How herbivore browsing strategy affects whole plant photosynthetic capacity

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20 **Abstract**

21 If a browse damage index indicates that a tree has been 50% browsed by herbivores, does this

22 mean half the leaves are entirely eaten or are all the leaves half eaten? Were the affected leaves

23 old or young? Large or small? In sunshine or shade? Understanding what effect browsing will have

24 on the photosynthetic capacity and the plant's survival ability clearly requires a greater

25 understanding of browsing strategy across the canopy than can be given by a single index value.

26 We developed stochastic models of leaf production, growth and consumption using data from

27 kamahi (*Weinmannia racemosa)* trees in New Zealand which have been browsed by possums

28 (*Trichosurus vulpecula*), to ascertain which of six feasible browsing strategies possums are most

29 likely to be employing. We compared the area distribution of real fallen leaves to model output in

30 order to select the best model, and used the model to predict the age distribution of leaves on the

31 tree and thus infer its photosynthetic capability.

32 The most likely browsing strategy that possums employ on kamahi trees is a preference for virgin

33 (i.e. previously unbrowsed) leaves, consistent with the idea that browsing increases the production

34 of chemical plant defences. More generally, our results show that herbivore browsing strategy can

35 significantly change the whole-plant photosynthetic capability of any plant and hence its ability to

36 survive, and therefore herbivore damage indices should be used in conjunction with more detailed

37 information about herbivore browsing strategy.

38

39 **Keywords**: browsing strategy, photosynthesis, individual based model, leaf growth.

1. Introduction

40

41 Plant growth, health and survival are closely related to photosynthetic capability being sufficient

42 to meet the needs of the plant (Taiz et al. 2015). The contribution of individual leaves to whole-

43 plant photosynthetic capability changes with leaf age: photosynthetic rates and leaf nitrogen

44 content decline with leaf age while leaf mass per area (LMA) increases with leaf age (Kitajima et

45 al. 1997; Shirke 2001). The realised whole-plant photosynthetic rate is therefore not proportional

46 to total leaf area, but the relationship is one of diminishing returns explained well by a saturating

47 curve such as the logistic equation (Koyama and Kikuzawa 2009). To determine the whole plant

48 photosynthetic rate one must know more about the distribution of both the size and the age of the

49 individual leaves.

50 When plants are browsed by herbivores, their photosynthetic capability is compromised by loss of

51 leaf area, a process which occurs at the level of the individual leaf. However, to predict the

52 response of growth, health and survival of the plant, we must scale up the effect of damage on

53 individual leaves to the plant level (Brown and Allen 1989). It is therefore necessary to know not

54 only the rate of herbivore damage to plant leaf area as a whole, but also the pattern of damage; i.e.

55 the age of each damaged or undamaged leaf and its relative contribution to plant function.

56 Field data on herbivore browse damage is usually estimated at the level of the whole plant using

57 an index of the proportion of browsed leaves (e.g. Department of Conservation 2014), percentage

58 or total leaf area or stems removed (Hörnberg 2001; Parsons et al. 2005), or the frequency and

59 severity of missing and damaged foliage (Stone et al. 2003). However, leaves within plants vary

60 in palatability and nutritional value, meaning that susceptibility of leaves to herbivore browsing

61 changes with age and position on the plant. Young leaves vary in texture and nutrient constituents

62 compared to older, thicker leaves (e.g. Roy and Barik 2012), while nitrogen content may be

63 correlated with leaf position (e.g. full sun vs. shade) (e.g. Kitajima et al. 2002). While leaf age has

64 a negative effect on photosynthetic capacity (Field et al. 1983; Kitajima et al. 1997), herbivore

65 preference for older or younger leaves, and the relative accessibility of older and younger leaves

66 to herbivores, may reduce or exacerbate this effect. Models used to predict community level

67 impacts of herbivore browsing clearly require more information about foraging strategies than

68 simple whole-plant browse indices.

69 One such case study of interest is the invasive brushtail possum, *Trichosurus vulpecula* (Kerr),

70 browsing native trees in New Zealand, causing enough damage to precipitate substantial tree

71 mortality at a regional scale (Gormley et al. 2012; Holland et al. 2013; Payton 2000). In particular,

72 kamahi (*Weinmannia racemosa)* is a broadleaf evergreen tree endemic to, and common in, the

73 North and South Islands of New Zealand. It forms a significant, though not preferred, part of the

74 possums' diet in many forest habitats (Nugent et al. 2000) and is commonly monitored as an index

75 of canopy condition due to its ubiquity across the country (Payton et al. 1997). Other more

76 preferred species such as Southern rata (*Metersideros umbellata*) and mistletoe (Loranthaceae)

77 suffer greater damage and mortality but have been removed from a number of areas as a result

78 (Rose et al. 1992; Sessions and Kelly 2001; Stewart and Rose 1988). Hence their use as predictors

79 is less widespread.

80 Kamahi continually produces new leaves throughout the growing season and the duration of

81 laminar leaf expansion is between one and two months (Green and Jane 1983). The leaves have a

82 lifespan of approximately 40 months though some leaves last over 120 months (Richardson et al.

83 2010). Holland et al. (2013) found that kamahi had a threshold leaf area such that browsing that

84 removed leaf area below the threshold rendered the tree vulnerable to death. Changing the

85   browsing strategy, for example from a preference for virgin leaves to a preference for already

86   browsed leaves, could change the threshold leaf area at which a tree became vulnerable to browse-

87   induced mortality by more than 20%. Understanding the way in which herbivores browse

88   individual trees is therefore clearly fundamental to being able to predict community impacts of

89   herbivore damage.

90   In this paper, we develop a generic model of leaf longevity on evergreen trees in order to estimate

91   the effect of different herbivore browsing strategies on individual leaves on the leaf area

92   distribution of the whole tree. We compare model output to browsed leaf fall data collected from

93   kamahi trees in New Zealand and infer what is the most likely strategy used by brushtail possums

94   browsing kamahi. We then use this model to predict the distribution of leaf ages and areas on a

95   whole tree and make predictions of the effect of possum browsing on photosynthetic rates.

96   **2. Materials, Methods and Results**

97   *2.1 Data*

98   1355 leaves were collected from seven leaf traps placed under six kamahi trees in the Tararuas

99   from August - November 2010. A single trap was placed under the canopy of each tree, and an

100 additional seventh trap was placed by the trunk of one tree. After collection, leaves were dried and

101 sorted into two categories: browsed by possums (relatively easily identified; Department of

102 Conservation 2014) and unbrowsed by possums. Individual leaf areas were measured using an

103 Epsom Expession 10000XL scanner and WinFOLIA 2012a software (Instruments). Leaf areas

104 ranged from $1 - 3738$ mm^2 with an average of 408 mm^2. Overall 33% of the leaves showed some

105 evidence of browse, and 67% were unbrowsed. The mean area of an unbrowsed leaf was 524 mm^2,

106 and the mean area of a browsed leaf was 185 mm^2, i.e. approximately 1/3.

107   Summary statistics for each leaf-fall trap are given in Table 1. There was no significant difference

108   (two-tailed t-test, logged variables) between the distribution of leaf areas collected from the two

109   traps (trunk, T20T, and canopy, T20C) under the same tree ($p = 0.25$) so these two sub-datasets

110   were pooled. Two trees (T20(C and T) and T23) had relatively few (less than 16%) browsed leaves.

111   There was no significant difference (two-tailed t-test, logged variables) between these two trees in

112   either the browsed leaf area distribution ($p = 0.17$) and the unbrowsed leaf area distribution ($p =$

113   0.08). Together these trees were designated unbrowsed and the data from these two trees were

114   pooled.

115   The remaining four trees had at least 39% of leaves browsed. There was no significant difference

116   (ANOVA, two-tailed, logged variables) in the browsed leaf area distributions for three (T15, T19

117   and T19B) of these trees ($p = 0.06$) and only a small difference in the unbrowsed leaf area

118   distributions ($p = 0.01$), where the mean unbrowsed leaf area for each tree was 550 mm^2, 520

119   mm^2 and 621 mm^2 respectively. When the fourth tree in this group (T22) was included in this

120   comparison it did show some significant differences, mainly resulting from the smaller size of

121   unbrowsed leaves from this tree compared to the other three. However, for simplicity, together

122   these trees were designated browsed and the data from these four trees were pooled. This pooled

123   data was used in all subsequent analyses.

124   *2.2 Model Overview*

125   We start by modelling leaf fall in the absence of browsing. The model parameters (mean and

126   variance of the area of a fully grown leaf) are found using basic statistical fitting methods on the

127   distribution of the areas of fallen leaves from the unbrowsed trees (pooled data).

128   We then develop a dynamical model of individual leaf growth and mortality on a whole plant, with

129   parameters including leaf longevity and growth rate which can be estimated using previously

130   published data. This model is combined with a model for possum browse with unknown

131   parameters for relative possum browse rate and relative possum bite size. The two unknown

132   possum model parameters are found by fitting the model output (fallen leaf area distribution) to

133   the leaf area distributions from the browsed trees (pooled data). The model can be modified to test

134   a range of browsing strategies. We explored six: no preference, a preference for young, old or big

135   leaves, and a preference for previously browsed or virgin (never browsed) leaves. For each

136   browsing strategy the unknown parameters were fitted independently to the pooled browsed leaf

137   area distribution and the best fit solutions for each strategy were compared to find the most likely

138   strategy.

139   *2.3 Predicting leaf area distribution – unbrowsed*

140   Growing kamahi leaves pass through three distinct phases: budbreak; leaves developing; and

141   leaves developed (mature) (cf. Green and Jane 1983). Initial growth is moderately fast compared

142   to tawari (*Ixerba brexioides*) and silver beech (*Lophozonia menziesii*) (Stewart and Rose 1988)

143   and, because kamahi leaves have a long life span (in the order of 4 years; Richardson et al. 2010),

144   the majority of leaves are in their final mature phase where growth is minimal (Choinski Jr and

145   Gould 2010). The final size of a mature leaf can vary widely (Wardle and MacRae 1966). To

146   model the growth of an individual leaf, whilst on the plant, we used a simple von-Bertalanffy

147   growth model (Kot 2001). The rate of change of area of individual leaf i, $A_i(t)$ is given by

148
$$\frac{dA_i}{dt} = r(K_i - A_i)$$

149 where r is the growth rate (assumed to be the same for all leaves on the plant) and K_i is the

150 maximum area of leaf i. Presuming the leaf starts with area 0 at time t_0 the leaf area at time t is

151
$$A_i(t) = K_i\big(1 - \exp(-r(t - t_0))\big).$$

152 The data describe the distribution of the area of fallen leaves only. We presumed that in the absence

153 of herbivore browse, leaves do not fall until they have reached their maximum size. Thus the

154 distribution of K_i equates to the distribution of the area of fallen leaves collected from the two trees

155 which were unaffected by browsing (see Fig 1). Three candidate distributions (gamma, log-normal

156 and Weibull) were tested to find which one best fitted the data. The Weibull distribution did not

157 provide a good fit (KS test $p < 0.05$) whereas the other two distributions did (KS test $p > 0.05$).

158 All three distributions have two parameters so were compared using log-likelihood (Lognormal

159 $L = -2621$, Weibull $L = -2648$, Gamma $L = -2625$). The log-normal provided the best fit

160 with mean 543mm^2 and standard deviation 387.

161 *2.4 Predicting leaf area distribution – browsed*

162 To predict the area of browsed leaves requires a more detailed knowledge of the life history of

163 each leaf. There is a seasonal component to both leaf production and fall in kamahi. Leaf

164 production begins in late winter (Wardle and MacRae 1966) but immature leaves are observed as

165 late as late summer (Choinski Jr and Gould 2010). Similarly leaf fall is highest in late summer but

166 occurs year round (Forsyth and Parkes 2005). Although we recognise that seasonal variations are

167 important the data collected do not reflect this as they were collected over a relatively short period.

168 For these reasons we start with a model that assumes constant leaf production through the year,

169 and new leaves with area 0 appear regularly with rate γ.

170   Leaf longevity is governed by a senescence process (Chabot and Hicks 1982) so simple models

171   driven by a homogeneous Poisson process are inappropriate. Instead we use a heterogeneous

172   Poisson process where the mortality rate (i.e. the rate at which a leaf detaches from the plant) for

173   an individual leaf is zero for the first L_0 months and constant thereafter. Hence the life span of a

174   leaf, L, is a random variable described by a shifted exponential

175
$$P(L = t) = \begin{cases} 0 & \text{if } t < L_0 \\ \dfrac{1}{\alpha}\exp\left(-\dfrac{1}{\alpha}(t - L_0)\right) & \text{if } t \geq L_0 \end{cases}.$$

176   Choosing $L_0 = 35$ months and $\alpha = 5$ months gives an expected leaf life span of 40 months

177   (Richardson et al. 2010). By explicitly including leaf longevity in the model we allow for the

178   possibility of a single leaf being affected by multiple browse events before it falls. Note that to

179   comply with the previous assumption that a fallen unbrowsed leaf will be at its maximum size, the

180   growth rate r must produce fast growth relative to the lifespan L. In this case we choose $r = 0.05$

181   so a leaf reaches 90% of its maximum size after 45 days (Green and Jane 1983).

182   The model for possum browse assumes that browse events occur with mean rate $N\gamma$ per day, with

183   each browse event reducing the size of a single leaf. We presume that a browse event will decrease

184   the leaf's area by some constant fraction B, which is the relative possum bite size (i.e. possums

185   take smaller absolute-sized bites from smaller leaves). After a browse event a leaf has not only lost

186   part of its current area but has also reduced the maximum size it can reach by the same fraction B

187
$$K_i \rightarrow K_i B.$$

188   An alternative browse model where browse events reduced the leaf area by a constant amount as

189   opposed to a fraction was also tested. The constant bite-size model gave very poor results in

190   comparison to the relative bite size that is presented.

191   The parameters N and γ control the rate of possum browse events. At each time step (of length

192   one day) γ new leaves are produced (each with area zero) and there are λ leaf browse events where

193   λ is a Poisson deviate with mean $N\gamma$. Note that the model does not make predictions about the

194   total number of leaves on a plant but only the distribution of leaf areas. By defining the rate of

195   browse events in conjunction with the leaf production rate, the leaf production rate can be chosen

196   arbitrarily (i.e. we do not need exact information about species-specific leaf growth rates), though

197   it must be large enough for relative numerical accuracy. We used $\gamma = 20$ which allows N to be

198   estimated to within approximately 0.05. Other values of γ were tested and the results did not

199   change though the computational efficiency decreases as γ is increased.

200   To run the stochastic simulation we start with 10,000 leaves with maximum areas chosen from the

201   best-fit log-normal area distribution for unbrowsed leaves, and uniformly distributed initial areas

202   between zero and 10% of the maximum leaf area seen in the data ($\sim U(0,374)$). Test simulations

203   were run with different initial conditions and the results were not affected provided enough leaves

204   were included in the simulation. Final simulations were run to a steady state where the change in

205   distribution was within the expected stochastic noise limits. Note that the model predicts two

206   separate distributions: the distribution of areas of fallen leaves and the distribution of areas of

207   leaves that are still attached to the tree. Allowing the unknown parameters to be normally

208   distributed with a CV of up to 10% did not substantially change the results but did increase the

209   computation time significantly. The total number of leaves at the end of the simulation depended

210   on both the choice of γ and the initial number of leaves but this did not affect the leaf area

211 distributions. Table 2 shows the parameter values and their estimates. The two unknown

212 parameters B, the relative possum bite size, and N, the relative browse rate, are estimated by fitting

213 the model prediction of fallen leaf area distribution to the pooled browsed tree data (including both

214 browsed and unbrowsed leaves from those trees).

215 Initially, we assume that possums have no preference for any type of leaf and all leaves (including

216 those that have been previously browsed) have an equal probability of being browsed. Extensive

217 numerical searches confirmed a single well-defined minimum set of parameter values (see for

218 example Fig 2, left panel). A search of the 2-dimensional unknown parameter space (B and N)

219 around this minimum shows that the root mean square error (RMSE) between the modelled fallen

220 leaf area cumulative distribution and the pooled browsed-tree leaf area data is minimised at $B =$

221 0.59, and $N = 0.65$. Using definitions in Burnham et al. (2002) RMSE can be converted to an

222 AIC value. Figure 2 (left panel) shows the optimisation surface in parameter space which has a

223 well-defined minimum and the resulting best fit solution (right panel). If we assume a typical

224 kamahi tree of 20 cm DBH has approximately 4 kg of foliar mass from 30,000 leaves, with a

225 lifespan of approximately 2.5 years (~1000 days) this implies 30 new leaves per day. The best fit

226 parameter values estimate $20 (= 30 * 0.65)$ browse events per day. With a foraging strategy where

227 all leaves are equally likely to be browsed (i.e. some browse events will affect already browsed

228 leaves), approximately 52% of leaves on the plant will never be browsed during their life span,

229 34% will experience a single browse event at some point in their lifespan and the remaining leaves

230 will undergo two or more browse events (c.f. Poisson distribution with mean 0.65). The data show

231 that on a browsed tree almost 56% of fallen leaves were unbrowsed which is a reasonable match

232 to the model estimate in this case.

233 *2.5 Browsing strategies*

234 With a plausible model to predict browsed and unbrowsed fallen leaf area distributions we

235 examined the effect of various leaf browsing strategies with a view to predicting the strategy most

236 likely used by possums. We present the results for six potential leaf browsing strategies

237 1. No preference – every leaf has an equal probability of being browsed.

238 2. Prefer big leaves – leaf browse probability is proportional to leaf area.

239 3. Prefer old leaves – leaf browse probability is proportional to leaf age.

240 4. Prefer young leaves – leaf browse probability is inversely proportional to leaf age.

241 5. Prefer virgin leaves – initially as per the no preference model, but once a leaf has been

242   browsed the probability of it being re-browsed is reduced by 90%.

243 6. Prefer browsed leaves – initially as per the no preference model, but once a leaf has been

244   browsed the probability of it being re-browsed is increased by 90%.

245 Again a search of the two-dimensional unknown parameter space (N, B) was carried out for each

246 strategy to find the best fit values for N and B, which appeared at a clearly defined minimum.

247 Figure 3 shows the best fit fallen leaf area distribution for each strategy, corresponding parameter

248 values and RMSE. The strategy that gives the lowest RMSE is "Prefer virgin leaves" where a leaf

249 that has been browsed is much less likely to undergo a subsequent browse event. This strategy has

250 best fit parameter values $N = 0.47$, $B = 0.69$. The second best strategy "No preference" has a far

251 greater AIC value (Table 3, $\Delta AIC = 228$) implying that the virgin leaves strategy is significantly

252 more likely to have generated the data than any other strategy tested (Burnham et al. 2002). If this

253 were a simple Poisson process this would give an estimate that 62% of fallen leaves are unbrowsed.

254 However, as the leaf preference is now for unbrowsed leaves, i.e. not a memoryless Poisson

255 process, the proportion of unbrowsed fallen leaves must be taken from the simulation process. In

256   this case 52% of fallen leaves were unbrowsed, which, as with the no preference strategy, is a

257   reasonable estimate of the data value of 56%.

258   *2.6 Consequences for photosynthesis*

259   The model predictions thus far have focussed on the area distribution of fallen leaves as found in

260   the data. However, the consequences of leaf area distribution on tree health depend on the

261   distribution of the area of leaves that are still attached to the tree. This distribution is harder to

262   measure and hence we have no comparative data, but it is available as a model output. Figure 4

263   shows the model predicted leaf area distributions for leaves on an unbrowsed tree and a tree

264   browsed using the "prefer virgin leaves" strategy . The unbrowsed and browsed distributions of

265   the data for fallen leaf areas are shown for comparison. It is interesting to note that on an

266   unbrowsed tree the distribution of fallen leaf areas is similar to the distribution of leaf areas still

267   on the tree . However, for browsed trees the fallen leaf area distribution is not a good estimate of

268   the area of leaves on the tree.

269   As our model predicts not only the area distribution of leaves upon the tree but also the age

270   distribution, we can use this information to make qualitative predictions of the effect of herbivore

271   browsing on the carbon uptake of a tree. Kitajima et al. (1997) found that 6-8 month old leaves

272   had 33-65% of the photosynthetic capacity per unit leaf area of 1-2 month old leaves. Leaf

273   photosynthetic rate therefore declines with age (cf. Field et al. 1983) and, we presume, is

274   proportional to leaf area. There is some argument that photosynthetic capacity is better related to

275   leaf mass (Givnish 1988), but we would expect there to be a close relationship between leaf mass

276   and leaf area. Leaf position also plays a role as photosynthetic rates positively correlate with light

277   availability (Kitajima et al. 2002). Relative depth in the canopy increases with age (e.g. Kitajima

278   et al. 2002) therefore light availability will decrease. To capture these effects as simply as possible

279   we assume that the photosynthetic capacity of the ith individual leaf (Ψ_i) decreases exponentially

280   over the leaf's life time at a rate such that a one year old leaf has very little capacity in comparison

281   to a new leaf:

282    $$\Psi_i = LA \exp(-\alpha T),$$

283   where LA is leaf area, T is leaf age and $\alpha = 0.01$ results in a reduction in photosynthesis (per unit

284   leaf area) to 1% after a year. Applying this relationship to the predicted distribution of leaves upon

285   the tree (age and area) gives a value of Ψ_i for each individual leaf, and an overall value of $\Psi =$

286    $E(\Psi_i)$ for an entire tree.

287   We define Ψ_0 as the baseline photosynthetic capacity of an unbrowsed tree. This can be calculated

288   using the simulation results from an unbrowsed tree. We then calculate the expected relative

289   change in photosynthetic capacity as $\Delta\Psi = \Psi / \Psi_0$ for each browsing strategy at the best fit

290   parameter values found previously. A browsing preference for young leaves results in the biggest

291   expected drop in both leaf area and photosynthesis rate compared to the unbrowsed state (Figure

292   5 and Table 3). Conversely a preference for previously browsed leaves has only a minimal effect

293   on photosynthesis but results in a large drop in leaf area as these leaves have already lost most of

294   their photosynthetic capability before they are browsed.

295

296

297   **3.   Discussion**

298   It is possible to estimate long term carbon gain of a plant with knowledge of leaf longevity, the

299   effect of leaf area on photosynthetic capacity, and the leaf population on the plant (Kitajima et al.

300   1997; Kitajima et al. 2002). However, under herbivore browsing pressure, we have shown that it

301   is also necessary to understand how herbivores browse individual leaves within a single plant, as

302   this affects photosynthetic capacity of the whole plant via both leaf area distribution and leaf

303   longevity.

304   Our results suggest that possums may have a targeted browsing strategy on kamahi trees, with the

305   only model to predict observed browsing on fallen leaves better than the null 'no preference' model

306   being a preference for browsing virgin leaves, i.e. leaves that have not been browsed previously.

307   The virgin leaf preference gives credence to the idea that kamahi leaves that have been browsed

308   may undergo changes in chemical composition rendering them less palatable in future. This is a

309   common trait in many plants as a result of coevolution of plant and herbivore populations (Freeland

310   and Janzen 1974) and some plants are even able to produce chemical defences, or plant secondary

311   metabolites (PSMs), on short time scales and in response to browsing on their neighbours as well

312   as themselves (Appel and Cocroft 2014). However, even these short time scales are unlikely to be

313   as short as a single browse event. There may be other reasons for a preference for unbrowsed

314   leaves, for example the predicted size of a browse event reduced the leaf area by 70% so browsed

315   leaves may be too small to be worth eating or the remaining leaf area may be unpalatable. Whether

316   possums actually use this strategy could be tested using captive possums offered kamahi leaves,

317   or by monitoring the pattern of leaf removal from kamahi trees browsed by wild possums.

318   The results noted that on an unbrowsed tree the distribution of fallen leaf areas is similar to the

319   predicted distribution of leaf areas still on the tree. This suggests that for trees such as kamahi,

320   which have leaves that grow quickly to their final size, the leaf area distribution of fallen leaves

321 may serve as a useful proxy for the actual area distribution of leaves on an unbrowsed tree. This

322 theory could be tested with observations. Conversely, on browsed trees the leaf area distributions

323 for fallen leaves and on-tree leaves are different. This suggests that leaves are not browsed

324 predominantly at the start of their natural life span. Again this would need observational evidence

325 to be confirmed.

326 The effect of heterogeneous resources on herbivore populations has been well studied: specific

327 examples include to assess how differences in palatability between individual trees influences

328 foraging behaviour (Moore et al. 2010) and how nutritional variation in diet affects reproductive

329 fitness (DeGabriel et al. 2009) while Provenza et al. (2003) provide extensive insight into the

330 relationship between herbivore foraging, diet and PSMs. The vast majority of work in this area

331 considers herbivores as individuals but plants as patches (e.g. biomass or individual plants) (e.g.

332 DeMay et al. 2014; McArthur et al. 2014; Shaffer 2014) between which herbivores may move in

333 order to maximise energy or nutritional intake, or to minimize (or evolve resistance to) toxins

334 (Speed et al. 2015). However, the distribution of herbivory within plant individuals is not usually

335 considered (although see Lambdon and Hassall 2005). There is indeed wide variation between

336 individual kamahi trees' browsing history and inferred palatability (see Gormley et al. 2012;

337 Holland et al. 2013). Our study suggests that acknowledging variation among individuals is not

338 enough. If differences that drive foraging patterns occur within tree canopies, targeted browsing

339 may have a significant effect on the ability of the individual tree to photosynthesize, with knock-

340 on effects to individual and population level tree mortality. For example, our models demonstrate

341 that a preference for browsing young leaves substantially reduces whole-tree photosynthetic

342 capacity relative to a preference for old leaves. There is little published research on differences in

343 palatability within individual tree canopies, for kamahi or any other species. Nonetheless, it would

344   be worth including as part of a sensitivity analysis where models must make an assumption about

345   how herbivore browsing removes leaf matter from a plant.

346   The second best fitting models were for no browsing preference, and for browsing preference for

347   young and old leaves, which all had significantly higher AIC values (Table 3). The effect of these

348   three browsing strategies on photosynthesis rates is very similar, i.e. it reduces photosynthesis by

349   around 3 or 4 %. Except for the strategy to browse on young leaves, this has a much more

350   substantial effect and reduces photosynthesis by almost 25%. This is due to the photosynthesis rate

351   decreasing strongly with leaf age.

352   Like any model ours is a simplification of the real world. Possibly the greatest limitation here is

353   that browsing might cause leaves to fall off sooner as intimated by Palacio et al. (2013). This

354   limitation could be tested with a long-term feeding study. However, as photosynthetic capacity in

355   the model drops so steeply with age we believe including this effect would make very little

356   difference to the overall photosynthesis level though it could feasibly affect leaf area distributions.

357   Another limitation is that there is some evidence that that young and old leaves are less

358   photosynthetically efficient than mature leaves (Shirke 2001). This is not included in the model

359   specifically, but it is implicit that young leaves are smaller and old leaves are larger, so the

360   photosynthetic capacity of a whole leaf will initially rise as the leaf grows before falling due to the

361   loss of synthetic capacity. Hence, this effect is captured albeit not explicitly. Given the apparent

362   preference of possums for virgin leaves shown in our results, an extension of the model could also

363   include a spatial element, with a preference for or against leaves close to those that have already

364   been browsed. This would allow for the likely tendency of herbivores to remain stationary for a

365   time while browsing leaves within reach, but also incorporate the potential for leaves closer to the

366   most recent damage to respond by producing chemical defenses (cf. Appel and Cocroft 2014).

367 A potential flaw in this study is the assumption that fallen leaves provide an adequate

368 representation of leaves upon the tree, in particular fallen leaves from trees that have been browsed

369 by possums. In some plants, for example *Schefflera digitata* and some *Pseudopanax* species,

370 possums tend to eat the petiole and very little of the leaf itself (Nugent et al 2000). For these species

371 a browsing event results in a fallen leaf. However, examples of browsed kamahi leaves in the

372 Foliar Browse Index field manual (Department of Conservation 2014) indicate that possums eat

373 from the leaf tip downwards, but not the stem or central area. In this case the leaf remains on the

374 tree and will fall in a more natural way. It would be unlikely there was no detritus even from a leaf

375 that has been almost entirely eaten. To fully confirm this assumption, captive feeding studies and

376 more field observations would be useful.

377 Clearly, the within-plant browsing strategy of a herbivore can change the ability of the plant to

378 survive, if not completely then indirectly by reducing the plant's photosynthetic capacity and hence

379 resilience to other disturbances. This is of concern for maintaining biodiversity and potentially for

380 carbon assimilation mediating global warming, and underlines the point that a simple index of leaf

381 area cannot be used alone to predict resilience at an individual plant, community or ecosystem

382 level.

383

384 **Data Availability**

385 Upon publication data from this study will be available via the Landcare Research data archive.

386

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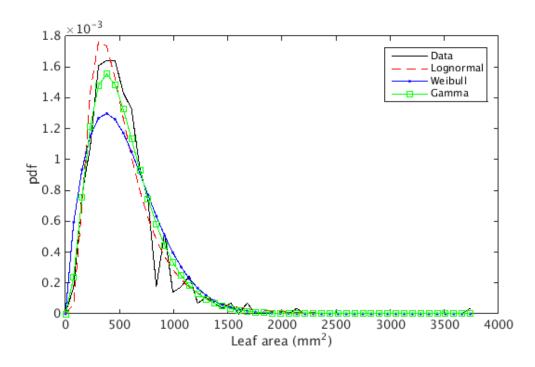486   stoichiometry PLoS ONE 8:e60360

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490   Figure 1: A lognormal distribution (red dashed line) provides the best fit to the fallen leaf area

491   distribution from unbrowsed trees (black solid line).
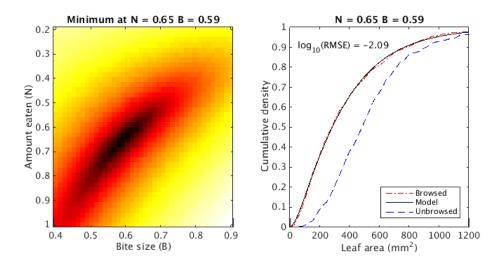
Figure 2: The best fit solution using the "eat anything" strategy. The optimisation surface (left panel) has a well-defined minimum (dark area) at the best fit solution. The corresponding best fit fallen leaf area distribution (right panel, solid line) is a good fit to the browsed tree leaf area data (dot-dash line). The data from unbrowsed trees are shown for comparison (dash line).
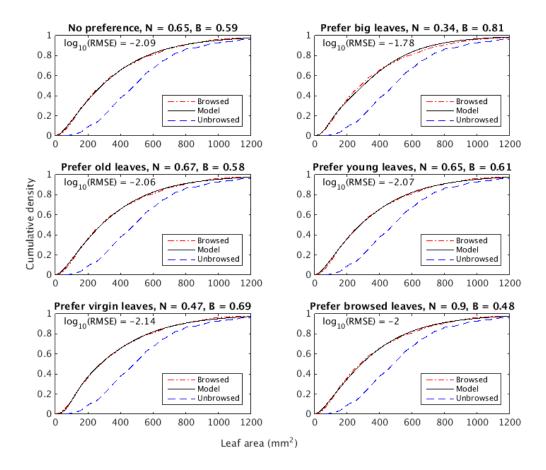
Figure 3: The best fit solutions for the six browsing strategies. Each panel shows the cumulative density function for the browsed tree fallen leaf area distribution data (dot-dash line), the best fit solution for that browsing strategy (solid line) and the data from unbrowsed trees (dash line) for comparison. Also given are the best fit parameter values B and N and the root-mean-square-error (RMSE) for the solution. The strategy with the best fit, i.e. lowest RMSE, is the preference for virgin (unbrowsed) leaves.
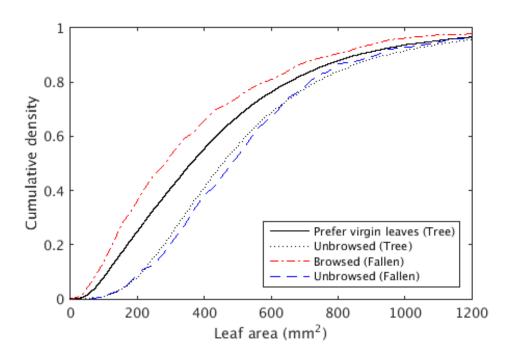
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505   Figure 4: The predicted distributions of the area of leaves remaining on a tree. The black dotted

506   line shows the leaf area distribution for an unbrowsed tree. The solid black line shows the

507   distribution of leaf areas on a browsed tree where the preference is for virgin (unbrowsed) leaves.

508   The data distributions for area of fallen leaves (red, dot-dash browsed trees, blue dash unbrowsed
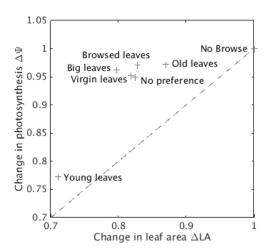
509   trees) are shown for comparison.

Figure 5: A comparison of the effect of the different browsing strategies on leaf area and photosynthesis. The 1:1 line (grey dashes) indicates a proportional reduction of photosynthesis and leaf area. Each strategy is simulated at the best fit parameter values particular to that strategy.

Tree	Number of leaves	Fraction Browsed	Leaf Areas Mean (std) (mm^2)	
			Browsed	Unbrowsed
T15	233	0.39	217 (165)	550 (360)
T19	244	0.45	173 (116)	520 (291)
T19B	200	0.40	208 (134)	621 (311)
T20C	*88*	*0.16*	*218 (150)*	*447 (218)*
T20T	*176*	*0.14*	*194 (174)*	*555 (335)*
T22	250	0.51	148 (99)	355 (235)
T23	*164*	*0.04*	*302 (142)*	*572 (380)*
All	1355	0.33	185 (134)	524 (327)
All Browsed trees (T15, T19, T19B, T22)	927	0.44	182 (130)	512 (318)
All Unbrowsed trees (T20T, T20C, T23)	*428*	*0.10*	*216 (163)*	*540 (337)*

514

515   Table 1: Summary tree statistics. Rows in italics represent trees designated as unbrowsed.

Parameter	Notation	Source	Value	Notes
Leaf growth rate	r	Green 1983	0.05 day^{-1}	Leaves grow to 90% of full size in 45 days.
Relative browse rate	N	Estimated from fitting to browsed data.	~ 0.35 – 0.9	Defined as a multiple of the production rate. Changes with browse model.
Mean maximum leaf area	$E(K_i)$	Estimated from fitting to unbrowsed data.	543 mm^2	
Standard deviation of maximum leaf area	$\sigma(K_i)$	Estimated from fitting to unbrowsed data.	387 mm^2	
Relative possum bite size	B	Estimated from fitting to browsed data.	~ 0.5 – 0.8	Changes with browse model.
Minimum leaf longevity	L_0	Richardson et al. (2010)	1060 days (35 months)	
Expected leaf lifespan	$L_0 + \alpha$	Richardson et al. (2010)	1220 days (40 months)	
Leaf production rate	γ	For numerical purposes only.	10	

516

517   Table 2: Model parameters used to explore the effect of possum browsing on the photosynthetic

518   capability of kamahi.

Strategy	N	B	$\log_{10}$ RMSE	ΔAIC	Fraction of leaves unbrowsed	$E(LA)$	ΔLA	ΔΨ
No Browse	0	0	--	--	0	534.6	1	1
No preference	0.65	0.59	-2.09	228	0.49	438.0	0.824	0.950
Prefer big leaves	0.34	0.81	-1.78	1549	0.52	432.2	0.798	0.963
Prefer old leaves	0.67	0.58	-2.06	345	0.67	469.0	0.870	0.972
Prefer young leaves	0.65	0.61	-2.07	292	0.52	380.9	0.711	0.772
Prefer virgin leaves	0.47	0.70	-2.14	0	0.52	434.5	0.818	0.951
Prefer browsed leaves	0.90	0.48	-2.00	598	0.55	443.7	0.827	0.971

519

520 Table 3: Model specific parameter values, best fit root-mean-square-error and corresponding

521 change in AIC for each browsing strategy. The effect of different browsing strategies on the

522 expected area of an individual leaf and the expected relative photosynthesis.