Article

Ease of access to an alternative food source enables wallabies to strip bark in Tasmanian *Pinus radiata* plantations

Anna H. Smith¹, David A. Ratkowsky¹, Timothy J. Wardlaw², Caroline L. Mohammed^{1,*}

- ¹ Tasmanian Institute of Agriculture, University of Tasmania, Private Bag 98, Hobart, TAS, 7001, Australia; annah.smith@hotmail.com (A.H.S.); d.ratkowsky@utas.edu.au (D.A.R.); caroline.mohammed@utas.edu.au (C.L.M.)
- ² ARC Centre for Forest Value, University of Tasmania, Private Bag 55, Hobart, TAS, 7001, Australia; timothy.wardlaw@utas.edu.au
- * Correspondence: caroline.mohammed@utas.edu.au

Abstract: Bark stripping by the Bennett's wallaby (Macropus rufogriseus rufogriseus) from the lower stems of 3-6-year-old radiata pine (Pinus radiata) causes significant damage in Tasmanian plantations. The usual diet of this generalist herbivore is mainly grasses and broadleaved forbs. As the factors that attract wallabies to supplement its diet by eating the bark of plantation pine trees are currently not elucidated, the present study aimed to determine how the incidence and severity of bark damage in 12 Tasmanian radiata pine plantations was influenced by various inter-site factors such as the floristic composition of the surrounding forest and by various intra-site factors such as the height and circumference of individual trees, the number of branches in the first two whorls at the base of the tree, and their internode lengths. Site differences in the observed percentage of bark stripping were found to be related to 'ease of access' variables such as bare ground, bracken, and moss, 'hindrance to access' variables such as rock and woody debris, and the percentage of grass, the wallaby's main food source, present in the five plots at each site. The difference between the mean minimum soil and air temperatures in spring, a driving force for carbohydrate production that occurs with tree growth in spring or early summer, was the only meteorological observation at the sites that was found to be statistically significant. Nevertheless, there was no direct evidence that it was the movement of sugars in the phloem tissue accompanying tree growth which provided wallabies with a supplementary food source.

Keywords: bark stripping; wallabies; supplementary food; radiata pine plantations

1. Introduction

Pinus radiata D. Don is a widely planted softwood species worldwide, estimated at over 4 million hectares globally [1], with approximately 770,000 ha growing in southern Australia (including Tasmania). The pests and diseases that currently affect radiata pine plantations can be controlled or tolerated, provided that the plantations are not on sites where the trees are stressed [1]. Less manageable is the damage consisting of bark stripping, girdling or partial girdling by native animals to trees in Australian plantations [2], and which may result in the death of the tree. Even when recovery takes place after less severe damage the tree may become deformed and substantially reduce its value as timber.

In Tasmania, wood quality losses and reduction of potential growth due to bark stripping damage is attributed mainly to the Bennett's wallaby *Macropus rufogriseus* (Desmarest) subsp. *rufogriseus* owing to the height of the damage occurring on the tree stems [3]. The only other animal that could cause the damage is the much larger Forester Kangaroo *Macropus giganteus* Shaw, 1790 subsp. *tasmaniensis*, but that species is restricted to isolated populations in the midlands and northeastern Tasmania [4] while Bennett's wallaby is found throughout Tasmania [5]. The Brushtail

possum *Trichosurus vulpecula* Kerr, 1792 is usually associated with stripped and broken stems in older, mid-rotation plantations ca. 10–15 years old [6].

Bennett's wallaby is a nocturnal, generalist herbivore with a diet of mainly grasses and broad-leaved forbs [7]. Previous field trials [8] found that browsing of *P. radiata* seedlings by herbivores was greatest when located in patches of palatable short vegetation such as grass and least in low-quality tall vegetation such as bracken and shrub. Night time feeding by wallabies is preferred in open grassland and young plantations, while closed canopy environments such as native forest are avoided. Daytime sheltering is preferred in older plantations [9].

In 3–6 year old radiata pine plantations, Bennett's wallabies tear off bark in strips near the base of trees [6]. The stripping exposes the cambium and usually results in extensive resin flow from the damaged section of the stem. When a tree is completely girdled or has had its bark severely stripped, it is at risk of dying. Partially ringbarked trees may survive, but sub-lethal bark stripping wounds may weaken the timber and reduce the wood quality around the location of the damage, resulting in large financial losses [6].

Limitations on food material may promote small mammal attack on trees, as has been observed in the Northern Hemisphere [10]. The availability of ground cover and the proximity to native vegetation and water is also important, as the mammals tend to harbour in such areas [2]. One overriding factor observed worldwide is that browsed trees are invariably young trees (seedlings or saplings), whether the browsing is done by ungulates as in Europe [11, 12], or by marsupials in Australia [13,14,15].

The social and political pressure to find alternatives to pesticides increased nationally within Australia during the latter part of the 20th Century. Formal health surveillance of state-owned forestry plantations in Tasmania commenced in 1997 using aerial, roadside and ground inspections [16]. Recognizing that a major risk to radiata pine plantations was crop loss and damage due to bark stripping by browsing mammals, the health surveillance program provided an opportunity to identify risk factors associated with the timing and location of severe outbreaks [16]. An earlier study [3] and the current study were undertaken in an endeavour to explore the factors that influence bark stripping by the Bennett's wallaby in Tasmanian pine plantations. The current study aimed to examine the risk factors at more than one spatial scale. Thus, intra-site factors (e.g. branch number, internode length, wallaby scat density and alternate feed) and inter-site factors (e.g. mean minimum soil and air temperatures, altitude and rainfall) that might affect the incidence and severity of bark stripping damage were investigated.

2. Materials and Methods

2.1. Study Sites

Data were collected from twelve commercial *Pinus radiata* plantations in Tasmania, Australia (Table 1, Figure 1). Sites were selected to represent a range of altitudes, rainfall and damage severity. Plantations were all second rotation, planted at a spacing of 2 m between trees and 3 m between rows with a single application of fertilizer after planting. For the purposes of within-site data collecting, five plots of 20 trees (4 rows x 5 trees) were established on each of the 12 sites, the plot locations being evenly spaced along a central road with approximately 50 m spacing between plots. The distance into the plantation from the central road was determined randomly using a random number generator.

2.2. Response Variables

The incidence and severity of bark stripping damage was spatially mapped at each site, between October 2006 and January 2007, to quantify damage that had occurred in the preceding winter and spring. Every tree in every 5th row per plantation was assessed (20% sample) and the location marked with a Garmin® eTrex handheld GPS. In addition to scoring the incidence (presence or absence) of old and fresh damage, the area damaged (cm²) was also determined by measuring the length and width of each bark stripping event. An overall percentage girdling score was derived as an estimate

Site name	Lat. (N)	Long. (E)	Alt. (m)	Ave. annual	Ave. annual	Ave. min. soil	Ave. min. air	Tdiff (diff. of	Average damage
				rainfall	air	temp.	temp.	min. soil	(%girdling)
				(mm)	temp.	(spring)	(spring)	and air	
					(°C)	(°C)	(°C)	temps.) (°C)	
Branchs Creek	-41.27	146.66	131	744	12.9	9.4	8.0	1.4	0.0
Franklin	-43.06	146.88	293	1123	9.7	10.9	4.7	6.2	25.5
Inglis River	-41.11	145.60	111	1353	11.3	8.8	6.2	2.6	22.9
Longhill	-41.34	146.49	120	988	11.6	7.3	6.2	1.1	2.5
Nicholas 1	-41.45	147.97	338	915	10.6	8.1	5.1	3.0	16.1
Nicholas 2	-41.47	147.98	324	915	10.6	8.6	5.1	3.5	4.7
Oonah	-41.23	145.62	454	1439	11.2	7.5	6.1	1.4	0.4
Plenty	-42.87	146.89	427	876	9.2	8.0	4.0	4.0	16.7
Springfield 1	-41.21	147.63	311	785	13.0	8.4	7.3	1.1	8.7
Springfield 2	-41.21	147.61	294	785	13.0	9.9	7.3	2.6	21.8
Styx	-42.77	146.83	539	714	11.6	8.0	5.6	2.4	1.3
Tower Hill	-41.53	147.91	512	716	11.5	6.2	5.6	0.6	41.6

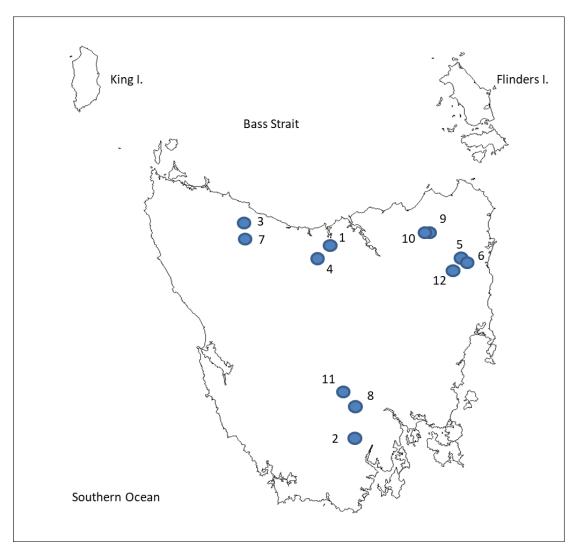


Figure 1. Location of *P. radiata* plantations in Tasmania at which the study was carried out (see Table 1 for latitude, longitude and other site information). 1. Branchs Creek; 2. Franklin; 3. Inglis River; 4. Longhill; 5. Nicholas 1; 6. Nicholas 2; 7. Oonah; 8. Plenty; 9. Springfield 1; 10. Springfield 2; 11. Styx; 12. Tower Hill.

of the percentage of the stem circumference that had its bark removed. An estimate of the age of each damage event was made by assessing the degree of desiccation and discoloration of the exposed sapwood, the presence of fresh resin around the wound and the degree of wound occlusion. From these data it could also be determined whether a tree sustained damage from multiple bark stripping events.

2.3. Explanatory Variables

Variables with the potential for explaining the observed percentage girdling fall into several categories: those which potentially aided access; those potentially hindering access; those potentially providing a food source; and climate attributes that may affect plant chemistry. Components of ground cover and projected plant cover were measured using ocular estimates of percent cover in each of three randomly located transects within each plot.

The variables (measured as a percentage cover) listed and coded in Table 2 that potentially aided access were: bare ground, Austral bracken (*Pteridium esculentum*), grass and moss/liverworts. The variables listed in Table 2 that may hinder the movement of a wallaby across a plot were: the percent cover by woody debris; the percent cover of rock. Several tree-level attributes that potentially aided or hindered access of wallabies were also measured. They included: tree height (measured using a height pole) and circumference at 20 cm above ground level (measured using a diameter tape); the number of branches in the first and second whorls (i.e. the more branches, the lesser the ease of access); and, the length of the internodes between whorls (i.e. the shorter the length, the lesser the ease of access).

Table 2. Description, abbreviations and units of plot variables measured in three transects in each of five plots at 12 sites in Tasmanian *Pinus radiata* plantations. Note: the category of variables comprising functional groups and species of vegetation as a food source is not shown.

Variable	Description	Units		
%Gird	Cumulative damage score, percentage of bark removed			
ang%Gird	Angular transformation of cumulative damage score %Gird			
BareGrd	Percentage of area as bare ground			
BBM	Composite variable, =BareGrd+Bracken+Moss			
BBMG	Composite variable, =BareGrd+Bracken+Moss+Grass	%		
Bracken	Percentage of area as Pteridium esculentum			
Grass	Percentage of area as grass			
height	Average height of the trees in the plot			
inter_1	Length of first internode of tree	mm		
inter_2	Length of second internode of tree	mm		
LiveMat	Percentage of area as live material (grasses, herbs, forbs, etc.)			
Moss	Percentage of area as mosses and liverworts			
P_radiata	Percentage of area containing wilding Pinus radiata	%		
Rock	Percentage of area occupied by rock	%		
RockWood	Composite variable, =Rock+WoodDeb	%		
SSpMinT	Minimum soil temperature in spring months, I-button	°C		
Tdiff	Difference between mean minimum soil and air	°C		
	temperatures in spring months, = SSpMinT-TminSpr			
TminSpr	Minimum air temperature in spring months (SILO)	°C		
whorl_1	No. of branches in first whorl of tree	integer		
whorl_2	No. of branches in second whorl of tree	integer		
WoodDeb	Percentage of area as woody debris	%		

The potential food source category of explanatory variable included two functional group of plant species: the percentage of plot area covered by grasses, which has a double role as they also aid access to the site; and, the percentage of live grasses, herbs and forbs. Together these two functional groups form the main constituents of the diet of the Bennett's wallaby [7]. The percent plot cover of wildling (i.e. unplanted) *Pinus radiata* was also included in the potential food source category. Other

vegetative variables, which are probably not food sources, include *Acaena novae-zelandiae*, *Acacia dealbata*, *Gonocarpus teucrioides*, species of *Juncus*, *Ozothamnus ferrugineus* and *Pomaderris apetala*.

A further set of potential explanatory variables involved climate data. Interpolated estimates (data drill) of various aspects of rainfall and temperature data were downloaded from SILO (an enhanced climate data bank [17]). These included average annual minimum and maximum temperature, average minimum and maximum temperature in each of the four seasons, as well as average annual rainfall, average radiation, average vapour pressure and average annual evaporation. The only climate variable actually measured on-site was the soil temperature, which was recorded continuously between March-December, 2007 using a Thermochron i-button (Dallas Communications, Texas). It has been reported that environmental stress in plants is associated with an increase in the conversion of starches to sugars [18,19]. That is, while increasing air temperature triggers shoot activity, low soil temperature and therefore low root activity means that the demand for nutrients and/or water exceeds their supply, potentially causing stress. It is hypothesized that the most attractive time for bark stripping by wallabies may be when soluble sugars and starch begin their flow in the phloem tissue of a tree. To test this, differences were calculated between the recorded soil temperature and the daily air temperatures obtained from the data drill in springtime. Thus, the derived temperature difference Tdiff (see Table 1), the difference between the minimum daily soil and air temperatures in spring, is an explanatory variable of interest.

2.4. Statistical Analysis

Multiple regression analysis was carried out on the mean values of all explanatory and response variables using PROC REG of SAS (Vers. 9.4, SAS Institute, Cary, NC, U.S.A.). For data at the plot level, there were 60 sampling units, made up of five plots at each of the 12 sites. For data at the site level, there were only 12 sampling units, made up by averaging 15 transects (i.e. three transects in each of five plots), thereby producing a site average. The response variable was percentage girdling (%Gird), which was transformed using the angular transformation, ang%Gird=sin¹(sqrt(%Gird)), this transformation producing a set of residuals which was closer to being normally distributed than %Gird itself or a logarithmic transformation of %Gird. The potential explanatory variables used for the regression analysis are tabulated in Table 2. To decide upon the best of several competing models, the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) were used as the main indicators [20]. In addition, the proportion of explained variation (R²) and adjusted proportion of explained variation (adj R²) were also calculated and contrasted with AIC and BIC.

3. Results

3.1. Percentage girdling at the plot level (n=60)

The best regression relationships, irrespective of whether the decision was based upon AIC, BIC or adj R², were obtained when bare ground, bracken and moss were all included in the model (Table 3), there being little difference between including these explanatory variables separately or as their sum in the composite variable BBM. These three variables are all associated with access, with large values of each indicating greater ease of access. No potential explanatory variable for percent girdling which related to a source of food, such as grass, herbs and forbs, whether alone or summed together, correlated with percentage girdling nor were they significant in any of the multiple regression models that were tried using them. Other vegetative components, such as internode length and the number of branches in the lowest two internodes, were also non-significant contributors to the explained variation in girdling damage.

3.2. *Percentage girdling at the site level (n=12)*

As was the case with the results at the plot level, the composite variable BBM, being the sum of the percentages of bare ground, bracken and moss, was positively correlated with the transformed percent girdling (ang%Gird) in the two best models (Table 4). Using either AIC or adj R^2 , the model

that included the percentage of area occupied by woody debris (WoodDeb) was adjudged to be the best model (Table 4), with its negative coefficient indicating that increasing the area occupied by woody debris inhibits bark stripping damage. BIC favours the parsimonious model lacking the woody debris term, a consequence of the fact that BIC incorporates a penalty for extra model terms and thereby tends to choose simpler models than does AIC. Figure 2 provides a graphical representation of the four components of ease of access for wallaby browsing, viz. bare ground, bracken, moss and grass (which is a food source as well as a component of ease of access). Sites on the right-hand side of Figure 2 (i.e. the ones with high percentage girdling) almost always have greater amounts of at least some of these variables than the sites with low percentage girdling (those on the left-hand side of Figure 2). It is noteworthy that the two best models both contain Tdiff, the mean difference between the minimum daily soil and air temperatures in the spring season, with a positive coefficient (Table 4), supporting the hypothesis that the trees are more attractive in spring, when soluble sugars and starch begin to flow in the phloem tissue.

No other potential explanatory variables associated with ease or difficulty of access, or vegetative components, were serious contenders as predictors of percentage girdling at the level of sites (n=12). These included variables that were expected to affect access (the number of branches in the first and second whorls of the tree, the length of the first and second internodes, the average height and average circumference of the tree). Of these six variables, only the pairwise correlation coefficient of whorl_1 with ang%Gird achieved statistical significance (r=0.654, P=0.021), but the regression coefficient was positive, not the expected negative value if a larger number of branches in the first whorl was inhibitory to wallaby attack.

Table 3 Regression relationships involving the angular transformation of percentage girdling (ang%Gird). Number of sampling units=60 (i.e. 5 plots at each of 12 sites).

Regression relationship	AIC	BIC	adj R ²
ang%Gird=0.106+0.00326(BareGrd)+0.0136(Bracken)+0.00947(Moss)	-187.9	-185.4	0.282
ang%Gird=0.09743+0.00500(BBM)	-187.8	-185.6	0.257

Notes: AIC = Akaike's Information Criterion, BIC = Bayesian Information Criterion and adj R^2 =the adjusted R^2 , i.e. the proportion of explained variation based upon the variance. BareGrd = Percentage of area as bare ground; Bracken = Percentage of area as *Pteridium esculentum*; Moss = Percentage of area as moss; BBM = BareGrd+Bracken+Moss; ang%Gird = Angular transformation of cumulative damage score.

Table 4 Regression relationships involving the angular transformation of percentage girdling (ang%Gird). Number of sampling units=12, one per site, derived by averaging over the 15 transects (3 transects in each of the 5 plots) in each of the 12 sites, thereby obtaining a single value for each site.

Regression relationship	AIC	BIC	adj R²
ang%Gird=-0.6288+0.01493(BBM)+0.01034(Grass)+0.06646(Tdiff)	-55.14	-49.64	0.834
ang%Gird=-0.4758+0.01424(BBM)+0.00865(Grass)+0.06216(Tdiff)-0.00484(WoodDeb)	-55.62	-46.72	0.845

Notes: AIC = Akaike's Information Criterion, BIC = Bayesian Information Criterion and $adj R^2$ the adjusted R^2 , i.e. the proportion of explained variation based upon the variance. The explanatory variables are BBM (= the sum of the percentages of area of bare ground, bracken and moss), the percentages of area as grass (Grass) and woody debris (WoodDeb), and Tdiff (=the difference between mean minimum soil and air temperatures in the spring months).

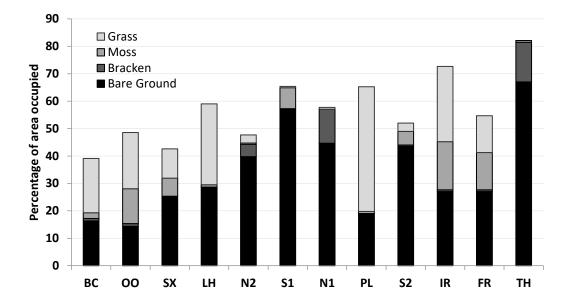


Figure 2. The stacked bar graph depicts four of the components of the vegetation. The total height of each bar corresponds to BBMG, the sum of the percentages of the area occupied by bare ground, bracken, moss and grass. The horizontal axis lists the 12 sites from left to right in order of increasing percentage girdling. BC = Branchs Creek; OO = Oonah; SX = Styx; LH = Longhill; N2 = Nicholas 2; S1 = Springfield 1; N1 = Nicholas 1; PL = Plenty; S2 = Springfield 2; IR = Inglis River; FR = Franklin; TH = Tower Hill.

4. Discussion

The statistically significant regression relationships given in Tables 3 and 4 indicate that bark stripping of plantation radiata pine may be determined principally by the ease to which Bennett's wallabies have access to the trees. The most significant variables in the regression equations were bare ground, bracken and moss, which appear in the most significant models either individually or collectively in the composite variable BBM. Although bracken in Tasmania can grow densely, forming extensive patches in areas which have been recently cleared or subject to severe disturbance, their pliable stems offer little resistance to the movement of animals the size of a wallaby and have the added advantage to them of providing shelter and cover. The extent of bare ground, bracken and moss varied greatly at the 12 sites of this study, as did the frequencies of occurrence of the various other components of the vegetation. For example, the site with the greatest percentage girdling, Tower Hill, had the greatest amount of bare ground (67%) but the least amount of grass (0%), whereas a site with a moderate percentage girdling, Plenty, had the most grass (45.5%) and the third least amount of bare ground (19%). Therefore, no single variable can be identified as being the most important for providing a wallaby easy access to the trees. The stacked bar graph given by Figure 2 reveals that bracken occurs in a substantial amount at only three of the sites (Nicholas 1, Nicholas 2 and Tower Hill), being present at 1% or less and barely visible on the scale of Figure 2 at the other nine sites. Similarly, the distribution of moss is very spotty, despite being present at all but one of the sites. Its abundance varies greatly, as well as having an almost zero pairwise correlation with percentage girdling, although it is an important explanatory variable in the models of Tables 3 and 4. This illustrates the dangers of accepting a multiple linear regression model at face value, without closer examination. The three sites that had substantial bracken had, in contrast, very little moss (Figure 2). Furthermore, no site was simultaneously abundant in all three of the components bare ground, bracken and moss, which may explain why the composite variable BBM may be a better explanatory variable for correlating with percentage girdling than the separate components. As there are only 12 sites, one spurious or atypical data point can have a strong

influence on which variables appear in the best predictive model. In Figure 2, the sites are arranged from left to right in order of increasing percentage girdling. If ease of access to the site were the full story, then the height of the bars in Figure 2 (BBMG) would tend to rise in tandem with increased percentage girdling. Although generally true, this is not entirely the case, as the Longhill site goes against the trend in the five sites that have <5% girdling, and Springfield 2 and Franklin go against the trend in the six sites that have <15% girdling.

Further attempts were made at finding components of the vegetation that correlate with percentage girdling. Some of the components, e.g. *Ozothamnus ferrugineus* and wildling *P. radiata*, the latter found to be attractive to browsing mammals and targeted in preference to crop trees [3], were abundant at only one of the sites and were absent or sparsely represented elsewhere. A consequence of this is that a high contribution of one of those components to the overall explained variation is likely to be spurious. Other non-vegetative site factors that were investigated for a possible link to percentage bark stripping damage include the number of whorls on the stem of the *P. radiata* tree and the distance between internodes. Although ang%Gird correlated significantly (P<0.05) with the average number of branches in the first whorl of the tree, the positive correlation obtained defies explanation, as the prevailing belief was that the more branches in a whorl, the more difficult it should be for a wallaby to gain access to the tree.

Bark stripping of Scots pine and lodgepole pine by moose in Sweden [21] and of the same and other tree species in Scotland by deer [22] is at its most intense in winter when alternative food resources are generally limiting. Seasonal changes in the carbohydrate physiology of the trees may contribute to when trees are the most susceptible to browsing damage. In Tasmania, browsing pressure on highly palatable forage species increased in winter and spring when soluble sugars were also at a seasonal peak [23]. Sugar levels increase in the bark and foliage of a number of pine species throughout autumn as part of the hardening process [24]. For example, both soluble sugar and shoot nitrogen concentrations increased in *P. halapensis* seedlings as minimum temperatures drop below 9°C [25]. Larger reserves of sugars are known to be associated with increased cold tolerance in lodgepole pine (*P. contorta*) and Scots pine (*P. sylvestris*) [26,27,28].

Previous held views on what promotes bark stripping damage due to browsing mammals in Tasmanian pine plantations are generally not supported by the results of the present survey. For example, although bark stripping in plantation P. radiata due to Bennett's wallaby was previously found to be significantly greater (P=0.002) at high elevation sites [3], we found no hint of an association, with both high and low bark damage occurring at sites of all elevations. The same was the case for rainfall; whereas the earlier study found significantly greater (P<0.001) bark stripping damage at wetter sites [3], no association was found in the present study. One should also keep in mind that the apparent low P-values previously reported [3] were not supported by high values of the proportion of explained variation in bark stripping incidence, those being R^2 =0.04 for elevation and R^2 =0.10 for rainfall. The significant associations are due to the large sample sizes (n=229 forest blocks) rather than due to strong relationships. Therefore, it would be unrealistic to expect a definitive result to be obtained from the present study, which had only 60 plots at the plot level occurring at 12 sites. Other potential factors such as aspect and slope of the sites, underlying geology, and proximity to, and vegetative composition of, nearby forests have little likelihood of being found to influence bark stripping damage, especially as their values were not allocated at random (or by any other process) when the plantations were established. Instead, the "levels" of these factors have highly unequal sample sizes, reducing the power of any statistical test.

Page et al. [23] found that there was a strong general positive association of high soluble sugar concentrations, particularly in the two exotic grasses *Poa annua* and *Holcus lanatus*, with elevated levels of browsing pressure in two large 4–5-year-old *Pinus radiata* plantations near Tarraleah in central western Tasmania, far from any of the 12 plantations in the present study which cover a wider geographical range (Figure 1) and encompass a much wider range of altitude, rainfall and temperature (Table 1). In the dry climate of eastern Tasmania, Bennett's wallabies were found to be the main cause of umbrella-shaped trees at 67 small dry eucalypt forest and woodland sites [14]. Those authors observed a "browsing cascade" in which the mammalian species consumed the preferred plant species when they were available, but foraged lesser species in the preference chain

when the preferred species were absent. This suggests that non-preferred species in small quantities form part of a mixed diet, which may have positive effects on nutrition and digestion, as is the case for browsers in other parts of the world, e.g. ungulates in Africa [29] and moose in Scandinavia [30].

5. Conclusions

The main conclusion to be drawn from the results of the present study is that a combination of four components to the vegetation, viz. bare ground, bracken, moss and grass, plays a major role in assisting wallaby browsing. However, the details of how the mechanism operates and how the components interact is not straightforward and is unlikely to be readily elucidated by small-scale surveys. In addition, it appears that a site can change its susceptibility to bark stripping with time. For example, in an earlier study [3], Oonah was one of the most severely affected sites, with a mean bark stripping of 47.3% compared to less than 1% in the present study. Therefore, chance is likely to play a role at any specific site and vary from year to year, increasing the difficulty of the task of unravelling the factors that are responsible for enticing wallabies to strip bark from *P. radiata* trees in Tasmanian plantations.

Author Contributions: A.H.S, T.J.W. and C.L.M. designed the experiment; A.H.S. carried out the field work; D.A.R. analyzed the data. All authors contributed to the writing of the manuscript.

Funding: This research was funded by the Australian Research Council Australian Research Council, LP0669742, and co-funded by industry; Forestry Tasmania, Hosking Forestry Ltd and Taswood Growers.

Acknowledgments: We thank David Page for his extensive help with sampling.

Conflicts of Interest: The authors declare no conflict of interest.

References

- Mead, D.J. Sustainable management of *Pinus radiata* plantations. FAO Forestry Paper No. 170, Rome, Italy, 2013.
- 2. McNally, J. Damage to Victorian exotic pine plantations by native animals. *Aust. Forestry* **1955**, *19*, 87–99.
- 3. Wotherspoon, K. An analysis of the factors influencing bark stripping by browsing mammals in *Pinus radiata* plantations. Division of Forestry Research and Development, Forestry Tasmania, Hobart, **2004**; 28pp.
- Department of Primary Industries, Parks, Water and the Environment, Tasmanian Government, 2014. http://dpipwe.tas.gov.au/wildlife-management/living-with-wildlife/living-with-kangaroos-and-wallabies, viewed 26 May 2017.
- 5. Calaby, J.H. Marsupials. In *The Complete Book of Australian Mammals*; Strahan, R., Ed.; Angus & Robertson: Sydney, Australia, 1983; pp. 239–241.
- 6. Wardlaw, T. A manual of health problems affecting *Pinus radiata* in Tasmania. Hobart: Forestry Tasmania, Division of Forest Research and Development, Technical Report 12/2003, **2003**.
- 7. Sprent, J.; McArthur, C. Diet and diet selection of two species in the macropodid browser-grazer continuum do they eat what they 'should'? *Aust. J. Zool.* **2002**, *50*, 183–192.
- 8. Pietrzykowski, E.; McArthur, C.; Fitzgerald, H.; Goodwin, A.N. Influence of patch characteristics on browsing of tree seedlings by mammalian herbivores. *J. Appl. Ecol.* **2003**, *40*, 458–469.
- 9. Le Mar, K.; McArthur, C. Comparison of habitat selection by two sympatric macropods, *Thylogale billardierii* and *Macropus rufogriseus rufogriseus*, in a patchy eucalypt-forestry environment. *Austral Ecol.* **2005**, *30*, 674–683. doi: 10.1111/j.1442-9993.2005.01510.x

- 10. Gill, R.M.A. A review of damage by mammals in North Temperate Forests: 2. Small mammals. *Forestry* **1992**, *65*, 281–308.
- 11. Díaz-Yáñez, O.; Mola-Yudego B.; González-Olabarria J.R. What variables make a forest stand vulnerable to browsing damage occurrence? *Silva Fennica* **2017**, *51* (2), article id 1693. https://doi.org/10.14214/sf.1693
- 12. Senn, J.; Suter, W. Ungulate browsing on silver fir (*Abies alba*) in the Swiss Alps: beliefs in search of supporting data. *Forest Ecol. Manage.* **2003**, *181*, 151–164.
- 13. Di Stephano, J. Mammalian browsing damage in the Mt. Cole State forest, southeastern Australia: analysis of browsing patterns, spatial relationships and browse selection. *New Forests* **2005**, 29, 43–61. doi: 10.1007/s11056-004-0258-9
- 14. Hazeltine, A., Kirkpatrick, J.B. Practical and theoretical implications of a browsing cascade in Tasmanian forest and woodland. *Aust. J. Bot.* **2015**, *63*, 435–443.
- 15. Stutz, R.S.; Banks, R.B.; Dexter, N.; McArthur, C. Herbivore search behaviour drives associational plant refuge. *Acta Oecol.* **2015**, *67*, 1–7. doi: 10.1016/j.actao.2015.05.004
- 16. Wardlaw, T. The evolution of forest health surveillance in Tasmania. Tasforests 2008, 17, 57–66.
- 17. Queensland Government. SILO climate data. Department of Science, Information Technology, Innovation and the Arts, The State of Queensland, Australia. http://www.longpaddock.qld.gov.au/. Accessed 2 January 2014.
- 18. Kobe, R.K. Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. *Oikos* **1997**, *80*, 226–233.
- 19. Kaelke, C.M.; Dawson, J.O. The accretion of nonstructural carbohydrates changes seasonally in *Alnus incana* ssp. *rugosa* in accord with tissue type, growth, N allocation, and root hypoxia. *Symbiosis* **2005**, *39*, 61–66.
- 20. Burnham, K.P.; Anderson, D.R. Multimodel inference: understanding AIC and BIC in model selection. *Sociol. Methods Res.* **2004**, *33*, 261–304.
- 21. Ball, J.P.; Dahlgren, J. Browsing damage on pine (*Pinus sylvestris* and *Pinus contorta*) by a migrating moose (*Alces alces*) population in winter: relation to habitat composition and road barriers. *Scand. J. For. Res.* **2002**, 17, 427–435. doi: 10.1080/028275802320435441
- 22. Gill, R.M.A.; Beardall, V. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry* **2001**, *74*, 209–218.
- 23. Page, D.E.; Close, D.; Beadle, C.L.; Wardlaw, T.J.; Mohammed, C.L. Seasonal dynamics in understorey abundance and carbohydrate concentration in relation to browsing and bark stripping of Tasmanian *Pinus radiata* plantations. *Forest Ecol. Manage.* **2013**, 296, 98–107.
- 24. Levitt, J. Response of Plants to Environmental Stresses. Volume I. Chilling, Freezing and High Temperature Stresses. Academic Press, New York, USA, 1980; 497pp.
- 25. Fernández, M.; Royo, A.; Gil, L.; Pardos, J.A. Effects of temperature on growth and stress hardening development of phytotron-grown seedlings of Aleppo pine (*Pinus halepensis* Mill.). *Ann. Forest Sci.* **2003**, 60, 277–284.
- 26. Ögren, E. Effects of climatic warming on cold hardiness of some northern woody plants assessed from simulation experiments. *Physiol. Plantarum* **2001**, *112*, 71–77.

- 27. Ögren, E.; Nilsson, T.; Sundblad, L.G. Relationship between respiratory depletion of sugars and loss of cold hardiness in coniferous seedlings over-wintering at raised temperatures: indications of different sensitivities of spruce and pine. *Plant, Cell Environ.* 1997, 20, 247–253.
- 28. Repo, T.; Leinonen, I.; Ryyppö, A.; Finér, L. The effect of soil temperature on the bud phenology, chlorophyll fluorescence, carbohydrate content and cold hardiness of Norway spruce seedlings. *Physiol. Plantarum* **2004**, *121*, 93–100.
- 29. Augustine, D.J.; McNaughton, S.J. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *J. Wildlife Manage.* **1998**, *62*, 1165–1183. doi: 10.2307/3801981
- 30. Milligan, H.T.; Koricheva, J. Effects of tree species richness and composition on moose winter browsing damage and foraging selectivity: an experimental study. *J. Anim. Ecol.* **2013**, *82*, 739–748. doi: 10.1111/1365-2656.12049