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Theme: Radiata Management
Site Productivity

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Soil Bacterial Community Properties: Interim Report on Relationships with Site Productivity

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Scion

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EXECUTIVE SUMMARY

The ability to access resources in forest soils is fundamental to the productivity and commercial sustainability of plantation forestry. Site productivity is influenced by many interrelated processes. Soil bacterial communities are involved in many of these processes, so the contribution of the soil bacterial community to productivity must be considered.

This project identifies opportunities to increase site productivity by making better use of existing soil bacterial resources. This fits in with the programme goals of acquiring more productivity for less input, and enhancing the sustainability of plantation forestry by decreasing reliance on external resources to maintain site productivity.

This project assessed the effect of:

- the production of two key chemicals produced by soil bacteria; and
- the catabolic capability of soil bacterial communities

on the productivity of established *Pinus radiata* D. Don plantations at 25 sites located on a range of soil types, with and without weed control.

The results of this project confirm the associations between site productivity and soil bacterial community properties. The bacterial production of two chemicals that enhance plant growth and stress tolerance was found to be greater under some conditions than others, but significant associations with site productivity were not found in all circumstances.

The relationships between site productivity and the utilisation of a number of substrates by soil bacteria were relatively consistent over a range of locations, and explained a substantial degree of variation in site productivity.

The results of this study were consistent with those of previous research. However, the new results represent a significant step forward in attempts to better understand and use the soil bacterial community, as the work presented here was conducted over a far greater range of sites and conditions than any previous research.

Some new opportunities to improve site productivity through the management of soil bacteria can be gained from this research. However, further research into the manipulation of substrate utilisation is critical to improving the usefulness of soil bacteria in increasing the productivity of *P. radiata.*

INTRODUCTION

Soil Bacterial Communities and Site Productivity

The ability to access resources from forest soils is fundamental to the productivity and commercial sustainability of plantation forestry[1,2,3]. Consequently, substantial research has been undertaken to assess variations in nutrient supply in forest soils[4,5] and to characterise the impacts of forest management on soil nutrient availability and the productive capacity of a given site[6,7,8]. The genome of plantation tree species has also been the subject of considerable attention[9,10]. Techniques to identify and propagate genes which influence tree growth and resource use[11,12] have the potential to increase productivity across a range of different climates and sites[13,14,15].

One avenue of research that has historically been less well explored is the contribution of soil bacterial communities to productivity in plantation forests. Soil bacteria underpin the functioning of terrestrial ecosystems[16], but research into the dynamics and functions of these communities has been hampered for many years by the inherent difficulties of working with soil[17,18]. However, advances in analytical techniques that enable the characterisation of soil bacterial activity based on genetic, molecular and enzymatic markers have reduced many of these problems. These new techniques provide opportunities to gain a greater understanding of the processes carried out by bacteria, and to explore the potential productivity implications of these processes[19,20].

Results obtained using these analytical techniques have enabled new models to be developed to explain how soil bacteria influence plant productivity. These models identify the role of soil bacteria in the provision of nutrients[21,22,23] and also the manipulation of growth behaviour by regulating plant hormone production and responses[24,25,26,27]. One such model is illustrated in Figure 1.

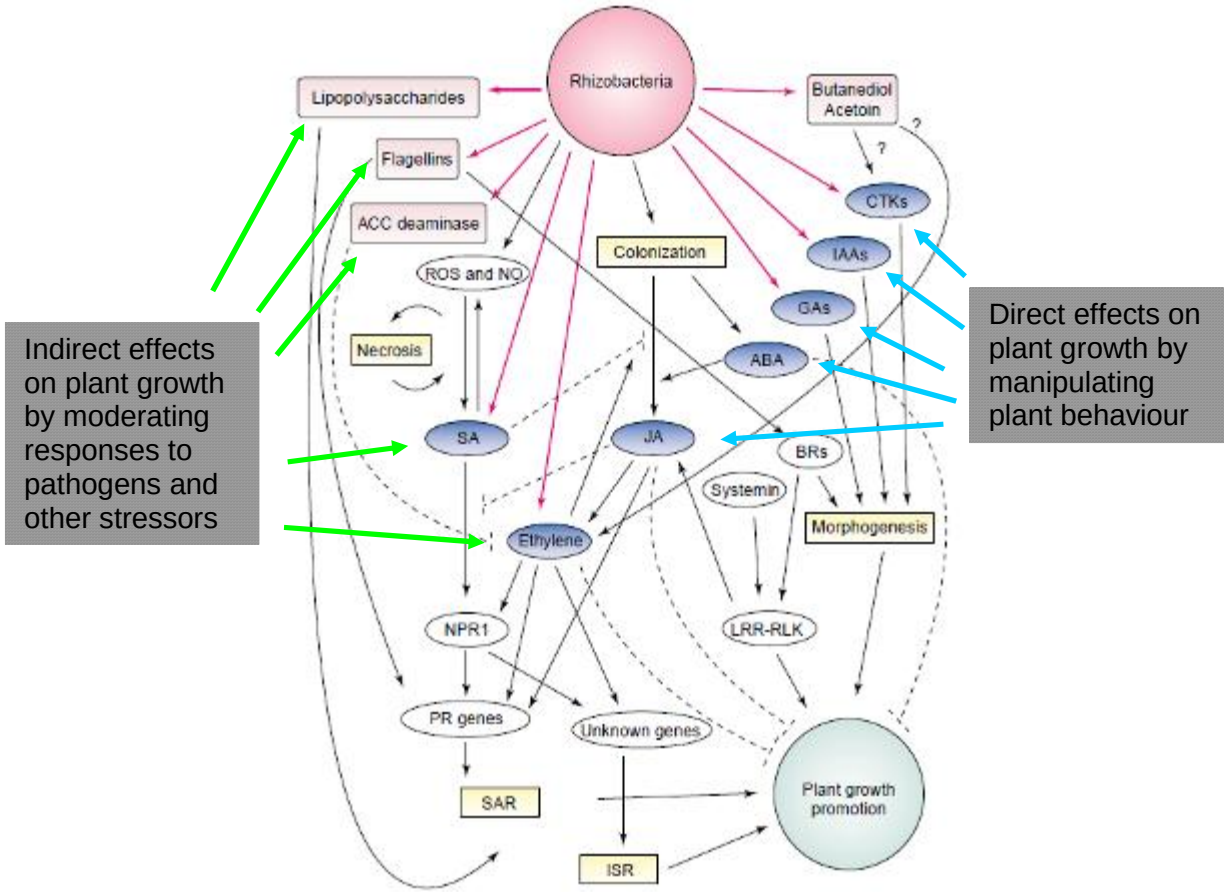

Figure 1: Network of signalling cascades involved in plant growth promotion by rhizobacteria. Modified from Ping, L., and Boland, W., *Signals from the underground: bacterial volatiles promote growth in Arabidopsis*. Trends in Plant Science, 2004. 9: p. 263-266.

Many significant knowledge gaps remain, as this field of research is still developing. These gaps generally relate to managed ecosystems and the effects of land management on the interactions between plants, soil and microbes. Consequently it is still not possible to predict accurately the effects of conventional forest management practices on the contribution of the soil bacterial community to site productivity at a wide scale, although localised studies have demonstrated the potential for significant effects, with implications for site productivity[26,28].

Establishment of Soil Bacteria Research Project

This project was established to address comprehensively several of these knowledge gaps by expanding on previous research and providing new information with direct relevance to the interests of the New Zealand forestry industry.

One aim of the project was to assess how site productivity is affected by the activity of two key chemicals produced by soil bacteria. These chemicals were the plant hormone indole acetic acid (IAA), and the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase. IAA was chosen because it is essential to the regulation of plant growth[24,27]; the enzyme ACC deaminase because it greatly increases stress tolerance in plants, allowing productivity to be maintained in adverse condtions[25,26]. The effects of weed control on the production and activity of these chemicals was assessed because of the proven potential for plantation management practices to influence soil bacterial properties[26,28].

Previous research indicates that strong relationships exist between the catabolic capability of soil bacterial communities and site productivity[29]. The other aim of this project was to determine if these relationships hold over the range of sites studies in this project. Catabolic profiling based on substrate utilisation[30] was used to produce profiles of the soil bacterial catabolic capability, which could then be examined against the productivity data from each site. The influence of weed control on these relationships was also examined.

The experimental framework used for the project was the Site Quality plot network[31], established across New Zealand in *P. radiata* plantations from 2000-2002 (example shown in Fig. 2).

Figure 2: A plot established as part of the Site Quality trial network immediately after installation. Note the substantial effect of weed control on the left side of the plot. Such differences in understory density were maintained during the life of the sites.

These sites were established in first and second rotation forests, installed in each case using the same stocking and site preparation techniques as the adjacent plantation. The only variation was that half of each site also received ongoing weed control application to reduce competition for resources during the life of the stand. Of 35 candidate sites, 25 were selected for use in this project based on stocking levels and the application of management treatments. These sites were distributed over various regions of New Zealand, providing substantial variations in climate and soil conditions (Appendix 1).

This report presents the interim findings from the examination of all 25 sites, describing the effects of weed control on site productivity, the relationships between soil bacterial community properties and site productivity, and the effects of weed control on the soil bacterial community properties.

METHODS

Site Details

The sites used in this study are presented in Table 1, with brief descriptions of soil conditions. Other site descriptors such as latitude, altitude and rainfall were also collated for use in subsequent analysis. Sites with Brown soil order dominated the dataset, but this was unavoidable due to the experimental framework available for this research.

Productivity at each site was determined by calculating the 300 Index[32] value for the weed control and no weed control half of each site, using the latest iteration of the 300 Index model. This provided a standardised value for the productivity of *P. radiata* for each site that could be compared to the value for any other site, regardless of differences in initial stocking or thinning regimes.

Table 1: List of sites used in this project

Name of Plantation	Soil Type	Soil Order
Longwoods	silt loam	Allophanic
Waimarino	steepland	Allophanic
Karioi	sandy loam	Allophanic
Tairua	silt loam	Allophanic
Tekapo	fine sandy loam	Brown
Eyrewell	stony sandy loam	Brown
Catlins	clay loam	Brown
Taringatura	stony silt loam	Brown
Otago Coast	stony silt loam	Brown
Rai Valley	clay loam	Brown
Golden Downs	silty clay loam	Brown
Aniseed Valley	stony silt loam	Brown
Bulls	black sand	Brown
Mahia	sandy loam	Brown
Ngaumu	fine sandy loam	Brown
Kaniere	stony silt loam	Brown
Ashley	silt loam	Pallic
Okuku	clay loam	Pallic
Pine Valley	silt loam	Pallic
Karatia	sand	Podzol
Hochstetter	humic silt loam	Podzol
Mawhera	humic silt loam	Podzol
Bottle Lake	sand	Raw
Woodhill	sand	Recent
Riverhead	clay loam	Ultic

Sampling Protocols

The owner or manager of the plantations containing each site was contacted prior to sampling and permission for site access was obtained. Soil samples were obtained by using a Hoffer tube to collect soil to a depth of 100 mm from four locations within both the weed control half and no weed

control half sections of each site. Additional samples of soil were collected from near the bases of four trees for mycorrhizal analysis; two in the weed control half and two in the no weed control half. All samples were kept chilled in transit and returned to the laboratory for analysis as soon as possible. The exception to this was the soils collected for mycorrhizal analysis, which were frozen at -20 ^{o}C. A selection of these will be analysed in the 2012-2013 year.

Each soil sample was transported to the laboratory and analysed as soon as possible after collection to reduce the risk of contamination or other changes in the nature and activity of the live soil bacterial community. This protocol meant that all 25 sites were sampled over a three month period from early February to early May 2012. Changes in climatic conditions with season were therefore a possible source of site-to-site variation in results, but no alternative approach to sampling was feasible.

Laboratory Analyses

Moisture Content

The moisture content of the soil samples was determined by taking a sub-sample and heating it to 105 ^{o}C for several days until a constant weight mass was obtained. This figure was then used to calculate soil microbial activity in all subsequent analyses on the basis of dry weight of soil.

IAA Production

The IAA concentration in the soil samples could not be determined directly using established techniques because the samples contained high concentrations of soil organic matter (SOM), which interferes with the analyses. Consequently, a new method was developed involving incubating soil samples in the presence of the IAA precursor L-tryptophan. Inocula of the bacteria in each fresh soil sample were prepared then incubated with L-tryptophan for 72 hours to stimulate IAA production. After this time, a sample of the culture was extracted and the amount of IAA present in each extract was determined using colorimetric analysis[26]. These data provided a relative measure of the rate at which each community could produce IAA.

ACC Deaminase Activity

The ability of the bacteria in the soil samples to produce and use the enzyme ACC deaminase was assessed by incubating a known mass of soil with ACC for 24 hours. The activity of the enzyme was then determined by measuring the amount of ACC converted into α-ketobutyrate with colorimetric analysis[26] . As with the measurements of IAA production in soils, this method had been developed specifically for forest soils to prevent interference by SOM.

Catabolic Capability

Inocula of the bacteria in each soil sample were prepared and inoculated into Biolog EcoPlates^{TM}. These plates contain 31 wells, each holding a single substrate which acts as the only carbon and nutrient supply for the bacteria. Examples of substrates included types of carbohydrates, amino acids, polymers and carboxylates. If the bacterial community introduced into the well is capable of metabolising the substrate, the associated respiration activates a dye, resulting in a measurable colour change. Colorimetric analysis of this change determined the relative ability of the soil bacterial community to use a range of molecules, and a profile of the catabolic capability of that community was generated. Each plate was incubated for 72 hours before the extent of colour change in the wells was determined.

Data Collection and Analysis

The effects of weed control on site productivity and the soil bacterial parameters were assessed using ANOVA. The relationships between the values for the 300 Index, ACC deaminase activity, IAA production and the catabolic capability of the bacterial community at each site were assessed using linear regression and multiple regression models.

It must be noted that more sites from the Brown soil order were present in this study than other orders, but given the experimental framework available for this research, this situation could not be avoided. In order to prevent the responses of the Brown soil sites from overwhelming overall results and obscuring any possible differences in response that may occur in other soil orders, results regarding the soil bacterial community were also considered in terms of soil order. As only one site each of the Ultic, Recent and Raw soil orders was able to be included in this project, these were placed together in a group designated “Other” to simplify data analysis.

RESULTS

Effect of Weed Control and Soil Order on 300 Index Values

The use of weed control significantly increased the mean value of the 300 Index across all 25 sites from 21.8 to 24.7, indicating a substantial increase in site productivity. However, when the effect was assessed across the different soil orders, it was clear that this increase was related to the soil order of each site (Table 2).

Table 2: Effect of weed control on 300 Index values varies with soil order

Soil Order	300 Index without Weed Control	300 Index with Weed Control	No. of Sites	Significant?
Allophanic	19.0	21.3	4	no
Brown	21.9	25.0	12	**yes**
Pallic	23.1	24.8	3	no
Podzol	21.1	25.9	3	**yes**
Other*	24.2	27.2	3	**yes**

*One site each of the Ultic, Recent and Raw soil orders.

Relationships between IAA Production, Weed Control and 300 Index Values

Across all sites and soil orders there was no significant correlation between IAA production by soil bacteria and 300 Index values. However, greater bacterial production of IAA was associated with increased 300 Index values at sites with Allophanic, Brown, and “Other” soil orders, but only in the absence of weed control (Table 3). The application of weed control disrupted any correlations between IAA production and site productivity. The effects of weed control on IAA production varied with soil order.

Table 3: IAA production and relationships with site productivity

Soil Order	Correlation without Weed Control	Correlation with Weed Control	Effect of Weed Control on IAA Production
All	**ns**	**ns**	No effect
Allophanic and Other	▲	**ns**	**Decreased**
Brown	▲	**ns**	**Increased**
Pallic and Podzol	**ns**	**ns**	**Decreased**

▲ indicates a significant positive relationship between IAA production and site productivity; **ns** indicates no significant relationship.

Relationship between ACC Deaminase Activity and 300 Index Values

No significant relationships were observed between ACC deaminase activity (measured by the production of α-ketobutyrate) and 300 Index values, regardless of soil order or the use of weed control. However, the productivity benefits associated with ACC deaminase are generally observed only when plants are under stress[25]. Therefore the productivity data were re-examined to determine if any correlations existed between ACC deaminase activity and 300 Index values at

sites where the *P. radiata* were likely to be more stressed, which would inherently be associated with lower 300 Index values.

When using only values of the 300 Index that where approximately 20 or less, a strong positive correlation between site productivity and ACC deaminase activity was observed (Fig. 3). This relationship was found to hold regardless of soil order or weed control treatments.

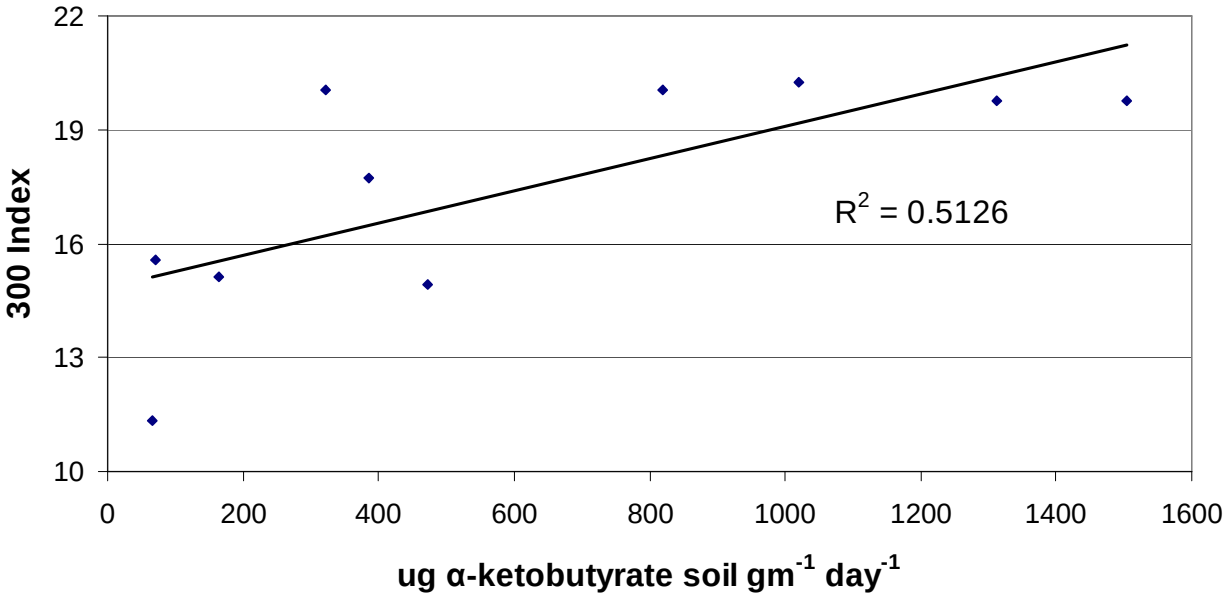

Figure 3: Relationship between ACC deaminase activity and lower 300 Index values.

Weed control significantly decreased ACC deaminase activity in soils from the Allophanic and "Other" soil order groups. It is not clear why this effect was observed only for these soil orders, but this result does suggest that the ongoing use of weed control on marginal Allophanic or "Other" sites may have a negative impact on site productivity. No other significant effects of weed control were observed.

Relationship between Catabolic Capability and 300 Index Values

The capability of the soil bacterial communities to utilise certain substrates was strongly associated with site productivity, regardless of soil order, climate or the value of the 300 Index. Key substrates were α-cyclodextrin (a cyclic polymer of glucose), threonine and glycyl glutamate (amino acids), phenylethylamine and the summed utilisation of five different types of carboxylate. The trends in the utilisation of these substrates combined to produce an alternative model for site productivity that could account for approximately 50% of the variation in the values of the 300 Index across all sites, regardless of the presence or absence of weed control. This relationship is illustrated in Figure 4.

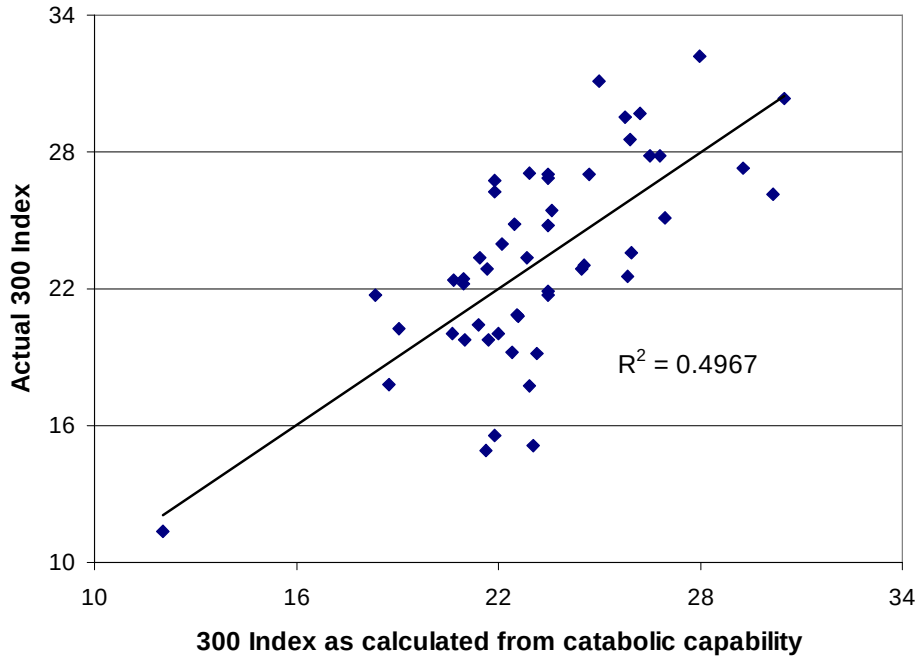

Figure 4: Relationship between 300 Index values calculated from a model using only bacterial catabolic capability data and 300 Index values produced by the established model[32].

Weed control significantly influenced the patterns of substrate utilisation by the soil bacteria within the plots (refer Appendix 2). An analysis was conducted to determine if weed control affected which substrates were directly related to the values of the 300 Index, and therefore site productivity. This was found to be the case (Table 4). For example, the utilisation of cellobiose was positively correlated with 300 Index values only where weed control was used. Another example was the utilisation of xylose, which was negatively correlated only where weed control had not been used.

Table 4: Effect of weed control on relationships between utilisation of key substrates and site productivity

Substrate	General Model (both treatments)	No Weed Control Model	With Weed Control Model
α-Cyclodextrin	▲	ns	ns
Threonine	▲	ns	▲
Glycyl glutamate	▼	▼	▼
Phenylethylamine	▲	▲	ns
Carboxylates	▼	ns	▼
Xylose	ns	▼	ns
Cellobiose	ns	ns	▲
α-Ketobutyrate	ns	ns	▲
Explanation of productivity:	**50%**	**49%**	**60%**

▲ indicates a significant positive relationship between the utilisation of this substrate and site productivity; **ns** indicates no significant relationship; ▼ indicates a significant negative relationship between the utilisation of this substrate and site productivity.

CONCLUSION

Comparisons to Previous Work

A previous study found that IAA production by soil bacteria was positively related to site productivity, as observed here for the Allophanic and "Other" soil orders[26]. This previous study also found that site management could influence the extent of this relationship, again as observed in the results presented here. However, this earlier research investigated bacterial IAA production at only one site, and therefore did not encounter differences in factors such as soil order, which have been demonstrated to be important to the relationship between IAA and site productivity. Consequently, the new research presented here is far more important and applicable than any previous work as it has been generated from multiple locations encompassing a variety of different factors.

The strong positive relationship between ACC deaminase activity and site productivity when site productivity is low agrees very well with past studies conducted in stressful conditions[25,26]. It is unclear why the weed control treatment substantially decreased ACC deaminase activity in soils from the Allophanic and "Other" orders. No direct comparisons to other work can be made on this issue as this is the first time this relationship has been studied over multiple sites, but it is speculated that the decreased mass and types of root exudates entering the soil following weed control forces the soil bacterial community to adapt to conditions with less contact with live plants. Consequently the production of ACC deaminase decreases, as this enzyme is useful only in close associations with live plants.

The substrate utilisation results demonstrate that an increased capability to utilise glycyl glutamate by the soil bacterial community is consistently associated with decreased site productivity. The utilisation of threonine, phenylethylamine and carboxylates was also related to site productivity in two of the three models. All these substrates (or classes of substrate) have previously been demonstrated to be significantly related to 300 Index values calculated from 122 plots distributed over six sites in New Zealand[29]. However, as these new data are generated from many more sites, the models explaining site productivity reported here are substantially more powerful than previous models, and clearly demonstrate that the activities and capabilities of soil bacteria communities are strongly related to the productivity of any given site.

How Can this Knowledge Help Improve Site Productivity?

Two implications for the use of the soil bacterial community as a resource can be drawn from this research. Firstly, the use of weed control on low productivity sites from Allophanic, Raw, Recent or Ultic soil orders may reduce site productivity in the mid-to-long term. As discussed above, the benefits of ACC deaminase manifest only when plants are in conditions that should be stressful, but in these soil orders it appears that ACC deaminase is less active if weed control is used, limiting the protection from stress and therefore decreasing site productivity.

Secondly, with regard to substrate utilisation, any management treatment that decreases the use of glycyl glutamate or carboxylates by soil bacteria while encouraging the use of threonine and phenylethylamine may also produce increased site productivity. Although there is little information to explain why the utilisation of these substrates is related to site productivity, it is clear that the relative degree of utilisation of these various substrates acts as an effective indicator of likely site productivity. Given the significance of the relationships and the degree of variation in productivity that can be explained over a wide range of sites and locations, further work to understand these relationships, and how they can be manipulated, is the next significant challenge in the use of soil bacterial communities as a resource for site productivity.

Further Work in this Project

Given that these results have been produced from only one set of measurements, a selection of sites of interest will be revisited for the collection of additional bacterial samples to provide more detail around aspects such as the response to weed control. This will also provide an opportunity to test the validity of the models referred to in this report.

The selection of these sites will be determined by site productivity values. More work will be done at low productivity sites to better understand the factors involved in the putative relationship with ACC deaminase activity. Patterns of substrate utilisation will be assessed, with particular focus on substrates known to be associated with lower productivity. Additional sampling will also take place at higher productivity sites, to attempt to better understand the contribution of the soil bacterial community in comparison to other factors that support good productivity, such as moisture, nutrient availability and climate. This research will examine the relative contribution of the soil bacterial community to site productivity, and will help determine if the bacterial parameters identified here are drivers of site productivity, or only indicators.

ACKNOWLEDGEMENTS

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REFERENCES

1. Jorgensen, J., Wells, C. and Metz, L., *The nutrient cycle: key to continuous forest production.* Journal of Forestry, 1975. **73:** p. 400-403.

2. Vitousek, P., *Nutrient cycling and nutrient use efficiency.* The American Naturalist, 1982. **119:** p. 553-572.

3. Nambiar, E.K.S., *Sustained productivity of forests is a continuing challenge to soil science*. Soil Science Society Journal of America, 1996. **60:** p. 1629-1642.

4. Keeney, D.R., *Prediction of soil nitrogen availability in forest ecosystems: a literature review.* Forest Science, 1980. **26:** p. 159-171.

5. Attiwill, P.M. and Adams, M.A., *Tansley review no. 50: Nutrient cycling in forests.* New Phytologist, 1993. **124:** p. 561-582.

6. Grigal, D.F., *Effects of extensive forest management on soil productivity.* Forest Ecology and Management, 2000. **138:** p. 167-185.

7. Nohrstedt, H.-Ö., *Response of coniferous forest ecosystems on mineral soils to nutrient additions: a review of Swedish experiences.* Scandinavian Journal of Forest Research, 2001. **16:** p. 555-573.

8. Stone, D.M. and Kabzems, R., *Aspen development on similar soils in Minnesota and British Columbia after compaction and forest floor removal.* Forest Chronicle, 2002. **78:** p. 886-891.

9. Whetten, R., and Sederoff, R., *Genetic engineering of wood.* Forest Ecology and Management, 1991. **43:** p. 301-316.

10. Griffin, A.R., *Genetically modified trees - The plantations of the future or an expensive distraction?* Commonwealth Forestry Review, 1996. **241:** p. 169-175.

11. Tang, W., and Newton, R.J., *Genetic transformation of conifers and its application in forest biotechnology*. Plant Cell Reports, 2003. **22:** p. 1-15.

12. Grant, J.E., Cooper, P.A., and Dale, T.M., *Transgenic Pinus radiata from Agrobacterium tumefaciens-mediated transformation of cotyledons.* Plant Cell Reports, 2004. **22:** p. 894-902.

13. Burdon, R.D., Carson, M.J., and Shelbourne, C.J.A., *Achievements in forest tree genetic improvement in Australia and New Zealand 10: Pinus radiata in New Zealand.* Australian Forestry, 2008. **71:** p. 263-279.

14. Weng, Y.H., Tosh, K., Adam, G., Fullarton, M.S., Norfolk, C., and Park, Y.S., *Realized genetic gains observed in a first generation seedling seed orchard for jack pine in New Brunswick, Canada*. New Forests, 2008. **36:** p. 285-298.

15. Lenz, P., Cloutier, A., MacKay, J., and Beaulieu, J., *Genetic control of wood properties in Picea glauca - An analysis of trends with cambial age*. Canadian Journal of Forest Research, 2010. **40:** p. 703-715.

16. Kennedy, A.C., and Gewin, V.L., *Soil microbial diversity: present and future considerations*. Soil Science, 1997. **167:** p. 607-617.

17. Wardle, D.A., and Giller, K.E., *The quest for a contemporary ecological dimension to soil biology.* Soil Biology and Biochemistry, 1996. **28:** p. 1549-1554.

18. Freckman, D.W., Blackburn, T.H., Brussaard, L., Hutchings, P., Palmer, M.A. and Snelgrove, P.V.R., *Linking biodiversity and ecosystem functioning of soils and sediments.* Ambio, 1997. **26:** p. 556-562.

19. Wargo, M.J., and Hogan, D.A., *Fungal-bacterial interactions: a mixed bag of mingling microbes.* Current Opinion in Microbiology, 2006. **9:** p. 359-364.

20. Frey-Klett, P., Garbaye, J., and Tarkka, M., *The mycorrhiza helper bacteria revisited*. New Phytologist, 2007. **176:** p. 22-36.

21. Gaskins, M.H., Albrecht, S.L., and Hubbell, D.H., *Rhizosphere bacteria and their use to increase plant productivity: A review*. Agriculture, Ecosystems and Environment, 1985. **12:** p. 99-116.

22. Sashidhar, B., and Podile, A.R., *Mineral phosphate solubilization by rhizosphere bacteria and scope for manipulation of the direct oxidation pathway involving glucose dehydrogenase*. Journal of Applied Microbiology, 2010. **109:** p. 1-12.

23. Balogh-Brunstad, Z., Keller, C.K., Gill, R.A., Bormann, B.T., and Li, C.Y., *The effect of bacteria and fungi on chemical weathering and chemical denudation fluxes in pine growth experiments*. Biogeochemistry, 2008. **88:** p. 153-167.

24. Morris, R.O., *Genes specifying auxin and cytokinin biosynthesis in prokaryotes.* In *Plant hormones and their role in plant growth and development*, Davies P.J. (Ed.), 1987. Dordrecht, The Netherlands: Martinus Nijhoff Publishers.

25. Glick, B.R., Penrose, D.M., and Jiping, L., *A model for the lowering of plant ethylene concentrations by plant growth-promoting bacteria.* Journal of Theoretical Biology, 1998. **190:** p. 63-68.

26. Smaill, S.J., Leckie, A.C, Clinton, P.W., and Hickson, A.C., *Plantation management induces long-term alterations to bacterial phytohormone production and activity in bulk soil*. Applied Soil Ecology, 2010. **45:** p. 310-314.

27. Ping, L., and Boland, W., *Signals from the underground: bacterial volatiles promote growth in Arabidopsis*. Trends in Plant Science, 2004. **9:** p. 263-266.

28. Smaill, S.J., Clinton, P.W., and Greenfield, L.G., *Legacies of organic matter removal: decreased microbial biomass nitrogen and net N mineralization in New Zealand* Pinus radiata *plantations*. Biology and Fertility of Soils, 2010. **46:** p. 309-316.

29. Smaill, S.J., *The effect of forest management practices on microbial community properties*. PhD Thesis, 2006: University of Canterbury, Christchurch, New Zealand.

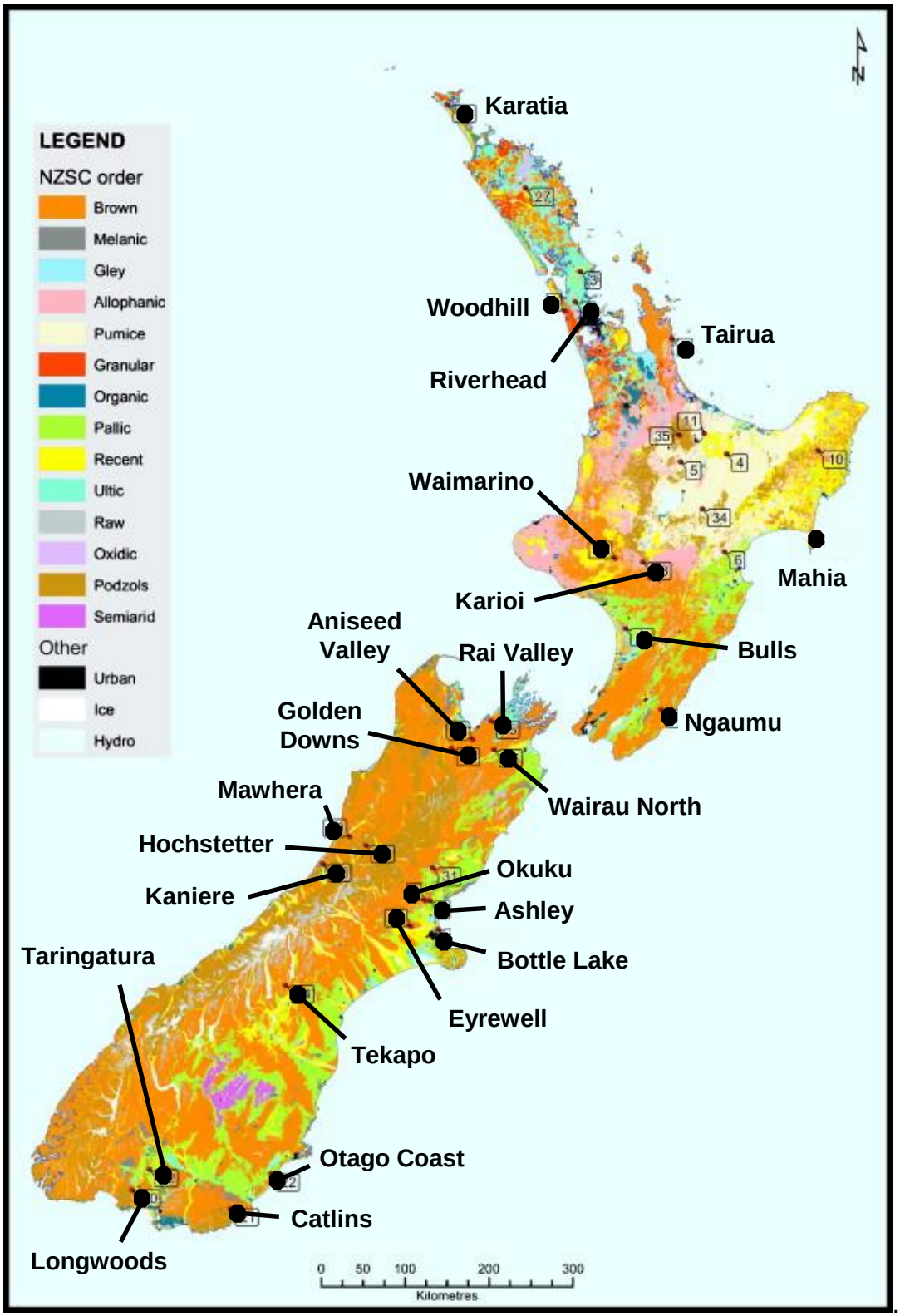
30. Garland, J.L. and Mills, A.L., *Classification and characterization of heterotrophic microbial communities on the basis of patterns of community-level sole-carbon-source utilization.* Applied and Environmental Microbiology, 1991. **57:** p. 2351-2359.

31. Watt, M.S., Coker, G., Clinton, P.W., Davis, M.R., Parfitt, R., Simcock, R., Garrett, L., Payn, T., Richardson, B. and Dunningham, A. *Defining sustainability of plantation forests through identification of site quality indicators influencing productivity - A national view for New Zealand*. Forest Ecology and Management, 2005. **216:** p. 51-63.

32. Kimberley, M., West, G., Dean, and M., Knowles, L., *The 300 Index: a volume productivity index for radiata pine.* New Zealand Journal of Forestry, 2005. **50:** p. 13–18.

APPENDICES

Appendix 1: Location of the Site Quality Plots used in this project



(Modified from Watt, M.S., Davis, M.R., Clinton, P.W., Coker, G., Ross, C., Dando, J., Parfitt, R.L., and Simcock, R., *Identification of key soil indicators influencing plantation productivity and sustainability across a national trial series in New Zealand*. Forest Ecology and Management, 2008. **256:** p. 180-190. Numbers indicate sites not used in this project.

Appendix 2: Response of substrate utilisation to weed control

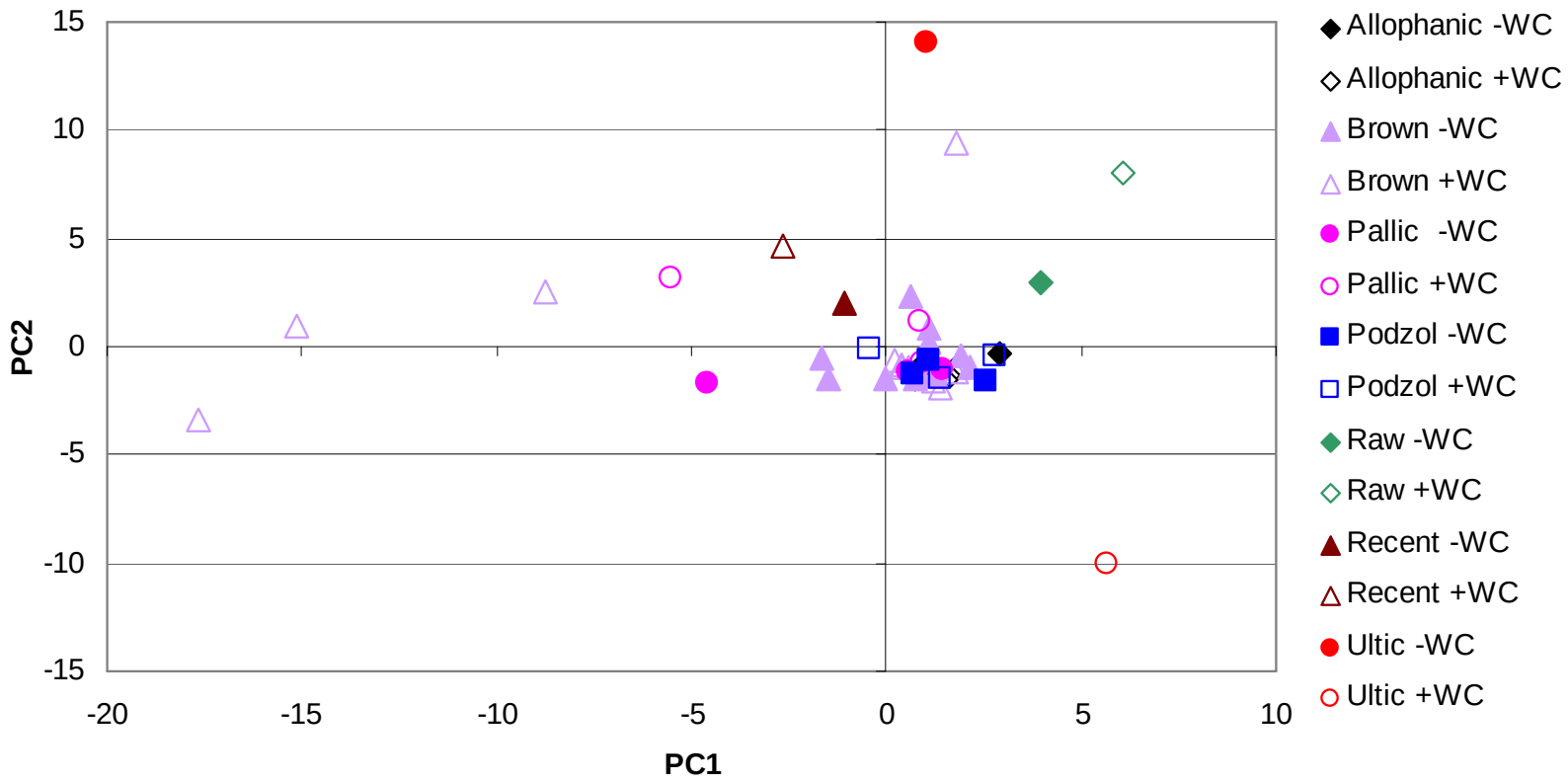


Figure A1: Relative differences between clusters of soil orders based on Principal Component Analysis of substrate utilisation data. Weed control significantly influenced the relative positioning of the sites on the axes (*P* = 0.002), and therefore significantly influenced the substrate utilisation at the different sites. +WC = with weed control; -WC = without weed control.

FFR SITE PRODUCTIVITY PUBLISHED REPORTS

Report No.	Date	Document Title	Author(s)
RSP-002	Aug 2010	Plantation Forest Nutrition	M Davis, J Xue and P Clinton
RSP-003	Jun 2011	Tree Species Effect on Soil Carbon	L Garrett, P Clinton, M Davis, H Jones
RS[-004	Jun 2012	Soil Bacterial Community Properties: Interim Report on Relationships with Site Productivity	S Smaill