



Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:

Keatley, MR;Bren, LJ;Hudson, IL

Title:

The historic flowering behaviour of River Red-gum and Black Box in a flooding forest

Date:

2021-06-01

Citation:

Keatley, M. R., Bren, L. J. & Hudson, I. L. (2021). The historic flowering behaviour of River Red-gum and Black Box in a flooding forest. *Austral Ecology*, 46 (4), pp.640-652. <https://doi.org/10.1111/aec.13021>.

Persistent Link:

<https://hdl.handle.net/11343/298303>

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31

DR. MARIE RUSSELL KEATLEY (Orcid ID : 0000-0001-5490-576X)

Article type : Research Article

Corresponding Author Email ID: mrk@unimelb.edu.au

Data declaration

The Eucalypt flowering data that support the findings of this study are available from the corresponding author upon request. Monthly flow in the River Murray was sourced from the gauging data of the Rural Water Corporation ([Rural Water Corporation of Victoria 1990](#)).

Funding statement

Funding was provided by Eucalypt Australia to digitise the eucalypt flowering data.

Conflict of interest disclosure

The authors have no conflicting interests to declare.

Permission to reproduce material from other sources

Figure S2 was sourced from the State Library of Victoria. The figures are based on maps produced by the Forest Commission of Victoria prior to 1969 and therefore are out of copyright.

The <https://www.communications.gov.au/copyright/duration-copyright> states that for Crown (Government) copyright material. Works made or first published, sound recordings and cinematograph films (made on or after 1 May 1969): 50 years from the end of the calendar year in which the material was made.

Your co-author details, including affiliation and email address.

Leon J Bren, School of Ecosystem and Forest Sciences, University of Melbourne, Creswick, Victoria, 3363, Australia. Email: lbren@ncable.net.au

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/AEC.13021](https://doi.org/10.1111/AEC.13021)

This article is protected by copyright. All rights reserved

32 Irene L Hudson, Mathematical Sciences, School of Science, Engineering and Health RMIT University,
33 Melbourne, Victoria 3000, Australia. Email: irene.hudson@rmit.edu.au

34
35

36

37 **The historic flowering behaviour of River Red-gum and Black Box in a flooding forest**

38

39 **Marie R. Keatley¹, Leon J. Bren¹, and Irene L. Hudson²**

40 1 School of Ecosystem and Forest Sciences, University of Melbourne, Creswick,
41 Victoria, 3363, Australia

42 2 Mathematical Sciences, School of Science, Engineering and Health RMIT University,
43 Melbourne, Victoria 3000, Australia

44

45 **Abstract**

46 River Red-gum (*Eucalyptus camaldulensis*) and Black Box (*E. largiflorens*) are the dominant
47 tree species of Barmah forest, Victoria; part of a floodplain ecosystem which has been
48 identified as being under threat due to the reduced frequency and duration and altered timing
49 of flooding associated with river regulation, water extraction and drought.

50

51 The flooding regime plays a significant role in the phenology in both these species. Hence
52 establishing past flowering behaviour using long-term records (1934 to 1973) provides a
53 historical baseline against which current and future flowering behaviour can be judged.

54

55 Black Box was more consistent in its flowering, with an annual failure recurrence interval of
56 1 in 36 years less compared to 1 in 9.25 years for River Red-gum. Black Box was also the
57 more intense flowering species and flowered for longer (4.0 ± 1.9 months compared to $2.1 \pm$
58 1.4 months), with its flowering period encompassing River Red-gum's. The flowering of the
59 two species was therefore synchronous. River Red-gum displayed evidence of flowering
60 more intensely every second year and therefore some dependence on the previous year's
61 flowering; this was absent in Black Box.

62

63 The influence of flooding on flowering intensity over this 40 year interval indicated that
64 flooding 10 years out of 13 years with an inundation period greater than 6 months has a

65 depressive effect on flowering intensity while flooding in 7 out of 13 years with an
66 inundation period of no greater than 5 months enhances flowering intensity. This is more so
67 for Black Box than River Red-gum. However, flooding is a recurring event in this study, and
68 therefore it is difficult to isolate the effect of a single flood on flowering.

69 **Keywords**

70 Barmah, *Eucalyptus camaldulensis*, *E. largiflorens*, flowering, flooding

71
72 **INTRODUCTION**

73 River Red-gum (*Eucalyptus camaldulensis*) is the most widespread eucalypt across mainland
74 Australia (Boland *et al.* 2006; Smith and Smith 2014). Historically it was of major
75 importance commercially (Colloff 2014). Consequently, facets of its biology have been well-
76 studied including its silviculture and regeneration (Dexter 1967; 1978). River Red-gum along
77 with Black Box (*Eucalyptus largiflorens*) are also important components of a suite of
78 eucalypts which sustain the bee-keeping industry (Paton *et al.* 2004; Somerville and
79 Nicholson 2005).

80

81 The largest River Red-gum forest is the Barmah-Millewa Forest, located on the floodplain of
82 the River Murray approximately 200 km north of Melbourne (Bren 2005). Black Box is
83 mostly associated with watercourses in the Murray-Darling system where it usually occurs
84 just above River Red-gum in areas subjected to flooding (Boland *et al.* 2006; Smith and
85 Smith 2014); in Barmah it is associated with areas of low flooding frequency (5 to 40% of
86 years flooded) and duration (Bren 1988b; Bren and Gibbs 1986).

87

88 The flooding regime plays a significant role in the distribution, health, recovery and
89 phenology in both these species (Bren 1988b; Bren and Gibbs 1986; Catelottia *et al.* 2015;
90 Moxham *et al.* 2018; Newell *et al.* 2009; Roberts 2004; Roberts and Marston 2011).

91

92 The floodplain ecosystem of which these two species are the dominant tree species has been
93 identified at being vulnerable to ecological collapse (Keith *et al.* 2013) due to the reduced
94 frequency and duration and altered timing of flooding associated with river regulation, water
95 extraction, drought and increases in salinity levels (CSIRO 2008; Mac Nally *et al.* 2011).

96 River Red-gum has been identified as being particularly impacted (Catelottia *et al.* 2015; Mac
97 Nally *et al.* 2011).

98

99 This study examines the flowering of River Red-gum and Black Box within Barmah Forest.
100 The data source is a 40-year record of monthly observations in “budding and flowering”
101 reports for the former forest management agency. As far as the authors are aware, this is the
102 longest record of flowering available for these species. The data were used to investigate the
103 following questions:

- 104 1. What are the flowering patterns of River Red-gum and Black Box along parts of the
105 River Murray?
- 106 2. Is the flowering of these two species synchronous?
- 107 3. How strong is the annual cyclicity of these species, and are there other underlying
108 cycles in the flowering records?
- 109 4. Is flowering in each year independent of flowering in the previous year?
- 110 5. Is there any relationship between the flooding status of the forest and flowering either
111 in the year of flooding or in the subsequent year after flooding?

112

113 **METHODS**

114 **Budding and Flowering Returns**

115 The original function of the early budding and flowering reports was to provide information
116 on the reproductive cycle of commercial eucalypts (Fig. S1). By 1935, however, there was a
117 focus on honey production. Observers – typically experienced overseers or young foresters –
118 made monthly observations on whether the trees were budding and/or flowering (Keatley *et*
119 *al.* 1999). These observers categorised their observations of flowering according to the
120 quantity and distribution of flowering across the population. Flowering quantity was ranked
121 from ‘No flowering’ to ‘Heavy flowering’, whilst distribution ranged from ‘Isolated’ to
122 ‘General’. These observations were then scored using the method of Keatley and Hudson
123 (2007) (Table 1). The result was a monthly discrete-valued time-series for each species with a
124 minimum score of 0 (no flowering) to a maximum score of 5 (which equates to heavy (scored
125 as 3) generally distributed flowering (scored as 2)).

126

127

128 In general, at Barmah, attempts were made to summarise budding and flowering over the
129 administrative region (Fig. S2) and forms filled out were a general summary rather than
130 observations on particular trees (B.D. Dexter, pers. comm. who was a young forester who
131 filled in some of these records in the mid-1950s). Observers’ marginal notes refer to issues

132 such as the difficulty of accessing stands due to flooding, so it is reasonable to assume that
133 the records covered areas subject to inundation.

134

135 The dataset covers the period December 1934 to December 1973 for River Red-gum and
136 January 1933 to December 1973 for Black Box. However, data were missing from both
137 series. In the River Red-gum data, a total of 36 months was missing: April to June 1934, July
138 to September 1936, 1947, 1952, 1959 and 1973, January to June 1948, October to December
139 1956 and 1965, January to March 1957, July to December 1958 and 1972. In the Black Box
140 data there was a total of 34 missing months. January to March 1948, 1956 and 1958,
141 September to December 1948, 1958 and 1972, October to December 1956, 1963 and 1965
142 and September in 1952 and 1959.

143

144 **Flowering behaviour and synchrony**

145 Flowering behaviour in these species was characterised using the method in Keatley and
146 Hudson (2007):

- 147 • Annual Flowering Success: the probability of flowering in each year and the flowering
148 failure recurrence,
- 149 • Mean Flowering Duration: the average period over which flowering occurred each
150 flowering year,
- 151 • Peak Flowering: the month in which highest flowering intensity occurred,
- 152 • The most probable month of commencement and finishing of flowering and the range
153 of months these phases occurred in.

154

155 Synchrony or the degree of overlap between River Red-gum and Black Box for individual
156 years and overall was calculated using the method described in Keatley et al. (2004).

157

158 **Flowering cycles and independence**

159 “Caterpillar” Singular Spectrum Analysis (SSA) (Golyandina and Zhigljavsky 2020) was
160 used to determine the trend and cycles within the flowering and the flooding time series. As
161 SSA requires a complete data set, missing values as detailed above were assigned the average
162 value for a particular month. Kendall’s rank correlation coefficient (τ) (Hollander *et al.* 2013)
163 was also used to examine the concordance between the annual maxima value of flowering of
164 the two species.

165

166 The flowering time series were also examined using cross-correlation for lags of up to 36
167 months to determine whether flowering in each year was independent of flowering in the
168 previous year(s).

169

170 **Flooding and flowering**

171 The percentage of the forest flooded was determined using the relationship between flooding
172 and peak flows based on a study of past flooding records as described in Bren (2005). The
173 flowering time series were used to provide the monthly distribution of flowering scores for
174 River Red-gum and Black Box. Examination of the relationship between flooding and
175 flowering used the “classical” hydrologic technique of “double mass plots” in which the
176 cumulative score of one sequence is plotted as a function of the cumulative score of a second
177 sequence (Searcy and Hardison 1960). In this instance the River Red-gum and Black Box
178 scores were divided by the maximum Black Box score to facilitate comparison. Similarly,
179 cumulative flooding was scaled (0,1) to facilitate direct comparison. Because the technique
180 uses integrated data, it is particularly good at depicting long-term trends that are hard to show
181 by more statistically-based techniques (Searcy and Hardison 1960). Additionally, Kendall’s
182 rank correlation coefficient (Hollander *et al.* 2013) was used to examine the concordance
183 between the percentage of the forest flooded and maximum value of flowering for either
184 species.

185

186 **RESULTS**

187 **Flowering behaviour and synchrony**

188 Both species, on average, reach peak flowering in December (Fig. 1 and Table 2) and to that
189 extent show synchronous behaviour. River Red-gum was also most likely to commence
190 flowering (0.69) in December. Black Box, however, was equally likely to commence
191 flowering in three months: September, October and December (0.26). River Red-gum was
192 equally as likely to stop flowering in both December and January (0.34) whereas February
193 (0.34) is the most probable month in which flowering ceases in Black Box. Black Box has a
194 longer mean flowering period and range of flowering: 4.0 and 9.0 months, respectively
195 compared to the 2.1 and 7.0 months, respectively of River Red-gum (Table 2). Not
196 surprisingly, a longer flowering period is associated with a greater flowering score.

197

198 The mean flowering of River Red-gum is significantly positively skewed (and for the
199 individual years it was positively skewed for 21 of the 24 years). In Black Box the mean
200 flowering pattern is not significantly skewed, and this was the case in 15 of the 29 individual
201 years. Comparing skewness between the species in the individual years; on 14 of the 22
202 occasions they were same; 12 of these 14 years were positively skewed; in the eight years
203 where they were differed River Red-gum was positively skewed and Black Box normally
204 distributed.

205

206 Flowering in Black Box was more consistent than River Red-gum over the observation
207 period: Black Box missed flowering once compared to the four years that River Red-gum
208 missed (Table 2). This equates to Black Box not flowering approximately once in 36 years
209 compared to about once in 9.25 years for River Red-gum. There is the possibility that neither
210 species flowered in 1957/1958 but both species have missing data for January to March 1958.
211 If this was the case the flowering failure recurrence rate would be once in 18 years for Black
212 Box and once in 7.4 years for River Red-gum.

213

214 Based on the most probable months of commencement and cessation of flowering (Table 2);
215 River Red-gum is totally synchronous with that of Black Box. However, when examined on a
216 yearly basis (for the years when there are no missing data), the flowering period of River
217 Red-gum is only totally synchronous with Black Box in 19 out of 25 years (mean = 0.93;
218 range 0.50 to 1.00). Consequently, the overlap of Black Box is less (mean = 0.56; range 0.17
219 to 1.00). In the remaining six years, flowering of Black Box finished earlier than River Red-
220 gum by two months in 1934 and one month in 1935, 1961 and 1969 and later in 1945 and
221 1949 (one and two months, respectively) one month later. The synchrony of individual years
222 ranges from 0.50 to 1.00 (mean = 0.74) between the two species.

223

224 Synchronicity was also shown by a cross-correlation plot of the River Red-gum and Black
225 Box scores as a function of monthly lag (Fig. 2). The peak in cross-correlation at 12, 24 and
226 36 months reflects the high synchronicity of December flowering. The smoothly curved
227 behaviour of the plot at 6, 18 and 24 months reflects that there is a longer period in which
228 River Red-gum does not flower and Black Box may or may not flower. Therefore, the species
229 are highly synchronous in peak flowering but not synchronous in their non-flowering.

230

231 **Flowering cycles and independence**

232 There was a weak, positive correlation ($\tau = 0.249$, $p = 0.039$) between the annual maxima
233 value of River Red-gum flowering and Black Box flowering. Therefore, it is likely that a
234 good flowering year for River Red-gum is a good flowering year for Black Box as well.
235 There was a weakly negative correlation between percentage of the forest flooded and
236 maximum value of flowering for both species, but this was not statistically significant (River
237 Red-gum $\tau = -0.149$, $p = 0.21$; Black Box $\tau = -0.198$, $p = 0.099$).

238

239 The autocorrelation between maximum annual flowering score for River Red-gum and Black
240 Box, respectively is shown in Figure 3. There is some indication of anti-cyclicality in River
241 Red-gum, as shown by a positive score for the two-year lags and a negative autocorrelation
242 for the one and three-year lags. Examination of the data showed that good flowering years of
243 River Red-gum tend to be followed by weaker years, although the species still flowers. SSA
244 also detected a very weak two-year flowering intensity signal (reconstructed series 8 and 9)
245 accounting for 2.9% of the variation in the data. There was no evidence of this, however, in
246 Black Box (by either autocorrelation or SSA), the score achieved in a given year appears to
247 be independent of that achieved in the previous year. SSA clearly identifies an annual cycle
248 (reconstructed series 2 and 3, Fig. 4.) within both species and in the flooding, accounting for
249 30.6% of the variation in Black Box, 23.7% in River Red-gum and just 8.2% in the flooding
250 series. The change in amplitude also indicates variation in the intensity flowering and
251 flooding within these cycles.

252

253 The autocorrelation functions for River Red-gum and Black Box flowering scores, as a
254 function of the monthly lag show a very strong annual cyclicality with maximum
255 autocorrelation being achieved at 12, 24, and 36 months. This is indicated by the peaks of the
256 autoregression coefficients at these time periods (Fig. 5). The autocorrelation values for both
257 species show similar behaviour, reflecting their synchrony in flowering. A consistent
258 difference is also apparent in the behaviour of the negative autocorrelation evident at 6, 18,
259 and 30 months. This reflects the longer period for which River Red-gum is not flowering
260 compared to Black Box (i.e., there is a much more sharply defined period for which Black
261 Box is not flowering than River Red-gum). An inference from this, for Black Box at least, is
262 that investigation of the periods when it is not flowering and the associated causal factors
263 may be equally illuminating as studying the period of flowering.

264

265 **Flooding and flowering**

266 The data sequences of flowering for the two species, the monthly flow in the River Murray at
267 Tocumwal, New South Wales, and the estimate of the percentage of forest flooded at that
268 time are illustrated in Figure 6. The cyclic nature of each of these variables is evident.

269

270 There was a weakly negative correlation between the percentage of the forest flooded and
271 maximum value of flowering for both species, but this was not statistically significant (River
272 Red-gum $\tau = -0.149$, $p = 0.21$; Black Box $\tau = -0.198$, $p = 0.099$).

273

274 The cumulative plots (Fig. 7) reveal that Black Box consistently achieves a higher cumulative
275 flowering score than River Red-gum (which reflects its long flowering period). Flowering of
276 both species, however, is aligned in that a good flowering period for River Red-gum tends to
277 also be a good flowering period for Black Box and vice versa. In addition, the cumulative
278 plots indicate that flowering behaviour is not homogeneous over longer time periods, with
279 differing behaviour evident over about thirteen-year blocks. Thus, for the period from 1934 to
280 about 1946 the flowering of both species was the most intense. From 1947 to about 1959 the
281 flowering was, on average, least intense for both species. The remaining period can be
282 viewed as intermediate. The accumulated plot of flooding percentage shows that the period of
283 least intense flowering corresponded to a period of substantial flooding, but this agreement is
284 not perfect. Analyses using the other flow variables give similar results. Therefore, heavy
285 flooding appears to be associated with relatively low flowering in both Black box and River
286 Red-gum, but the agreement is not close enough to infer “cause and effect.”

287

288 The reduction in flowering intensity during flooding, however, is supported by the results of
289 the cross correlation of the trends delineated by SSA (Fig. 8: in Black Box the three periods
290 of flowering intensity are clearly seen, less so in River Red-gum). At zero lag, Black Box is
291 more strongly negatively influenced ($\rho = -0.72$; $P = 0.05$) than River Red-gum ($\rho = -0.44$; $P <$
292 0.05) by flooding. The trend accounts for a large amount of the variance in flooding (52.2%)
293 but less so in flowering of Black Box (31.7%) and River Red-gum (14.9%). It should also be
294 noted that SSA indicates that there is an overall reduction in flowering intensity in both the
295 species examined over the observation period.

296

297 **DISCUSSION**

298

299 **Flowering periods**

300 The results present an interesting historical picture of two species more or less working in
301 synchrony but also functioning with rather different modalities. River Red-gum has a closely
302 defined flowering period and evidence of flowering more intensely every second year Black
303 Box has a much longer duration of flowering, is more uniform in its behaviour, and its
304 flowering behaviour appears not to be influenced by its behaviour in a previous year.

305

306 The flowering period within River Red-gum is location dependent (Paton *et al.* 2004; Wykes
307 1947). In general, this is attributable to variation in climate and geographical influences at
308 sites (Ashton 1975; Griffin 1980; Rawal *et al.* 2015) and specifically to genetic variation
309 between subspecies (McDonald *et al.* 2009). Along the Murray River and therefore within
310 Barmah only the subspecies *camaldulensis* occurs (McDonald *et al.* 2009). This subspecies
311 has been recorded as being in flower in each month of the year (Dexter 1967; George 2004).
312 Over the 40-year observation period of this study, River Red-gum was recorded flowering
313 between September and March. However, flowering in March and September occurred only
314 once in 1935 and 1939, respectively. The early flowering in September was attributed to the
315 “... *excellent bud development early in the year it was expected that flowering would have*
316 *commenced much earlier*” by the Forest Officer. The most probable flowering period
317 delineated in this study is December and January ($\geq 50\%$ chance of flowering (Keatley *et al.*
318 1999)), this agrees with that reported by others (Beuhne 1922; George 2004; Somerville and
319 Nicholson 2005) as well as being in agreement with Colloff (2014) who undertook
320 observations in Barmah. Dexter (1967) also studied flowering in Barmah and found the major
321 flowering period to be between November and January.

322

323 The agreement with other studies on the flowering range of Black Box is less-evident. As
324 with River Red-gum, Black Box has also been recorded flowering in each month of the year
325 (Boland *et al.* 2006; George 2004; Jensen *et al.* 2007; Somerville and Nicholson 2005). In
326 Black Box some of this variation is likewise attributable to different locations (Roberts and
327 Marston 2011) where flowering might occur opportunistically in relation to rainfall and flood
328 (Parsons and Zubrinich 2010).

329

330 In this study Black Box has a nine month range from August to April. Flowering in August
331 was only recorded twice over the observation period in 1939 and 1966 and in April just once
332 in 1966. The most probable months of flowering are October to January: hence a spring and
333 summer main flowering season. An eight-month range of June to January was recorded by

334 Boomsma (1972) with the main period being October to November. Other flowering periods
335 are noted as January to February (Beuhne 1922), January to March (Somerville and
336 Nicholson 2005) and April to January (Jensen 2008). Intense spot-flowering has been
337 recorded in the months of June, September and December in Black Box which has received
338 environmental watering in the Lower Murray Valley (Jensen and Walker 2017).

339

340 **Flowering synchrony**

341 Flowering within River Red-gum is usually within the flowering period of Black Box with
342 both species peak flowering occurring in the same month indicating facilitation in relation to
343 attracting pollinators, rather than competition - particularly given that the flowering pattern is
344 positively skewed. A positively skewed pattern indicates the majority of flowers being
345 opened rapidly at the beginning of a flowering period to enable potential pollinators to
346 quickly adjust to an unaccustomed food source (Makino and Sakai 2007; Thomson 1980) and
347 pollinators then remaining faithful to the plant even as the number of flowers decline. This
348 pattern may also ensure that the majority of seeds are available as soon as possible (Forrest
349 and Thomson 2009; Keatley and Hudson 1998).

350

351 Black Box flowering was either normally distributed or positively skewed. The normal
352 distribution implies that early or late flowers should have access to fewer pollinators but with
353 less competition for them (Elzinga *et al.* 2007; Wyatt 1982).

354

355 **Flowering cycles and intensity**

356 SSA and autocorrelation clearly identify the annual cycle of flowering within both species.
357 Each method also indicates flowering in River Red-gum was more intense every second year
358 Cycles in flowering intensity are known in eucalypts (Ashton 1975; Hudson and Keatley
359 2010; Hudson *et al.* 2011; Law *et al.* 2000) which is in part explained by cycles in budding
360 (Hudson *et al.* 2015). In River Red-gum a two year cycle within individuals has long been
361 reported (Beuhne 1922; Jensen *et al.* 2007; Paton *et al.* 2004; Rayment 1916; Somerville and
362 Nicholson 2005). However, this current study examines flowering intensity at the population
363 level. Therefore, it is not surprising that the contribution to the variation indicated by either
364 method is quite small but significant.

365

366 Only an annual flowering cycle was detected for Black Box in this study. In general at the
367 population level, this seems to be the case; Boomsma (1972) using a 19 year observation

368 period for Black Box only found evidence of an annual cycle. At the individual level biennial
369 flowering has been noted (Beuhne 1922; Jensen *et al.* 2007).

370

371 Additionally, flowering in both species became less intense over the observation period;
372 whether this has remained the case is not known and could only be determined if
373 phenological monitoring was again undertaken. Methods could follow those are previously
374 undertaken or those detailed in Bassett (2014) or possibly a combination of both. It is
375 tempting to suggest that the reduction is related, at least in part, to the shift in flooding regime
376 post-construction of the Hume Reservoir (Dexter *et al.* 1986). Various analyses (e.g., Bren
377 1988a; Colloff 2014) have quantified changes in the flooding regime of the River Murray
378 since the advent of river regulation began with the first filling of Hume Weir in 1934. In
379 general, these have shown a decrease in the number of larger winter-spring floods, an
380 increase in the variability of these floods compared to the natural river, and a substantial
381 increase in summer flooding in near-river environments associated with “rejections” of
382 irrigation flows in summer.

383

384 **Flooding and flowering**

385 Although flooding is a requirement to maintain the health of both tree species and their
386 flowering, extended flooding can cause stress (Kozlowski 1997; Roberts and Marston 2011)
387 which can result in less buds, flowers and fruits (Kozlowski 1997). Drought-stressed Black
388 Box and River Red-gum trees are also known to flower less and produce smaller buds
389 (Blackwood *et al.* 2010; George 2004; Somerville and Nicholson 2005).

390

391 In this study, the period which coincides with the least intense flowering (approximately 1947
392 to about 1959) occurred when the forest was effectively flooded (effective flooding only
393 considers months May to December (Dexter *et al.* 1986)) in 10 out of the 13 years (Dexter *et*
394 *al.* 1986) (see Fig. 6). On three occasions, 1952, 1955 and 1956, the effective flooding
395 duration was greater than 6 months with the period 1955 to 1956 being when the forest was
396 flooded continuously (Bren 1987). For the two more intense flowering periods (1934 to 1946
397 and 1960 to 1973) the forest was effectively flooded 7 times with a median of three months in
398 both periods (Dexter *et al.* 1986) (Fig. 6). In these two periods the maximum effective
399 flooding was five months in 1935, 1939, 1964 and 1973. They also include two extended dry
400 periods of approximately 18 months for much of the forest in 1944 and 1967 (Bren 1987;
401 Dexter *et al.* 1986).

402

403 As the condition of forests and woodlands have been deteriorating within the Murray Darling
404 Basin (Chesterfield 1986; Cunningham *et al.* 2007; Dexter 1967; Mac Nally *et al.* 2014; Wen
405 *et al.* 2009) much work has been undertaken to determine the water regime to optimally
406 maintain and improve their condition (e.g. Catelottia *et al.* 2015; Doody *et al.* 2015; George
407 2004; Roberts and Marston 2011; Wen *et al.* 2009). The flooding frequency and flooding
408 durations during the more intense flowering periods broadly align with these. To maintain
409 their condition River Red-gum forests require a range of three to seven months duration with
410 a flooding frequency ranging from four to seven years out of ten (Catelottia *et al.* 2015;
411 Doody *et al.* 2015; Murray–Darling Basin Authority 2012; DSE 2008 in Roberts and Marston
412 2011; Ward and Colloff 2010). However, an upper flooding frequency threshold of 9 years
413 out of ten has been nominated by the Murray-Darling Basin Authority (2012). Not
414 surprisingly, the requirements for woodlands is less: a duration of one to four months with a
415 flooding frequency ranging from three years to five years out of ten (with a preference for
416 flooding to occur over winter and spring (Murray–Darling Basin Authority 2012; DSE 2008
417 in Roberts and Marston 2011; Ward and Colloff 2010). Each of the flood frequency values
418 with the exception of the Murray-Darling Basin Authority’s is less frequent than the least
419 intense flowering period.

420

421 The flooding frequency suggested for Black Box ranges from 1 in 10 to 10 in 22 years (Bren
422 2005; Murray–Darling Basin Authority 2012; Roberts and Marston 2011). For Black Box a
423 range of two to six months of flooding is nominated as a requirement for maintaining
424 moderate to vigorous flowering (Roberts and Marston 2011; Rogers 2011) whereas the
425 Murray-Darling Basin Authority advises one to three months specifically for Barmah
426 (Murray–Darling Basin Authority 2012). Rogers (2011) suggests two to four months for
427 inundation with a cut point of 4 months of inundation as it results in reduced reproductive
428 success attributed to a flood adaption response of stomatal closure and increased
429 transpiration. A contributing factor could be soil type as stress was observed after 2.5 months
430 on sodic clays (Akeroyd *et al.* 1998). The flooding frequency and inundation during the least
431 intense flowering period exceeded these values.

432

433 **CONCLUSIONS**

434 The 40-year data sequence examined has enabled the flowering patterns of both these species
435 over that interval to be established and indicates that they flower more or less in synchrony. It

436 also showed that flowering in both species has become less intense over the observation
437 period. Determining whether this reduction is related to the change in flooding regime is
438 worthy of future research. There is an indication, more so for Black Box than River Red-gum,
439 that flooding in 10 out of the 13 years with inundation greater than 6 months has a depressive
440 effect on its flowering intensity while flooding in 7 out of 13 years with inundation of no
441 greater than 5 months enhances flowering intensity. However, as flooding is a recurrent event
442 (in this data set) it is difficult to isolate the effect of a single flood.

443

444 **ACKNOWLEDGEMENT**

445 We thank the Forest Officers who collected the original data and Eucalypt Australia for their
446 support in the digitizing of the flowering data. We also thank the reviewers for their time in
447 critically reading the manuscript and providing constructive comments.

448

449 **REFERENCES**

- 450 Akeroyd M. D., Tyerman S. D., Walker G. R. & Jolly J. D. (1998) Impact of flooding on the
451 water use of semi-arid eucalypts. *J. Hydrol.* **206**, 104-17.
- 452 Ashton D. H. (1975) Studies of flowering behaviour in *Eucalyptus regnans* F. Muell. *Aust. J.*
453 *Bot.* **23**, 399-411.
- 454 Bassett O. D. (2014) *Seed Crop Monitoring and Assessment. Native Forest Silvicultural*
455 *Guidelines No 1.* Dept of Primary Industries, Victoria.
- 456 Beuhne F. R. (1922) *The Honey Flora of Victoria.* Department of Agriculture, Melbourne.
- 457 Blackwood A., Kingsford R. T., Nairn L. & Rayner T. (2010) The effect of river red gum
458 decline on woodland birds in the Macquarie Marshes. School of Biological,
459 Environmental and Earth Sciences, University of New South Wales, Sydney.
- 460 Boland D. J., Brooker M. I. H., Chippendale G. M., Hall N., Hyland B. P. M., Johnston R. D.,
461 Kleinig D. A., McDonald M. W. & Turner J. D. (2006) *Forest Trees of Australia.* CSIRO
462 Publishing, Melbourne.
- 463 Boomsma C. D. (1972) *Native trees of South Australia. Bulletin No 19.* Woods and Forests
464 Department, South Australia.
- 465 Bren L. J. (1987) The duration of inundation in a flooding river red gum forest. *Aust. For.*
466 *Res.* **17**, 191-202.

- 467 Bren L. J. (1988a) Effects of river regulation on flooding of a riparian red gum forest on The
468 River Murray, Australia. *Regul. River* **2**, 65-77.
- 469 Bren L. J. (1988b) Flooding characteristics of a riparian red gum forest. *Aust. For.* **51**, 57-
470 62.
- 471 Bren L. J. (2005) The changing hydrology of the Barmah-Millewa forests and its effects on
472 vegetation. *Proc. Roy. Soc. Victoria* **117**, 61-76.
- 473 Bren L. J. & Gibbs N. L. (1986) Relationships between flood frequency, vegetation and
474 topography in a River Red Gum forest. *Aust. For. Res.* **16**, 357-70.
- 475 Catelottia K., Kingsford R. T., Bino G. & Bacon P. (2015) Inundation requirements for
476 persistence and recovery of river red gums (*Eucalyptus camaldulensis*) in semi-arid
477 Australia. *Biol. Conserv.* **184**, 346–56.
- 478 Chesterfield E. A. (1986) Changes in the vegetation of the river red gum at Barmah, Victoria.
479 *Aust. For.* **49**, 4-15.
- 480 Colloff M. J. (2014) *Flooded Forest and Desert Creek: Ecology and History of the River Red*
481 *Gum*. CSIRO Publishing, Collingwood.
- 482 CSIRO. (2008) Water availability in the Murray-Darling Basin. A report to the Australian
483 Government from the CSIRO Murray-Darling Basin Sustainable Yields Project. CSIRO,
484 Canberra, ACT, Australia.
- 485 Cunningham S. C., Read J., Baker P. J. & Mac Nally R. (2007) Quantitative assessment of
486 stand condition and its relationship to physiological stress in stands of *Eucalyptus*
487 *camaldulensis* (Myrtaceae). *Aust. J. Bot.* **55**, 692-9.
- 488 Dexter B. D. (1967) Flooding and regeneration of River Red Gum, *Eucalyptus*
489 *camaldulensis*, Dehn. Forests Commission of Victoria, Melbourne.
- 490 Dexter B. D. (1978) Silviculture of the River red gum forests of the central Murray flood
491 plain. *Proc. Roy. Soc. Victoria* **90**, 175-91.
- 492 Dexter B. D., Rose H. J. & Davies N. (1986) River regulation and associated forest
493 management problems in the River Murray red gum forests. *Aust. For.*, 16-27.
- 494 Doody T. M., Colloff M. J., Davies M., Koul V., Benyon R. G. & Nagler P. L. (2015)
495 Quantifying water requirements of riparian river red gum (*Eucalyptus camaldulensis*) in

- 496 the Murray–Darling Basin, Australia – implications for the management of environmental
497 flows. *Ecohydrology* **8**, 1471-87.
- 498 Elzinga J. A., Atlan A., Biere A., Gigord L., Weis A. E. & Bernasconi G. (2007) Time after
499 time: flowering phenology and biotic interactions. *Trends Ecol. Evol.* **22**, 432-9.
- 500 Forrest J. & Thomson J. D. (2009) Pollinator experience, neophobia and the evolution of
501 flowering time. *Proc. R. Soc. B* **276**, 935-43.
- 502 George A. K. (2004) Eucalypt regeneration on the Lower Murray floodplain, South Australia.
503 PhD thesis, *School of Earth and Environmental Studies*. The University of Adelaide.
- 504 Golyandina N. & Zhigljavsky A. (2020) *Singular Spectrum Analysis for Time Series*.
505 Springer-Verlag, Berlin Heidelberg.
- 506 Griffin A. R. (1980) Floral phenology of a stand of mountain ash (*Eucalyptus regnans* F.
507 Muell.) in Gippsland, Victoria. *Aust. J. Bot.* **28**, 393-404.
- 508 Hollander M., Wolfe D. A. & Chicken E. (2013) *Nonparametric Statistical Methods*. John
509 Wiley and Sons, Hoboken, New Jersey.
- 510 Hudson I., Kang I. & Keatley M. (2015) Wavelet characterisation of eucalypt flowering and
511 the influence of climate and budding. In: *Partnering with industry and the community for
512 innovation and impact through modelling. MODSIM2015, 21st International Congress on
513 Modelling and Simulation* (eds T. Weber, M. J. McPhee and R. S. Anderssen) pp. 1813–9.
514 Modelling and Simulation Society of Australia and New Zealand, Gold Coast.
- 515 Hudson I. L. & Keatley M. R. (2010) Singular spectrum analysis: climatic niche
516 identification. In: *Phenological Research: Methods for environmental and climate change
517 analysis* (eds I. L. Hudson and M. R. Keatley) pp. 393-424. Springer, Dordrecht.
- 518 Hudson I. L., Keatley M. R. & Kang I. (2011) Wavelet characterization of eucalypt flowering
519 and the influence of climate. *Environ. Ecol. Stat.* **18**, 513-33.
- 520 Jensen A. E. & Walker K. F. (2017) Sustaining recovery in red gum, black box and lignum in
521 the Murray River Valley: clues from natural phenological cycles to guide environmental
522 watering. *Trans. R. Soc. S. Aust.* **141**, 209-29.
- 523 Jensen A. E., Walker K. F. & Paton D. C. (2007) Using phenology of eucalypts to determine
524 environmental watering regimes for the River Murray floodplain, South Australia. In:
525 *Proceedings of the 5th Australian Stream Management Conference. Australian rivers:*

- 526 *making a difference.* (eds A. L. Wilson, R. L. Dehaan, R. J. Watts, K. J. Page, K. H.
527 Bowmer and A. Curtis) pp. 175-80, Charles Sturt University, Thurgoona, New South
528 Wales.
- 529 Keatley M. R. & Hudson I. L. (1998) The influence of fruit and bud volumes on Eucalypt
530 flowering: An exploratory analysis. *Aust. J. Bot.* **46**, 281-304.
- 531 Keatley M. R. & Hudson I. L. (2007) A comparison of the long-term flowering patterns of
532 Box-Ironbark species in Havelock and Rushworth forests. *Environ. Model. Assess.* **12**,
533 279-92.
- 534 Keatley M. R., Hudson I. L. & Fletcher T. D. (1999) The use of long-term records for
535 describing flowering behaviour: A case-study in Victorian Box-Ironbark Forests. In:
536 *Australia's Ever-changing Forests IV* (eds J. Dargavel and B. Wasser) pp. 311-28.
537 Australian University Press, Canberra.
- 538 Keatley M. R., Hudson I. L. & Fletcher T. D. (2004) Long-term flowering synchrony of Box-
539 Ironbark eucalypts. *Aust. J. Bot.* **52**, 47-54.
- 540 Keith D. A., Rodríguez J. P., Rodríguez-Clark K. M., Nicholson E., Aapala K., Alonso A.,
541 Asmussen M., Bachman S., Basset A., Barrow E. G., Benson J. S., Bishop M. J.,
542 Bonifacio R., Brooks T. M., Burgman M. A., Comer P., Comín F. A., Essl F., Faber-
543 Langendoen D., Fairweather P. G., Holdaway R. J., Jennings M., Kingsford R. T., Lester
544 R. E., Mac Nally R., McCarthy M. A., Moat J., Oliveira-Miranda M. A., Pisanu P., Poulin
545 B., Regan T. J., Riecken U., Spalding M. D. & Zambrano-Martínez S. (2013) Scientific
546 foundations for an IUCN Red List of ecosystems. *PLoS ONE* **8**, e62111.
- 547 Kozłowski T. T. (1997) Responses of woody plants to flooding and salinity. *Tree Physiology*
548 *Monograph No. 1*, 1-17.
- 549 Law B., Mackowski L. & Tweedie T. (2000) Flowering phenology of myrtaceous trees and
550 their relation to climate, environmental and disturbance variables in northern New South
551 Wales. *Austral Ecol.* **25**, 160-78.
- 552 Mac Nally R., Cunningham S. C., Baker P. J., Horner G. J. & Thomson J. R. (2011)
553 Dynamics of Murray-Darling floodplain forests under multiple stressors: The past,
554 present, and future of an Australian icon. *Water Resour. Res.* **47**.

- 555 Mac Nally R., Lada H., Cunningham S. C., Thomson J. R. & Fleishman E. (2014) Climate-
556 change-driven deterioration of the condition of floodplain forest and the future for the
557 avifauna. *Global Ecol. Biogeogr.* **23**, 191–202.
- 558 Makino T. T. & Sakai S. (2007) Experience changes pollinator responses to floral display
559 size: from size-based to reward-based foraging. *Func. Ecol.* **21**, 854–63.
- 560 McDonald M. W., Brooker M. I. H. & Butcher P. A. (2009) A taxonomic revision of
561 *Eucalyptus camaldulensis* (Myrtaceae). *Aust. Syst. Bot.* **22**, 257–85.
- 562 Moxham C., Duncan M. & Moloney P. (2018) Tree health and regeneration response of
563 Black Box (*Eucalyptus largiflorens*) to recent flooding. *Ecol. Manag. Restor.* **19**, 58–65.
- 564 Murray–Darling Basin Authority. (2012) Barmah–Millewa Forest: Environmental Water
565 Management Plan. Murray–Darling Basin Authority, Canberra.
- 566 Newell G., White M. & Griffioen P. (2009) Potential impacts of a changing climate on
567 selected terrestrial ecosystems of Northern Victoria. Arthur Rylah Institute for
568 Environmental Research, Heidelberg, Victoria.
- 569 Parsons R. F. & Zubrinich T. M. (2010) The green-leaved variant of *Eucalyptus largiflorens*:
570 a story involving hybridization and observant local people. *Cunninghamia* **11**, 413–6.
- 571 Paton D. C., Crossfield E. L., Hurrell B. & Rogers D. J. (2004) *Floral Resources used by the*
572 *South Australian Apiary Industry*. Rural Industries Research and Development
573 Corporation, Barton, ACT.
- 574 Rawal D. S., Kasel S., Keatley M. R. & Nitschke C. R. (2015) Herbarium records identify
575 sensitivity of flowering phenology of eucalypts to climate: implications for species
576 response to climate change. *Austral Ecol.* **40**, 117–25.
- 577 Rayment T. (1916) *Money in bees in Australasia. A practical treatise on the profitable*
578 *management of the Honey Bee in Australasia* Whitcombe and Tombs Ltd, Melbourne.
- 579 Roberts J. (2004) Floodplain forests and woodlands in the southern Murray–Darling Basin.
580 Canberra ACT.
- 581 Roberts J. & Marston F. (2011) *Water regime of wetland and floodplain plains in the*
582 *Murray-Darling Basin. A source book of ecological knowledge*. National Water
583 Commission, Canberra.

- 584 Rogers K. (2011) Vegetation. In: *Floodplain wetland biota in the Murray Darling Basin:*
585 *Water and habitat requirements* (eds K. Rogers and T. J. Ralph). CSIRO Publishing,
586 Collingwood.
- 587 Searcy J. K. & Hardison C. H. (1960) Double-mass curves, manual of hydrology: Part 1.
588 General surface-water techniques. *U.S. Geological Survey Water-Supply Paper 1541-B*,
589 31-65.
- 590 Smith P. & Smith J. (2014) Floodplain vegetation of the River Murray in 1987–1988: an
591 important pre-drought benchmark for subsequent studies *Cunninghamia* **14**, 97–151.
- 592 Somerville D. C. & Nicholson D. (2005) The primary melliferous flora and other aspects
593 associated with beekeeping within State forests of New South Wales as determined by
594 surveys of beekeepers. *Aust. For.* **68**, 9-16.
- 595 Thomson J. D. (1980) Skewed flowering distributions and pollinator attraction. *Ecology* **61**,
596 572-9.
- 597 Ward K. & Colloff M. J. (2010) Ecosystem response modelling for the Barmah-Millewa
598 Forest: the interface between science and management. In: *Ecosystem Response Modelling*
599 *in the Murray-Darling Basin* (eds N. Saintilan and I. Overton). CSIRO Publishing,
600 Collingwood Victoria.
- 601 Wen L., Ling J., Saintilan N. & Rogers K. (2009) An investigation of the hydrological
602 requirements of River Red Gum (*Eucalyptus camaldulensis*) Forest, using Classification
603 and Regression Tree modelling. *Ecohydrology* **2**, 143–55.
- 604 Wyatt R. (1982) Inflorescence architecture: How flower number, arrangement and phenology
605 affect pollination and fruit-set. *Am. J. Bot.* **69**, 585-94.
- 606 Wykes G. R. (1947) Part II: Investigations into Nectar Secretion of Species of the Genus
607 *Eucalyptus*, and the Possible Relationship of Starch Stored in the Sapwood to the Honey
608 Flow. Masters thesis, University of Melbourne.

609

610 **Figures**

611 Fig. 1. Monthly distribution of flowering scores (July to June) for River Red-gum and Black
612 Box.

613

614 Fig. 2. Cross-correlation as a function of months lag between the River Red-gum and the
615 Black Box flooding score.

616

617 Fig. 3. Autocorrelation of maximum flowering score achieved as a function of annual lag.

618

619 Fig. 4. Annual cycle as determined by SSA. Reconstructed series 2 and 3: (A) Black Box, (B)
620 River Red-gum and (C) flooding. Note the different starting points on the x axes.

621

622 Fig. 5. Autocorrelation coefficient of monthly flowering score as a function of monthly lag
623 for River Red-gum and Black Box.

624

625 Fig. 6. River Red-gum and Black Box scores, flow in the River Murray at Tocumwal, and
626 estimated percentage of the Barmah forest flooded for the period of the flowering sequence.

627

628 Fig. 7. Accumulated flowering score for Black Box and River Red-gum, and accumulated
629 monthly percentage of the forest flooded. The values for Black Box and flooding have been
630 scaled by the maximum value achieved. The value for River Red-gum has been scaled by the
631 maximum value achieved by Black Box to show the parity of flowering.

632

633 Fig. 8. SSA trend results for River Red-gum, Black Box and monthly flooding (note the
634 different scales on both vertical axes). The trends highlight the decline in flowering intensity,
635 more evident in River Red-gum, over the observation period.

636

637 **Tables**

638

639 **Table 1.** Terms used to describe flowering intensity and their assigned value (after Keatley
640 and Hudson 2007).

641

642 **Table 2.** Flowering behaviour of River Red-gum and Black Box.

Observation parameter	Description	Assigned Value
Quantity	No flowering	0
	Very scattered or isolated	0.5
	Light Flowering	1
	Medium Flowering	2
	Heavy Flowering	3
Distribution	Isolated	0.5
	Scattered	1
	Fairly General	1.5

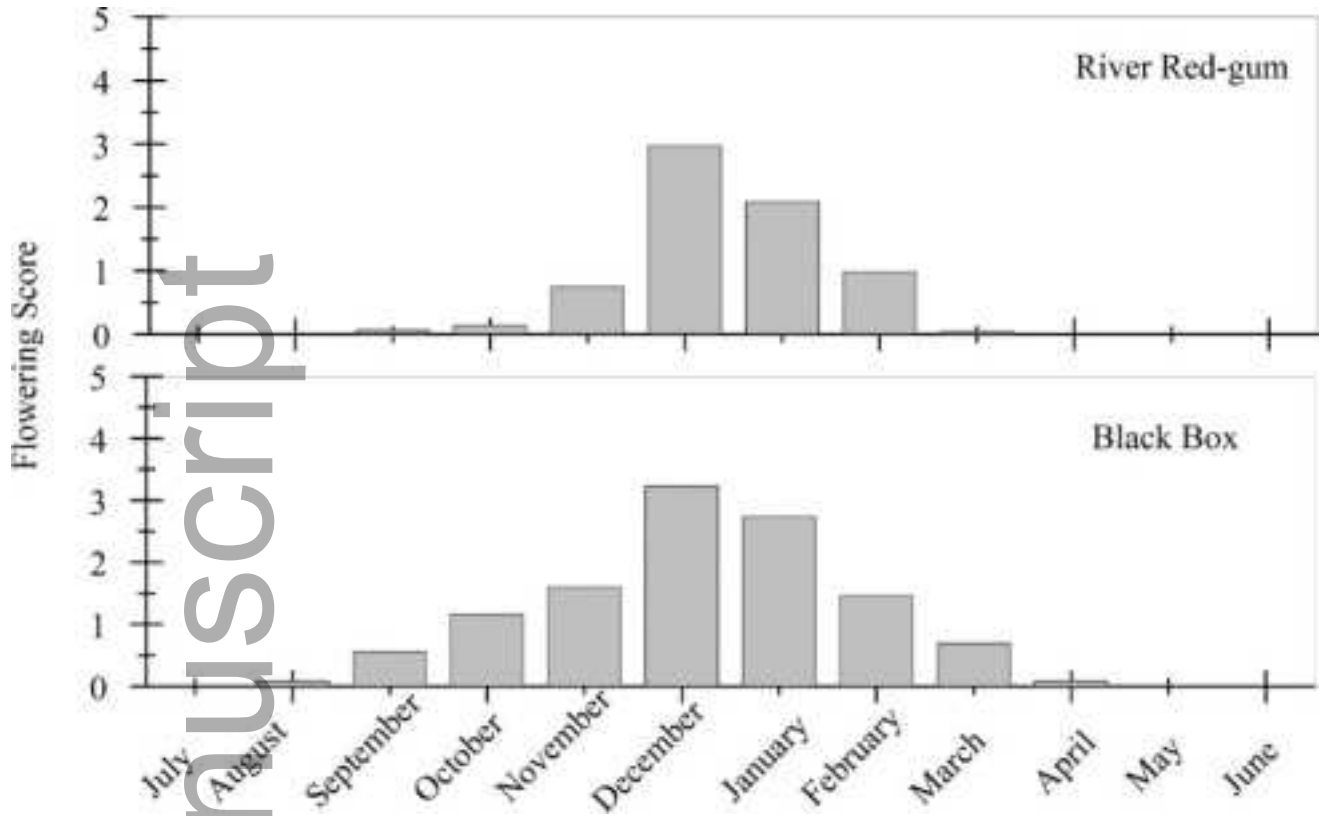
1

Author Manuscript

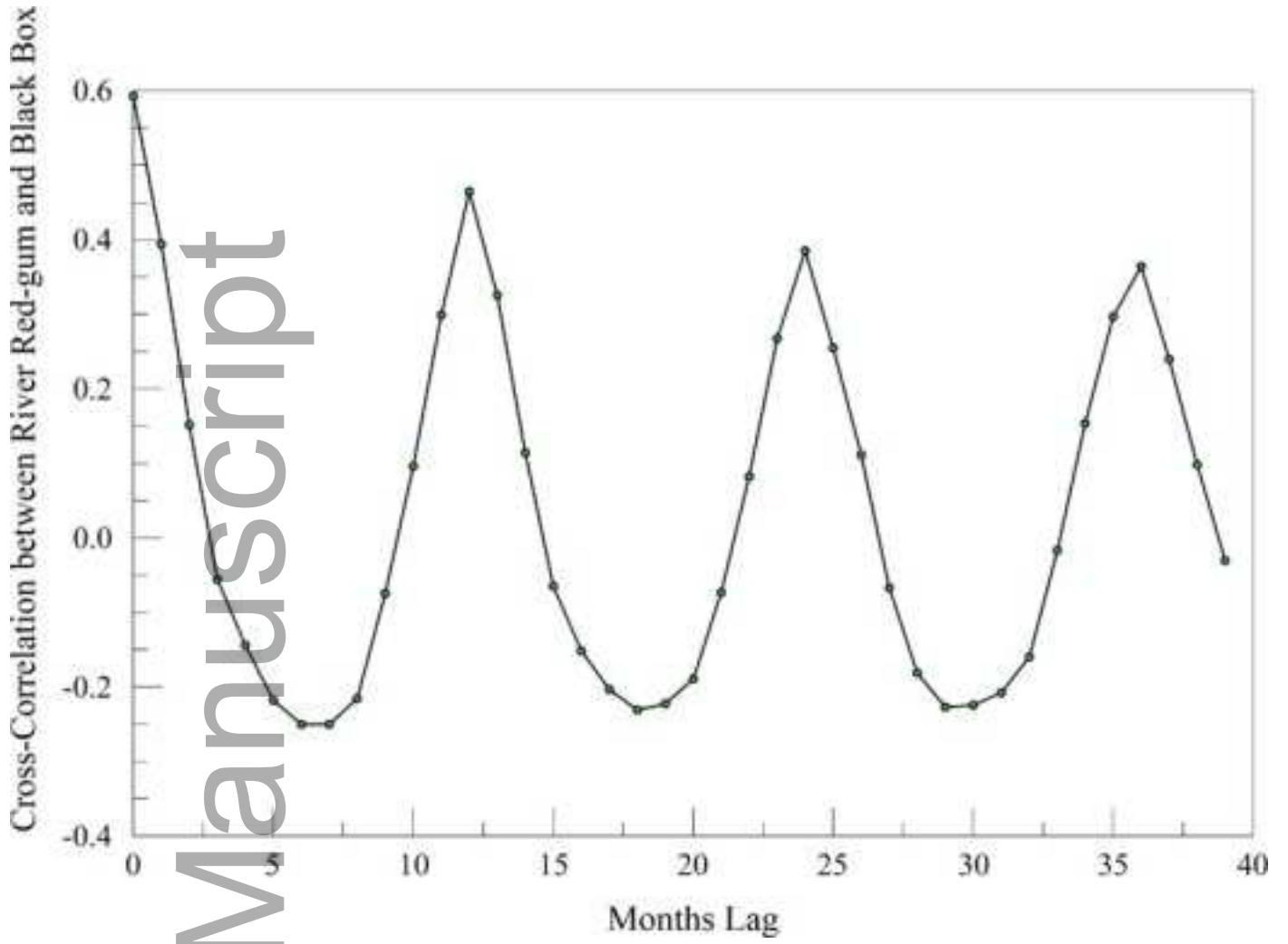
	River Red-gum	Black Box
Missed years (July to June)	1941/42, 1962/63, 1966/67, 1971/72	1971/1972
Annual flowering success	0.89	0.97
Flowering failure recurrence	1 in 9.25 yrs	1 in 36 yrs
Month of peak flowering (intensity)	December	December
Most probable month of commencement (range)	December (Sept to Dec)	Sept, Oct, Dec (Aug to Jan)
Most probable month of cessation (range)	December, January (Dec to Mar)	February (Dec to Apr)
Flowering range	September to March	August to April
Mean flowering period (months)	2.1 ± 1.4	4.0 ± 1.9

1

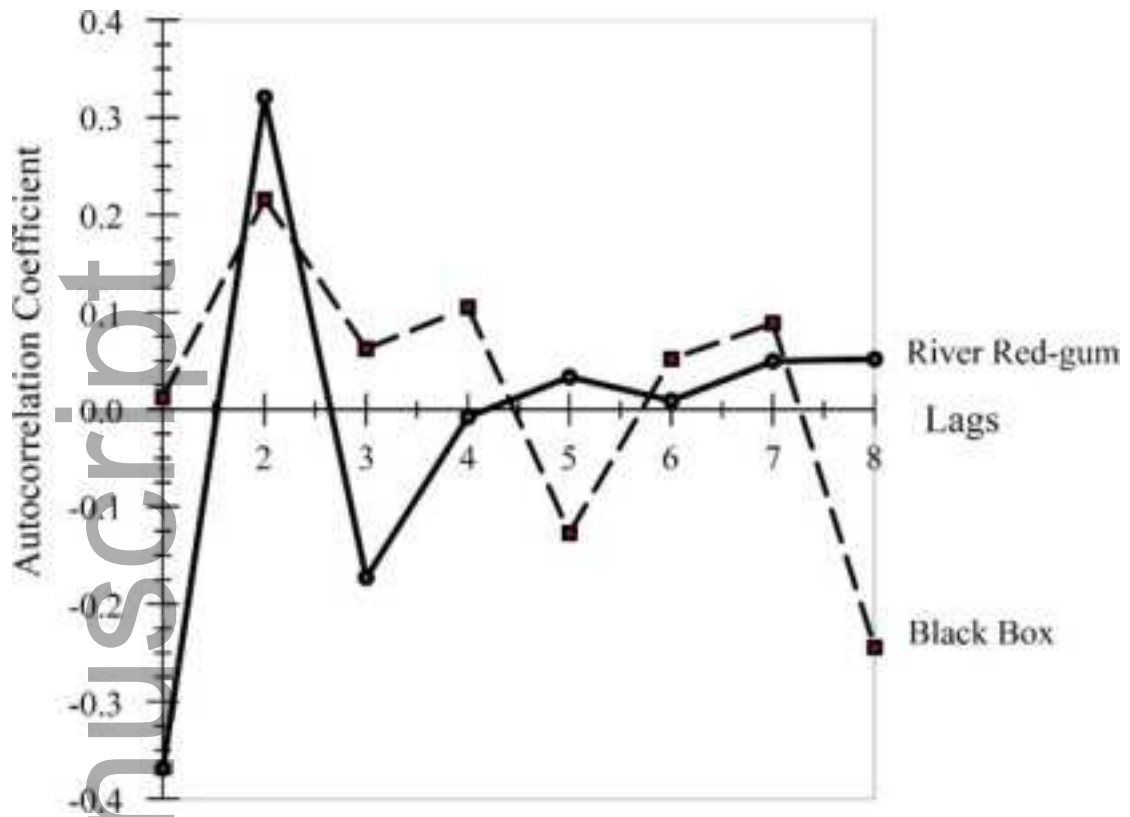
Author Manuscript



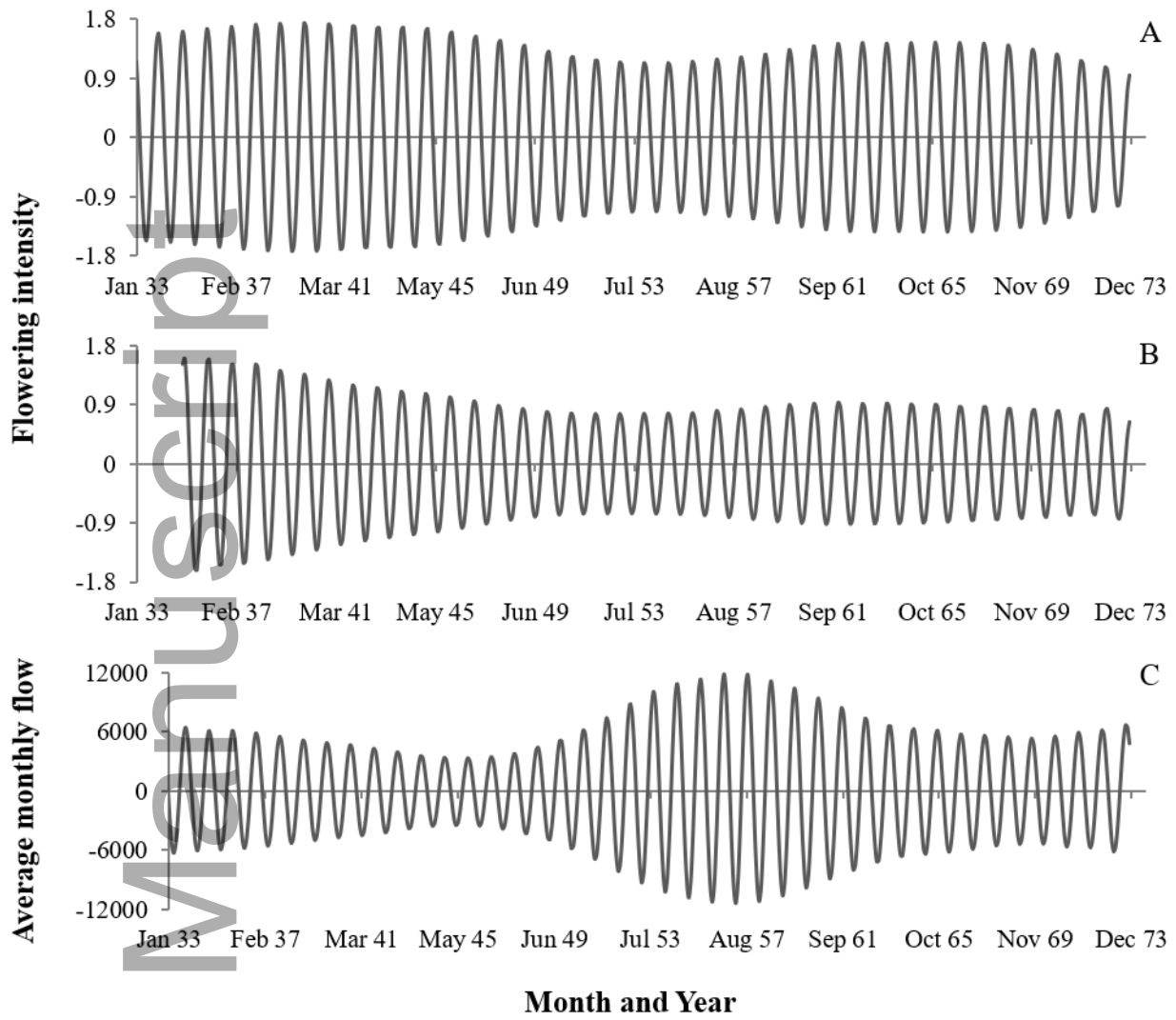
aec_13021_f1.tif



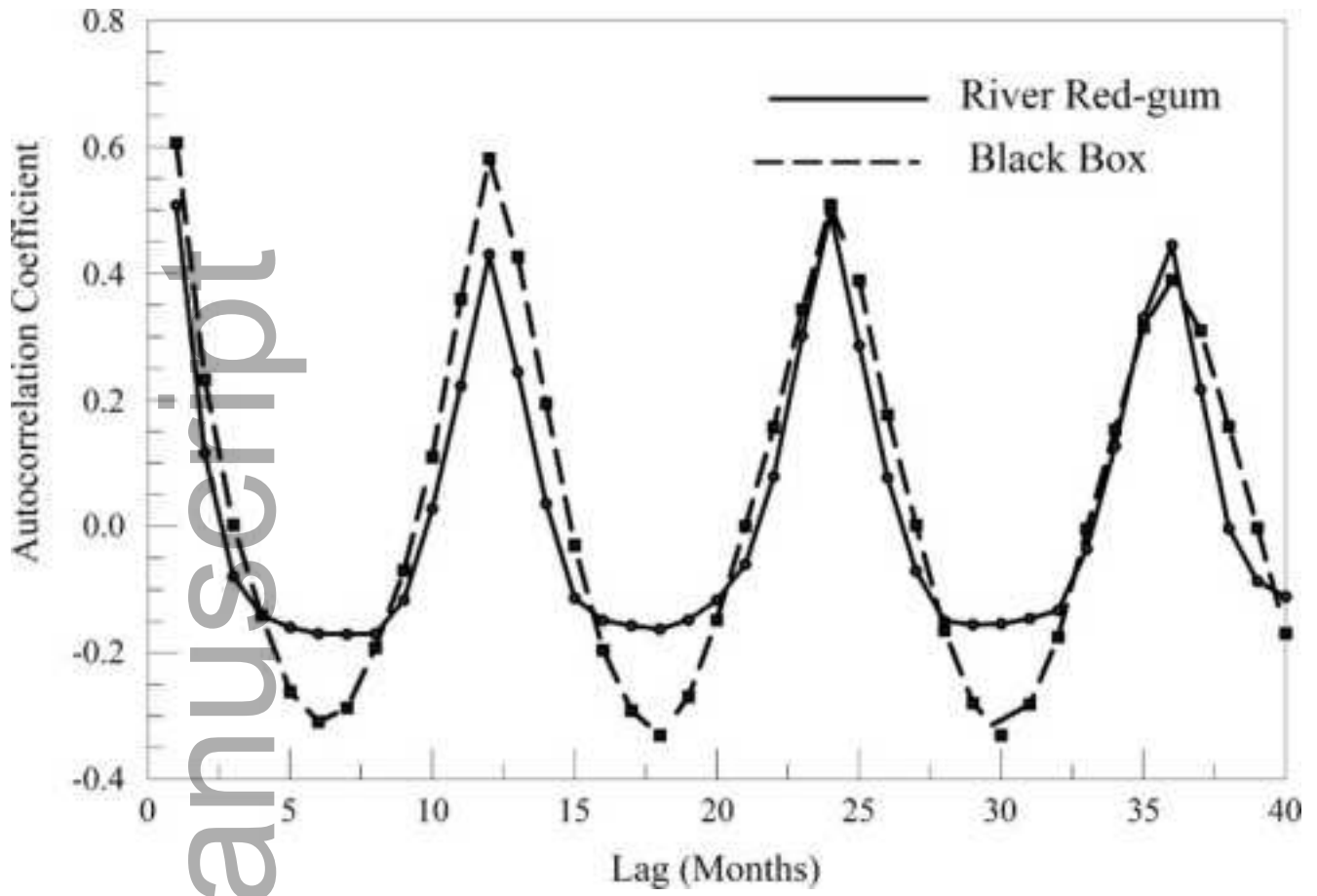
aec_13021_f2.tif



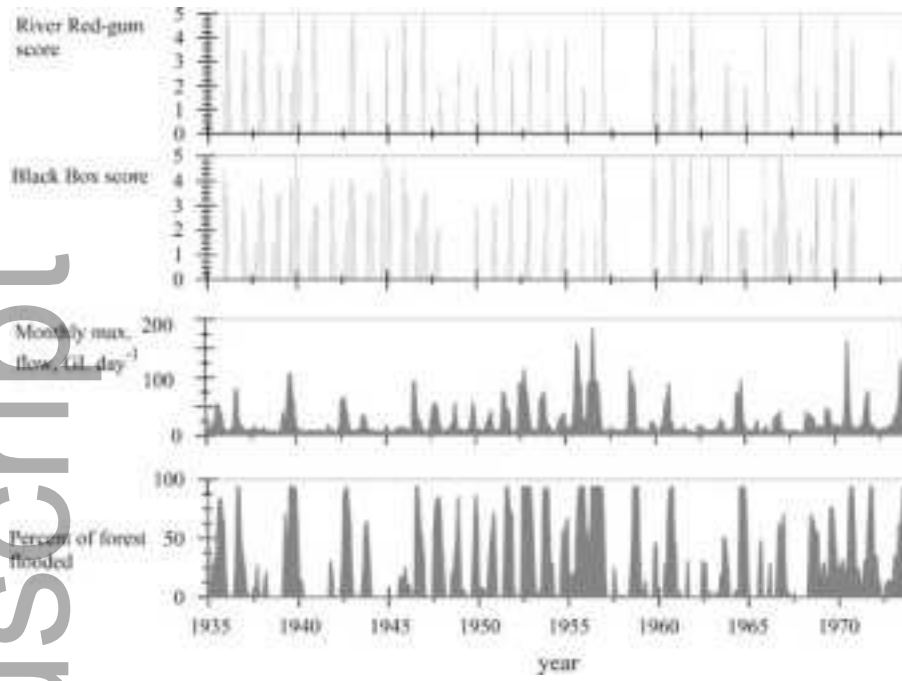
aec_13021_f3.tif



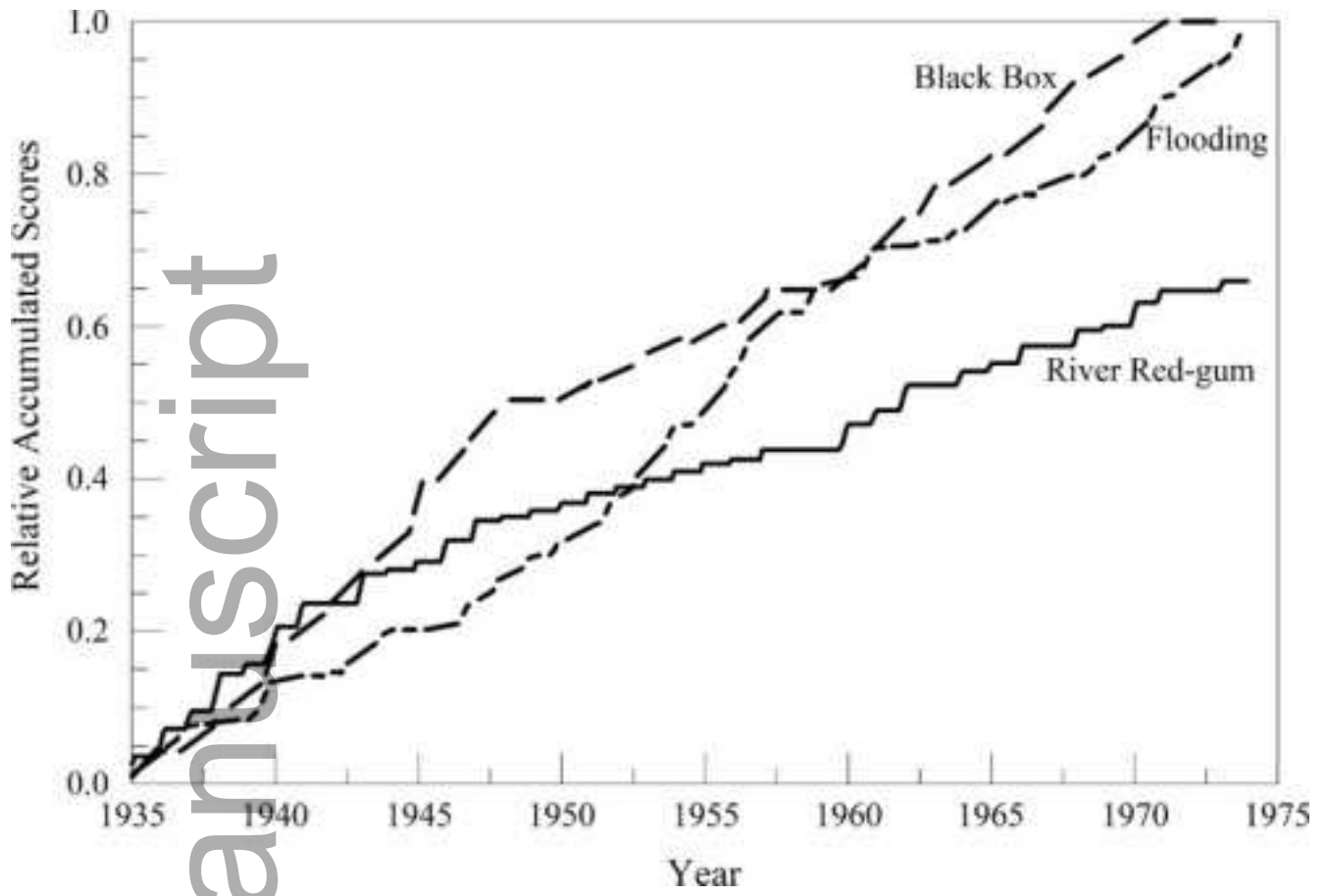
aec_13021_f4.tif



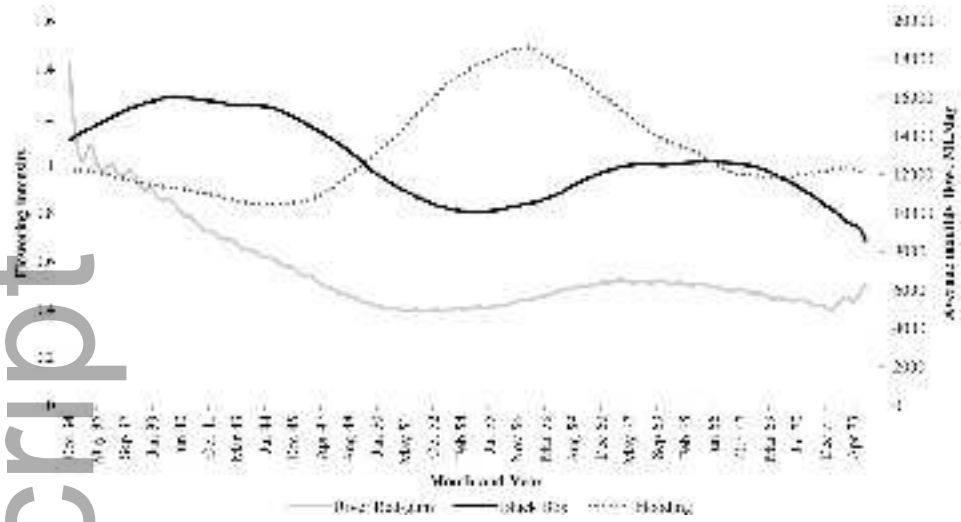
aec_13021_f5.tif



aec_13021_f6.tif



aec_13021_f7.tif



aec_13021_f8.tif