Determinants of seasonal changes in availability of food patches for elephants (*Loxodonta africana*) in a semi-arid African Savanna

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Loss of biodiversity caused by impact of elephants (*Loxodonta africana*) on African woodlands may require a management response, but any action should be based on an understanding of why elephants choose to utilise trees destructively. Comprehension of elephant feeding behaviour requires consideration of the relative value of the plant groups they may potentially consume. Profitability of available food is partly determined by the time to locate a food patch and, therefore, as a foundation for understanding the influence of food availability on diet selection, key controls on the density of grass, forb, and browse patches were investigated across space and time in a semi-arid African savanna. Density of food patches changed seasonally because plant life-forms required different volumes of soil water to produce green forage; and woody plants and forbs responded to long-term changes in soil moisture, while grasses responded to short-term moisture pulses. Soil texture, structure of woody vegetation and fire added further complexity by altering the soil water thresholds required for production of green forage. Interpolating between regularly-timed, ground-based measurements of food density by using modelled soil water as the predictor in regression equations may be a feasible method of quantifying food available to elephants in complex savanna environments.

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2 **a*fricana*) in a semi-arid African Savanna**

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23   **ABSTRACT**

24   Loss of biodiversity caused by impact of elephants (*Loxodonta africana*) on African woodlands

25   may require a management response, but any action should be based on an understanding of why

26   elephants choose to utilise trees destructively. Comprehension of elephant feeding behaviour

27   requires consideration of the relative value of the plant groups they may potentially consume.

28   Profitability of available food is partly determined by the time to locate a food patch and,

29   therefore, as a foundation for understanding the influence of food availability on diet selection,

30   key controls on the density of grass, forb, and browse patches were investigated across space and

31   time in a semi-arid African savanna. Density of food patches changed seasonally because plant

32   life-forms required different volumes of soil water to produce green forage; and woody plants

33   and forbs responded to long-term changes in soil moisture, while grasses responded to short-term

34   moisture pulses. Soil texture, structure of woody vegetation and fire added further complexity by

35   altering the soil water thresholds required for production of green forage. Interpolating between

36   regularly-timed, ground-based measurements of food density by using modelled soil water as the

37   predictor in regression equations may be a feasible method of quantifying food available to

38   elephants in complex savanna environments.

INTRODUCTION

African savannas are characterised by a predominance of woody plants and grasses (Huntley 1982), but they also support a richness of herbaceous dicotyledons (forbs). Savanna elephants (*Loxodonta africana*) harvest food from all these plant types (Barnes 1982; Field 1971; Kabigumila 1993), but their conspicuous impact on woody plants has the greatest potential to cause long-term vegetation change (Lamprey et al. 1967; Laws 1970b; Leuthold 1977). Over time, this behaviour may simplify the structure and composition of woodlands (O'Connor & Page 2014), jeopardising the persistence of impacted species (Lombard et al. 2001; O'Connor et al. 2007) and the biota that are dependent on the original complexity (Cumming et al. 1997; Herremans 1995; Kerley & Landman 2006). Extensive impact on woodlands by elephants was first noticed in the 1930s (Laws 1970a) and since then many wooded areas in Africa have been converted to shrubland or grassland (Spinage 1994). The threat of local extirpation of some impacted woody species (O'Connor et al. 2007) begs a management response, but any action should be founded upon an understanding of why elephants choose to use woody plants in a destructive manner.

Comprehension of elephant feeding patterns requires consideration of the relative value of the plant groups they may potentially consume. Savanna elephants may utilise grasses, including roots (de Boer et al. 2000; de Longh et al. 2004; Wyatt & Eltringham 1974), forbs (Barnes 1982; Field 1971), and all components of woody plants (Field 1971; Guy 1976). They adjust their diet seasonally depending on food availability (Cerling et al. 2004; Owen-Smith 1988). During the wet summer months large amounts of grass and forbs are eaten, but when these food types dry out in winter, elephants consume an increasing amount of leaves and twigs from woody plants, followed by bark and roots as leaves are shed.

67   Impact on woody vegetation by elephants is greatest when their feeding involves

68   breaking branches, debarking stems, or toppling, pollarding or uprooting whole plants, and less

69   when trunkloads of leaves are stripped without breaking branches (Clegg 2010). When diet is

70   composed solely of grass and forbs there is no damage to woody plants. Prediction of diet is

71   therefore a crucial step towards forecasting impact on woody vegetation.

72   Large mammalian herbivores exercise a hierarchy of decisions, from patch to landscape,

73   when deciding where to forage and what to eat (Senft et al. 1987), which necessitates a

74   landscape-level assessment of the relative availability of forage types. Elephants may forage for

75   18 hours a day to meet their needs (Wyatt & Eltringham 1974), thus searching time for food

76   patches is critical. Patch density of a forage type therefore provides a functional measure of food

77   availability because the distance between patches determines the searching time to locate food,

78   which is a constraint to intake (Fortin et al. 2015). Food availability therefore differs among

79   vegetation types in relation to differences in food-patch densities. Food availability also varies

80   seasonally over an annual cycle. Accordingly, environmental influences on the leaf phenology of

81   forage types were examined.

82   Short-term changes in soil water govern grass growth but are apparently less important

83   for leaf flush and drop of woody plants, for which levels of internally stored water (Borchert

84   1994; Chapotin et al. 2006; Kulmatiski et al. 2010), photoperiod and temperature play an

85   important role (Archibald & Scholes 2007; Choler et al. 2010). However, evidence for an

86   influence of soil water on the phenology of woody plants includes early leaf drop in response to

87   low rainfall in the preceding wet season (Borchert et al. 2002), woody plants that receive early

88   rain flush first (Borchert et al. 2002; Clegg 2010), and that internally stored water has to be

89   recharged from the soil store. Environmental influences on the growth of forbs in African

90   savannas are unstudied.

91   The amount of soil water that is available for uptake by plants is a function of rainfall

92   pattern, soil storage capacity as influenced by profile depth and soil texture, and evapo-

93   transpirative demand (Ritchie 1981). Clay-rich soils store more water at field capacity than sandy

94   soils but this is partly offset by clay soils holding a greater proportion of water more tightly

95   within the pores (Foth 1990). A tendency for higher water-use efficiency (WUE) of tropical C_4

96   grasses relative to tropical C_3 forbs and woody plants (Ehleringer & Monson 1993) may lead to

97   differences in leaf phenology between these plant groups. Inter-plant competition for soil

98   moisture influences the duration of leaf carriage in savanna (Smit 2001).

99   Available nutrients and fire also influence food availability. The influence of soil

100 nutrients corresponds directly with that of soil texture (Foth 1990), an effect that cannot be

101 isolated from the influence of soil texture on soil water availability. That fire has an immediate

102 effect on food availability is obvious, but subsequent effects on plant phenology and available

103 forage are poorly understood.

104 The aim of this study was to investigate key determinants of food available to elephants

105 across space (vegetation types) and time (annual cycle) as a foundation for understanding forage

106 selection. The following specific questions were addressed. (1) Can plant-available water in the

107 soil be used to predict the availability of the main food types? (2) Do different food types differ

108 in their annual pattern of availability? (3) Is the relation between food availability and soil water

109 influenced by soil texture? (4) Does soil texture influence the effect of fire on food availability?

110 (5) Does the structure of woody vegetation influence the annual phenological pattern?

111   The study formed the foundation of a landscape scale analysis of elephant foraging

112   behaviour that will be reported elsewhere. The findings are relevant to savanna elephants

113   throughout Africa, and are also applicable to other herbivores that inhabit savannas globally. The

114   results concerning the relationship between soil water and the leaf phenology of the plant

115   growth-forms are novel and, although particular emphasis was given to foraging elephants, the

116   findings also make a contribution to the general theory of savanna function.

117

118   **MATERIALS & METHODS**

119   The study was conducted in the semi-arid savanna of Malilangwe Wildlife Reserve in south-

120   eastern Zimbabwe (20°58′–21°15′ S, 31°47′–32°01′ E). The reserve has a hot wet season from

121   November to March, a cool dry season from March to August, and a hot dry season from

122   September to October. Mean annual rainfall is 557 mm (n = 64; CV = 34.2%), with

123   approximately 84 % falling in the hot wet season. Rainfall during the year under study was 716

124   mm. The average minimum and maximum monthly temperatures range from 13.4 °C (July) to

125   23.7 °C (December), and 23.2 °C (June) to 33.9 °C (November) respectively (Clegg 2010). Frost

126   is rare. Thirty-eight vegetation types, from open grassland to dry deciduous forest, have been

127   identified on seven geological types, with soils ranging from 90 % sand to 41 % clay (Clegg &

128   O'Connor 2012). Fire has been used as a tool for rangeland management since 1994.

129   Management burns were conducted in October 2001, 5 months prior to the start of the study

130   period. Permission to conduct the study was granted by the Director of The Malilangwe Trust.

131   The study focused on grass, forbs, and leaves and bark from woody plants because these

132   constitute the bulk of an elephant's diet (Barnes 1982; de Boer et al. 2000; Field 1971; Guy

133   1976). Maps of the areas burnt during the previous year and areas that experienced early woody

134   leaf flush (identified from an October 2002 landsat 7 ETM+ image using a Normalized

135   Vegetation Index) were combined with a fine-scale vegetation map (Clegg & O'Connor 2012) to

136   create a spatial framework for sampling with 65 landscape units. Within each unit, the

137   relationship between the density of grass, forb, or leaf patches and soil water was investigated

138   between March 2002 and March 2003. The density of bark patches, whose availability was

139   considered constant for a year, was estimated for each landscape unit. Sampling was undertaken

140   between November 2001 and July 2003 at approximately three-month intervals. On each

141   occasion, five sample points were positioned in each landscape unit using a stratified random

142   strategy and located in the field using a GPS. Plant nomenclature follows Mapaura and

143   Timberlake (2004).

144

145   **Estimation of the density of food patches**

146   *Grass and forbs*

147   An individual grass tuft or forb plant would constitute a patch if it was growing in isolation, but

148   at high plant densities a trunkload would be made up of material from multiple plants. A 1 m^2

149   area was therefore arbitrarily defined as the patch size for grasses and forbs.

150   The nutritional quality of savanna grasses varies over the annual cycle (Buxton &

151   Redfearn 1997; Lyons et al. 1996). Elephants avoid eating senescent forage, so a plant can only

152   be considered a patch if it offers a sufficient ratio of green to dry material (Clegg 2010; Loarie et

153   al. 2009). Accordingly, the density of patches with green grass only, or a mixture of green and

154   dry grass were estimated. In support of recognising two grass patch types, elephants require

155   twice the time to harvest, clean by shaking, chew and ingest a trunkload of mixed grass than one

156   of green grass (Clegg & O'Connor 2016). When most forbs senesce their leaves are abscised and

157   their stems wither, therefore only the density of patches with green forbs was estimated.

158   At each sampling point, 25 1 m^2 quadrats were sampled along a 50 m tape. The cover of

159   green grass, dry grass and green forbs was estimated in each quadrat using an eight point scale (0

160   %; 1 %; 2-10 %; 11-25 %; 26-50 %; 51-75 %; 76-95 %; 96-100 %). A quadrat was assigned to a

161   patch type using the following criteria: green grass = green grass cover $\geq$ 1 %, $\geq$ 90 % of total

162   grass biomass green, and total grass cover $\geq$ 1 %; mixed green and dry grass $\leq$ 90 % and $\geq$ 10 %

163   of total grass biomass green; green forb = green forb cover $\geq$ 2 %. The density of patches (m^{-2})

164   with green grass, mixed green and dry grass, and green forbs was calculated per site.

165

166   **Leaves from woody plants**

167   Individual shrubs and trees were considered patches. Elephants avoid eating senescent leaves

168   (Clegg 2010) and for this reason only woody plants with > 25 % of their canopies with green leaf

169   were used to estimate patch density. Below this level it becomes difficult for elephants to harvest

170   a trunkload that is comprised solely of green leaves (Clegg 2010). Elephants also avoid very

171   young, red leaves of *Colophospermum mopane* possibly because of a high concentration of

172   polyphenols and resins (Styles & Skinner 1997), and therefore mopane plants with this leaf type

173   were excluded. Other species that were also excluded because they were avoided by elephants

174   were *Courbonia glauca*, *Euclea divinorum*, *Salvadora persica*, and *Thilachium africanum*.

175   The density of woody plants with green leaf was estimated in the following way. At each

176   site the nearest woody plant was assessed and the following recorded: (1) species, (2) shrub ($\leq$ 3

177   m) or tree (> 3 m), (3) per cent of canopy volume with new leaves, and (4) per cent of canopy

178 volume with mature green leaves, using the eight-point scale. Then the next nearest individual

179 was assessed in the same way. This process was repeated until five trees and five shrubs of each

180 species had been sampled. To reduce sampling, only species with a canopy volume > 25 and >

181 15 m³ha⁻¹ were sampled for trees and shrubs respectively (calculation of volume given in Clegg

182 & O'Connor (2012)). For each species of tree and shrub, an average (n = 25) estimate was

183 derived for each date. To improve the temporal resolution for each shrub and tree species, data

184 were pooled across landscape units with similar topo-edaphic conditions. The per cent canopy

185 volume with new green leaf (V_{new}) and mature green leaf (V_{mature}) was estimated, on a daily basis,

186 for each species of shrub and tree in a landscape unit by interpolating between data points using

187 a smoothing spline regression (KyensLab 2002). The total per cent canopy volume with green

188 leaf was calculated, for each shrub and tree species in a landscape unit, as:

189
$$V_{total} = V_{new} + V_{mature}$$

190   Bull elephants are taller than cows and are therefore capable of stripping leaves from a

191 greater height. It was determined from field measurements that bulls and cows (n = 200 each)

192 can feed from a maximum height of just over 6 and 4 m, respectively (see Clegg 2010 for

193 details). The density of woody plants with green leaf available to bulls (D_{bull}) was calculated on a

194 daily basis, for each vegetation unit, as:

195
$$D_{bull} = \sum_{i=1}^{n} d_{i,tree,bull}\, p_{i,tree} + \sum_{i=1}^{n} d_{i,shrub}\, p_{i,shrub} \; ,$$

196 where $d_{i,tree,bull}$ is the density of the ith tree species with canopy volume below 6 m (see (2012) for

197 how density of each species was calculated), $p_{i,tree}$ is the Boolean probability (0 or 1) that

198 $V_{total,i,tree} > 25$ %, $d_{i,shrub}$ is the density of the ith shrub species and $p_{i,shrub}$ is the Boolean probability

199   (0 or 1) that $V_{total,i,shrub} > 25$ %. The calculation was the same for cows except $d_{i,tree,cow}$ was based

200   on trees and shrubs with canopy volume below 4 m.

201

202   **Bark**

203   Individual shrubs and trees of species whose branches were commonly chewed for bark were

204   considered patches. The density of patches with bark available to bulls, in each landscape unit,

205   was calculated as:

206
$$D_{bull} = \sum_{i=1}^{n} d_{i,shrub} + \sum_{i=1}^{n} d_{i,tree,bull} \,,$$

207   where $d_{i,shrub}$ is the density of the ith shrub species utilised for bark and $d_{i,tree,bull}$ is the density of

208   the ith tree species that was utilised for bark with canopy below 6 m. The calculation was the

209   same for cows except $d_{i,tree}$ was based on the density of trees with canopy below 4 m.

210

211   **Estimation of soil water**

212   A simple model of soil water that estimated water in the upper soil layer and ignored the process

213   of deep drainage was considered adequate. Daily moisture in the top 30 cm of soil was extracted

214   for each sample site from maps generated by linking a model of soil moisture balance (Hobbs et

215   al. 1994) to a geographic information system. A constant profile depth of 30 cm was used

216   because 50 % of the study area had soil ≤ 30 cm deep (Clegg & O'Connor 2012) and in savannas

217   most active roots of woody and herbaceous plants occur within this depth (Kulmatiski et al.

218   2010). Daily moisture loss from the 0-30 cm profile was modelled using a negative exponential

219 function that was dependent on available soil moisture and driven by daily rainfall and potential

220 evaporation:

221
$$M_t = (M_{t-1} + R_t) \times \exp^{-k.PE},$$

222 where M is the soil moisture fraction, R is the rainfall fraction, PE is potential evaporation (mm)

223 and k is an evaporative constant. M was scaled between 0 and 1, and was calculated as:

224
$$M = \frac{m_{soil} - m_{min}}{m_{FC} - m_{min}}$$

225 where m_{soil} is the moisture (mm) in the 0 - 30 cm profile, m_{min} is the minimum air dried moisture

226 (mm), and m_{FC} is the field capacity of the 0 - 30 cm profile. If the soil profile was less than 30

227 cm, m_{FC} was calculated for the actual soil depth. Minimum air dried moisture was calculated for

228 each vegetation unit from per cent silt and clay (Clegg & O'Connor 2012) using the equation of

229 Bennie et al. (1988). Field capacity was calculated using the equation of Hutson (1984). R was

230 scaled between 0 and 1 and was calculated by dividing daily rainfall (mm) by $m_{FC} - m_{min}$.

231 Rainfall data were collected from 14 gauges within and 12 gauges outside the study area. A

232 rainfall surface was generated for each rainfall event by interpolating between gauges using a

233 triangular irregular network (Eastman 2003). Following Hobbs et al. (1994) the evaporative

234 constant k was derived from m_{min}. Daily PE data were collected from two class A evaporation

235 pans that were located at the Zimbabwe Sugar Association, 27 km to the west of Malilangwe

236 headquarters.

237

238 **Relationship between density of food patches and soil water**

239 *Curve fitting*

240 For each landscape unit, the average density of food patches (D) on a particular date was plotted

241 against average soil moisture for the previous 5, 10, 15, 20, 25, 30, 45, 60, 75, 90, 105, 120, 135

242 and 150 days. The relationship for green grass and forbs could be described by a monotonically

243 increasing sigmoidal curve, with lower and upper asymptotes 0 and 1 respectively (Fig 1). Green

244 leaves from woody plants showed a similar relationship, but the data for each land unit required

245 standardisation to achieve asymptotes of 0 and 1. Consequently, for these forage types the

246 logistic equation:

247
$$D = \frac{1}{1 + \exp^{a-bM}},$$

248 where a and b are constants, was fitted to the data from each land unit using Systat 9 (SPSS

249 1998).

250 The relationship between the density of mixed grass patches and soil moisture was

251 initially a monotonically increasing sigmoidal curve that was followed at higher levels of soil

252 moisture by a monotonically decreasing sigmoidal curve (Fig 1). Consequently, the following

253 model was fitted to the data for density of mixed grass patches:

254
$$D = \left(\frac{1}{1 + \exp^{a-bM}} \right) \times \left(\frac{1}{1 + \exp^{c-dM}} \right),$$

255 where a, b, c and d are constants.

256 For each landscape unit, the curve from the predictor variable with the best fit was chosen

257 to represent the relationship between the density of the food type and soil water.

258

259   **Soil water thresholds**

260   The sigmoidal relationship between the density of forage patches and soil water can be divided

261   into lag, exponential and plateau phases. The soil water thresholds marking the start and end

262   points of these phases can be represented by the points of maximum curvature on the sigmoidal

263   curves (Fig 1). The first threshold (M_1) represents the point at which availability begins to

264   increase rapidly (green-up) and the second (M_2) the point when availability nears its maximum

265   (plateau). Mixed grass had two additional thresholds, M_3 and M_4, for the declining phase of its

266   relationship with soil water when mixed grass is converted into green grass. For each landscape

267   unit, these thresholds were determined for the food types by calculating the local maxima of

268   curvature.

269

270   **Influence of soil texture, plant life-form and fire on food availability**

271   Moderated multiple regression (Aguinis 2004) was used to determine whether the linear

272   relationship between soil water threshold and soil clay content was dependent on the value of a

273   dichotomous moderator variable, which was either dummy coded plant life-form (e.g., green

274   grass = 1, green forbs = 0) or dummy coded fire (burnt = 1, unburnt = 0). Separate analyses were

275   conducted for green-up and plateau thresholds and for each paired combination of plant life-

276   form. We used the standard method of determining whether a moderating effect existed, which

277   entailed the addition of a linear interaction term in the multiple regression model,

278    $$Y = b_0 + b_1 X + b_2 Z + b_3 XZ \,,$$

279   where Y is the soil water threshold (mm), X is soil clay content (%) and Z is the dichotomous

280   moderator variable (either plant life-form or fire). A significant interaction term (b_3) indicates

281   that the association between X and Y varied as a function of Z, but does not specify the form of

282   the interaction. Consequently, a significant ($P < 0.05$) interaction was probed further by using the

283   Johnson-Neyman technique (Kowalski et al. 1994) to calculate the regions along the textural

284   gradient where the moderating factor had a significant effect. The regions of significance (RoS)

285   were calculated using the online application: Probing Interactions in Moderated Multiple

286   Regression and Differential Susceptibility Research

287   (http://www.yourpersonality.net/interaction/) that was designed by R. C. Fraley as a supplement

288   to Roisman *et al.* (2012).

289   Tests of the assumptions of moderated regression were conducted following Lund &

290   Lund (2013). Outliers (deleted studentized residuals $> \pm 2.0$) were removed only if there was an

291   obvious ecological reason (e.g., soil water estimates were inaccurate because of a steep slope or

292   proximity to a perennial river), and if removal had a significant effect on the regression results.

293

294   **Effect of soil texture and structure of woody vegetation on retention of green leaf patches**

295   The maximum density of woody green leaf patches (when all woody plant canopies have > 25 %

296   green leaf) for each landscape unit was determined. The predictable seasonal decline in patch

297   density due to leaf drop as the dry season progresses and increase with leaf flush following

298   commencement of rains allowed per cent patch retention to be calculated for each unburnt

299   landscape unit by dividing the sum of daily patch density estimates by the maximum possible

300   patch density over the annual cycle. The relationship between per cent patch retention, soil

301   texture and woody canopy volume was then explored using the multiple non-linear regression

302   routine of Labfit (Silva & Silva 2011). Labfit searches a library of 280 functions and outputs the

303   one that best fits the data. Six landscape units were removed from the analysis because they were

304   affected by water-related environmental anomalies.

305

RESULTS

306

307   **Temporal pattern of soil water**

308   Soil water increased sharply when it rained and declined more slowly as soil dried (Fig 2). As

309   expected, soil water was highest in the wet season and clay soils stored more water per unit depth

310   than sandy ones. Time series constructed using short time lags had large, frequent fluctuations,

311   while longer lags resulted in smoother profiles.

312

313   **Relationship between density of food patches and soil water**

314   Density of herbaceous forage patches was successfully modelled from soil water using the

315   sigmoidal functions (Fig 3). Average R^2_{adj} values (± SD) were 0.92 ± 0.14, 0.90 ± 0.11, and 0.89

316   ± 0.11 for green grass, mixed grass and green forbs respectively. Density of woody plants with

317   green leaves was successfully modelled (average $R^2_{adj} = 0.90 ± 0.08$) during leaf drop and flush

318   (Fig 3) but not during the period prior to leaf drop because at this time woody plants had more

319   green leaf than predicted by soil water (Fig 4).

320   Plant life-forms responded to changes in soil water over different time scales. Grass

321   responded to short-term fluctuations, with a best predictor average (± 95 % confidence interval)

322   of 29.7 ± 5.5 and 29.9 ± 5.6 days for green and mixed grass respectively. Forbs responded to

323   medium-term fluctuations, with a best predictor average of 40.6 ± 5.9 days, and leaves from

324   woody plants to long-term fluctuations, with an average of 99.2 ± 8.0 days.

325

Influence of soil texture and food type on soil water thresholds

327   For all food types, the volume of soil water required to start green-up and reach maximum patch

328   density increased linearly with clay content (P < 0.01) (Fig 5). Thresholds for woody green

329   leaves and mixed grass were well below the field capacity of the soil, the gap between field

330   capacity and threshold increasing with clay content. In contrast, plateau thresholds for green

331   grass were almost at field capacity and were above field capacity for green forbs on clay-rich

332   substrates, indicating that the assumed plateau density of 1 patch m^{-2} was too high for green

333   forbs.

334   Woody plants required significantly (P < 0.05) less soil water to start greening up and

335   reach maximum patch density than green grass and forbs (Tables 1 and 2, Figs 6 and 7). Green

336   grass and forbs had the same green-up thresholds (P > 0.05), but plateau thresholds were higher

337   for forbs on soils with greater than 14.2 % clay. Thresholds for mixed grass were generally

338   similar to woody plants, but differences occurred on some soil types.

339

Temporal pattern of food availability

341   Availability of green and mixed grass was characterised by large, short-term fluctuations (Fig 8).

342   In contrast, green forbs and woody green leaves had smooth temporal profiles, giving the

343   impression that availability was unrelated to soil water. Mixed grass had lower green-up and

344   plateau thresholds than green grass and was therefore more consistently available over the annual

345   cycle. Green grass only became plentiful for a short period during the late rainy season when its

346   thresholds were exceeded.

347   Maximum patch density was higher for herbaceous food types than for woody green

348   leaves and bark. The plateau threshold was not reached for forbs. Food was less available on

349   clay-rich substrates than on sandy ones, but considering the higher growth thresholds on clay

350   soils, the difference was lower than expected.

351

352   **Effect of fire on food availability**

353   The relationship between soil water and density of woody green leaf patches was not affected by

354   fire, but green-up and plateau thresholds of green grass and green forbs, and the M_3 and M_4

355   thresholds of mixed grass were affected (Table 2). Fire lowered ($P < 0.05$) the thresholds for

356   these food types on clay-rich soils but not on sandy ones (Fig 9). This meant that on clay-rich

357   substrates, density of green grass or green forb patches was higher on burnt than unburnt areas

358   for a given volume of soil water, and that mixed grass was converted to green grass at lower

359   levels of soil water on burnt compared to unburnt sites (Fig 10).

360

361   **Effect of soil texture and woody vegetation structure on retention of green leaf patches**

362   The effect of soil clay content and woody canopy volume on retention of green leaf patches was

363   best represented ($P < 0.005$, $R^2_{adj} = 0.379$) by the power function

364
$$Y = a * \left(\frac{X_1}{X_2}\right)^b,$$

365   where Y is per cent patch retention, X_1 is per cent clay content of the top 30 cm of soil, X_2 is

366   woody canopy volume (m³ ha⁻¹) and a and b are constants. Estimates of a and b were 106.9 and

367   0.059 respectively. Patch retention increased as clay content increased and woody canopy

368   volume decreased (Fig 11).

369

370   **DISCUSSION**

371   **Determinants of seasonal changes in food availability**

372   Savannas have been intensively studied (Sankaran et al. 2005), but drivers of forage production

373   in these environments are still only superficially understood. In this study, food availability for

374   elephants changed seasonally primarily because grasses, forbs and woody plants required

375   different volumes of soil water for development and maintenance of green foliage, and they

376   responded to fluctuations in soil moisture over different time scales. Soil texture, the structure of

377   woody vegetation and fire added further complexity by altering the soil water thresholds required

378   by the plant groups for production of green forage. Differences were apparent among growth

379   forms despite each plant group being comprised of a large number of species (woody plants =

380   89, grasses = 66, forbs = 72).

381   Woody plants required less water per unit volume of soil than grasses and forbs to

382   produce green foliage. This is possibly because they have more laterally extensive root systems

383   that harvest water over a wider area, some species are deeply-rooted allowing access to deep-

384   stored water, or because they have access to an additional source of water stored in their wood

385   that can be drawn upon when soil is dry (Borchert 1994; Chapotin et al. 2006; Kulmatiski et al.

386   2010).

387   Grasses responded to short-term fluctuations in soil water, while woody plants and forbs

388   responded to longer seasonal changes. Grasses appear to be geared for exploiting moisture pulses

389   even if they are short-lived (< 1 month) and unseasonal, while woody plants and forbs are more

390   conservative, only responding to the more predictable, longer-term (1 − 3 month) seasonal

391   moisture cycles (Archibald & Scholes 2007). This difference may be explained by the ability of

392   woody plants to store water internally.

393   Soil texture in combination with plant life-form added further complexity to the

394   relationship between food availability and soil water. For all food types, green-up and plateau

395   soil water thresholds increased linearly with increasing clay content. This was expected because

396   although clay soils store more water per unit volume than sandy soils, water is more difficult to

397   extract from clay soils (Foth 1990). Despite this, woody plants retained leaf for longer on clay-

398   rich than on sandy soils. This suggests that the effect of soil texture on food availability is

399   determined by the difference between field capacity and soil water threshold rather than the

400   magnitude of the soil water threshold alone. Density of forage patches will remain at maximum

401   until soil water drops below the plateau threshold, and how long this takes to happen is

402   determined by the volume of water that the soil can store over and above the plateau threshold

403   (field capacity - plateau soil water threshold). For woody green leaves and mixed grass this

404   volume is relatively large on sandy soils and becomes even larger with increasing clay content

405   (Fig 7). For green grass and green forbs, however, the volume stored in excess of the plateau

406   threshold is relatively small on sandy soils and becomes even smaller with increasing clay

407   content. The net result is that leaves on woody plants and mixed grass stay green for longer on

408   clay-rich substrates compared to sandy ones, with the reverse being true for green grass and

409   green forbs. However, this will only happen if rainfall is sufficient to fill the clay soils to

410   capacity, as was the case in this study.

411   On sandy soils forbs required the same volume of soil water as grass to reach maximum

412   patch density, but required more water than grass on clay-rich substrates. A possible explanation

413   is that greater water use efficiency of C_4 photosynthesis affords grasses an advantage over C_3

414   forbs on clay-rich substrates, where soil water is more difficult to extract, but not on sandy soils

415   where water is held less tightly (Ehleringer & Monson 1993).

416   Woody vegetation structure in combination with soil texture further influenced the

417   availability of green browse. Shrubs and trees retained green leaves for longer when the canopy

418   volume of woody plants was low, which was generally the case on clay-rich substrates, and shed

419   leaves earlier when canopy volume was high, which was often the case on sandy soils. In

420   accordance, mopane trees carried leaves for longer into the dry season following tree thinning

421   (Smit 2001), ostensibly as a result of reduced inter-tree competition when trees are widely

422   spaced (Smith & Goodman 1986; Walker & Smith 1983). The net result of woody vegetation

423   structure was a high maximum density of browse patches on sandy and loam soils that declined

424   to low density early in the dry season; and a low maximum density of browse patches on clay-

425   rich substrates that persisted for long into the dry season. Clay-rich substrates may therefore

426   support a higher density of browse patches than sandy soils during the mid-dry season, despite a

427   lower density of woody plants.

428   Fire influenced the temporal availability of food for elephants, but only for herbaceous

429   vegetation growing on clay-rich substrates. The study was conducted during the second growing

430   season after fire when the immediate effects of fire, such as barren, blackened soil surfaces, had

431   already been ameliorated by regrowth of herbaceous vegetation during the 2001/2002 growing

432   season. For a given volume of soil water, density of mixed grass, green grass, and green forb

433   patches was higher at burnt than unburnt sites. At Malilangwe, clay soils support greater grass

434   biomass than sandy ones (Clegg 1999) and therefore greater competition among grass plants for

435   soil water is expected on clay-rich substrates. In savannas, biomass of grass may be reduced for

436   several years post-fire (Frost & Robertson 1985; Savadogo et al. 2009; Snyman 2005), with the

437   extent of reduction determined by fire temperature (Frost & Robertson 1985). At Malilangwe,

438   hotter fires because of larger fuel loads, and therefore greater post-fire reductions in grass

439   biomass are expected on clay compared to sandy substrates. This may result in the available soil

440   water being spread over less herbaceous biomass post-fire on clay-rich soils, and hence the lower

441   green-up and plateau soil water thresholds at burnt sites. In addition, because senescent material

442   carried over from previous seasons is removed by fire, grass has a higher ratio of live-to-dead

443   material at burnt compared to unburnt sites (Shombe et al. 2008; Van de Vijver et al. 1999),

444   which further explains the higher density of green herbaceous patches in post-fire regrowth.

445   Plants defoliated by fire may also have higher root-to-shoot ratios (Snyman 2005), and a larger

446   number of secondary and fine tertiary roots (Hartnett et al. 2005) than unburnt plants which

447   could enable them to rehydrate and green-up using less water (Fisher 1978).

448   Although fire reduced the canopy volume of the shrub layer, it had little effect on total

449   woody canopy volume because the tree layer was mostly out of reach of the flames.

450   Consequently fire did not reduce inter-tree competition for soil water, which may explain why

451   there was no post-burn effect on the temporal availability of green browse.

452   Although findings concerning the relationship between soil water, soil texture, fire,

453   structure of the woody layer and leaf phenology have been presented in the context of food for

454   elephants, they also have obvious significance for savannas in general. Specifically, the results

455   support the hypothesis that soil water plays a central role in the tree-grass interaction (Walter

456   1939; Walter 1970) and that explanation of this role is a key challenge towards understanding the

457 functioning of savannas. Furthermore, we believe the insight gained into the phenological pattern

458 of forbs suggests that the hitherto reported tree-grass interaction of savannas should be expanded

459 to a tree-grass-forb interaction. However, the study was not perfectly designed to address these

460 issues so we have purposely chosen not to elaborate further on these points.

461

462 **Implications for foraging elephants**

463 In savannas elephants are confronted with a broad spectrum of food choices that change across

464 space and time. Change over the annual cycle is predictable because there is a progressive drying

465 of soil from the onset of the dry season, with food types being lost from the choice set in a

466 sequence determined by their relative soil water requirements. Food types with the highest

467 requirement are lost first, followed by the next highest and so on until only the most drought

468 resistant types remain. This corresponds with reported seasonal changes in the diet of elephants

469 from consumption of forbs and grass (high water requirement) in the rainy season to mostly

470 leaves from woody plants (medium water requirement) when rains end, followed by an

471 increasing amount of bark and roots (low water requirement) in the late dry season (Barnes 1982;

472 Cerling et al. 2004; Field 1971; Guy 1976). This understanding enables prediction of diet under

473 different scenarios. For example, in semi-arid savannas grass is expected to be utilised for longer

474 in wet than in dry years, and consumption of bark is expected to increase during drought.

475   Knowledge of the mechanisms that cause spatial variation in food availability can help to

476 explain seasonal movements of elephants. For example, because trees and grasses have different

477 soil water requirements, key browse and grass resources are often separated geographically and

478 elephants must undertake seasonal movements between them if they are to exploit their different

479   phenological patterns. This may partly explain why elephants are often reported to move

480   between a wet season range, where grass makes up the bulk of the diet, and a dry season range

481   where browse from woody plants is the dominant food type (Cerling et al. 2006; Field 1971;

482   Loarie et al. 2009). To locate and utilise patches of green grass elephants inhabiting savanna

483   environments must track rain storms that are typically isolated and scattered (Eisinger &

484   Wiegand 2008), which forces them to move fast (Birkett et al. 2012) and widely during the rainy

485   season (Bohrer et al. 2014; Thouless 1995; Young et al. 2009). In contrast, browse from woody

486   plants is a less ephemeral source of food and therefore elephants can move more slowly (Birkett

487   et al. 2012) and occupy a relatively confined area during the dry season (Bohrer et al. 2014;

488   Thouless 1995; Young et al. 2009).

489   A key challenge to the study of feeding behaviour of a wide-ranging herbivore in a

490   complex environment is to quantify available food at an adequate spatial and temporal

491   resolution. The approach described in this study may meet this need. The daily food supply for

492   elephants at Malilangwe was successfully mapped for one annual cycle using this method (Clegg

493   2010), and the results successfully used to interpret foraging decisions that yielded generalised

494   insight into elephant feeding behaviour that has Africa wide relevance (for monthly maps

495   showing the spatial availability of the different forage types over the study area see Clegg 2010

496   pgs 60, 61, 66, 72-74). Although time consuming, a ground-based approach was identified as a

497   key to this success because estimates of patch density and the vertical distribution of browse on a

498   species-specific basis could be derived for each food type, which is currently not possible with

499   existing satellite technology. These measures were essential for estimating the mass and energy

500   content of trunkloads harvested from food patches (Clegg 2010).

501   The findings of this study also have relevance for other large mammalian herbivores that

502   inhabit savanna environments. However, when extrapolating the results it should be recognised

503   that elephant-centric nuances were embedded in the approach and methodology of this study. For

504   example, availability of browse patches was calculated using a maximum reach height of 4 and 6

505   m for cows and bulls respectively, and browse patches were only considered available if they had

506   >25 % green leaf. These nuances make the results specific to elephants. However, despite this,

507   the discerning reader should still be able to recognise the implications for other herbivores.

508

509   **CONCLUSIONS**

510   The types of food available to elephants changed seasonally because (1) plant life-forms required

511   different volumes of soil water to produce green forage; (2) woody plants and forbs responded to

512   long-term changes in soil moisture, while grasses responded to short-term moisture pulses; and

513   (3) soil texture, the structure of woody vegetation and fire added further complexity to the

514   pattern of food availability by altering the soil water thresholds required by the plant groups for

515   the production of green foliage.

516   Interpolating between regularly-timed, ground-based measurements of food density by

517   using modelled soil water as the predictor in regression equations proved to be a feasible method

518   of for quantifying the food available to elephants over an annual cycle. In complex

519   environments, stratification on the basis of soil texture, woody vegetation structure and recent

520   fire history is essential.

521

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526

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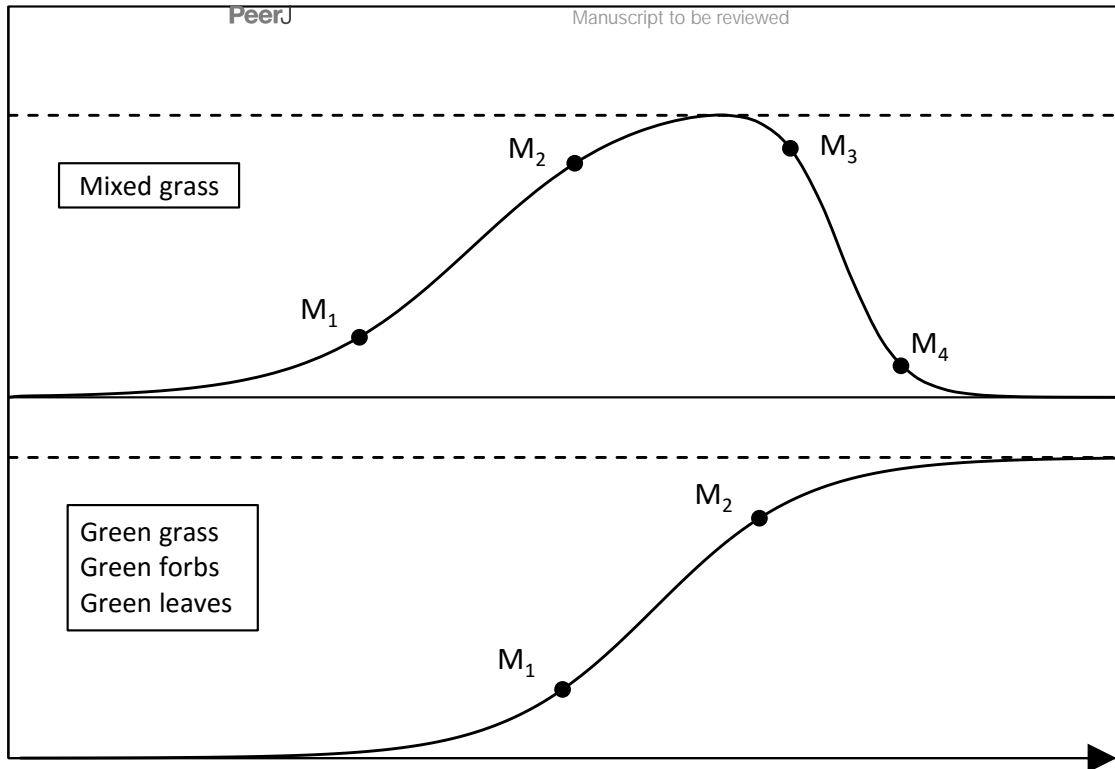
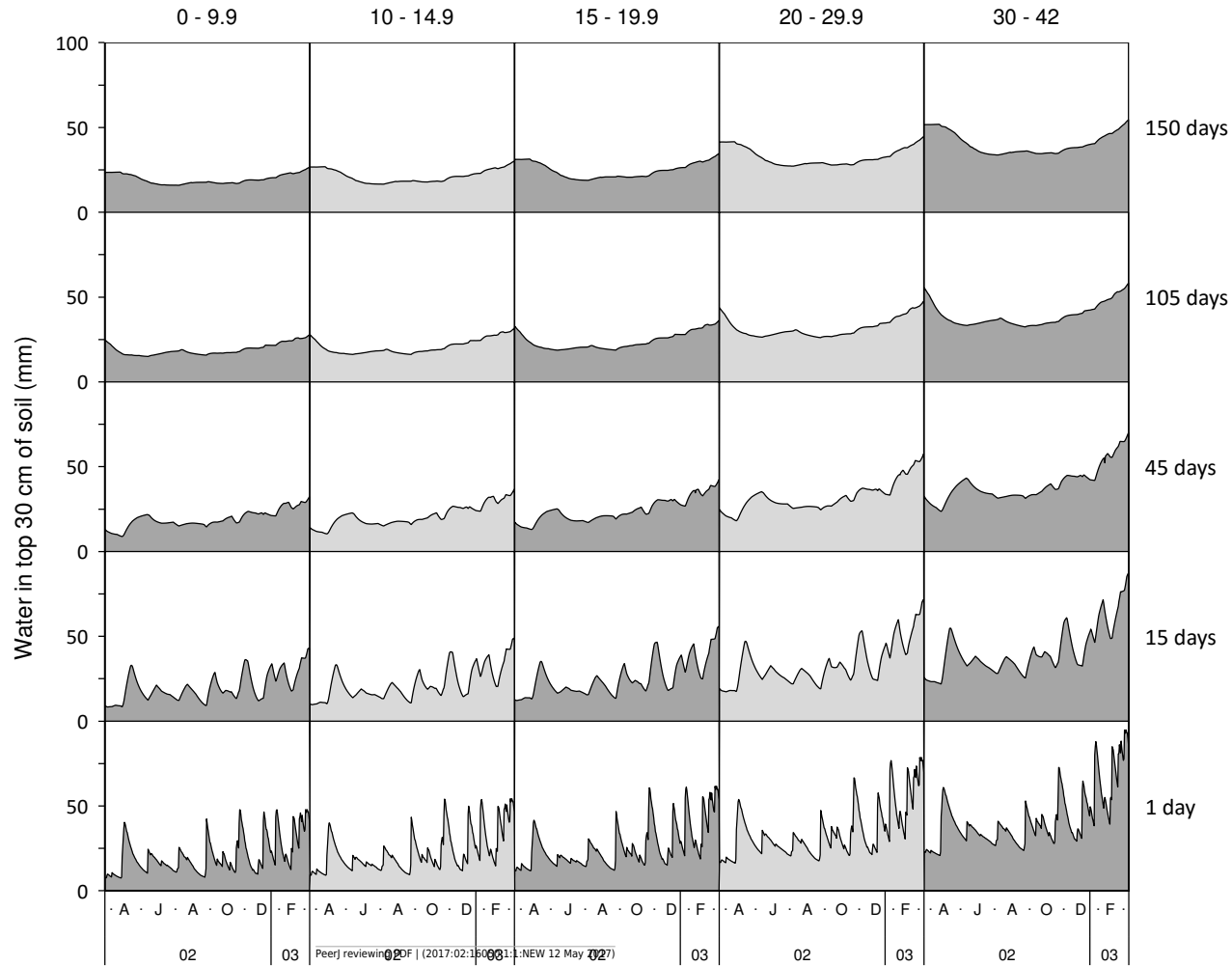
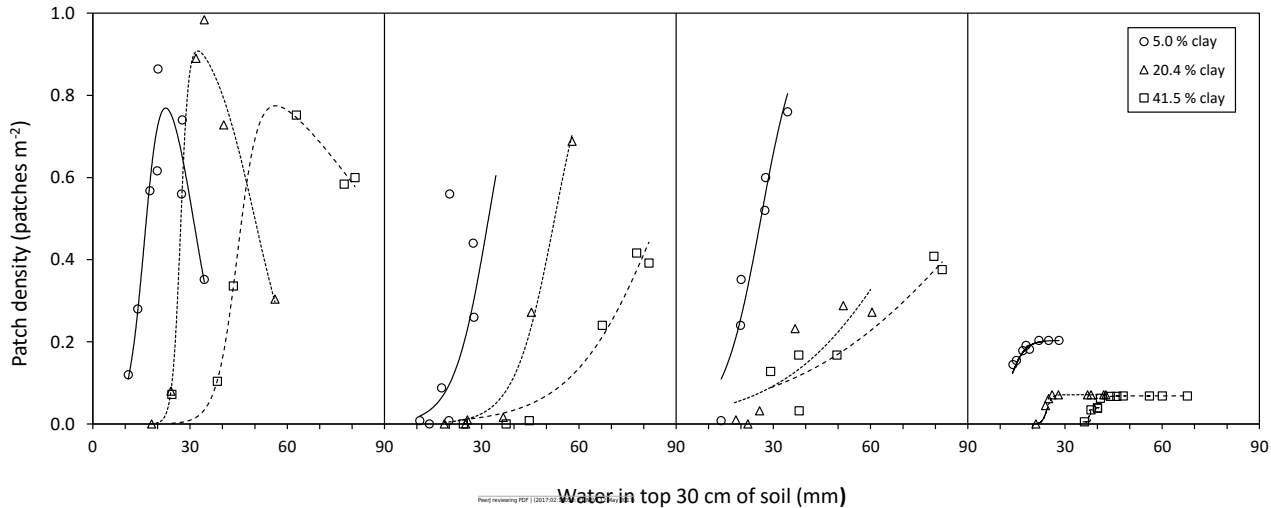
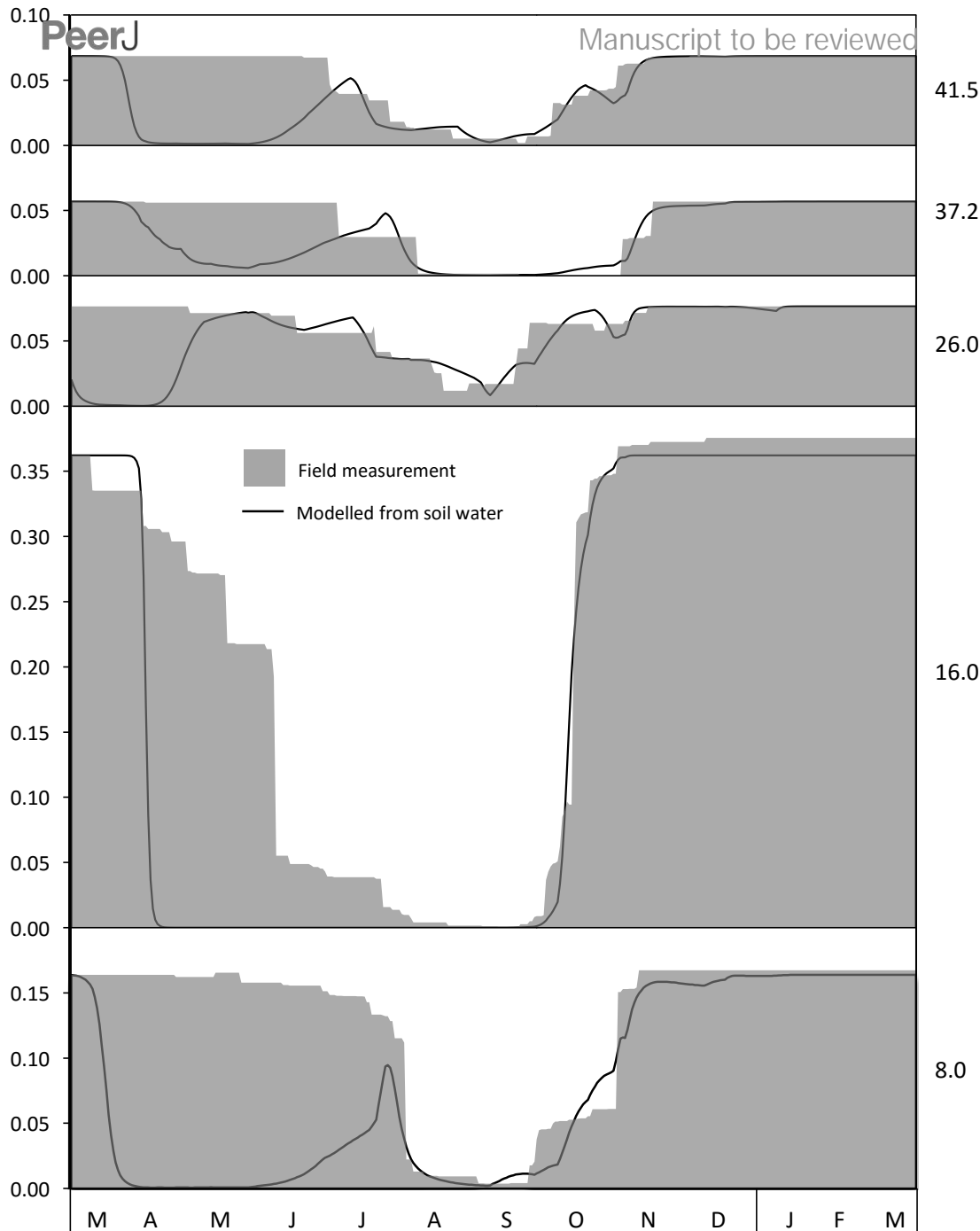
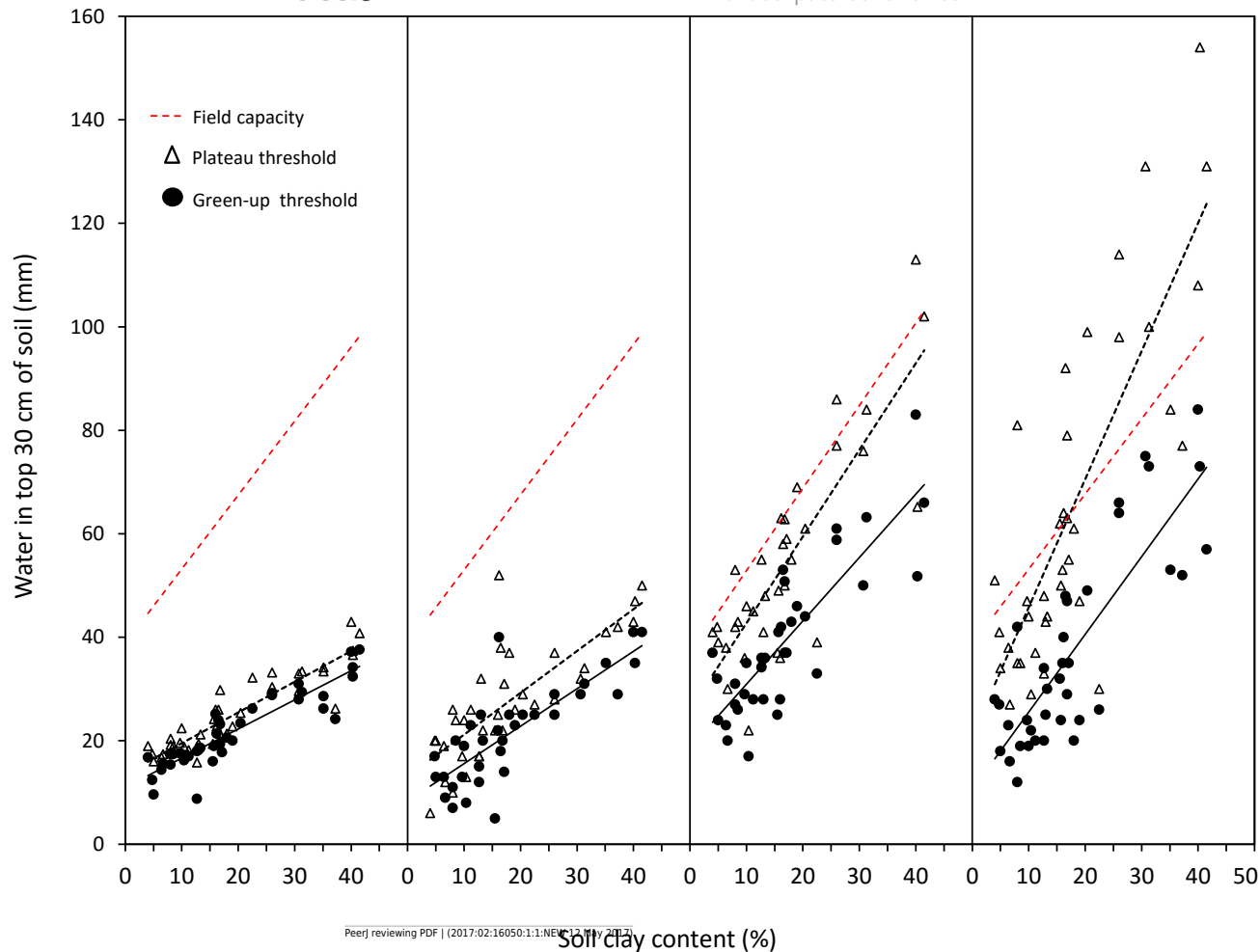
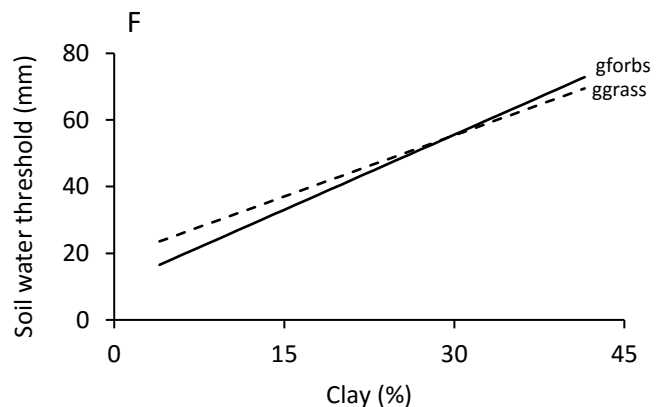
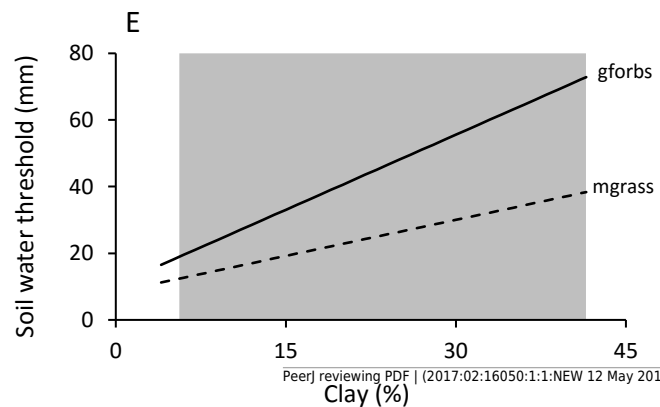
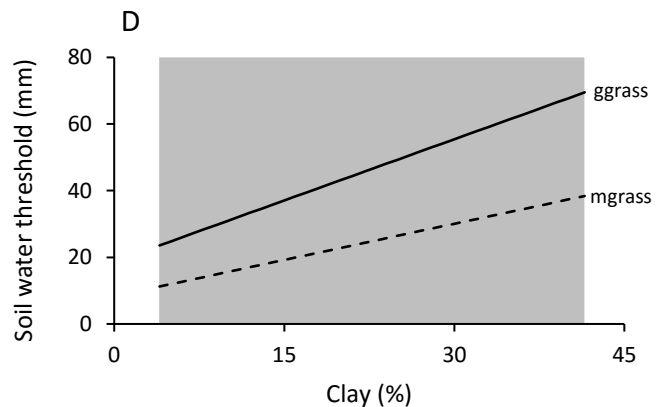
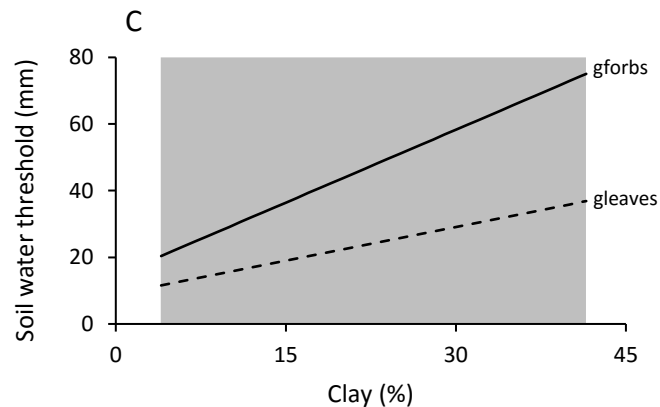
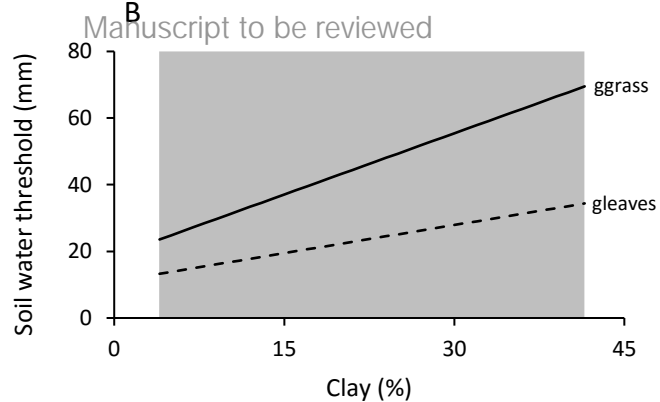
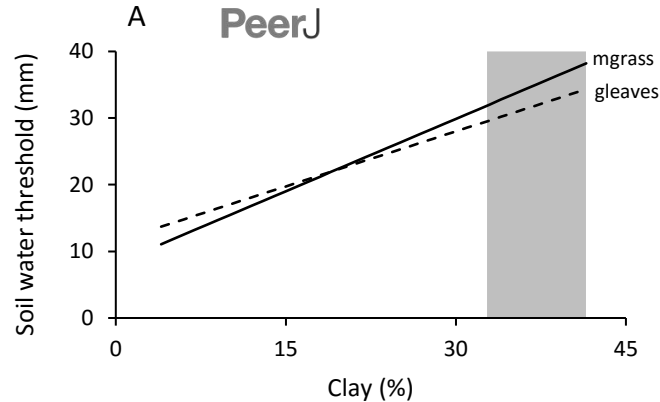
Sigmoidal curves representing the relationship between availability and soil water for the forage types.

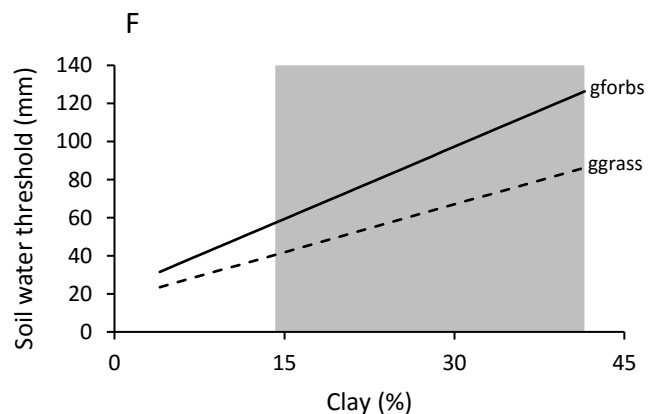
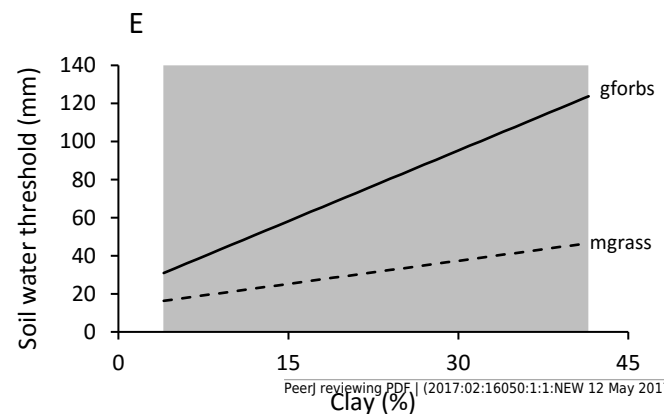
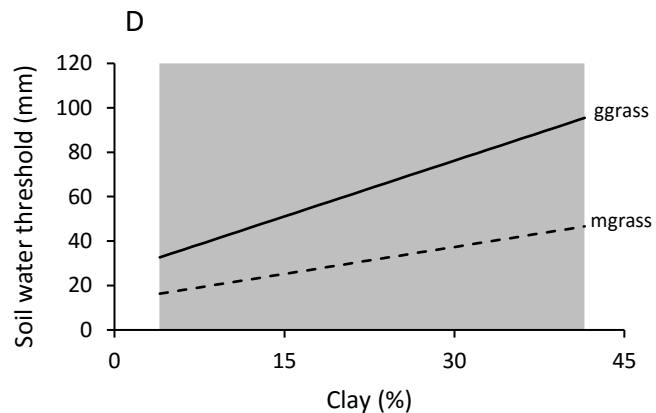
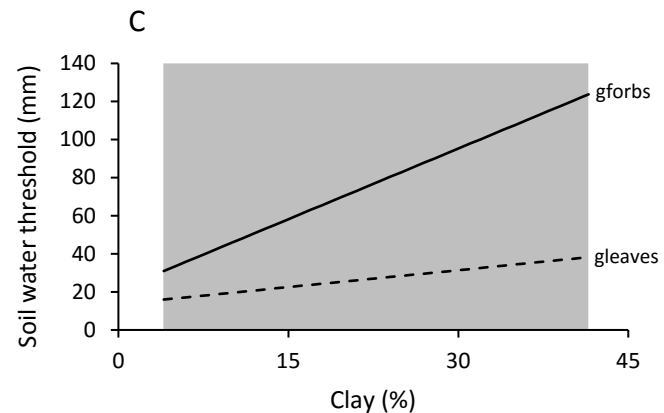
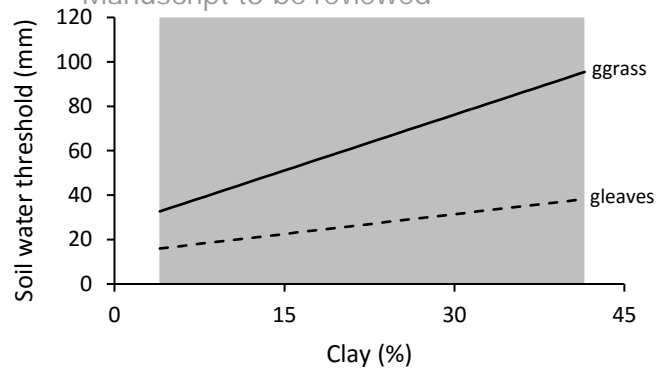
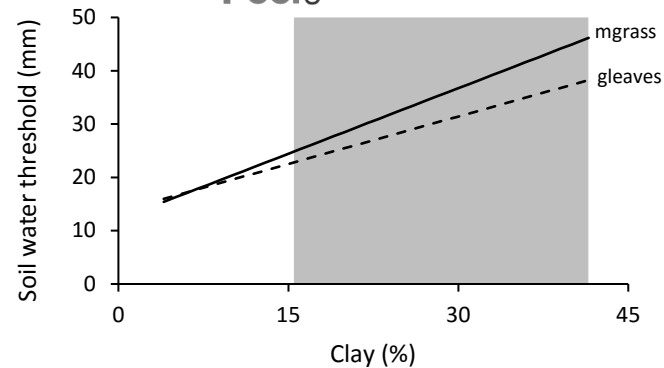
M_1 = threshold between lag and exponential phases (green-up), M_2 = threshold between exponential and plateau phases (plateau), M_3 = threshold between plateau and exponential phases of the decline in mixed grass patches and M_4 = threshold between exponential and lag phases of the decline in mixed grass patches.

Effect of soil clay content and lag period on the temporal pattern of soil water.

Examples of the relationship between availability of food types and soil water in relation to increasing clay content.

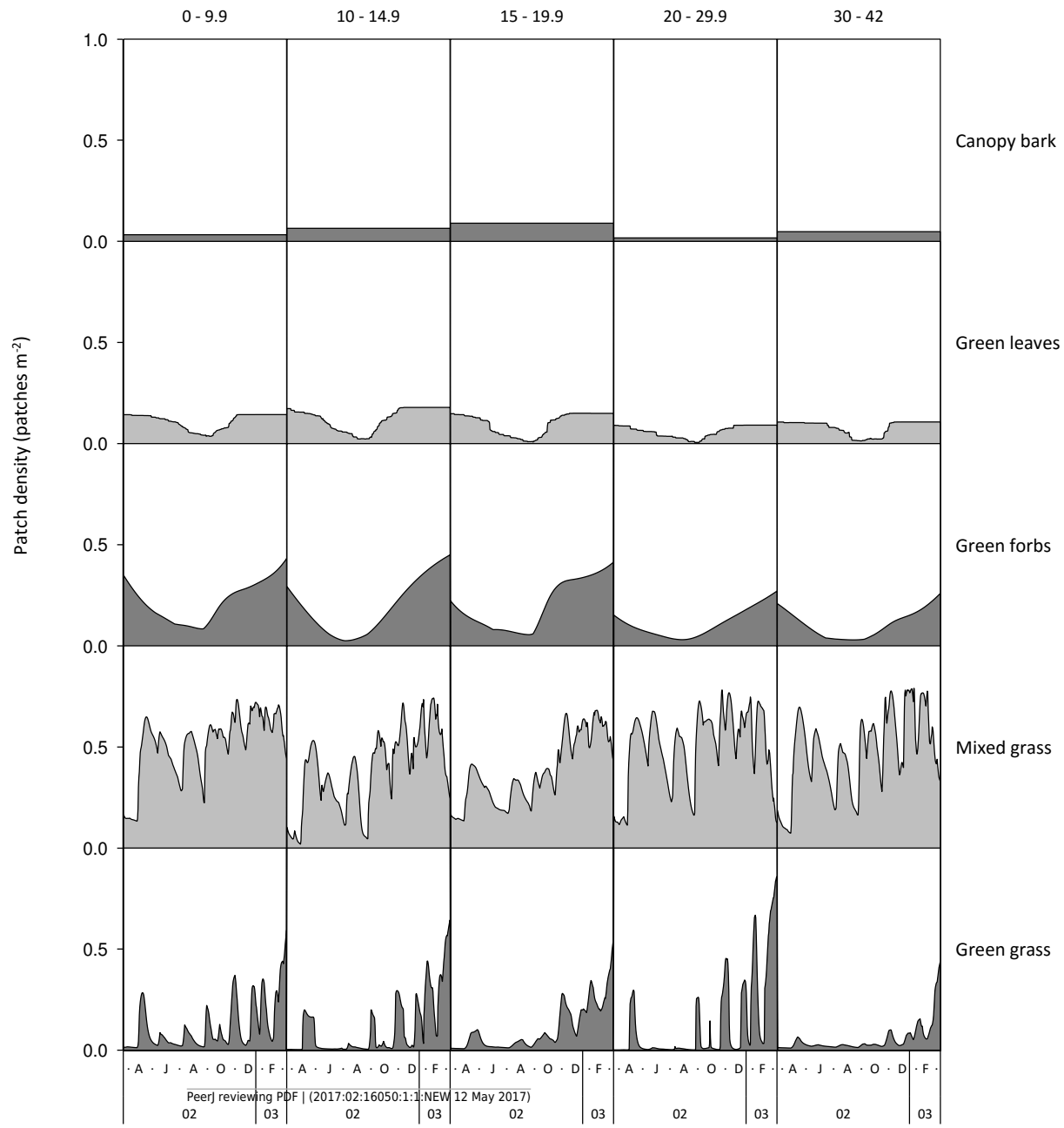
Mixed grass (A); green grass (B); green forbs (C); green leaves (D). Data for green leaves from woody plants are restricted to the period from the start of leaf drop, through leaf flush, to maximum patch density.

Examples of temporal estimates of availability of woody green leaf available to adult bull elephants from field measurements and modelling along a gradient of increasing soil clay content.

Measured and modelled estimates corresponded well except for the period before leaf drop.

Linear regressions between clay content and field capacity of the 30 cm soil profile and green-up (M1) and plateau (M2) soil water thresholds for each food type.

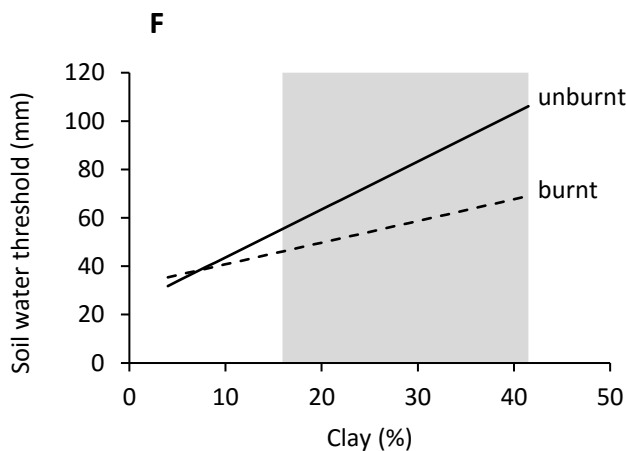
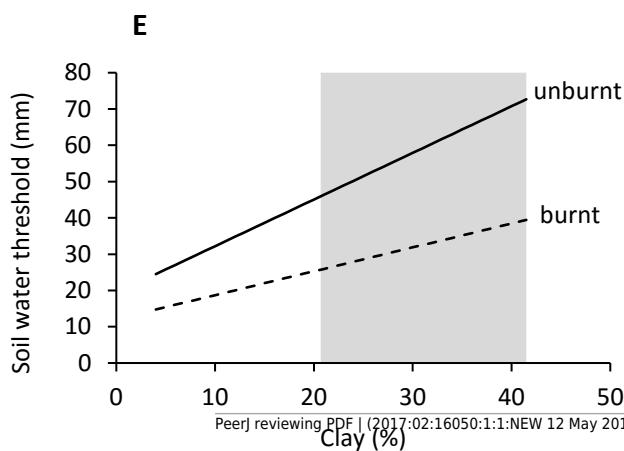
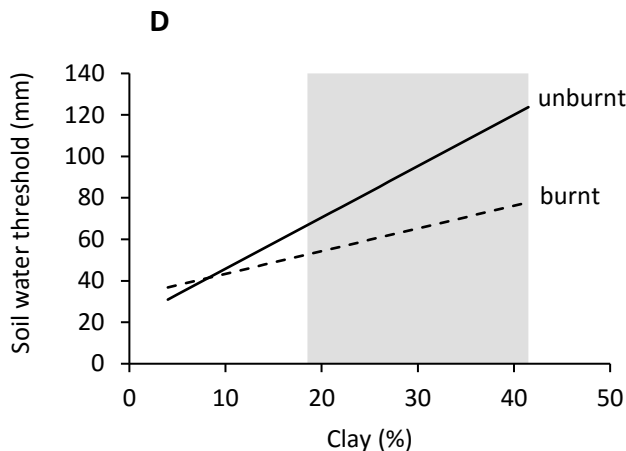
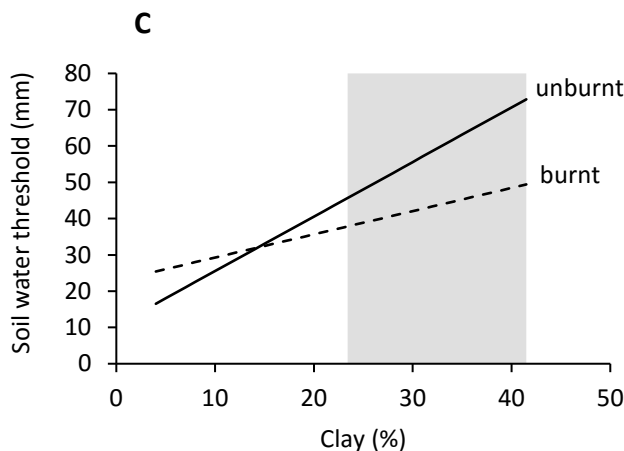
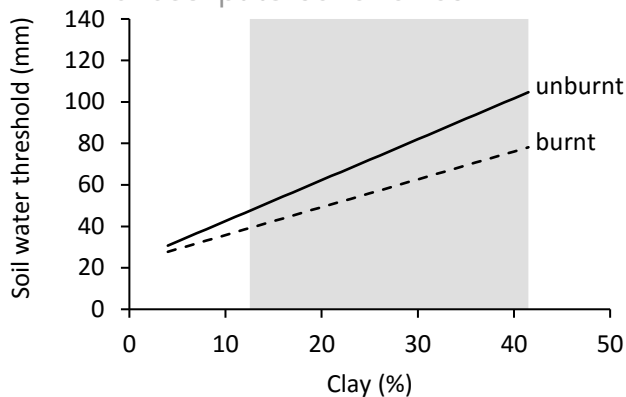
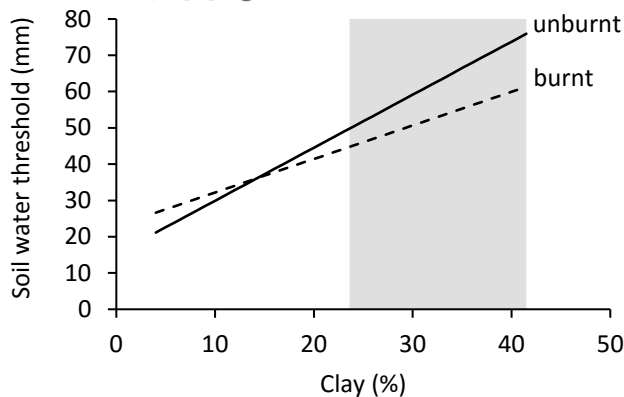
Green leaves (A); mixed grass (B); green grass (C); green forbs (D). Equations, adjusted R^2 and P values for regressions: green leaves, $M_1 = 11.022 + 0.563X$ ($R^2 = 0.81$, $P < 0.001$), $M_2 = 12.645 + 0.663X$ ($R^2 = 0.87$, $P < 0.001$); mixed grass, $M_1 = 8.346 + 0.724X$ ($R^2 = 0.64$, $P < 0.001$), $M_2 = 13.423 + 0.774X$ ($R^2 = 0.54$, $P < 0.001$); green grass, $M_1 = 18.671 + 1.225X$ ($R^2 = 0.69$, $P < 0.001$), $M_2 = 26.22 + 1.673$ ($R^2 = 0.70$, $P < 0.001$); green forbs, $M_1 = 10.52 + 1.502X$ ($R^2 = 0.68$, $P < 0.001$), $M_2 = 18.493 + 2.63X$ ($R^2 = 0.68$, $P < 0.001$).

Effect of soil clay content and food type on green-up (M1) soil water thresholds.

Regions of significant (P < 0.05) differences between green leaves and mixed grass (A), green leaves and green grass (B), green leaves and green forbs (C), mixed grass and green grass (D), mixed grass and green forbs (E), and green grass and green forbs (F) are shaded grey.

Effect of soil clay content and food type on plateau (M2) soil water thresholds.

Regions of significant (P < 0.05) differences between green leaves and mixed grass (A), green leaves and green grass (B), green leaves and green forbs (C), mixed grass and green grass (D), mixed grass and green forbs (E), and green grass and green forbs (F) are shaded grey.

Temporal availability of forage types along a gradient of increasing clay content.

Data for woody green leaves are for adult bulls. Availability of woody green leaf was slightly lower for cows, but otherwise followed the same pattern.

Soil clay content (%)

Effect of a significant interaction between soil clay content and fire (>5 months previously) on soil water thresholds for green grass, green forbs and mixed grass.

Green grass M_1 (A); green grass M_2 (B); green forbs M_1 (C); green forbs M_2 (D); mixed grass M_3 (E); mixed grass M_4 (F). Regions of significant ($P < 0.05$) difference between burnt and unburnt areas are shaded grey.

Examples of the effect of fire (>5 months previously) on the patch density – soil water relationship for herbaceous forage types along a gradient of increasing clay content.

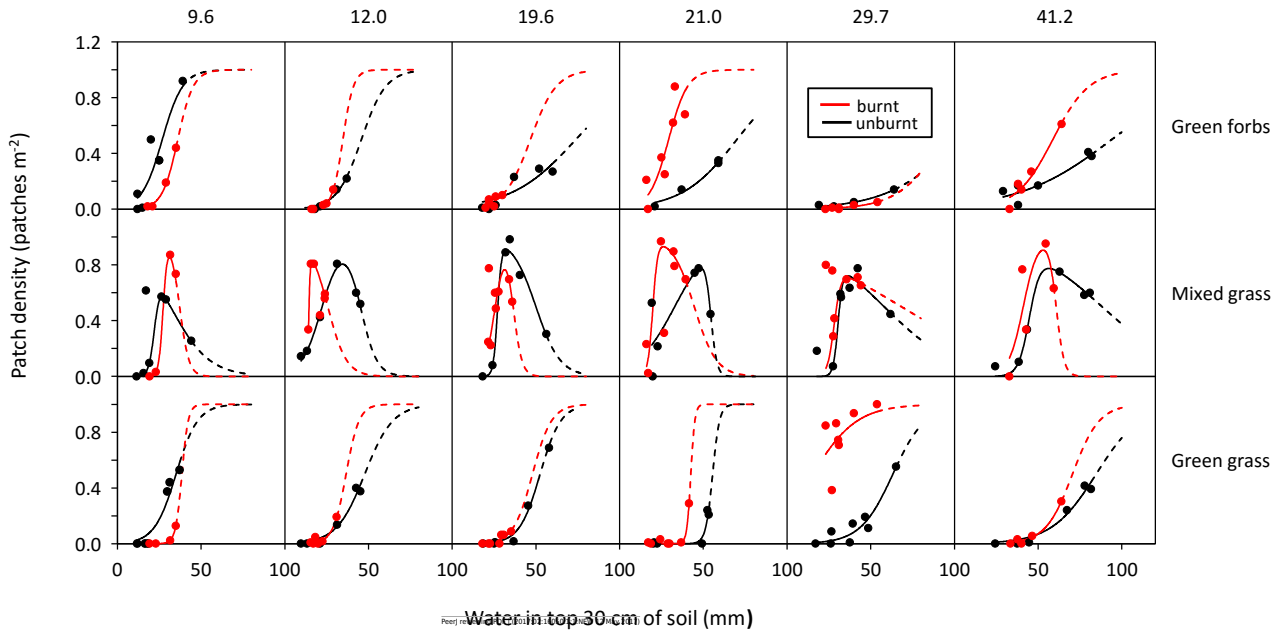
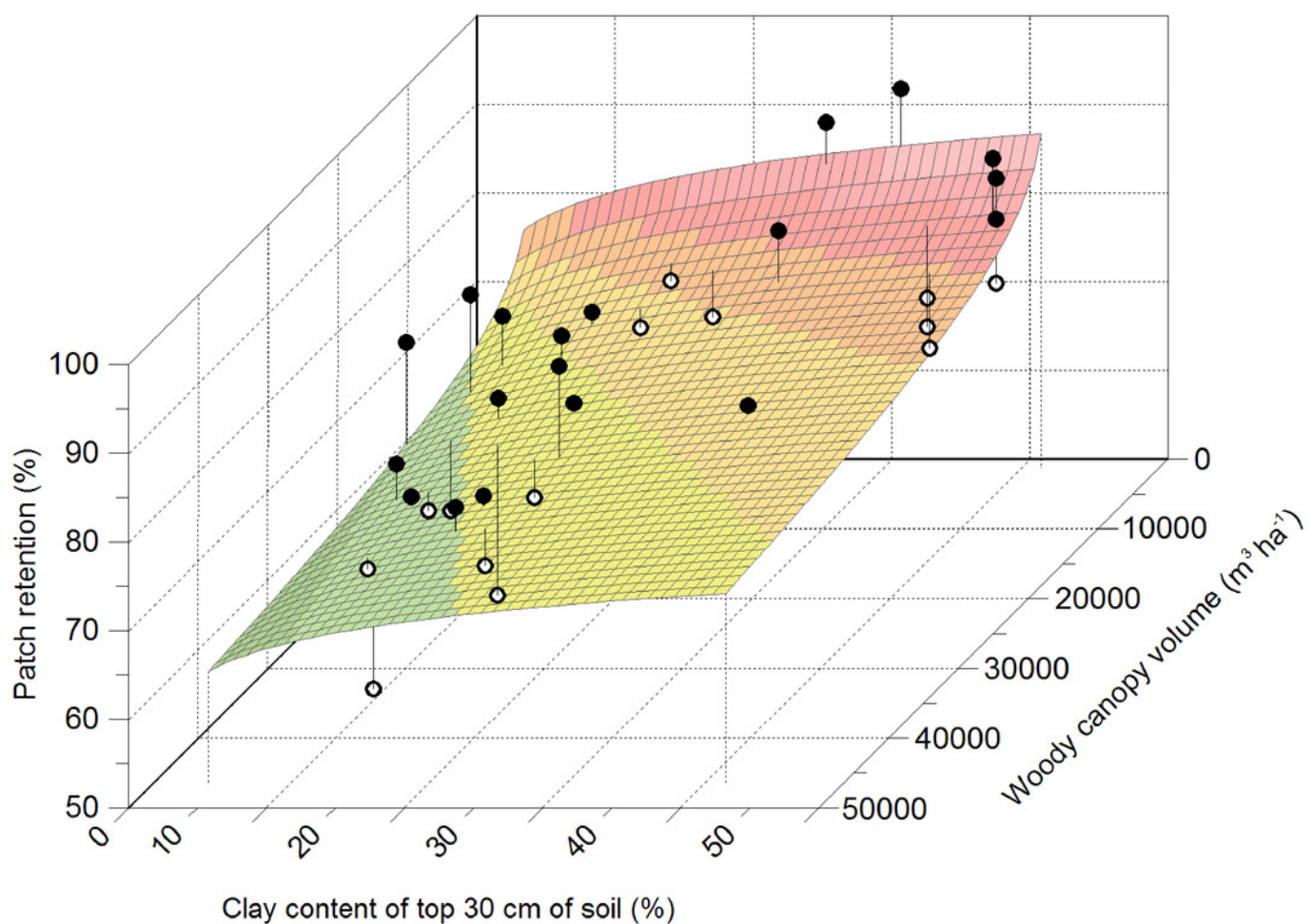



Figure 11

Influence of soil clay content and woody canopy volume on retention of green leaf patches.

Y = a*(X1/X2)b, where Y = patch retention, X1 = soil clay content, X2 = woody canopy volume, and a and b are constants.

Regression estimates and region of significance limits (RoS X) for the influence of soil texture and plant life-form on soil water thresholds.

Threshold (Y)	Dummy coded Moderator variable (Z)		Regression estimates						RoS X (Clay %)	
	1	0	b_0	b_1	b_2	b_3	$XZ\,\Delta R^2$	p	Lower bound	Upper bound
M_1	G. leaves	M. grass	8.164**	0.724**	3.342*	-0.174*	0.015	0.019	32.8	41.5
M_1	G. leaves	G. grass	18.671**	1.225**	-7.650**	-0.662**	0.06	0.0005	4.0	41.5
M_1	G. leaves	G. forbs	14.543**	1.458**	-5.682*	-0.783**	0.087	0.0005	4.0	41.5
M_1	M. grass	G. grass	18.671**	1.225**	-10.325	-0.501**	0.027	0.0005	4.0	41.5
M_1	M. grass	G. forbs	10.518**	1.502**	-2.172	-0.779**	0.058	0.0005	5.6	41.5
M_1	G. grass	G. forbs	10.518**	1.502**	8.153	-0.278	0.007	0.22	-	-
M_2	G. leaves	M. grass	12.129**	0.82	1.469	-0.226*	0.02	0.016	15.5	41.5
M_2	G. leaves	G. grass	25.984**	1.674**	-12.386**	-1.080**	0.075	0.0005	4.0	41.5
M_2	G. leaves	G. forbs	21.025**	2.475**	-7.427	-1.882**	0.111	0.0005	4.0	41.5
M_2	M. grass	G. grass	25.984**	1.674**	-12.883**	-0.866**	0.046	0.0005	4.0	41.5
M_2	M. grass	G. forbs	21.025**	2.475**	-7.924	-1.667**	0.084	0.0005	4.0	41.5
M_2	G. grass	G. forbs	21.374**	2.529**	4.610	-0.855*	0.025	0.018	14.2	41.5

1   *P < 0.05, **P < 0.01

Regression estimates and region of significance limits (RoS X) for the influence of soil texture and fire (>5 months previously) on soil water thresholds.

Threshold (Y)	Dummy coded moderator variable (Z)		Regression estimates						RoS X (Clay %)	
	1	0	b_0	b_1	b_2	b_3	$XZ\ \Delta R^2$	p	Lower bound	Upper bound
G. leaves M_1	Burnt	Unburnt	11.134**	0.581**	0.498	-0.077	0.003	0.202	-	-
M. grass M_1	Burnt	Unburnt	8.346**	0.724**	6.861*	-0.301	0.026	0.1	-	-
G. grass M_1	Burnt	Unburnt	15.298**	1.461**	7.626	-0.536*	0.029	0.022	23.6	41.5
G. forbs M_1	Burnt	Unburnt	10.518**	1.502**	12.336	-0.862*	0.052	0.012	23.4	41.5
G. leaves M_2	Burnt	Unburnt	13.144**	0.631**	-0.776	-0.059	0.002	0.403	-	-
M. grass M_2	Burnt	Unburnt	12.129**	0.820**	5.742	-0.277	0.018	0.130	-	-
G. grass M_2	Burnt	unburnt	22.807**	1.973**	-0.463	-0.629*	0.021	0.040	12.5	41.5
G. forbs M_2	Burnt	unburnt	21.025**	2.475**	11.389	-1.381*	0.046	0.025	18.5	41.5
M. grass M_3	Burnt	Unburnt	19.349**	1.285**	7.228	-0.627*	0.041	0.016	20.7	41.5
M. grass M_4	Burnt	Unburnt	23.848**	1.983**	7.985	-1.087**	0.053	0.006	15.9	41.5

1   *$P < 0.05$, **$P < 0.01$