the size of the regression models fitted for the other stand density indices ($RMSE \geq 18.52$) (Table 3.3). On an individual site basis, with trees of similar size and form, these three stand density indices were strongly related to Zone 3 %DIFN (Table 3.4; Figure 3.6). However, when pooled together, the scatter plots of the data (and also the model residuals) clearly indicated that some other unaccounted difference between the sites was also influencing PAR transmission (Figure 3.6). In particular, there were marked differences in the relationship for young/small trees at Ballantrae compared to mature/large trees at Kiwitea and Hautope 1 (Figure 3.6).

Table 3.3 Regression equations, and their respective coefficients, developed for overstorey (stand) density indices to estimate the percentage of above-canopy PAR (%DIFN) transmitted at the centre of a vertically projected canopy gap (Zone 3) between fully in leaf *P. x euramericana* trees.

Index	Equation	Coefficients			
		<i>a</i>	<i>b</i>	<i>c</i>	<i>r</i> ²
DBH [†]	$Y = a + b \cdot \text{sqrt}(x)$	100.81 (4.57)	-7.88 (0.85)		0.62
BA	$Y = a + b \cdot \exp(c \cdot x)$	18.58 (3.07)	78.25 (3.09)	-10.32 x 10 ⁻² (1.17 x 10 ⁻²)	0.95
GCL [†]	$Y = a + b \cdot \text{sqrt}(x)$	98.23 (4.72)	-1.13 (0.13)		0.57
HPCD [†]	$Y = a + b \cdot \text{sqrt}(x)$	100.29 (5.19)	-1.72 (0.22)		0.54
HPCC	$Y = a + b \cdot \ln(x+1) + c \cdot \ln(x+1)^2$	94.10 (1.86)	9.82 (2.03)	-5.80 (0.44)	0.96
CEV	$Y = a + b \cdot x + c \cdot x^2$	91.59 (1.65)	-0.97 (0.07)	0.34 x 10 ⁻² (0.05 x 10 ⁻²)	0.91
CCL	$Y = a + b \cdot x$	95.48 (1.06)	-0.96 (0.02)		0.97

Standard errors of regression coefficients are in *parentheses*. All fitted models were highly significant ($P < 0.0001$). Pooled number of observations for the equations = 53. Pooled mean estimated PAR transmission (%DIFN) in the open = 94.77% ± 1.42% (mean ± standard error, $n=10$). Abbreviations: DBH, sum of stem diameters over bark at breast height (1.4m) per hectare (m/ha); BA, sum of stem basal areas at breast height per hectare (m²/ha); GCL, sum of vertically projected green crown lengths per hectare (m/ha); HPCD, sum of the horizontally projected crown diameters per hectare (m/ha); HPCC, horizontally projected canopy closure ratio (%); CEV, sum of the crown ellipsoidal volumes per hectare (‘000 m³/ha); CCL, canopy closure ratio (%) measured with a standard digital camera when the trees were fully in-leaf; sqrt, square root; ln, natural logarithm; exp, base of natural logarithm; *r*², adjusted coefficient of determination (approximated for non-linear models); RMSE (root mean square error), standard error of prediction. [†] Systematic trends in the residuals for DBH, GCL, and HPCD indicated that at least another parameter or concomitant variable was required for the regression models.

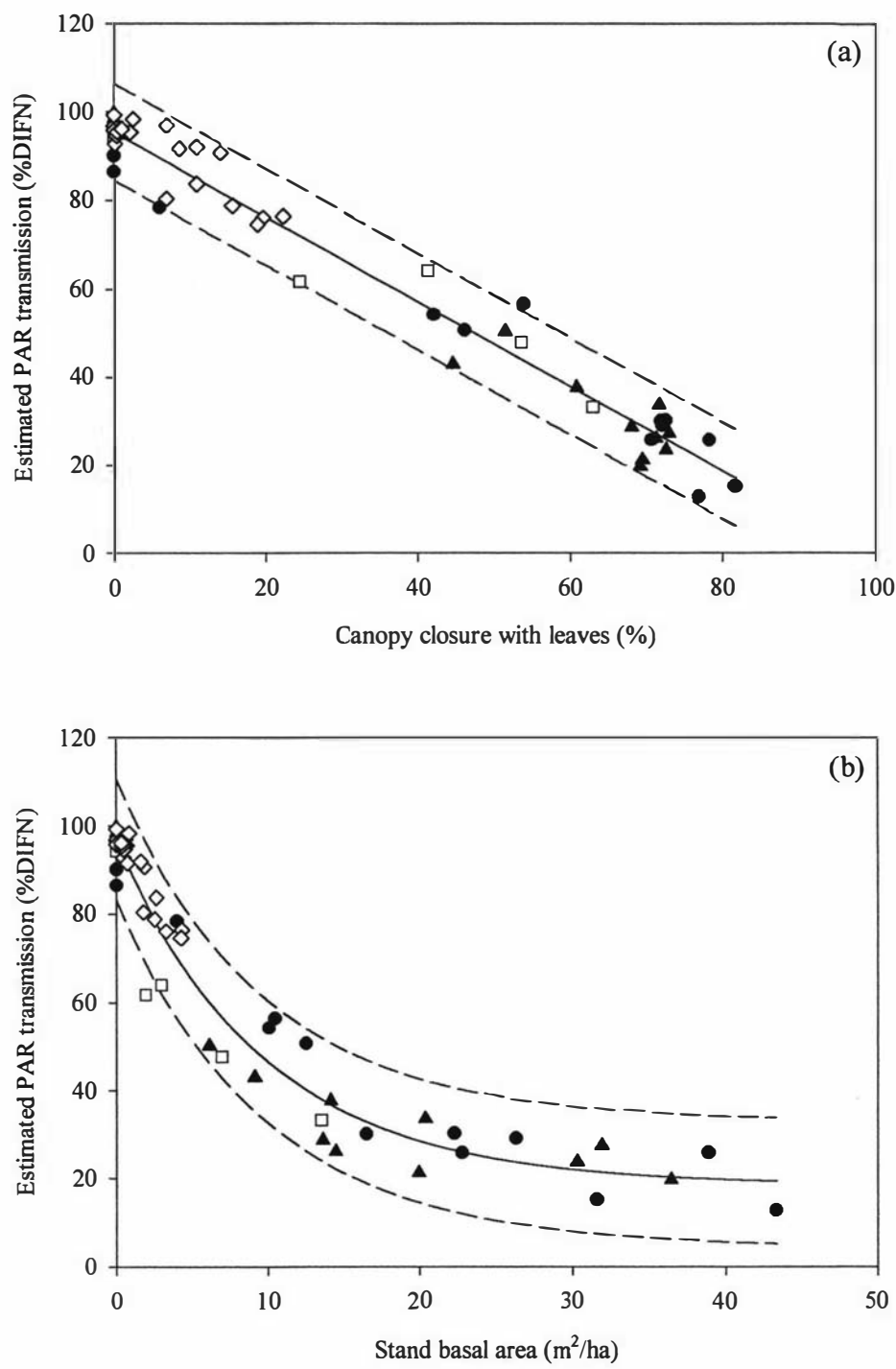


Figure 3.4 The estimated percentage of above-canopy PAR (%DIFN) transmitted at the centre of a vertically projected canopy gap (Zone 3) between fully in leaf poplars, over a range of (a) canopy closure ratios (CCL) measured with a standard digital camera and (b) stand basal areas (BA). Solid line - mean predicted response. Dashed lines - upper and lower 95% prediction limits. Symbols: (●) Kiwitea, (▲) Hautope 1, (□) Hautope 2, and (◇) Ballantrae.

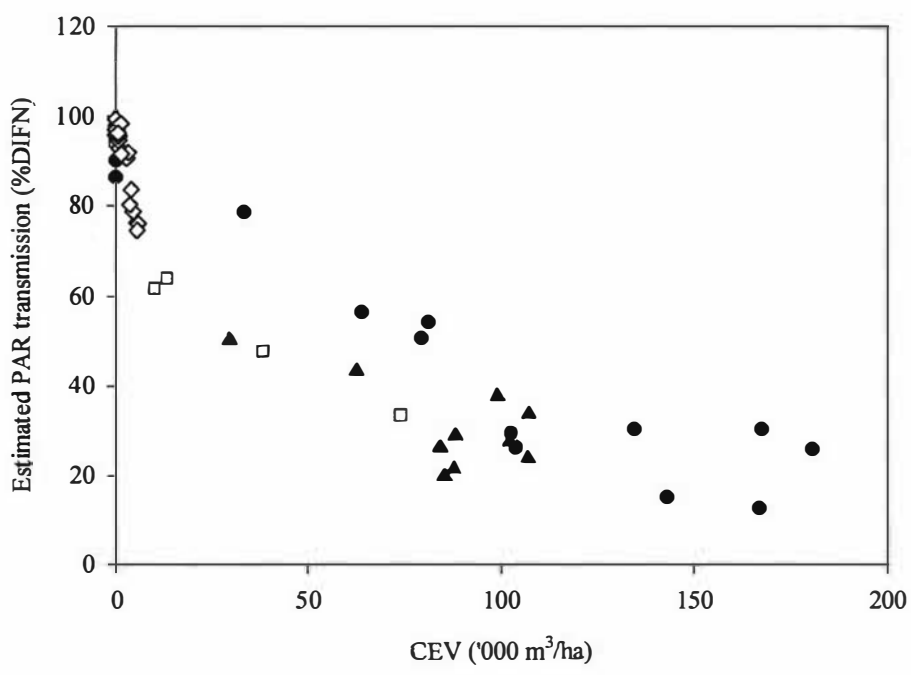


Figure 3.5 The estimated percentage of above-canopy PAR (%DIFN) transmitted at the centre of a vertically projected canopy gap (Zone 3) between fully in-leaf poplars, over a range of stand crown ellipsoidal volumes (CEV) at each farm site. Symbols: (●) Kiwitea, (▲) Hautope 1, (□) Hautope 2, and (◇) Ballantrae.

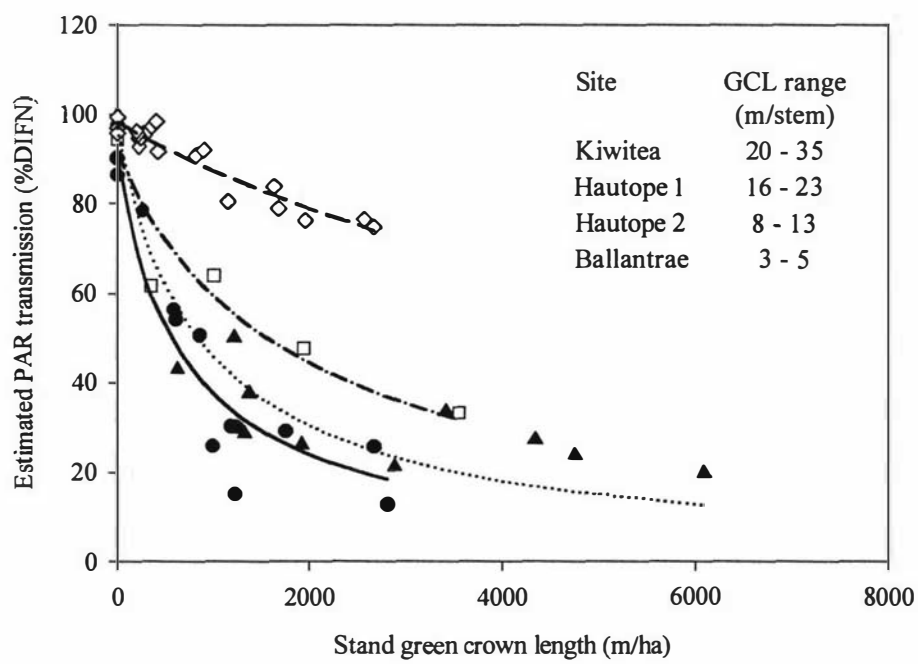


Figure 3.6 The estimated percentage of above-canopy PAR (%DIFN) transmitted at the centre of a vertically projected canopy gap (Zone 3) between fully in-leaf poplars, over a range of stand green crown lengths (GCL) at each farm site. The sum of the stem diameters over bark at breast height (DBH; 1.4m) and the sum of the horizontally projected crown diameters per hectare (HPCD) also showed very similar relationships with Zone 3 %DIFN. Symbols: (—●—) Kiwitea, (···▲···) Hautope 1, (—□—) Hautope 2, and (—◇—) Ballantrae.

Table 3.4 Regression parameters (standard errors in parentheses) for equations predicting estimated PAR transmission (Zone 3 %DIFN) from stand green crown length (m/ha), where $Y=(a*b)/(b+x)$.

Site	<i>a</i>	<i>b</i>	r^2	RMSE	n	P
Kiwitea	91.24 (4.99)	719.83 (120.48)	0.90	8.89	14	<0.0001
Hautope 1	96.88 (6.31)	922.93 (169.85)	0.90	9.06	12	<0.0001
Hautope 2	91.66 (5.41)	1891.93 (480.95)	0.89	8.21	6	<0.0028
Ballantrae	98.28 (0.85)	8092.99 (709.08)	0.90	2.57	21	<0.0001

Out of the range of potential functions tested the non-linear hyperbolic decay function was ranked the best for all of the sites. Abbreviations: r^2 , approximated adjusted coefficient of determination; RMSE (Root mean square error), standard error of prediction; n, total number of observations.

3.4.2 %DIFN directly underneath a fully in-leaf poplar crown

When going from open pasture to low poplar stand densities estimated PAR transmission directly below the fully in-leaf tree crowns (Zone 1 %DIFN) decreased at a much faster rate than within the vertically projected gap between the trees (Zone 3) (Figure 3.4 vs. 3.7). For each of the sites, Zone 1 %DIFN became relatively constant from a low stand density onwards, irrespective of the actual index used (Figure 3.7a,b). However, the average level of PAR transmitted below the trees varied significantly between the four sites. On average, Zone 1 %DIFN at Kiwitea, Hautope 1, Hautope 2, and Ballantrae was $11\% \pm 2\%$ (mean \pm SEM), $26\% \pm 2\%$, $28\% \pm 4\%$, $76\% \pm 2\%$, respectively. The difference in Zone 1 %DIFN between Hautope 1 and 2 was not significant ($P=0.6098$).

Out of the different stand density indices tested, CCL, BA, HPCC, and CEV accounted for at least 90% of the variation in Zone 1 %DIFN (Table 3.5). However, the above site differences, along with the pooled datasets generally being unbalanced, reduced confidence in the appropriateness of the assigned regression models. In particular, the datasets for these four independent variables lacked data points for young/small and old/large trees at high and very low stand densities, respectively (Figure 3.7a,b).

Similarly to Zone 3, for the pooled data both BA and CEV had clear thresholds above which Zone 1 %DIFN became relatively constant. However, these thresholds were about half that for Zone 3, with %DIFN becoming constant at around 17% beyond roughly $10 \text{ m}^2/\text{ha}$ (Figure 3.7b) and $50,000 \text{ m}^3/\text{ha}$ (data not shown), respectively, for the two stand density indices. In contrast, Zone 1 %DIFN decreased at a diminishing rate for CCL (Figure 3.7a) and HPCC (data not shown) over their entire ranges, reaching approximately 15-18% at the maximum canopy cover measured in the field (Table 3.5). Nonetheless, for all of the above stand density indices it was clearly evident that at least another variable was required to account for site differences (as shown for CCL and BA in Figures 3.7a & b).

The datasets for DBH, GCL, and HPCD were generally more balanced – having greater integration of data points from each site along the x-axis (data not shown). Even so, these three independent variables each accounted for only 70-75% of the variation in Zone 1 %DIFN and their regression models RMSE were larger than for the other investigated stand

density indices (Table 3.5). Similarly to Zone 3, the lower quality of fit and precision of the assigned regression models for the pooled data was likely caused by more pronounced relationship differences at each site for these three independent variables (data not shown).

Table 3.5 Regression equations, and their respective coefficients, developed for overstorey (stand) density indices to estimate the percentage of above-canopy PAR (%DIFN) transmitted directly below (Zone 1) the fully in-leaf *P. x euramericana* crowns.

Index	Equation	Coefficient			
		<i>a</i>	<i>b</i>	<i>c</i>	<i>r</i> ²
DBH [†]	$Y = a + b \cdot \ln(x+1)$	93.18 (5.21)	-18.37 (1.70)		0.75
BA	$Y = a + b \cdot \exp(c \cdot x)$	16.83 (2.22)	77.63 (3.48)	-0.36 (0.06)	0.93
GCL [†]	$Y = a/(1 + b \cdot x)$	94.33 (5.78)	0.23×10^{-2} (0.05×10^{-2})		0.72
HPCD [†]	$Y = a/(1 + b \cdot x)$	94.48 (5.58)	0.42×10^{-2} (0.08×10^{-2})		0.74
HPCC	$Y = 1/(a + b \cdot x)$	1.06×10^{-2} (0.03×10^{-2})	0.08×10^{-2} (0.01×10^{-2})		0.92
CEV	$Y = a + (b \cdot x)/(c+x)$	93.84 (2.27)	-80.86 (2.91)	5.62 (1.32)	0.95
CCL	$Y = a + b \cdot \ln(x+1)$	94.57 (3.10)	-18.07 (0.95)		0.90

Standard errors for regression coefficients are in *parentheses*. All fitted models were highly significant ($P < 0.0001$). Pooled number of observations for the models = 40. Pooled mean estimated PAR transmission (%DIFN) in the open = 94.74% \pm 1.41% (mean \pm standard error, $n=10$). Abbreviations: DBH, sum of stem diameters over bark at breast height (1.4m) per hectare (m/ha); BA, sum of stem basal areas at breast height per hectare (m²/ha); GCL, sum of vertically projected green crown lengths per hectare (m/ha); HPCD, sum of the horizontally projected crown diameters per hectare (m/ha); HPCC, horizontally projected canopy closure ratio (%); CEV, sum of the crown ellipsoidal volumes per hectare ('000 m³/ha); CCL, canopy closure ratio (%) measured with a standard digital camera when the trees were fully in-leaf; ln, natural logarithm; exp, base of natural logarithm; *r*², adjusted coefficient of determination (approximated for the non-linear models); RMSE (root mean square error), standard error of prediction. [†] Systematic trends in the residuals for DBH, GCL, and HPCD were detected, indicating that at least another parameter or concomitant variable was required for the regression models.

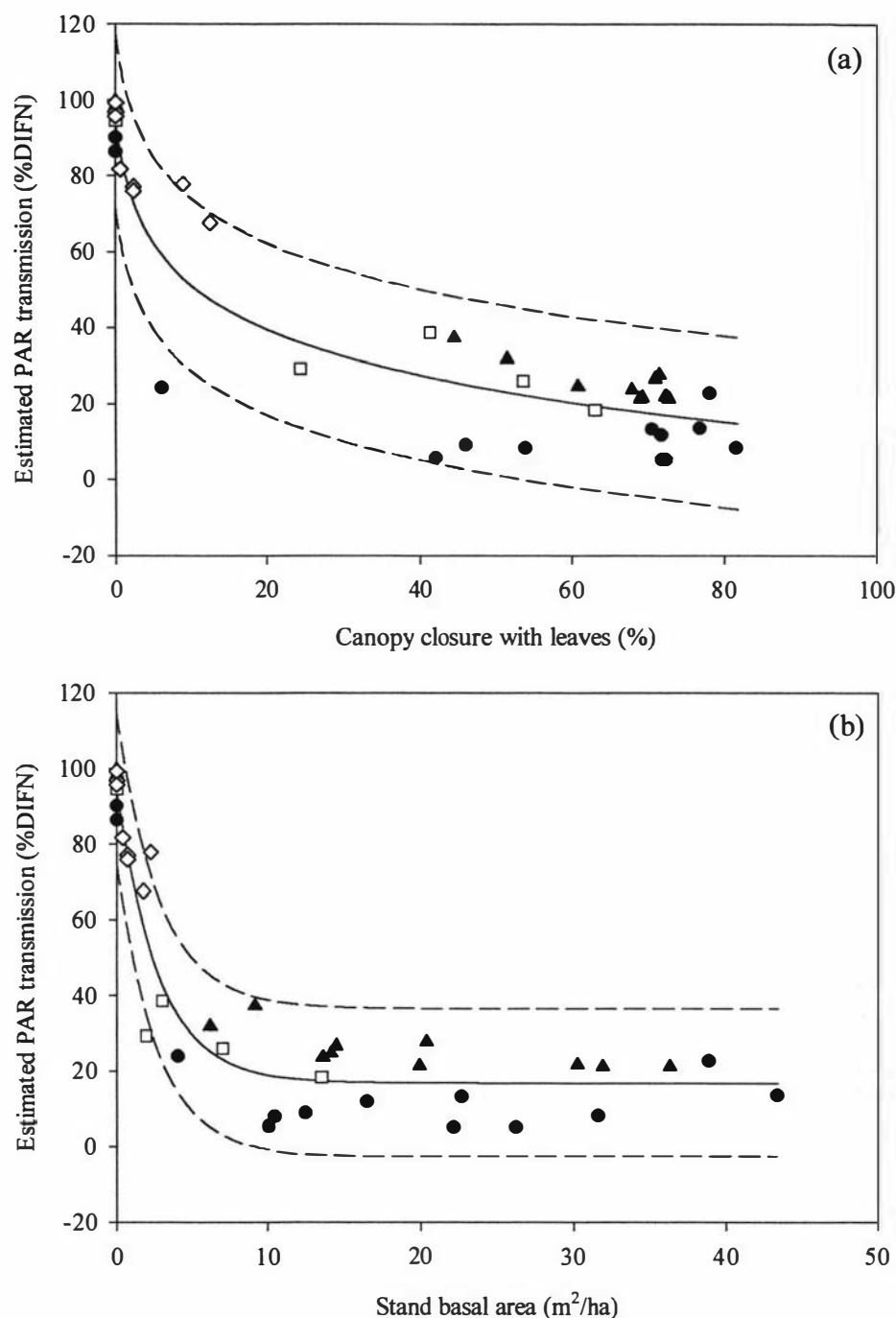


Figure 3.7 The estimated percentage of above-canopy PAR (%DIFN) transmitted directly below the fully in-leaf poplar crowns (Zone 1), over a range of (a) stand canopy closure ratios (CCL) measured with a standard digital camera and (b) stand basal areas (BA). Symbols: (●) Kiwitea, (▲) Hautope 1, (□) Hautope 2, and (◇) Ballantrae. Solid line - mean predicted response. Dashed lines - upper and lower 95% prediction limits. The data point clearly outside the lower 95% prediction limit for CCL vs Zone 1 %DIFN was identified as an outlier (R-student statistic, $\alpha = 0.05$), but was not removed from the natural logarithm regression analysis. Note: the clumping or segregation of data points for the different sites (along the Y-axis) indicated that another unaccounted factor was also influencing Zone 1 %DIFN.

3.4.3 %DIFN within the vertically projected gap between leafless poplars

After leaf fall, Zone 3 %DIFN remained inversely related to each of the stand density indices, when all four of the sites were pooled together (Table 3.6). However, in comparison to summer with the trees fully in leaf, Zone 3 %DIFN increased across the entire range of stand densities - more so towards the mid to higher end of the stand density range (Tables 3.3 & 3.6). For example, at a stand basal area of 5 m²/ha and 40 m²/ha %DIFN was predicted to increase by 15% and 38%, respectively, once the trees had lost all of their leaves (Figure 3.4b vs. 3.8b).

On average, the regression models fitted using CCNL, BA, HPCC, and CEV had a RMSE 44% greater than their summer counterparts when the trees were fully in leaf ($P=0.0193$; Tables 3.3 & 3.6). Out of these four indices, the simple linear model based on CCNL produced the highest adjusted coefficient of determination ($r^2=0.82$) and smallest standard error of prediction (RMSE=8.24; Table 3.6). BA, CEV, and HPCC, on the other hand, each accounted for approximately 70% of the variation in Zone 3 %DIFN (Table 3.6). Although the regression models fitted with DBH, GCL, and HPCD as single independent variables had a smaller RMSE than their equivalent models in summer, they still had the weakest relationship with Zone 3 %DIFN among the different stand density indices investigated ($r^2 \leq 0.43$; Tables 3.3 & 3.6). Again, the unbalanced nature of the datasets for CCNL, BA, HPCC, and CEV (refer to Section 3.4.2) reduced confidence that the shape of the assigned curves was an accurate representation of the 'true' relationship.

Residual scatter plots along with formal test statistics (e.g. Levene Median Test) of the above regression models indicated that each, except for CCNL and BA, contained heterogeneous variance (data not shown). This looked to be because of marked site differences in the relationships between Zone 3 %DIFN and the various stand density indices. All of the relationships at both Kiwitea and Hautope 2 were generally negative and linear. Whereas, at Hautope 1 and Ballantrae, once amongst the stands, there was no clear trend between Zone 3 %DIFN and any of the tested stand density indices. Nevertheless, Zone 3 %DIFN did vary significantly between these two sites ($P<0.0001$). On average, the younger/smaller trees at Ballantrae allowed $96\% \pm 1\%$ (mean \pm SEM) of incident PAR

to be transmitted to the understorey, while the older/larger trees at Hautope 1 allowed $54\% \pm 2\%$ to be transmitted.

Based only on Kiwitea and Hautope 2 in winter, the relationships for BA, HPCC, and CEV versus Zone 3 %DIFN changed from having some degree of negative concave curvature when the trees were fully in leaf in summer (Table 3.3) to a negative straight-line (linear) relationship when the trees were completely without leaf in winter (Table 3.7). In contrast, the relationship between CC and Zone 3 %DIFN was linear for both periods. However, the slope of the relationships did not remain constant, with the rate of decrease in Zone 3 %DIFN associated with increasing CC being 26% less in winter, when the trees were completely without leaf (Table 3.3 vs. 3.7). Overall, BA, HPCC, and CEV accounted for over 80% of the variation in Zone 3 %DIFN, while CCNL accounted for a slightly lesser amount at around 70% (Table 3.7).

The datasets for DBH, GCL, and HPCD were generally more balanced than for the other stand density indices (Figure 3.8 vs. 3.9). Similarly in summer, the relationships for these three independent variables clearly depended on the site, as shown for GCL in Table 3.8 and Figure 3.9. Site differences in the slope of the relationships were particularly marked between Ballantrae, Hautope 2, and Kiwitea (Table 3.8; Figure 3.9). At each site, the individual relationships between these three independent variables and Zone 3 %DIFN also looked to change from being curvilinear in summer to linear in winter, as again shown for GCL (Figure 3.6 vs. 3.9).

Table 3.6 Regression equations, and their respective coefficients, developed for overstorey (stand) density indices to estimate the percentage of above-canopy PAR (%DIFN) transmitted at the centre of the vertically projected canopy gap (Zone 3) between the leafless *P. x euramericana* trees.

Index	Equation	Coefficients				
		<i>a</i>	<i>b</i>	<i>c</i>	<i>r</i> ²	RMSE
DBH	$Y = a + b \cdot x$	95.06 (2.75)	-0.42 (0.07)		0.43	13.90
BA	$Y = a + b \cdot \ln(x+1)$	101.64 (2.39)	-11.74 (1.17)		0.66	10.69
GCL	$Y = a + b \cdot x$	93.91 (2.68)	-8.79×10^{-3} (1.44×10^{-3})		0.41	14.09
HPCD	$Y = a + b \cdot x$	94.96 (3.16)	-2.09×10^{-2} (0.41×10^{-2})		0.33	15.04
HPCC	$Y = a + b \cdot x$	98.13 (1.97)	-0.48 (0.04)		0.70	10.04
CEV	$Y = a + b \cdot x + c \cdot x^2$	97.11 (1.94)	-0.55 (0.08)	0.20×10^{-2} (0.05×10^{-2})	0.70	10.14
CCNL [†]	$Y^2 = a + b \cdot x$	9379.17 (215.05)	-137.79 (8.85)		0.82	8.24

[†]Zone 3 %DIFN was power transformed to improve the underlying assumptions of the linear model; nevertheless, the RMSE is given in natural units (Myers 1990). Standard errors for regression coefficients are in *parentheses*. All fitted models were highly significant ($P < 0.0001$). Pooled number of observations for the equations = 52. Pooled mean %DIFN in the open = 97.6 % \pm 1.3% (mean \pm standard error, $n=9$). Abbreviations: DBH, sum of stem diameters over bark at breast height (1.4m) per hectare (m/ha); BA, sum of stem basal areas at breast height per hectare (m²/ha); GCL, sum of vertically projected green crown lengths per hectare (m/ha); HPCD, sum of the horizontally projected crown diameters per hectare (m/ha); HPCC, horizontally projected canopy closure ratio (%); CEV, sum of crown ellipsoidal volumes per hectare ('000 m³/ha); CCNL, canopy closure ratio (%) measured with a standard digital camera when the trees were completely without leaves; ln, natural logarithm; *r*², adjusted coefficient of determination; RMSE (root mean square error), standard error of prediction.

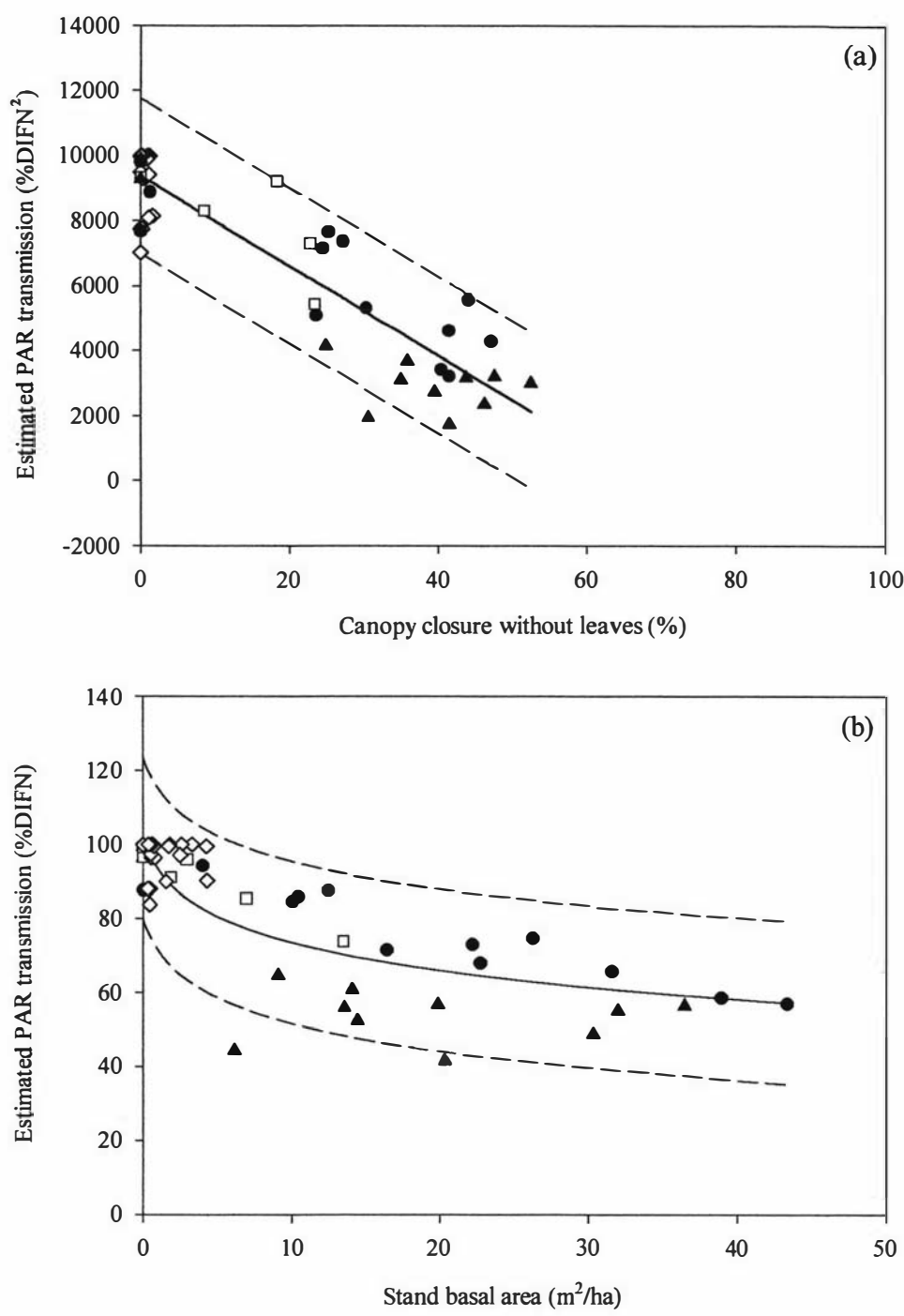


Figure 3.8 The estimated percentage of above-canopy PAR (%DIFN) transmitted at the centre of a vertically projected gap between leafless poplars (Zone 3), over a range of (a) canopy closure ratios (CCNL) measured with a standard digital camera and (b) stand basal areas (BA). Note: %DIFN was squared to normalise the data in (a). Symbols: (●) Kiwitea, (▲) Hautope 1, (□) Hautope 2, and (◇) Ballantrae. Solid line - mean predicted response. Dashed lines - upper and lower 95% prediction limits. The data point clearly outside the lower 95% prediction limit for BA was identified as an outlier (R-student statistic, $\alpha = 0.05$), but was not removed. For BA, the clumping or segregation of (▲) Hautope 1 data points away from the other sites (along the Y-axis) indicates that another unaccounted factor was also influencing Zone 3 %DIFN.

Table 3.7 Regression parameters (standard errors in parentheses) for equations predicting estimated Zone 3 %DIFN individually from CCNL, BA, HPCC and CEV, where $Y = a + b \cdot x$.

Index	<i>a</i>	<i>b</i>	r^2	RMSE
CCNL	97.10 (2.75)	-0.71 (0.10)	0.73	7.05
BA	94.58 (1.49)	-0.94 (0.08)	0.89	4.48
HPCC	98.26 (2.34)	-0.37 (0.04)	0.81	5.92
CEV	96.07 (1.87)	-0.20 (0.02)	0.85	5.23

Dataset for the above simple linear relationships includes only Kiwitea and Hautope 2 sites. All models were highly significant ($P < 0.0001$). Pooled number of observations for the equations = 19. Pooled mean PAR transmission (%DIFN) in the open = 95.61 ± 2.75 (mean \pm stand error, $n=4$). Abbreviations: r^2 , adjusted coefficient of determination; RMSE (Root mean square error), standard error of prediction.

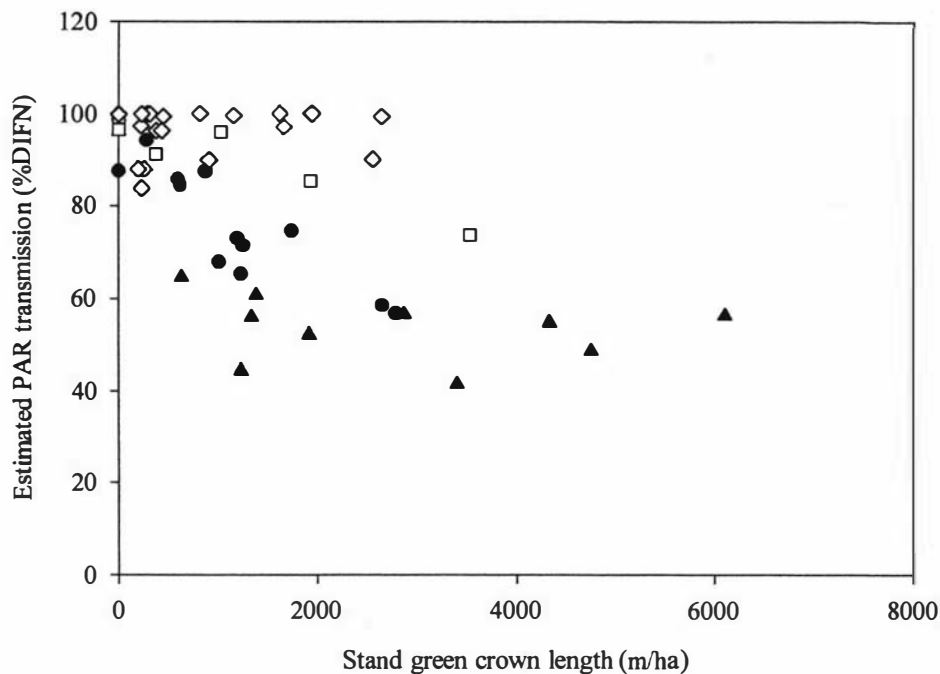


Figure 3.9 The estimated percentage of above-canopy PAR (%DIFN) transmitted at the centre of a vertically projected canopy gap (Zone 3) between leafless poplars, over a range of stand green crown lengths (m/ha). Symbols: (●) Kiwitea, (▲) Hautope 1, (□) Hautope 2, and (◇) Ballantrae. Stem diameter over bark at breast height (DBH; 1.4m) and horizontally projected crown diameter (HPCD) also showed similar relationships with Zone 3 %DIFN.

Table 3.8 Regression parameters (standard errors in parentheses) for equations predicting estimated PAR transmission (Zone 3 %DIFN) from stand green crown length (m/ha), where $Y = a + b \cdot x$.

Site	<i>a</i>	<i>b</i>	<i>r</i> ²	RMSE	<i>n</i>	<i>P</i>
Kiwitea	92.2 (2.9)	-0.0134 (0.0021)	0.78	6.3	13	<0.0001
Hautope 1	83.4 (7.5)	-0.0139 (0.0041)	0.56	13.7	9	0.0118
Hautope 2	97.8 (1.9)	-0.0065 (0.0011)	0.87	3.4	6	0.0041
Ballantrae	NS	NS	-	-	21	0.8490

Out of the range of potential functions tested the simple linear function was ranked the best for all four sites. Abbreviations: *r*², adjusted coefficient of determination; RMSE (Root mean square error), standard error of prediction; *n*, total number of observations.

3.4.4 %DIFN directly underneath a leafless poplar crown

The general trend of the winter relationships between Zone 1 %DIFN and the different stand density indices was similar to in summer. All of the fitted regression models for the pooled data maintained strong negative concave curvature (Table 3.9). The decrease in Zone 1 %DIFN was particularly large when going from open pasture to low stand densities, and thereafter %DIFN remained relatively constant (Figures 3.10a,b). As in summer, with increasing stand density %DIFN decreased at a much faster rate in Zone 1 compared to Zone 3. The only exception was at Hautope 1, where %DIFN in both zones of tree influence was not significantly different, irrespective of the stand density ($P=0.5415$; Figure 3.8 vs. 3.10).

One of the main differences between the two periods was a significant increase in the average level of estimated PAR transmission (%DIFN) in winter, when the trees were completely without leaves ($P<0.0001$). On average, Zone 1 %DIFN increased by $31\% \pm 5\%$ (mean \pm SED) between summer and winter (excluding open pasture values). However, on an individual site basis, the increase in %DIFN relative to in summer was greater under the more mature/larger trees at Kiwitea, followed by those at Hautope 1 and 2, and then the younger/smaller trees at Ballantrae (Figure 3.11). As a result, Zone 1 %DIFN at Kiwitea, Hautope 1, Hautope 2, and Ballantrae in winter averaged $54\% \pm 2\%$ (mean \pm SEM), $51\% \pm 3\%$, $68\% \pm 3\%$, and $83\% \pm 4\%$, respectively; the difference between Kiwitea and Hautope 1 was not significant ($P=0.3787$). In winter, the greater increase in Zone 1 %DIFN at Kiwitea compared to Ballantrae also meant that there was less variation amongst the sites than in summer (Figure 3.11).

Overall, the regression models based on CCNL, BA, HPCC, and CEV explained about 80% to 85% of the variation in Zone 1 %DIFN, while DBH, GCL, and HPCD explained around 70% (Table 3.9). On average, the proportion of variation accounted for did not change significantly between the two periods ($P=0.2228$; Table 3.5 & 3.9).

For the pooled data, both CCNL and HPCC had clear thresholds (10% and 45%, respectively) above which Zone 1 %DIFN became constant at 54% (Figure 3.10a; Table 3.9). This contrasted with the relationships fitted for summer, which decreased at a

diminishing rate over the entire ranges of CCL and HPCC (Figure 3.7a; Table 3.5). Site differences and also the unbalanced nature of the pooled dataset may have caused the inconsistency in the form of the relationships between periods, as previously discussed in Section 3.4.2.

Both BA and CEV had similar threshold values to in summer, above which Zone 1 %DIFN became relatively constant (Figure 3.10b; Table 3.9). However, the same factors influencing the choice of regression model for CCNL and HPCC were also present for BA and CEV (Figure 3.10b).

Again, similar to in summer, the datasets for DBH, GCL, and HPCD were more balanced (along the x-axis) than for the other stand density indices and showed more pronounced site differences in their relationship with Zone 1 %DIFN (data not shown). The site differences likely reduced the above regression models quality of fit and precision in comparison to the other stand density indices.

Based on the maximum canopy closure ratio for in summer (82% CCL) and winter (52% CCNL), Zone 1 %DIFN for the pooled data was predicted to increase from $15\% \pm 5\%$ (estimate \pm standard error) to $52\% \pm 4\%$ (Figures 3.7a & 3.10a). These values, and the corresponding vertical shift in Zone 1 %DIFN between the two periods, closely resembled Zone 3 at the same stand density (Figures 3.4a & 3.8a). This indicates that the stand was effectively closed at this density, and thus, the canopy gap fractions 'seen' from Zones 1 and 3 were similar.

Table 3.9 Regression equations, and their respective coefficients, developed for overstorey (stand) density indices to estimate the percentage of above-canopy PAR (%DIFN) transmitted directly below (Zone 1) the leafless *P. x euramericana* crowns.

Index	Equation	Coefficients				
		<i>a</i>	<i>b</i>	<i>c</i>	<i>r</i> ²	RMSE
DBH	$Y = a + b \cdot \ln(x+1)$	96.34 (3.33)	-10.45 (1.07)		0.71	10.73
BA	$Y = a + b \cdot \sqrt{x} + c \cdot x$	97.52 (2.30)	-19.93 (1.94)	2.13 (0.33)	0.86	7.60
GCL	$Y = 1/(a + b \cdot \sqrt{x})$	1.04×10^{-2} (0.04×10^{-2})	0.02×10^{-2} (0.00×10^{-2})		0.68	11.35
HPCD	$Y = 1/(a + b \cdot \sqrt{x})$	1.03×10^{-2} (0.04×10^{-2})	0.03×10^{-2} (0.00×10^{-2})		0.69	11.07
HPCC	$Y = a + b \cdot \exp(c \cdot x)$	53.87 (1.91)	43.04 (3.08)	-0.08 (0.02)	0.84	8.12
CEV	$Y = a + b \cdot \sqrt{x} + c \cdot x$	95.92 (2.09)	-8.95 (0.95)	0.45 (0.08)	0.87	7.24
CCNL	$Y = a + b/(x+1)$	53.63 (1.82)	41.98 (3.28)		0.81	8.71

Standard errors for regression coefficients are in *parentheses*. All fitted models were highly significant ($P < 0.0001$). Total pooled number of observations for the models = 39. Pooled mean estimated PAR transmission (%DIFN) in the open = 97.6 % \pm 1.3% (mean \pm standard error, $n=9$). Abbreviation: DBH, sum of stem diameters over bark at breast height (1.4m) per hectare (m/ha); BA, sum of stem basal areas at breast height per hectare (m²/ha); GCL, sum of vertically projected green crown lengths per hectare (m/ha); HPCD, sum of the horizontally projected crown diameters per hectare (m/ha); HPCC, horizontally projected canopy closure ratio (%); CEV, sum of the individual crown ellipsoidal volumes per hectare ('000 m³/ha); CCNL, canopy closure ratio (%) measured with a standard digital camera when the trees were completely without leaves; sqrt, square root; ln, natural logarithm; *r*², adjusted coefficient of determination (approximated for non-linear models); RMSE (root mean square error), standard error of prediction.

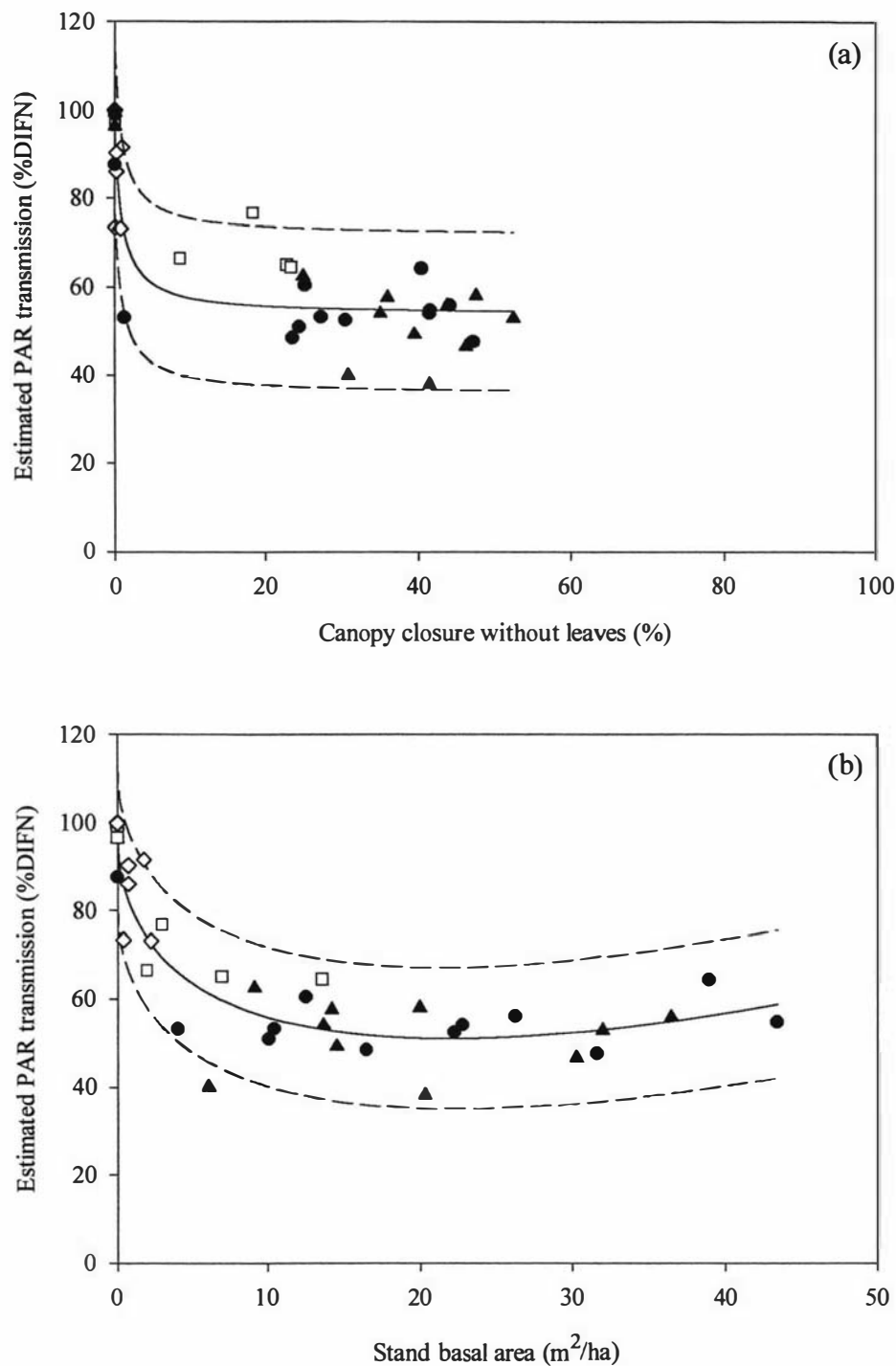


Figure 3.10 The estimated percentage of above-canopy PAR (%DIFN) transmitted directly below (Zone 1) the leafless poplar crowns, over a range of (a) stand canopy closure ratios (CCNL) measured with a standard digital camera and (b) stand basal areas (BA). Symbols: (●) Kiwitea, (▲) Hautope 1, (□) Hautope 2, and (◇) Ballantrae. Solid line - mean predicted response. Dashed lines - upper and lower 95% prediction limits.

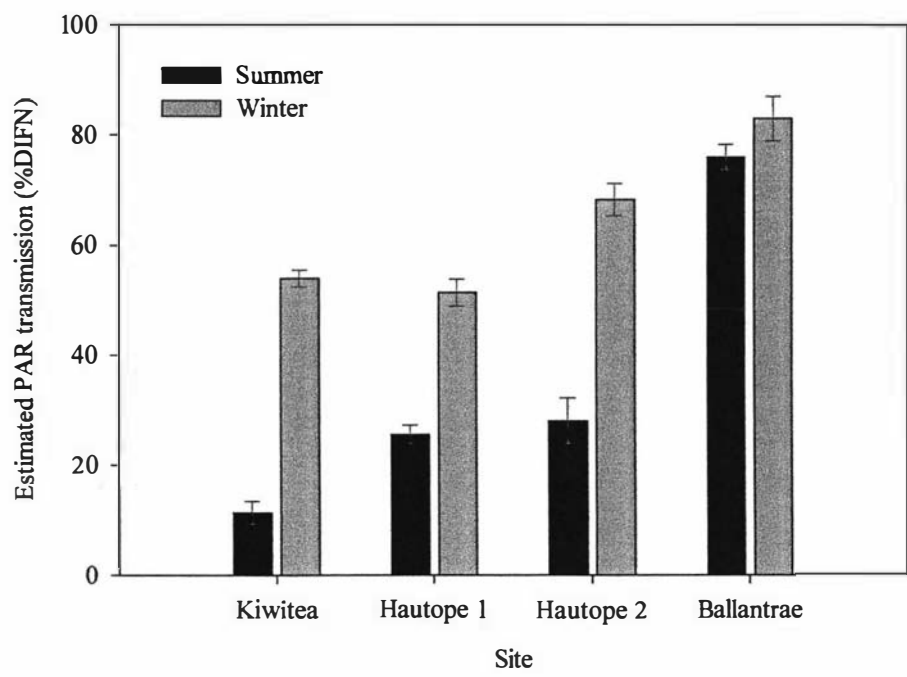


Figure 3.11 Mean estimated percentage of above-canopy PAR (%DIFN) transmitted directly underneath the individual poplar crowns (Zone 1) at each site. Vertical bars represent the standard error of the mean.

3.4.5 Selective relationships between stand density indices

When pooled across all four sites, the winter canopy closure ratio (CCNL) increased by 6% for every 10% increase in the summer canopy closure ratio (CCL) (Table 3.10; Figure 3.12a). However, based on the scatter of the data points, differences in the relationship between these two variables were particularly marked between the younger trees at Ballantrae and the older, more fully developed, trees at Kiwitea and Hautope 1 and 2 (Figure 3.12a). A comparison of slopes from simple linear functions for each site using ANCOVA confirmed that Ballantrae was significantly different from the other three sites ($P<0.01$). As a result, a further two simple linear functions are presented in Table 3.10 representing the different groups - separated as young (Ballantrae) and mature (Kiwitea & Hautope) stands.

HPCC, BA, and CEV were all strongly related to CCL (Table 3.10; Figures 3.12b,c,d). Initially, when going from open pasture to low BA and CEV the increase in CCL was rapid, with CCL becoming relatively constant at around 70-80% beyond a BA of approximately 20 m²/ha (Figures 3.12c,d).

Table 3.10 Regression models, and their respective coefficients, developed for selected stand indices to predict canopy closure (CC).

Index	Equation	Coefficients			
		<i>a</i>	<i>b</i>	<i>r</i> ²	RMSE
BA	$Y=a*(1-\exp(-b*x))$	78.69 (3.25)	0.105 (0.012)	0.94	7.44
CEV	$Y=a*x^b$	9.14 (1.62)	0.428 (0.039)	0.90	9.49
HPCC	$Y=a*(1-\exp(-b*x))$	136.28 (28.82)	0.010 (0.003)	0.95	6.48
CCL [†]	$Y= a + b*x$	-3.79 (1.34)	0.600 (0.030)	0.92	5.37
CCL [†] categorised into stand age groups:					
Young	$Y= a + b*x$	0.08* (0.06)	- 0.061 (0.006)	0.87	0.18
Mature	$Y= a + b*x$	-4.31* (4.30)	0.615 (0.067)	0.77	6.18

[†]Index used to estimate the without leaf canopy closure ratio (CCNL). *Coefficients (intercepts) were not significant ($P>0.05$). Standard errors are presented in parentheses. All fitted models were highly significant ($P<0.0001$). Abbreviations: *r*², adjusted coefficient of determination; RMSE, standard error of prediction. Total number of observations for the models based on all four sites, young, and mature categories were 43, 18, and 26, respectively. Analysis of the linear model residuals for CCL-young and -mature indicated that transformations were required to meet the underlying assumption of homogenous variance. However, these models were left untransformed for ease of comparison.

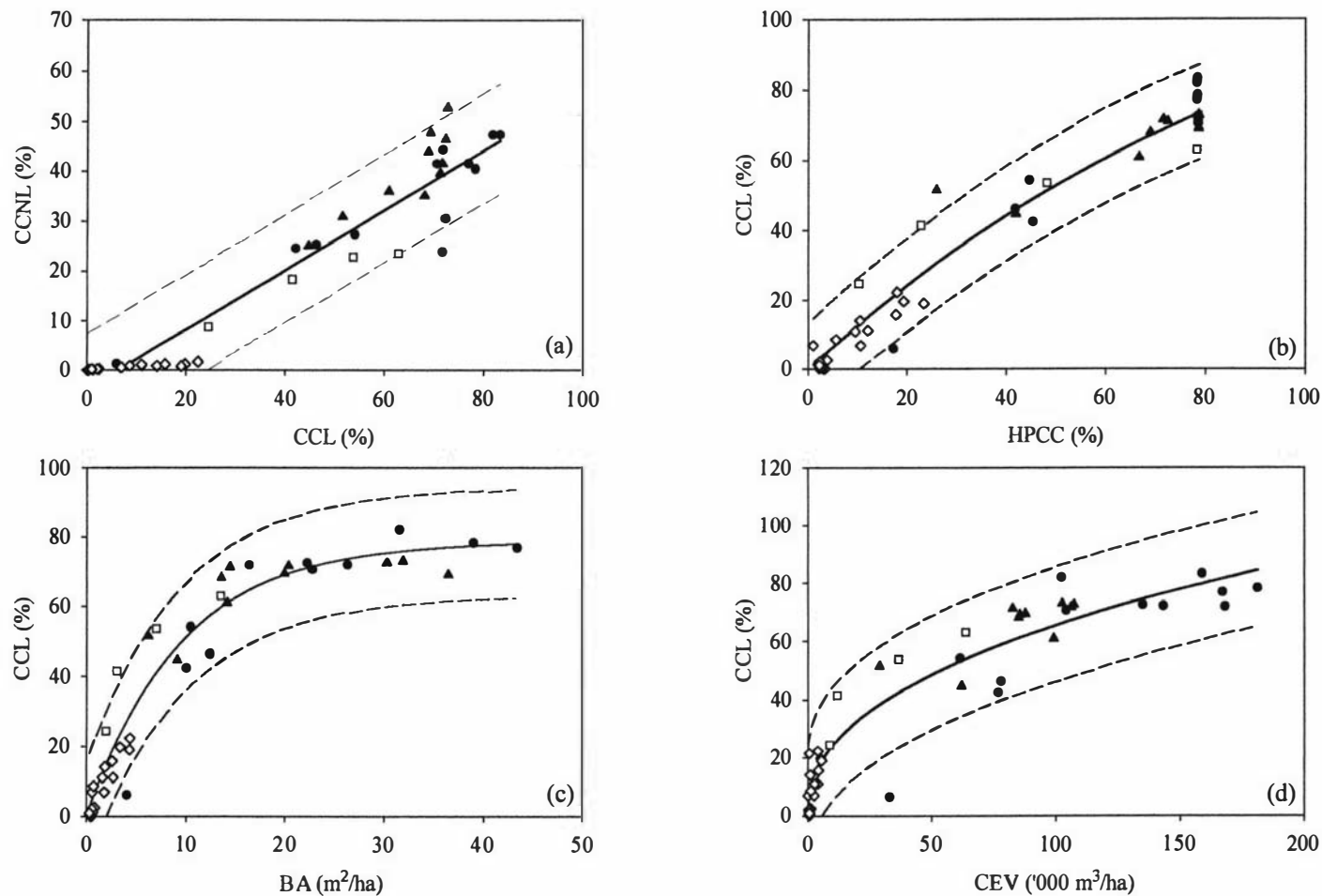


Figure 3.12 Relationships between overstorey (stand) density indices. Abbreviations: CCL, canopy closure ratio when trees are fully in leaf; CCNL, canopy closure ratio when trees are completely without leaf (no leaf); HPCC, horizontally projected canopy closure ratio; BA, stem basal areas at breast height (1.4m) per hectare; and CEV, crown ellipsoidal volumes per hectare. Symbols: (●) Kiwitea, (▲) Hautope 1, (□) Hautope 2, and (◇) Ballantrae. Solid line - mean predicted response. Dashed lines - upper and lower 95% prediction limits. Datum clearly outside the lower 95% prediction limit for CEV vs. CCL was identified as an outlier (R-student test, $\alpha=0.05$) (Myers 1990), but was not removed from the regression.

3.4.6 Weighted (stand level) %DIFN over a range of canopy closures

In summer, the relationship between CCL and stand-level PAR transmission (weighted %DIFN) was curvilinear, with the rate of change in weighted %DIFN decreasing at higher CCLs (Table 3.11; Figure 3.13a). For example, at a CCL of 40% weighted %DIFN was reduced by 48% compared to the open pasture, whereas going from a CCL of 40% to 80% (near the maximum CCL measured in the field) it was only reduced by a further 33%. Overall, the regression model accounted for a very high proportion of variation in weighted %DIFN ($r^2=0.97$).

Conversely, in winter the rate of change in weighted %DIFN increased at higher CCLs (Table 3.11; Figure 3.13b). At a high CCL of 80% weighted %DIFN was predicted to be over 3-fold greater under the leafless trees in winter than under the fully foliated trees in summer (Figures 3.13a,b).

Table 3.11 Relationships between the in-leaf canopy closure ratio (CCL) and estimated stand-level PAR transmission (weighted %DIFN).

Season	Equation	Coefficients			r^2	RMSE	n
		<i>a</i>	<i>b</i>	<i>c</i>			
Summer	$Y = a - b \cdot x + c \cdot x^2$	94.94 (1.51)	1.42 (0.13)	0.005 (0.002)	0.97	5.68	40
Winter [†]	$Y^2 = a - b \cdot x$	9367 (260)	88.38 (5.17)	-	0.88	7.56	39

[†]%DIFN was squared to normalise the distribution of the regression residuals; nevertheless, the RMSE for the winter season is given in natural units (Myers 1990). Standard errors of the coefficients are given in parentheses. Both regressions were highly significant ($P<0.0001$). Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction, n, total number of observations.

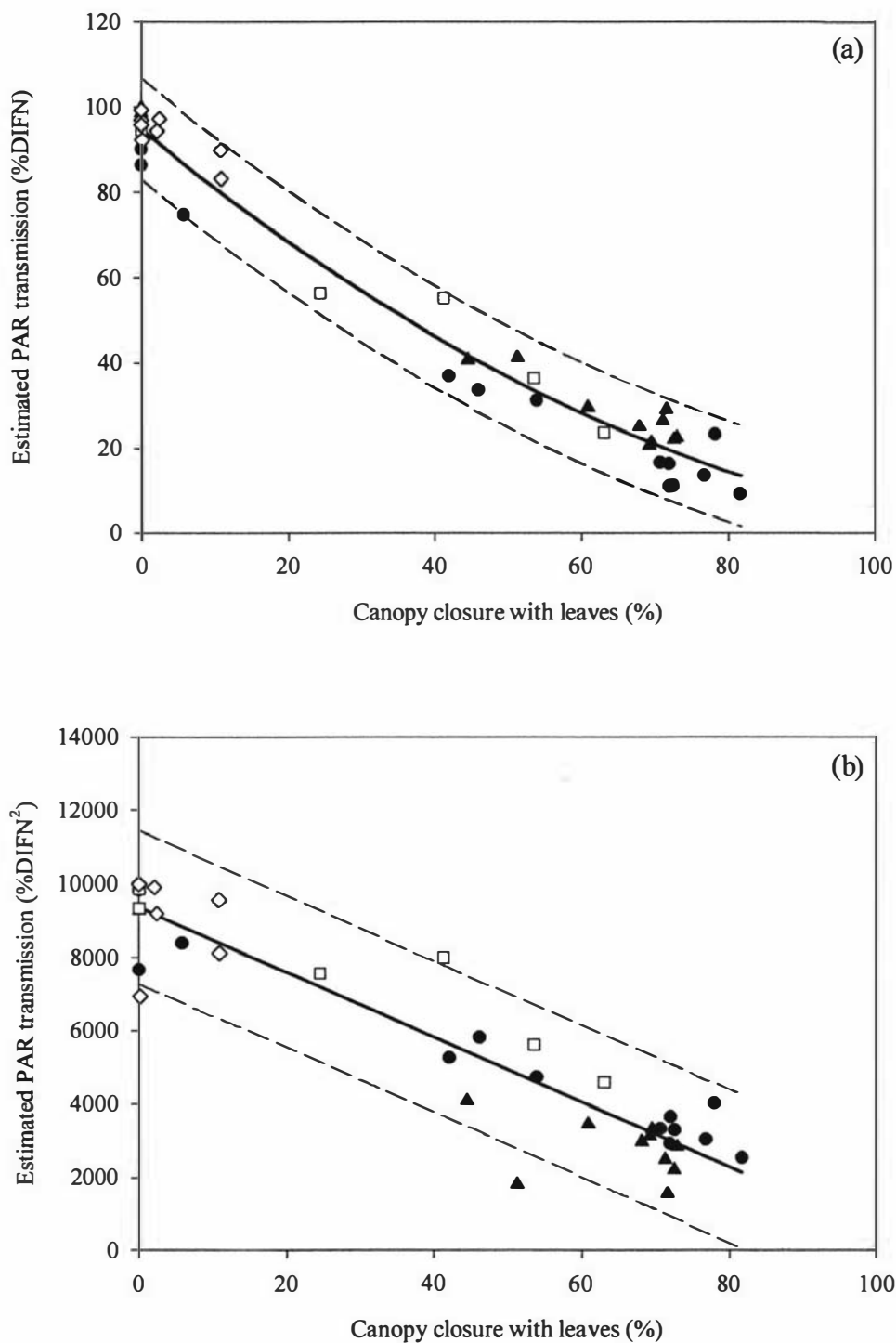


Figure 3.13 Estimated stand-level PAR transmission (weighted %DIFN) across a range of in-leaf canopy closure ratios (CCL) in (a) summer and (b) winter (%DIFN squared to normalise data). Solid line - mean predicted response. Dashed lines - upper and lower 95% prediction limits. Symbols: (●) Kiwitea, (▲) Hautope 1, (□) Hautope 2, and (◇) Ballantrae.

3.4.7 The relationship between R:FR and %DIFN

In summer, the red to far-red ratio (R:FR), relative to that received in the open pasture, progressively declined with reduced levels of estimated PAR transmission (%DIFN) under the fully in-leaf poplar stands (Table 3.12; Figure 3.14a). The decrease was especially pronounced below a %DIFN level of approximately 40% (Figure 3.14a). In contrast, the R:FR underneath the leafless poplar stands in winter, relative to the open pasture ratio, decreased less markedly ($P<0.0001$) under reduced %DIFN and the rate of change was more constant over the entire range of measured transmission levels. There was also less variation around the fitted relationship in winter than summer (Table 3.12; Figure 3.14b). The regression model fitted for summer showed signs of systematic variation in the residuals around the highest %DIFN levels, with the model tending to underestimate R:FR, relative to the open pasture ratio (Figure 3.14a).

Table 3.12 Regression parameters (standard errors in parentheses) for equations predicting understorey R:FR, relative to open pasture (%), from estimated PAR transmission (%DIFN), where $Y = a + b \cdot \ln(x)$.

Season	<i>a</i>	<i>b</i>	r^2	RMSE	n
Summer	11.53 (2.76)	18.50 (0.73)	0.89	5.42	83
Winter	62.48 (3.72)	8.30 (0.86)	0.62	1.93	58

Models were highly significant ($P<0.0001$). Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction; n, total number of observations.

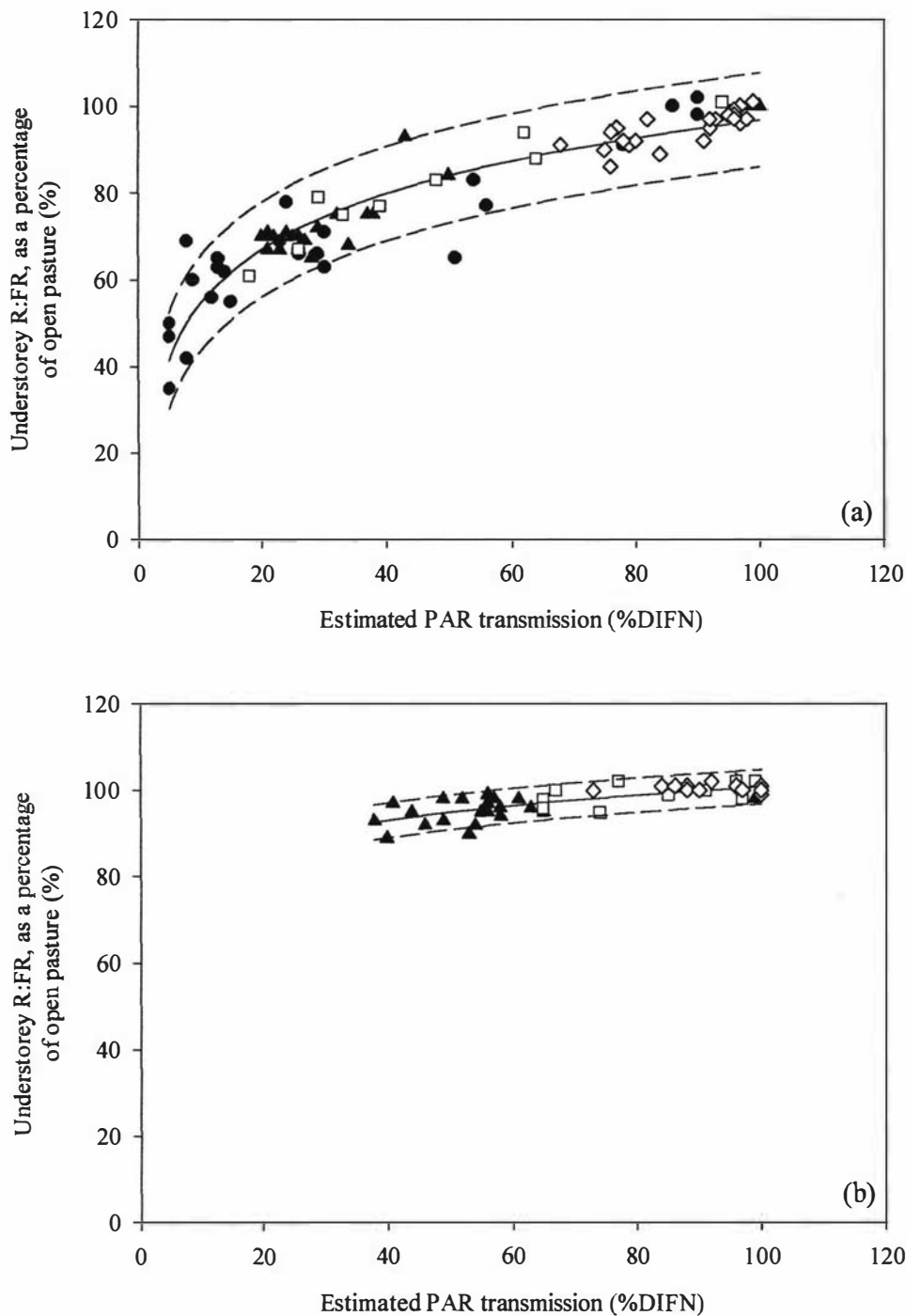


Figure 3.14 The relationship between the understorey R:FR, relative to the open pasture, and estimated PAR transmission (%DIFN) through the poplar canopy in (a) summer (in-leaf) and (b) winter (no-leaf). Symbols: (●) Kiwitea, (▲) Hautope 1, (□) Hautope 2, and (◇) Ballantrae. Solid line - mean predicted response. Dashed lines - upper and lower 95% prediction limits. The two data points clearly outside the 95% prediction limits for the summer (in-leaf) relationship were identified as outliers (R-student test, $\alpha=0.05$) (Myers 1990), but were not removed from the simple logarithm regression. No R:FR measurements were taken at the Kiwitea site for the winter period.

3.5 Discussion

3.5.1 The relationship between stand density indices and Zone 3 %DIFN for summer and winter

3.5.1.1 General relationship

In both summer and winter PAR transmission at the centre of a vertically projected gap between the tree crowns (Zone 3 %DIFN) was inversely related to all of the tested stand density indices (Tables 3.3 & 3.6). However, after leaf fall in autumn Zone 3 %DIFN increased especially in the mid to high poplar stand density range, which in turn reduced the slope of the relationships. As a result, at higher stand densities a greater proportion of annual PAR received on the ground would occur during leafless periods of the year (i.e. autumn through until spring). Using the depth of a canopy to vary its density, Wang & Baldocchi (1989) found the same trend under a mixed deciduous oak-hickory stand (*Quercus* and *Carya* spp.). Anderson (1964b) also noted that the more heavily shaded a deciduous forest site was in summer the greater the percentage of the total year's radiation budget was received in spring.

3.5.1.2 Rankings of stand density indices for estimating Zone 3 %DIFN

Out of the stand density indices tested, CCL/NL measured with a standard digital camera had the simplest relationship with Zone 3 %DIFN for both summer and winter periods. CCL/NL consistently had one of the highest adjusted coefficients of determination (r^2) and one of the lowest standard errors of prediction (RMSE) out of the indices tested. In particular, the regression statistics for CCL suggested that the simple linear model fitted was a very good first approximation of the actual relationship, and that any gain in precision by including other independent (explanatory) variables was likely to be negligible. The -1:1 slope of the regression line, along with the intercept not being significantly different from open pasture values, indicated a directly proportional inverse relationship between estimated Zone 3 %DIFN and CCL. Thus, overall, CCL appears to be a very good surrogate of Zone 3 %DIFN across a wide range of poplar stand densities. This result agrees with Buckley *et al.* (1999), who found similar relationships for stands dominated with either deciduous red oak (*Quercus rubra* L.) or evergreen red pine (*Pinus resinosa* Ait.). Nevertheless, there

were notable differences in the methodologies used by the two studies. More specifically, in the study by Buckley *et al.* (1999) light measurements were based on instantaneous quantum-sensor readings taken from a number of different locations for each stand density, and CCL was determined with a concave spherical densiometer.

The relationship between CCNL and Zone 3 %DIFN was more complicated, with the unbalanced nature of the pooled dataset making it difficult to ascertain its general 'true' form. For the pooled data, when going from open pasture to a low CCNL, Zone 3 %DIFN decreased initially at a much slower rate in winter than summer. However, as CCNL continued to increase so too did the rate of decline in Zone 3 %DIFN. This contrasted with the constant (linear) rate of decline found for in summer. Factors contributing to the change in the relationship may have been the less specific absorption of PAR wavelengths by the leafless canopy, and also a greater proportion of diffuse radiation making up global (direct + diffuse) radiation penetrating to the stand floor.

Site differences in the relationship between CCNL and Zone 3 %DIFN caused further complications (Figure 3.8a). At Ballantrae the small nature of the trees (i.e. height, trunk and branch size) resulted in stands having only a very low CCNL and thus they caused little obstruction even when they were closely planted. However, the lack of relationship amongst the trees at Hautope 1 was less easy to explain. Potentially, the boundary trees projecting outwards from the four nuclei trees of each experimental unit at this site may have been more closely and similarly spaced apart. As a consequence, the incoming radiation could have been blocked similarly by the mass of tree trunks collectively visible low on the horizon, while, the trees nearest the point of interest caused little obstruction as they only appeared as narrow tapering columns (Anderson 1964b).

BA, HPCC, and CEV all had very strong relationships with Zone 3 %DIFN in summer (Table 3.3) and moderately strong relationships in winter (Table 3.6). In general, these relationships were either more complicated or their strengths weaker than for CCL/NL (Tables 3.3 & 3.6). It is likely that the same factors influencing the form of the winter relationship for CCNL also caused the relationships for BA, HPCC, and CEV in winter to straighten. Wang & Baldocchi (1989) showed a similar effect to the above when using the

leaf area index (LAI) and woody biomass area index (WBI) of a stand to predict PAR transmission for foliated and non-foliated periods, respectively.

Several researchers for a variety of different tree species have found strong inverse relationships between BA and PAR transmission (Perry *et al.* 1969; Vales & Bunnell 1988; Buckley *et al.* 1999). The BA and LAI of a stand are highly correlated (Buckley *et al.* 1999). Thus, normally the form of the relationship shares similarities with Beer's law (Monsi & Saeki 1953, cited Vales & Bunnell 1988) and contains negative exponential curvature (as shown in Figure 3.4b). However, one notable exception between the assigned regression model for the summer period and Beer's law was that in the former there was no light extinction point. Instead, Zone 3 %DIFN approached a lower asymptote of around 20% (Table 3.3; Figure 3.4b).

Canham *et al.* (1999) noted that since most of the light that reaches a stand floor in summer penetrates through regions of the sky near the zenith, shading would be determined more by the horizontal cross-sectional shape/area of the crown rather than its vertical cross section. This may have been one of the primary reasons why HPCC was strongly related to Zone 3 %DIFN especially over the fully in-leaf summer period (Table 3.3). Kuuluvainen & Pukkala (1987) also showed, using a theoretical model, that differences in the vertical shape of a tree had little effect on the area of shade it produced when the sun was positioned at a high elevation above the horizon. However, Sibbald *et al.* (1994) found that within stands of Sitka spruce (*Picea sitchensis* [Bong.] Carr.) at Scottish latitudes the horizontal component of incident light was more important for understorey pasture production than the vertical component. This would seem logical, as a high proportion of annual pasture production would occur in spring with the sun at a mid-elevation above the horizon. If the vertical component of the canopy was especially important in determining Zone 3 %DIFN then CEV should have provided a stronger relationship, as it takes into account both the horizontal and vertical components of the tree crowns. However, for the in-leaf summer period CEV had a higher RMSE and lower adjusted r^2 than HPCC (Table 3.3); whereas, in the leafless winter period the strength of the relationships for these two independent variables were similar (Table 3.6). This indicates that in the present study the horizontal component of the canopy more strongly influenced Zone 3 %DIFN.

Variation in foliage density per unit of crown volume for the different aged trees (Wang *et al.* 1995) at each site could have caused the marked site differences in the relationship between CEV and Zone 3 %DIFN for in summer (Figure 3.5). Hybrid phenology or environmental stresses (e.g. soil moisture) may also have affected the density of foliage present on the individual tree crowns (Yates & McKennan 1989; Messier *et al.* 1998; Lieffers *et al.* 1999).

When pooled across all four sites DBH, GCL, and HPCD individually were poor to moderate predictors of Zone 3 %DIFN for both summer and winter periods (Tables 3.3 & 3.6). This contrasts with findings by Vales & Bunnell (1988) and Comeau *et al.* (1998) who found that DBH was strongly related to light transmission. These previous studies each related light transmission to DBH through the use of a single exponential decay type curve. Although the work by Vales & Bunnell (1988) was based on a broad range of stand structures, both previous studies were limited to small- to mid-sized trees stocked at a comparatively high rate per hectare. Conversely, in the present study there were large differences in the average size of the trees at each site, especially Ballantrae versus Kiwitea and Hautope 1 (data not shown).

On an individual site basis, under trees of similar size and form, GCL, DBH, and HPCD were all strongly related to Zone 3 %DIFN, as shown for GCL. The general shape (i.e. negative concave curvature) of the relationships were also similar to those presented by Vales & Bunnell (1988) and Comeau *et al.* (1998). Therefore, to improve the assigned regression models quality of fit for the pooled data and to generally make them more robust, another independent variable was likely required to account for the average size/form differences of the trees at each site. Similarly, in investigating the relationship between GCL and understorey pasture production for *Pinus radiata* D.Don stands, Percival *et al.* (1984) and Percival & Knowles (1988) found that the mean GCL per tree was a useful covariate for combining data taken from a number of sites. This covariate became increasingly important as the range of tree ages increased (Percival *et al.* 1984).

Comeau *et al.* (1998) stated that further testing was required to determine if their developed relationship between DBH (*sensu* 'Lorimer's competition index') and PAR transmission for paper birch (*Betula papyrifera* Marsh.) could be generalised to other sites. The results from

this study indicate that the above relationship would be in error if applied to stands containing trees of vastly different average size/form for a given DBH/ha.

Miller (1959, cited Vales & Bunnell 1988) proposed the hypothesis that canopy closure alone would not accurately predict light transmission because it does not take into account crown depth, which also influences light attenuation. However, out of the stand density indices that were tested, CCL/NL measurements centred on Zone 3 were the least affected by site differences likely related to tree size. Pyke & Zamora (1982) and Vales & Bunnell (1988) noted that any estimate of canopy closure made using an instrument with at least a moderate angle of view will include some crown depth and possibly serve as a better integrator of the three dimensional nature of the intercepting surface.

3.5.2 The relationship between stand density indices and Zone 1 %DIFN for summer and winter

3.5.2.1 General relationship

In both summer and winter, as the stand density increased from open pasture to low stand densities there was a more marked decline in PAR transmission (%DIFN) directly below the poplar crowns (Zone 1) than in the vertically projected gap between the crowns (Zone 3). A number of factors likely contributed to the initially more rapid decline in Zone 1 compared to Zone 3 %DIFN. In Zone 1, the tree crown directly overhead, along with the surrounding trees, would obscure a larger portion of the total sky hemisphere. The tree crown directly above Zone 1 in particular would block out the disproportionately brighter region of the sky, which is generally located towards the zenith (Anderson 1964a, 1966). Furthermore, in comparison to Zone 3, a greater proportion of PAR transmitted from in-between the tree crowns to Zone 1 would strike the ground at angles of incidence other than perpendicular to the plane of irradiation, this resulting in the energy received being spread over a larger area, as formalised in Lambert's cosine law (Barnes *et al.* 1997).

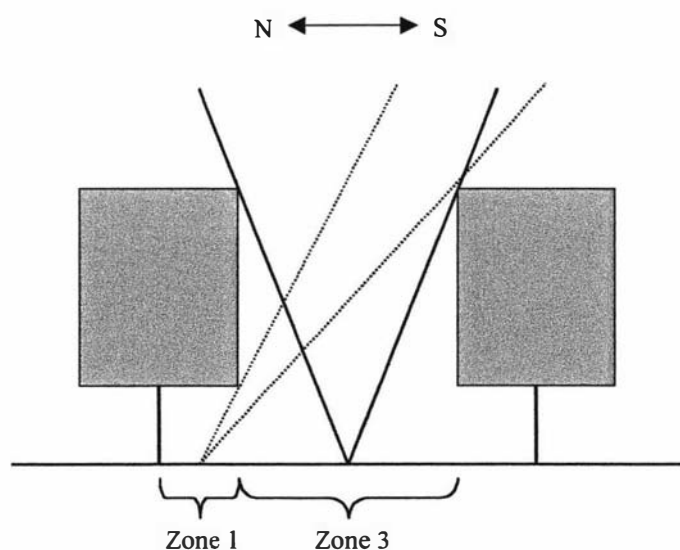


Figure 3.15 Schematic diagram illustrating the smaller angle of sky view seen from Zone 1 and its general skew away from the zenith compared to Zone 3.

Figure 3.15 illustrates the smaller angle of sky view seen from Zone 1 and its general skew away from the zenith. From this figure it is apparent that at low stocking rates, smaller trees with either a greater crown height or less width will increase the angle of sky view seen from Zone 1; the latter two attributes in particular increasing the sky view towards the zenith. A greater crown height relative to total tree height would also reduce crown depth (GCL/stem) and thus the overall path length that light must pass through the canopy. Shorter path lengths usually increase the probability of light passing through the canopy without being intercepted (Hanan & Bégué 1995). Differences in such tree attributes may have caused the significant differences in Zone 1 %DIFN found between the sites in both summer and winter. The aspect and slope of a site would also have influenced the region of sky seen from Zone 1 (Takenaka 1988) and the angle of incidence at which light strikes the ground (Barnes *et al.* 1997).

Variation in the above tree and site attributes would likely affect each of the relationships developed for Zone 1. For example, shorter, thinner, and higher pruned trees would reduce the initial rate of decrease in %DIFN when going from open pasture to low tree stocking rates. Differences in average crown depth may also affect the %DIFN as the stand becomes closed. Therefore, in order to make the developed regression models for Zone 1 more robust and precise, additional independent variables related to the above attributes will likely be required.

Even in their current form, the predicted response for Zone 1 %DIFN compared well with light measurements made by Guevara-Escobar *et al.* (1997) for a mature *Populus x euramericana* stand. Under a stand very similar to at Kiwitea and Hautope 1, with an average BA of 14 m²/ha, PAR transmission was 20% directly below large untended trees. At the same stand density the predicted response was 17% PAR transmission, when using BA as the independent (predictor) variable (Figure 3.7b).

On the other hand, there was considerable variation between field measurements taken by Douglas *et al.* (2001) and the predicted response for Zone 1 %DIFN at an equivalent stand density. Based on the analysis of hemispherical photographs, Douglas *et al.* (2001) estimated that solar irradiance under medium size *Populus maximowiczii* x *P. nigra* trees was 62% and 91% of adjacent open-pasture plots in summer and winter, respectively. The

BA for this study ranged between 2-8 m²/ha. In comparison, the predicted transmission of PAR at the lower end of this BA range for the present study was 55% and 73%, respectively (Figures 3.7b & 3.10b). Differences in phenology between the poplar hybrids and the aforementioned tree and site attributes may have caused the above discrepancies. In addition, Douglas *et al.* (2001) measured total short-wave radiation, which has a higher level of transmission compared to PAR, since it includes a greater range of wavebands not selectively absorbed by the tree leaves (e.g. near-infrared radiation) (Wang & Baldocchi 1989).

Similarly to Zone 3, between summer and winter the relative increase in Zone 1 %DIFN was greater under high compared to low stand densities (Figures 3.7a,b vs. 3.10a,b). As a result, the variation in Zone 1 %DIFN across the range of stand densities was comparatively less in winter. Anderson (1964b) also found that, while the total daily radiation received in the understorey of three deciduous forest sites was very different in summer, there was little difference once the trees lost their leaves in winter. Two of the forest sites had an almost continuous tree canopy, while the other contained a large canopy gap of approximately 20m in diameter (Anderson 1964b). The greater uniformity amongst the three forest sites in winter was attributed to the incoming radiation being blocked similarly by the mass of tree trunks collectively visible low on the horizon, while, the trees nearest the point of interest caused little obstruction as they only appeared as narrow tapering columns (Anderson 1964b).

3.5.2.2 Rankings of stand density indices for estimating Zone 1 %DIFN

For the pooled data of both summer and winter periods the regression models fitted using CCL/NL, BA, HPCC, and CEV as single independent variables accounted for a greater proportion of the variation in Zone 1 %DIFN and had smaller RMSE than those using DBH, GCL, or HPCD (Tables 3.5 & 3.9). However, site differences in the relationships were evident for all of the tested stand density indices, as shown for CCL/NL and BA in Figures 3.7a,b and 3.10a,b. The differences were particularly marked for DBH, GCL, and HPCD as their datasets were generally more balanced. The imbalanced nature of the pooled datasets for CCL/NL, BA, HPCC, and CEV may have contributed to the inconsistency in the form of relationships between the two periods. Generally, as a result of the above

factors no single index was clearly better than any of the others in estimating Zone 1 %DIFN. Further sampling under young/small and old/large trees at high and very low stand densities, respectively, along with the investigation of covariates to account for site differences, is required to strengthen the developed relationships.

3.5.3 Practical considerations

The stand density indices based on physical tree measurements had a number of practical advantages over the digital camera technique. Out of the stand density indices, DBH and BA followed by HPCD and HPCC were the easiest to measure and required minimal equipment. In comparison, the measurement of GCL and CEV generally took longer, especially under large trees, and required more specialised equipment in the form of a measuring pole and hypsometer. All of the above stand density indices can be sampled throughout the year under almost any weather conditions (Comeau *et al.* 1998).

Using a tape measure, tripod, and digital camera, the collection of canopy images was also relatively quick and easy. However, uniformly overcast conditions were needed to optimise contrast between the canopy and sky. This limits the usefulness of the technique in remote locations, where there may be only a narrow ‘window’ of opportunity for gathering data. Furthermore, the digital image analysis can take a considerable amount of time (Englund *et al.* 2000; Brandeis *et al.* 2001), especially if the images were not taken under optimum conditions.

3.5.4 Relationships between the best stand density indices for estimating PAR transmission (%DIFN)

3.5.4.1 Relationship between canopy closure with leaves (CCL) and basal area (BA)

Many researchers have found a strong relationship between the CCL and BA of a stand, for a variety of deciduous and conifer species, and also using a variety of techniques for measuring canopy cover (e.g. spherical densiometers, canopy digital images, etc.). Similar to the relationship developed for the present study (Table 3.10; Figure 3.12c), most take the form of a growth model with an exponential rise to a maximum (upper asymptote) (Mitchell & Popovich 1996; Buckley *et al.* 1999; Knowles *et al.* 1999; McElwee & Knowles 2000).

In Figure 3.16, the data and the predicted response from the present study are compared with functions developed by McElwee & Knowles (2000) and Buckley *et al.* (1999) for deciduous poplar and oak stands, respectively. The study by McElwee & Knowles (2000) encompassed 40 different poplar stands (mainly *P. deltoides* x *P. nigra*) from the Bay of Plenty and East Coast regions of the North Island, New Zealand; while, the study by Buckley *et al.* (1999) was based on even-aged oak stands (dominated by *Q. rubra* L.) located in northern Lower Michigan, USA. Both of the functions developed in these studies were within the 95% prediction limits of the present study's growth model (data not shown). However, in comparison to McElwee & Knowles (2000), the present study's growth model tended to predict a higher CCL for a given BA, especially between 15m²/ha to 25m²/ha (Figure 3.16). The similarity between the function developed by Buckley *et al.* (1999) and the present study was surprising given the innate differences in crown phenology between the two tree species.

There are a number of potential reasons why there was systematic variation between the growth model of McElwee & Knowles (2000) and the present study. The crown-height-to-tree-height ratio (i.e. height ratio⁸) of the respective stands of trees from the two studies may have been markedly different. Generally, stands with greater height ratios for a given BA, have a lower CCL (Knowles *et al.* 1999; McElwee & Knowles 2000). For example, through the pruning of lower branches, Devkota (2000) increased the height ratio of an even-aged and -stocked Italian grey alder (*Alnus chordata*) stand from 0.24 to 0.71, causing CCL to decrease from 89% to 41% (Devkota 2000; Devkota *et al.* 2001). For stands of *P. radiata*, Knowles *et al.* (1999) included the height ratio as an independent variable to take into account the effects of green crown pruning and found it was a significant factor. McElwee & Knowles (2000) also investigated adding the height ratio into their empirical model, but it was not a statistically significant addition. An insufficient range of height ratios may have inhibited the reflection of this effect (McElwee & Knowles 2000).

⁸ Height ratio is defined as the vertical height from ground level to the base of the live tree crown (crown height) divided by the vertical height from ground level to the top of the tree (total height) (Knowles *et al.* 1999; McElwee & Knowles 2000).

The local site conditions may have been important, with environmental stresses, such as a soil moisture deficit, reducing normal leaf area display (Yates & McKennan 1989). Given that similar poplar species and hybrids were sampled in the two studies it is unlikely that variation in individual crown phenology was, at least partially, responsible for differences between the functions describing the relationship between BA and CCL - although this could be a factor when applying the developed functions to newer hybrids.

The different techniques and apparatus used to sample CCL could also have contributed to the variation found between the two studies. Bunnell & Vales (1990) reported that from a common point in a forest understorey, techniques/apparatus that measure a wider angle of view of the upward sky-hemisphere gave a higher estimate of canopy closure (*sensu* crown completeness), with less variation around the mean. In general, the difference was greater under low CCLs (Bunnell & Vales 1990). Similarly, underexposing canopy photographs causes an increase in the estimate of CCL (Vales & Bunnell 1988; Chen *et al.* 1991).

Frazer *et al.* (2001) found that differences in the resolution of digital-images of dense overstorey canopies have a small effect on the estimate of CCL (<5% difference). In comparison, the subjectivity involved in techniques used to visually separate canopy and sky pixels of digital-images could be a greater source of error (Machado & Reich 1999; Englund *et al.* 2000). Several researchers have repeated the processing and analysis of each image several times to reduce this potential error (McKennan 1995; Gendron *et al.* 1998; Englund *et al.* 2000; Frazer *et al.* 2001).

Overall, the above factors indicate that any future model development of the relationship between CCL and BA should include the average height ratio of individual trees as an independent variable to make the function more robust in regards to common silvicultural management practices. In addition, the methodology for taking digital canopy-images (e.g. lens field of view & image exposure) and image analysis (e.g. repeated analyses) needs to be standardised to reduce the error incurred when estimating CCL/NL.

3.5.4.2 Relationship between canopy closure with (CCL) and without leaves (CCNL)

The clear site differences between Ballantrae and the other three sites for the relationship between CCL and CCNL indicated that at least some other unaccounted factor was significantly influencing the relationship (Figure 3.12a; Table 3.10). It is uncertain what factor or factors may have influenced this relationship, but obvious differences were the trees at Ballantrae were less than one-fifth the age and had a height ratio two to five times greater than at the other sites (Table 2.1). A young tree would have considerably less woody biomass area index (WBI) associated with its main stem and branches (Scanlan 1991; Wang *et al.* 1995); while, a greater height ratio would reduce the WBI associated with branches and reduce the depth of the canopy. Based on a simple linear function forced through the origin, McElwee & Knowles (2000) estimated that CCNL was 31% of CCL. In comparison, when the simple linear functions for the young (Ballantrae) and mature (Kiwitea & Hautope) stands were also forced through the origin CCNL was 7% and 55% of CCL, respectively (Figure 3.17). It is difficult to speculate whether the differences in slope between these functions were due to the above aforementioned factors, as McElwee & Knowles (2000) did not disclose the specific age or height ratio of the stands used for developing their simple linear relationship.

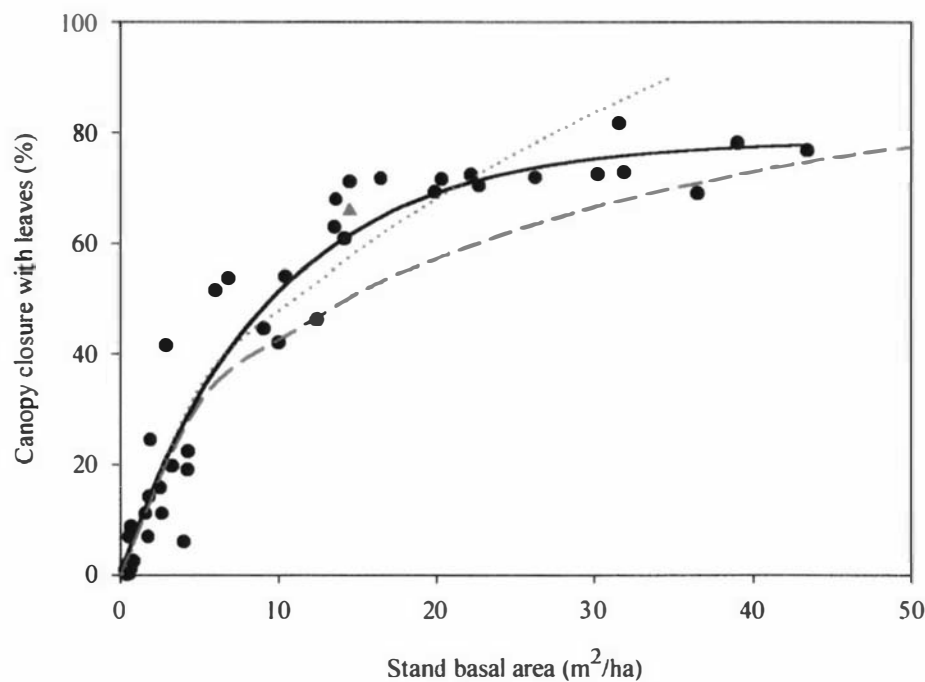


Figure 3.16 Relationships between in-leaf canopy closure (CCL) and basal area (BA). Symbols: (—●—) data points and predicted response from the present study, (▲) data point for a single poplar stand (Guevara-Escobar 1999), predicted response for a range of (---) poplar (McElwee & Knowles 2000) and (.....) red oak stands (Buckley *et al.* 1999).

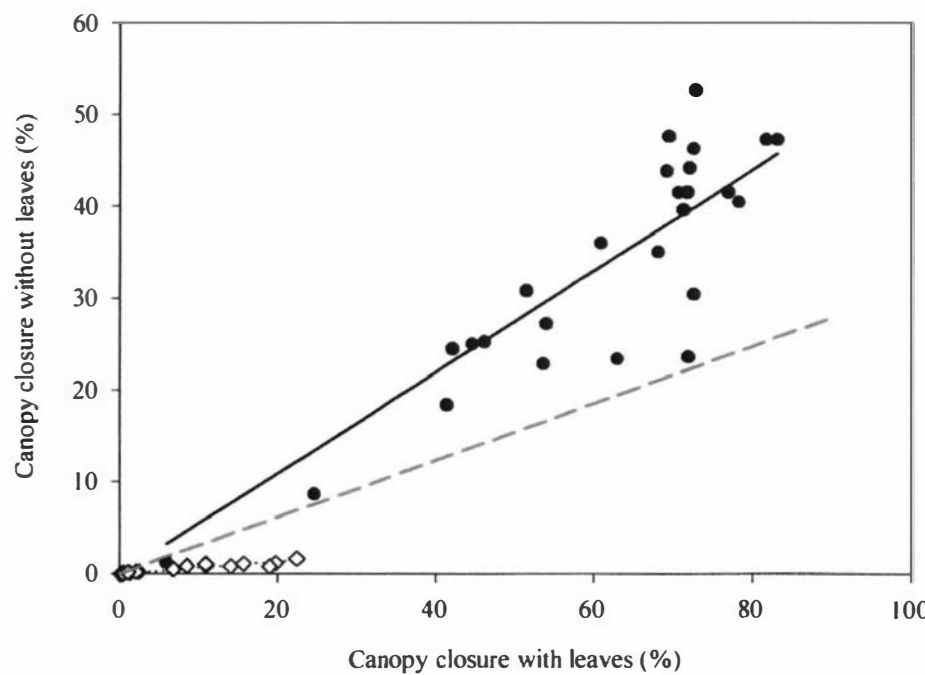


Figure 3.17 Comparison of relationships between no-leaf canopy closure (CCNL) and in-leaf canopy closure (CCL). Symbols: (—●—) mature (Kiwitea & Hautope) and (—◇—) young stands (Ballantrae), and (—) predicted response for a range of poplar stands from McElwee & Knowles (2000).

3.5.5 Stand level %DIFN across a range of canopy closure ratios in summer and winter.

Similar to the summer relationship derived in the present study, Vales & Bunnell (1988), Barnes *et al.* (1997), and Buckley *et al.* (1999) also reported strong inverse relationships between CCL and PAR transmission. The relationships given by Vales & Bunnell (1988) and Barnes *et al.* (1997) for conifer tree species contained negative curvature, with the slope decreasing towards higher CCLs. This contrasted with Buckley *et al.* (1999) who found a negative 1:1 linear relationship for both deciduous and conifer species. The sampling methods used (Anderson 1964b; Vales & Bunnell 1988; Englund *et al.* 2000) and structure of the stands (Barnes *et al.* 1997) could have caused the differences in the form of the above relationships.

Parallel with Zone 3 %DIFN in winter, it is likely that less specific absorption of PAR wavelengths by the woody biomass and greater downward reflection of incident light at low CCNLs caused the relationship for weighted %DIFN to change shape from being concave to convex (Figure 3.13a,b). Overall, both the summer and winter relationships for weighted %DIFN compared well with single density measurements previously taken under the closed canopies of various deciduous tree species (Table 3.13). Nevertheless, further sampling under young/small and old/large trees at high and very low stand densities, respectively, and especially covering the range between 10-40% CCL, would clearly strengthen the developed relationships for weighted %DIFN.

Table 3.13 Light transmission through various closed stands of deciduous trees.

Source	Genus	BA	Total Height	Light transmission (%)	
		(m ² /ha)	(m)	Summer	Winter
Hughes <i>et al.</i> (1985)	<i>Quercus</i>	47	18	10	55
Messier <i>et al.</i> (1998)	<i>Populus</i>	33	20	10	-
	<i>Betula</i>	21	17	14	-
Chen <i>et al.</i> (1997)	<i>Populus</i>	26	21	26	55
Carlson & Groot (1997) [†]	<i>Populus</i>	36	19	18	-
Mourelle <i>et al.</i> (2001)	<i>Populus</i>	-	17	15	-
Reifsnyder <i>et al.</i> (1971/72) [†]	Mixed hardwood	18	-	9	-
Wang & Baldocchi (1989)	<i>Quercus</i> & <i>Carya</i>	-	21	-	60

[†]Light transmission was measured using pyranometers, which measure a wider range of short-wave radiation wavelengths compared to quantum sensors. Given that leaves preferentially absorb PAR over near-infrared radiation wavelengths the above transmission values would likely be an overestimate of PAR transmission. In the study by Reifsnyder *et al.* (1971/72) maple were the dominant species, along with a considerable admixture of oak and ash.

3.5.6 Potential error incurred through using %DIFN measurements

A number of researchers have voiced concerns about using instantaneous measurements, such as %DIFN, to characterise seasonal PAR transmission levels (Anderson 1964a,b; Gay *et al.* 1971; Hutchison & Matt 1977b; Canham 1988; Canham *et al.* 1990; Stadt *et al.* 1997; Tang *et al.* 1999). The measurement of only diffuse short-wave radiation expressed as a percentage of open conditions (e.g. %DIFN) can mask important features of spatial and temporal variation in global (diffuse + direct) short-wave radiation below a stand of trees (Anderson 1964b; Gay *et al.* 1971).

Due to scattering in the atmosphere diffuse radiation emanates from the sky hemisphere rather similarly from all compass directions (azimuths) with its brightness distribution increasing from a minimum at the horizon to a maximum at the zenith (Hutchison & Matt 1976; Stadt *et al.* 1997). As a result, within an inter-tree gap the general pattern of diffuse radiation tends to be quite uniform/symmetrical with the greatest level at the centre, roughly decreasing at a similar rate in all directions towards the gap edge and beyond (Takenaka 1988; Canham *et al.* 1990; Runkle *et al.* 1995).

In contrast, outside of the tropics large diurnal and seasonal changes in the apparent position of the sun (solar disk) causes direct-beam radiation to have a much more varied asymmetrical distribution. For example, at New Zealand's temperate latitude the sun never actually passes directly overhead, but instead during the course of a day appears to cross from east to west in the northern part of the sky (Sturman & Tapper 1996). As a consequence of the sun's angle with the ground considerably more direct-beam radiation is often transmitted to understorey areas adjacent to the sun (north⁹) facing edges of either widely spaced trees or large canopy gaps compared to opposite understorey areas adjacent to shade (south) facing edges. Yet both have a similar sky view and thus receive roughly equal amounts of diffuse radiation (Sibbald & Griffiths 1992; Runkle *et al.* 1995; Stadt *et al.* 1997; Douglas *et al.* 2001). Therefore, by measuring only diffuse radiation spatially amongst stands with large inter-tree gaps global (diffuse plus direct) radiation transmission will likely be under- and overestimated in some areas (Lieffers *et al.* 1999).

The extent of the above skewed north-south gradient varies with the sun's elevation above the horizon, but also depends on the inter-tree gap configuration relative to tree size/form, cloud cover, and the topography of the site (Canham 1988; Takenaka 1988; Sibbald & Griffiths 1992; Canham *et al.* 1990; Lieffers *et al.* 1999). Even though the latitude of the four sampled sites was generally similar, and thus so was the solar track across the sky, the latter factors varied considerably. At Kiwitea and Hautope 2 the steep north-facing hillsides that the stands of trees were situated on would likely have allowed direct-beam radiation to penetrate inter-tree gaps at an angle much closer to perpendicular to the ground than at Ballantrae and Hautope 1 reducing the skewed distribution (especially around the summer solstice). Table 3.14 shows that during the growing season direct-beam radiation must generally pass through gaps in the tree crowns to reach their base at Kiwitea and Hautope 2, while the shadow length produced by the same trees is much smaller than for the other two sites.

⁹ In Northern Hemisphere latitudes outside of the tropics (>23.5°N) it is the opposite way around with the sun facing edges southward (Poulson & Platt 1989; Canham *et al.* 1990; Runkle *et al.* 1995).

Table 3.14 Maximum solar angle[‡] above the horizon allowing direct-beam radiation to pass below the crown of an average sized tree to its base and also the shadow length produced by the same tree.

Season	Time	Solar elevation (degrees)	Shadow length as a proportion of crown radius			
			Kiwitea	Hautope 1	Hautope 2	Ballantrae
Autumn/spring equinox	morn./after. [†]	22.5	9.9	13.0	10.7	17.5
	noon	50.0	2.7	6.9	2.9	6.1
Summer solstice	morn./after.	37.4	5.4	7.1	5.8	9.5
	noon	73.4	1.2	1.9	1.3	2.2
Winter solstice	morn./after.	5.5	42.6	56.0	46.2	75.2
	noon	26.6	4.5	42.0	4.9	14.5
Crown radius (m)			7.3	4.6	3.0	1.0
‡ Max. angle (degrees)			21.7	49.6	36.2	74.5

[†]Morning and afternoon times were taken as 4 hours either side of solar noon. Formulas for determining the solar elevation and shadow lengths were obtained from Takenaka (1988), Sturman & Tapper (1996), and Ban *et al.* (1998). Latitude was assumed to be 40°S for all sites. Average crown height/radius ratio at Kiwitea, Hautope 1, Hautope 2, and Ballantrae was 0.4, 1.2, 0.7, and 3.6, respectively. Ground slope for morning/afternoon was assumed to be 0°, while at noon slopes were 28°N, 20°S, 27°N, and 0°N for Kiwitea, Hautope 1, Hautope 2, and Ballantrae, respectively. Dates for autumn/spring (vernal) equinox, summer and winter solstices were: 21 March / 22 September, 21 December, and 21 June, respectively (Sturman & Tapper 1996). It should also be noted that radiation hitting the ground at angles other than perpendicular to the plane of irradiance is distributed over a greater area, causing the amount of energy received per unit area to be less (Lambert's cosine law). Thus, at low angles of incidence, the intensity of direct-beam radiation will be considerable less than at higher angles (Barnes *et al.* 1997).

Nevertheless, several other researchers have shown that single point-in-time measures of solely diffuse radiation can provide a very good estimate of mean daily or seasonal global PAR transmission (Washitani & Tang 1991; Hanan & Bégué 1995; Messier & Puttonen 1995; Parent & Messier 1996; Comeau *et al.* 1998; Gendron *et al.* 1998; Machado & Reich 1999). These studies spanned a wide range of stand types, including both homogenous and heterogeneous canopies, and measurements were taken from a number of different microsites. In fact, Comeau *et al.* (1998), Gendron *et al.* (1998), and Machado & Reich (1999) reported that for estimating global PAR transmission diffuse radiation methods including %DIFN were as good as hemispherical (fisheye) photography, which does take into account changes in solar elevation.

3.5.7 The relationship between R:FR and %DIFN

3.5.7.1 Under a fully in-leaf poplar canopy in summer

As shown in Figure 3.14a, the red to far-red ratio (R:FR) decreased from open pasture values at an increasing rate as the transmission of PAR (%DIFN) through the poplar canopy declined. This relationship shared similarities with the idealised relationships postulated by Lieffers *et al.* (1999) for deciduous and coniferous dominated stands. Both of the above empirical and idealised relationships showed marked decreases in the R:FR below a PAR transmission level of about 40%. Within the vertically projected gap between the poplar crowns (Zone 3), estimated PAR transmission (%DIFN) was lower than 40% at a canopy closure >58% (Figure 3.4a); whereas, directly below the crowns (Zone 1) of the mature unpruned trees at Hautope and especially Kiwitea this critical point was surpassed over the entire range of canopy closures (Figure 3.7a). Conversely, at Ballantrae the %DIFN underneath the crowns (Zone 1) of the young pruned trees did not fall below 65% (Figure 3.7a); and as a result would have lessened the magnitude of variation in R:FR across the tree-gap continuum.

In the idealised relationships of Lieffers *et al.* (1999) the R:FR reached a maximum at around 40% light transmission and thereafter remained relatively constant. This contrasted with the logarithmic relationship developed in the present study, which did not reach a maximum until 100% PAR transmission (Figure 3.14a). Similarly, Ritchie (1997) measured a logarithmic increase in the R:FR with decreasing plant density based on a greenhouse experiment using Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco.) seedlings, which were systematically spaced apart in a miniature “Nelder” (Nelder 1962) design.

A number of previous studies, which measured the light environment under clear sky conditions and allowed data points to be converted to values relative to the open pasture, fitted the developed relationship well (Figure 3.18). The good fit of Ross *et al.* (1986) and Messier *et al.* (1989) data from coniferous stands was inconsistent to that of other researchers who have found differences in the spectral absorbance characteristics between broadleaf and conifer species (Coombe 1957; Federer & Tanner 1966; Vézina & Boulter 1966; Tasker & Smith 1977; Morgan & Smith 1981). In general, the light spectrum under conifers tends to be more uniform, with a greater intensity of blue light (455-500 nm) and a

lower intensity of infrared (>700 nm) light on clear days compared to under broadleaf species (Federer & Tanner 1966; Morgan & Smith 1981; Smith 1982). However, in more recent studies by Ross *et al.* (1986) and Endler (1993) little difference in the attenuation of various light spectra, including the R:FR, were found between these two broad groups. Some of the variation observed among the studies in Figure 3.18 could have been the consequence of different sampling/measurement techniques (Smith 1982; Morgan *et al.* 1985). In particular, atmospheric conditions (e.g. the degree of cloud cover) at the time of measurement can have a marked effect on the understorey R:FR (Morgan *et al.* 1985; Messier *et al.* 1989; Messier & Puttonen 1995; Lieffers *et al.* 1999; Reitmayer *et al.* 2002). Overall, confirmation of the appropriateness of the assigned logarithmic relationship using previously published research was hindered by their lack of data points above 40% PAR transmission (Figure 3.18).

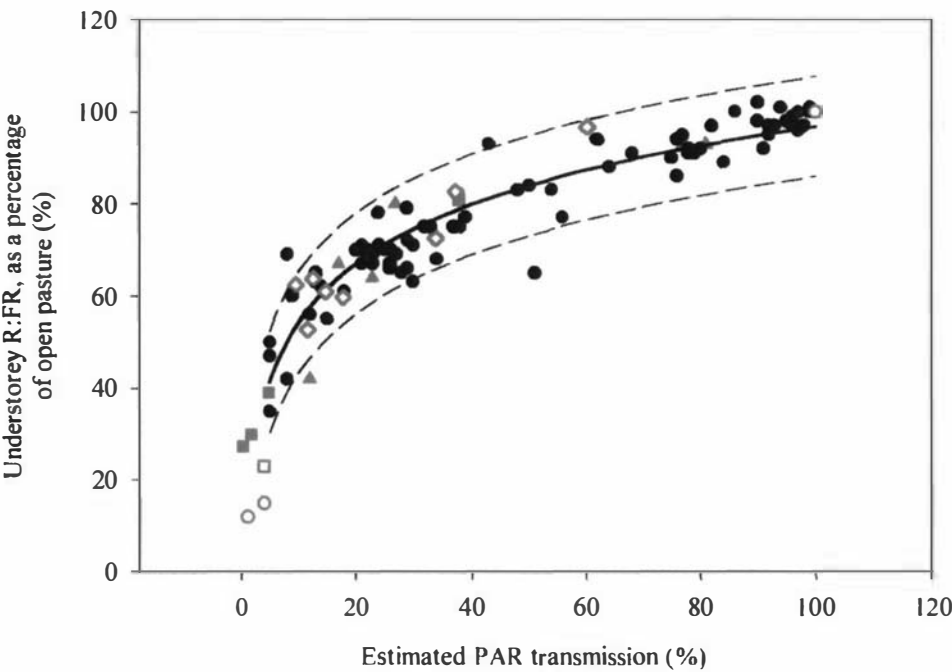


Figure 3.18 Comparison of the developed relationship between R:FR and estimated PAR transmission with data from other sources. Symbol: (●) present study, (□) Morgan & Smith (1981), (○) Ross *et al.* (1986), (○) Messier & Bellefleur (1988), (■) Messier *et al.* (1989), (▲) Devkota (2000). All of the R:FR measurements were taken under predominantly clear sky conditions, except for the present study, where measurements were taken under a range of atmospheric conditions. The sky conditions in the study by Morgan & Smith (1981) were not specified. Solid line – mean predicted response from the present study; dashed lines - upper and lower 95% prediction limits.

Under forest stands dominated by deciduous trees, Tasker & Smith (1977), Pons (1983), Hughes *et al.* (1985), and Ross *et al.* (1986) all measured marked decreases in the average R:FR with leaf emergence in spring. Thereafter, the R:FR remained relatively stable over the main growing season until leaf senescence began in autumn. Nevertheless, similar to PAR transmission, over the course of a single day there may be considerable variation in the R:FR at any point on the ground, especially under open stands during clear-sky conditions (Ross *et al.* 1986; Turnbull & Yates 1993; Messier & Puttonen 1995; Reitmayer *et al.* 2002). As discussed in Section 3.5.5, this temporal variation is caused by interactions between the changing sun-angle relative to the ground, stand biomass distribution, and cloud cover (Endler 1993; Messier & Puttonen 1995; Reitmayer *et al.* 2002). Single point-in-time measurements, such as those used in the present study, cannot take into account such variation (Anderson 1964a,b). As a result, this may limit the applicability of the developed relationships in this study to certain understorey plant responses where the time scale over which the variation in the R:FR occurs is important (e.g. phytochrome-mediated responses). Conversely, the light environment below a closed canopy tends to be much more uniform over time (Ross *et al.* 1986; Turnbull & Yates 1993).

3.5.7.2 Under a leafless poplar canopy in winter.

In contrast to summer (Figure 3.14a), as the percentage of PAR transmitted through the leafless poplar canopy in winter decreased, there was correspondingly a much smaller and more constant rate of decrease in the R:FR (Figures 3.14b). With all of Hautope 1's data points clumped at lower estimated PAR transmission (%DIFN) levels away from the other sites (Figure 3.14b), it is difficult to distinguish whether the pooled trend is significant or simply an artefact of variation between the sites. Regardless, the scatter of data points in Figure 3.14b show that without spectrally selective absorbing leaves the poplar overstorey has relatively little effect on the understorey R:FR, irrespective of stand density. The decrease in the impact of the overstorey may actually start to occur prior to leaf fall through chlorophyll degradation of the senescencing leaves (Ross *et al.* 1986). Hughes *et al.* (1985) found that under a deciduous oak (*Q. robur* L.) canopy, transmitted light was spectrally neutral (unaltered) after leaf fall in autumn and remained so up until bud break in the following spring. During the non-foliated period the R:FR remained close to unity under the oak canopy (Hughes *et al.* 1985).

3.5.8 The ecological significance of changes in the understorey light environment for pasture plants.

Decreases in PAR and the R:FR ratio under a poplar stand can have a number of effects on understorey pastures. With PAR wavelengths being directly involved in photosynthesis, a decrease in transmission through the tree canopy normally leads to a reduction in pasture carbohydrate and net dry matter (DM) production compared to in open pastures (Seo *et al.* 1989; Wong & Stür 1996; Devkota *et al.* 1997; Sanderson *et al.* 1997). However, the reduction is not always in proportion to the decrease in PAR as plants can make compensatory changes (adaptations) in their morphology and physiology, which help to increase light interception and enhance the efficiency of carbon use in both photosynthesis and respiration (Ludlow *et al.* 1974; Corré 1983a; Assmann 1992; Sanderson *et al.* 1997; Wilson 1997; Healey *et al.* 1998). Nevertheless, below some critical threshold, even the above adaptations cannot compensate for the overall lower level of incident PAR reaching the plant, this resulting in decreased growth and development (Ludlow *et al.* 1974; Corré 1983a; Stuefer & Huber 1998). Conversely, several researchers have found that a change in the R:FR ratio of incident PAR does not directly influence the total aboveground DM production of individual pasture plants (Casal *et al.* 1985; Deregibus *et al.* 1985; Heraut-Bron *et al.* 1999; Devkota 2000).

Combining the developed PAR transmission curves from Sections 3.4 with pasture production data given by Devkota *et al.* (1997) provides an initial estimate of the likely shape of the understorey pasture response to changes in the density of the poplar overstorey (Figure 3.19a,b). It is important to note that the pasture production data of Devkota *et al.* (1997) come from a glasshouse experiment, which used a range of spectrally neutral¹⁰ shade cloth densities (each providing a constant level of shade) to vary the intensity of PAR, and that soil nutrients and water were non-limiting for plant growth. Based on Figure 3.19a, pasture DM production in Zone 3 would decrease at a constant rate (i.e. linearly) with increasing CCL. In contrast, pasture production decreases initially at a much faster rate in Zone 1 than Zone 3, but thereafter falls at a diminishing rate. As discussed in Section 3.5.2.1 for PAR transmission directly below the poplar crowns (Zone 1 DIFN%), reducing the crown depth and width of the individual trees (via pruning and species selection,

respectively) would likely reduce the degree of negative curvature of the pasture production response. However, as the canopy becomes more uniformly closed both zones of tree influence approach similar rates of production regardless of the individual crown dimensions. The extinction point for pasture production in Figure 3.19a was at 85% CCL, which is the same as visual estimates made in the field by McElwee & Knowles (2000), and considerably higher than the 67% CCL estimated for *P. radiata* agroforestry (Knowles *et al.* 1999; McElwee & Knowles 2000).

The general shape of the pasture production response estimated for the two main zones of tree influence for the winter period was comparable to summer (Figures 3.19a,b). However, given that the maximum CCNL did not block more than 50% of the sky-hemisphere, pasture dry matter production was not estimated to fall below a similar value (Figure 3.19b).

¹⁰ Transmission of PAR through the shade cloth did not alter the R:FR from that measured in full sunlight.

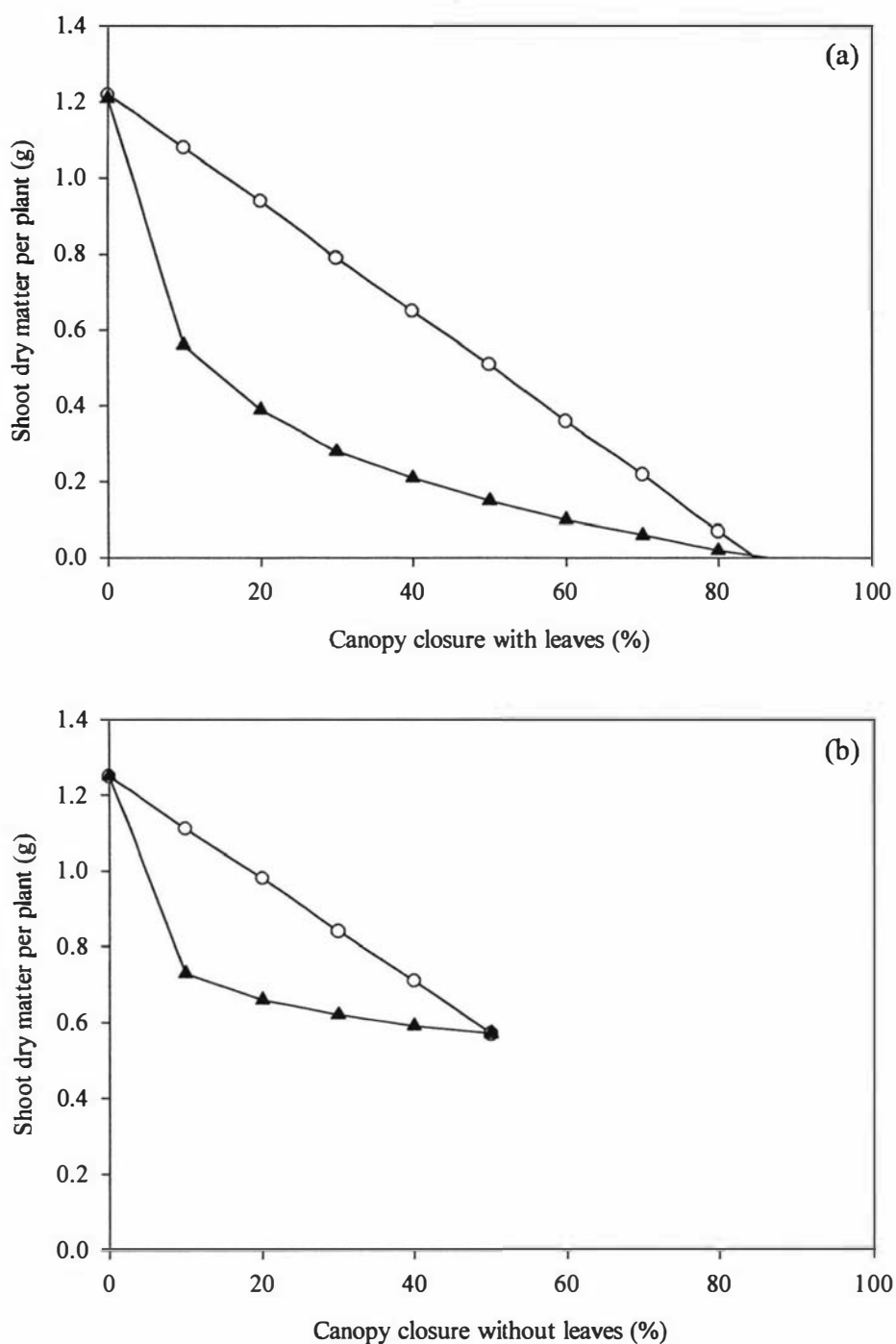


Figure 3.19 Estimated pasture dry matter production (○) at the centre of a vertically projected canopy gap (Zone 3) and (▲) directly below the poplar crowns (Zone 1), over a range of stand canopy closure ratios in (a) summer and (b) winter. The linear and non-linear relationships relating PAR transmission in the two main zones of tree influence (i.e. Zones 1 & 3) to stand canopy closure are given in Section 3.4; whereas, the linear relationships between pasture production and PAR transmission are given in Devkota *et al.* (1997). For the latter, spectrally neutral shade cloth was used to vary the PAR transmission levels under glasshouse conditions; soil nutrients and water were non-limiting (Devkota *et al.* 1997). The botanical species composition for the above relationships was assumed to be 70% perennial ryegrass (*Lolium perenne*) and 30% white clover (*Trifolium repens*).

In general, plant morphology is more affected by changes in the intensity of PAR rather than the R:FR ratio (Lee *et al.* 1996; Lieffers *et al.* 1999; Devkota 2000). Typical responses to reduced levels of PAR in the range of tree-shade include: an increase in leaf area ratio¹¹ (Ludlow *et al.* 1974; Corré 1983a,b; Kephart *et al.* 1992) and specific leaf area¹² (Corré 1983a,b; Samarakoon *et al.* 1990; Devkota *et al.* 1997; Meziane & Shipley 1999); leaf and petiole elongation in grasses (Taylor *et al.* 1968; Wong & Wilson 1980; Sanderson *et al.* 1997) and legumes (Solangaarachchi & Harper 1987; Stuefer & Huber 1998); and a decrease in tiller/branch appearance (Ludlow *et al.* 1974; Wong & Stür 1996; Devkota *et al.* 1997; Gautier *et al.* 1999) and root biomass (Corré 1983a; Eriksen & Whitney 1981; Samarakoon *et al.* 1990; Wilson 1996). Overall, these changes generally produce more open (less dense) and etiolated understorey pastures, with higher shoot-to-root ratios than in the open (Wong & Wilson 1980; Eriksen & Whitney 1981). A reduction in the R:FR can also cause similar morphological responses (Casal *et al.* 1985, 1987b; Solangaarachchi & Harper 1987; Thompson 1993; Sanderson *et al.* 1997). However, the responses tend to be more related to changes that enable plants to physically avoid impending shade (or alternatively, “forage for light”) at the expense of leaf area development (Smith 1982; Corré 1983b; Schmitt & Wulff 1993; Heraut-Bron *et al.* 1999). Regardless of the R:FR ratio, under very low PAR intensities, compensatory changes in plant morphology will be inhibited through restricted carbon nutrition (Morgan & Smith 1981; Casal *et al.* 1986; Messier *et al.* 1989; Stuefer & Huber 1998; Heraut-Bron *et al.* 1999).

Again, combining the developed PAR transmission curves with pasture production data given by Devkota *et al.* (1997) provides an initial estimate of the likely shape of the understorey pasture response in tillering/branching to changes in overstorey tree density (Figure 3.20a,b). Within the vertically projected canopy gap (Zone 3) the relationship between tiller/branch production and CCL was more convex in shape compared to the linear response shown for DM production (Figure 3.19a,b vs. 3.20a,b). Directly below the poplar crowns (Zone 1), on the other hand, had a similar shaped response for both attributes (Figure 3.19a,b vs. 3.20a,b). According to the simplified model developed, tiller/branch

¹¹ Leaf area ratio (LAR) is the amount of leaf area displayed per unit of total plant biomass (m²/kg plant DM).

¹² Specific leaf area (SLA) is the leaf area per unit of leaf weight (cm²/g DM).

production in the perennial ryegrass/white clover sward would cease at around 85% CCL in summer (Figure 3.20a). This contrasted with only a 30% reduction from open pasture levels at maximum canopy closure (52% CCNL) under the leafless poplars in winter (Figure 3.20b).

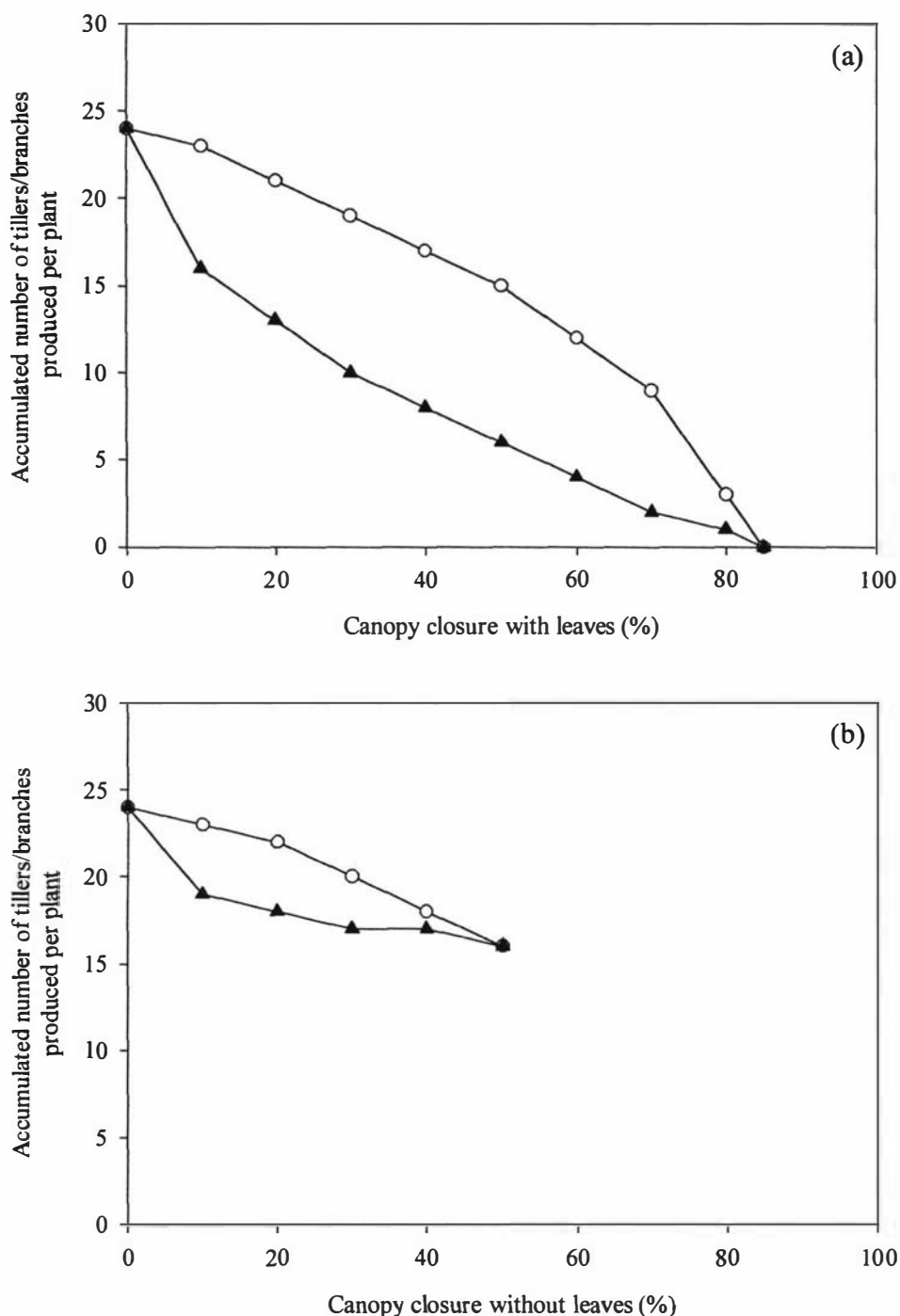


Figure 3.20 Estimated tillering/branching (○) at the centre of a vertically projected canopy gap (Zone 3) and (▲) directly below the poplar crowns (Zone 1), over a range of stand canopy closure ratios in (a) summer and (b) winter. The linear and non-linear relationships relating PAR transmission in the two main zones of tree influence (i.e. Zones 1 & 3) to stand canopy closure are given in Section 4.4; whereas, the relationships between tillers/branches and PAR transmission were derived from data given in Devkota *et al.* (1997). For the latter, spectrally neutral shade cloth was used to vary the PAR transmission levels under glasshouse conditions; soil nutrients and water were non-limiting (Devkota *et al.* 1997). The botanical species composition for the above relationships was assumed to be 70% perennial ryegrass (*Lolium perenne*) and 30% white clover (*Trifolium repens*).

Solangaarachchi & Harper (1987), Gautier *et al.* (1999), and Devkota (2000) have all reported that a concomitant decrease in the R:FR enhances the effect of reduced PAR on tillering/branching. In the glasshouse experiment of Devkota *et al.* (1997) the R:FR was held constant at around that measured in open pastures, irrespective of the actual shade level. Therefore, in the developed relationships for summer, when the trees were fully in-leaf (Figure 3.20a), the rate of decline in tillering/branching would probably be underestimated over certain parts of the curves. A small reduction in the R:FR of incident light has been shown to cause marked changes in the morphology of some plant species (Smith 1982; Casal *et al.* 1986; Teuber & Laidlaw 1996). For example, Casal *et al.* (1987a) measured a strong decrease in the tillering of *Lolium multiflorum* resulting from a small reduction in the R:FR below values typical of full sunlight.

There are a number of other factors that can also influence the response of understorey pastures to decreases in the level of PAR and R:FR ratio. The extent of changes in sward structure and total dry matter production under tree-shade will depend on the botanical species composition of the pasture (Figure 3.21a,b). This is because there is considerable variation in shade tolerance and potential yield amongst and within different pasture species (Solangaarachchi & Harper 1987; Skálová & Krahulec 1992; Devkota *et al.* 1997, 1998; Naumburg *et al.* 2001). Shade tolerant ('shade') plants usually have lower growth rates in full sunlight, but in comparison to their shade intolerant ('sun') counterparts can maintain dry matter (DM) production closer to their maximum potential yields under reduced levels of PAR (Figure 3.21a,b) (Boardman 1977; Björkman 1981; Corré 1983b; Devkota *et al.* 1997; Reich *et al.* 1998; Naumburg *et al.* 2001). In relation to changes in plant morphology, shade intolerant species are normally more sensitive (or show greater plasticity) to small-to-moderate decreases in the intensity of PAR and R:FR below open habitat values (Corré 1983a,b; Devkota *et al.* 1997; Wilson 1997; Devkota 2000); typical responses include allocating a greater proportion of assimilates to organs that help move the plant's photosynthetic area into more favourable light conditions (Smith 1982; Corré 1983b). In contrast, shade tolerant species are less plastic, except when under very heavy shade (Devkota *et al.* 1997), and respond mainly to decreases in the intensity of PAR (Smith 1982; Corré 1983b; Caldwell 1987) by allocating a greater proportion of assimilates into the development or maintenance of leaf area (Wong *et al.* 1985; Naumburg *et al.* 2001).

Nevertheless, there are exceptions to the above generalisations (Corré 1983b; Naumburg *et al.* 2001).

The effect of shade on understorey pasture growth can also depend on the stage of phenological development of the plants. Based on a glasshouse experiment using five grass species native to Arizona *Pinus ponderosa* forests, Naumburg *et al.* (2001) showed that a reduction in net assimilation rate (NAR) with increasing shade was greater for grasses when they were shifting to reproductive growth, compared to at flowering. In addition, shading slowed flower development for the naturally late flowering species by bringing forward the onset of reproductive growth with a similar or later date of actual flower emergence (Naumburg *et al.* 2001).

Simply describing PAR and the R:FR relative to open pasture values can be misleading, as it is the daily integral of these factors (in absolute values of moles photons m^{-2}) that determines plant growth and morphology (Wilson & Ludlow 1991; Wilson 1997; McKenzie *et al.* 1999). For example, in tropical and temperate climates the intensity of PAR in summer usually greatly exceeds the photosynthetic capacity of open pasture plants. Thus, even under moderate levels of shade the intensity of PAR may still actually exceed, or at least be near, the understorey plant's maximum photosynthetic capacity, causing little effect on growth and development. However, in winter the intensity of PAR in the open is normally much lower than in summer (often less than half the average daily total), which means that a similar level of shade in this season would likely have a much more pronounced impact on the understorey plants (Wilson 1997). Furthermore, relative values based on single point-in-time measurements disguise important temporal variation in the understorey light environment (Anderson 1964a,b), including sunfleck activity, which can have a significant impact on plant growth and development (Chazdon 1988; Chazdon & Pearcy 1991; Washitani & Tang 1991; Wayne & Bazzaz 1993; Healey *et al.* 1998; Tang *et al.* 1999). Studies using shade cloth to vary the intensity of PAR also ignore the potential effects of sunflecks (Turnbull & Yates 1993; Lee *et al.* 1996).

Soil fertility, water availability, and temperature also influence the response of pastures to changes in the level of light (Alberda 1965; Eriksen & Whitney 1981; Corré 1983c; Sanderson *et al.* 1997; Meziane & Shipley 1999). Under soil nutrient, water, or low

temperature stress, a plant's photosynthetic response curve shows full saturation (or reaches its maximum) at a lower level of light compared to when these abiotic factors are non-limiting for plant growth and development (Alberda 1965; Wilson 1997). As a result, a moderate decrease in the level of PAR from open pasture values may have little impact on plant growth and development when other abiotic factors are more limiting. This was shown in an experiment by Blackman & Templeman (1938, cited Eriksen & Whitney 1981), where under low soil nitrogen (N) levels the dry matter production of *Agrostis capillaris* and *Festuca rubra* was unaffected by up to 39% and 56% shade, respectively. In situations where the tree canopy improves the above abiotic factors, it is even possible to increase understorey photosynthesis over open conditions in full sunlight (Wong & Wilson 1980; Wild *et al.* 1993; Wilson 1996, 1997).

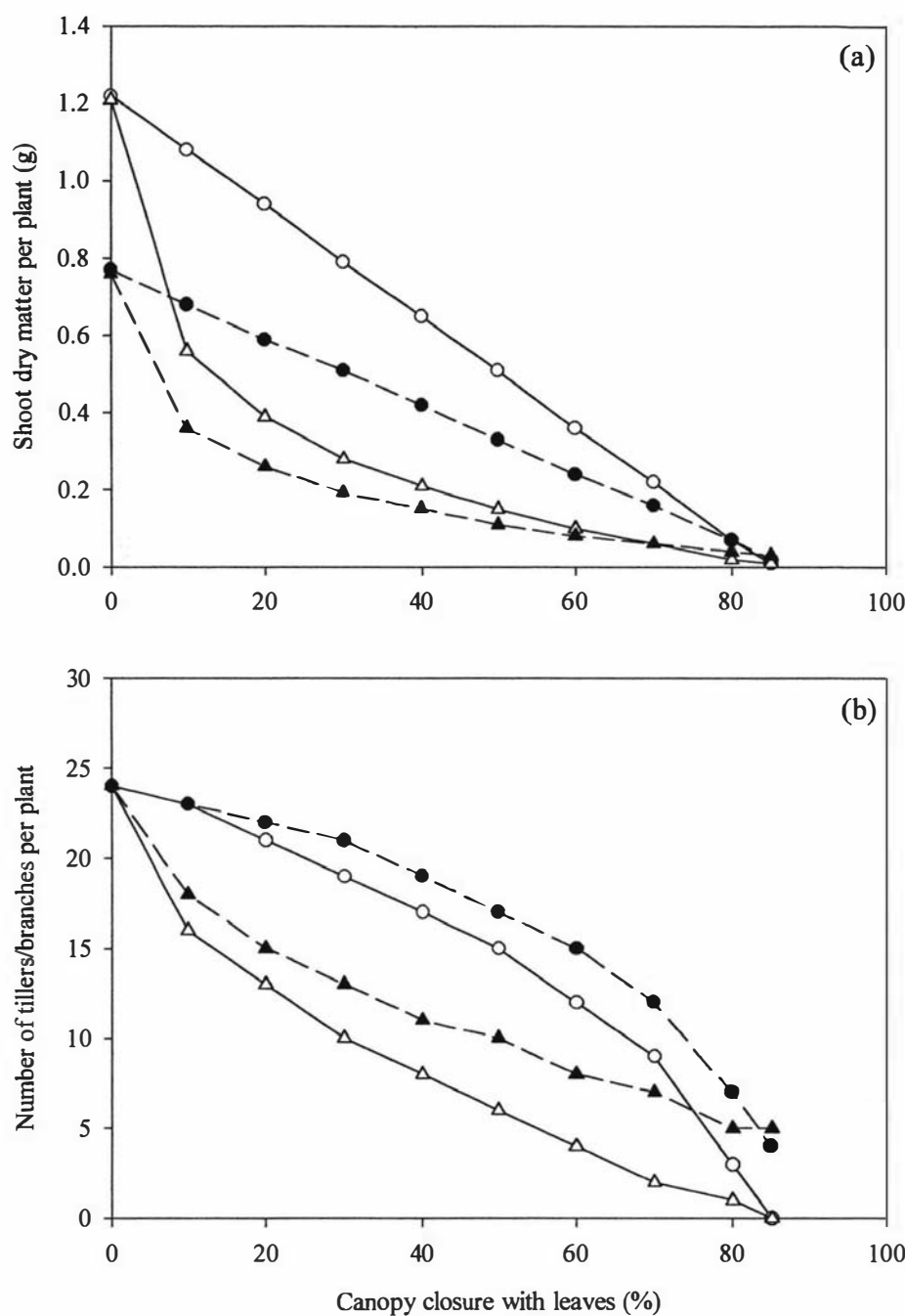


Figure 3.21 Estimated (a) dry matter production and (b) tillers/branches per plant for (○) perennial ryegrass/white clover and (●) cocksfoot/lotus pastures at the centre of a vertically projected canopy gap (Zone 3) and for (△) perennial ryegrass/white clover and (▲) cocksfoot/lotus pastures directly below the poplar crowns (Zone 1), over a range of CCLs in summer. Cocksfoot and lotus are considered shade tolerant species (Devkota 2000). The botanical species composition for the above relationships was assumed to be a mix of 70% grass and 30% legume. The linear and non-linear relationships relating PAR transmission in the two main zones of tree influence (i.e. Zones 1 & 3) to stand canopy closure are given in Section 3.4; whereas, data relating pasture production variables to PAR transmission were obtained from Devkota *et al.* (1997). For the latter, spectrally neutral shade cloth was used to vary the PAR transmission levels under glasshouse conditions; soil nutrients and water were non-limiting (Devkota *et al.* 1997).

3.6 Conclusion

Estimated PAR transmission (%DIFN) was inversely related to all of the stand density indices tested. However, there were marked differences in the general form, complexity, and precision of the above relationships depending on the location (zone) within the stand, season, and stand density index used. When initially going from the open pasture to low poplar stand densities %DIFN decreased at a faster rate in Zone 1 than Zone 3. After the initial rapid decrease in Zone 1 %DIFN it then became relatively constant, with the level depending on the average size of the trees. Under a completely closed canopy, %DIFN in both zones of tree influence converged at around 15-20% and 50-55% in summer (in-leaf) and winter (no leaf), respectively. The relative increase in %DIFN between summer and winter was greater at higher stand densities and under larger, more mature, trees. This reduced the slope of the inverse relationships associated with Zone 3 %DIFN in winter, and also reduced the magnitude of decline in Zone 1 %DIFN.

In summer, the R:FR decreased from open pasture values at an increasing rate as the transmission of PAR (%DIFN) through the fully in-leaf poplar canopy declined. The decrease was particularly marked below a %DIFN of 40%. In contrast, without spectrally selective leaves, in winter the poplar canopy had little effect on the understorey R:FR.

Across multiple sites, CCL/NL, BA, HPCC, and CEV were more strongly related to %DIFN than DBH, HPCD, or GCL. In particular, there was a directly proportional inverse relationship between CCL and Zone 3 %DIFN in summer. Unaccounted for site differences in the relationships for Zone 1 %DIFN were evident to varying degrees for all of the stand density indices investigated. One of the main factors not accounted for was likely the difference in average tree-crown size between sites. This factor also probably contributed to the lower quality of fit and precision of the regression models fitted for Zone 3 %DIFN when using DBH, HPCD, and GCL as single independent variables. Site variation in the average foliage density of the trees may have confounded the summer relationship between CEV and Zone 3 %DIFN.

Further investigation of factors causing the above site differences is clearly required to improve the strength and robustness of the developed regression models. The average height ratio of the trees is likely an important factor that warrants investigation. Increasing the number of samples taken under young/small and old/large trees at high and very low stand densities, respectively, would also help to strengthen the regression models for both %DIFN and the R:FR ratio. Overall, the results show that the developed regression models should not be applied/extrapolated to stands with vastly different crown size or form.

In general, canopy closure (CCL/NL) based on digital images taken with at least a moderate angle of view was able to account for variations in silvicultural management (e.g. pruning), crown shape, and crown density/porosity more than any of the other stand density indices investigated. However, there is a need for greater standardisation of the techniques used for capturing and analysing digital canopy images.

BA, HPCC, and CEV were all strongly related to CCL. Similarly, CCNL and CCL were also strongly related. However, for the latter relationship there were marked differences between sites with young/pruned and mature/unpruned trees.

Combining data from the present study with a previously conducted shade trial indicates that understorey pasture production would follow a similar pattern to changes in %DIFN. In summer, understorey pasture DM production was estimated to cease at 85% CCL, while not falling below 50% of open pasture in winter at the same overstorey (stand) density.

3.7 References

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4 The effect of poplar overstorey density on soil chemical properties

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4.1 Introduction

Chapter 3 showed how a decrease in PAR transmission directly below poplar trees and with increasing stand density was likely to have a negative effect on understorey pasture production. Also briefly discussed in Section 3.5.8 was that other limiting factors, such as soil moisture and nutrient stress, can have an impact on a pasture plant's response to changes in PAR. Trees can intercept and reduce significant amounts of effective rainfall reaching the soil surface (Guevara-Escobar 1999; Guevara-Escobar *et al.* 2000; Douglas *et al.* 2001; McIvor *et al.* 2003). Nevertheless, several recent studies have shown that the soil moisture content in upper soil layers does not vary widely between tree and open pasture/grassland environments (Wilson & Kleb 1996; Guevara-Escobar *et al.* 1997; Guevara-Escobar 1999; Power *et al.* 1999, 2003; Herman *et al.* 2003; James *et al.* 2003; McIvor *et al.* 2003). In contrast, Guevara-Escobar *et al.* (2002) found the pH and levels of exchangeable base cations (Ca, Mg, & K) in the topsoil were higher directly under poplar trees than in adjacent open pasture and concluded that the soil from the former environment was superior in supporting pasture production, when no other factors were limiting.

However, Guevara-Escobar *et al.* (2002) study was limited to a summer-moist climate (annual rainfall 1100mm-1300mm), covered a very small range of stand densities, and spatially, comparisons were restricted to between directly below trees (analogous to Zone 1) and in adjacent open pasture. Trees affect soils mainly through their litter, root activity, and changes to the microclimate (Van Goor 1985). As such, variation in the regional climate, stand density, and proximity to trees in a stand will all likely strongly influence the impact of trees on soil properties (Fuller & Anderson 1993; Nwaigbo *et al.* 1997; Perrott *et al.* 1999). Therefore, the objective of this chapter was to determine the spatial variation in the effect of poplar trees on soil properties, over a range of stand densities, and to evaluate whether any changes will likely affect understorey pasture production. To increase the scope of the study, measurements were taken from two climatically contrasting regions (summer-wet & -dry) where poplar trees are often planted for soil conservation work.

4.2 Methodology

4.2.1 General site characteristics and treatment structure

The broad range of overstorey (stand) densities previously developed in Chapter 2 for Kiwitea and Hautope 1 formed the main treatment structure of this study. These two sites, as opposed to Hautope 2, were selected because their larger/more fully developed trees would likely have had a greater impact on the nutrient balance of the mixed tree-pasture system, and also their poplar stands contained a wider range of densities. Both of these factors should help to clarify any trends in soil properties related to changes in stand density (Alban 1982; Myers 1990; Guevara-Escobar 1999). The Kiwitea and Hautope 1 sites represent summer-wet and summer-dry climates, respectively (refer to section 2.3.1.3).

The poplars at each farm site had mainly been planted to control or prevent mass movement and fluvial soil erosion (refer to Section 2.3). As a consequence, tree spacing was not constant, instead being closer in areas with severe soil erosion and more widely spaced on relatively stable parts of the hill slopes. This typical planting pattern used for soil conservation trees (Wall *et al.* 1997; Wilkinson 1999) caused higher stand density experimental units to be situated on areas that showed greater visual signs of previous soil disturbance (refer to Section 2.3).

Grasses dominated the pastures at both sites (refer to Section 5.4.4). At Kiwitea, grasses comprised over 50% of the total sward biomass, while at Hautope 1 this value exceeded 60% and was often around 80%. Directly below the poplar crowns (Zone 1) at Kiwitea the proportion of high fertility responsive grasses (HFG¹) tended to be greater than in either the vertically projected canopy gap (Zone 3) or open pasture. Out of the different HFG, *Lolium perenne* and *Poa* spp. dominated the open pasture and Zone 1, respectively, whereas, these two species were found in similar abundance in Zone 3. All three main overstorey environments had a legume content around 8% of the total sward biomass (refer to Section 5.4.4.1). At Hautope 1, both Zones 1 and 3 contained a greater proportion HFG than in the adjacent open pasture. *Lolium perenne* and *Poa* spp. were the main high fertility responsive species in Zones 1 and 3, whereas, *Lolium perenne* and *Holcus lanatus*

¹ HFG included: *Lolium perenne*, *Poa* spp., *Holcus lanatus*, and *Dactylis glomerata*.

dominated the open pasture. Less than 5% legume was present in Zones 1 and 3. In comparison, the open pasture had around 10% legume in spring, but this decreased markedly to below 5% in late summer (refer to Section 5.4.4.3).

4.2.2 Field sampling

Soil samples were taken at Hautope 1 and Kiwitea on 5 September and 17 October 2000, respectively. A 25 mm-diameter soil corer was used to collect samples from 0-75 mm and 75-150 mm soil depths. The upper 0-75 mm soil stratum was sampled for all of the experimental units (microsites) that were selected in Chapter 2, except for the paired units located on a south facing aspect at Kiwitea. These two experimental units were excluded to limit comparisons at this site to a single northerly aspect (refer to Section 2.3, Table 2.2). The lower 75-150 mm stratum was sampled from a more limited range of experimental units at each of the sites. This range consisted of an open pasture control, and experimental units under low, medium, and high overstorey densities. Experimental units were stratified into overstorey density classes based on the proportion of diffuse non-intercepted radiation (%DIFN) received at the centre of their vertically projected canopy gap (Zone 3). Within each overstorey density class, two experimental units were randomly selected for sampling (Appendix 4.1).

Amongst the stands of poplar the two main overstorey environments (or zones of tree influence) previously described in Section 3.2.3.3 were sampled separately. From within these overstorey environments, and also within the open pasture, 10 soil cores were randomly collected and bulked together for each soil stratum. Sampling near patches with visual signs of dung or urine spots was avoided (Cornforth 1980) and the soil cores were only taken from a medium hill-slope (13-25 degrees) category (Saggar *et al.* 1990; López 2000).

The bulked soil samples were analysed for: $\text{pH}_w(\text{H}_2\text{O})$; basic plant-available cations - calcium (Ca), magnesium (Mg), potassium (K), and sodium (Na); plant-available anions - phosphate (P) and sulfate-sulfur ($\text{SO}_4\text{-S}$); anion storage capacity (ASC); soil organic carbon (SOC) and related soil organic matter (SOM).

4.2.3 Chemical and biochemical analysis techniques

Prior to analysis, the bulked soil samples were air dried at 33-35° for 18 hours, crushed, and then ground to pass through 2 mm-hole stainless steel sieves (Cornforth 1980).

To measure soil pH, 12 ml of a soil sample was suspended in 25 ml of distilled water, vigorously stirred, and then left to equilibrate overnight (16 hours) at 20°C. After briefly re-stirring the 1:2.1 v/v water slurry, the soil pH was read using a combined glass-calomel electrode and direct reading digital pH meter (Cornforth 1980; Blakemore *et al.* 1987).

AgResearch Quick-test² procedures were used to measure plant-available K, Ca, Mg, and Na, as outlined by Cornforth (1980) and Lee *et al.* (1991). The method involved shaking 4.4 ml of soil with a 20 ml solution of 1M ammonium acetate (NH₄OAc) at pH 7 for 2 minutes; after which, from the filtered extract, the displaced K, Ca, and Na were measured by flame emission spectrophotometry, while Mg was measured by atomic absorption spectrophotometry.

Plant-available P was determined based on the method of Olsen *et al.* (1954). P was extracted from 4 ml of soil with an 80 ml solution of 0.5M sodium bicarbonate (NaHCO₃) at pH 8.5 for 30 minutes. The concentration of P (units: µg/ml) in the filtered extract was measured through an Autoanalyser system, using a modified method of Murphy & Riley (1962) and Watanabe & Olsen (1965).

Immediately plant-available SO₄-S was determined by extraction of 4 g of soil with a 20 ml solution of 0.02M potassium phosphate (K₂HPO₄) at pH 4.0 for 30 minutes. The concentration of SO₄-S (units: ppm) in the filtered extract was measured by high performance ion chromatography (HPIC) (Watkinson & Kear 1994).

The ASC³ of the soil was determined by the method of Saunders (1965). This procedure involved mixing 5 g of soil with 25 ml of potassium dihydrogen phosphate buffer for 16 hours. After this time lapsed, the remaining phosphate in the filtered solution was measured by spectrophotometry (Saunders 1965; Cornforth 1980).

² Formally known as Ministry of Agriculture and Fisheries (MAF) Quicktest procedures.

³ Formally known as Phosphate retention (Cornforth 1980).

SOC was measured by combusting solid soil samples and determining by infrared the amount of carbon dioxide (CO₂) produced. SOC content was converted to SOM by multiplying by a factor of 1.724 (Foth 1978; Nelson & Sommers 1982; Park *et al.* 1994).

4.3 Data analyses

For each site, a split-plot analysis of variance (ANOVA) was conducted, using the general linear model (GLM) procedure of SAS[®] (version 8.02 for Windows[®], SAS Institute, Inc. 1999), to test the effects of overstorey environment (main plots), soil depth (subplots), and their interactions on the soil properties. In the GLM, a 'replicate nested within overstorey environment' parameter was treated as a random-effect, while all other parameters were considered fixed (Hedderley per. comm. 2002). The 3 x 2 factorial design was unbalanced, with treatment combinations having 2-11 replicates (Figure 4.1). As a result, Type 3 sums of squares were used instead of Type 1, due to their more conservative nature. Diagnostic options provided in SAS[®] were used to check the underlying ANOVA assumptions. These included studentised residual and normal probability plots, along with more formal test statistics (SAS 1990). Several soil properties required transformation to meet either the assumption of normality or homogeneity of variance. These soil properties are clearly identified in the appropriate results tables. One data point was identified as an outlier and removed for the analysis of plant-available Mg at Kiwitea. Separation of treatment means was by the Tukey-Kramer multiple comparison method (PDIFF ADJUST=TUKEY) for unequal sample sizes (SAS 1990).

Simple linear regression analyses, using the GLM procedure of SAS[®], were performed to examine the relationship between the soil properties and the in-leaf poplar canopy cover ratio (CCL). Separate regression analyses were carried out for the two main overstorey environments amongst the poplar stands (Zones 1 & 3) and also for the two soil strata (0-75mm & 75-150mm). Differences between the regression equations were tested by analysis of covariance (ANCOVA), using the GLM procedure of SAS[®] (Littell *et al.* 1991; Kleinbaum *et al.* 1998). Where the regression equations for the two main overstorey environments amongst the poplar stands (Zones 1 & 3) coincided (i.e. were not significantly different in intercept or slope) the data were combined into a single function representing the entire understorey environment. The quality of fit of the simple linear

regressions was checked through inspection of scatter, residual, and normal probability plots, along with more formal test statistics (SAS 1990).

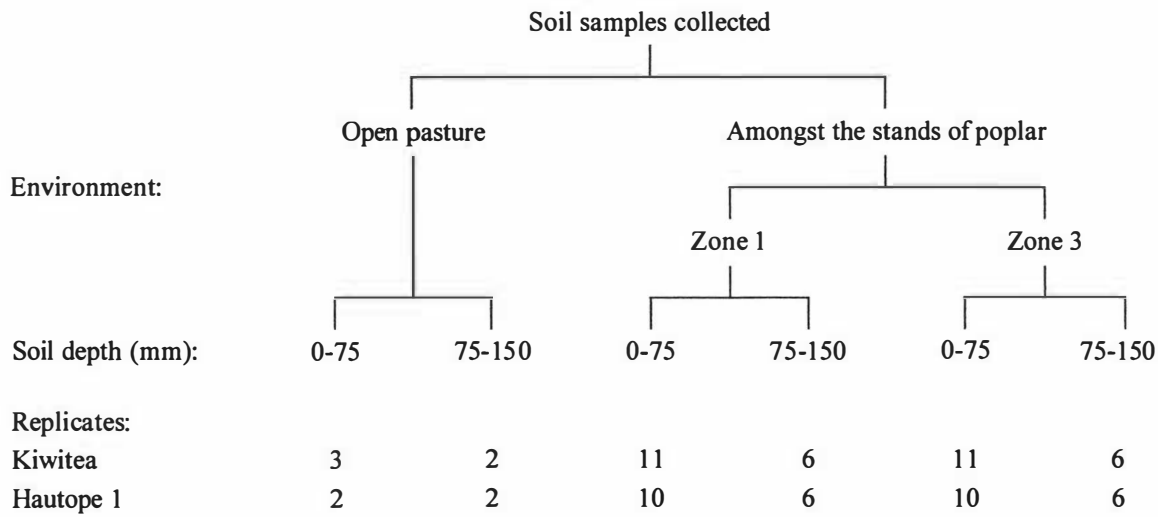


Figure 4.1 Unbalanced nested factorial-treatment structure. Abbreviations: Zone 1, area directly below the poplar crown in the north-eastern corner of an experimental unit with trees; Zone 3, area within the vertically projected canopy gap between the four nuclei trees defining an experimental unit (refer to Section 3.2.3.3, Figure 3.3); open pasture, adjacent open pasture area (control) away from the influence of the poplar trees.

4.4 Results

4.4.1 Effect of overstorey environment on soil properties within two separate soil strata at Kiwitea

When averaged over both 0-75 mm and 75-150 mm soil strata, soil pH_w and plant-available SO₄-S levels varied significantly between the three main overstorey environments (Table 4.1). Also, there was weak evidence of an overstorey environment effect on the levels of K, Ca, and SOC (Table 4.1). Soil pH_w and SO₄-S levels were 0.4 units and 1-2 ppm, respectively, higher amongst the poplar trees (Zones 1 & 3) than in the adjacent open pasture. The concentrations of K tended to be greater in the vertically projected canopy gap between the trees (Zone 3), followed by directly below the poplar crowns (Zone 1), and then open pasture. Similarly, plant-available Ca was marginally higher in Zone 3 than in the open pasture. However, the Ca concentration in Zone 1 was not significantly different from either of the other two main overstorey environments. The soil in the open pasture contained 1% more SOC than amongst the poplar stands. Plant-available P, Mg, and Na in the soil, along with ASC, did not vary significantly between the

three main overstorey environments (Table 4.1). All of the soil chemical properties, except for ASC, decreased significantly with increasing soil depth (Table 4.1).

4.4.2 Effect of poplar overstorey density on soil properties within two separate soil strata at Kiwitea

In the upper 0-75 mm of soil pH_w generally increased under greater CCL (Figure 4.2a). The simple linear relationship, which included both main zones of tree influence (Zones 1 & 3), was strong ($r^2=0.66$; $P<0.0001$) with little variation around the fitted function (CV=3%). The rate of increase in soil pH_w amongst the poplar trees was 0.1 units for every 10% increase in CCL (Figure 4.2a). In the lower 75-150 mm of soil pH_w was not significantly related to CCL.

The concentrations of Ca, Mg, and K in the upper 0-75 mm of soil also increased under greater CCL (Figure 4.2b,c,d). Similar relationships occurred in both Zones 1 and 3 for Ca and Mg (Figure 4.2b,c), while for K the relationship was restricted to Zone 3 (Figure 4.2d). Overall, Ca, Mg, and K increased at a rate of 0.3, 1.7, and 1.2 quick-test units, respectively, for every 10% increase CCL (Figure 4.2b,c,d). However, the strength of the above relationships was generally weak ($r^2\leq 0.41$) and there was considerable variation around the fitted functions (CV=15-46%). In the lower 75-150 mm of soil, Ca, Mg, and K were not significantly related to CCL.

In contrast, the ASC in the upper 0-75 mm of soil decreased under greater CCL (Figure 4.3a). The relationship did not differ significantly between the two main overstorey environments amongst the poplar trees (Zones 1 & 3); and in Zone 3 a similar response also occurred further down the soil profile within the 75-150 mm stratum (Figure 4.3c). The strength of the linear relationship for 0-75 mm soil depth was weak ($r^2=0.25$; $P=0.007$), increasing to a moderate level ($r^2=0.51$; $P=0.03$) further down the soil profile (75-150 mm).

The SOC content also decreased under greater CCL (Figure 4.3b,d). The relationship was limited to Zone 1 for the upper 0-75 mm of soil (Figure 4.3b), while it occurred in both zones further down the soil profile (75-150 mm) (Figure 4.3d). SOC decreased at a rate of

0.17% for every 10% increase CCL, and the relationship did not vary significantly ($P>0.05$) between the two soil strata (Figures 4.3b,d).

The concentrations of Na, P, and $\text{SO}_4\text{-S}$ in the soil did not change significantly ($P>0.05$) with increasing CCL.

Table 4.1 Kiwitea soil chemical properties¹: directly below the poplar crowns (Zone 1), at the centre of the vertically projected canopy gap between the trees (Zone 3), and within the open pasture (Open pasture).

Soil depth	Environment	pH _w	P (µg/ml)	K (QT)	SO ₄ -S (ppm)	Ca (QT)	Mg (QT)	Na (QT)	ASC (%)	SOC (%)	SOM (%)
			(lnY)	(lnY)	(lnY)	(lnY)		(1/Y)	(lnY)		
0-75 mm	Open pasture	5.5	17.8 (2.74)	6.2 (1.78)	3.2 (1.03)	5.5 (1.70)	26.5	5.7 (0.18)	20.5 (3.02)	4.7	8.2
	Zone 1	6.1	18.7 (2.79)	10.8 (2.31)	5.5 (1.67)	6.8 (1.90)	36.7	6.0 (0.17)	14.5 (2.62)	3.8	6.5
	Zone 3	6.2	19.8 (2.88)	13.1 (2.44)	4.5 (1.43)	7.7 (2.03)	36.0	6.4 (0.16)	15.1 (2.70)	3.9	6.8
	Grand mean	5.9	19.1 (2.80)	11.3 (2.18)	4.8 (1.38)	7.1 (1.88)	33.1	6.1 (0.17)	15.5 (2.78)	4.1	7.2
75-150 mm	Open pasture	5.6	14.0 (2.22)	4.3 (1.26)	2.0 (0.38)	4.8 (1.59)	24.0	4.5 (0.23)	22.3 (3.05)	3.4	6.0
	Zone 1	5.9	7.8 (1.98)	7.0 (1.89)	3.2 (1.11)	5.7 (1.71)	28.7	5.8 (0.19)	19.8 (2.87)	2.5	4.3
	Zone 3	5.9	10.5 (2.26)	8.7 (2.09)	2.5 (0.90)	6.3 (1.82)	27.2	4.8 (0.22)	17.3 (2.89)	2.5	4.3
	Grand mean	5.8	9.9 (2.15)	7.3 (1.75)	2.7 (0.80)	5.8 (1.71)	26.6	5.2 (0.21)	19.1 (2.94)	2.8	4.9
Overall 0-150 mm	Open pasture	5.6	16.3 (2.48)	5.4 (1.52)	2.7 (0.70)	5.2 (1.65)	25.2	5.2 (0.20)	21.2 (3.03)	4.1	7.1
	Zone 1	6.0	14.9 (2.38)	9.5 (2.10)	4.6 (1.39)	6.4 (1.81)	32.7	5.9 (0.18)	16.4 (2.74)	3.1	5.4
	Zone 3	6.0	16.5 (2.57)	11.5 (2.26)	3.8 (1.17)	7.2 (1.93)	31.6	5.8 (0.19)	15.9 (2.80)	3.2	5.5
	Grand mean	6.0	15.8 (2.58)	9.8 (2.14)	4.0 (1.28)	6.6 (1.86)	32.2	5.8 (0.18)	16.8 (2.78)	3.4	5.9
Analysis of variance											
Environment (A)		P<0.05	NS	P<0.1	P<0.05	P<0.1	NS	NS	NS	P<0.1	P<0.1
Soil depth (B)		P<0.1	P<0.001	P<0.001	P<0.001	P<0.05	P<0.001	P<0.05	P<0.01	P<0.001	P<0.001
Interaction (A*B)		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
SD		0.1	(0.22)	(0.14)	(0.24)	(0.14)	3.3	(0.03)	(0.09)	0.2	0.3

¹Averaged across a range of different poplar stand densities. Abbreviations: QT, AgResearch Quick test units; lnY, natural-logarithm transformed; SD, standard deviation; NS, non significant (P>0.1); P, Phosphate; K, potassium; SO₄-S, sulfate-sulfur; Ca, calcium; Mg, magnesium; Na, sodium; ASC, anion storage capacity; SOC, soil organic carbon; and SOM, soil organic matter.

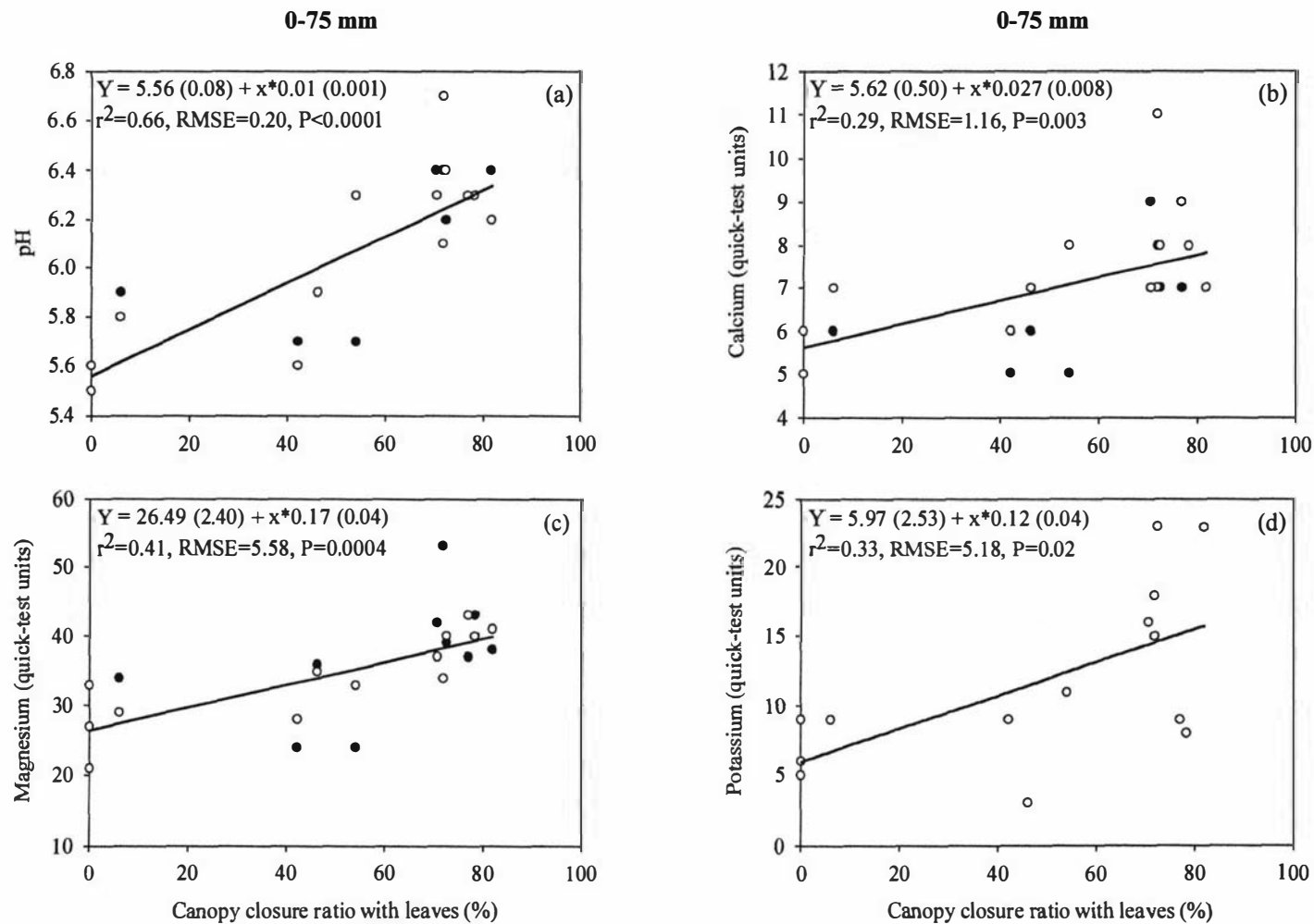


Figure 4.2 Kiwitea 0-75 mm soil chemical properties linearly related to poplar canopy closure (CCL). Symbols: (●) directly below the poplar crowns (Zone 1) and (○) at the centre of the vertically projected canopy gap between the trees (Zone 3). Standard errors for the simple linear regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction.

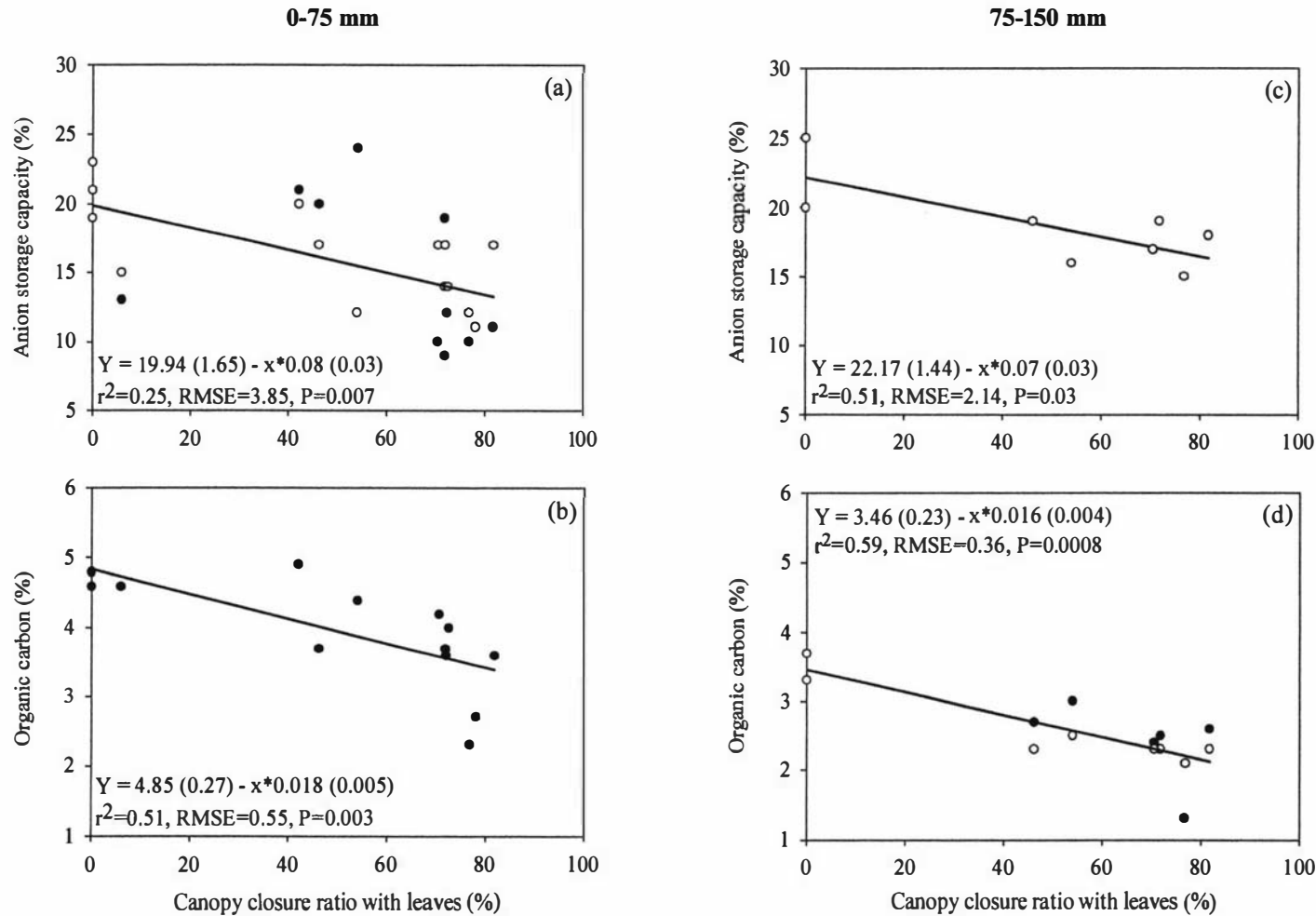


Figure 4.3 Kiwitea soil chemical properties linearly related to poplar canopy closure (CCL). Symbols: (●) directly below the poplar crowns (Zone 1) and (○) at the centre of the vertically projected canopy gap between the trees (Zone 3). Standard errors for the simple linear function coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction.

4.4.3 Effect of overstorey environment on soil properties within two separate soil strata at Hautope 1

In the upper 0-75 mm of soil pH_w was 0.2-0.3 units higher amongst the poplar trees (Zones 1 & 3) than in open pasture (Table 4.2). However, the reverse occurred in the lower 75-150 mm of soil as a result of the open pasture pH_w increasing by 0.3 units, while pH_w decreased in Zone 1 and did not change significantly in Zone 3 (Table 4.2). At this lower soil depth the difference in pH_w between Zone 1 and open pasture was only marginal ($P=0.07$).

The concentration of K in the upper 0-75 mm of soil was highest in Zone 1, followed by Zone 3, and then the open pasture (Table 4.2). With increasing soil depth, K decreased by 3-5 quick-test units in Zones 1 and 3, while not changing significantly in the open pasture (Table 4.2). The decrease in Zone 3 K made it comparable with the open pasture, whereas in Zone 1 the concentration remained significantly higher than in the other two overstorey environments (Table 4.2).

For Mg there was a weak interaction ($P=0.07$) between overstorey environment and soil depth (Table 4.2). Mg in the upper 0-75 mm of soil tended to be 13.1-14.2 quick-test units greater in both Zones 1 and 3 compared to in the open pasture (Table 4.2). However, further down in the 75-150 mm soil stratum, Mg did not vary significantly between the three main overstorey environments (Table 4.2).

Ca in the upper 0-75 mm of soil did not differ significantly among the three main overstorey environments (Table 4.2). Nevertheless, in Zones 1 and 3 the concentration tended ($P=0.06$) to decrease by 0.8 quick-test units with increasing soil depth, whereas, in the open pasture it did not change significantly. As a result, in the 75-150 mm of soil, Zone 1 Ca tended ($P=0.06$) to be slightly lower than in the open pasture (Table 4.2).

Again, little difference was found with Na. When averaged across both soil depths, the highest concentrations of Na were in Zone 1, followed by Zone 3, and then open pasture (Table 4.2).

For both soil depths Zone 1, followed by Zone 3, tended ($P=0.08$) to have the greatest concentration of P (Table 4.2). In all three main overstorey environments P decreased with soil depth (Table 4.2).

In the upper 0-75 mm of the open pasture soil $\text{SO}_4\text{-S}$ was around 11 ppm greater ($P=0.06$) than amongst the poplar trees (Table 4.2). However, in the lower 75-150 mm of soil the reverse occurred as a result of a significant ($P<0.001$) decrease in the level of $\text{SO}_4\text{-S}$ in the open pasture.

The ASC increased significantly with soil depth when averaged across all three main overstorey environments (Table 4.2). Also, there tended ($P=0.05$) to be an interaction between the overstorey environment and soil depth (Table 4.2). In the upper 0-75 mm soil stratum, the ASC in Zone 3 was marginally higher than in Zone 1 or the open pasture. Whereas, further down in the 75-150 mm soil stratum, Zones 1 and 3 both had an ASC around 6% greater than in the open pasture (Table 4.2).

When averaged over both soil depths, Zone 1 had 0.5-0.6% more SOC than in Zone 3 or the open pasture (Table 4.2). The SOC in all three main overstorey environments decreased significantly with soil depth (Table 4.2).

4.4.4 Effect of poplar overstorey density on soil properties within two separate soil strata at Hautope 1

In the upper 0-75 mm of soil K, Na, and Mg increased under greater CCL (Figure 4.4). The simple linear relationship for K did not differ significantly ($P>0.05$) between the two main overstorey environments amongst the poplars (Figure 4.4a). In contrast, for Na and Mg the relationships only occurred in Zone 1 and Zone 3, respectively (Figure 4.4b,c). The rate of increase for these basic cations was 0.9, 0.5, and 2.3 quick-test units, respectively, for every 10% increase CCL. However, the strength of the above relationships was weak ($r^2\leq 0.35$), with a large amount of variation around the fitted functions. Furthermore, data points were concentrated around the two extremes in CCL, which reduced confidence in the fitted functions.

Soil pH_w, Ca, P, SO₄-S, ASC, SOC in the upper soil stratum (0-75 mm) did not change significantly ($P>0.05$) over the limited range of CCLs.

In the lower 75-150 mm of soil, P and Na, along with ASC, increased under greater CCL (Figure 4.5b,c,d). This contrasted with soil pH_w, which at the same depth decreased with increasing CCL (Figure 4.5a). P and Na increased by 0.6 µg/ml and 0.4 quick-test units, respectively, for every 10% increase in CCL (Figure 4.5c,d). The slope of the simple linear relationship for Na was not significantly different ($P>0.05$) from the same relationship found in the upper 0-75 mm of soil (Figures 4.4b & 4.5d). Conversely, soil pH_w decreased by 0.05 units for every 10% increase in CCL (Figure 4.5a). Overall, the strength of the above relationships ranged from weak to strong ($r^2=0.34-0.64$). However, the relationships were based on a very limited range of CCLs and the soil properties, except for soil pH_w, exhibited disproportionately greater variation towards higher CCLs.

Table 4.2 Hautope 1 soil chemical and biochemical properties¹: directly below the poplar crowns (Zone 1), at the centre of the vertically projected canopy gap between the poplar trees (Zone 3), and within the open pasture (Open pasture).

Soil depth	Environment	pH _w	P (µg/ml)	K (QT)	SO ₄ -S (ppm)	Ca (QT)	Mg (QT)	Na (QT)	ASC (%)	SOC (%)	SOM (%)
			(lnY)		(lnY)			(lnY)			
0-75 mm	Open pasture	5.5	15.0 (2.62)	7.5	24.0 (3.03)	8.5	39.0	7.0 (1.94)	16.0	4.3	7.4
	Zone 1	5.8	20.7 (2.96)	16.5	13.5 (2.51)	8.6	52.1	10.3 (2.32)	16.9	4.9	8.5
	Zone 3	5.7	16.2 (2.76)	11.6	12.4 (2.50)	8.8	53.2	9.0 (2.18)	20.6	4.2	7.3
	Grand mean	5.6	18.1 (2.78)	11.9	14.0 (2.68)	8.6	48.1	9.4 (2.15)	17.8	4.5	7.8
75-150 mm	Open	5.8	3.5 (1.24)	6.0	4.5 (1.44)	9.0	49.0	6.0 (1.79)	16.0	2.3	3.9
	Zone 1	5.6	7.3 (1.93)	11.7	11.5 (2.38)	7.8	49.1	9.8 (2.35)	22.1	2.8	4.8
	Zone 3	5.6	5.8 (1.75)	8.6	10.7 (2.39)	8.0	51.7	9.3 (2.29)	22.8	2.4	4.2
	Grand mean	5.7	6.1 (1.64)	8.8	10.1 (2.07)	8.2	49.9	9.1 (2.14)	20.3	2.6	4.4
Overall 0-150 mm	Open	5.6	9.3 (1.93)	6.7	14.3 (2.24)	8.8	44.0	6.5 (1.86)	16.0	3.3	5.7
	Zone 1	5.7	14.0 (2.44)	14.1	12.5 (2.44)	8.2	50.6	10.1 (2.33)	19.5	3.8	6.7
	Zone 3	5.6	11.0 (2.26)	10.1	11.5 (2.44)	8.4	52.4	9.2 (2.24)	21.7	3.3	5.7
	Grand mean	5.6	13.5 (2.42)	11.7	12.5 (2.41)	8.4	51.1	9.3 (2.21)	19.8	3.8	6.5
Analysis of variance											
Environment (A)		NS	P<0.1	P<0.01	NS	NS	NS	P<0.001	P<0.1	P<0.01	P<0.001
Soil depth (B)		NS	P<0.001	P<0.001	P<0.001	P<0.1	NS	NS	P<0.01	P<0.001	P<0.001
Interaction (A*B)		P<0.001	NS	P<0.05	P<0.001	P=0.05	P<0.1	P<0.1	P=0.05	NS	NS
SD		0.1	(0.17)	1.0	(0.20)	0.4	4.4	(0.08)	1.8	0.3	0.5

¹Averaged across the range of poplar stand densities. Abbreviations: QT, AgResearch Quick test units; SEM, standard error of the mean; NS, non significant; P, phosphate; K, potassium; SO₄-S, sulphate-sulphur; Ca, calcium; Mg, magnesium; Na, sodium; ASC, anion storage capacity; SOC, soil organic carbon; and SOM, soil organic matter.

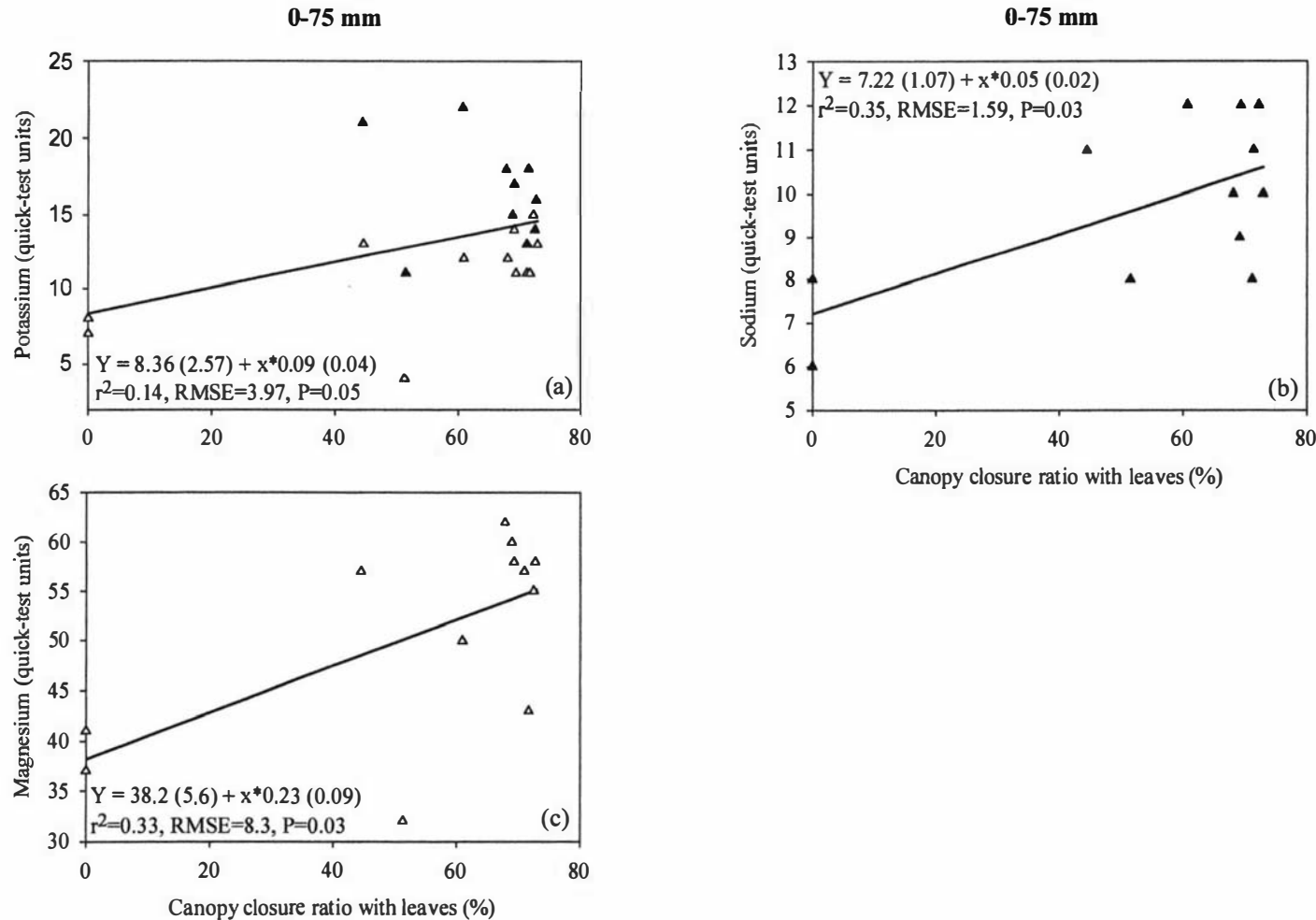


Figure 4.4 Hautepe 1 0-75 mm soil chemical properties linearly related to poplar canopy closure (CCL). Symbols: (▲) directly below the poplar crowns (Zone 1) and (Δ) at the centre of the vertically projected canopy gap between the trees (Zone 3). Standard errors for the simple linear function coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction.

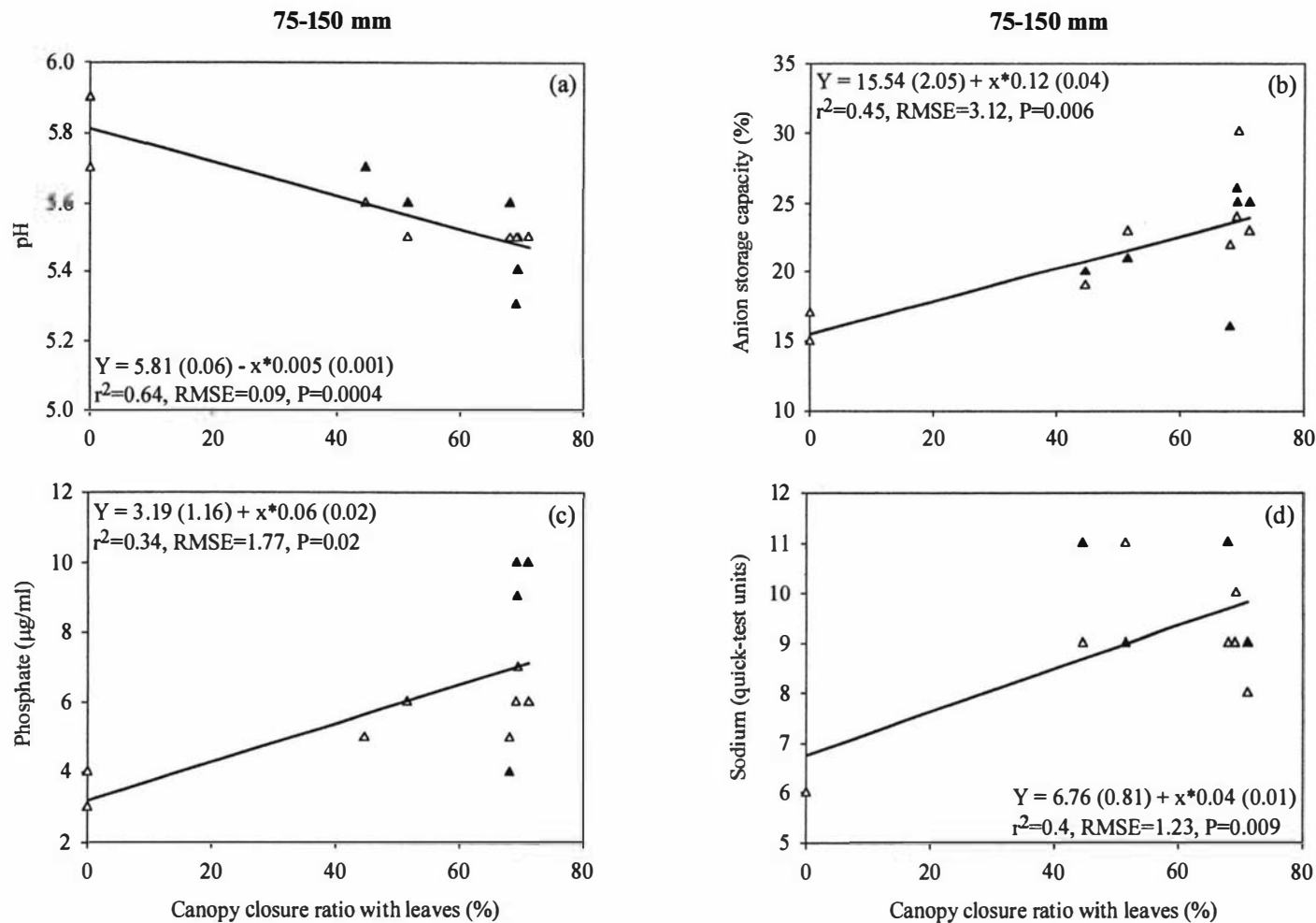


Figure 4.5 Hautope 1 soil chemical properties linearly related to poplar canopy closure (CCL). Symbols: (▲) directly below the poplar crowns (Zone 1) and (Δ) at the centre of the vertically projected canopy gap between the trees (Zone 3). Standard errors for the simple linear function coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction.

4.5 Discussion

4.5.1 Soil pH

In the upper 0-75 mm of soil at both Kiwitea and Hautope 1 one of the main impacts that poplar trees had was a 0.2-0.7 unit increase in soil pH_w compared to the adjacent open pasture (Tables 4.1 & 4.2). At Kiwitea, the elevation in soil pH_w was greater under higher CCL (Figure 4.2a). However, no such effect was found at Hautope 1. Based on the scatter plot of the data, the poor range of CCL sampled (skewed between 45-75% CCL) and the high amount of variation in soil pH_w under the trees possibly contributed to the lack of any significant relationship at this site (data not shown). The greater concentration of organic matter in the soil under the trees at Hautope 1 than at Kiwitea (*t*-test, $P=0.0006$) could have increased its pH buffering capacity (Helyar 1987; Curtin & Rostad 1997; Giddens *et al.* 1997; Alfredsson *et al.* 1998). A similar effect would also be achieved through higher clay content in the soil (During 1984; McBride 1994; Wong *et al.* 2000).

Using a similar “paired-site” approach to this study, Guevara-Escobar *et al.* (2002) measured the soil pH_w at 10 different sites in the same Manawatu-Wanganui region as Kiwitea. In the upper 0-75 mm of soil, pH_w directly under poplar trees (> 5 years old) was 0.5-1.2 units higher than in open pasture. In general, the soil pH_w was around 5.5 units in the open pasture and 6.1 units directly under the trees. This corresponded very closely to the soil pH_w levels measured under the same respective overstorey environments at Kiwitea (Table 4.1). However, the increase in soil pH_w under the trees was more marked than at Hautope 1 (Table 4.2).

Spatially, Guevara-Escobar *et al.* (2002) measurements were restricted to directly below the trees (analogous to Zone 1) and in the open pasture. The more intensive stratified sampling used in the present study indicates that poplar trees have a similar effect on soil pH_w both directly under and in the gaps between their crowns (Tables 4.1 & 4.2; Figures 4.2a & 4.5a).

The higher soil pH_w under poplars is the opposite of that normally found under the main exotic tree species planted in New Zealand - *Pinus radiata* D. Don. In general, *P. radiata* has been shown to acidify the soils of unimproved (Alfredsson *et al.* 1998) and improved

(Hawke & O'Connor 1993; Giddens *et al.* 1997; Parfitt *et al.* 1997; Cossens & Hawke 2000) pasture/grassland. Based on the Tikitere Agroforestry Research Area near Rotorua, Hawke & O'Connor (1993) reported that greater soil acidification occurred under older stands of *P. radiata* planted at a higher stocking rate; both attributes are associated with greater CCL.

Soils under legume-based pasture also generally become more acidic with time (Ridley *et al.* 1990; Bolan *et al.* 1991; Haynes & Williams 1993). If unchecked this can cause pasture production losses (especially pH <5.5) through reduced nutrient availability and phytotoxic effects of elevated Al and Mn levels in the soil solution (Edmeades 1986; Dodd *et al.* 1992; McLaren & Cameron 1996; Wheeler & O'Connor 1998). Adding lime to pastures is widely used in New Zealand to control/ameliorate soil acidification (Sinclair 1995; Wheeler 1997). However, on hill pastures that do not allow ground-based applications, liming is generally considered uneconomic owing to high aerial-application costs (Sinclair 1995; MacLaren 1996; de Klein *et al.* 1997). For example, on moderately buffered New Zealand sedimentary soils 6-10 tonnes/ha of good quality limestone (approx. 80% CaCO₃) is usually required to raise the soil pH by 1 unit (Morton *et al.* 1994; Sinclair 1995). Therefore, the integration of widely spaced poplar trees across hill pastures could potentially be used as an alternative bioremediation measure for controlling soil acidification.

4.5.1.1 Potential processes causing a greater decrease in open pasture soil pH, compared to amongst the poplar stands

Many different processes affect the balance of hydrogen ions (H⁺) and hydroxyl ions (OH⁻) in soil solution, which in turn determines pH (Van Breemen *et al.* 1983; Binkley & Richter 1987; Helyar & Porter 1989; Sinclair 1995). In temperate legume-based pastures generally the most important processes are associated with the carbon (C) and nitrogen (N) cycles (Helyar & Porter 1989; Ridley *et al.* 1990b; Bolan *et al.* 1991; Tang *et al.* 1999; Bolan *et al.* 2003).

Carbon (C) cycle

Additional H⁺ ions are added to soil solutions from the C cycle via: the dissociation of carbonic acid (H₂CO₃), formed originally from carbon dioxide (CO₂) respired by plant roots and heterotrophic soil organisms; and from the synthesis and dissociation of organic

acids (Van Breemen *et al.* 1983; Binkley & Richter 1987; Bolan *et al.* 1991; de Klein *et al.* 1997).

Dissociation of carbonic acid (H_2CO_3)

The dissociation of H_2CO_3 releases both H^+ and bicarbonate (HCO_3^-) into the soil solution (Binkley & Richter 1987; de Klein *et al.* 1997). Where rainfall exceeds evapotranspiration, these HCO_3^- anions are leached from the topsoil in association with companion cations (e.g. exchangeable Ca^{2+} , Mg^{2+} , K^+ , Na^+). This leaves a pool of additional H^+ , which either replace some of the removed cations on soil colloid exchange complexes (along with Al^{3+}), or are used in the weathering (e.g. hydrolysis) of minerals (Binkley & Richter 1987; McBride 1994; Fisher & Binkley 2000).

de Klein *et al.* (1997) noted some studies have shown that the extra pool of H^+ created through the dissociation of H_2CO_3 is relatively small compared to other acidifying processes. Nevertheless, Parfitt *et al.* (1997), Chen *et al.* (2000), and Saggar *et al.* (2001) all measured significantly higher concentrations of CO_2 in soils under open pastures compared to under adjacent conifer (*Pinus* spp.) stands. In the study by Parfitt *et al.* (1997), the resulting elevated concentration of HCO_3^- in the open pasture soil was the main inorganic anion regulating the leaching of base cations.

Parfitt *et al.* (1997) attributed elevated CO_2 and HCO_3^- concentrations in open pasture soil to higher rates of root and microbial respiration and also to a lower rate of gas diffusion. Similarly to Kiwitea (Table 4.1), the open pasture had a greater amount of SOM than under the trees, and this, along with a lower soil C:N ratio, was postulated to favour enhanced microbial respiration. In contrast, at Hautope 1 the SOM content directly below the trees (Zone 1) was higher than in the open pasture (Table 4.2). Nevertheless, the biochemical composition of this SOM may still have inhibited its rate of turnover. Köchy & Wilson (1997) reported that the aboveground litter from a mixed-grass prairie decomposed faster than senesced leaves shed from an adjacent *Populus tremuloides* (aspen) forest. Differences in the decomposition rate, and thus presumably CO_2 production, was mainly related to the biochemical nature of the litter, rather than to plant-induced changes to the microclimate, although both had a significant effect. Overall, it was postulated that the decomposition rate of the senesced poplar leaves was limited by a lower N concentration, in comparison to the prairie litter (Köchy & Wilson 1997).

Another possible cause of lower CO₂ concentrations in the soil atmosphere under poplar trees is the presence of substances that restrict the growth of heterotrophic decomposer communities. *Populus* species contain condensed tannins (proanthocyanidins) (Driebe & Whitman 2000; Kemp *et al.* 2001). These high molecular weight secondary compounds form resilient complexes with proteins, making them less available as substrates for decomposer soil organisms, and can inhibit the activity of many different enzymes associated with the breakdown of organic matter (Benoit *et al.* 1968; Benoit & Starkey 1968; Lewis & Starkey 1968; Schimel *et al.* 1996; Fierer *et al.* 2001; Schofield *et al.* 2001). Also, some tannins are toxic to certain groups of soil organisms (Baldwin *et al.* 1983; Schimel *et al.* 1996; Fierer *et al.* 2001). In contrast, most hill pasture plants either do not contain or have only trace amounts of condensed tannins (Jackson *et al.* 1996; Wang *et al.* 1996).

Warmer soil temperatures, as a catalyst of enhanced plant root and microbial respiration, and slower gas diffusion through wetter soils in autumn and spring, could also increase the HCO₃⁻ concentration in open pasture (Kowalenko *et al.* 1978; Taylor & Parkinson 1988; Parfitt *et al.* 1997). The soil under poplar trees is normally 0.5-5.0° cooler than in adjacent open pasture (Crowe 1993; Guevara-Escobar *et al.* 1997) and can also be drier at certain key times of the year, such as late autumn through until early spring (Guevara-Escobar *et al.* 1997; Douglas *et al.* 2001).

Synthesis and dissociation of organic acids

If cations and anions are not taken up in equilibrium by plant roots then either H⁺ or OH⁻ ions are released back into the soil solution to maintain charge neutrality within the soil-plant system (Binkley & Richter 1987; Sinclair 1995; Tang *et al.* 2003). These H⁺ and OH⁻ ions are generated inside the plants mainly through the dissociation of organic acids and decarboxylation of organic acid anions, respectively (Bolan *et al.* 1991). Therefore, the absorption of a greater ratio of inorganic cations-to-anions by plants causes two main effects: the excretion of H⁺ into the soil solution, which lowers the soil solution pH; and the formation of large quantities of charge-balancing organic acid anions inside the plants (Sinclair 1995; de Klein *et al.* 1997; Tang *et al.* 1999, 2003). However, the complete recycling and mineralisation of this plant material back into the same soil releases the inorganic ions taken up, and oxidation of the synthesized organic acid anions, along with the ammonification of the organic nitrogen compounds, consumes the previously excreted

H⁺ resulting in no net change in soil solution pH (Binkley & Richter 1987; Sinclair 1995; de Klein *et al.* 1997; Fisher & Binkley 2000).

Many temperate pasture legumes in particular take up an excess of cations over anions (Braschkat & Randall 2004), thus releasing H⁺ back into the soil solution to maintain charge neutrality (Bolan *et al.* 1991; Haynes & Williams 1993; Sinclair 1995; de Klein *et al.* 1997). If grazing animals consume this legume material and then permanently remove it from the system (via animal products or the transfer of dung and urine to camp areas) then the cycle described above is uncoupled and the H⁺ previously released cannot be neutralised, this causing soil acidification (Bolan *et al.* 1991; Sinclair 1995; Fisher & Binkley 2000). In hill pastures, grazing animals usually ingest herbage from over a wide area of the paddock and return a large proportion of this material, in the form of dung and urine, back to relatively small camp areas (Gillingham & During 1973; Gillingham *et al.* 1980). At both Kiwitea and Hautope 1, this effect (i.e. net transference of alkalinity) was likely enhanced in the open environment because of the greater pasture/legume production and animal carrying capacity than amongst the poplar trees (refer to Section 5.4.1).

Nitrogen (N) cycle

In legume-based pastures where new N inputs are solely added through symbiotic N₂ fixation, a permanent change in soil pH occurs via the N cycle only when nitrate (NO₃⁻) is leached from the system (Binkley & Richter 1987; de Klein *et al.* 1997). Generally NO₃⁻ is weakly held in the soil and, if not absorbed by plants or soil microbes, is prone to being leached with companion cations in drainage water (Bolan *et al.* 1991). This prevents H⁺ produced during the nitrification process from being neutralised and leads to a permanent increase in soil acidity (Helyar 1976; Bolan *et al.* 1991; Sinclair 1995; de Klein *et al.* 1997; Fisher & Binkley 2000). Assuming the pastures within all three main overstorey environments at Kiwitea and Hautope 1 were equally utilised by grazing animals, then the greater pasture/legume production in the open, compared to amongst the poplar stands (refer to Section 5.4.1), would result in a larger quantity of N being returned to the soil in dung and urine patches (Steele *et al.* 1984; Heng *et al.* 1991; Scholefield *et al.* 1993). The high N concentration aggregated in dung and especially urine patches (30-100 g N/m²) usually far exceeds the immediate requirements of pasture plants and soil microbes (Ball & Ryden 1984; Haynes & Williams 1991, 1993). Thus, in the open pasture there would be

greater potential for excess N to be transformed into NO_3^- and leached as a salt than under the trees (Zones 1 & 3).

NO_3^- leaching normally occurs in late autumn and winter (Holland & During 1977; Field *et al.* 1985; Sherwood & Fanning 1989; Scholefield *et al.* 1993; Ridley *et al.* 2001). Often NO_3^- levels build up during summer when plant sinks are inactive due to water stress and the wetting up of soil in early autumn can also cause a flush in N mineralisation and nitrification (Helyar 1976; Heng *et al.* 1991; Scholefield *et al.* 1993; Herman *et al.* 2003). However, the large quantity of poplar litter and aqueous leachates released in autumn (Taylor *et al.* 1989; Guevara-Escobar 1999) could reduce the size of the labile NO_3^- pool. Thibault *et al.* (1982) found that dormant bud and foliar leachates from balsam poplar (*Populus balsamifera* L.) specifically inhibited nitrification. Lodhi & Killingbeck (1980) and Baldwin *et al.* (1983) reported similar effects in ponderosa pine (*Pinus ponderosa* Dougl.) and balsam fir (*Abies balsamea* [L.] Mill) stands, respectively, and attributed the inhibition to tannin and phenolic compounds from the trees. These C-rich secondary compounds can also decrease soil NO_3^- levels by stimulating N immobilisation, while at the same time reducing N mineralisation (Azhar *et al.* 1986; Fox *et al.* 1990; Palm & Sanchez 1991; Schimel *et al.* 1996; Fierer *et al.* 2001). Lower soil water content under the trees, compared to in the open pasture through autumn to spring would also reduce NO_3^- leaching (refer to C cycle).

An additional pathway: Alkalisiation of incident precipitation by the poplar canopy and litter

The flux of H^+ reaching the mineral soil in precipitation may be greater under open pasture compared to the combined effects of poplar trees and understorey pasture. Throughfall and stemflow under broadleaved trees is usually less acidic than incident rainfall (Parker 1983; Pastor & Bockheim 1984; Potter *et al.* 1991; McBride 1994; Houle *et al.* 1999; Neal 2002). Also, a significant proportion of free H^+ ions can be neutralised in reactions with forest floor organic horizons (Richter *et al.* 1983; Richter 1986; Pohlman & McColl 1988; Shibata *et al.* 1995). Cation exchange reactions on foliage, bark, and litter surfaces appear to be the primary mechanism for the neutralisation of this acidity (Potter *et al.* 1991; Cappellato *et al.* 1993; Shibata *et al.* 1995). However, if this was a major pathway for soil pH_w differences, then Zone 1 would be expected to have a higher pH_w than Zone 3. This was clearly not the case, as the soil pH_w in Zones 1 and 3 were not significantly different at either of the sites (Tables 4.1 & 4.2; Figure 4.2a). The annual fluxes of H^+ deposited,

especially in unpolluted regions, may also be relatively small compared with native soil acidity (Richter 1986). Furthermore, low CEC soils such as at Kiwitea are typically acidic and as a consequence are less susceptible to base cation displacement and leaching by atmospheric acids (Richter 1986).

4.5.1.2 Potential processes causing an increase in soil pH amongst the poplar stands, compared to in the open pasture

Before the stands of poplar were planted at Kiwitea, Suckling (1975) had measured a soil pH of 5.4 to 5.5 units in the same paddocks used for the present study. Based on this historical data, soil pH_w in the open pasture has not appreciably decreased over time, but instead has increased amongst the poplar trees. Furthermore, the significant relationships between soil pH_w and CCL at the two farm sites indicate that the trees have a direct effect on soil pH_w (Figure 4.2a & 4.5a).

Guevara-Escobar *et al.* (2002) found that simply mixing poplar leaf litter into soil from an open pasture increased its pH_w. Noble *et al.* (1996) reported a similar effect for several other different tree species and also showed that the change in soil pH was dependent on the amount of litter added. In the latter study, the leaf litter contained an excess of inorganic cations over anions, with the charge balance maintained by synthesised organic acid anions. From this it was reasoned that during the decomposition of leaf litter, oxidation (decarboxylation) of organic acid anions would consume H⁺ from the soil, causing an increase in soil solution pH. Other alkalising-mechanisms proposed are that organic acid anions and functional groups are protonated (Hoyt & Turner 1975; Wong *et al.* 1998; Marx *et al.* 2002) or exchange with the terminal OH⁻ ions of soil minerals (Hue *et al.* 1986; Hue & Amien 1989). Out of the major cations in leaf litter, the level of Ca was highly correlated with ash alkalinity, which in turn was used as an estimate (index) of the organic acid anion content (Noble *et al.* 1996; Noble & Randall 1999). In summer, the Ca concentration in the poplar leaves at Kiwitea and Hautope 1 was 4- and 6-times greater than in the open pasture herbage, respectively (refer to Sections 5.4.7 & 5.4.8).

Several studies have shown that poplar leaves contain a greater ratio of major inorganic cations-to-anions (Lousier & Parkinson 1976; Pastor & Bockheim 1984; Noble *et al.* 1996; Singh 1998; Berthelot *et al.* 2000), with very little Ca or Mg, relative to other

ions, being retranslocated prior to leaf fall (Baker & Blackmon 1977; McColl 1980; Pastor & Bockheim 1984; Singh 1998). Thus, at both Kiwitea and Hautope 1, the oxidation of synthesised organic acid anions, during the decomposition of fallen poplar litter, could have been a major pathway for increasing the soil pH_w (Haynes & Mokolobate 2001). The effect depending on the amount of poplar leaf added to the soil, which in turn is related to CCL. Alternatively, the organic acid anions may have leached from the poplar foliage as a salt with mobile inorganic cations such as K and been carried into the soil via throughfall and stemflow (Parker 1983).

However, as previously discussed for the C cycle in Section 4.5.1.1, an excess uptake of inorganic cations over anions into plant roots must be matched by the excretion of H⁺ back into the soil to maintain charge neutrality (Binkley & Richter 1987; Bolan *et al.* 1991). This counter-balancing any alkalinity created from the oxidation of the organic acid anions. Therefore, in order for the above process to make the topsoil more alkaline an equal amount of acidity has to be imparted somewhere else within the soil profile (Noble *et al.* 1996; Tang *et al.* 1999; Marschner & Noble 2000). In other words, alkalinity is not independently synthesised through this mechanism, but is simply transferred (Haynes & Mokolobate 2001). This could explain why in the 75-150 mm of soil at Hautope 1 pH_w was lower amongst the poplar trees, compared to the open pasture, while the situation was reversed in the top 75 mm of soil (Table 4.2). Greater cycling of nutrients through denser stands of poplar would have a compounding effect, and this occurred in the lower, less well buffered, 75-150 mm of soil at Hautope 1 (Figure 4.5a). In contrast, pH_w levels within both soil strata at Kiwitea were higher amongst the poplar trees than in the open pasture. These site differences may have been caused by the dense subsoil (fragipan) at Hautope 1 (refer to Section 2.3.1.2) forcing the poplar trees to absorb nutrients from shallower soil horizons, whereas, the more permeable soils at Kiwitea would have allowed deeper and more extensive root development.

Uncoupling of the C cycle through the accumulation of SOM in Zone 1 at Hautope 1 (Table 4.2) could also enhance soil acidification, if the excess inorganic cations over anions in the accumulated SOM were originally sourced *in situ* (Richter 1986; Bolan *et al.* 1991; de Klein *et al.* 1997; Giddens *et al.* 1997; Parfitt *et al.* 1997; Tang *et al.* 1999; Marschner & Noble 2000).

Another pathway in which organic matter, rich in organic acid anions and inorganic cations, could have been added to the topsoil amongst the poplar trees was through the camping of grazing animals. Sibbald & Agnew (1996) found that widely spaced trees acted as a focal point where sheep congregated, rested, defecated, and urinated to a greater extent than in the inter-canopy gap areas. If this dung and urine came from ingested open pasture herbage, which in turn was rich in organic acid anions and inorganic cations, then its decomposition and mineralisation in the soil under the trees would cause the net consumption of H^+ (or release of OH^-) (Wong & Swift 2003). This is because the counter-balancing acidifying processes originally associated with the synthesis of this herbage, before it was ingested, occurred in the open pasture and not under the trees (refer to Section 4.5.1.1). Animal dung containing a high concentration of Ca and Mg relative to inorganic anions is normally balanced with carbonate (CO_3^{2-}), giving it a pH in the range of 7.0-8.0 (Haynes & Williams 1993). Several researchers have measured significant increases in soil pH below dung patches (During *et al.* 1973; Haynes & Williams 1991; Whalen *et al.* 2000). Nguyen & Goh (1992) found consistently higher soil pH levels in animal camp areas compared with non-camp areas in permanent pastures that had been grazed and fertilised for more than 15 years.

Out of the two farm sites investigated, the potential for transferring alkalinity from the open pasture to amongst the trees in the form of dung deposits was greater at Hautope 1. This was because the paddocks at this site had a greater mix of tree and large open pasture areas, whereas, at Kiwitea the poplar stands more homogeneously covered the paddocks. The K concentration in soils has been used as an indicator of nutrient transfer by grazing animals (Hawke & Tombleson 1993; Hawke & Gillingham 1996; Gillingham & Hawke 1997). At Hautope 1, soil K was greater amongst the poplar stands, especially directly below the poplar crowns (Zone 1), compared to in the open pasture (Table 4.2). This indicated that at this site animal camping under the trees could have been a significant factor. Conversely, amongst the poplar stands at Kiwitea the concentration of soil K tended ($P < 0.1$) to be greater at the centre of the inter-canopy gap (Zone 3) in comparison to the open pasture (Table 4.1).

The translocation of exchangeable Al from upper to lower soil strata could also have contributed to the changes in soil pH at each site (Smith *et al.* 1995). Al contributes to soil acidity through the way in which it undergoes hydrolysis (depending on the pH of the soil

solution) to produce H^+ (Binkley & Richter 1987; McBride 1994). Many organic compounds (e.g. tannins, phenolics, other soluble organic acids/anions) released into the soil from tree leachates, root exudates, litter and its decomposition products can temporarily complex Al (Malcolm & McCracken 1968; Pohlman & McColl 1988). In soluble form, these organic-Al complexes can be leached down the soil profile (Bloomfield 1954; DeLong & Schnitzer 1955), where they are subsequently broken down by oxidation and microbial attack, or alternatively they become saturated with metals and precipitate out of solution (Davies 1971; David *et al.* 1995; Fox 1995). However, at both sites the overall contribution of exchangeable Al to soil acidity was likely relatively small due to the low amount of sesquioxides present (as indicated by the low ASC) and relatively high soil pH (Noble *et al.* 1996; Wong *et al.* 1998, 2000).

4.5.2 The effect of overstorey environment on major plant-available cations

Overall, the concentrations of major plant available cations (K, Ca, Mg, & Na) in both Zones 1 and 3 were either similar to or greater than in the open pasture (Table 4.1 & 4.2). Most cations were also positively, but weakly, related to CCL (Figure 4.2 & 4.4). However, the relative differences in cation concentration amongst the three main overstorey environments, and with increasing CCL, varied markedly between the two farm sites. For example, at Kiwitea a positive linear relationship between CCL and Mg in the upper 0-75mm of soil was found in both Zones 1 and 3, while for K it was restricted to Zone 3 (Figure 4.2c,d), whereas, the exact opposite occurred at Hautope 1 (Figure 4.4a,c). Guevara-Escobar *et al.* (2002) also measured similar or greater concentrations of major cations in the topsoil directly below young (5 year old) and mature (>25 year old) poplar trees when compared with adjacent open pastures. However, the present study shows that the trees influence is not solely restricted to within the crown domain, but can extend well into the inter-canopy gap area.

Hawke & O'Connor (1993) and Perrott *et al.* (1999) found the concentration of exchangeable cations (K, Ca, Mg, & Na) in the top 0-75mm of soil decreased under older stands and greater tree stocking rates of *P. radiata*. Nevertheless, for New Zealand paired-site studies the relative difference between tree and adjacent open pasture/grassland areas has been variable in magnitude and direction (Maclaren 1996; Giddens *et al.* 1997; Parfitt *et al.* 1997; Alfredsson *et al.* 1998).

Potassium (K)

At both farm sites, plant available K in the upper 0-75mm of soil was higher amongst the poplar trees (Zones 1 & 3) than in the open pasture, which supports the findings of Guevara-Escobar *et al.* (2002) under mature poplar trees, but not young trees, in the same region as Kiwitea. High rates of nutrient return in litterfall, throughfall, and stemflow, along with nutrient transfer by grazing animals and reduced leaching all likely contributed to the elevated levels of K in the topsoil amongst the trees (Adams & Boyle 1979; Pastor & Bockheim 1984; Sibbald & Agnew 1996; Parfitt *et al.* 1997). In forest ecosystems K is largely cycled in throughfall rather than litterfall (Carlisle *et al.* 1966; Parker 1983; Swank 1986, cited Blair 1988). Nevertheless, Guevara-Escobar (1999) found that adding senesced poplar leaves to an open pasture soil increased the level of exchangeable K 4-fold after two months of incubation. Little K, Mg, or Ca is stored in poplar tissue over winter (Baker & Blackmon 1977). The higher soil pH amongst the poplar trees would also enhance K adsorption through its positive effect on the soil's cation exchange capacity (CEC; Haynes & Williams 1993).

In comparing the two sites for levels of K there was no consistent pattern between the two overstorey environments amongst the trees. As noted above, at Hautope 1 plant available K in the upper 0-75mm of soil was significantly greater in Zone 1 than Zone 3, which was the reverse of what was found at Kiwitea. In Hautope 1's more extreme summer-dry climate grazing animals seeking shade directly below the poplar crowns (Zone 1) may have transferred K in dung and urine above that required by the trees and understorey pasture or lost through soil leaching. Furthermore, the higher SOM content in Zone 1 (Table 4.2) would have increased the soil's CEC and thus its ability to retain K (Williams 1980). In contrast, at Kiwitea under a milder and less heterogeneous microclimate created by the higher proportion of tree cover, the K returned to the soil in dung and urine may have been more evenly distributed over the entire paddock. A higher concentration of K in Zone 3 could then have resulted from an overall lower demand from the pasture in comparison to the combined demand from the trees and understorey pasture. Alternatively, grazing animals may have actually preferred the limited canopy-gap areas and thus returned a greater amount of dung and urine to this overstorey environment.

Sodium (Na)

At Hautope 1, the higher concentration of plant available Na in Zone 1, followed by Zone 3, and then the open pasture was probably influenced by the same factors affecting the relative concentrations of K. Additional Na from outside of the tree-pasture system would also have been added to Zone 1 by the large surface area of the trees catching sea salt (Parker 1983; Parfitt *et al.* 1997). Dry deposition of Na in sea salt would also have occurred at Kiwitea. However, it is unclear why the concentrations of plant available Na at this site did not vary significantly between the three main overstorey environments, or change with increasing CCL. The elevated concentration of other major cations (e.g. Ca, Mg, & K) in the soil amongst the trees may have displaced or prevented Na from being adsorbed onto the more limited cation exchange sites (Fisher & Binkley 2000), with the Na in soil solution leaching from the free draining soil under high rainfall (refer to Section 2.3).

Calcium (Ca)

At Kiwitea several factors likely caused the increase in plant available Ca in the upper 0-75mm of soil under greater CCL (Figure 4.2b). In comparison to the open pasture, more Ca would have been added to the soil surface through the Ca rich poplar leaf litter. As previously discussed in Section 4.5.1.2, the Ca concentration in poplar leaves at Kiwitea in summer was 4-times greater than in the open pasture herbage, with little re-translocation or leaching of this cation likely occurring from tree leaves before leaf fall (Parker 1983; Pastor & Bockheim 1984; Potter *et al.* 1991). Assuming this site had a net primary production (NPP) capacity of 13 t DM/ha/yr, with poplar leaves making up 3.1 t DM/ha/yr in the tree-pasture system (Guevara-Escobar 1999), it was estimated that annually twice as much Ca was added to the soil under the trees relative to the open pasture (Appendix 4.2). However, for enrichment to occur, the Ca mineralised from leaf litter needed to originally have come from some other soil stratum (Alban 1982; Parfitt *et al.* 1997). Under increasing CCL, tree leaf litter makes up a larger proportion of the total organic matter cycled in the soil, while less Ca would be lost from the system through nutrient leaching or the grazing animals. The higher soil pH amongst the trees (Table 4.1; Figure 4.2a) would also increase the soil's ability to retain Ca, but this may have been negated to some extent by the lower SOM content (Table 4.1; Figure 4.3b). The absorption of soil Ca by trees is usually high (Fisher & Binkley 2000). This could explain why the concentration of Ca in Zone 3 was

only significantly greater than the open pasture, instead of both Zones 1 and 3 when averaged over the entire range of CCLs (Table 4.1).

At Hautope 1, the similar level of plant available Ca in the upper 0-75 mm of soil across the three main overstorey environments may have been caused by the less marked differences in soil pH (Table 4.2), more restricted rooting zone caused by the dense subsoil, and overall lower leaching potential of the site (refer to Section 2.3). The restricted rooting zone would reduce the ability of the trees to absorb Ca from lower soil horizons and transfer it to the soil surface, while the lower leaching potential of the site would reduce the amount of Ca lost especially from the open pasture. In addition, considerable amounts of Ca may have been immobilised in the build up of SOM directly below the trees (Zone 1; Table 4.2). Within the 75-150 mm soil stratum at Hautope 1, the lower levels of plant available Ca amongst the poplar trees (Zones 1 & 3) than in the open pasture was likely related to the lower soil pH, along with the trees being forced to take up Ca from this soil depth because of the dense subsoil (refer to Section 2.3.1.2).

Magnesium (Mg)

Similarly to Ca at Kiwitea, the increase in plant available Mg in the upper 0-75mm of soil under higher CCL at both farm sites (Figures 4.2c & 4.4c) was likely related to considerable Mg inputs from poplar leaf litter (Parfitt *et al.* 1997; Davis 1998; Guevara-Escobar 1999; Sharma *et al.* 2001). Adams & Boyle (1979) found that adding *Populus grandidentata* Michx. leaf leachate to the topsoil of a sandy Michigan spodosol enriched the latter with Mg (and also K). In marine climates, throughfall and stemflow transferred to the soil directly below trees (Zone 1) can also be enriched in Mg through the deposition of sea salt (Parker 1983; Giddens *et al.* 1997; Parfitt *et al.* 1997). This latter process would help counter the loss of Mg from the soil through tree uptake. Alternatively, at Hautope 1 there may have been considerable transfer in dung (Hawke & Tomblinson 1993) and greater weathering of Mg-rich clays (Saunders 1978) in the more restricted root zone (Alban 1982).

4.5.3 The effect of overstorey environment on major plant-available anions

Phosphate (P)

The similar Olsen-P values among the three main overstorey environments at Kiwitea was somewhat surprising, given that the soil amongst the trees contained less SOM (Table 4.1), which was also likely to be more recalcitrant (refer to Section 4.5.1.1) than in the open pasture. A lower SOM concentration would reduce the total size of the organic P pool, while the greater refractory nature of the SOM would reduce the rate at which the organic P is mineralised. Amongst the trees, the higher soil pH_w (Table 4.1) and also the release of appreciable quantities of organic acid anions (refer to Section 4.5.1.2) could have increased the Olsen-P by reducing the ASC of the soil (Figure 4.3a,c); with the organic acid anions also directly competing for anion exchange sites (Saunders 1965; Roberts *et al.* 1996; Perrott *et al.* 1999). Furthermore, organic acid anions (e.g. oxalate) can release inorganic P into the soil solution through the dissolution of oxide surfaces (Fox & Comeford 1992; Fox 1995). Prior to leaf fall, a high proportion of phosphorus is retranslocated out of poplar leaves back into perennial tissue (Baker & Blackmon 1977; Pastor & Bockheim 1984). As a result, it is unlikely that poplar leaf litter is a major factor determining soil Olsen-P levels.

Based on soil samples taken in spring under young (5 year old) and mature (> 25 year old) poplar trees, Guevara-Escobar *et al.* (2002) also did not find any significant difference in Olsen-P between tree and adjacent open pasture environments. In contrast, most New Zealand studies investigating the effect of afforestation with pines have found that trees increase plant available P in the soil (Davis & Lang 1991; Hawke & O'Connor 1993; Condon *et al.* 1996; Chen *et al.* 2000; Cossen & Hawke 2000; Chen *et al.* 2003). This has been partly attributed to the enhanced mineralisation of organic P previously built up under pasture/grassland (Condon *et al.* 1996; Chen *et al.* 2000). Competition for adsorption sites by organic acid anions produced by the trees, desorption or dissolution of organic species, and the breakdown of soil aggregates exposing previously protected SOM may also be involved (Perrott *et al.* 1999).

All of the previously discussed mechanisms operating under poplar trees at Kiwitea would also likely be present at Hautope 1. However, at this site there was greater SOM in Zone 1 (Table 4.2), increasing the organic P pool available for mineralisation, and also there was

greater probability of nutrient transfer occurring by the grazing animals (refer to Section 4.5.1.2). This may have resulted in the elevated Olsen-P level in Zone 1 compared to Zone 3 and the open pasture (Table 4.2). Giddens *et al.* (1997) also attributed greater Olsen-P levels under *P. radiata* stands to animal transfer at 'paired sites' where grazing animals had free access to both environments.

In the lower 75-150mm of soil at Hautope 1, the increase in Olsen-P with greater CCL was probably due to the lower soil pH_w (Table 4.2; Figure 4.5a), increasing the positive charge on soil colloids, and a greater concentration of sesquioxides (Section 4.5.1.2). Both mechanisms would lead to a higher ASC, which at this soil depth was also positively related to CCL (Figure 4.5b).

Sulfate (SO₄-S)

Given that >90% of sulfur (S) in most topsoils is tied up in organic matter (McLaren & Cameron 1996; Fisher & Binkley 2000), it was surprising that at Kiwitea the immediately available SO₄-S levels in Zones 1 and 3 were marginally, but significantly, higher than in the adjacent open pasture (Table 4.1). At both farm sites in summer, the concentration of S in the tree leaves was around 2-fold greater than in the open pasture herbage (refer to Sections 5.4.7 & 5.4.8). Therefore, the addition of poplar leaf litter to the topsoil in both Zones 1 and 3 could have been a major pathway for SO₄-S enrichment. Based on a glasshouse soil incubation experiment, Guevara-Escobar (1999) reported that adding senesced poplar leaves (at a rate typical of a dense plantation) to an open pasture soil caused a 5-fold increase in immediately available SO₄-S after two months of incubation. In contrast, at Hautope 1 the concentration of immediately available SO₄-S in the upper 0-75 mm of soil was markedly higher in the open pasture compared to amongst the poplar trees (Table 4.2). This may have been caused by an uneven rate of SO₄-S added to the two systems through recent fertiliser applications (refer to Section 2.3.2.2).

Parfitt *et al.* (1997) also attributed a higher concentration of SO₄-S under *P. radiata* than in open pasture to the trees absorbing this nutrient from lower soil horizons and redistributing it in leaf litter onto the soil surface. In addition, a significant quantity of S from sea salt was also trapped by the tree crowns and transferred to the soil in throughfall (Parfitt *et al.* 1997). Soil SO₄-S enrichment via the latter process would also be expected in Zone 1 at

Kiwitea and Hautope 1 because of each of the sites relatively close proximity to the coastline.

The lower net herbage accumulation (NHA) amongst the trees at both farm sites (refer to Section 5.4.1) would reduce $\text{SO}_4\text{-S}$ taken up by pasture and lost through grazing animals (via product and excreta) (Saggar *et al.* 1990). Furthermore, similar mechanisms described for the N cycle in Section 4.5.1.1, such as greater net immobilisation and less leaching at key times of the year may also play a role in reducing the amount of $\text{SO}_4\text{-S}$ lost from the tree-pasture system.

4.5.4 Differences in soil organic carbon (SOC) between the overstorey environments

The effect of poplar trees on the SOC concentration was also not consistent across both farm sites. For example, when averaged over the range of overstorey densities (CCLs) investigated at Kiwitea, there was weak evidence ($P < 0.1$) that the open pasture had around 1% more SOC than amongst the poplar trees (Table 4.1). A weak-to-moderate negative linear relationship between CCL and SOC also occurred especially for Zone 1 (Figure 4.3b,d). This contrasted with Hautope 1, where Zone 1 contained approximately 0.5% more SOC than the other two main overstorey environments (Table 4.2) and CCL did not significantly affect the SOC concentration.

Several researchers have measured an increase in SOC (or associated SOM) when poplar trees are planted into previously cultivated (arable) agricultural land (Singh *et al.* 1989; Hansen 1993; Makeschin 1994; Park *et al.* 1994; Thevathasan & Gordon 1997; Marquez *et al.* 1999; Jha *et al.* 2000; Kaur *et al.* 2000; Tolbert *et al.* 2000; Saviozzi *et al.* 2001). Afforestation of permanent pasture/grassland is more variable, with the concentration of SOC usually being similar to or lower than in open pasture (Crowe 1993; Fuller & Anderson 1993; Saviozzi *et al.* 2001; Guevara-Escobar *et al.* 2002). Similar New Zealand results have also been found for afforestation of pasture/grassland with *P. radiata* and other conifer species (Giddens *et al.* 1997; Parfitt *et al.* 1997; Alfredsson *et al.* 1998; Perrott *et al.* 1999; Chen *et al.* 2000, 2003; Halliday *et al.* 2003). Davis & Condon (2002) concluded from an extensive review of these predominantly paired-site studies that, on average, conifers initially reduce the organic carbon concentration of pastoral soils;

however, after about 20 years there is generally little difference between the two ecosystems.

The organic carbon, or associated organic matter, content of a soil is governed simultaneously by the amount of organic matter added and lost from the soil (Foth 1978; Van Cleve & Powers 1995; Post & Kwon 2000). Therefore, at the Kiwitea farm site there are two possible ways for the SOC (and associated SOM) content to be greater in the open pasture than amongst the poplar trees: either there has been a comparatively greater amount of organic matter added to the open pasture soil, relative to its decomposition; or a greater amount of organic matter has been lost amongst the poplars, relative to its addition. Without baseline data taken prior to the trees being planted it is difficult to establish which of these mechanisms was mainly responsible for the observed difference, especially given that it is uncertain whether the soils of the improved hill pasture had attained a 'steady-state' in their carbon content.

Using the annual net herbage accumulation of pasture legume from Section 5.4.1 as a proxy for N₂-fixation (Lambert 1987; Guevara-Escobar 1999), a larger amount of organic matter would likely have been cycled in the open pasture through overall greater net primary production (NPP) compared to amongst the poplar trees (Walker 1956; Paustian *et al.* 1992; Cole *et al.* 1995; Murata *et al.* 1995). Given that the open pasture and poplar stands at Kiwitea were split into separate paddocks, little of the extra N or organic matter produced in the open pasture could have been transferred, via animal dung and urine, to among the poplar trees.

Counteracting the higher biomass-C inputs in the open pasture is the likelihood that poplar litter is more recalcitrant (refer to Section 4.4.2.1). However, the increase in soil pH and potentially the greater release of organic acid anions (refer to Section 4.4.2) would reduce bonding between organic matter and inorganic colloids (e.g. clays), this increasing the formers exposure to microbial and biochemical decomposition processes (Curtin *et al.* 1998; Perrott *et al.* 1999). Alternatively, the difference in SOC content may simply be the effect of soil erosion of the site prior to the planting of poplars, with the soil still in the process of slowly accumulating organic carbon back to previous non-eroded levels. Davis & Condon (2002) postulated that large differences in SOC for many of the paired-

site studies they reviewed could also have been caused by initial differences in soil carbon stocks rather than effects of afforestation *per se*.

Similarly, based on annual legume net herbage accumulation (refer to Section 5.4.1) as a proxy for N_2 -fixation at Hautope 1, amongst the poplar stands (Zones 1 & 3) would be expected to be more N limited than in the open pasture. However, unlike at Kiwitea, the poplar stands were intermixed with large open pasture areas in the same paddock, allowing greater opportunity for the transfer of N and organic matter to amongst the trees in the form of animal urine and dung (During *et al.* 1973; Paustian *et al.* 1992; Haynes & Williams 1993; Haynes & Naidu 1998; Metherell 2003). Also, in comparison to the open pasture, the trees ability to access soil water at depth in the summer-dry environment, along with higher levels of essential macro-nutrients, such as P and K, could have led to a greater NPP and thus litter-C inputs.

4.5.5 The ecological significance of the soil nutrient status at each site in relation to pasture production

The slightly-to-moderately acid soil pH_w and the medium-to-high levels of plant-available P and K in the upper 0-75 mm of soil at Kiwitea (Table 4.1) were all close to the biological optimum⁴ for maximum pasture production on New Zealand sheep and beef farms, irrespective of the overstorey environment (Edmeades *et al.* 1984; Morton *et al.* 1994). In contrast, the level of immediately available SO_4^{2-} -S at the time of sampling in spring was low for all three main overstorey environments and potentially could have limited pasture production (Morton *et al.* 1994).

Nevertheless, SO_4^{2-} -S deficiency throughout the rest of the year in the well-developed pasture was unlikely because of substantial inputs through: the addition of superphosphate fertiliser (refer to Section 2.3.2.1), mineralisation of SOM, and to a lesser extent, from rainfall (wet) and dry deposition (Saunders *et al.* 1981; Cornforth *et al.* 1983; Ledgard & Upsdell 1991). This was confirmed using Sinclair & Saunders (1984) mass-balance model, which accounts for such gains to the S cycle (Nguyen *et al.* 1993). Based on this model, it was estimated that the application of superphosphate at a rate of 220 kg/ha/yr should have

⁴ Soil test values that, on average for New Zealand sedimentary soils, are associated with 97% maximum pasture production (Morton *et al.* 1994).

provided the soil at Kiwitea with an extra 5.5 kg of S/ha above maintenance requirements (Appendix 4.1). Some additional SO_4^{2-} -S may also have been absorbed by pasture plants from further down the soil profile (Gregg *et al.* 1977), but was probably only a small amount given the very low levels of immediately available SO_4^{2-} -S measured within the 75-150 mm soil stratum (Guevara-Escobar 1999).

In the upper 0-75 mm of soil at Hautope 1, the moderately acid soil pH_w and medium-to-high levels of plant-available P, K, and SO_4^{2-} -S were close to the optimum for maximum pasture production on New Zealand sheep and beef farms (Edmeades *et al.* 1984; Morton *et al.* 1994).

The higher pH_w in the upper 0-75 mm of soil amongst the trees than in the open pasture at Kiwitea and Hautope 1 should have enhanced legume N_2 -fixation by increasing rhizobial nodulation (McKenzie *et al.* 1999) and molybdenum (Mo) availability (Sherrell & Metherell 1985; Wheeler & O'Connor 1998). However, as previously discussed for the C and N cycles in Section 4.5.1.1, the large pulse of C-rich poplar residues (including secondary organic compounds such as tannins) added to the soil in autumn could potentially reduce the size of the inorganic N, S, and P pools available for the understorey pasture plants. Furthermore, in the following spring, mineralisation of this stored N could reduce the competitive advantage of legumes over grasses in the generally N deficient sites, resulting in depressed understorey legume growth and N_2 -fixation from late-spring through until autumn (Luscombe & Fletcher 1982).

For New Zealand sedimentary soils the level of plant-available Ca and Na in the upper 0-75 mm of soil at Kiwitea was generally medium-to-low and low, respectively, whereas the level of Mg was high (Cornforth 1980; Blakemore *et al.* 1987). Hautope 1 also contained high levels of plant-available Mg, but had medium, as opposed to medium-to-low, levels of Ca and Na (Cornforth 1980; Blakemore *et al.* 1987). However, while these major soil cations play significant roles in the general chemistry, biology, and physical properties of soils, and are also important in relation to animal nutrition and health, the varying levels found in New Zealand soils seldom directly limit pasture production (During 1984; McLaren & Cameron 1996).

4.6 Conclusion

At Kiwitea and Hautope 1 the soil pH_w and concentration of essential major cations (Ca, Mg, K, & Na) and anions (P & SO_4-S) in the top 0-75 mm of soil amongst the poplar trees (Zone 1 & 3) were similar to, or greater than, in the adjacent open pasture. Nevertheless, based on the standard basic soil tests taken in spring, the soil fertility of both tree and open pasture environments was close to the biological optimum required for maximum pasture production on New Zealand sheep and beef farms. The only exception was SO_4-S at Kiwitea, which at the time of measurement was low in all three main overstorey environments. Therefore, it appears that poplar trees in summer-wet and summer-dry regions of the North Island, New Zealand, do not limit understorey pasture production through their effects on soil chemical properties.

Soil pH_w in the upper 0-75mm of soil was 0.2-0.7 units higher amongst the poplar trees than in adjacent open pasture. The increase in soil pH_w depended on CCL, but was also strongly affected by the pH_w buffer capacity of the soil. The influence of the trees on soil pH_w extended across the inter-tree gap (Zones 3) and was not restricted only to directly below the tree crowns (Zone 1). Chemical reactions involved with the addition of poplar organic material to the soil (e.g. ligand exchange, oxidation, and/or protonation of synthesised organic acid anions, & release of inorganic cations) were probably the main causes of the increase in soil pH_w . Lower HCO_3^- and NO_3^- leaching may also have reduced the rate of natural acidification in the soil amongst the trees (Zones 1 & 3). Conversely, greater transference of alkalinity away from the open pasture, in the form of animal products and excreta, may have occurred through this environment's overall higher grazing-animal carrying capacity. Comparison between the Kiwitea and Hautope 1 sites indicates that impact of poplars on soil pH_w is affected by the structure of the soil and poplars can even cause acidification (via excess cation/anion uptake) in the rhizosphere just above impermeable soil horizons such as fragipans.

In general, the concentration of major plant available cations in the top 0-75mm of soil increased under higher CCL, although there was considerable variation between sites and overstorey environments amongst the trees. Enrichment was likely caused by the redistribution of cations from lower soil horizons through poplar leaf litter and leachates, an increase in the CEC of the soil associated with higher soil pH_w , and lower soil water

leaching. External sources Na and Mg would also be added through the trees catching sea-salts. Variation in relationships between the two sites was probably caused by differences in SOM content, leaching potential, nutrient transfer by grazing animals, and soil structure (affecting tree rooting depth).

Amongst the trees (Zones 1 & 3), the release of appreciable quantities of organic acid anions into the soil (via poplar leaf litter and leachates) and the higher soil pH_w likely increased Olsen-P values. Site differences were then determined by the variation in SOM content between the three main overstorey environments. The level of $\text{SO}_4\text{-S}$ in the soil amongst the trees was probably enhanced directly from the tree litter itself and also from sea-salt deposition, while less $\text{SO}_4\text{-S}$ would have been lost through the grazing animals and soil water leaching. Similarly to cations, differences in animal grazing behaviour between the sites may have been a confounding factor for both Olsen-P and $\text{SO}_4\text{-S}$.

The poplar trees had contrasting effects on the levels of SOC at Kiwitea and Hautope 1. Without baseline data taken prior to tree planting, it is difficult to speculate what the probable causes were for the site differences. Variation in N availability may have been a significant factor through its affect on NPP and thus C inputs.

Amongst the trees (Zones 1 & 3), the addition of large quantities poplar litter and leachate to the soil (especially in autumn), reduced leaching via less soil water drainage, and a lower animal carrying capacity could potentially close/tighten the N, P, and S cycles. Further study of temporal changes (fluxes) in these major nutrients is needed, as changes in their concentrations could affect seasonal understorey pasture production, reduce fertiliser input costs, and also lower pollution of the wider environment. Some processes involved, such as the timing and quantity of leaf fall, could also be manipulated to improve synchronization between the supply of these soil nutrients and demand by understorey pasture plants.

4.7 References

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5 The effect of poplar overstorey density on understorey pasture production

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5.1 Introduction

The effect of poplar trees on annual pasture dry matter production, relative to adjacent open pasture, has been shown to range from a negligible decrease under young isolated trees (Gilchrist *et al.* 1993) to a 40-50% decrease under mature trees with high inter-crown interference (Crowe 1993; Guevara-Escobar *et al.* 1997). Similarly, in stands with low inter-crown interference poplars have little impact on the nutritive value of understorey pastures (Douglas *et al.* 2005). However, below mature stands with high inter-crown interference Guevara-Escobar *et al.* (1997) found the understorey pasture had a slightly lower nutritive value for grazing animals compared to an adjacent open pasture.

In New Zealand, pasture production measurements around poplars have been restricted to within close proximity of individual tree crowns (Gilchrist *et al.* 1993; Guevara-Escobar *et al.* 1997; Douglas *et al.* 2001, 2005). Although a tree's influence on understorey pasture decreases with greater distance from the base of its stem (Clements *et al.* 1988; Gilchrist *et al.* 1993) this relationship also depends on the size and proximity of the surrounding trees (Sibbald *et al.* 1991). Lack of information about how pasture production within the inter-tree gap area is affected over a range of stand densities is inhibiting the development of a predictive stand level model, which could be used by farmers and resource managers to gauge the impact of poplars on farm pastoral productivity. This information would also help to develop management strategies that minimise any negative effects that these trees might have when integrated into hill pasture systems.

In Chapter 3 canopy closure (CC) measured with a standard digital camera was shown to be a very good index of stand density and accounted for both the size and proximity of trees within a stand. As such, this index is used in this chapter to characterise the density of the poplar stands and is used to relate how changes in stand density affects understorey pasture productivity both directly below and in the gap between trees.

5.2 Methodology

5.2.1 Treatments and sampling positions

Similarly to Chapters 3 and 4, the broad range of overstorey (stand) densities previously developed in Chapter 2 formed the main treatment structure of this study. At all three farm sites, sampling amongst the poplar stands was restricted to within two main overstorey environments (or zones of tree influence): Zone 1, area directly below the vertical projection of the tree crown on the north-eastern corner of an experimental unit; and Zone 3, area at the centre of the vertically projected gap between the crowns of the four nuclei trees (Figure 5.1). To evaluate how representative the above sampling method was for an entire experimental unit, sampling was intensified at Kiwitea for two stand densities (50% & 70% CCL, each replicated twice). The total number of sampling zones was increased to five, spaced out along a linear transect running diagonally between two of the 'nuclei' trees defining an experimental unit (Figure 5.1).

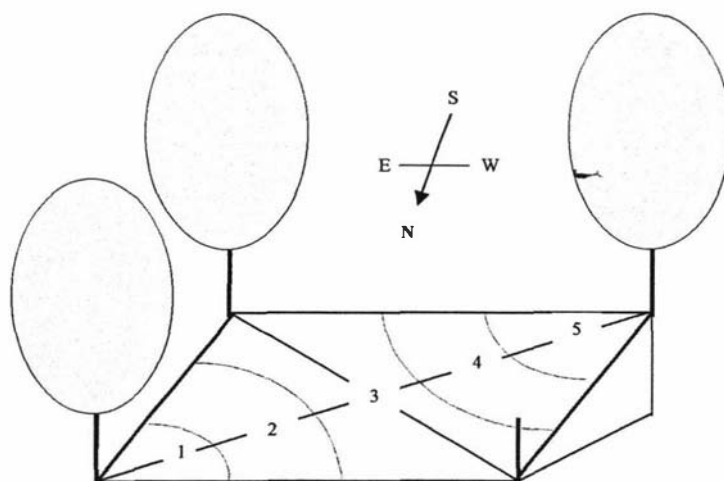


Figure 5.1 Intensified sampling zones used for a limited number of experimental units at Kiwitea: Zones 1 & 5 – directly below the individual tree crowns on the northeast and southwest corners of an experimental unit, respectively; Zone 3 - at the centre of the vertically projected canopy gap between the trees; and Zones 2 & 4 – transitional area midway between the centre of the vertically projected canopy gap and its respective northeast and southwest edge.

5.2.2 Measurements

5.2.2.1 Net herbage accumulation

Pasture net herbage accumulation (NHA) was measured on a dry weight basis using the standard double-trim technique (Radcliffe 1974; Lucas & Thompson 1994). Measurements were taken over two years at Kiwitea (October 1998 - September 2000), and for one year at Hautope 1 and 2 (May 1999 – April 2000). Under 0.7m² grazing exclusion cages pastures were trimmed with a portable shearing hand-piece to a uniform height of 25mm above ground. After a month, all re-growth above the pre-trimmed height was harvested from inside a 0.1m² metal quadrat and taken to the laboratory for processing. Following each harvest, the grazing exclusion cages were moved to a new location that was raked free of tree debris and trimmed. Each exclusion cage did not return to the same area for at least three months. Placement of cages was restricted to a medium hill-slope (13-25°) category (Saggar *et al.* 1990; López 2000). Harvests were missed in some winter and late summer/autumn months because of slow pasture growth. Overall, 6-7 harvests were taken each year.

In the laboratory, all tree material (leaves, catkins, small twigs, bark, etc.) was discarded from the herbage samples by hand sorting. The samples were then washed to remove any soil contamination and dried in a forced-draught oven at 80°C for 24 hours. Dried samples were weighed on electronic scales to 2 decimal places (d.p.). The NHA per unit area per day was calculated by dividing the dried herbage collected from each quadrat by the total number of days separating the initial trim and harvest cuts.

NHA data from individual cuts was pooled to provide seasonal and annual totals, which are presented relative to the open pasture environment. Where a NHA cut interval overlapped across two seasons, the measurement was assigned to the latter season, because this is when the vast majority of herbage accumulated (Radcliffe 1974). Seasons were related to the phenological cycle of the trees: spring - bud burst to full leaf; summer - full leaf; autumn – leaf fall; and winter – no leaf. At all three farm sites, bud burst began in September and full leaf display was not attained until late October. Summer lasted from November until February, when premature leaf fall occurred, likely because of a combination of soil moisture stress and leaf-rust disease (McElwee & Knowles 2000).

At Kiwitea and Hautope 2 the trees were completely devoid of leaves by June. In contrast, leaf fall finished one month earlier in May at Hautope 1.

NHA was scaled up to a stand-level (weighted) estimate using the general equation:

$$\text{Weighted NHA}_{(\text{Zones 1 \& 3})} = (\text{Zone 1 NHA} \times \text{Zone 1 area}) + (\text{Zone 3 NHA} \times \text{Zone 3 area})$$

The two area variables for the above equation were calculated as the proportion of an experimental unit that each zone covered on a horizontal plane. This, in turn, was derived from a simple linear relationship between HPCC and CCL (refer to Section 3.2.2). At Kiwitea, NHA for the more intensively stratified experimental units was scaled up to a stand-level estimate using the equation:

$$\text{Weighted NHA}_{(\text{Zones 1-5})} = (\text{Zone 1 NHA} \times \frac{1}{2} \text{ Zone 1 area}) + (\text{Zone 2 NHA} \times \frac{1}{3} \text{ Zone 3 area}) + (\text{Zone 3 NHA} \times \frac{1}{3} \text{ Zone 3 area}) + (\text{Zone 4 NHA} \times \frac{1}{3} \text{ Zone 3 area}) + (\text{Zone 5 NHA} \times \frac{1}{2} \text{ Zone 1 area})$$

5.2.2.2 Residual herbage mass below 25mm trimming height

At the end of each season, an area similar to where each grazing exclusion cage was sited was trimmed to 25mm above ground level, with the cut herbage above this height removed and discarded. Immediately afterwards, a second cut to ground level was made inside a 0.1m² quadrat, with all of the remaining herbage harvested and taken to the laboratory for processing (refer to Section 5.2.2.1). Residual herbage mass (RHM) was calculated in kg DM/ha for each season. Quadrat cuts were taken at Kiwitea on 22/10/99, 11/03/00, 17/05/99, and 10-11/08/99 for spring, summer, autumn, and winter, respectively. Whereas, at Hautope 1 and 2, residual herbage cuts were made on the 1-2/10/99, 12-13/03/00, 14/05/99, and 17-18/08/99 for the same respective seasons. The summer season cut for all three farm sites was delayed for two months because of very low pasture cover in February and March 2000.

5.2.2.3 Pasture composition by weight

Coinciding with the timing of NHA measurements, additional 0.1m² quadrat samples for pasture composition analysis were cut from under the grazing exclusion cages in both late spring and summer. Field-sampling dates at Kiwitea over the two-year period were 29-30/10/98 and 22/10/99 for spring, and 07/01/99 and 4-5/03/00 for summer. In comparison,

Hautope 1 and 2 were sampled on the 1-2/10/99 and 12-13/03/00 for spring and summer, respectively. All of the experimental units (microsites) selected in Chapter 2 were sampled, except for the paired units located on a south facing aspect at Kiwitea. These experimental units were excluded to limit comparisons at this site to a single northerly aspect (refer to Section 2.3, Table 2.2). Amongst the trees, sampling was restricted to Zones 1 and 3 (Figure 5.1).

In the laboratory, each fresh sample was initially spread out over a clean bench and any particularly large pieces of plant material (e.g. *Plantago lanceolata* leaves) were torn into smaller pieces so that all plant material was of a fairly similar size. The quantity of herbage was reduced down to a manageable size for hand sorting by repeatedly mixing and then discarding half of the sample. Sub-samples prepared for sorting were dissected into high fertility responsive (HFR) grasses, low fertility tolerant (LFT) grasses, legume species, other species, and dead pasture material. HFR grasses consisted of *Lolium perenne*, *Dactylis glomerata*, *Holcus lanatus*, and *Poa* spp. LFT grasses included species such as *Agrostis tenuis*, *Cynosurus cristatus*, and *Anthoxanthum odoratum*. Tree material was excluded from the analyses. Dissected herbage was separately dried in an oven at 60°C for 48 hrs and weighed using electronic scales to 3 d.p. The dry weight of each category was expressed as a percentage of the total herbage dry weight in the dissected sub-sample (excluding tree material).

5.2.2.4 Pasture nutritive value

At Kiwitea and Hautope 1, a third 0.1m² quadrat for pasture nutritive value analysis was cut from under the grazing exclusion cages at the same time as the pasture botanical composition samples. However, sampling was restricted to a limited range of stand densities at each of these sites. This range consisted of an open pasture control, and experimental units under low and medium-to-high overstorey densities (Appendix 5.1). Each overstorey-density class was replicated twice and contained two sub-units (e.g. Zones 1 and 3 amongst the trees).

In the laboratory, each sample was thoroughly mixed and a sub-sample taken to measure dry matter content. The latter was calculated from measurements of the sub-samples fresh (wet) and dry weights (measured to 2 d.p.). On the same day of collection in the field, about 200g of mixed herbage from each main sample was washed and placed separately in

an oven to be dried at 60°C for 48hrs. The dried herbage was ground in a 'Cyclotec Mill' to pass through a 1 mm diameter sieve and then stored in airtight containers until subjected to chemical analysis. Feed value indices were measured by near infrared reflectance spectroscopy (NIRS; Corson *et al.* 1999) at the ICP Facility, Grasslands Research Centre, Palmerston North. Samples were analysed for crude protein (CP), lipid, soluble carbohydrates (Sol CHO), neutral detergent fibre (NDF), acid detergent fibre (ADF), *in vitro* organic matter digestibility (OMD), and metabolisable energy (ME).

5.2.2.5 Pasture mineral content

Two strips of pasture, each approximately 0.5m long, were cut with a portable shearing handpiece (75mm wide) from around the same locations and at the same time as the nutritive value cuts. However, the samples were taken from outside of the grazing exclusion cages to prevent possible contamination by the cages galvanised coating (Guevara-Escobar 1999; Mackay *et al.* 1995). The methodology for processing the samples in the laboratory was the same as that used for nutritive value analysis, except the dry matter content of the fresh herbage was not measured. The mineral concentration in the samples was measured by Plasma Emission Spectrometry, at the ICP Facility, Grasslands Research Centre, Palmerston North.

5.2.2.6 Nutritive value and mineral content of poplar leaves

At Kiwitea and Hautope 1, poplar leaves (lamina + petioles) were plucked from lower tree branches in spring, summer, and autumn for nutritive value and mineral content analysis. Samples were taken from one nuclei tree associated with each of the experimental units used for determining pasture nutritive value and mineral contents (i.e. 4 trees were sampled per site per season). Leaves collected in autumn were senescing and had started to turn yellow. Field-sampling dates at Kiwitea were 22/10/99, 07/01/00, and 04/04/00, for spring, summer, and autumn, respectively. In comparison, Hautope 1 was sampled on the 17/10/99, 05/01/00, and 29/03/00 for the same respective seasons. The methodology for processing the samples in the laboratory was the same as that used for nutritive value analysis. The nutritive value of the poplar leaves was measured by Near Infrared Reflectance Spectroscopy (NIRS), while the mineral content was measured by Plasma Emission Spectrometry.

5.3 Data analyses

5.3.1 Net herbage accumulation and residual herbage mass

The relationship between NHA and CCL was examined by regression analysis, using the REG and NLIN procedures of SAS[®] (version 8.02 for Windows[®], SAS Institute, Inc. 1999). For each site, the above relationship was separately studied for Zone 1, Zone 3, and at the stand level (weighted across an experimental unit). Regression model selection was by the 'forward method', where initially the most appropriate model is assumed to be a straight-line (Kleinbaum *et al.* 1998). The adequacy (quality of fit) of each regression model was checked via inspection of scatter, residual, and normal probability plots, along with more formal test statistics (SAS 1990). CurveExpert[®] (version 1.37 for Windows[®], Hyams 2001) and applicable published ecological studies were also used to determine potential regression models for the data. For each relationship, the simplest model with the smallest standard error of prediction (RMSE) and no trend in the residual plots was selected. Slopes of the relationships for different sites, seasons, or years (Kiwitea), were compared using t-tests (comparisons only made between the same regression models).

A split plot analysis of variance (ANOVA) was conducted for the more intensively sampled experimental units at Kiwitea, using the GLM procedure of SAS[®], to test the effects of CCL (main plots), understorey location (subplots), and their interaction on NHA. Where appropriate, individual treatments, including an open pasture control, were compared using 95% CI.

Similar statistical analyses were carried out for residual herbage mass.

5.3.2 Pasture composition, nutritive value, and mineral content

For each site, a split-plot-in-time analysis of variance (ANOVA) was conducted, using the GLM procedure of SAS[®], to test the effects of the overstorey environment (main plots), season (subplot), and their interactions on the various pasture characteristics. In the general linear model, a 'replicate nested within overstorey environment' parameter was treated as a random-effect, while all other parameters were considered fixed (Hedderley per. comm. 2002).

The 3 x 2 factorial design for the botanical species composition data was unbalanced, with treatment combinations having 4-10 replicates. As a result, Type 3 sums of squares were used instead of Type 1, due to their more conservative nature. The data sets were balanced for nutritive value and mineral concentration analyses.

Separate regression analyses were carried out for the two main overstorey environments amongst the poplar stands (Zones 1 & 3) and also for the two seasons (spring and summer). Differences between regression equations were tested by analysis of covariance (ANCOVA), using the GLM procedure of SAS[®] (Kleinbaum *et al.* 1998; Littell *et al.* 1991). Where regression equations for the two main overstorey environments amongst the poplar stands (Zones 1 & 3) coincided (i.e. were not significantly different in intercept or slope) the data were combined into a single function representing the entire understorey environment.

5.3.3 Poplar leaves nutritive value and mineral content

Differences in poplar leaf nutritive value and mineral content between spring, summer, and autumn were analysed by multivariate analysis of variance (MANOVA), using the ANOVA procedure of SAS[®] (Littell *et al.* 1991).

5.3.4 A check of underlying model assumptions

Diagnostic options provided in SAS[®] were used to check the underlying regression and ANOVA assumptions. These included studentised residual and normal probability plots, along with more formal test statistics (SAS 1990). Several data sets required transformation to meet either the assumption of normality or homogeneity of variance. Pasture characteristics that required transformation are clearly identified in the appropriate figures and tables.

5.4 Results

5.4.1 Annual net herbage accumulation

5.4.1.1 Directly underneath the poplar crowns

Annual net herbage accumulation (ANHA) in the open pasture was 13.2 ± 0.9 , 13.4 ± 0.9 , 10.9 ± 0.2 , and 13.5 ± 1.7 t DM/ha (mean \pm SEM) at Kiwitea in 1998-99, 1999-00, and at Hautope 1 and 2, respectively. At all of the sites, ANHA was lower directly below the poplar crowns (Zone 1) than in the open pasture (Figure 5.2a). In particular, the rate of decline in ANHA was very high when initially going from the open environment to a low poplar canopy cover (CCL). The lack of data points between 0-40% CCL made it difficult to identify the exact form of the relationship and as a result, a number of potential regression models, ranging from a gentle exponential to a sharp hyperbolic decay curve, fitted the data reasonably well. Out of the potential regression models tested, a simple power curve was selected because of its slightly better fit in relation to the RMSE and distribution of residuals. Overall, Zone 1 ANHA averaged across all three sites became relatively constant at around 50% of open pasture beyond approximately 20% CCL (Figure 5.2a). Again, the lack of data points over the lower CCL range inhibited a more accurate estimation of this threshold.

The trees effect on Zone 1 ANHA varied significantly between sites (Appendix 5.1.1 & 5.2a). At Hautope 1, the rate of decline in ANHA with increasing CCL was less than at Kiwitea, and on average ANHA was reduced to $65\% \pm 1\%$ of the open pasture, compared to 47%, 38%, and $44\% \pm 3\%$ for Kiwi98-99, Kiwi99-00, and Hautope 2, respectively. Although the rate of decline in ANHA, relative to the open pasture, did not vary significantly between the two measured years at Kiwitea (Appendix 5.1.1 & 5.2a), ANHA directly below poplar crowns was on average marginally higher in 1998-99 than 1999-00 (paired t-test; $P < 0.0001$). The high level of error associated with the small sample size ($n=8$) and high variance, especially for open pasture measurements, in the relationship for Hautope 2 reduced its statistical power for making comparisons with the other sites (Appendix 5.1.1 & 5.2a).

5.4.1.2 Within the vertically projected canopy gap between trees

ANHA in the vertically projected gap between the trees (Zone 3) decreased from open pasture values at a constant rate with increasing CCL (Figure 5.2b). Across all sites, the rate of decline was $6.6\% \pm 0.5\%$ of open pasture production for every 10% increase in CCL (Figure 5.2b). Between the sites, Zone 3 ANHA at Hautope 1 and Kiwi98-99 appeared to decrease at a lesser rate than at Hautope 2 and Kiwi99-00. However, only the difference in the slope of the relationship for Hautope 1 and Kiwi99-00 was statistically significant (Appendix 5.1.2 & 5.2b). Zone 1 and 3 ANHA converged at around 80% CCL, indicating that at this level the poplar overstorey had become relatively homogeneous and closed (Figures 5.2a,b).

5.4.1.3 Weighted across the inter-tree space (stand level)

Stand level (weighted) ANHA decreased at a slightly diminishing rate with increasing CCL (Figure 5.2c). Pooled across all sites, ANHA under a CCL of 25%, 50% and 75% was estimated to be 77%, 60%, and 48% of the open pasture, respectively. Overall, the simple exponential decay regression model accounted for a high proportion of the variation in ANHA ($r^2=0.77$). However, the degree of negative curvature varied significantly between sites. Hautope 1 exhibited the least negative curvature, followed by Kiwi98-99, and then Kiwi99-00 and Hautope 2 (Appendix 5.1.3 & 5.2c). The high standard error associated with the Hautope 2 relationship resulted in it not being significantly different from any of the other sites (Appendix 5.1.3). Based on the individual site relationships predicted ANHA at 75% CCL varied anywhere between 35% and 65% of the open pasture (Appendix 5.1.3 & 5.2c).

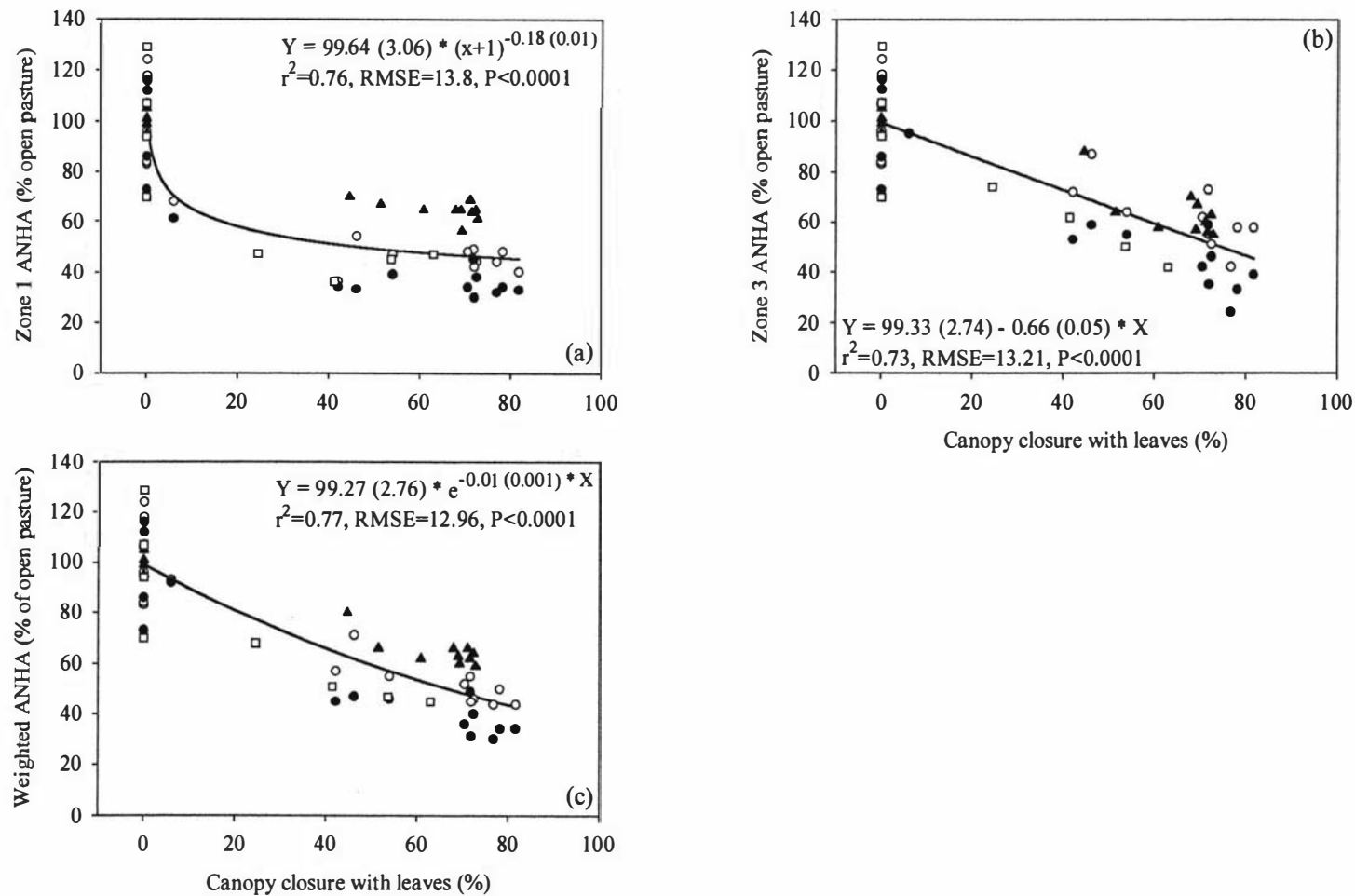


Figure 5.2 Annual net herbage accumulation (ANHA) over a range of in-leaf canopy closure ratios. Standard errors for regression coefficients are given in parentheses. Symbols: (○) Kiwitea98-99 (●) Kiwitea99-00, (▲) Hautope 1, (□) Hautope 2. Solid line - mean predicted response. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction.

5.4.1.4 Intensively stratified across the inter-tree space at Kiwitea

Across the inter-tree space, ANHA was significantly affected by the interaction between the density of the poplar stand, defined by its CCL, and the understory location (zone of tree influence) ($P=0.033$; Figure 5.3). Directly below the poplar crowns, on either the shade-facing (Zone 1) or sun-facing (Zone 5) side of the trees, ANHA was similar at around 42% of open pasture, irrespective of CCL. At a stand density of 70% CCL, ANHA within the gap centre (Zone 3) and adjacent intermediate/transitional areas (Zones 2 & 4) also did not differ significantly from Zones 1 and 5 ($P>0.05$). In contrast, at 50% CCL, ANHA in Zones 2, 3, and 4 increased to around 62% of open pasture production ($P<0.05$). The difference between Zone 4 ANHA at 50% CCL and Zone 3 ANHA at 70% CCL was not statistically significant ($P>0.05$; Figure 5.3).

In general, there was good comparability between stand level (weighted) estimates of ANHA made using either two or five zones of tree influence. Weighted ANHA based on Zones 1 & 3 was $55 \pm 4.2\%$ and $41.1 \pm 2.9\%$ of the open pasture under a CCL of 50% and 70%, respectively. This compared with $52.7 \pm 4.2\%$ and $41.1 \pm 3.7\%$ of open pasture production, respectively, estimated using the five zones of tree influence (Zones 1-5). Thus, while there is little difference between the methods in estimating ANHA at high stand densities, the more simplified method marginally overestimates herbage production ($<5\%$) at medium stand densities (Paired t-test; $P=0.0035$).

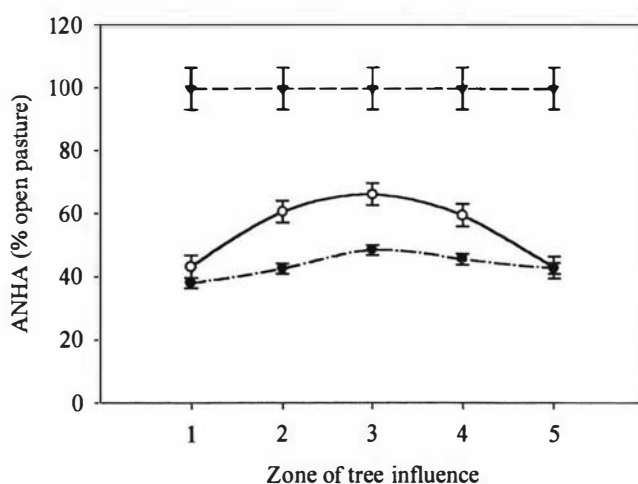


Figure 5.3 Annual net herbage accumulation (ANHA) stratified across the inter-tree space at Kiwitea (1998-2000). Vertical bars represent the standard error of the mean (SEM). Symbols: (▼) open pasture (○) 50% CCL (●) 70% CCL. Sample size: 20 experimental units with trees and 6 experimental units without trees (open pasture).

5.4.2 Seasonal net herbage accumulation

5.4.2.1 Summer and autumn

In summer (Figure 5.4) and autumn (Figure 5.5) the shape of the relationships for Zone 1, 3 and stand level (weighted) NHA was generally similar to those for ANHA (Figure 5.2). Overall, the rate of decline in NHA associated with increasing CCL did not vary significantly between the two consecutive seasons for each environment ($P>0.05$).

Averaged over both seasons, Zone 1 NHA became relatively constant at around 36% of open pasture production by at least 20% CCL (Figures 5.4a & 5.5a). Nevertheless, there were significant differences in the trees effect on Zone 1 NHA between sites/years. In summer, Zone 1 NHA at Kiwi99/00 was reduced to $27 \pm 3\%$ of open pasture production, compared with $45 \pm 4\%$, $38 \pm 2\%$, and $47 \pm 5\%$ for Kiwi98/99, Hautope 1 and Hautope 2, respectively. In autumn, Zone 1 NHA at Kiwi99/00 was reduced further to $18 \pm 3\%$ of open pasture production, while at Kiwi98/99, Hautope 1 and Hautope 2 understorey herbage accumulation was $44 \pm 4\%$, $42 \pm 4\%$, and $30 \pm 5\%$, respectively. Zone 1 NHA in the latter three sites/years did not vary significantly between the two consecutive seasons ($P>0.05$). However, unlike in summer, the difference between Kiwi99/00 and Hautope 2 in autumn was not significant ($P>0.05$).

In contrast to Zone 1, NHA in Zone 3 and at the stand level (weighted) decreased more slowly with increasing CCL (Figures 5.4b,c & 5.5b,c). For example, at 20% CCL Zone 3 and weighted NHA was 79% and 76% of the open pasture, respectively, when pooled across all sites and the two consecutive seasons. In both summer and autumn, Zone 3 NHA decreased at a significantly faster rate at Kiwitea in 1999-00 than 1998-99 ($P<0.05$). Whereas, at the stand level (weighted), over the same two seasons, the rate of decline in NHA at Kiwi99/00 was also significantly greater than Kiwi98/99 and Hautope 1 ($P<0.05$). Similarly to ANHA, the high error associated with the relationships determined for Hautope 2 would likely have reduced the statistical power for making comparisons with other sites (data not shown).

Overall, the strength of the summer relationships was strong (Figure 5.4). However, the strength of these relationships decreased to a more moderately strong level in autumn, mainly due to a disproportionately large amount of variation in the open pasture (Figure 5.5).

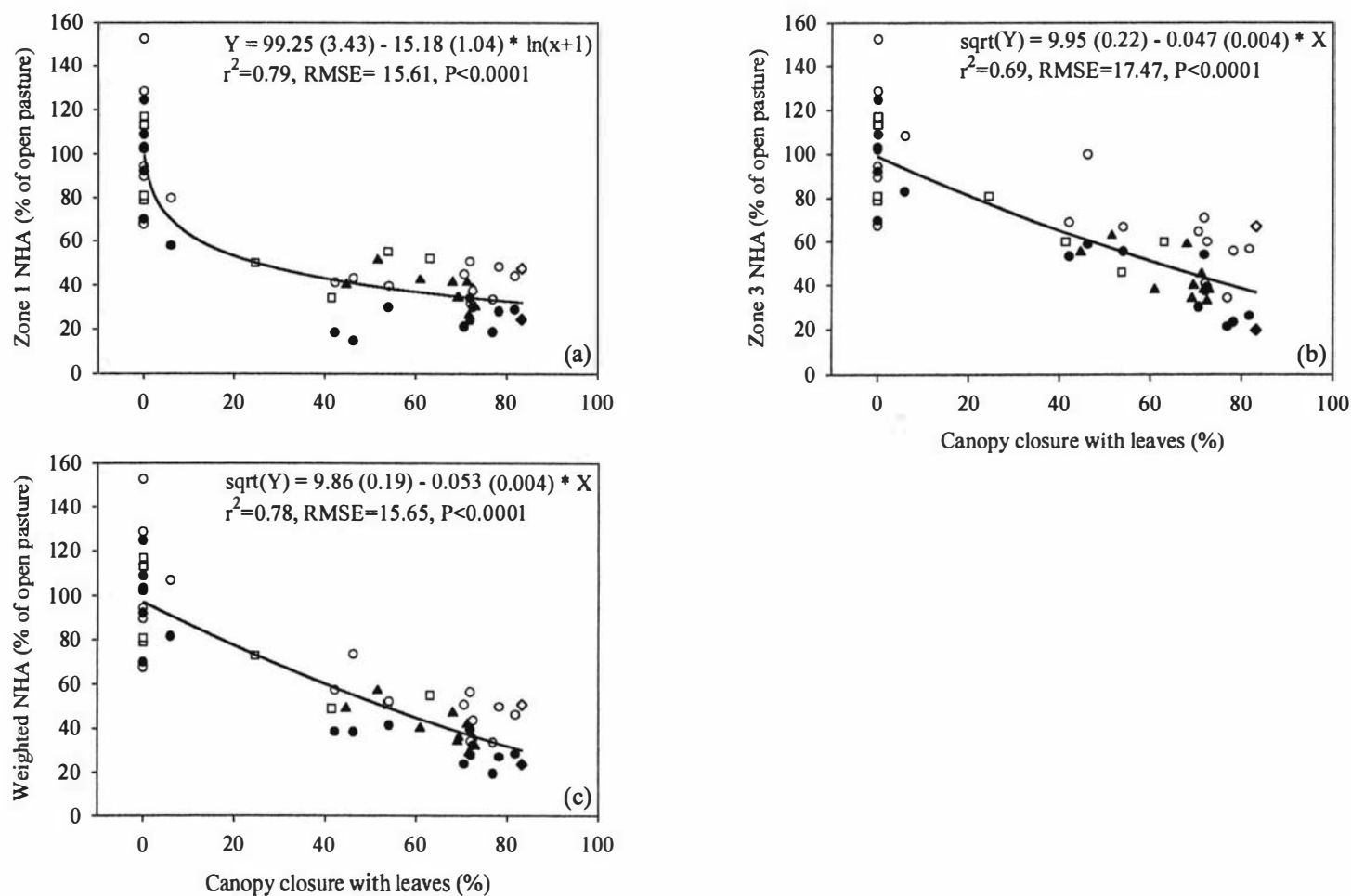


Figure 5.4 Summer net herbage accumulation (NHA) over a range of in-leaf canopy closure ratios. Standard errors for regression coefficients are given in parentheses. Symbols: (○) Kiwitea98-99 (●) Kiwi99-00, (◊) Southern aspect Kiwi98-99 (◆) Southern aspect Kiwi99-00, (▲) Hautope 1, (□) Hautope 2. Solid line - mean predicted response. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction.

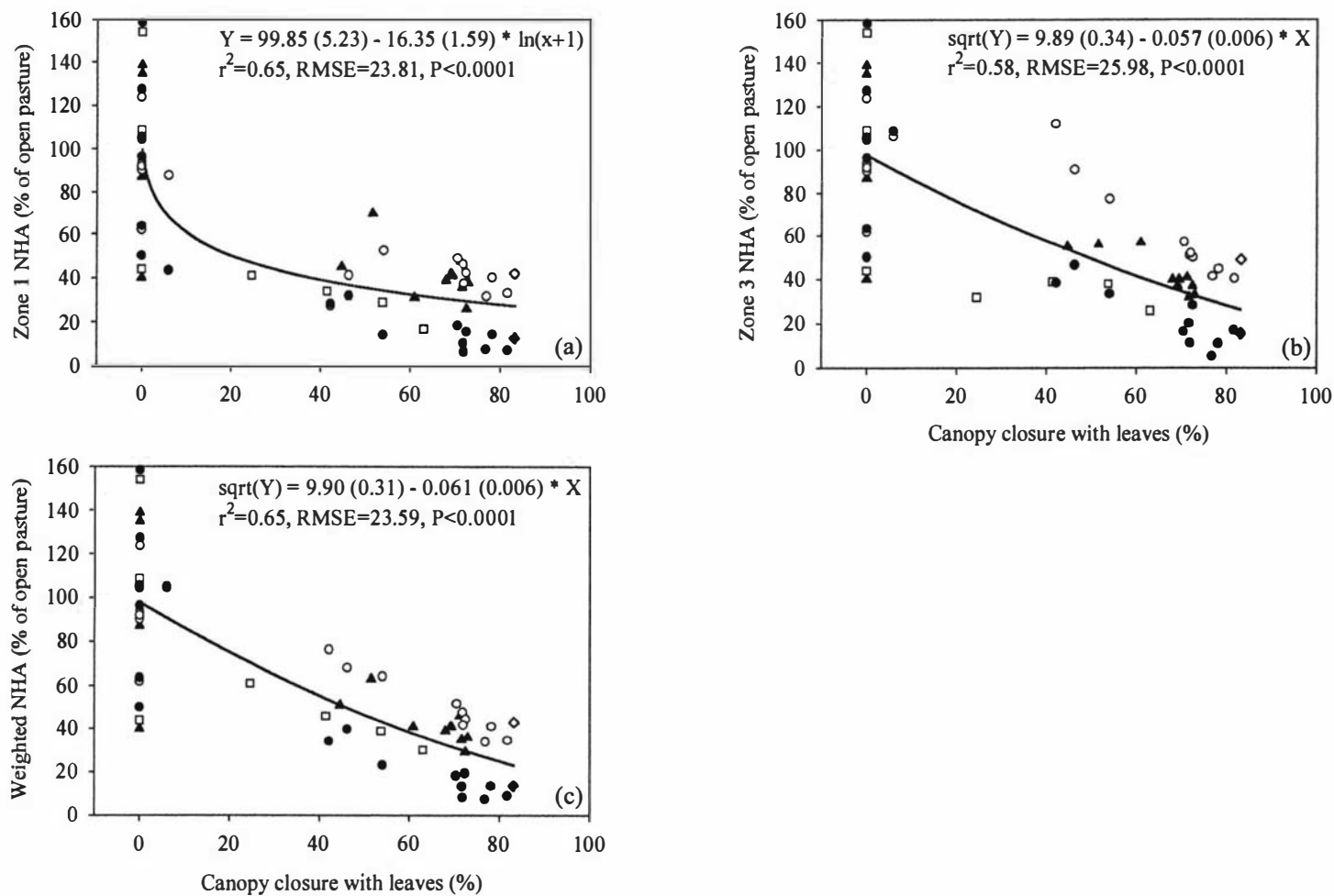


Figure 5.5 Autumn net herbage accumulation (NHA) over a range of in-leaf canopy closure ratios. Standard errors for regression coefficients are given in parentheses. Symbols: (○) Kiwitea98-99 (●) Kiwi99-00, (◇) Southern aspect Kiwi98-99 (◆) Southern aspect Kiwi99-00, (▲) Hautope 1, (□) Hautope 2. Solid line - mean predicted response. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction.

5.4.2.2 Winter and spring

At Kiwitea and Hautope 2 in winter the relationship between NHA and CCL for Zones 1 and 3, and also at the stand level (weighted), did not change significantly from the preceding two seasons ($P>0.05$; Table 5.1; Figure 5.6). In comparison, at Hautope 1 NHA particularly under higher CCLs recovered towards open pasture levels. As a result, Zone 1 and 3 NHA for this site decreased at only a marginal rate with increasing CCL (Table 5.1; Figure 5.6).

Table 5.1 Regression models, and their respective coefficients, developed for CCL to predicted winter understorey NHA, relative to open pasture production.

Zone	Site	Equation	Coefficients				
			<i>a</i>	<i>b</i>	<i>r</i> ²	RMSE	P
1	1&3	$Y=a-b*\ln(x+1)$	99.22 (3.50)	14.88 (1.09)	0.81	14.30	<0.0001
1	2	$Y=a-b*x$	100.61 (4.72)	0.21 (0.08)	0.29	9.68	0.0277
3	1&3	$\text{sqrt}(Y)=a-b*x$	9.86 (0.22)	0.048 (0.004)	0.74	16.00	<0.0001
3	2	$Y=a-b*x$	99.99 (6.74)	0.28 (0.12)	0.24	13.81	0.0418
Weighted	1&3	$\text{sqrt}(Y)=a-b*x$	9.83 (0.21)	0.052 (0.004)	0.79	15.12	<0.0001
Weighted	2	$Y=a-b*x$	100.41 (3.97)	0.24 (0.07)	0.43	8.14	0.0063

Standard errors for coefficients are presented in parentheses. Abbreviations: Y, understorey NHA relative to open pasture production (unit: %); X, in-leaf canopy cover (unit: %); Site 1, Kiwitea; Site 2, Hautope 1; Site 3, Hautope 2; *r*², adjusted coefficient of determination; RMSE, standard error of prediction; Total number of observations for regression models based on Sites 1&3 and Site 2 were 44 and 14, respectively. At Site 2 (Hautope 1) the slope of the relationship for Zone 1 and 3 were not significantly different ($P>0.05$).

At Hautope 1 in spring, NHA did not change significantly with increasing CCL, irrespective of environment amongst the trees (Figure 5.7). On average, Zone 1 NHA at this site was $18 \pm 6\%$ higher than in the open pasture, while Zone 3 NHA did not differ significantly from either Zone 1 or the open pasture environment. Zone 1 NHA also remained relatively constant across the range of CCLs at Kiwitea and Hautope 2, but averaged only 59% of open pasture production (Figure 5.7a). There was also significant yearly variation, with Zone 1 NHA at Kiwitea in 1998-99 and 1999-00 averaging $51 \pm 3\%$ and $68 \pm 3\%$ of the open pasture, respectively. Similarly to Hautope 1 in winter and spring (Figure 5.6 & 5.7), NHA at Kiwitea and Hautope 2 in spring recovered to a greater extent at higher CCLs. Thus, the overall magnitude of decline in NHA amongst the trees was less than for other seasons.

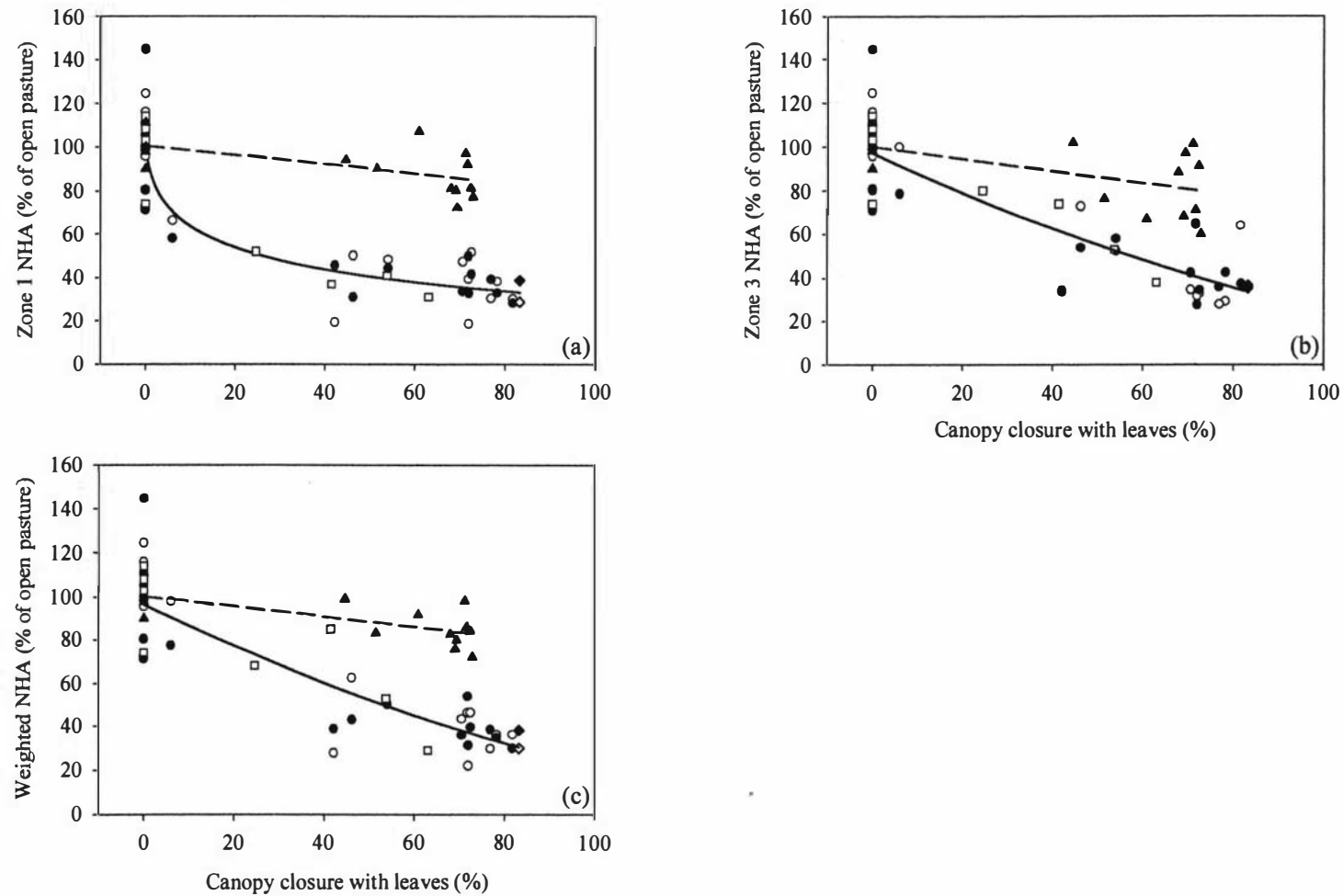


Figure 5.6 Winter net herbage accumulation (NHA) over a range of in-leaf canopy closure ratios. Symbols: (○) Kiwitea98-99 (●) Kiwi99-00, (◇) Southern aspect Kiwi98-99 (◆) Southern aspect Kiwi99-00, (▲) Hautope 1, (□) Hautope 2. Solid line - mean predicted response for Kiwitea and Hautope 2. Dashed line – mean predicted response for Hautope 1.

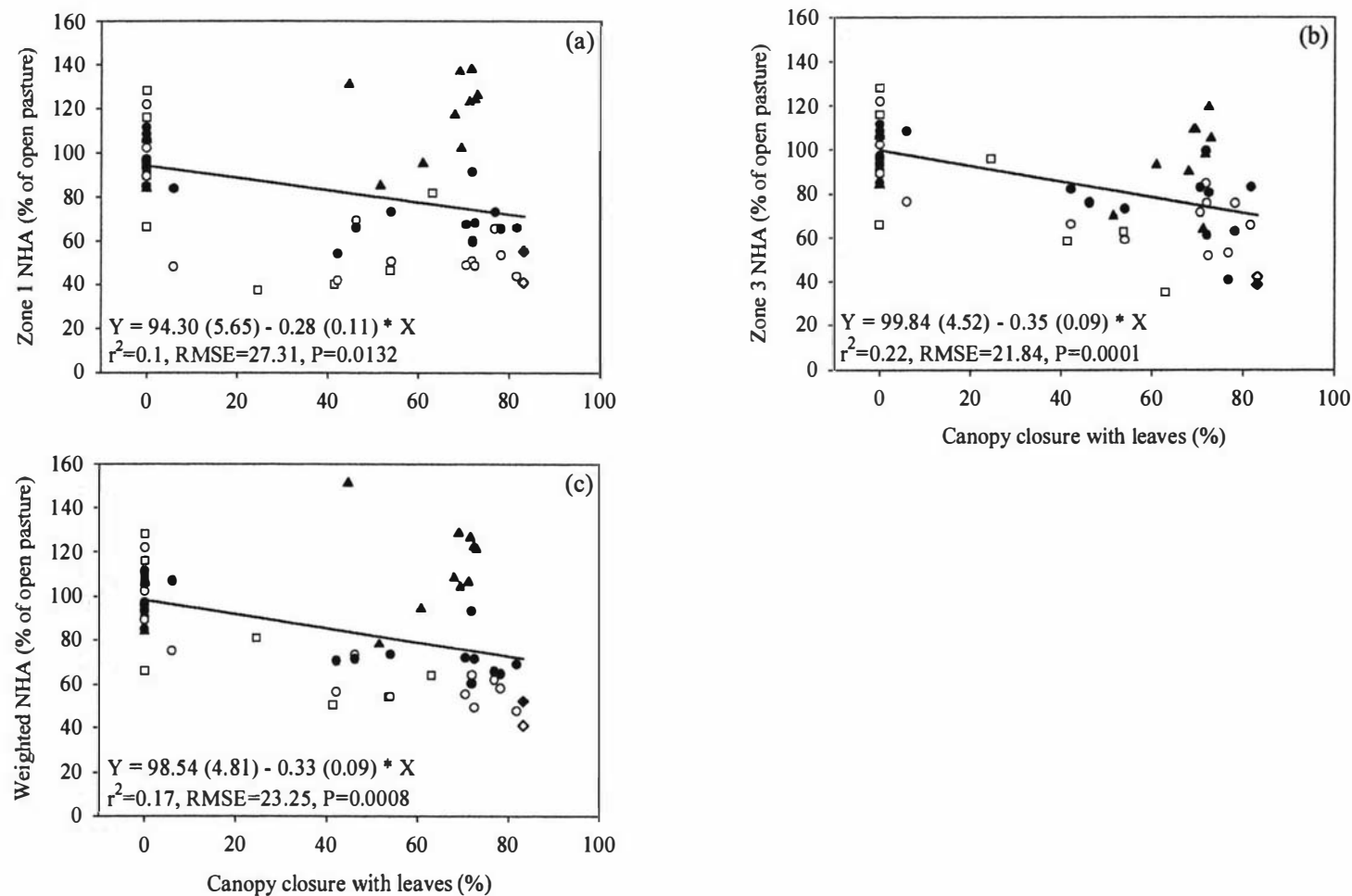


Figure 5.7 Spring net herbage accumulation (NHA) over a range of in-leaf canopy closure ratios. Standard errors for regression coefficients are given in parentheses. Symbols: (○) Kiwitea98-99 (●) Kiwi99-00, (◊) Southern aspect Kiwi98-99 (◆) Southern aspect Kiwi99-00, (▲) Hautope 1, (□) Hautope 2. Solid line - mean predicted response. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction.

5.4.2.3 Intensively stratified across the inter-tree space at Kiwitea

In summer, NHA varied significantly across the space between the trees ($P=0.0006$). Averaged over both 50% and 70% CCL, NHA directly below the trees on the shade-facing (Zone 1) and sun-facing (Zone 5) sides of the canopy gap was reduced to 30% of the open pasture (Figure 5.8a). In contrast, NHA within the centre of the gap (Zone 3) and transitional areas (Zones 2 and 4) was reduced to 50% of open pasture production (Figure 5.8a). Overall, when averaged across the entire space between the trees, NHA tended ($P=0.0696$) to be 14% higher (relative to the open pasture) under 50% than 70% CCL (data not shown).

Depending on the density (CCL) of the poplar stand, understorey NHA in autumn varied significantly with location between the trees ($P=0.011$). At 50% CCL, NHA in Zones 2, 3, and 4 was not significantly different from the open pasture ($P>0.05$; Figure 5.8b). However, directly below the trees on both sides of the canopy gap (Zones 1 and 5) NHA was reduced to 35% of open pasture production. NHA did not vary significantly across the entire inter-tree space (Zones 1-5) under 70% CCL and was maintained at a level similar to directly below the trees at 50% CCL (Figure 5.8b). The difference in NHA between Zone 4 at 50% CCL and Zone 3 at 70% CCL was not statistically significant ($P>0.05$; Figure 5.8b).

In winter and spring there were no significant differences in NHA across the inter-tree space (Zones 1-5) or between stand densities (50 and 70% CCL). On average, NHA amongst the poplar trees was 46% of open pasture production in winter (Figure 5.8c). This increased to 70% in spring (Figure 5.8d).

For each season, there was good comparability between estimates of stand level (weighted) NHA using either two or five zones of tree influence. Relative to estimates based on all five zones of tree influence, alternative estimates using just Zones 1 and 3 marginally overestimated weighted NHA in summer by 9% (Paired t-test; $P=0.0457$). Similarly, autumn NHA at the medium stand density of 50% CCL was slightly overestimated by 10% when weighted using Zones 1 and 3 (Paired t-test; $P=0.0431$). Otherwise, there were no significant differences between these two methods.

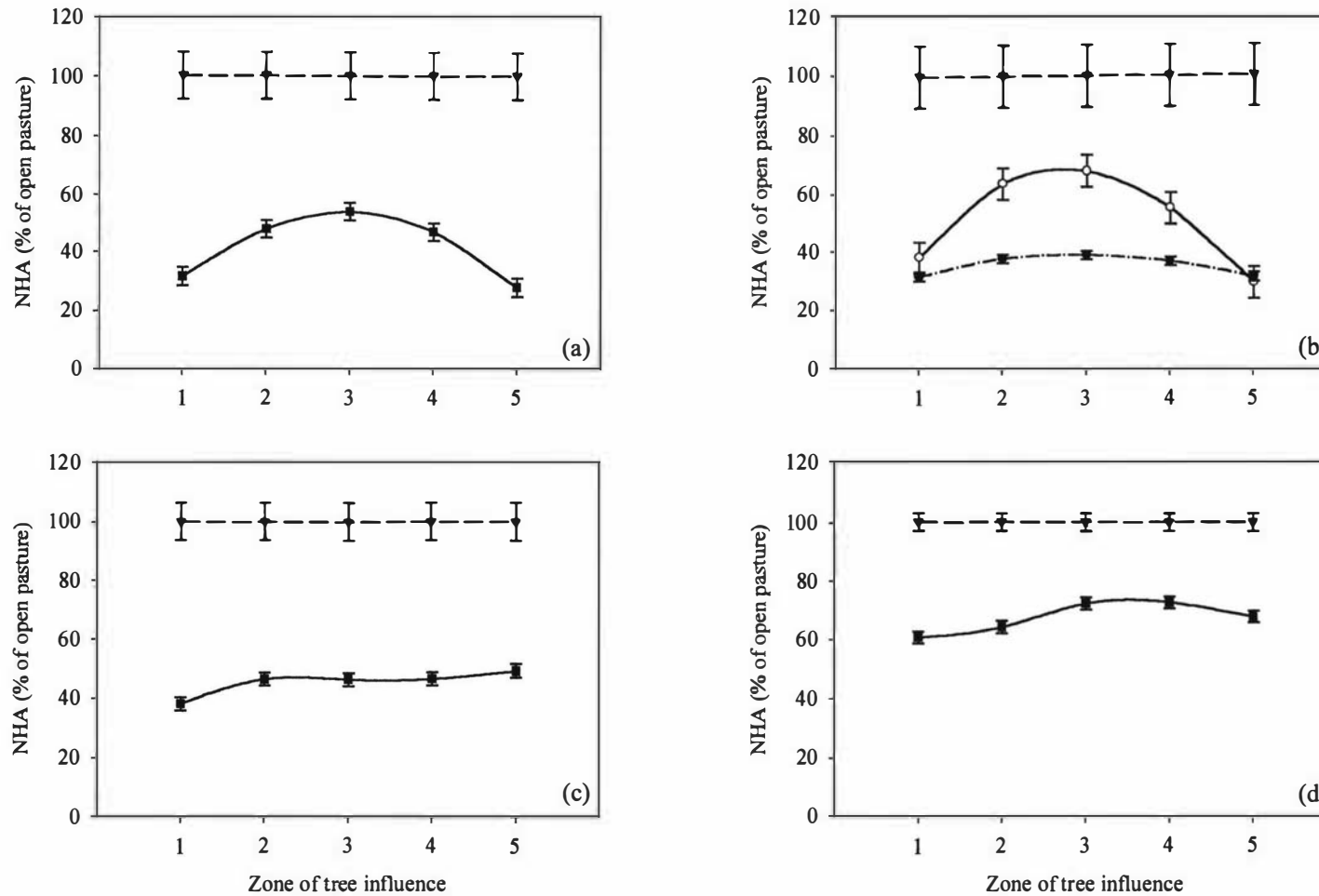


Figure 5.8 Net herbage accumulation (NHA), relative to the open pasture, across the inter-tree space at Kiwitea (1998-00) in: (a) summer, (b) autumn (c) winter, and (d) spring. Vertical bars represent the standard error of the mean (SEM). Symbols: (\blacktriangledown) open pasture, (\circ) 50% CCL, (\bullet) 70% CCL, and (\blacksquare) 50% and 70% CCL averaged together.

5.4.3 Residual herbage mass below 25 mm trimming height

5.4.3.1 Effect of overstorey environment on Kiwitea residual herbage mass

In late spring, the residual herbage mass (RHM) of the open pasture was 784 ± 74 kg DM/ha (Figure 5.9a). In comparison, Zone 1 RHM was 30% lower than in the open pasture ($P=0.0224$), whereas Zone 3 was not significantly different from either of the other two main overstorey environments (Figure 5.9a). By late summer, the RHM in the open pasture had increased to 1572 ± 189 kg DM/ha (Figure 5.9a). This amount of herbage was 2.4-fold ($P=0.004$) and 1.9-fold ($P=0.009$) greater than in Zone 1 and 3, respectively (Figure 5.9a). The relative differences between the three main overstorey environments in late autumn were similar to those measured in summer. Nevertheless, the overall amount of RHM was markedly reduced, with the open pasture having around 700 kg DM/ha (Figure 5.9a). In late winter, the RHM ranged between 300-500 kg DM/ha, and was not significantly different between the three overstorey environments (Figure 5.9a).

5.4.3.2 Effect of poplar overstorey density on Kiwitea residual herbage mass

In late spring, the RHM in Zone 1 and 3 was relatively constant at approximately 550 kg DM/ha and 700 kg DM/ha, respectively, over the entire range of poplar canopy closures (data not shown). Similarly, in late summer the RHM in Zone 1 also remained relatively constant at around 700 kg DM/ha (data not shown). This contrasted with the RHM in Zone 3, which decreased from open pasture levels at a rate of 120 ± 23 kg DM/ha for every 10% increase in CCL (Figure 5.10a). In autumn, the RHM in both Zones 1 and 3 decreased at a lesser ($P<0.05$) rate of 46 ± 6 kg DM/ha for every 10% increase CCL (Figure 5.10b). The strength of both the summer and autumn linear relationships was strong ($r^2=0.62-0.66$; $P<0.0001$). However, a more accurate determination of the general shape of the relationships was hindered by the lack of data points between 0-40% CCL (Figures 5.10a,b). In late winter, the RHM in Zones 1 and 3 was relatively constant at approximately 350 kg DM/ha, irrespective of CCL (data not shown).

5.4.3.3 Effect of overstorey environment on Hautope 1 & 2 residual herbage mass

Over the entire year at Hautope 1, the RHM in the open pasture was at least twice as high as amongst the trees (Zones 1 & 3) ($P < 0.05$; Figure 5.9b). At the same time, the RHM was not significantly different in Zones 1 and 3 ($P > 0.05$; Figure 5.9b). The open pasture RHM reached a maximum of 1700 kg DM/ha in late spring and a minimum of 850 kg DM/ha in late autumn/winter (Figure 5.9b).

At Hautope 2 in spring, there was little difference in the RHM amongst the three main overstorey environments ($P > 0.05$; Figure 5.9c). In summer, the RHM amongst the trees (Zones 1 & 3) was 38% lower than in the open pasture ($P < 0.05$; Figure 5.9c). This increased further to between 55%-60% in late autumn and winter in Zone 1 ($P < 0.05$), while the RHM in Zone 3 was not significantly different from either of the other two main overstorey environments (Figure 5.9c).

5.4.3.4 Effect of poplar overstorey density on Hautope 1 & 2 residual herbage mass

In late spring and summer the RHM amongst the trees (Zones 1 & 3) remained constant at around 500-600 kg DM/ha, irrespective of the CCL (data not shown). Whereas, in late autumn the RHM decreased from open pasture levels at a rate of 82 ± 7 kg DM/ha for every 10% increase in CCL (Figure 5.11a). Similarly to Kiwitea, the determination of the precise form of the relationship was hindered by the lack of data points between 0-40% CCL (Figures 5.10a,b & 5.11a). Analysis of the residual errors, for the individual zones of tree influence, indicated that the relationship between Zone 3 RHM and CCL might have convex curvature; while, there was weak evidence for some form of concave curvature associated with Zone 1 (Figure 5.11a). Nevertheless, the poor and unbalanced spread of the data points, especially towards the lower range of poplar canopy closures, inhibited the use of such relationships with confidence. A similar relationship to autumn also occurred in winter ($P > 0.05$; Figure 5.11b). Variation in RHM around the fitted function in winter was greater than in autumn (Figure 5.11a,b).

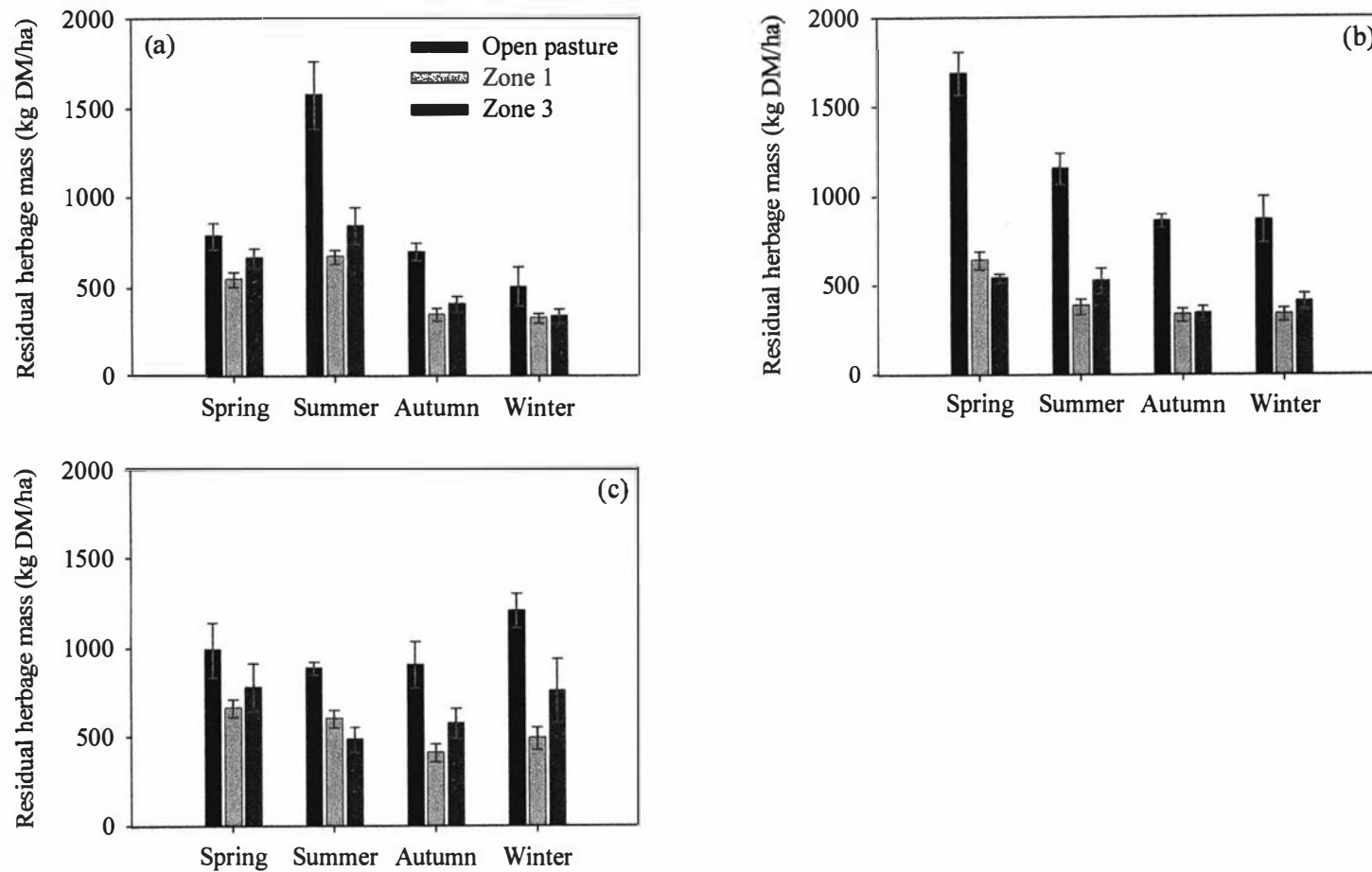


Figure 5.9 Residual herbage mass in each of the three main overstorey environments at (a) Kiwitea, (b) Hautope 1, and (c) Hautope 2. Vertical bars represent the standard error of the mean (SEM). Abbreviations: Zone 1, directly below the crowns of individual trees; and Zone 3, at the centre of the vertically projected canopy gap between trees.

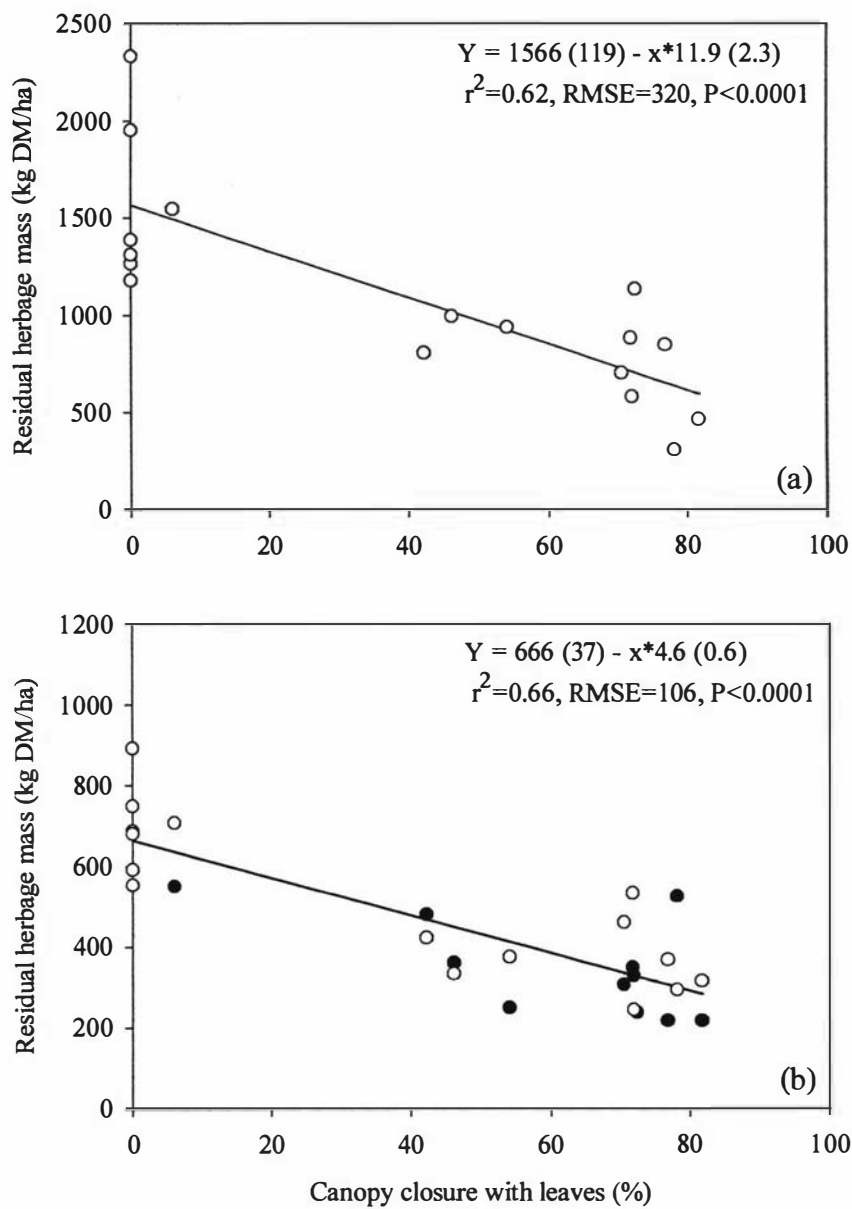


Figure 5.10 Post-trimming Kiwitea residual herbage mass in (a) summer and (b) autumn over a range of poplar canopy closure ratios (CCL): (●) directly below the individual tree crowns (Zone 1), and (○) at the centre of the vertically projected canopy gap between trees (Zone 3). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction.

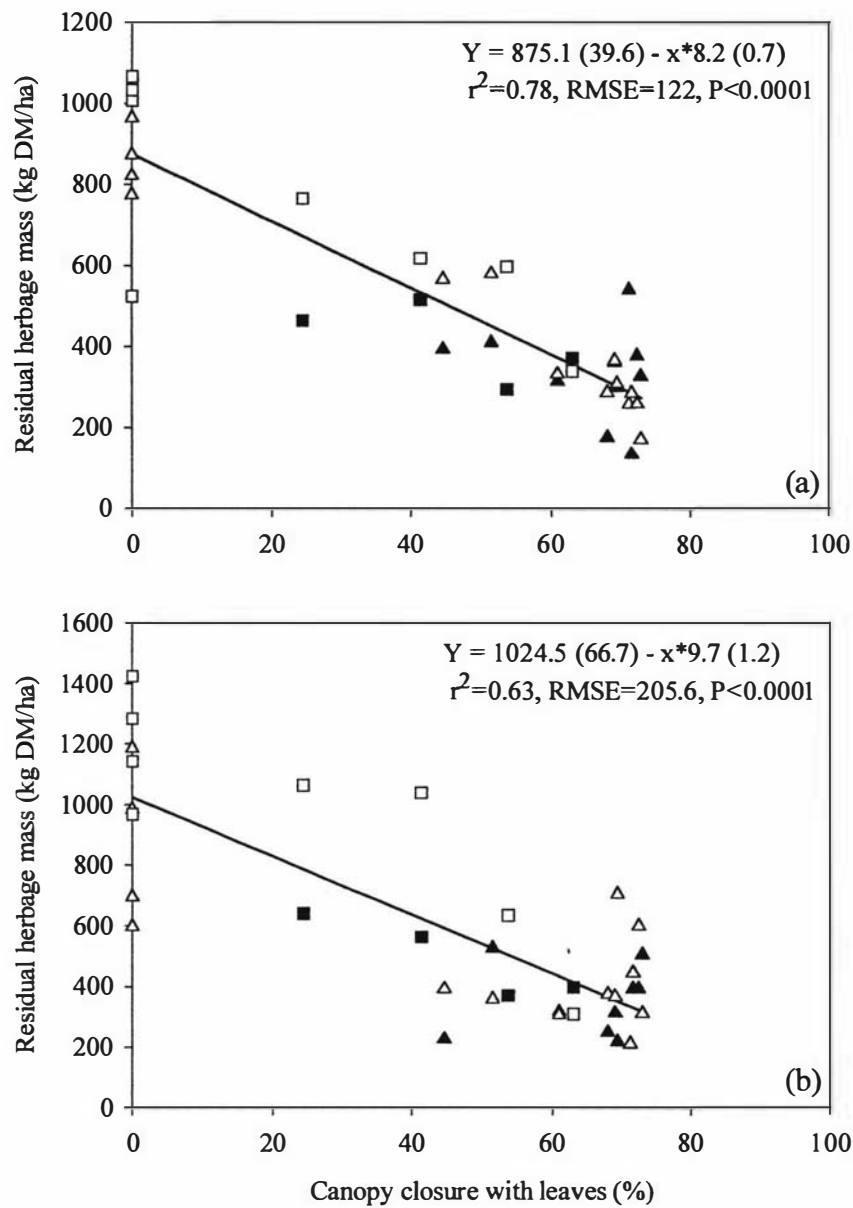


Figure 5.11 Post-trimming Hautope 1 & 2 residual herbage mass in (a) autumn and (b) winter over a range of poplar canopy closure ratios (CCL). Directly below the individual tree crowns (Zone 1) at (▲) Hautope 1 and (■) Hautope 2, and at the centre of the vertically projected canopy gap between trees (Zone 3) at (Δ) Hautope 1 and (□) Hautope 2. Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction.

5.4.3.5 Spatial variation in residual herbage mass between the trees at Kiwitea

In late summer, depending on the density (CCL) of the poplar stand, the RHM varied significantly with location between the trees ($P=0.045$; Figure 5.12a). Under 50% CCL, RHM in Zone 3 was 55% greater than in Zone 1 (Figure 5.12a). The RHM in Zone 3 also tended ($P\leq 0.1$) to be at least 49% greater than in all of the zones of tree influence at 70% CCL, except for Zone 4. However, these differences were only significant at $P\leq 0.05$ for Zone 2 and 5 (Figure 5.12a). In general, the RHM in Zone 5 at 70% CCL, was significantly lower than all other zones of tree influence, except for Zone 2 at the same CCL, and also Zone 1 at 50% CCL (Figure 5.12a). Overall, the summer RHM in the open pasture was significantly greater than in all of the stratified zones of tree influence, except for Zone 3 at 50% CCL (Figure 5.12a). On average, the difference in RHM was 2.3-fold greater in the open pasture.

The RHM was not significantly different between any of the zones of tree influence or stand densities in late autumn ($P>0.05$; Figure 5.12b). However, under both 50% and 70% CCL the RHM in Zone 1 was approximately 55% less than in the open pasture (Figure 5.12b). In late winter and spring, the post trimming RHM did not vary significantly across the inter-tree space or between the different stand densities, including the open pasture ($P>0.05$; data not shown).

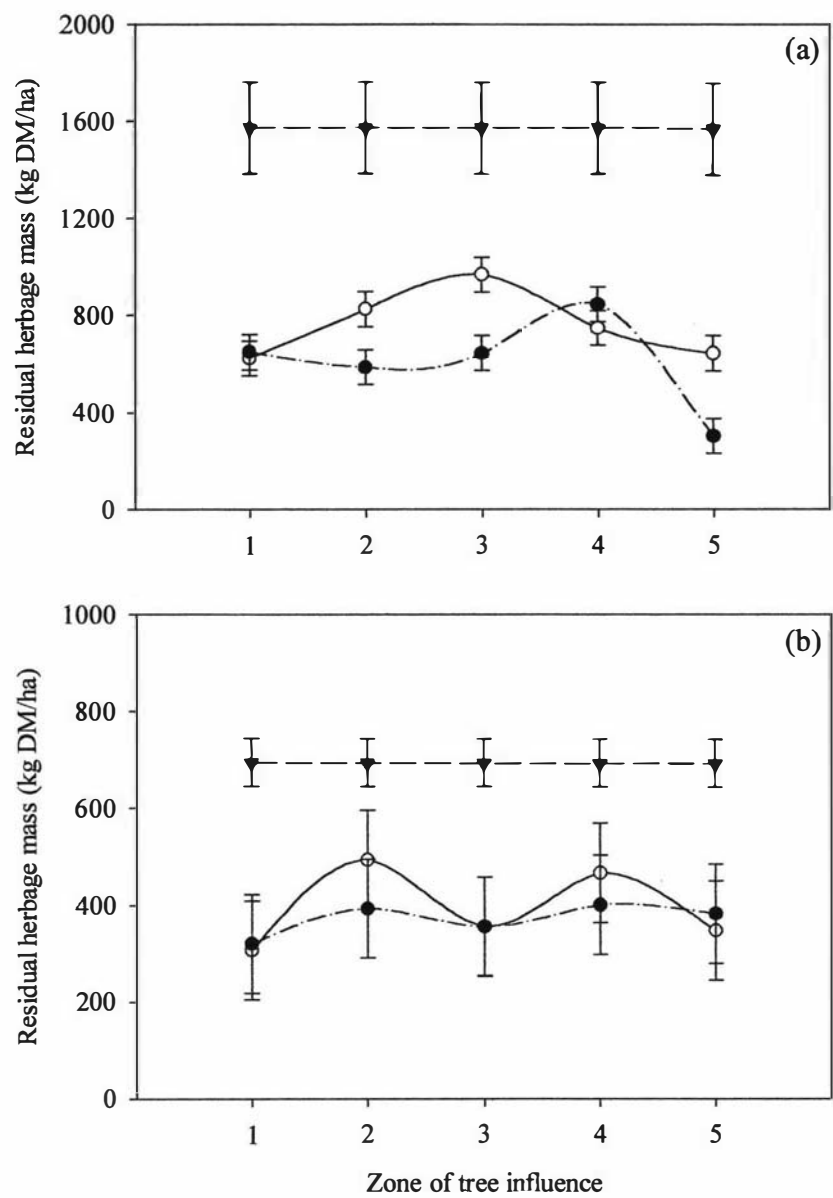


Figure 5.12 Residual herbage mass (RHM) stratified across the inter-tree space at Kiwitea in (a) late summer and (b) late autumn (1999-2000). Vertical bars represent the standard error of the mean (SEM). Symbols: (▼) open pasture, (○) 50% CCL, and (●) 70% CCL.

5.4.4 Pasture botanical species composition

5.4.4.1 Effect of overstorey environment and season on Kiwitea pasture composition

General pasture composition

Grasses dominated the pasture botanical composition, accounting for over 70% and 50% of total sward biomass in spring and summer, respectively (Table 5.2). Overall, Zone 1 tended to contain 10-18% more high fertility responsive (HFR) grasses than either Zone 3 or the open pasture ($P=0.05$; Table 5.2). In contrast, no significant differences between the three main overstorey environments were evident for low fertility tolerant (LFT) grasses, legumes, other species (flat weeds, thistles, etc.), or dead pasture material (Table 5.2). Between spring and summer, the proportion of HFR grasses, when averaged across all three main overstorey environments, decreased by 20% in the sward, with a compensatory 4% and 18% increase in other species and dead pasture material, respectively. Over the same period of time, the total legume content decreased from 10% to 6% (Table 5.2).

Main high fertility responsive grasses and legumes

The most abundant HFR grass in the open pasture was *Lolium perenne*, with a small amount of *Poa* (Table 5.3) and trace amounts of *Dactylis glomerata* and *Holcus lanatus* also present ($<0.5\%$ DM). Averaged over both seasons, the open pasture contained 11-14% more *Lolium perenne* than in Zones 1 and 3 ($P<0.0001$). However, the difference between these three main overstorey environments tended to fall in summer due to a reduction of *Lolium perenne* in the open pasture ($P=0.0646$; Table 5.3).

Poa and *Lolium perenne* were the dominant HFR grasses in Zones 1 and 3 (Table 5.3). In spring, Zone 1, followed by Zone 3, and then the open pasture, had the greatest *Poa* content (Table 5.3). Between spring and summer, the proportion of *Poa* in Zone 3 was reduced to a level comparable with the open pasture. Similarly, the proportion in Zone 1 also decreased, but remained significantly greater than in the other two main overstorey environments (Table 5.3).

When averaged over both seasons, Zone 1 contained 4-5% more *Holcus lanatus* than Zone 3 or the open pasture (Table 5.3). This contrasted with *Dactylis glomerata*, which did not vary significantly between the three main overstorey environments (Table 5.3). The sward content of both these species did not change between spring and summer (Table 5.3).

The main legumes in the swards were *Trifolium repens* and to a lesser extent various *Lotus* species (Table 5.3). The proportion of these legumes varied little between the three main overstorey environments or two consecutive seasons. Overall, the sward biomass contained around 8% legume (Table 5.2).

5.4.4.2 The effect of poplar overstorey density on Kiwitea pasture composition

General pasture composition

In spring, the proportion of high fertility responsive grasses in Zone 1 showed a strong ($r^2=0.59$, $P=0.0002$) positive linear relationship with increasing CCL (Figure 5.13a). Conversely, the proportion of low fertility tolerant grasses within the same zone of tree influence decreased at a similar absolute rate ($P>0.05$), although the strength of this relationship was much weaker ($r^2=0.37$, $P=0.006$) (Figure 5.13b). The rate of change for both relationships was approximately 2-4% of the total sward biomass for every 10% increase in CCL (Figure 5.13a,b).

No clear trends were evident in summer for any of the general pasture composition categories. The only exception was a weak ($r^2=0.25$, $P=0.02$) negative linear relationship between the dead pasture material content in Zone 3 and increasing CCL (Figure 5.14a).

Main high fertility responsive grasses

Lolium perenne and *Poa* showed clear trends with increasing CCL (Figure 5.13c,d). In both Zones 1 and 3, the proportion of *Lolium perenne* in the sward decreased at a constant rate of $2.6\% \pm 0.4\%$ (prediction \pm SE) for every 10% increase in CCL (Figure 5.13c). This contrasted with *Poa* in Zone 1, which increased at a higher ($P\leq 0.05$) rate of $5.3\% \pm 0.6\%$ for every 10% increase in CCL (Figure 5.13d). Thus, the positive linear relationship between the content of HFR grasses in Zone 1 and CCL (Figure 5.13a) was, at

least in part, due to a more than compensatory increase in *Poa* over the decrease in *Lolium perenne*.

Overall, the *Lolium perenne* content of the open pasture had disproportionately greater variability around the fitted function, compared to the two main zones of tree influence amongst trees (Zones 1 & 3) (Figure 5.13c). This contrasted with the *Poa* spp. content, which was more variable in Zones 1 and 3 (Figure 5.13d). The intercept for the latter simple straight-line function was not significantly different from zero ($P=0.1336$; Figure 5.13d).

In summer, the proportion of *Lolium perenne* in Zone 1 also showed a clear negative trend with increasing CCL (Figure 5.14b). However, both the intercept and slope of this simple linear relationship were significantly ($P \leq 0.05$) lower than in spring (Figures 5.13c & 5.14b).

Table 5.2 Pasture composition at Kiwitea¹, expressed as a percentage of total sward biomass (%DM).

Season	Environment	HFR grasses	LFT grasses	Legume	Other species	Dead matter
			(lnx)			(√x)
Spring'98&'99	Open pasture	37	37 (3.6)	9	15	3 (3.5)
	Zone 1	60	23 (3.0)	8	6	3 (2.3)
	Zone 3	47	25 (3.0)	13	13	2 (3.2)
	Grand mean	50	27 (3.1)	10	11	3 (2.9)
Summer'98&'99	Open pasture	24	29 (3.3)	8	17	22 (4.0)
	Zone 1	35	27 (3.2)	5	11	22 (3.0)
	Zone 3	29	28 (3.2)	6	18	19 (3.8)
	Grand mean	30	28 (3.2)	6	15	21 (3.5)
Overall	Open pasture	30	33 (3.4)	9	16	12 (3.7)
	Zone 1	48	25 (3.1)	7	9	12 (2.7)
	Zone 3	38	27 (3.1)	10	15	11 (3.5)
	Grand mean	40	27 (3.2)	8	13	12 (3.2)
Analysis of variance						
Environment (A)		P=0.05	NS	NS	NS	NS
Season (B)		P<0.001	NS	P<0.05	P<0.05	P<0.001
Interaction (A*B)		NS	NS	NS	NS	NS
SD		10	(0.4)	5	7	(0.4)

¹Averaged across the entire range of poplar stand densities over a two year period (1998-2000). Transformed values are given in parentheses. Abbreviations: Zone 1, directly below the crowns of individual poplar trees; Zone 3, at the centre of the vertically projected gap between poplar crowns; lnx, natural-logarithm transformed; √x, square-root transformed; SD, standard deviation; NS, not significant ($P \geq 0.1$); DM, dry matter; HFR grasses, high fertility responsive grasses (*Lolium perenne*, *Dactylis glomerata*, *Holcus lanatus*, and *Poa* spp.); LFT grasses, low fertility tolerant grasses (*Agrostis capillaris*, *Cynosurus cristatus*, and *Anthoxanthum odoratum*).

Table 5.3 Main high fertility responsive (HFR) grasses and legumes at Kiwitea¹, expressed as a percentage of total sward biomass (%DM).

Season	Environment	<i>Lolium perenne</i>	<i>Dactylis glomerata</i>	<i>Holcus lanatus</i>	<i>Poa</i> spp.	<i>Trifolium repens</i>	<i>Lotus</i> spp.
			(ln[x+1])	(√x)	(√x)		
Spring'98&'99	Open pasture	32	0 (0.03)	0 (0.35)	4 (2.04)	8	1
	Zone 1	12	3 (0.92)	6 (2.12)	38 (5.99)	6	2
	Zone 3	16	3 (0.75)	1 (0.78)	26 (4.72)	10	3
	Grand mean	18	3 (0.66)	3 (1.21)	26 (4.64)	8	2
Summer'98&'99	Open pasture	23	0 (0.00)	0 (0.22)	1 (0.58)	6	2
	Zone 1	14	4 (1.00)	4 (1.56)	12 (3.09)	5	1
	Zone 3	15	6 (1.02)	1 (0.70)	6 (1.56)	6	0
	Grand mean	17	4 (0.79)	2 (0.93)	7 (1.95)	6	1
Overall	Open pasture	27	0 (0.01)	0 (0.28)	3 (1.31)	7	2
	Zone 1	13	4 (0.96)	5 (1.84)	25 (4.54)	5	1
	Zone 3	16	5 (0.88)	1 (0.74)	16 (3.14)	8	2
	Grand mean	17	3 (0.73)	3 (1.07)	17 (3.30)	7	1
Analysis of variance							
Environment (A)		P<0.001	NS	P<0.01	P<0.01	NS	NS
Season (B)		NS	NS	NS	P<0.001	NS	NS
Interaction (A*B)		P<0.1	NS	NS	P<0.05	NS	NS
SD		7	(0.39)	(0.63)	(0.92)	5	3

¹Averaged across a range of poplar stand densities over a two-year period (1998-2000). Transformed values are given in parentheses. Abbreviations: Zone 1, directly below the crowns of individual poplar trees; Zone 3, at the centre of the vertically projected gap between poplar crowns; ln[x+1], natural-logarithm transformed; √x, square-root transformed; SD, standard deviation; NS, not significant ($P \geq 0.1$); DM, dry matter.

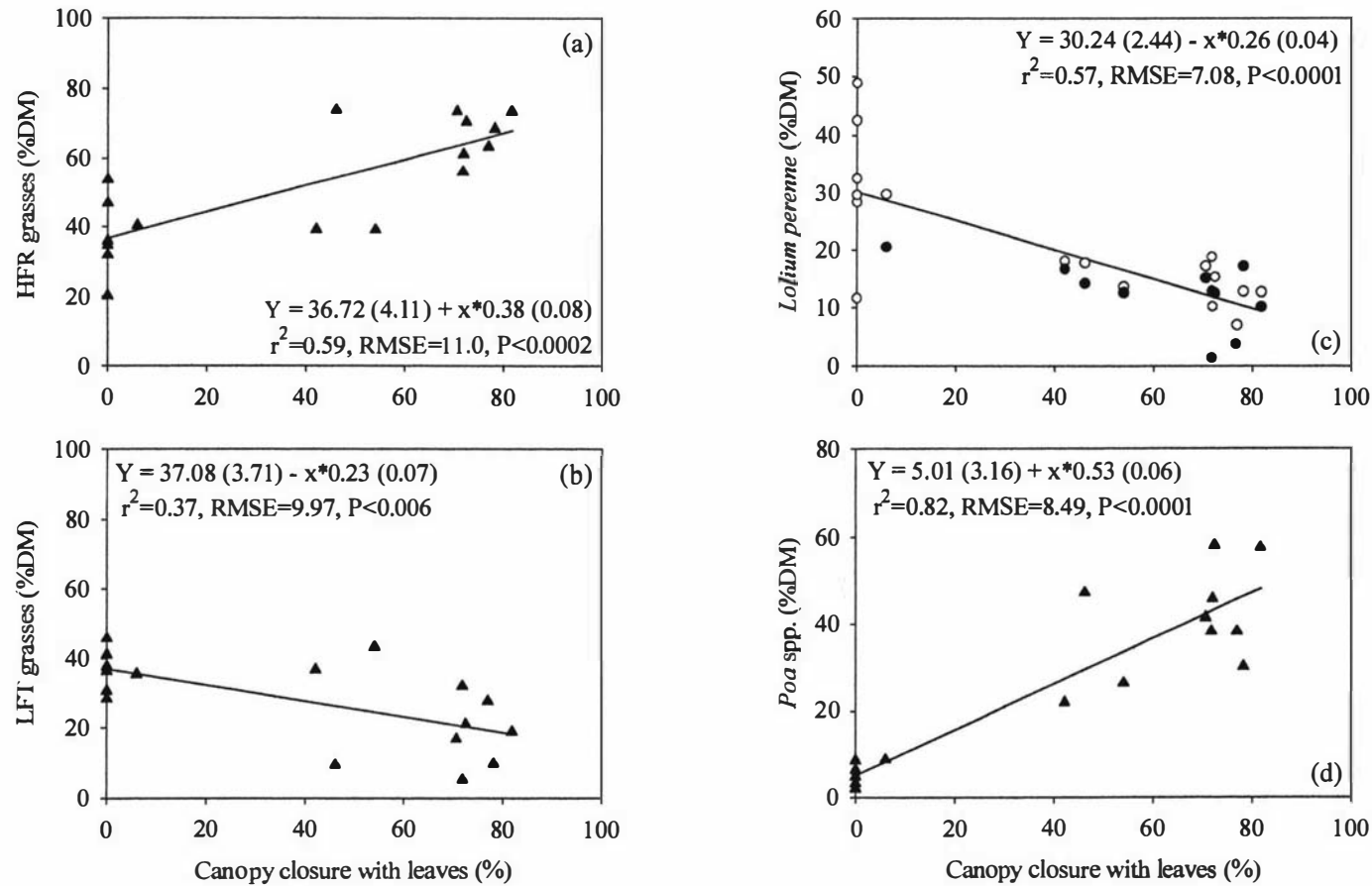


Figure 5.13 Relationship between spring pasture composition and poplar canopy closure (CCL) at Kiwitea. Symbols: (\blacktriangle) directly below the poplar crowns (Zone 1) and (\circ) at the centre of the vertically projected canopy gap between the trees (Zone 3). Standard errors for simple linear regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction; HFR grasses, high fertility responsive grasses, LFT grasses, low fertility tolerant grasses.

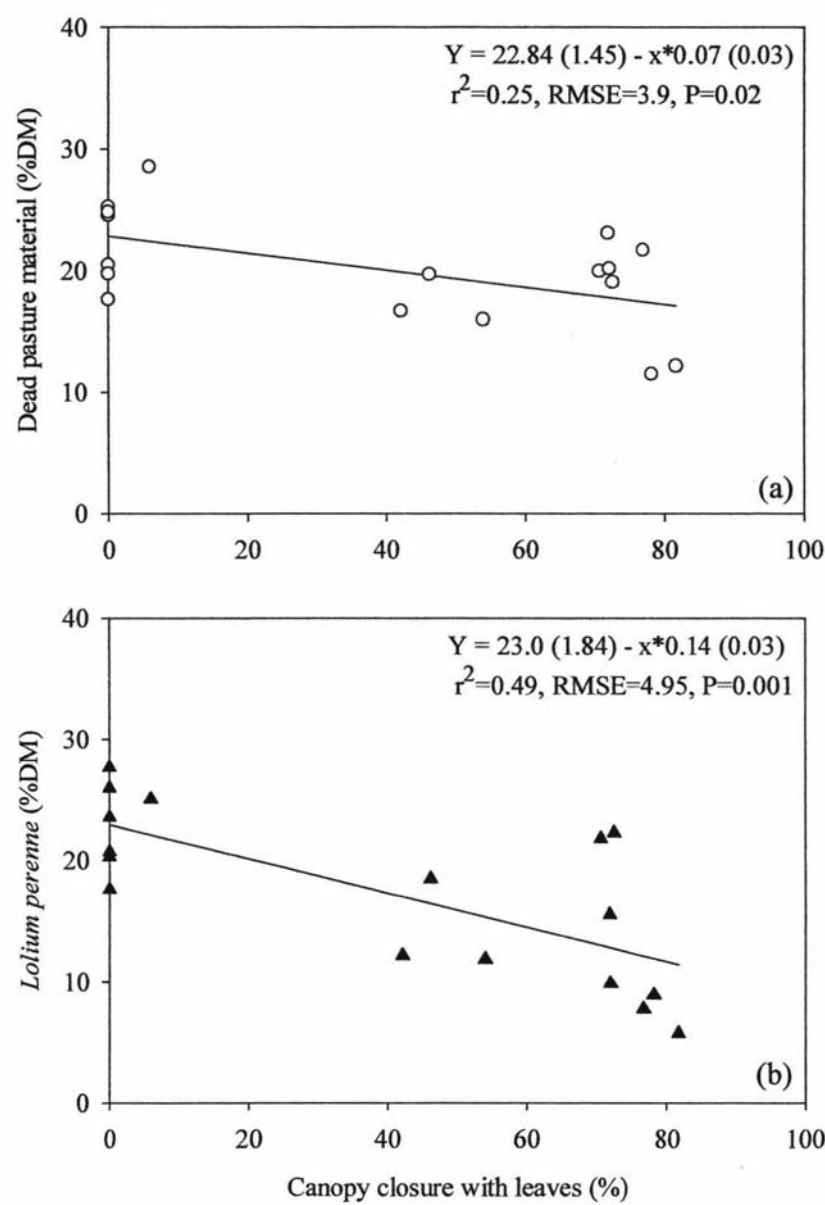


Figure 5.14 Relationship between the summer pasture composition and poplar canopy closure at Kiwitea. Symbols: (▲) directly below the poplar crowns (Zone 1) and (○) at the centre of the vertically projected canopy gap between the trees (Zone 3). Standard errors for simple linear regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction.

5.4.4.3 Effect of overstorey environment and season on Hautope 1 pasture composition

General pasture composition

Grasses made up at least 60%, and usually exceeded 80%, of the total sward biomass (Table 5.4). Averaged over the two consecutive seasons, Zones 1 and 3 contained around 27% more HFR grasses compared to the open pasture (Table 5.4). Conversely, the proportion of LFT grasses in the pastures did not differ significantly amongst the three main overstorey environments, but did decrease by about 10% between spring and summer (Table 5.4). Both Zones 1 and 3 contained very little legume in their swards ($\leq 1\%$). This contrasted with the open pasture, which in spring had 12% legume (Table 5.4). Between spring and summer, the legume content in the open pasture decreased to 2%, but still remained significantly higher than amongst the trees (Zones 1 & 3) (Table 5.4). The main 'other species' in the pastures were flat-weeds, such as *Plantago lanceolata*, *Taraxacum officinale*, and *Cerastium glomeratum*. Collectively, these species accounted for less than 6% of the total sward biomass, and were generally in similar abundance amongst the three main overstorey environments (Table 5.4). Dead pasture material also made up only a small proportion ($<10\%$) of the pasture in spring, irrespective of overstorey environment (Table 5.4). However, between spring and summer, this general category increased by 30% in the open pasture, and by approximately 7% amongst the trees (Zone 1 & 3) (Table 5.4).

Main high fertility responsive grasses and legumes

In the open pasture the main HFR grass was *Lolium perenne*, followed by *Holcus lanatus* (Table 5.5). Amongst the trees (Zone 1 & 3) both *Lolium perenne* and *Poa* were co-dominant (Table 5.5). All three main overstorey environments in spring had about 22% *Lolium perenne*. During the ensuing summer, the proportion of *Lolium perenne* did not change significantly in the open pasture, but did tend to increase by 14% and 9% in Zones 1 and 3, respectively ($P=0.0894$; Table 5.5). Averaged over the two consecutive seasons, the open pasture contained 6-7% more *Holcus lanatus* than in Zones 1 & 3 (Table 5.5). In contrast, the understorey pastures in Zones 1 and 3 had around 23% more *Poa*, with only a trace amount ($<0.5\%$ DM) of this species evident in the open pasture environment (Table 5.5). Between spring and summer the *Poa* content decreased (Table

5.5). *Dactylis glomerata* made up only a small proportion of total sward biomass in all three main overstorey environments (<5%DM; Table 5.5).

The two main legume species in the open pasture were *Trifolium repens* and *T. dubium*; the latter was not evident in summer (data not shown). In comparison, over both consecutive seasons, only a trace amount ($\leq 1\%$ DM) of *Trifolium repens* was present in Zones 1 and 3 (Table 5.5).

5.4.4.4 Effect of poplar overstorey density on Hautope 1 pasture composition

General pasture composition

In both spring and summer, the proportion of HFR grasses amongst the trees (Zones 1 & 3) increased exponentially with increasing CCL (Figure 5.15). However, this relationship was based on a very limited range of CCLs and accounted for only 40% of the variation shown by this general category (Figure 5.15).

In summer, the proportion of dead pasture material in the sward was negatively related to CCL (Figure 5.16). Amongst the trees (Zones 1 & 3), the dead material content of the sward decreased at a constant rate of $3\% \pm 0.5\%$ for every 10% increase in CCL (Figure 5.16). The strength of this relationship was moderate ($r^2=0.56$; $P<0.0001$).

Table 5.4 Pasture composition at Hautope 1¹, expressed as a percentage of total sward biomass (%DM).

Season	Environment	HFR grasses	LFT grasses	Legume	Other species	Dead matter
				(\sqrt{x})	($1/[x+1]$)	($\ln x$)
Spring'99	Open pasture	30	52	12 (3.35)	2 (0.40)	4 (1.40)
	Zone 1	52	40	0 (0.37)	0 (0.78)	7 (1.83)
	Zone 3	55	35	1 (0.57)	5 (0.75)	5 (1.52)
	Grand mean	50	40	2 (0.95)	2 (0.71)	6 (1.58)
Summer'99	Open pasture	25	36	2 (1.22)	2 (0.51)	34 (3.48)
	Zone 1	60	26	0 (0.34)	0 (0.86)	13 (2.43)
	Zone 3	56	29	0 (0.30)	1 (0.72)	14 (2.54)
	Grand mean	52	29	1 (0.47)	1 (0.74)	17 (2.82)
Overall	Open pasture	28	44	7 (2.29)	2 (0.46)	19 (2.44)
	Zone 1	56	33	0 (0.36)	0 (0.82)	10 (2.13)
	Zone 3	55	32	1 (0.44)	3 (0.73)	10 (2.03)
	Grand mean	51	34	2 (0.71)	2 (0.72)	11 (2.14)
Analysis of variance						
Environment (A)		P<0.01	NS	P<0.001	P<0.1	NS
Season (B)		NS	P<0.01	P<0.01	NS	P<0.001
Interaction (A*B)		NS	NS	P<0.01	NS	P<0.01
SD		12	13	(0.69)	(0.22)	(0.46)

¹Averaged across the entire range of poplar stand densities over a one-year period (1999-2000). Transformed values are given in parentheses. Abbreviations: Zone 1, directly below the crowns of individual poplar trees; Zone 3, at the centre of the vertically projected gap between poplar crowns; $\ln x$, natural-logarithm transformed; \sqrt{x} , square-root transformed; $1/[x+1]$, inverse transformed; SD, standard deviation; NS, not significant ($P \geq 0.1$); DM, dry matter; HFR grasses, high fertility responsive grasses (*Lolium perenne*, *Dactylis glomerata*, *Holcus lanatus*, and *Poa* spp.); LFT, low fertility tolerant grasses (*Agrostis capillaris*, *Cynosurus cristatus*, and *Anthoxanthum odoratum*).

Table 5.5 Main high fertility responsive grasses and legume species at Hautope 1¹, expressed as a percentage of total sward biomass (%DM).

Season	Environment	<i>Lolium perenne</i>	<i>Dactylis glomerata</i>	<i>Holcus lanatus</i>	<i>Poa</i> spp.	<i>Trifolium repens</i>
				(1/[x+1])	(x ^{1/3})	
Spring'99	Open pasture	22	1	8 (0.22)	0 (0.23)	4
	Zone 1	20	3	1 (0.83)	29 (2.97)	0
	Zone 3	24	2	0 (0.86)	28 (2.92)	1
	Grand mean	22	2	2 (0.74)	24 (2.04)	1
Summer'99	Open pasture	17	1	7 (0.19)	0 (0.10)	2
	Zone 1	34	4	3 (0.58)	19 (2.47)	0
	Zone 3	33	2	2 (0.79)	18 (2.34)	0
	Grand mean	31	3	3 (0.60)	15 (1.64)	1
Overall	Open pasture	19	1	8 (0.21)	0 (0.16)	3
	Zone 1	27	4	2 (0.70)	24 (2.72)	0
	Zone 3	29	2	1 (0.83)	23 (2.63)	1
	Grand mean	26	3	3 (0.67)	20 (2.26)	1
Analysis of variance						
Environment (A)		NS	NS	P<0.01	P<0.001	P<0.001
Season (B)		P<0.1	NS	NS	P<0.05	NS
Interaction (A*B)		P<0.1	NS	NS	NS	NS
SD		9	5	(0.27)	(0.52)	1

¹Averaged across the entire range of poplar stand densities over a one-year period (1999-2000). Transformed values are given in parentheses. Abbreviations: Zone 1, directly below the crowns of individual poplar trees; Zone 3, at the centre of the vertically projected gap between poplar crowns; (1/[x+1]), inverse transformed; x^{1/3}, cubic-root transformed; SD, standard deviation; NS, not significant (P≥0.1); DM, dry matter.

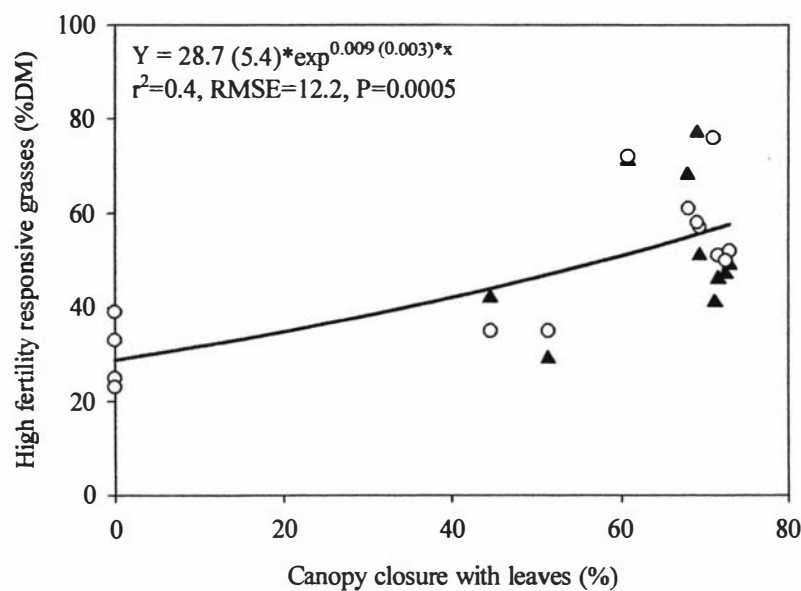


Figure 5.15 Relationship between HFR grasses and poplar canopy closure (CCL) at Hautope 1 in spring and summer: (▲) directly below the poplar crowns (Zone 1), and (○) at the centre of the vertically projected canopy gap between the trees (Zone 3). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination (approximated for the non-linear function; refer to Section 4.3); RMSE, standard error of prediction.

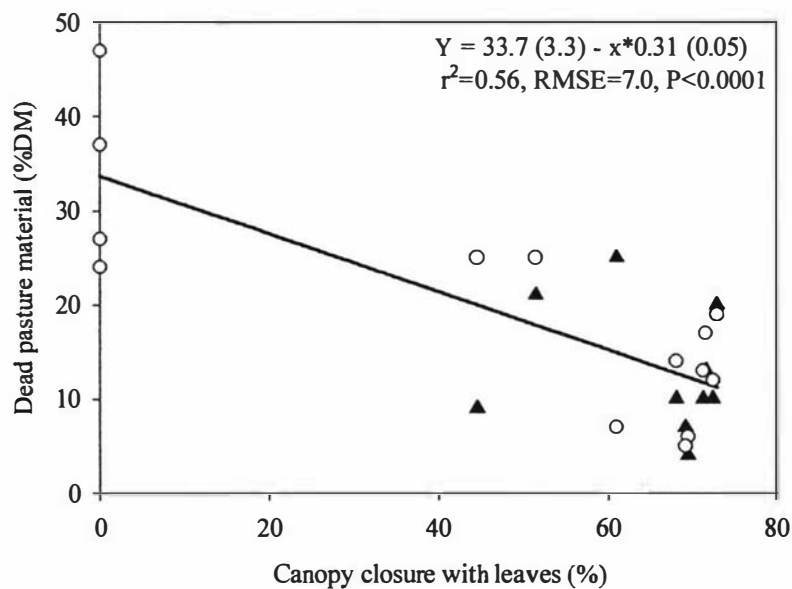


Figure 5.16 Relationship between dead pasture material and poplar canopy closure (CCL) at Hautope 1 in summer: (▲) directly below the poplar crowns (Zone 1), and (○) at the centre of the vertically projected canopy gap between the trees (Zone 3). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction.

5.4.4.5 Effect of overstorey environment and season on Hautope 2 pasture composition

General pasture composition

Overall, LFT grasses made up over 75% of the total sward biomass and thus, dominated the pastures at this site (Table 5.6). In spring, Zone 1 contained a significantly higher proportion of LFT grasses compared to the open pasture. Nevertheless, in summer no significant differences were evident amongst the three main overstorey environments (Table 5.6). HFR grasses, legumes, and other species collectively made up less than 15% of the total sward biomass; and their proportions in the pasture varied little amongst the three main overstorey environments or over the two consecutive seasons (Table 5.6). The legume species included *Trifolium subterraneum*, *T. repens* and *T. dubium*, while the HFR grasses consisted almost entirely of *Lolium perenne*, except for trace amounts of *Holcus lanatus* and *Poa* (<1%DM; data not shown). All three main overstorey environments in spring had a similar proportion of dead pasture material (Table 5.6). Between spring and summer the dead pasture material content in Zones 1 and 3 increased by 9-15%, while not changing significantly in the open pasture. As a result, in summer Zone 1 had a significantly higher dead pasture material content than in the open pasture (Table 5.6).

No significant relationships between the pasture composition categories and CCL were detected at this site.

Table 5.6 Pasture composition at Hautope 2¹, expressed as a percentage of total sward biomass (%DM).

Season	Environment	HFR grasses	LFT grasses	Legume	Other species	Dead matter
		(ln[x+1])				
Spring'99	Open pasture	6 (1.33)	72	5	0	17
	Zone 1	4 (1.30)	87	0	0	9
	Zone 3	2 (0.58)	84	0	0	14
	Grand mean	4 (1.07)	81	2	0	13
Summer'99	Open pasture	4 (1.17)	80	1	0	15
	Zone 1	7 (1.84)	68	0	1	24
	Zone 3	4 (1.17)	73	0	1	23
	Grand mean	5 (1.39)	74	0	0	21
Overall	Open pasture	5 (1.25)	76	3	0	16
	Zone 1	5 (1.57)	78	0	0	17
	Zone 3	3 (0.87)	78	0	0	18
	Grand mean	4 (1.23)	77	1	0	17
Analysis of variance						
Environment (A)		NS	NS	NS	NS	NS
Season (B)		NS	P<0.05	NS	NS	P<0.01
Interaction (A*B)		NS	P<0.05	NS	NS	P<0.05
SD		(0.84)	7	3	0.5	5

¹Averaged across the entire range of poplar stand densities over a one-year period (1999-2000). Natural logarithm transformed (ln[x+1]) values are given in parentheses. Abbreviations: Zone 1, directly below the crowns of individual poplar trees; Zone 3, at the centre of the vertically projected gap between poplar crowns; DM, dry matter; HFR grasses, high fertility responsive grasses (*Lolium perenne*, *Dactylis glomerata*, *Holcus lanatus*, and *Poa* spp.); LFT grasses, low fertility tolerant grasses; SD, standard deviation; NS, not significant ($P \geq 0.1$).

5.4.5 Pasture nutritive values (proximate analysis)

5.4.5.1 Effect of overstorey environment and season on Kiwitea pasture nutritive values

Dry matter

In spring, the dry matter (DM) content of the freshly cut (wet) pasture amongst the trees (Zones 1 & 3) was on average 5.2% lower than in the open pasture (Table 5.7). Between spring and summer, there was little change in the DM content of the open pasture, whereas, in Zones 1 and 3 it increased to a level comparable with the open pasture environment (Table 5.7).

Organic matter digestibility and related metabolisable energy

In spring, the organic matter digestibility (OMD) of the pasture in the three main overstorey environments was similar (Table 5.7). However, between spring and summer all three decreased, with a greater degree of reduction in the open pasture. Thus, in summer the OMD of the understorey pasture amongst the trees (Zones 1 & 3) was on average 5.9% greater than in the open pasture (Table 5.7). The differences in the metabolisable energy (ME) content of the pastures mirrored those for OMD (Table 5.7).

Crude protein

Crude protein (CP) in the pastures decreased between spring and summer, irrespective of the overstorey environment (Table 5.7). Overall, Zones 1 and 3 tended to contain 1.6-2.1% more CP than the open pasture ($P=0.0815$; Table 5.7).

Neutral detergent fibre

In general, the variation in neutral detergent fibre (NDF) across the three main overstorey environments and two consecutive seasons was not large ($\leq 6\%$ DM; Table 5.7). However, the concentration of NDF in the pasture tended to depend on an interaction between the overstorey environment and season ($P=0.0747$; Table 5.7). In spring, Zone 1 had 4.6% more NDF than in the open pasture; whereas, the concentration in Zone 3 was not significantly different from either of the other two main overstorey environments (Table 5.7). Between spring and summer, the NDF in Zones 1 and 3 did not change significantly, whereas in the open pasture it increased to a level comparable with the other two overstorey environments (Zones 1 & 3) (Table 5.7). Unlike in spring, the concentration of NDF in Zone 3 in summer was marginally (but significantly) lower than in Zone 1 (Table 5.7).

Acid detergent fibre

Overall, Zone 1 had 1.6% and 2.4% more acid detergent fibre (ADF) than in Zone 3 and the open pasture, respectively (Table 5.7). Averaged across all three main overstorey environments, the concentration of ADF in the pasture also slightly increased over the two consecutive seasons (Table 5.7).

Soluble carbohydrate

Overall, the concentration of soluble carbohydrate (Sol CHO) was greatest in the open pasture, followed by Zone 3, and then Zone 1 (Table 5.7). Nevertheless, there tended to be an interaction between the overstorey environment and season ($P=0.0848$). In spring, the open pasture contained 2.4%-3.8% more Sol CHO than amongst the trees (Zones 1 & 3); whereas, at the same time, Zone 3 tended to have a greater concentration of Sol CHO than Zone 1 ($P=0.0533$). In summer, the open pasture continued to have a greater Sol CHO level than in Zone 1. However, the concentration in Zone 3 was not significantly different from either of the other two main overstorey environments (Table 5.7).

Lipid

Averaged across the three main overstorey environments, the amount of lipid in the pasture decreased by 0.6% between spring and summer (Table 5.7). There also tended to be an overstorey environment by season interaction ($P=0.0828$). In spring, Zones 1 and 3 had 0.4% more lipid (on average) than in the open environment. However, between spring and summer the lipid content in all three main overstorey environments decreased to a similar level (Table 5.7).

Ash

Overall, the ash content in Zone 3 was marginally greater than in the open pasture; whereas, in Zone 1 the ash content was not significantly different from either of the other two main overstorey environments (Table 5.7).

Dietary anion-cation difference

Averaged across the three main overstorey environments, the dietary anion-cation difference (DACD) of the pasture decreased by 28% between spring and summer (Table 5.7).

Table 5.7 Nutritive value indices for the mixed-species pasture¹ at Kiwitea: directly below the crowns of individual trees (Zone 1), at the centre of the vertically projected gap between trees (Zone 3), and in the open pasture.

Season	Environment	DM (%)	CP (% DM)	Lipid (% DM)	Ash (% DM)	ADF (% DM)	NDF (% DM)	Sol CHO (% DM)	DCAD (meq/kg DM)	OMD (% DM)	ME (MJ/kg DM)
Spring'98&'99	Open pasture	21.8	20.0	4.6	12.0	26.6	45.5	6.7	537	74.4	10.7
	Zone 1	16.3	21.9	5.1	11.6	28.9	50.1	2.9	530	72.9	10.5
	Zone 3	16.9	21.8	4.9	12.6	28.1	47.5	4.3	560	73.1	10.5
	Grand mean	18.4	21.2	4.8	12.1	27.9	47.7	4.6	542	73.5	10.6
Summer'99&'00	Open pasture	24.1	15.8	4.1	10.7	29.0	49.9	5.9	356	60.8	8.8
	Zone 1	25.4	17.1	4.3	11.8	31.6	50.9	4.2	405	66.4	9.5
	Zone 3	24.3	18.2	4.3	12.0	29.2	47.2	5.3	400	67.0	9.6
	Grand mean	24.6	17.0	4.2	11.5	29.9	49.3	5.1	387	64.7	9.3
Overall	Open pasture	23.0	17.9	4.4	11.3	27.8	47.7	6.3	447	67.6	9.8
	Zone 1	20.8	19.5	4.7	11.7	30.2	50.5	3.6	467	69.6	10.0
	Zone 3	20.6	20.0	4.6	12.3	28.6	47.3	4.8	480	70.0	10.0
	Grand mean	21.5	19.1	4.5	11.8	28.9	48.5	4.9	465	69.1	9.9
Analysis of variance											
Environment (A)		NS	P<0.1	NS	P<0.05	P<0.01	NS	P<0.05	NS	NS	NS
SEM (A)		0.6	0.5	0.05	0.3	0.3	0.6	0.3	11.8	0.8	0.09
Season (B)		P<0.001	P<0.001	P<0.001	NS	P<0.001	P<0.1	NS	P<0.001	P<0.001	P<0.001
SEM (B)		0.5	0.4	0.05	0.2	0.2	0.5	0.2	9.6	0.6	0.08
Interaction (A*B)		P<0.01	NS	P<0.1	NS	NS	P<0.1	P<0.1	NS	P<0.05	P<0.01
SEM (A*B)		0.9	0.7	0.08	0.4	0.4	0.9	0.4	16.7	1.1	0.13

¹Averaged across the entire range of poplar stand densities over a two-year period (1998-2000). Abbreviations: SEM, standard error of the mean; NS, not significant ($P \geq 0.1$); DM, dry matter; CP, crude protein; ADF, acid detergent fibre; NDF, neutral detergent fibre; Sol CHO, soluble carbohydrate; DCAD, dietary cation-anion difference; OMD, *in vitro* organic matter digestibility; ME, metabolisable energy.

5.4.5.2 The effect of poplar overstorey density on Kiwitea pasture nutritive values

In spring, the DM content of the freshly cut (wet) pasture decreased at a constant rate of $0.7\% \pm 0.1\%$ for every 10% increase in CCL (Figure 5.17a). Similarly, the Sol CHO concentration of the pasture also decreased with increasing CCL (Figure 5.17b). However, based on the limited spread of data points, the form of the latter relationship was exponential as opposed to linear. For both nutritive (feed) value indices, their relationships with CCL were not significantly different ($P>0.05$) between the two main zones of tree influence (Zones 1 & 3) (Figure 5.17a, b).

Conversely, the CP, lipid, NDF, and ADF contents of the pasture increased marginally with increasing CCL (Figure 5.17c,d,e,f). The relationships for NDF and ADF were significant only in Zone 1 (Figure 5.17d,e), whereas, for CP the relationship was significant only in Zone 3 (Figure 5.17c). Similar ($P>0.05$) relationships occurred for lipid in both of the main zones of tree influence (Zones 1 & 3) amongst the poplar stands (Figure 5.17f).

In summer, the rate of change in Zone 1 ADF was similar ($P>0.05$) to that observed in spring (Figures 5.17e & 5.18c). The OMD and related ME content of the pasture were also positively related to increasing CCL (Figure 5.18a,b); however, the maximum variation in these nutritive value indices was less than 8% DM and 1 MJ/kg DM, respectively, over the entire measured range of canopy covers (Figure 5.18a,b).

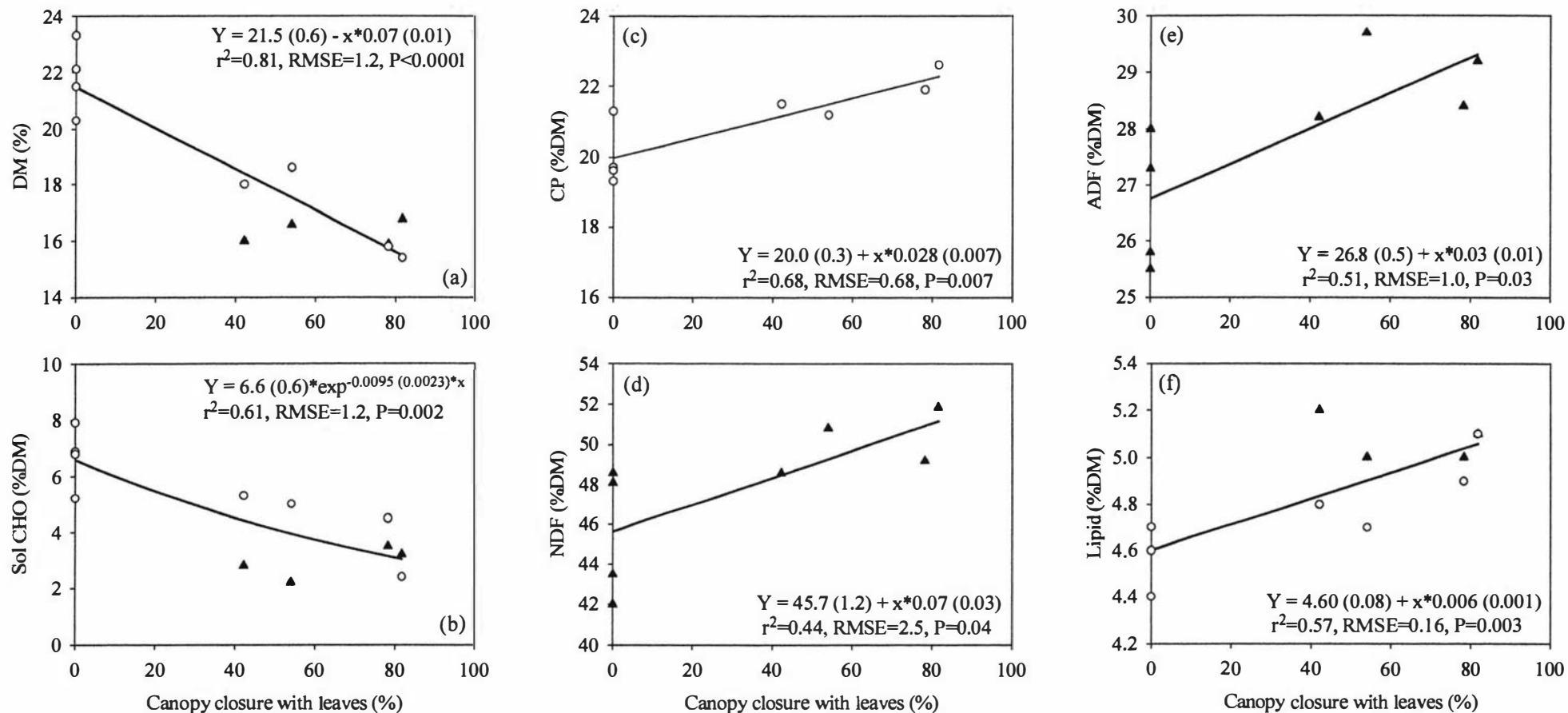


Figure 5.17 Spring relationships between pasture nutritive (feed) value indices and poplar canopy closure (CCL) at Kiwitea: (▲) directly below the crowns of individual trees (Zone 1), and (○) at the centre of the vertically projected canopy gap between trees (Zone 3). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction; DM, dry matter content; Sol CHO, soluble carbohydrates; CP, crude protein; NDF, neutral detergent fibre; ADF, acid detergent fibre.

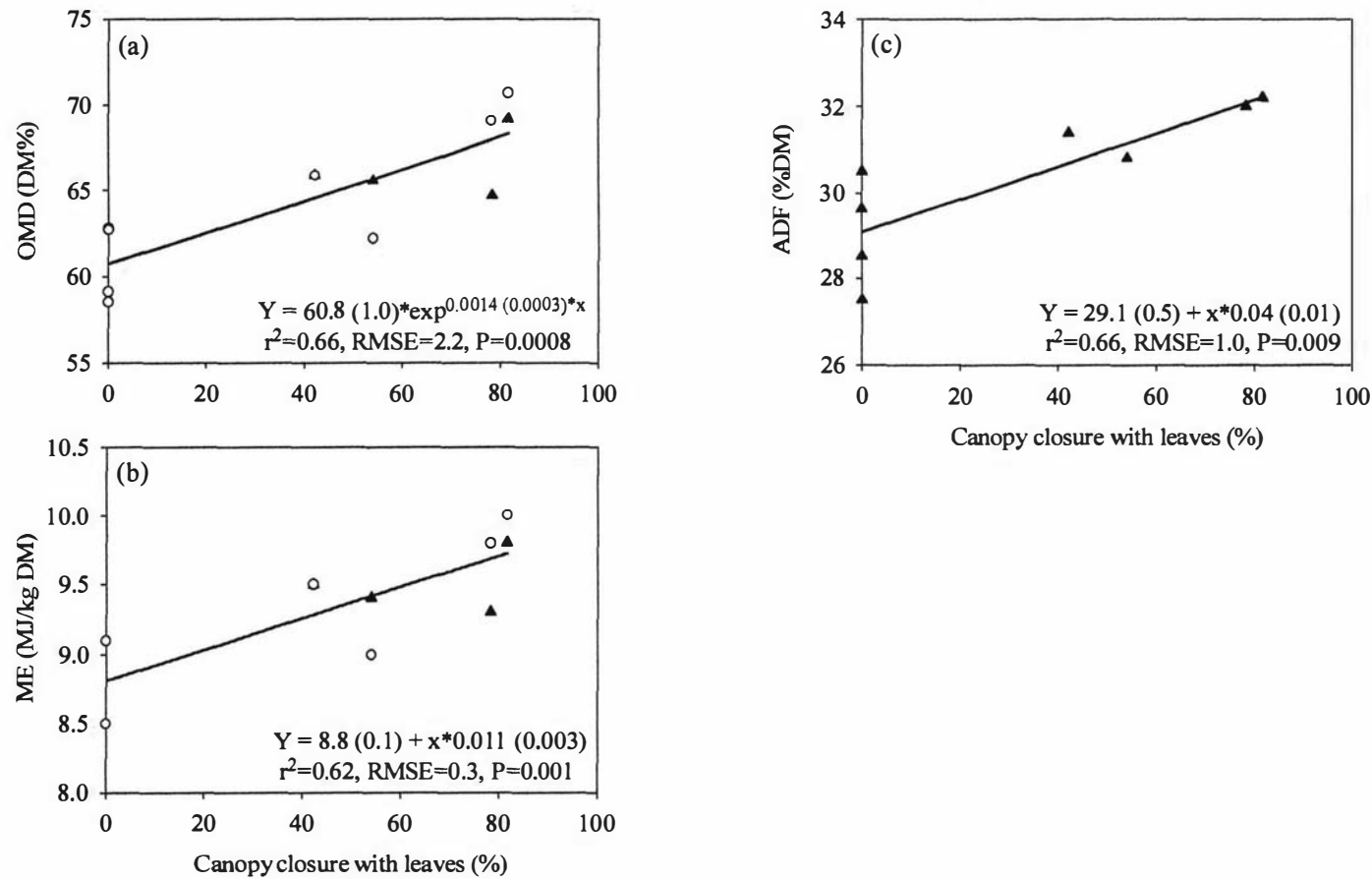


Figure 5.18 Summer relationships between pasture nutritive (feed) value indices and poplar canopy closure (CCL) at Kiwitea: (▲) directly below the crowns of individual trees (Zone 1), and (○) at the centre of the vertically projected canopy gap between trees (Zone 3). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction; OMD, *in vitro* organic matter digestibility; ME, metabolisable energy; ADF, acid detergent fibre.

5.4.5.3 Effect of overstorey environment and season on Hautope 1 pasture nutritive values

Dry matter

Overall, the DM content of the freshly cut (wet) pasture amongst the trees (Zones 1 & 3) was on average 4.7% lower than in the open pasture (Table 5.8). In spring, the DM content of the pastures was very high at above 80%, whereas, in summer this decreased markedly to around 20% (Table 5.8).

Organic matter digestibility and related metabolisable energy

In spring, the OMD of the pasture was similar for all three main overstorey environments (Table 5.8). However, over the ensuing season, while the OMD of the open pasture decreased slightly by 8%, it increased (Zone 1) and tended to increase ($P=0.0870$; Zone 3) by on average 6% amongst the trees (Table 5.8).

The differences in ME mirrored those for OMD. Thus, the three main overstorey environments were not significantly different in spring, but the understorey pasture (Zones 1 & 3) had a greater ME content compared to the open pasture in summer (Table 5.8). This divergence was caused mainly by a drop in the ME content of the open pasture between spring and summer, as opposed to an increase amongst the poplar trees (Zones 1 & 3) (Table 5.8).

Crude protein

Overall, the understorey pasture amongst the trees (Zones 1 & 3) had 4% more CP than in the open pasture (Table 5.8). When averaged across the three main overstorey environments, the CP in the pastures also increased by 4.8% over the two consecutive seasons (Table 5.8).

Neutral detergent fibre

In spring, the open pasture had on average 4.7% less NDF compared to the understorey pasture (Zones 1 & 3) (Table 5.8). However, between spring and summer, the NDF content in the open pasture increased by 4%, whereas, it decreased in Zones 1 and 3 by on average 6.1%. Thus, the difference in NDF concentration, between the three main overstorey environments, was reversed in summer (Table 5.8).

Acid detergent fibre

In spring, the level of ADF in the pastures was similar for all three main overstorey environments (Table 5.8). Between spring and summer, the ADF content in the open pasture did not change significantly. This contrasted with amongst the trees (Zones 1 & 3), which decreased by on average 3.6% (Table 5.8).

Soluble carbohydrate

Overall, the open pasture had 2.9% more Sol CHO than in Zones 1 and 3 (Table 5.8). When averaged across the three main overstorey environments, the concentration of Sol CHO in the pastures slightly decreased over the two consecutive seasons ($P=0.0514$; Table 5.8).

Lipid

Between spring and summer the concentration of lipid in the pastures increased by on average 1.3% (Table 5.8). Nevertheless, an interaction tended to occur between the overstorey environment and season ($P=0.0843$). In spring, all three main overstorey environments contained approximately 3.4% lipid. Over the ensuing summer season this concentration increased further, but was especially marked in Zones 1 and 3. Thus, in summer, the understorey pasture directly below the tree crowns (Zone 1) and at the centre of the inter-canopy gap (Zone 3) had, and tended ($P=0.0586$) to have, respectively, a greater concentration of lipid compared to the open pasture (Table 5.8).

Ash

In spring, the ash content of the pastures was not significantly different between the three main overstorey environments (Table 5.8). Generally, the amount of ash produced increased over the two consecutive seasons, but was again especially marked in Zones 1 and 3. As a result, the understorey pastures (Zone 1&3) contained on average 1.8% more ash than in the open pasture in summer (Table 5.8).

Dietary anion-cation difference

In spring, the DACD of the pastures in all three main overstorey environments was similar (Table 5.8). Between spring and summer, the DACD in the open pasture decreased by 18%, while in Zone 1 it increased by 17%. No significant change occurred in Zone 3. Thus, overall in summer, the DACD of the understorey pastures (Zone 1 & 3) was on average 31% greater than in the open pasture (Table 5.8).

Table 5.8 Nutritive value indices for mixed-species pasture¹ at Hautope 1: directly below the crowns of individual poplar trees (Zone 1), at the centre of the vertically projected gap between the poplar crowns (Zone 3), and in the open pasture.

Season	Environment	DM (%)	CP (% DM)	Lipid (% DM)	Ash (% DM)	ADF (% DM)	NDF (% DM)	Sol CHO (% DM)	DCAD (meq/kg DM)	OMD (% DM)	ME (MJ/kg DM)
(lnx)											
Spring'99	Open pasture	87.2	12.2	3.5	10.2	32.2	54.1	8.2	531	66.2	9.4 (2.24)
	Zone 1	84.1	14.8	3.5	10.5	33.5	58.6	4.1	496	63.7	9.0 (2.20)
	Zone 3	83.2	13.2	3.2	10.4	34.1	59.0	5.1	546	64.5	9.2 (2.21)
	Grand mean	84.9	13.4	3.4	10.4	33.2	57.2	5.8	524	64.8	9.2 (2.22)
Summer'00	Open pasture	25.3	14.0	4.4	11.3	33.1	58.1	6.4	438	58.3	8.1 (2.09)
	Zone 1	19.2	20.6	5.0	13.1	29.7	51.6	4.2	579	71.3	9.7 (2.27)
	Zone 3	19.3	19.9	4.9	13.1	30.7	53.8	4.2	570	69.1	9.4 (2.24)
	Grand mean	21.3	18.2	4.7	12.5	31.2	54.5	4.9	529	66.2	9.1 (2.20)
Overall	Open pasture	56.2	13.1	3.9	10.7	32.6	56.1	7.3	484	62.3	8.8 (2.16)
	Zone 1	51.7	17.7	4.3	11.8	31.6	55.1	4.1	537	67.5	9.4 (2.23)
	Zone 3	51.3	16.6	4.0	11.8	32.4	56.4	4.6	558	66.8	9.3 (2.23)
	Grand mean	53.1	15.8	4.1	11.4	32.2	55.8	5.3	527	65.5	9.1 (2.21)
Analysis of variance											
Environment (A)		P<0.01	P<0.05	NS	P<0.001	NS	NS	P<0.05	P≤0.05	P<0.1	NS
SEM (A)		1.2	0.8	0.1	0.2	0.5	0.8	0.3	18	1.2	(0.02)
Season (B)		P<0.001	P<0.001	P<0.001	P<0.001	P<0.01	P<0.05	P=0.05	NS	NS	NS
SEM (B)		1.0	0.6	0.1	0.1	0.4	0.6	0.3	15	1.0	(0.01)
Interaction (A*B)		NS	NS	P<0.1	P<0.05	P<0.05	P<0.01	NS	P<0.05	P<0.01	P<0.05
SEM (A*B)		1.7	1.1	0.2	0.3	0.7	1.1	0.5	25	1.7	(0.03)

¹Averaged across the entire range of poplar stand densities over a one-year period (1999-2000). Transformed values are given in parentheses. Abbreviations: lnx, natural-logarithm transformed; SEM, standard error of the mean; NS, not significant ($P \geq 0.1$); DM, dry matter; CP, crude protein; ADF, acid detergent fibre; NDF, neutral detergent fibre; Sol CHO, soluble carbohydrates; DCAD, dietary cation-anion difference; OMD, *in vitro* organic matter digestibility; ME, metabolisable energy.

5.4.5.4 Effect of poplar overstorey density on Hautope 1 pasture nutritive values

In spring, the Sol CHO concentration in the pasture decreased at a constant rate of $0.6\% \text{ DM} \pm 0.1\% \text{ DM}$ for every 10% increase in CCL (Figure 5.19a). Both of the main zones of tree influence (Zones 1 & 3) had similar ($P>0.05$) negative linear relationships, and the overall strength of the combined relationship was strong ($r^2=0.76$; $P=0.0001$). In Zone 1, the DCAD of the understorey pasture also decreased marginally with increasing CCL (Figure 5.19e). However, the strength of this negative linear relationship was moderate ($r^2=0.44$; $P=0.04$).

Conversely, the CP, NDF, and ADF in the pasture were positively related to CCL (Figure 5.19b,c,d). These nutritive value indices increased at $0.4 \pm 0.1\% \text{ DM}$, $0.7 \pm 0.1\% \text{ DM}$, and $0.2 \pm 0.1\% \text{ DM}$, respectively, for every 10% increase in CCL. However, the rate of change relative to the open pasture level was at least twice as large for CP compared to the other two indices (Figure 5.19b,c,d). In addition, the relationships for CP and ADF were restricted to Zone 1 (Figure 5.19b,d); whereas, similar ($P>0.05$) relationships for NDF occurred in both Zones 1 and 3 (Figure 5.19c). No clear trends were evident for DM, OMD, ME, lipid, or ash in the spring pastures.

In summer, all of the nutritive value indices, except for the DM, Sol CHO, and lipid contents, showed significant relationships with CCL (Figure 5.20). The OMD, ME, ash, and DCAD in the pasture increased at a constant rate of $2.1 \pm 0.3\% \text{ DM}$, $0.3 \pm 0.04 \text{ MJ/kg DM}$, $0.27 \pm 0.06\% \text{ DM}$, and $24 \pm 5 \text{ meq/kg DM}$, respectively, for every 10% increase in CCL (Figures 5.20a,b,f & 5.21). Similarly, the concentration of CP also increased with increasing CCL (Figure 5.20c). However, based on the very limited spread of data points the form of this relationship was exponential as opposed to linear. In the open pasture the predicted CP content was 14% DM, increasing to 22% at maximum measured CCL (Figure 5.20c). Conversely, the level of NDF and ADF in the pasture decreased at a constant rate of $1.0 \pm 0.2\% \text{ DM}$ and $0.6 \pm 0.1\% \text{ DM}$, respectively, for every 10% increase in CCL (Figure 5.20d,e). In general, for each of the above nutritive value indices, the relationships in both main zones of tree influence (Zones 1&3) were similar ($P>0.05$) (Figures 5.20 & 5.21).

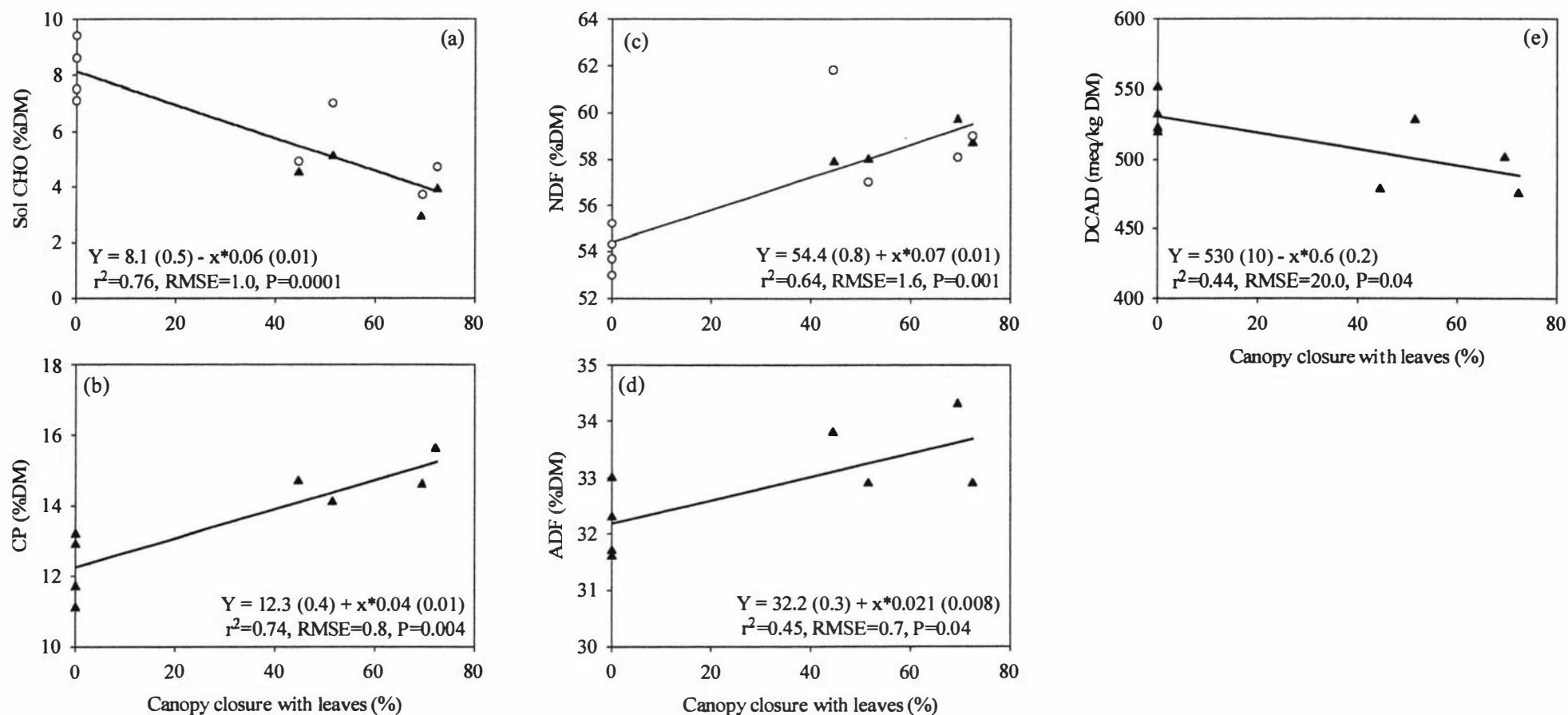


Figure 5.19 Spring relationships between pasture feed value indices and poplar canopy closure (CCL) at Hautope 1: (\blacktriangle) directly below the crowns of individual trees (Zone 1), and (\circ) at the centre of the vertically projected canopy gap between trees (Zone 3). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction; CP, crude protein; ADF, acid detergent fibre; NDF, neutral detergent fibre; Sol CHO, soluble carbohydrates; DCAD, dietary cation-anion difference.

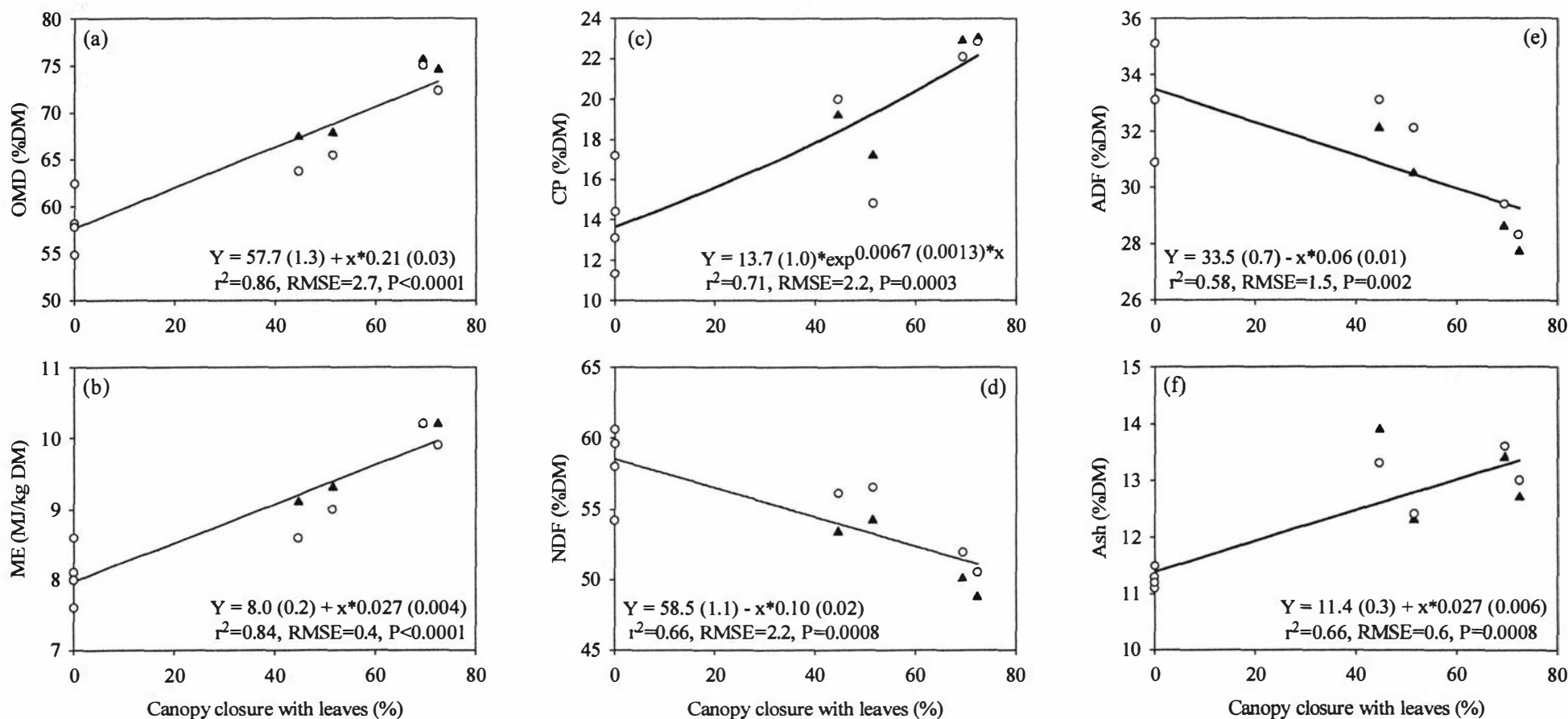


Figure 5.20 Summer relationships between pasture feed value indices and poplar canopy closure (CCL) at Hautope 1: (▲) directly underneath the crowns of individual trees (Zone 1), and (○) at the centre of the vertically projected canopy gap between trees (Zone 3). Standard errors for regression coefficients are in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction; CP, crude protein; ADF, acid detergent fibre; NDF, neutral detergent fibre; OMD, *in vitro* organic matter digestibility; ME, metabolisable energy.

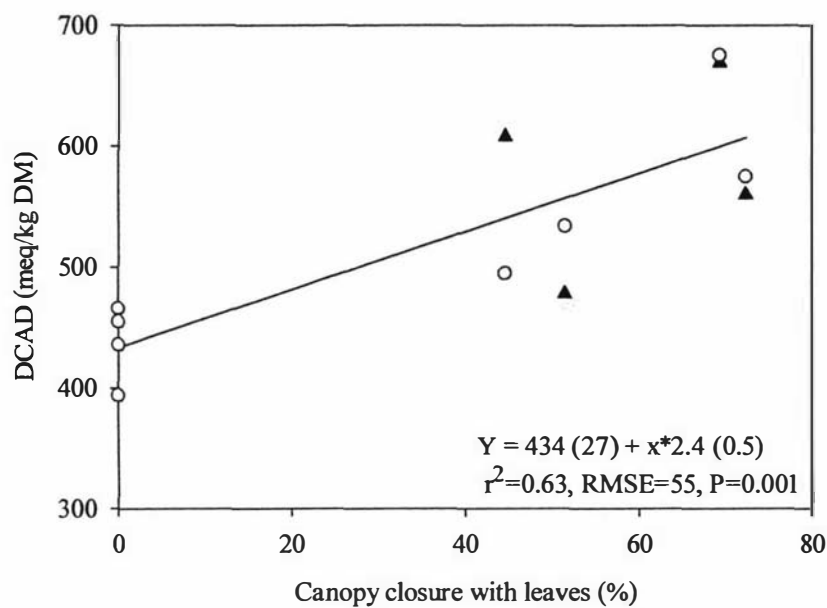


Figure 5.21 Summer relationship between the dietary cation-anion difference (DCAD) and poplar canopy closure (CCL) at Hautope 1: (▲) directly below the crowns of individual trees (Zone 1), and (○) at the centre of the vertically projected canopy gap between trees (Zone 3). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction.

5.4.6 Poplar leaf nutritive values

5.4.6.1 Seasonal effects at Kiwitea

The DM content of the fresh (wet) poplar leaves increased from spring through until autumn (Table 5.9). In spring the DM content was $26\% \pm 1\%$ and this increased by 4.2% and then a further 2.4% over the spring-summer and summer-autumn intervals, respectively (Table 5.9). Between spring and summer the concentrations of Sol CHO, CP, and lipid in the leaves did not change significantly. However, over the ensuing autumn season these three indices decreased by 5.2%, 7.5%, and 0.2% DM, respectively (Table 5.9). Similarly, while the OMD and ME content of the leaves decreased slightly between spring and summer, these two indices also decreased markedly over the ensuing autumn period (Table 5.9). Over the same period the ADF and NDF concentration increased by around 9% DM (Table 5.9). The ash content and DCAD of the leaves varied little over time (Table 5.9).

In both spring and summer, the DM, Sol CHO, OMD and ME content of the poplar leaves were 6-8%, 6-7%, 5-12% DM, and 0.8-1.8 MJ/kg DM, respectively, higher than in the mixed-species pasture ($P < 0.001$; Tables 5.7 & 5.9). Conversely, over the same two consecutive seasons, the ADF, NDF, and ash concentrations were 4-5%, 13-14%, and around 2%, respectively lower in the poplar leaves, compared to the mixed-species pasture ($P < 0.001$; Tables 5.7 & 5.9). There was little difference in lipid and the DCAD between the two types of plant material in spring ($P > 0.05$). However, both of these feed value indices were significantly higher in the poplar leaves in summer ($P < 0.01$; Tables 5.7 & 5.9). The concentration of CP in the two types of plant material was not significantly different in either spring or summer ($P > 0.05$; Tables 5.7 & 5.9).

5.4.6.2 Seasonal effects at Hautope 1

The DM content of the fresh (wet) poplar leaves tended to increase from spring through until late autumn (Table 5.10). In spring, the leaves contained $30\% \pm 3\%$ DM and this increased by 5% and then 16% over the summer and autumn seasons, respectively (Table 5.10). Similarly, between spring and summer the Sol CHO content of the leaves increased marginally by 2% DM. However, this concentration then decreased by 8% DM during the ensuing summer/autumn period (Table 5.10). Over the same latter period, the

CP, OMD and ME content of the leaves also decreased by 5.8%, 17.1%, and 2.4 MJ/kg DM, respectively, while the ADF and NDF concentration tended to increase by around 8% DM (Table 5.10). In spring the DCAD was 531 meq/kg DM. This decreased by 12.8% and then 35.8% in summer and autumn, respectively (Table 5.10). The lipid and ash concentrations of the leaves did not vary significantly over time (Table 5.10).

In spring, the DM content of the fresh (wet) poplar leaves was 35% of that in the mixed-species pasture. However, in summer the reverse occurred, with the DM content of the latter being 61% of that in the poplar leaves ($P < 0.001$; Tables 5.8 & 5.10). Analogous to Kiwitea, the concentration of Sol CHO, OMD, and ME content of the poplar leaves were 5-8%, 10-12%, and 1.4-1.8 MJ/kg DM, respectively, higher than in the mixed-species pasture, over both spring and summer ($P < 0.05$; Tables 5.8 & 5.10). At the same time, the ADF and NDF concentrations in the poplar leaves were 4.4-6.9% and 21.8-23%, respectively, lower than in the mixed-species pasture ($P < 0.05$; Tables 5.8 & 5.10). Also similar to Kiwitea in spring, the DCAD did not differ significantly between the two types of plant material ($P > 0.05$). However, in summer the DCAD of the poplar leaves was marginally (12%) lower than the mixed-species pasture ($P < 0.05$; Tables 5.8 & 5.10). In spring, the CP and Lipid concentrations were 5.5% and 0.9% DM, respectively, higher in the poplar leaves than mixed-species pasture ($P < 0.01$). However, in the following summer, the lipid concentration was 0.6% DM greater in the pasture ($P < 0.001$), while there was little difference in CP between the two types of plant material (Tables 5.8 & 5.10).

Table 5.9 Nutritive value indices for *P. x euramericana* leaves at Kiwitea.

Season	DM (%)	CP (%DM)	Lipid (%DM)	Ash (%DM)	ADF (%DM)	NDF (%DM)	Sol CHO (%DM)	DCAD (meq/kg DM)	OMD (%DM)	ME (MJ/kg DM)
Spring	26.8	19.8	5.0	10.0	24.0	34.4	11.3	562	78.8	11.4
Summer	31.0	18.5	4.9	9.7	25.3	35.5	11.2	519	76.6	11.1
Autumn	33.4	11.0	4.7	10.3	34.2	44.0	6.0	448	63.4	9.2
Grand mean	30.4	16.4	4.9	10.0	27.8	37.9	9.5	510	72.9	10.5
Analysis of variance										
Significance	P<0.05	P<0.01	P<0.05	NS	P<0.01	P<0.01	P<0.05	NS	P<0.01	P<0.05
SEM (n=12)	0.9	1.3	0.1	0.1	1.4	1.3	0.8	18	2.1	0.3

Averaged over a two-year period (1998-2000). Abbreviations: SEM, standard error of the mean; NS, not significant ($P \geq 0.1$); DM, dry matter; CP, crude protein; ADF, acid detergent fibre; NDF, neutral detergent fibre; Sol CHO, soluble carbohydrate; DCAD, dietary cation-anion difference; OMD, *in vitro* organic matter digestibility; ME, metabolisable energy.

Table 5.10 Nutritive value indices for *P. x euramericana* leaves at Hautope 1.

Season	DM (%)	CP (%DM)	Lipid (%DM)	Ash (%DM)	ADF (%DM)	NDF (%DM)	Sol CHO (%DM)	DCAD (meq/kg DM)	OMD (%DM)	ME (MJ/kg DM)
Spring	30.1	18.9	4.3	10.0	26.3	35.4	11.1	531	75.3	10.6
Summer	34.7	17.1	4.1	11.0	26.8	31.5	13.2	463	78.3	10.9
Autumn	50.9	11.3	4.1	10.0	34.5	39.1	5.6	297	61.2	8.5
Grand mean	38.6	15.7	4.1	10.3	29.2	35.3	10.0	430	71.6	10.0
Analysis of variance										
Significance	P<0.1	P<0.05	NS	NS	P<0.1	P<0.1	P<0.1	P<0.05	P<0.05	P<0.05
SEM (n=12)	2.8	1.1	0.1	0.4	1.3	1.2	1.2	32	2.4	0.3

Averaged over a one-year period 1999-2000. Abbreviations: SEM, standard error of the mean; NS, not significant ($P\geq 0.1$); DM, dry matter; CP, crude protein; ADF, acid detergent fibre; NDF, neutral detergent fibre; Sol CHO, soluble carbohydrate; DCAD, dietary cation-anion difference; OMD, *in vitro* organic matter digestibility; ME, metabolisable energy.

5.4.7 Pasture mineral content

5.4.7.1 Effect of overstorey environment and season on Kiwitea pasture mineral concentrations

Major mineral elements

Overall, the concentrations of potassium (K) and magnesium (Mg) in the understorey pasture amongst the trees (Zones 1 & 3) were 31% and 13%, respectively, greater than in the adjacent open pasture (Table 5.11). When averaged across all three main overstorey environments, these two major cations decreased significantly between spring and summer (Table 5.11). In spring, the concentration of phosphorus (P) in Zones 1 and 3 was 19% greater than in the open pasture. Nevertheless, all three main overstorey environments decreased to a similar level of 0.3%DM over the ensuing season (Table 5.11). Between spring and summer the concentration of sulfur (S) in Zones 1 and 3 decreased by 20-22%, whereas, it did not change significantly in the open pasture. As a result, Zone 1 contained significantly less S than in the open environment (Table 5.11). For both calcium (Ca) and sodium (Na) there were no significant differences between overstorey environments or seasons (Table 5.11).

Trace mineral elements

Averaged over the two consecutive seasons, the concentration of manganese (Mn) was 50% greater in the open pasture than in Zones 1 and 3 (Table 5.12). On the other hand, strontium (Sr) tended ($P=0.0531$) to form a graded series, with Zone 3 having the greatest and the open pasture having the lowest concentration (Table 5.12). Both of these trace elements, along with iron (Fe) and aluminium (Al), accumulated in the pastures between spring and summer (Table 5.12). Conversely, copper (Cu) and nickel (Ni) decreased over the same period of time (Table 5.12). The levels of zinc (Zn), boron (B) and cobalt (Co) in the pastures were not significantly different between overstorey environments or seasons (Table 5.12).

Table 5.11 Major mineral elements ($\mu\text{g/g DM}$) in the mixed-species pasture¹ at Kiwitea: directly below the crowns of individual poplar trees (Zone 1), at the centre of the vertically projected gap between poplar crowns (Zone 3), and in the open pasture.

Season	Environment	Ca	K	Mg	Na	P	S
					(lnx)		
Spring'98&'99	Open pasture	4228	21672	1961	1135	3722	2679
	Zone 1	4189	30449	2400	1038	4513	2898
	Zone 3	5049	29358	2251	1200	4338	2961
	Grand mean	4488	27159	2204	1124	4191	2846
Summer'98&'99	Open pasture	3953	18773	1932	1491	3217	2572
	Zone 1	4783	22733	2102	1319	3252	2246
	Zone 3	4912	23113	2080	1193	3270	2361
	Grand mean	4549	21540	2038	1334	3246	2393
Overall	Open pasture	4090	20223	1946	1313	3470	2626
	Zone 1	4486	26591	2251	1178	3882	2572
	Zone 3	4980	26235	2166	1197	3804	2661
	Grand mean	4519	24350	2121	1229	3719	2620
Analysis of variance							
Environment (A)		NS	P<0.05	P=0.05	NS	NS	NS
SEM (A)		175	767	40	(0.07)	65	67
Season (B)		NS	P<0.001	P<0.01	NS	P<0.001	P<0.001
SEM (B)		145	626	33	(0.06)	53	55
Interaction (A*B)		NS	NS	NS	NS	P<0.01	P<0.05
SEM (A*B)		247	1084	57	(0.11)	92	95

¹Averaged across the entire range of poplar stand densities over a two-year period (1998-2000). Transformed values are given in parentheses. Abbreviations: lnx, natural-logarithm transformed; SEM, standard error of the mean; NS, not significant ($P \geq 0.1$); DM, dry matter; Ca, calcium; K, potassium; Mg, magnesium; Na, sodium; P, phosphorus; S, sulfur.

Table 5.12 Trace mineral elements ($\mu\text{g/g DM}$) in the mixed-species pasture¹ at Kiwitea: directly below the crowns of individual poplar trees (Zone 1), at the centre of the vertically projected gap between poplar crowns (Zone 3), and in the open pasture.

Season	Environment	Cu	Fe	Mn	Zn	Al	B	Co	Ni	Sr
			(lnx)	(lnx)		($\text{x}^{-1} \times 10^{-3}$)				
Spring'98&'99	Open pasture	19.4	211 (5.30)	137.1 (4.90)	36.3	206.5 (5.25)	20.2	0.50	0.55	24.6
	Zone 1	17.9	182 (5.20)	62.7 (4.13)	36.1	236.3 (4.50)	22.5	0.55	0.70	24.9
	Zone 3	17.5	168 (5.12)	84.1 (4.42)	45.6	189.3 (5.39)	20.0	0.40	0.55	30.2
	Grand mean	18.3	182 (5.21)	86.1 (4.48)	39.3	211.5 (5.05)	20.9	0.48	0.60	26.6
Summer'99&'00	Open pasture	15.0	265 (5.57)	155.0 (5.03)	36.6	401.8 (2.63)	17.7	0.48	0.35	26.2
	Zone 1	14.1	327 (5.76)	120.9 (4.71)	33.8	574.0 (2.01)	19.0	0.73	0.43	32.2
	Zone 3	14.5	273 (5.59)	122.5 (4.79)	41.8	477.3 (2.30)	19.8	0.63	0.53	33.1
	Grand mean	14.6	293 (5.64)	128.3 (4.84)	37.4	500.9 (2.32)	18.8	0.64	0.43	30.5
Overall	Open pasture	17.2	238 (5.43)	146.1 (4.96)	36.5	304.1 (3.94)	18.9	0.49	0.45	25.4
	Zone 1	16.0	255 (5.48)	91.8 (4.42)	34.9	405.1 (3.26)	20.8	0.64	0.56	28.5
	Zone 3	16.0	220 (5.35)	103.3 (4.60)	43.7	333.3 (3.85)	19.9	0.51	0.54	31.7
	Grand mean	16.4	238 (5.42)	107.2 (4.66)	38.4	356.2 (3.68)	19.8	0.56	0.52	28.5
Analysis of variance										
Environment (A)		NS	NS	P<0.01	NS	NS	NS	NS	NS	P=0.05
SEM (A)		0.3	(0.10)	(0.09)	3.2	(0.52)	1.2	0.06	0.06	0.9
Season (B)		P<0.001	P<0.01	P<0.01	NS	P<0.01	NS	NS	P<0.05	P<0.01
SEM (B)		0.3	(0.08)	(0.08)	2.6	(0.42)	1.0	0.05	0.05	0.8
Interaction (A*B)		NS	NS	NS	NS	NS	NS	NS	NS	NS
SEM (A*B)		0.5	(0.14)	(0.13)	4.5	(0.73)	1.7	0.08	0.08	1.3

¹Averaged across the entire range of poplar stand densities over a two-year period (1998-2000). Transformed values are given in parentheses. Abbreviations: lnx, natural-logarithm transformed; $\text{x}^{-1} \times 10^{-3}$, inverse transformed; DM, dry matter; SEM, standard error of the mean; NS, not significant ($P \geq 0.1$); Cu, copper; Fe, iron; Mn, manganese; Zn, zinc; Al, aluminium; B, boron; Co, cobalt; Ni, nickel; Sr, strontium. The values for Al, B, Co, Ni, and Sr are based on one year (1999-2000).

5.4.7.2 The effect of poplar overstorey density on Kiwitea pasture mineral concentrations

Major mineral elements

In spring, the concentrations of K, Mg, P, and S in the pasture showed moderate through to strong ($r^2=0.59-0.79$) positive linear relationships with increasing CCL (Figure 5.22). Similar ($P>0.05$) linear relationships were evident in both Zone 1 and 3 for K, Mg, and P, whereas, for S the relationship solely occurred in Zone 3 (Figure 5.22). The rate of change in K, Mg, P, and S was $1220 \pm 190 \mu\text{g/g DM}$, $56 \pm 12 \mu\text{g/g DM}$, $115 \pm 28 \mu\text{g/g DM}$, and $50 \pm 12 \mu\text{g/g DM}$, respectively, for every 10% increase in CCL (Figure 5.22). No clear trends were apparent for either Ca or Na in the spring pastures.

In summer, linear relationships similar to those found in spring occurred for K and Mg (Figure 5.23a,b). However, the intercept of the relationship for K was 19% lower than in spring ($P=0.05$), and for Mg the relationship was significant only in Zone 3. In addition to these two major cations, the concentration of Ca also showed a moderate ($r^2=0.42$), but positive, linear relationship with increasing CCL. This major cation accumulated at a rate of $144 \pm 48 \mu\text{g/g DM}$ for every 10% increase in CCL (Figure 5.23c). No clear trends were apparent for P, S, or Na in the summer pastures.

Trace mineral elements

Amongst the trees (Zone 1 & 3) in spring, the concentrations of Cu and Mn decreased at a constant rate of $0.3 \pm 0.1 \mu\text{g/g DM}$ and $9.0 \pm 2.0 \mu\text{g/g DM}$, respectively, for every 10% increase in CCL (Figure 5.24). The strength of the relationship for Cu was moderate ($r^2=0.56$), whereas, for Mn it was strong ($r^2=0.65$) (Figure 5.24).

Sr was the only trace element that showed a significant relationship with CCL in summer (Figure 5.25). However, the strength of this relationship was a moderate fit ($r^2=0.51$). In both Zones 1 and 3 Sr increased at a constant rate of $1.0 \pm 0.3 \mu\text{g/g DM}$ for every 10% increase in CCL (Figure 5.25).

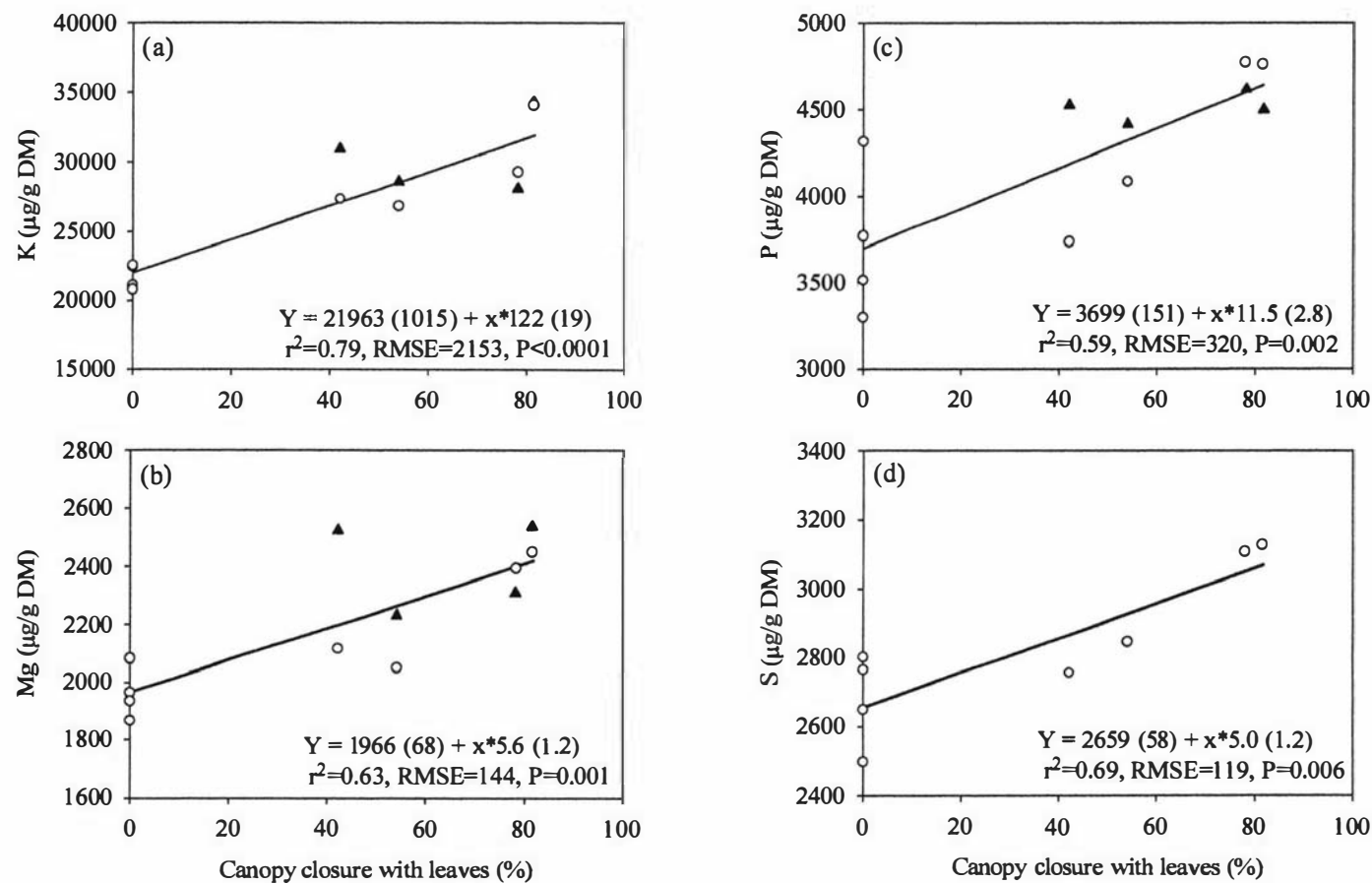


Figure 5.22 Spring relationships between major pasture minerals and poplar canopy closure (CCL) at Kiwitea: (▲) directly below the crowns of individual trees (Zone 1), and (○) at the centre of the vertically projected canopy gap between trees (Zone 3). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction; K, potassium; Mg, magnesium; P, phosphorus; and S, sulfur.

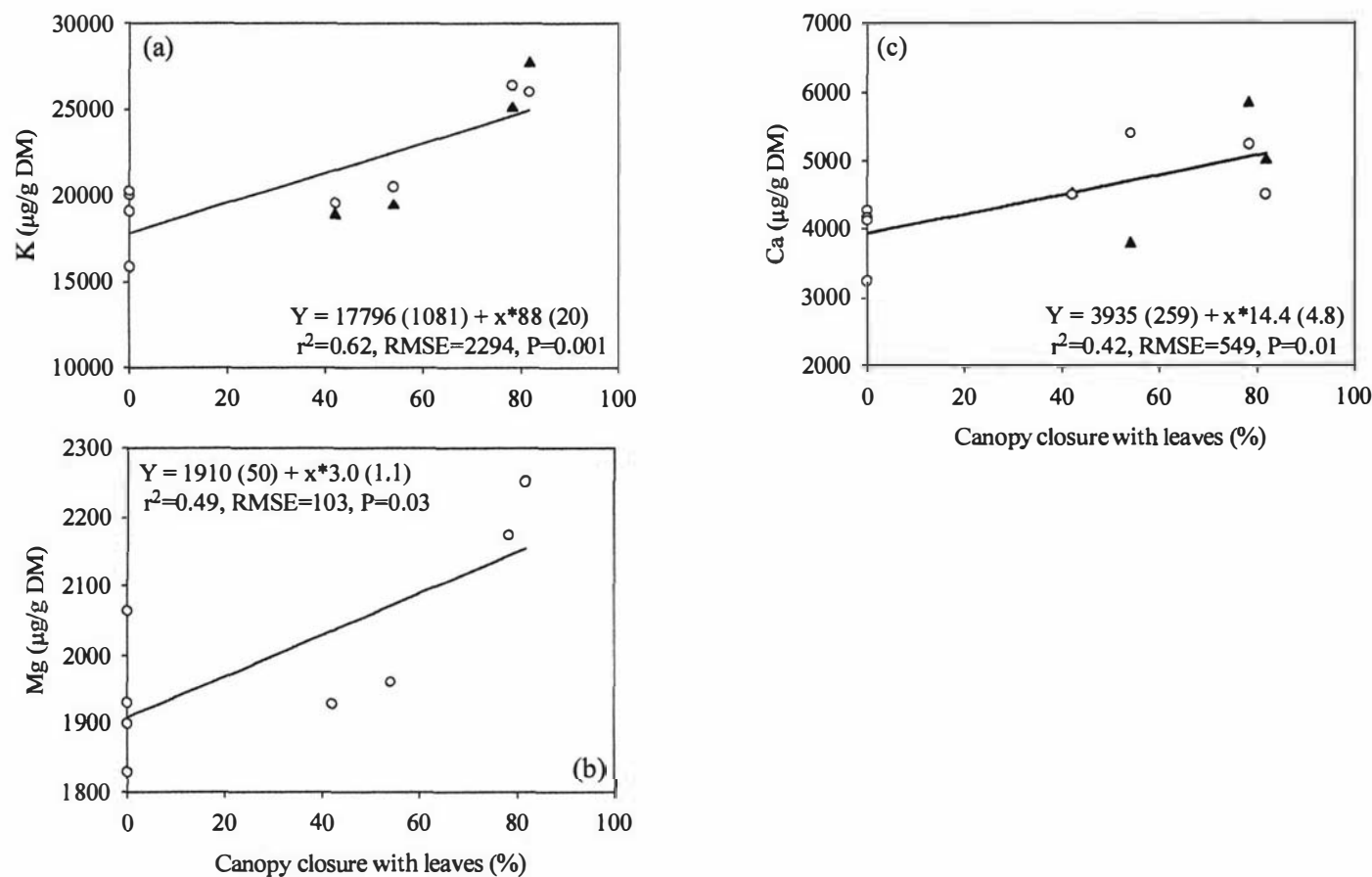


Figure 5.23 Summer relationships between major pasture minerals and poplar canopy closure (CCL) at Kiwitea: (\blacktriangle) directly below the crowns of individual trees (Zone 1), and (\circ) at the centre of the vertically projected canopy gap between trees (Zone 3). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction; K, potassium; Mg, magnesium; and Ca, calcium.

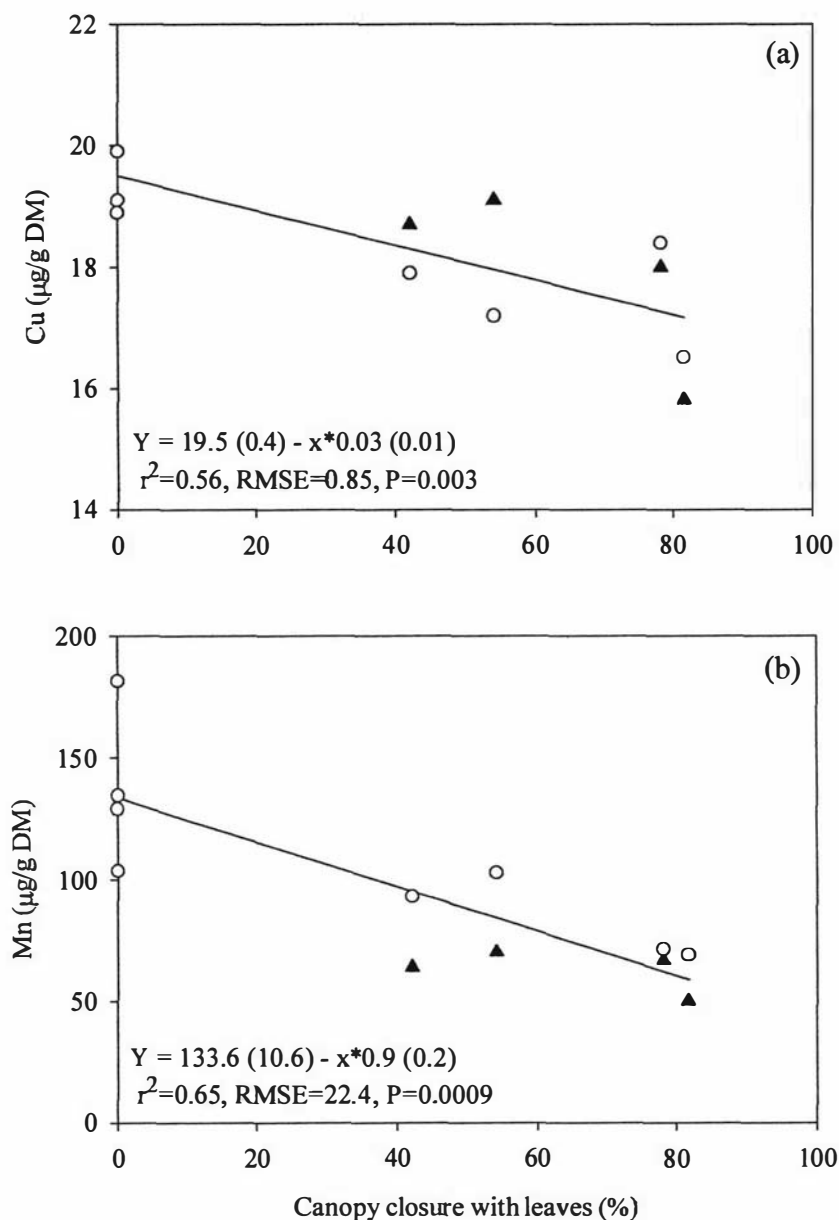


Figure 5.24 Spring relationships between pasture trace minerals and poplar canopy closure (CCL) at Kiwitea: (\blacktriangle) directly below the crowns of individual trees (Zone 1), and (\circ) at the centre of the vertically projected canopy gap between trees (Zone 3). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction; Cu, copper; and Mn, manganese.

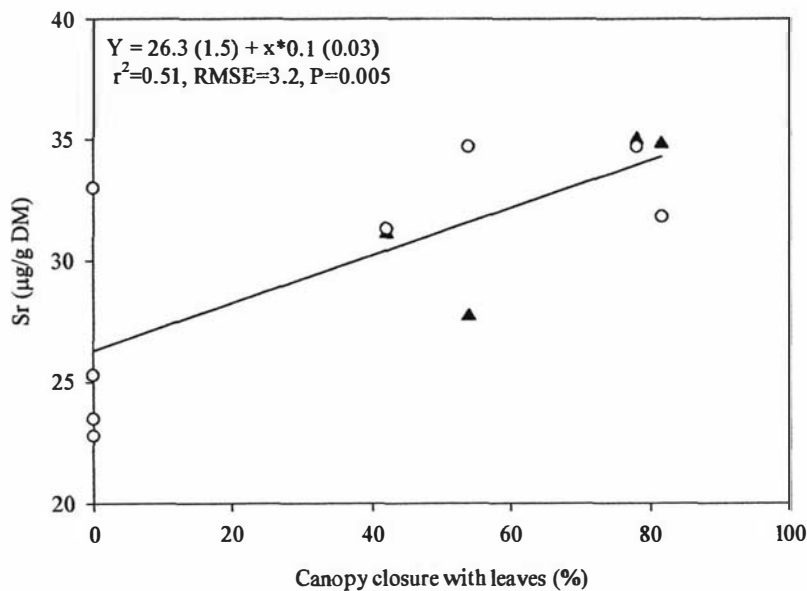


Figure 5.25 Summer relationship between strontium (Sr) and poplar canopy closure (CCL) at Kiwitea: (▲) directly below the crowns of individual trees (Zone 1), and (○) at the centre of the vertically projected canopy gap between trees (Zone 3). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction.

5.4.7.3 Effect of overstorey environment and season on Hautope 1 pasture mineral concentrations

Major mineral elements

Overall, the K and Mg concentrations in the understorey pastures amongst the trees (Zones 1 & 3) were 66% and 47% greater than in the open pasture, respectively (Table 5.13). Across the three main overstorey environments, Mg increased by 16% between spring and summer (Table 5.13). Similarly, over the same two consecutive seasons, K increased in Zone 3, but did not change significantly in Zone 1 or the open pasture ($P=0.0492$; Table 5.13). While the level of Ca in the pastures did not differ among the three main overstorey environments, this major mineral element also increased by 26% over spring and summer (Table 5.13).

The understorey pasture in Zone 1 had the greatest concentration of Na, followed by Zone 3, and then the open pasture environment (Table 5.13). However, unlike the former major cations, across the three main overstorey environments, the level of Na decreased by 28% between spring and summer (Table 5.13).

In spring, the average concentration of P in the understorey pasture amongst the trees (Zones 1 & 3) was 24% greater than in the open pasture (Table 5.13). This difference increased to 63% in summer, as the level in the understorey pasture (Zone 1 & 3) increased further, while it did not change significantly in the open pasture (Table 5.13). Overall, the concentration of S also tended to be 16% greater in Zones 1 and 3, compared to in the open pasture ($P=0.08$; Table 5.13).

Trace mineral elements

In spring, the understorey pasture amongst the trees (Zones 1 & 3) contained 58% more Fe than in the open pasture (Table 5.14). At the same time, the concentration of Al in Zone 1 was also 27% greater than in the open pasture, whereas, Zone 3 was not significantly different from either of the other two main overstorey environments (Table 5.14). Nevertheless, during the ensuing summer the respective concentrations of Fe and Al in all three main overstorey environments increased to a similar level (Table 5.14).

Overall, the concentrations of Zn and Sr in the understorey pasture amongst the trees (Zones 1 & 3) were 20% and 32%, greater than in the open pasture, respectively (Table 5.14). These trace minerals, along with all of the others measured, except for B and Ni, accumulated in the pastures over spring and summer (Table 5.14).

5.4.7.4 Effect of poplar overstorey density on Hautope 1 pasture mineral concentrations

Major mineral elements

In spring, the respective concentrations of Na, K, Mg, and P in the pasture increased at a constant rate of 203 ± 44 $\mu\text{g/g DM}$, 1160 ± 180 $\mu\text{g/g DM}$, 102 ± 16 $\mu\text{g/g DM}$, and 105 ± 16 $\mu\text{g/g DM}$, respectively, for every 10% increase in CCL (Figure 5.26). The strengths of these positive linear relationships were strong ($r^2=0.65-0.79$), and the relationships were not significantly different ($P>0.05$) between Zones 1 and 3 (Figure 5.26). No clear trends were apparent for either Ca or S in the spring pastures.

In summer, the concentrations of Na, K, Mg, and P in the pasture showed strong to very-strong ($r^2=0.71-0.84$) positive linear relationships with increasing CCL (Figure 5.27). For Na the rate of change was significantly ($P<0.05$) different between the two main zones of tree influence, with the level increasing twofold in Zone 1 compared to Zone 3 (Figure 5.27c). Nevertheless, both of these relationships (i.e. the intercepts and slopes) were not significantly different ($P>0.05$) from the single combined relationship that was observed in spring (Figures 5.26c & 5.27c). Similarly, the rate of change in Mg was not significantly different ($P>0.05$) between the two consecutive seasons (Figures 5.26b & 5.27b). In contrast, the rate of change in K and P was 1.8- and 2.4-fold, respectively, greater in summer compared to spring ($P\leq 0.05$) (Figures 5.26a,d & 5.27a,e).

Unlike in the spring pastures, Ca and S showed significant, but moderate fit ($r^2=0.42-0.49$), positive linear relationships with increasing CCL (Figure 5.27d,f). These two major minerals increased at a rate of 81 ± 29 $\mu\text{g/g DM}$ and 98 ± 33 $\mu\text{g/g DM}$, respectively, for every 10% increase in CCL (Figure 5.27d,f). The relationship for Ca was restricted to Zone 1 (Figure 5.27d).

Trace mineral elements

In spring, the concentrations of Cu, Zn, Fe, and Sr increased at a constant rate of $0.17 \pm 0.05 \mu\text{g/g DM}$, $1.2 \pm 0.3 \mu\text{g/g DM}$, $7.3 \pm 1.8 \mu\text{g/g DM}$, and $1.0 \pm 0.3 \mu\text{g/g DM}$, respectively, for every 10% increase in CCL (Figure 5.28). For each of these trace minerals the relationships found in Zone 1 and 3 were similar ($P>0.05$). Overall, the strengths of fit of the combined (Zones 1 & 3) linear relationships were moderate to moderately strong ($r^2=0.53\text{-}0.63$) (Figure 5.28).

In summer, the rate of change in Sr was not significantly different ($P>0.05$) from that observed in spring (Figures 5.28d & 5.29b). Unlike in spring, the concentration of Mn in Zone 1 was significantly related to CCL. Mn decreased by $28.6 \pm 8.0 \mu\text{g/g DM}$ for every 10% increase in CCL (Figure 5.29a).

Table 5.13 Major mineral elements ($\mu\text{g/g DM}$) in the mixed-species pasture¹ at Hautope 1: directly below the crowns of individual poplar trees (Zone 1), at the centre of the vertically projected gap between poplar crowns (Zone 3), and in the open pasture.

Season	Environment	Ca	K	Mg	Na	P	S
			(lnx)	(lnx)	(\sqrt{x})	(\sqrt{x})	
Spring'99	Open pasture	3437	15562 (9.65)	1351 (7.21)	1225 (34.66)	2387 (48.83)	2294
	Zone 1	3585	23210 (10.05)	1998 (7.59)	2698 (51.87)	3015 (54.88)	2453
	Zone 3	3367	20952 (9.94)	1817 (7.50)	2173 (46.23)	2900 (53.80)	2371
	Grand mean	3463	19908 (9.88)	1722 (7.43)	2032 (44.25)	2768 (52.50)	2373
Summer'00	Open pasture	4064	13881 (9.53)	1485 (7.30)	751 (27.32)	2483 (49.76)	2132
	Zone 1	4524	27268 (10.20)	2279 (7.73)	2190 (46.76)	4156 (64.34)	2700
	Zone 3	4509	26464 (10.15)	2255 (7.71)	1437 (37.87)	3921 (62.37)	2781
	Grand mean	4365	22538 (9.96)	2006 (7.58)	1459 (37.32)	3520 (58.83)	2537
Overall	Open pasture	3750	14722 (9.59)	1418 (7.25)	988 (30.99)	2435 (49.30)	2213
	Zone 1	4054	25239 (10.13)	2139 (7.66)	2444 (49.31)	3585 (59.61)	2576
	Zone 3	3938	23708 (10.04)	2036 (7.60)	1805 (42.05)	3411 (58.09)	2576
	Grand mean	3914	21223 (9.92)	1864 (7.50)	1746 (40.79)	3144 (55.67)	2455
Analysis of variance							
Environment (A)		NS	P<0.01	P<0.01	P<0.001	P<0.01	P<0.1
SEM (A)		101	(0.04)	(0.03)	(1.56)	(0.98)	84
Season (B)		P<0.001	NS	P<0.01	P<0.01	P<0.001	NS
SEM (B)		82	(0.03)	(0.02)	(1.27)	(0.80)	68
Interaction (A*B)		NS	P=0.05	NS	NS	P<0.05	P<0.1
SEM (A*B)		143	(0.06)	(0.04)	(2.21)	(1.39)	118

¹Averaged across the entire range of poplar stand densities over a one-year period (1999-2000). Transformed values are given in parentheses. Abbreviations: lnx, natural-logarithm transformed; \sqrt{x} , square-root transformed; SEM, standard error of the mean; NS, not significant ($P\geq 0.1$); DM, dry matter; Ca, calcium; K, potassium; Mg, magnesium; Na, sodium; P, phosphorus; and S, sulfur.

Table 5.14 Trace mineral elements ($\mu\text{g/g DM}$) in the mixed-species pasture¹ at Hautope 1: directly below the crowns of individual poplar trees (Zone 1), at the centre of the vertically projected gap between poplar crowns (Zone 3), and in the open pasture.

Season	Environment	Cu		Fe		Mn		Zn		Al		B		Co		Ni		Sr	
		lnx		$x^{-1} \times 10^{-3}$		lnx		$x^{-1} \times 10^{-3}$		$x^{-1} \times 10^{-3}$		$x^{-1} \times 10^{-3}$		$x^{1/3}$		\sqrt{x}			
Spring'99	Open pasture	11.0	(2.39)	68.5	(14.81)	248.0	(5.50)	27.3	(36.85)	113.8	(8.83)	16.8	(68.86)	0.43	(0.73)	0.95	(0.97)	17.0	
	Zone 1	11.8	(2.47)	116.4	(8.67)	152.5	(4.93)	34.9	(29.11)	144.5	(7.00)	17.5	(59.82)	0.28	(0.65)	0.98	(0.97)	23.0	
	Zone 3	12.1	(2.49)	99.8	(10.90)	181.3	(5.14)	32.7	(30.87)	128.0	(8.17)	11.8	(86.06)	0.30	(0.67)	1.13	(1.06)	21.6	
	Grand mean	11.7	(2.45)	100.1	(11.46)	183.1	(5.19)	32.5	(32.28)	131.8	(8.00)	15.1	(71.58)	0.32	(0.68)	1.03	(1.00)	21.2	
Summer'00	Open pasture	14.8	(2.68)	381.0	(2.99)	362.3	(5.87)	92.8	(11.70)	412.0	(2.99)	14.7	(72.53)	0.58	(0.82)	1.20	(1.09)	21.0	
	Zone 1	14.6	(2.67)	259.0	(4.20)	193.0	(5.22)	120.2	(8.86)	266.0	(4.30)	16.9	(65.98)	0.50	(0.79)	1.13	(1.05)	28.1	
	Zone 3	15.7	(2.75)	276.8	(3.64)	282.3	(5.47)	100.8	(10.38)	248.5	(4.07)	15.4	(65.49)	0.48	(0.78)	1.20	(1.09)	27.5	
	Grand mean	15.1	(2.70)	290.5	(3.61)	262.6	(5.52)	107.0	(10.31)	288.2	(3.79)	15.9	(68.00)	0.51	(0.80)	1.17	(1.07)	26.4	
Seasons combined	Open pasture	12.9	(2.54)	224.7	(8.90)	305.1	(5.68)	60.0	(24.28)	262.9	(5.91)	15.8	(70.69)	0.50	(0.78)	1.08	(1.03)	19.0	
	Zone 1	13.2	(2.57)	187.7	(6.43)	172.8	(5.08)	77.6	(18.99)	205.3	(5.65)	17.2	(62.90)	0.39	(0.72)	1.05	(1.01)	25.6	
	Zone 3	13.9	(2.62)	188.3	(7.27)	231.8	(5.31)	66.7	(20.62)	188.3	(6.12)	13.6	(75.78)	0.39	(0.72)	1.16	(1.07)	24.5	
	Grand mean	13.4	(2.58)	195.3	(7.53)	222.8	(5.35)	69.7	(21.29)	210.0	(5.89)	15.5	(69.79)	0.41	(0.74)	1.10	(1.04)	23.8	
Analysis of variance																			
Environment (A)		NS		P<0.1		NS		P=0.05		NS		NS		NS		NS		P<0.05	
SEM (A)		(0.03)		(0.59)		(0.07)		(1.08)		(0.36)		(8.07)		(0.01)		(0.04)		0.70	
Season (B)		P<0.001		P<0.001		P<0.01		P<0.001		P<0.001		NS		P<0.001		NS		P<0.001	
SEM (B)		(0.02)		(0.48)		(0.06)		(0.89)		(0.29)		(6.59)		(0.01)		(0.04)		0.57	
Interaction (A*B)		NS		P<0.01		NS		NS		P<0.05		NS		NS		NS		NS	
SEM (A*B)		(0.04)		(0.83)		(0.10)		(1.53)		(0.51)		(11.42)		(0.01)		(0.06)		0.99	

¹Averaged across the entire range of poplar stand densities over a one-year period (1999-2000). Transformed values are given in parentheses. Abbreviations: lnx, natural-logarithm transformed; $x^{-1} \times 10^{-3}$, inverse transformed; $x^{1/3}$, cubic-root transformed; \sqrt{x} , square-root transformed; DM, dry matter; SEM, standard error of the mean; NS, not significant ($P \geq 0.1$); Cu, copper; Fe, iron; Mn, manganese; Zn, zinc; Al, aluminium; B, boron; Co, cobalt; Ni, nickel; Sr, strontium.

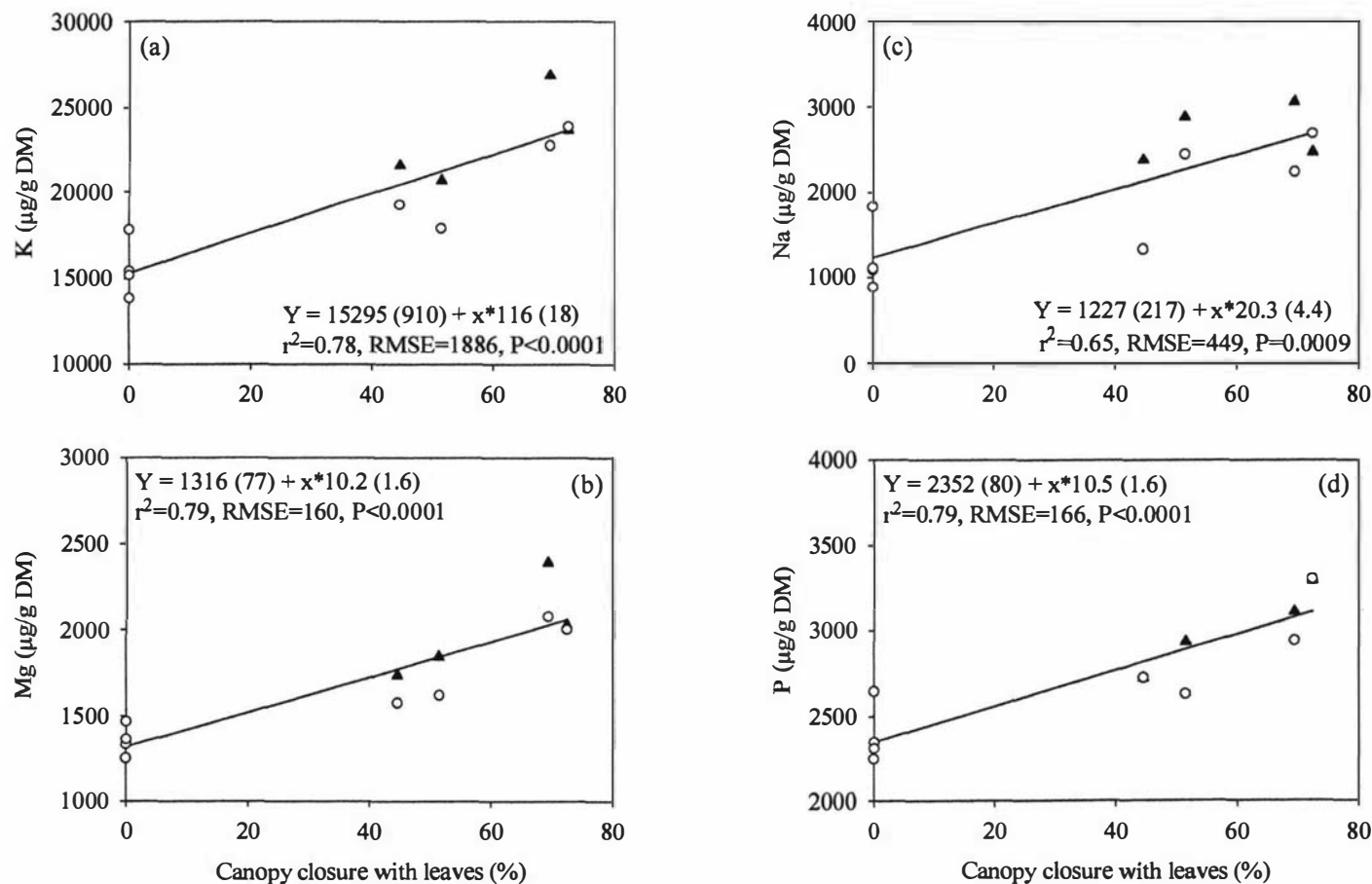


Figure 5.26 Spring relationships between major pasture minerals and poplar canopy closure (CCL) at Hautope 1: (▲) directly below the crowns of individual trees (Zone 1), and (○) at the centre of the vertically projected canopy gap between trees (Zone 3). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction; Na, sodium; K, potassium; Mg, magnesium; and P, phosphorus.

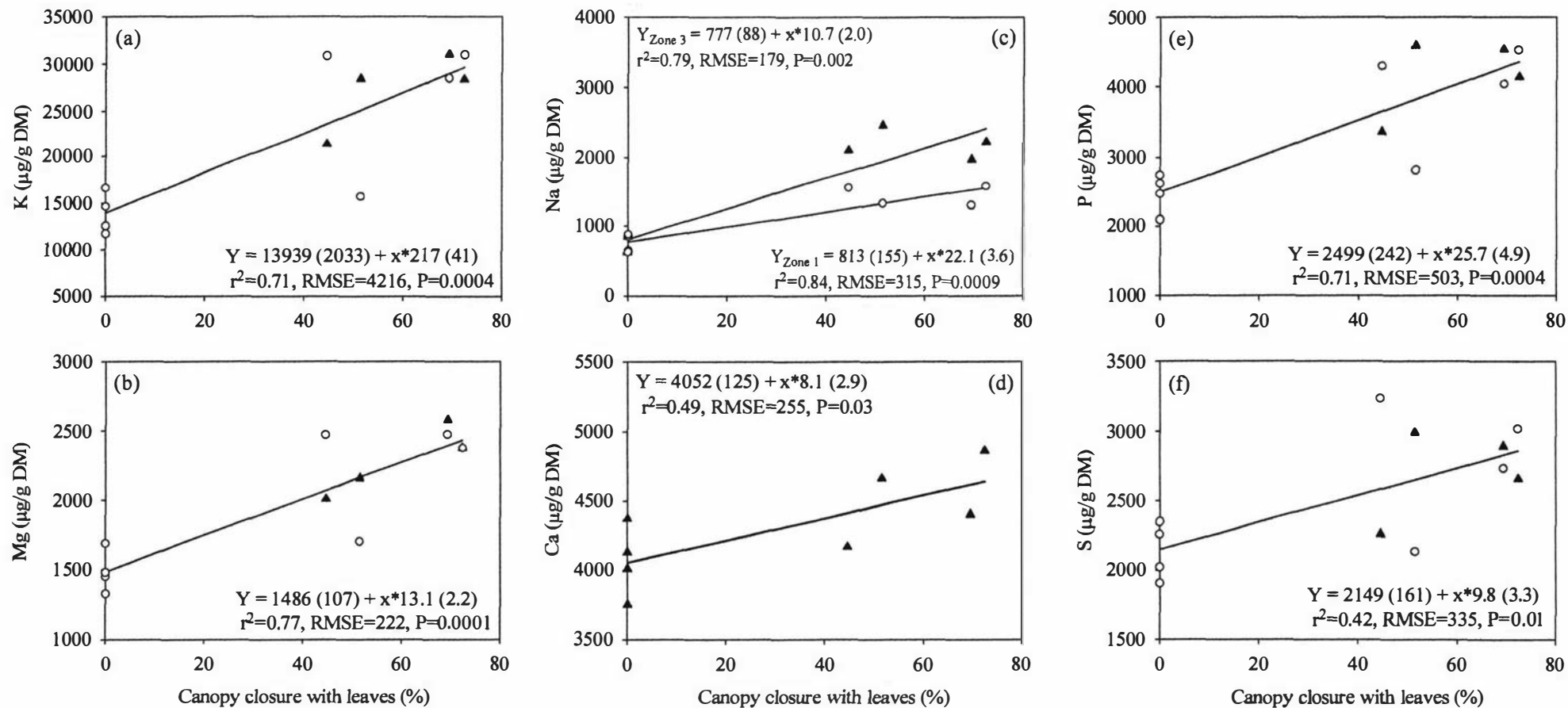


Figure 5.27 Summer relationships between the major pasture minerals and poplar canopy closure (CCL) at Hautope 1: (\blacktriangle) directly below the crowns of individual trees (Zone 1), and (\circ) at the centre of the vertically projected canopy gap between trees (Zone 3; \circ). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction; Na, sodium; K, potassium; Mg, magnesium; Ca, calcium; P, phosphorus; and S, sulfur.

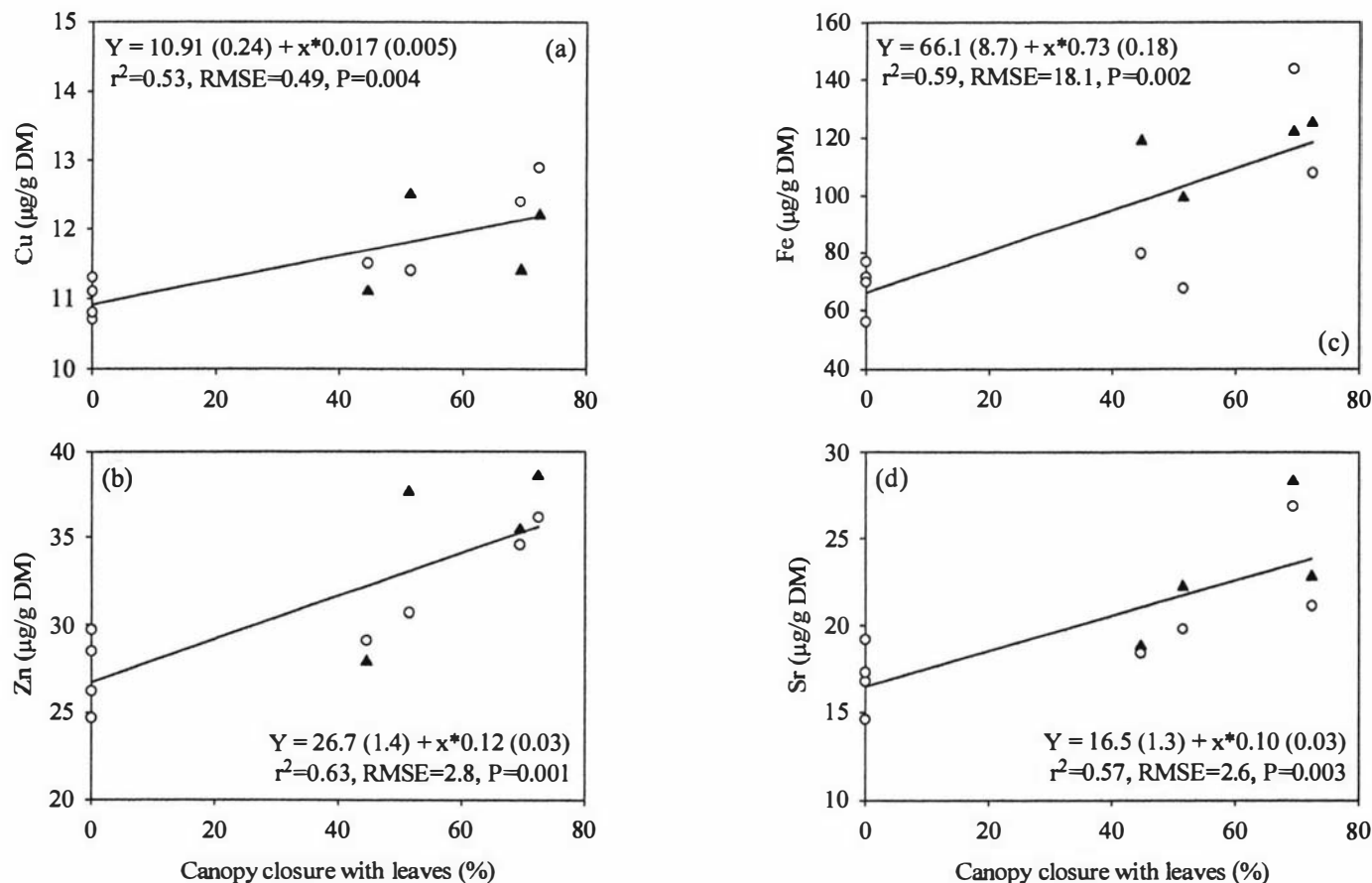


Figure 5.28 Spring relationships between the trace pasture minerals and poplar canopy closure (CCL) at Hautope 1: (▲) directly below the crowns of individual trees (Zone 1), and (○) at the centre of the vertically projected canopy gap between trees (Zone 3). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction; Cu, copper; Zn, zinc; Fe, iron; and Sr, strontium.

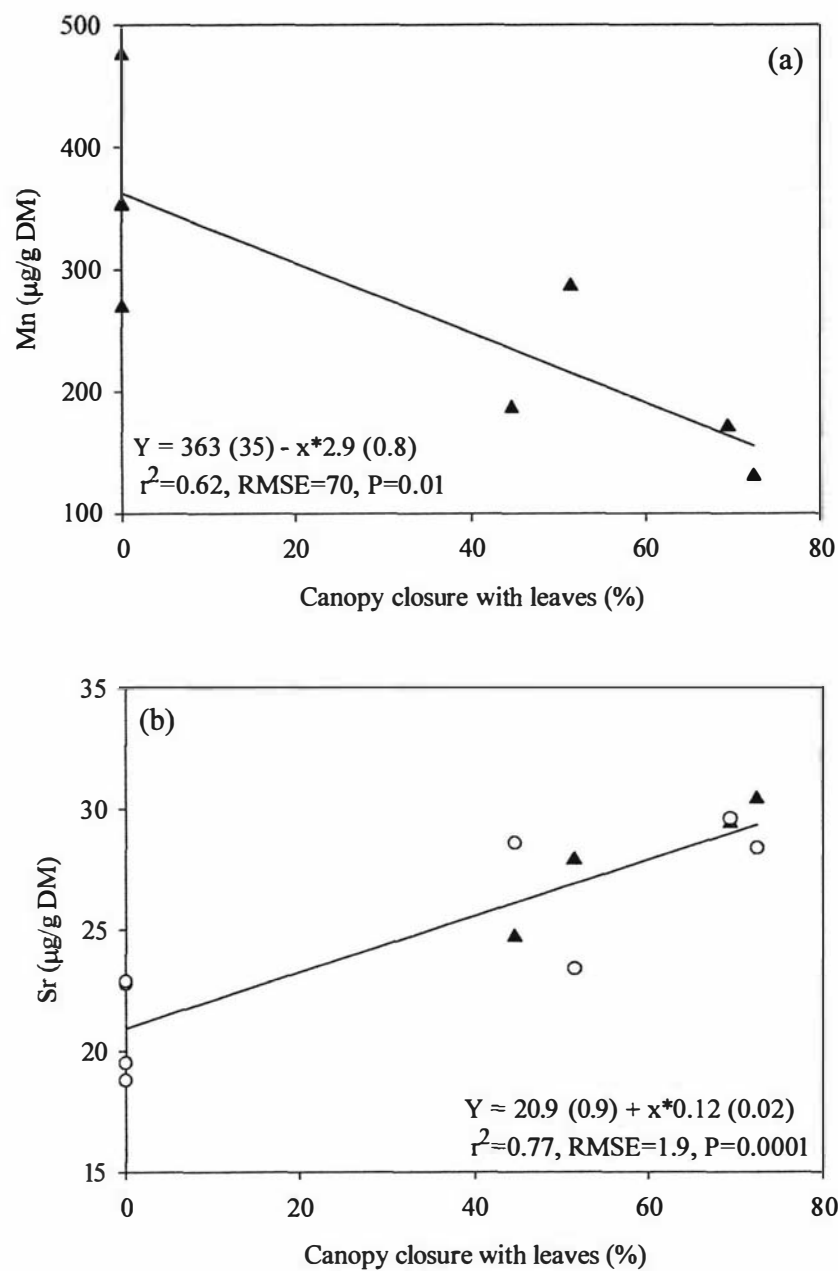


Figure 5.29 Summer relationships between the trace pasture minerals and poplar canopy closure (CCL) at Hautope 1: (\blacktriangle) directly below the crowns of individual trees (Zone 1), and (\circ) at the centre of the vertically projected canopy gap between trees (Zone 3). Standard errors for regression coefficients are given in parentheses. Abbreviations: r^2 , adjusted coefficient of determination; RMSE, standard error of prediction; Mn, manganese; and Sr, strontium.

5.4.8 Poplar leaf mineral contents

5.4.8.1 Seasonal effects at Kiwitea

Major mineral elements

Ca and Na accumulated in the poplar leaves from spring through until late autumn (Table 5.15). These two major minerals increased by 42% and 80%, respectively, between spring and summer, and then increased a further 30% and 22%, respectively, between summer and just prior to leaf fall in autumn (Table 5.15). In contrast, the concentration of P decreased by 28% and then 21% over the same two intervals (Table 5.15). No significant changes occurred in the levels of K, Mg, or S over the three consecutive seasons (Table 5.15).

In spring, the respective concentrations of Ca, Mg, and S in the poplar leaves were 2.6- ($P<0.01$), 2.1- ($P<0.001$), and 1.6-fold ($P<0.05$) greater than the average concentration in the mixed-species pasture for all three main overstorey environments (Tables 5.11 & 5.15). This contrasted with P and Na, which were 35% ($P<0.001$) and 29% ($P\leq 0.05$) lower in the poplar leaves compared to the mixed-species pastures (Tables 5.11 & 5.15).

In summer, the difference in Ca, Mg, and S increased further to 3.6- ($P<0.001$), 2.5- ($P<0.001$) and 2.0-fold ($P<0.05$), respectively (Tables 5.11 & 5.15). On the other hand, the difference in P remained at around 40%, and for Na there was no significant difference ($P>0.05$) between the poplar leaves and mixed-species pasture (Tables 5.11 & 5.15). Both types of plant material had similar ($P>0.05$) levels of K in spring and summer (Tables 5.11 & 5.15).

Trace mineral elements

Mn, Co, and Sr accumulated in the poplar leaves from spring through until late autumn (Table 5.16). Similarly, Fe, Al, and B also increased between spring and summer, but thereafter did not change significantly (Table 5.16). The concentrations of Cu, Zn, and Ni did not vary significantly over the three consecutive seasons (Table 5.16).

In spring the respective concentrations of Zn, B, Co, and Sr in the poplar leaves were 2.6- ($P<0.01$), 2.9- ($P<0.01$), 4.9- ($P<0.05$), and 3.6-fold ($P<0.001$) greater than the average

concentrations in the mixed-species pasture (Tables 5.12 & 5.16). Conversely, Cu, Fe, and Al were 1.8- ($P<0.01$), 2.5- ($P<0.001$) and 6.2-fold ($P<0.001$), respectively, greater in the mixed-species pasture compared to the poplar leaves (Tables 5.12 & 5.16).

In summer, the differences in B, Co, Sr, Fe, and Al, increased further to 5.7- ($P<0.01$), 6.9- ($P<0.05$), 4.7- ($P<0.001$), 2.9- ($P<0.001$), and 6.5-fold ($P<0.001$), respectively. Conversely, Zn decreased slightly to 2.5-fold ($P<0.01$), and, unlike in spring, the concentration of Cu was similar between the two types of plant material. Over both seasons the poplar leaves and the mixed-species pasture had similar ($P>0.05$) concentrations of Mn and Ni (Tables 5.12 & 5.16).

5.4.8.2 Seasonal effects at Hautope 1

Major mineral elements

Ca accumulated in the poplar leaves from spring through until late autumn (Table 5.17). In contrast, the concentration of K tended ($P=0.0789$) to decrease between spring and summer, and then significantly decreased between summer and autumn (Table 5.17). No significant changes occurred for Mg, Na, P, or S over the three consecutive seasons (Table 5.17).

In spring, the respective concentrations of Ca, Mg, and S in the poplar leaves were 5.2- ($P<0.01$), 2.2- ($P<0.001$), and 1.6-fold ($P<0.05$) greater than the average concentration in the mixed-species pasture (Tables 5.13 & 5.17). Conversely, P was 29% ($P<0.05$) lower in the poplar leaves compared to the mixed-species pasture (Tables 5.13 & 5.17). Overall, the relative differences in Mg, S, and P were very similar to those measured at the Kiwitea site (Section 5.4.8.1). Both types of plant material had similar ($P>0.05$) levels of K and Na (Tables 5.13 & 5.17).

In summer, the concentration of Ca in the poplar leaves was 5.8-fold ($P<0.01$) greater than in the mixed-species pasture, whereas the differences for Mg and S varied little from spring (Tables 5.13 & 5.17). Unlike in spring, the mixed-species pasture contained 43% more K than the poplar leaves ($P<0.05$). Similarly, P was also 2.5-fold ($P<0.001$) greater in the pasture compared to the poplar leaves (Tables 5.13 & 5.17).

Trace mineral elements

Between spring and summer the concentrations of Al, Co, and Sr in the poplar leaves increased by 49%, 71%, and 48%, respectively, but thereafter did not change significantly (Table 5.18). Similarly, Mn increased by 26% between spring and summer, but in autumn decreased to a level that was not significantly different from either spring or summer (Table 5.18). The concentration of Zn was similar in spring and summer. However, this trace mineral increased by 57% between summer and autumn (Table 5.18). Cu, Fe, B, and Ni varied little over the three consecutive seasons (Table 5.18).

In spring, the average concentration of Fe and Al in the mixed-species pasture was 1.6- ($P<0.01$) and 2.3-fold ($P<0.001$), respectively, greater than in the poplar leaves (Tables 5.14 & 5.18). In contrast, the respective concentrations of Zn, B, Co, and Sr in the poplar leaves were 4.9- ($P<0.001$), 5.3- ($P<0.01$), 8.4- ($P<0.001$), and 5.0-fold ($P<0.001$) greater than in the mixed-species pasture (Tables 5.14 & 5.18). Both types of plant material contained similar amounts of Cu, Mn, and Ni ($P>0.05$; Tables 5.14 & 5.18).

In summer, the average concentrations of Fe, Al, Cu, and Ni in the mixed-species pasture were 6.0- ($P<0.001$), 3.7- ($P<0.001$), 1.4- ($P<0.01$), and 1.7-fold ($P<0.01$), respectively, greater than in the poplar leaves (Tables 5.14 & 5.18). Similarly to spring, the levels of Zn, B, Co, and Sr in the poplar leaves were 1.4- ($P<0.05$), 6.1- ($P<0.01$), 9.2- ($P<0.01$), and 6.0-fold ($P<0.01$) greater than in the mixed-species pasture (Tables 5.14 & 5.18). This contrasted with Mn, which was not significantly different between both types of plant material ($P>0.05$; Tables 5.14 & 5.18).

Table 5.15 Major mineral elements (µg/g DM) in *Populus x euramericana* leaves at Kiwitea.

Season	Ca	K	Mg	Na	P	S
Spring	11574	24010	4636	799	2711	4664
Summer	16392	22152	5031	1440	1945	4709
Autumn	21355	22397	5735	1755	1536	4240
Grand mean	16441	22853	5134	1331	2064	4538
Analysis of variance						
Significance	P<0.01	NS	NS	P<0.05	P<0.05	NS
SEM (n=12)	1283	799	198	148	168	215

Abbreviations: DM, dry matter; SEM, standard error of the mean; NS, not significant ($P\geq0.1$); Ca, calcium; K, potassium; Mg, magnesium; Na, sodium; P, phosphorus; S, sulfur.

Table 5.16 Trace mineral elements (µg/g DM) in *P. x euramericana* leaves at Kiwitea.

Season	Cu	Fe	Mn	Zn	Al	B	Co	Ni	Sr
Spring	10.1	75.1	96.6	103.7	34.0	61.3	2.4	0.6	94.7
Summer	13.3	98.4	149.3	93.5	75.1	107.3	4.2	0.3	142.3
Autumn	13.0	88.7	191.0	131.6	75.5	89.3	5.3	0.4	167.8
Grand mean	12.1	87.4	145.6	109.6	61.5	86.0	4.0	0.4	134.9
Analysis of variance									
Significance	NS	P<0.05	P<0.05	P<0.01	P<0.05	P<0.1	P<0.05	NS	P<0.01
SEM (n=12)	0.6	4.3	12.9	7.7	6.2	6.7	0.5	0.0	10.1

Abbreviations: DM, dry matter; SEM, standard error of the mean; NS, not significant ($P\geq0.1$); Cu, copper; Fe, iron; Mn, manganese; Zn, zinc; Al, aluminium; B, boron; Co, cobalt; Ni, nickel; Sr, strontium.

Table 5.17 Major mineral elements (µg/g DM) in *Populus x euramericana* leaves at Hautope 1.

Season	Ca	K	Mg	Na	P	S
Spring	17845	20388	3722	1747	1967	3747
Summer	25231	15718	4633	2810	1387	4419
Autumn	33768	12917	4644	2834	1397	3098
Grand mean	25615	16341	4333	2463	1584	3755
Analysis of variance						
Significance	P<0.1	P<0.01	NS	NS	NS	NS
SEM (n=12)	2378	1081	209	256	107	267

Abbreviations: DM, dry matter; SEM, standard error of the mean; NS, not significant ($P\geq0.1$); Ca, calcium; K, potassium; Mg, magnesium; Na, sodium; P, phosphorus; S, sulfur.

Table 5.18 Trace mineral elements (µg/g DM) in *P. x euramericana* leaves at Hautope 1.

Season	Cu	Fe	Mn	Zn	Al	B	Co	Ni	Sr
Spring	13.5	58.8	183.3	156.5	55.7	82.0	2.8	1.0	103.0
Summer	10.9	50.7	231.0	147.3	83.0	96.2	4.8	0.7	152.3
Autumn	11.6	51.6	226.3	230.8	80.4	112.3	7.4	0.7	200.0
Grand mean	12.0	53.7	213.5	178.2	73.0	96.9	5.0	0.8	151.8
Analysis of variance									
Significance	NS	NS	P<0.05	P<0.1	P<0.05	NS	P<0.05	NS	P<0.1
SEM (n=12)	0.7	3.1	17.7	12.9	4.3	6.5	0.7	0.1	14.5

Abbreviations: DM, dry matter; SEM, standard error of the mean; NS, not significant ($P\geq0.1$); Cu, copper; Fe, iron; Mn, manganese; Zn, zinc; Al, aluminium; B, boron; Co, cobalt; Ni, nickel; Sr, strontium.

5.5 Discussion

5.5.1 Annual net herbage accumulation (ANHA)

5.5.1.1 At the stand level

Most previous silvopastoral studies in wet and dry climates have typically shown that understorey pasture dry matter (DM) production is negatively related to tree canopy closure. However, the slope and general shape of these relationships varies markedly between tree species (Jameson 1967; Pyke & Zamora 1982; Percival & Knowles 1988; Mitchell & Bartling 1991; Knowles *et al.* 1999; Devkota *et al.* 2001; Power *et al.* 2001). For *Pinus radiata*, Knowles *et al.* (1999) found a strong negative linear relationship with pasture DM production ceasing at around 70% canopy closure (pasture growth extinction point). Similarly, Mitchell & Bartling (1991) and Fernández *et al.* (2002) also measured little pasture growth at canopy closures greater than 70% for *Pinus ponderosa* Doug. (Laws). In contrast to the study by Knowles *et al.* (1999), pasture DM production (weighted ANHA) under the poplars decreased at a diminishing rate over the range of CCLs measured (i.e. the shape of the relationship was concave in nature) and was still 50% of open pasture at 70% CCL (Figure 5.2c). Power *et al.* (1999) also showed that young *Acacia melanoxylon* trees (6-9 years old) were able to maintain a greater level of understorey pasture DM production than under *P. radiata*, especially towards higher tree canopy closures. Pasture DM production under 25%, 50%, and 75% *A. melanoxylon* canopy closure was 83%, 65% and 35% of the open pasture, respectively (taken directly from figure), which is very similar to that measured for the poplars in the present study (Power *et al.* 2001). However, the overstorey/understorey relationship for *A. melanoxylon* was convex in shape, which differs from the linear and concave relationships found for *P. radiata* and poplar, respectively.

5.5.1.2 Directly underneath the tree crown (Zone 1)

Out of the two main zones of tree influence amongst the poplars (Zones 1 & 3) the rate of decline in ANHA was particularly marked in Zone 1 when initially going from the open pasture to a low CCL (Figures 5.2a,b). Beyond 20% CCL Zone 1 ANHA became relatively constant at around 50% of the open pasture (Figure 5.2a). The strong negative concave curvature of this relationship shared many similarities with the relationship between Zone

1 estimated PAR transmission (%DIFN) and CCL/NL (Figure 3.7a & 3.10a). Estimates from the developed logarithm model, using CCL as the independent variable, also compared well with previous single stand density measurements taken under untended poplars in New Zealand (Table 5.19). At sites with low, low-to-medium, and high inter-crown interference Gilchrist *et al.* (1993), Douglas *et al.* (2001), and Guevara-Escobar *et al.* (1997) measured 11% (not significant), 14-34%, and 40% reductions in understorey pasture DM production compared to the open pasture, respectively (Table 5.19). It is likely that differences in stand canopy closure, tree age (size), and hybrid phenology would have confounded comparisons between these studies. The trees in Gilchrist *et al.* (1993) and Douglas *et al.* (2001) studies were approximately one-third to one-half the age of the trees in the present study. As discussed in Section 3.5.2.1 at low tree stocking rates, smaller trees with either greater crown height or less width will increase the quantity of PAR transmitted to the understorey pasture directly below their crowns. The understorey pasture DM production in the study by Douglas *et al.* (2001) was also probably greater than predicted (Table 5.19) because the sampling area for pasture measurements extended out beyond the vertical projection of the tree crown.

Table 5.19 New Zealand studies measuring annual net herbage accumulation (ANHA) under poplars.

Source	Region	Poplar hybrid	BA (m ² /ha)	CCL (%)	ANHA (%OP)	Predicted Zone 1 ANHA
Gilchrist <i>et al.</i> (1993)	Gisborne	<i>Populus x</i> <i>euramericana</i>	NA	NA	89	NA
Douglas <i>et al.</i> (2001) [‡]	Manawatu	<i>P. maximowiczii x</i> <i>P. nigra</i>	2-8	15-45	86	60-50
	Otago	<i>P. x euramericana</i>	1-3	8-20	66	67-58
Guevara-Escobar <i>et al.</i> (1997)	Manawatu	<i>P. x euramericana</i>	14	70	60	46

[‡] Includes measurements that were taken only on the shaded (south) side of the trees and up to 0.45 tree height distances away from the base of the tree stems. Where not provided CCL was estimated from BA/ha (Table 3.10). Predicted Zone 1 ANHA was calculated from the logarithm model in Figure 5.2a. Abbreviations: BA, stand basal area per hectare; CCL, stand in-leaf canopy closure; NA, not available.

5.5.1.3 Within the vertically projected gap between trees (Zone 3)

Within the vertically projected gap between the trees (Zone 3) ANHA decreased by 6.6% of open pasture production for each 10% increase in CCL. This linear relationship differed markedly from the strong negative concave curvature found directly below the trees (Zone 1) with increasing CCL. However, it did share similarities with the linear relationship found between Zone 3 %DIFN and CCL (Figure 3.4a), although the slope of the relationship for ANHA was significantly (*t*-test; $P < 0.0001$) less than for %DIFN. Zone 1 and 3 ANHA converged at around 80% CCL, which supports the finding in Section 3.4.4 that poplar stands are effectively closed beyond this CCL.

McIvor *et al.* (2003) measured pasture DM production at the midpoint (analogous to Zone 3) between young 6 year-old 'Veronese' poplar (*Populus x euramericana*) with an estimated CCL of 20% (estimated from a BA of 2.75m²/ha). Pasture DM production was 10-15% lower amongst the trees than in adjacent open pasture. This compared very well with the predicted 14% lower pasture DM production (ANHA) estimated from the developed function for Zone 3 ANHA (Figure 5.2b). In scaling up pasture DM production measurements taken from directly under poplar trees to a stand level, Guevara-Escobar (1999) assumed the gap was equal to open pasture. However, results from this study clearly show that pasture DM production (ANHA) within the gap between trees (Zone 3) varies with gap size or overall stand canopy closure.

5.5.1.4 Spatial variation around the trees at Kiwitea

Across the inter-tree space any change in ANHA depended on the CCL (Figure 5.3). In the United Kingdom, Sibbald *et al.* (1991) reported a similar effect amongst 3-8m tall Sitka spruce (*Picea sitchensis* [Bong.] Carr.) trees planted on a square-grid pattern at 156, 278, and 625 stems/ha. Amongst small (3-5m tall) unpruned trees, pasture DM production was lower near the corners of the inter-tree space, particularly on the shaded north-eastern¹ side of the trees. In contrast, there was less spatial variation in pasture DM production amongst taller (8m) pruned trees at the same stocking rates, which would have had a more uniformly closed canopy 'seen' from any position in the understorey (refer to Section 3.5.2.1).

¹The forest site was located at latitude 55°42'N. In the Southern hemisphere the side of a tree shaded from direct solar radiation is on the south side of the tree.

However, the greater reduction in pasture DM production on the shaded, relative to the sunny, side of the trees at low overall stand canopy closures in the study by Sibbald *et al.* (1991) differed from the results found in the present study. Instead, the distribution of ANHA between mature unpruned poplar trees was symmetrical in shape, irrespective of CCL (Figure 5.3). Douglas *et al.* (2001) also measured significantly lower pasture DM production within close proximity to the shaded side of small (11m tall) relatively isolated poplar trees, compared to the opposite sunny side of the trees. However, around larger (17.4m tall) trees at another site in the same study there was no significant difference between shaded and sunny sides of the trees. Similarly, Clements *et al.* (1988) also did not find any significant difference in pasture DM production with orientation around widely spaced ash (*Fraxinus excelsior*) trees (15m tall) at Chiddingfold in the United Kingdom. Since the stand level (weighted) model developed in Section 5.4.1.3 assumes that ANHA in all directions directly below the trees is similar to the shaded side of the tree (Zone 1), this may lead to weighted ANHA being underestimated for stands with small, widely spaced trees (refer to area shaded red in Figure 5.30). Nevertheless, the weighted model may have compensated for this by assuming that beyond the tree-crown periphery (e.g. in Zones 2 & 4) ANHA increases rapidly to the same level found at the centre of the vertically projected gap (Zone 3) (refer to area shaded grey in Figure 5.30). This latter assumption for the simplified 'two zones of tree influence' model also likely contributed to the slight (<5%) overestimation of weighted ANHA at medium stand densities (e.g. 50% CCL) when compared to estimates based on five zones of tree influence (Section 5.4.1.4).

5.5.2 Seasonal net herbage accumulation (NHA)

5.5.2.1 Directly underneath (Zone 1) and within the gap (Zone 3) between tree crowns

Differences in NHA amongst the three main overstorey environments (open pasture, Zone 1 & 3) varied with season and largely reflected the presence or absence of leaves on the poplar trees. The greatest decrease in Zone 1 and 3 NHA with increasing CCL occurred when the trees were fully in-leaf in summer and also during leaf fall in autumn. Over these two consecutive seasons Zone 1 NHA was reduced to around 36% of the open pasture beyond approximately 20% CCL. In contrast, Zone 3 NHA decreased at a slower and more

constant rate with increasing CCL, reaching a similar level to Zone 1 once the canopy had become closed at about 80% CCL (Figures 5.4a,b & 5.5a,b).

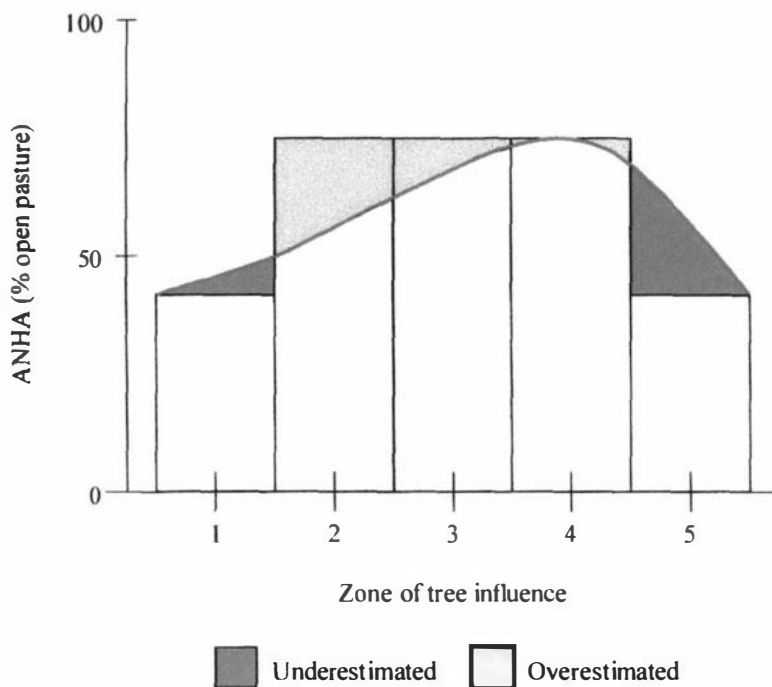


Figure 5.30 Schematic diagram (not to scale) of annual net herbage accumulation (ANHA) across an inter-tree space: (—) skewed distribution with less ANHA on the shaded (south) side of the trees and (---) assumed distribution for the simplified 'two zones of tree influence' model.

Previous research has also shown that the greatest reduction in pasture DM production under poplar trees usually occurs around summer (Crowe & McAdam 1992b; Crowe 1993; Gilchrist *et al.* 1993; Guevara-Escobar *et al.* 1997; Guevara-Escobar 1999; Douglas *et al.* 2001, 2005). However, the timing and extent of pasture recovery towards open pasture levels from autumn through until spring varies between different studies. In Ireland, understorey pasture NHA below mature (>30 year old) evenly spaced (278 stems/ha) *Populus serotina* trees was similar to the open pasture at the end of the growing season in autumn (Crowe 1993). Whereas, in New Zealand, pasture NHA under relatively isolated poplars did not fully recover to open pasture levels until winter (Gilchrist *et al.* 1993; Douglas *et al.* 2001, 2005).

Guevara-Escobar (1999) reported more variable results based on a two-year study with mature (unpruned) poplar trees that had high inter-crown interference. In the first winter understorey pasture NHA recovered to 76% of the open pasture and was not significantly

different from the latter environment, but in the second winter it remained suppressed at only 47% of the open pasture. Similarly, across the three farm sites in the present study there were inconsistencies in the extent and rate at which the understorey pasture recovered back towards open pasture levels after autumn. At Kiwitea and Hautope 2 there was no significant recovery until spring; whereas at Hautope 1, understorey pasture NHA was at least 83% of the open pasture in winter and was slightly greater than the open pasture in spring.

5.5.2.2 Spatial variation around the trees at Kiwitea

The more intensively stratified measurements taken across the inter-tree space showed NHA directly below the mature unpruned trees on both their shaded (Zone 1) and sunny (Zone 5) sides was similar, irrespective of CCL or season. In contrast, NHA within the vertically projected canopy gap (Zones 2, 3, & 4) varied significantly depending on both CCL and season (Figure 5.8). Similarly to ANHA, in summer and autumn stand level NHA was marginally overestimated ($\leq 10\%$) by assuming pasture DM production immediately beyond the tree crowns (Zones 2 & 4) equalled that at the centre of the vertically projected canopy gap (Zone 3). From Figure 5.8a,b it is apparent that there is actually a more graduated increase in NHA with distance from the trees during these two seasons. In contrast, with there being little variation in NHA across the inter-tree space in winter and spring (Figure 5.8c,d), omitting the two intermediate/transitional zones had little impact on stand level estimates.

5.5.3 Residual herbage mass (RHM) below 25 mm trimming height

At Kiwitea the RHM in the open pasture and in the understorey amongst the trees (Zones 1 & 3) had a similar seasonal pattern to that measured by Cossens (1984) for a *P. radiata* agroforestry trial in Otago, New Zealand. Maximum and minimum RHM in both studies occurred during summer and winter, respectively (Figure 5.9a). In late spring, the RHM in the open pasture was above 700 kg DM/ha (Figure 5.9a) indicating that the herbage mass was within the 700-2000 kg DM/ha range for set-stocked pastures where enough residual leaf area should have remained so not to detrimentally affect NHA markedly (Bircham & Hodgson 1983, 1984; Smetham 1990). However, Zone 1 RHM was around 550 kg DM/ha. Hence, trimming the understorey pasture in Zone 1 down to 25mm could have caused a

pronounced lag in the rate of pasture re-growth at this time through insufficient remaining green (photosynthetic) leaf tissue. Although the RHM in Zone 3 was not significantly different from Zone 1 or the open pasture, the actual mean level across the range of stand densities studied was around 700 kg DM/ha (Figure 5.9a). In late spring neither Zone 1 or 3 RHM was affected by CCL.

Averaged over the range of stand densities studied, the greatest difference in RHM between the open pasture and amongst the trees (Zones 1 & 3) occurred in late summer, and in general the open pasture contained at least twice as much RHM than in Zone 1 and 3 (Figure 5.9a). However, the significant relationship between Zone 3 RHM and CCL indicated that the effect of the trees on RHM depended on their density (Figure 5.10a). Crowe & McAdam (1992a) reported the largest difference in sward biomass density (kg DM/ha/cm) for pastures maintained at 50 mm surface height also occurred in summer, with the open pasture being significantly greater than understorey pasture below mature *Populus serotina* trees.

Based on previous sward-dynamics research for *Lolium perenne*-dominant open pastures, the late summer RHM in all three main overstorey environments should have contained enough residual leaf area not to adversely affect NHA (Figure 5.9a). However, due to morphological changes in sward structure caused by tree-shade the residual leaf area in Zone 1 and 3 may actually have been much lower than predicted for the given level of herbage mass. Changes in plant morphology under tree-shade include increases in specific leaf area (SLA) via taller and thinner leaves and an increase in stem/petiole length (Solangaarachchi & Harper 1987; Samarakoon *et al.* 1990a; Skálová & Krahulec 1992; Balocchi & Phillips 1997b; Sanderson *et al.* 1997; Wilson 1997). As a result, a higher proportion of total plant leaf area could have been positioned in upper sward horizons reducing the leaf area available in the lower horizons for re-growth after defoliation. Crowe (1993) reported shading *Holcus lanatus* and *Lolium perenne* pasture for more than 4 weeks caused the leaf biomass and leaf area index (LAI) further down the sward to decrease with a corresponding increase in stem biomass.

In late autumn, both Zones 1 and 3 had a very low RHM of 300-400 kg DM/ha, when averaged over the range of stand densities studied, whereas the RHM in the open pasture was around 700 kg DM/ha (Figure 5.9a). The low RHM in Zones 1 and 3 along with

morphological adaptations brought about by tree-shade likely resulted in very little leaf area remaining under 25mm trimming height, and thus would have detrimentally affected the rate of pasture re-growth. The significant relationship between RHM and CCL indicated that the effect of the trees on RHM also depended on their density (Figure 5.10b). However, the slope of the relationship was lower than in summer, indicating the RHM was less affected by CCL in autumn. Two factors that may have lessened the effect of the trees on RHM could have been an increase in PAR transmission and a change in the quality of light towards levels found in the open pasture, especially at higher CCLs (refer to Sections 3.5.2 and 3.5.7).

In late winter, the RHM in Zone 1 and 3 changed little from autumn, but was in the range (300-500 kg DM/ha) typically found in open pastures for that particular time of the year (Nicol & Nicoll 1987; Thompson & Poppi 1990). Crowe & McAdam (1992a) also found the herbage biomass density below 50mm sward surface height in winter was similar for open and understorey pastures. However, unlike at Kiwitea, the herbage biomass density in the two environments converged in the preceding autumn season. Similarly to Kiwitea, Zone 1 and 3 RHM at Hautope 1 and 2 was particularly low in summer and autumn, compared to the open pasture, with the levels likely affecting the rate of pasture re-growth (Figure 5.9b,c).

Overall, the differences in RHM between the three main overstorey environments suggest that understorey pasture below poplar trees should not be grazed as hard as in the open during summer and autumn, in order to leave adequate residual leaf area so not to markedly reduce herbage re-growth and thus NHA. This could be achieved through shorter grazing times on the particular paddock or through the use of stock such as cattle, which cannot graze as closely to the ground as sheep. However, the grazing intensity would need to be intensive enough, at least periodically, so not to allow excessive herbage loss from tissue death and decay (leaf senescence).

5.5.4 Botanical composition

5.5.4.1 Kiwitea

Averaged over the range of stand densities studied, the understorey pasture in Zone 1 contained 10-20% more high fertility responsive (HFR) grasses than either Zone 3 or the open pasture (Table 5.2). This difference was mainly due to a greater content of *Poa* spp. and to a lesser extent *Holcus lanatus* in Zone 1 compared to Zone 3 and the open pasture (Table 5.3). Previous research has shown that both these species often make up a high proportion of pastures under trees. Under poplars the content of *Poa* has been found to increase in stands with low (Guevara-Escobar 1999) and high (Guevara-Escobar 1999; Crowe & McAdam 1992b) inter-crown interference. Crowe & McAdam (1992b) also measured a greater content of *Holcus lanatus*, than in adjacent open pasture, under mature *Populus serotina* trees with high inter-crown interference. Similarly, the proportion of *Poa* spp. and *Holcus lanatus* has also been shown to increase in New Zealand agroforestry trials with *Pinus radiata* (Percival *et al.* 1984; West *et al.* 1991).

In the poplar understorey (Zones 1 & 3) the *Poa* spp. content likely increased through proliferation over autumn-spring into gaps created by tree-shade (Section 3.5.8) and the smothering effect of fallen poplar leaf litter (Eason 1988; McAdam 1996). Wells & Haggard (1984) found the most favourable time of the year for colonisation of newly sown *Lolium perenne* swards by *Poa annua* was in autumn, rather than in spring. *Poa* spp. generally have good winter growth and tillering ability compared to many other temperate grasses, including *Lolium perenne* (Vartha 1973a; Harris 1990). Also, coming into autumn, prolonged tree-shade may have reduced below ground competition from other resident pasture species by inhibiting their root development (Devkota *et al.* 1998).

In autumn, the density of the understorey pasture decreased with increasing CCL, as indicated by Figure 3.20a for tillering and Figure 5.10b for RHM. Based on the above discussion, such sward conditions would be more conducive for the ingress of *Poa* spp., and may explain why in spring the proportion of *Poa* spp. in Zone 1 was positively related to CCL (Figure 5.13d). After *Poa annua* sets seed in spring it then dies as part of the obligate cycle of an annual (Harris 1990). This, along with the intolerance of *Poa* spp. to soil moisture stress (Vartha 1973b; Garwood & Sinclair 1979) could have caused the

significant decrease in the content of *Poa* spp. in Zone 1 and 3 between spring and summer (Table 5.3).

Several factors may have lead to the higher content of *Holcus lanatus* in Zone 1 than Zone 3 or the open pasture (Table 5.3). Based on an artificial shade experiment, Devkota *et al.* (1997) found *Holcus lanatus* had greater DM production and tillering ability than most other common hill country pasture species screened under very low PAR transmission levels (14% of incident radiation). This high level of shade was similar to in Zone 1 at Kiwitea in summer (Section 3.4.2). Devkota (2000) also found sheep had greater preference to graze away from heavy shade if given the choice. Laxer grazing in the shade under trees along with the strong mid-season (summer) growth of *Holcus lanatus* would increase its competitiveness against other common hill country pasture species (Watt & Haggard 1980; Frame 1991). The increase in *Holcus lanatus* under *Pinus radiata* has been attributed to lower grazing pressure imposed during the initial years of tree establishment (Gillingham 1984; Percival *et al.* 1984). A temporary 2-3 year period of retirement from grazing is also required for successfully establishing poplar trees if unprotected planting stock is used (Stace 1996).

Averaged over both seasons, the open pasture contained 11-14% more *Lolium perenne* than amongst the trees in Zones 1 and 3 (Table 5.3). In the understorey of mature poplar stands with high inter-crown interference both Crowe (1993) and Guevara-Escobar (1999) measured a lower proportion of *Lolium perenne* than found in adjacent open pastures. However, in stands with low to medium inter-crown interference the proportion of *Lolium perenne* in the understorey has been found to be similar to (Douglas *et al.* 2005) or greater than (Guevara-Escobar 1999) in the open pasture. This indicates that the proportion of *Lolium perenne* in understorey pastures depends on stand density, which was confirmed by the negative relationships between *Lolium perenne* and CCL in Figures 5.13c and 5.14b. Similarly, the proportion of *Lolium perenne* under *Pinus radiata* has also been reported to decrease with increasing tree stocking rate or age (Cossens 1984; Percival *et al.* 1984; Hawke 1991).

Up to medium-to-high levels of shade the performance of *Lolium perenne* in terms of DM production is comparable to more shade tolerant grasses such as *Holcus lanatus* and *Dactylis glomerata* (Devkota *et al.* 1997; 1998). However, as shading increases, the rate of

tiller production by *Lolium perenne* is suppressed to a greater extent than for shade tolerant species, this reducing the ability of *Lolium perenne* to proliferate vegetatively and withstand defoliation (Devkota *et al.* 1997; 1998). In New Zealand agroforestry trials with *Pinus radiata*, lower *Lolium perenne* contents under trees have also been partly attributed to reduced grazing pressure during tree establishment (Gillingham *et al.* 1976; Cossens 1984; Knowles 1991).

Between spring and summer the proportion of *Lolium perenne* in the open pasture decreased towards levels found in Zone 1 and 3 (Table 5.3). This may have been due to a greater rate of senescence in the open pasture than amongst the trees (Crowe & McAdam 1992b; Crowe 1993) or due to delayed phenological development (e.g. inflorescence) in the tree understorey (Guevara-Escobar 1999).

The similar legume, other species (weeds), and dead matter content in each of the three main overstorey environments (Table 5.2) confirms previous findings by Guevara-Escobar (1999) based on trees of a comparable age. Douglas *et al.* (2001) also did not find any significant differences in each of the above botanical composition categories when comparing the understorey pasture on the shaded side of intermediate aged (8-15 years) poplar trees (similar to Zone 1) with adjacent open pasture. However, at a site in the same region as Kiwitea the legume and weed content was lower on the sunny side of the trees. Douglas *et al.* (2005) also reported significant seasonal variation in the legume content at the same site. In summer and autumn, the proportion of legume in the open pasture was 5-7% higher than in swards beneath the trees, whereas in winter and spring there was little difference between environments.

5.5.4.2 Hautope 1 and 2

In contrast to Kiwitea, at Hautope 1 both Zone 1 and 3 contained a higher proportion of HFR grasses than in the open pasture, when averaged over the range of stand densities studied (Table 5.4). In spring this difference was mainly due to a greater content of *Poa* spp. in Zone 1 and 3 compared to in the open pasture, whereas in summer Zone 1 and 3 contained a greater proportion of *Lolium perenne* (Table 5.5). The same factors contributing to the increase in *Poa* amongst the trees at Kiwitea were also likely present at Hautope 1. However, it is less clear why the proportion of *Lolium perenne* in Zone 1 and 3

tended to increase between spring and summer, while not changing significantly in the open pasture (Table 5.5). Site differences in the effect of the trees on soil fertility, soil moisture, and animal grazing behaviour, relative to the open pasture, are possible contributing factors. The greater content of *Holcus lanatus* in the open pasture (Table 5.5) was opposite to Kiwitea and could indicate that either grazing pressure or soil N availability was lower in the open pasture, as both factors increase this species competitiveness against other grasses such as *Lolium perenne* (Watt & Haggard 1980; Frame 1991).

The lower proportion of legume and weeds in Zone 1 and 3 was similar to that found by Douglas et al. (2001) when comparing the understorey pasture on the sunny side of intermediate aged trees (8-11 years) with adjacent open pasture. The lower dead matter content in Zone 1 and 3 in summer may have been caused by a lower rate of senescence (Crowe & McAdam 1992b; Crowe 1993) or delayed phenological development (e.g. inflorescence) (Guevara-Escobar 1999).

In comparison to Kiwitea and Hautope 2, the higher content of winter active grasses (e.g. *Lolium perenne* and *Poa* spp.) and lower content of dead matter amongst the trees than in the open pasture at Hautope 1 (Table 5.4 & 5.5) could account, at least partly, for the greater recovery in understorey NHA measured at this site in winter and spring (Section 5.4.2.2). Other factors such as nutrient cycling may also be involved, especially nitrogen (N) availability in spring (Section 4.5.5). Several studies have shown that low to moderately high levels of shade can actually improve pasture growth in naturally low N environments (Wong & Wilson 1980; Wild et al. 1993; Wilson 1996, 1997). The high spring NHA in Zone 1 and 3 despite a low legume content strongly indicates the understorey pasture was obtaining soil N from an alternative source.

At Hautope 2 there was little variation in botanical composition between the three main overstorey environments (Table 5.6). The most prominent difference was in summer Zone 1 and 3 had a greater proportion of dead matter than in the open pasture (Table 5.6), which contrasted with both of the other sites (Table 5.2 & 5.4).

5.5.5 Pasture and poplar leaf feed values

The nutritive value of the spring pastures at Kiwitea and Hautope 1 for all three main overstorey environments (Table 5.7 & 5.8) was high and would easily meet the requirements of grazing sheep and cattle (Hodgson & Brooks 1999). In summer as the pastures matured their nutritive values declined. However, primary indicators of nutritive value, such as *in vitro* organic matter digestibility (OMD) and metabolisable energy (ME), remained higher in Zone 1 and 3 than in the open pasture (Table 5.7 & 5.8) and were positively related to CCL (Figure 5.18 & 5.20). Averaged for both seasons over the range of stand densities studied, the crude protein (CP) content of the understorey pasture in Zone 1 and 3 was also higher than in the open pasture (Table 5.7 & 5.8). At Hautope 1 in summer the higher nutritive value amongst the trees in Zone 1 and 3 was likely related to the lower dead matter content in the understorey pasture (Table 5.4), which was also positively related to CCL (Figure 5.16). Soluble carbohydrate (Sol CHO) was the only nutritive value component in the understorey pasture that was lower than in the open pasture (Table 5.7 & 5.8) and in spring was negatively related to CCL (Figure 5.17 & 5.19). Low carbohydrate reserves would detrimentally affect initial plant re-growth after defoliation, especially if only low residual leaf area remained (Hodgson 1990). In contrast to the mature poplar stands, Douglas *et al.* (2005) found very little difference in the nutritive value of pastures under widely spaced intermediate aged trees (8-11 years) and in the open environment. Douglas *et al.* (2005) attributed this to the similar botanical composition in the tree and open pasture environments.

The spring nutritive value of fresh poplar leaves at Kiwitea and Hautope 1 was similar to pasture, while the summer comparisons showed poplar leaves to have markedly higher nutritive values (Table 5.9 & 5.10). Thus, fresh poplar leaf material would serve very satisfactory as a supplementary feed during either the spring or summer months. Even though the senescing autumn leaves had lower nutritional values (Table 5.9 & 5.10) than in spring and summer they still would have considerable potential as an emergency fodder source. However, both Guevara-Escobar (1999) and Douglas *et al.* (2005) found poplar leaves quickly lose their nutritional value once they are on the ground for more than a few days.

The mineral content in spring and summer pastures at Kiwitea (Table 5.11 & 5.12) and Hautope 1 (Table 5.13 & 5.14) was sufficient to meet the dietary requirements of sheep

and cattle (Grace 1984). At both sites, the concentrations of major mineral elements in the pastures of each overstorey environment mirrored differences previously identified for soil fertility (Section 4.4.1). All of the minerals measured in poplar leaves at Kiwitea (Table 5.15 & 5.16) and Hautope 1 (Table 5.17 & 5.18), except for phosphorous (P), were also above minimum requirements for sheep and cattle (Grace 1984). As a sole feed, dietary P may be deficient especially as the high calcium (Ca) concentration that was also present in the leaves would depress P absorption.

5.6 Conclusion

At the stand level, ANHA decreased at a diminishing rate with increasing CCL. However, the suppression of ANHA under the poplar stands was less than for other tree species such as *Pinus radiata*, especially towards higher levels of canopy closure. Below 30-40% CCL stand level (weighted) ANHA was greater than 75% of open pasture production. Amongst the trees, the rate of decline in ANHA was much greater in Zone 1 than Zone 3 when initially going from the open pasture to a low CCL. This decrease appeared to be strongly related to the level of PAR transmission in the respective environments. Seasonally, the greatest decrease in NHA amongst the trees occurred in summer and autumn, with the change also strongly related to CCL. However, there was considerable variation in the rate of recovery in winter and spring between sites, which was probably caused by site-specific differences in pasture botanical composition and in spring soil fertility. During summer and autumn low RHM amongst the trees indicated understorey pasture should not be grazed as hard as open pasture for these seasons.

The most consistent difference in pasture botanical composition between the three main overstorey environments was a greater proportion of *Poa* spp. amongst the trees than in the open pasture, especially in spring. Other differences also occurred for *Holcus lanatus* and *Lolium perenne*. However, these differences were inconsistent across sites and were likely confounded by variation in PAR transmission (%DIFN) under the trees, soil fertility and moisture, and animal grazing behaviour.

The nutritive value of the understorey pasture amongst the trees was as good and often slightly better than in the open pasture, particularly in summer. Fresh leaf prunings from the trees in summer had a forage value comparable to open pasture and could be used to

partly offset any reduction in understorey pasture NHA. However, once the tree leaves reach the ground they would reduce the nutritive value of the total feed on offer if they are not quickly consumed within 2-3 days. The concentration of major and minor minerals in the understorey pasture was generally greater than in the open pasture and likely reflected the higher soil pH and fertility under the trees.

5.7 References

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6 Conclusions

The research presented in this thesis provides the following conclusions:

When initially going from the open pasture to low poplar stand densities estimated PAR transmission (%DIFN) decreases at a much faster rate directly below the trees (Zone 1) than in the inter-tree gap (Zone 3). Thereafter, Zone 1 %DIFN becomes relatively constant, with the level depending on the average size of the tree. At complete canopy closure %DIFN is 15-20% and 50-55% of the open pasture in summer and winter, respectively. In summer the poplar canopy also reduces the R:FR, especially when PAR transmission levels fall below 40% of the open.

Based on previous pasture-shade trials the above reduction in %DIFN will have a major effect on pasture net herbage accumulation (NHA) and general sward structure. Again, the impact will initially be more marked in Zone 1 rather than Zone 3. However, as the density of the poplar stand increases the productivity and structure of the understorey pasture becomes spatially homogeneous. Under conditions where the level of PAR is the only limiting factor, understorey NHA should cease at around 85% CCL, while not falling below 50% of the open pasture in winter because of reduced shading. At low stand densities the use of smaller trees with either a greater crown height (through pruning) or less crown width improves Zone 1 %DIFN and thus reduces any negative impact that the trees initially have on understorey pastures.

Canopy closure (CCL/CCNL), measured with a standard digital camera, is a very good predictor of %DIFN. In particular, there is a directly proportional inverse-relationship between Zone 3 %DIFN and CCL. However, unaccounted for site differences in the relationship for Zone 1 %DIFN was evident to varying degrees for all of the stand density indices investigated. One of the main factors unaccounted for is likely the difference in average tree-crown size between sites. Especially for DBH, HPCD, and GCL as single independent variables, the above unaccounted for factors markedly reduced their ability to accurately predict %DIFN. As such, these three stand density indices should be used with caution when applied across multiple sites.

The soil pH_w and concentration of essential major cations (Ca, Mg, K, & Na) and anions (P & SO₄-S) in the upper 75 mm of soil under mature stands of poplar are as good as, and in some cases slightly better than, in the adjacent open pasture. Also, the influence of the trees on soil properties is not restricted to within the crown domain (Zone 1), but instead often extends out into the inter-tree gap (Zone 3). One of the main impacts that mature poplars have is an increase in soil pH_w, although the extent of change depends on the soil texture and tree rooting depth. The cycling of excess cations over inorganic anions from lower soil horizons to the topsoil is a major pathway for many of the changes in soil chemical properties that occur under the trees. Overall, the basic soil tests taken indicate poplars do not adversely affect understorey pastures through their effects on the soil. However, the seasonal changes in soil N, P, and SO₄-S availability associated with leaf fall could have both positive and negative impacts and requires further investigation.

Under increasing CCL the change in ANHA of the understorey pasture broadly follows a similar pattern to %DIFN. Beyond 20% CCL, Zone 1 ANHA becomes relatively constant at around 50% of the open pasture. In contrast, Zones 3 ANHA decreases from open pasture levels at a constant rate of 6.6% for every 10% increase in CCL. Given the decrease in ANHA appeared to be strongly related to the change in %DIFN, the use of short, narrow, or high pruned trees should reduce the suppression of ANHA in Zone 1. Seasonally, the greatest decrease in NHA amongst the trees from open pasture levels occurs in summer and autumn. Thereafter, understorey pasture production recovers towards open pasture levels. However, there were site differences, with the trees at Hautope 1 having a less detrimental impact on NHA than at Kiwitea and Hautope 2 in winter and spring. The cause may have been site-specific differences in botanical composition and in spring soil fertility. Fresh leaf prunings from poplars in summer have a nutritive value similar to open pasture and could be used to partly offset any reduction in understorey pasture production during this season.

The botanical composition and feed value of the understorey pasture is broadly similar to that of the open pasture. The most consistent difference in botanical composition was a greater content of *Poa* spp. in the understorey pasture. In contrast, the decrease in ANHA directly below mature unpruned trees (Zone 1) and amongst trees at high stand densities is substantial and will have a significant impact on farm profitability if situated over a large area of a farm. Therefore, ongoing management of poplar stand density is necessary to

minimise the negative impact that trees have on pasture ANHA. To maintain ANHA levels at around 75% of the open pasture CCL should not exceed 30-40%. At Kiwitea and Hautope 1, this is equivalent to less than 30 mature unpruned trees per hectare.

Appendix 4.1 Experimental unit selections for soil samples taken at 75-150mm soil depth.

4.1.1 Kiwitea

Experimental unit	Zone 3 %DIFN	Overstorey density class	Selection
42	90	Open	*
40	90		
41	86		*
39	78	Low	
30	56		*
36	54		
23	51		*
28	30	Medium	
38	30		*
3	29		
29	26		*
24	26		
7	15	High	*
6	13		*

4.1.2 Hautope 1

Experimental unit	Zone 3 %DIFN	Overstorey density class	Selection
2	100	Open	*
1	99		*
6	50	Low	*
3	43		*
4	38		
8	34	Medium	
5	29		*
10	27		
7	26		*
11	24	High	
9	21		*
12	20		*

Appendix 4.2 Annual Ca returned in the pasture and tree biomass at Kiwitea.

Assumptions:

- a. Net primary production = 13 t DM/ha/yr (refer to section 5.4.1);
- b. Poplar leaf biomass = 3.1 t DM/ha/yr (Guevara-Escobar 1999);
- c. Ca concentration in autumn tree leaves = 2.13% (refer to section 5.4.8.1);
- d. Ca concentration in understorey and open pasture = 0.48% and 0.41%, respectively (refer to section 5.4.7.1); and
- e. All organic material is returned to the soil

Quantity of Ca returned to the soil in the poplar-pasture system.		kg Ca/ha/yr
Poplar leaf litter:	3100 kg DM/ha/yr x 2.13% Ca	= 66.0
Understorey pasture:	9900 kg DM/ha/yr x 0.48% Ca	= 47.5
Total		= 113.5
Quantity of Ca returned to the soil in the open pasture system.		
Open pasture	13000 kg DM/ha/yr x 0.41% Ca	= 53.3
Difference between systems.		= 60.2

Appendix 4.3 Mass-balance sulfur cycling model

Based on formulas given by Sinclair & Saunders (1984) and Nguyen & Goh (1993).

Assumptions¹:

- a. Annual stocking rate² = 12.65 stock units per hectare (SU/ha)
- b. Total sulfate lost in animal products (assuming steep hill) = 1.4 kg S/SU
- c. End of season leaching of sulfate = 6 kg S/ha
- d. Net sulfate immobilisation = nil
- e. Atmospheric sulfate input = (Ledgard & Upsdell 1991)
- f. Fraction of rainfall sulfate leached = 0.25
- g. Soil test (0-75 mm depth) = 4.8 Quick test units

1. Pasture development index (PDI)

$$\begin{aligned}
 \text{PDI} &= \text{years since pasture improvement commenced (to a maximum of 20)} \\
 &\times \text{average stocking rate over that period} \\
 &\times 0.005 \text{ for steep hill country.} \\
 &= 20 \times 12.65 \times 0.005 \\
 &= \mathbf{1.27}
 \end{aligned}$$

2. Sulfate leaching index (SLI) classification = 5

3. Maintenance sulfate requirement (S)

$$\begin{aligned}
 S &= \text{loss in animal products (a} \times \text{b)} + \text{end of season leaching (c)} + \text{immobilisation (d)} \\
 &\quad - \text{sulfate added from rainfall (e} \times \text{1-f).} \\
 &= (12.65 \times 1.4) + 6 + 0 - (e \times (1 - 0.25)) \\
 &= 23.71 \text{ kg S/ha} - 1.5 \text{ kg S/ha} \\
 &= \mathbf{22.21 \text{ kg S/ha}}
 \end{aligned}$$

4. Modification of the maintenance requirement (MS) due to previous pasture development

$$\begin{aligned}
 \text{MS} &= \text{maintenance requirement (S)} \times [2 - 0.125 \times \text{soil test (g)} - 0.5 \times \sqrt{\text{PDI}}] \\
 &= 22.21 \times [2 - 0.125 \times 4.8 - 0.5 \times \sqrt{1.27}] \\
 &= \mathbf{18.66 \text{ kg S/ha}}
 \end{aligned}$$

5. Sulfate added (SA) from annual topdressing with single superphosphate @ 11% sulfate

$$\begin{aligned}
 \text{SA} &= 220 \text{ kg/ha} \times 0.11 \\
 &= \mathbf{24.2 \text{ kg S/ha}}
 \end{aligned}$$

6. Excess sulfate added in fertiliser above the modified maintenance requirements

$$\begin{aligned}
 &= 24.2 \text{ kg S/ha} - 18.66 \text{ kg S/ha} \\
 &= \mathbf{5.5 \text{ kg S/ha}}
 \end{aligned}$$

¹ Many of the assumptions are directly related to the sulfate-leaching index (SLI) (Sinclair & Saunders 1984).

² Average stocking rate between the maximum of 14.8 SU/ha achieved on the farm in 1969 and the current rate of 10.5 SU/ha. The grazing system was classified as "set-stocking or extensive rotational grazing" given that the current stocking rate was less than 75% of the potential carrying capacity (Metherell & Morrison 1984, cited Nguyen & Goh 1993).

Appendix 5.1 Regression parameters (standard errors in parentheses) for equations predicting ANHA from in-leaf stand canopy cover (CCL).

5.1.1 Zone 1 ANHA (% open pasture), where $Y = 100 \cdot (X+1)^b$

Site	b	r^2	RMSE	N	P<
Kiwitea98-99	-0.1896 (0.0209) a ^ψ	0.85	10.829	17	0.0001
Kiwitea99-00	-0.2495 (0.0241) a	0.90	10.388	17	0.0001
Hautope 1	-0.1044 (0.0062) b	0.95	3.686	14	0.0001
Hautope 2	-0.2184 (0.0597) ab	0.72	18.039	8	0.01

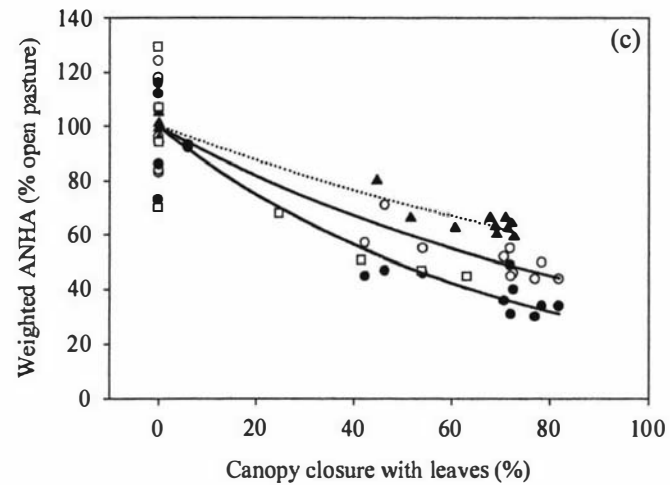
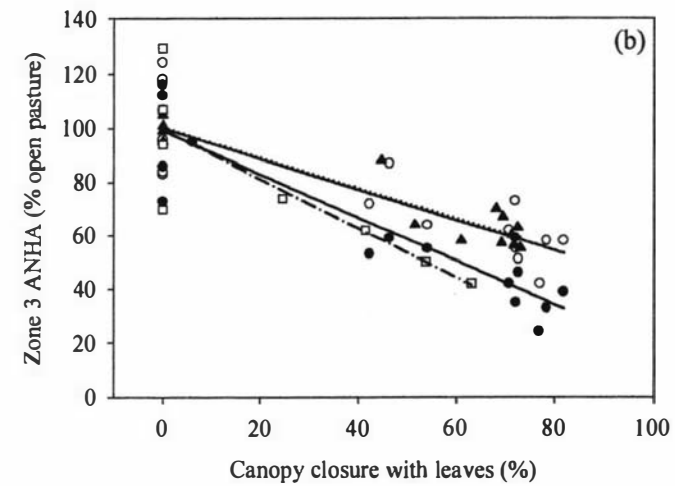
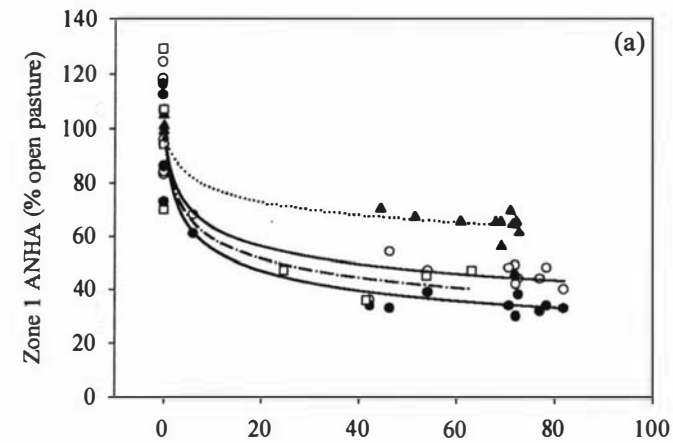
5.1.2 Zone 3 ANHA (% open pasture), where $Y = 100 + b \cdot X$

Site	b	r^2	RMSE	N	P<
Kiwitea98-99	-0.5723 (0.0868) a	0.73	12.1438	17	0.0001
Kiwitea99-00	-0.8122 (0.0859) ab	0.85	12.0198	17	0.0001
Hautope 1	-0.5664 (0.0564) ac	0.88	6.4311	14	0.0001
Hautope 2	-0.9248 (0.2474) abc	0.65	17.4939	8	0.01

5.1.3 Weighted ANHA (% open pasture), where $Y = 100 \cdot e^{b \cdot X}$

Site	b	r^2	RMSE	N	P<
Kiwitea98-99	-0.0099 (0.0012) a	0.84	10.7215	17	0.0001
Kiwitea99-00	-0.0142 (0.0015) b	0.89	10.8431	17	0.0001
Hautope 1	-0.0067 (0.0004) c	0.95	3.7757	14	0.0001
Hautope 2	-0.0143 (0.0043) abc	0.67	17.6511	8	0.01

^ψWithin column, regression parameters with the same letter were not significantly different ($P > 0.05$).



Appendix 5.2 Annual net herbage accumulation (ANHA) over a range of in-leaf canopy closures. Symbols: (○) Kiwitea98-99 (●) Kiwitea99-00, (▲) Hautope 1, (□) Hautope 2.