Seed survival of Australian *Acacia* in the Western Cape of South Africa in the presence of biological control agents and given environmental variation

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Abstract

Studies of invasive Australian *Acacia* have shown that many seeds are still produced and accumulate in soil stored seed banks regardless of the presence of seed-targeting biological control agents. This is despite claims of biological control success, although there is generally a lack of data on the seed production of invasive Australian *Acacia* before and after the release of the respective agents. We aimed to quantify seed production and seed survival of invasive Australian *Acacia* currently under biological control. The seed production and survival (proportion of aborted, predated and surviving seeds) of *A. longifolia*, *A. pycnantha* and *A. saligna* were each studied at four to five sites in the Western Cape of South Africa. The relationships between seed production and stand characteristics were determined and the relative effects of seed predation and abortion on seed survival were established. The investigated invasive Australian *Acacia* produced many seeds that survived the pre-dispersal stage despite long-term presence of released biological control agents. It was shown that seed crop size is the only significant factor influencing seed survival of the studied Australian *Acacia* species. Furthermore, the seeds surviving per tree and per square meter were related to tree size. No quantitative evidence was found to suggest that seed-reducing biological control agents are having an impact on the population dynamics of their Australian *Acacia* hosts. This study illustrates the importance of studying the seed ecology of invasive plants before biological control agents are selected and released.

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17 ## Abstract

18 Studies of invasive Australian *Acacia* have shown that many seeds are still produced and

19 accumulate in soil stored seed banks regardless of the presence of seed-targeting biological

20 control agents. This is despite claims of biological control success, although there is generally a

21 lack of data on the seed production of invasive Australian *Acacia* before and after the release of

22 the respective agents. We aimed to quantify seed production and seed survival of invasive

23 Australian *Acacia* currently under biological control. The seed production and survival

24 (proportion of aborted, predated and surviving seeds) of *A. longifolia*, *A. pycnantha* and *A.*

25 *saligna* were each studied at four to five sites in the Western Cape of South Africa. The

26   relationships between seed production and stand characteristics were determined and the relative

27   effects of seed predation and abortion on seed survival were established. The investigated

28   invasive Australian *Acacia* produced many seeds that survived the pre-dispersal stage despite

29   long-term presence of released biological control agents. It was shown that seed crop size is the

30   only significant factor influencing seed survival of the studied Australian *Acacia* species.

31   Furthermore, the seeds surviving per tree and per square meter were related to tree size. No

32   quantitative evidence was found to suggest that seed-reducing biological control agents are

33   having an impact on the population dynamics of their Australian *Acacia* hosts. This study

34   illustrates the importance of studying the seed ecology of invasive plants before biological

35   control agents are selected and released.

36   **Introduction**

37   Assessment of the seed bank dynamics of invasive alien plants provides a framework to

38   determine when control measures would be most effective during population development (e.g.

39   at what stage are seed banks the smallest) to reach management goals (Richardson & Kluge,

40   2008). In addition, it gives an indication to whether control measurements will be successful

41   before they are applied (Kriticos et al., 1999). However, this aspect of the population dynamics

42   of invasive alien plants is generally poorly understood (Gioria et al., 2012). Invasive Australian

43   *Acacia* have become a model system to illustrate the importance of a focus on seed bank

44   dynamics to understand the invasion process as well as to recommend appropriate management

45   interventions (Richardson & Kluge, 2008).

46   Australian *Acacia* are of great commercial value and have been introduced worldwide (Griffin et

47   al., 2011). Many of these plants have become naturalised and a few have become invasive

48   (Richardson et al., 2011). Invasive Australian *Acacia* often cover vast areas of natural and

49   agricultural land (Bar (Kutiel), Cohen & Shoshany, 2004; Henderson, 2007; Marchante, Freitas

50   & Hoffmann, 2011b) and have significant impacts on natural capital (e.g. reduced water

51   availability) (Le Maitre et al., 2011; Rascher et al., 2011; Cohen & Bar (Kutiel), 2017). Their

52   impact has led to chemical and mechanical clearing operations (van Wilgen et al., 2012) and

53   biological control programs (Impson et al., 2011; Marchante, Freitas & Hoffmann, 2011a).

54   Especially, in South Africa many resources have been spent in an effort to control these plants

55   (van Wilgen et al., 2012).

56   The invasive potential of Australian *Acacia* has been attributed to their pre-adaptation to

57   environmental conditions (Roux & Middlemiss, 1963), high growth rates (Witkowski, 1991) and

58   copious seed production (Milton & Hall, 1981; Dennill, 1985; Neser, 1985; Pieterse & Cairns,

59   1986b; Holmes, Dennill & Moll, 1987; Donnelly, 1992; Impson, Moran & Hoffmann, 2004).

60   The prolific production of seeds by invasive Australian *Acacia* has been widely proposed and

61   ascribed to a lack of natural enemies (Van den Berg, 1977; Milton, 1980; Impson, Moran &

62   Hoffmann, 2004; Richardson & Kluge, 2008); however, the natural enemy release hypothesis

63   remains controversial and lacks quantitative proof (Maron & Vila, 2001; Colautti et al., 2004;

64   Parker, Burkepile & Hay, 2006).

65   In contrast to the view that natural enemies are lacking, many studies have demonstrated that

66   Australian *Acacia* seeds may be lost to indigenous insects (Holmes & Rebelo, 1988; Donnelly &

67   Stewart, 1990; Pieterse, 1998), birds (Middlemiss, 1963; Winterbottom, 1970; Glyphis, Milton &

68   Siegfried, 1981; Pieterse, 1986) and mammals (Middlemiss, 1963; Holmes, 1990; Pieterse &

69   Cairns, 1990; Mokotjomela & Hoffmann, 2013). Pieterse (1998) showed that whole seed crops

70   of *A. implexa* may be lost to a native insect. Likewise, Holmes (1990) demonstrated that native

71   rodents have the potential to completely consume annual seed crops of invasive Australian

72   *Acacia*. Indigenous seed predators can therefore have substantial impacts on the seed survival of

73   invasive Australian *Acacia*. Nevertheless, in South Africa, the enemy release hypothesis is still

74   used as a basis for the rationale to search for and release biological control agents on Australian

75   *Acacia* (Van den Berg, 1977; Richardson & Kluge, 2008; Zachariades et al., 2017).

76   Based on this premise, ten biological control agents, namely five seed-feeding weevils

77   (*Melanterius* spp), two bud-galling wasps (*Trichilogaster* spp.), two flower-galling flies

78   (*Dasineura* spp.) and a rust fungus (*Uromycladium* sp.), have been released on Australian *Acacia*

79   in South Africa to decrease both the invasive potential of these plants as well as management

80   costs (Zimmermann et al., 2004; Impson et al., 2011). The use of seed-reducing agents was

81   further motivated, as these are generally host-specific and would not harm the useful parts of the

82   plants, resolving conflicts of interest for commercially valuable species (e.g. *A. mearnsii* that is

83   used for tannin and wood chip production in South Africa) (Dennill & Donnelly, 1991; Pieterse

84   & Boucher, 1997; Impson et al., 2011; Zachariades et al., 2017). All of the agents reduce seed

85   production and usually a combination of two agents, a gall-former and a seed-feeding weevil, is

86   used on a targeted invasive Australian *Acacia* species. The impact of most of these agents has

87   been described as extensive (almost no seeds surviving) or considerable (>50 % reduction)

88   (Impson et al., 2011; Zachariades et al., 2017). It has also been indicated that no (e.g. *A.*

89   *longifolia*) active management (mechanical clearing) or substantially less management than in

90   the past (e.g. *A. saligna*) is required to control the targeted Australian *Acacia* (Zimmermann et

91   al., 2004; Zachariades et al., 2017). Based on this apparent success, it is upheld that seed-

92   reducing agents are the only cost-effective and sustainable way to manage these plants

93   (Richardson & Kluge, 2008; Wilson et al., 2011).

94   Despite the reported success of using seed-reducing agents to control Australian *Acacia* in South

95   Africa, many agents failed as biological control agents (Myers et al., 1988; Myers & Risley,

96   2000). Invasive *Acacia* possess many of the characteristics described as likely candidates for

97   failed use of insect herbivores (Crawley, 1989) and more specifically seed-reducing agents

98   (Myers & Risley, 2000; Van Klinken et al., 2003). These attributes are (as suggested by Crawley,

99   1989): a long growing period, a tough woody stem, high powers of regrowth, high tannin content

100   and large seed banks with protracted dormancy. These are the same qualities possessed by

101   *Vachellia nilotica* (syn *Acacia nilotica*), against which a seed-reducing agent was documented as

102   unsuccessful in Australia (Kriticos et al., 1999). Characteristics that make invasive Australian

103   *Acacia* poor candidates for biological control through the use of seed-reducing agents are (as

104   suggested by Van Klinken et al., 2003): high plant fecundity, short maturation period, high seed

105   viability and protracted seed dormancy. Crawley (1989) and Kriticos et al. (1999) further suggest

106   that seed-reducing agents will fail against plants that are not seed limited, i.e. where seeds do not

107   limit recruitment rates and stand density. Andersen (1989), for example, showed that a reduction

108   of 95 % in the seed production of four long-lived perennials plants did not impact on their

109   population recruitment.

110   Despite the claimed impact of released biological control agents, Australian *Acacia* seed banks

111   remain a challenge to management (Strydom, Esler & Wood, 2012; Strydom et al., 2017). Many

112   Australian *Acacia* are adapted to fire driven systems through the accumulation of persistent seed

113   banks (i.e. storage effects) (Auld, 1996). These soil reserves increase in size with time since fire

114   (Milton & Hall, 1981). Seed persistence in the soil is the consequence of physically imposed

115   dormancy, requiring hot temperatures (fire or non-fire) or mechanical injury to stimulate

116   germination (Pieterse & Cairns, 1986; Jeffery et al., 1988). Recent seed bank studies have shown

117   that Australian *Acacia* seed banks in their invaded ranges in South Africa are still large (1017 to

118   17261 seeds m^{-2}), currently accumulating (Strydom, 2012; Strydom, Esler & Wood, 2012;

119   Strydom et al., 2017) and are of similar size to that measured prior to biological control agent

120   release (Strydom, 2012; Strydom et al., 2017). Therefore, these data suggest that seed production

121   and survival are still high and that the released biological control agents are having little overall

122   effect. Consequently, the seed bank data and prior assessments of biological control agent

123   success are contradictory (Zimmermann et al., 2004; Impson et al., 2011; Zachariades et al.,

124   2017). Furthermore, data on the reproductive capacity of invasive Australian *Acacia* are

125   generally scarce (Gibson et al., 2012), so making sense of the estimated proportion of seeds lost

126   to biological control is difficult. For example, in South Africa, no seed bank and seed rain data

127   have previously been collected for *A. pycnantha,* or assessed for *A. longifolia* over the past 30

128   years.

129   Our study assessed the seeds lost to predation within the pods, as well as the impact of seed

130   predation on the survival of invasive Australian *Acacia* seeds. The seeds surviving per tree (i.e.

131   not lost to predation or abortion during the pre-dispersal phase) as well as the seed rain m^{-2} of

132   *Acacia* cover, i.e. the annual input into the seed bank, were quantified. Rate of seed loss within

133   the soil after a year and the presence of gall-forming agents on trees were also determined. These

134   data therefore allow the assessment of the current impact of the introduced biological control.

135   Therefore, these data were collected to test the following hypothesis that was derived from the

136   results of Strydom et al. (2017):

137   Seed banks of invasive Australian *Acacia* accumulate within their invaded ranges over time as a

138   consequence of constant seed input in the presence of released gall-forming biological control

139   agents.

140 **Methods**

141 Study sites

142 Seed survival of *A. longifolia*, *A. mearnsii*, *A. pycnantha* and *A. saligna* were studied. Three to

143 five study sites within the Western Cape of South Africa were chosen for each of the four

144 investigated Australian *Acacia* species. All studied sites contained monospecific stands of the

145 investigated species. Sites were selected on the same basis as described in Strydom et al. (2017).

146 In addition to the criteria listed by Strydom et al. (2017), dense stands were also chosen as this is

147 the predominant condition of these plants in South Africa (Henderson 2007; Henderson &

148 Wilson, 2017). Sites were also selected to include different levels of precipitation and therefore

149 over an environmental gradient. Investigations at the studied sites were conducted during 2012

150 and / or 2013.

151 The study area is characterised by a Mediterranean climate (Roura-Pascual et al., 2011). The

152 mean annual rainfall (MAR) over the sampled range varied between 412 to 955 mm with most of

153 the rain (60 to 81 %) being received during the winter months (Table S1). The mean annual

154 temperature varied between 15 to 19 °C over the sampled range, the recorded average minimum

155 temperature of the coldest month was 5 to 10 °C while the average maximum temperature of the

156 warmest month was 27 to 33 °C. The first sampled season (2012) received less rainfall (MAR =

157 621 mm) than the second sampled season (2013, MAR = 809 mm).

158 Sampling procedure

159 Sampling of trees or selection of plots within sampled monospecific Australian *Acacia*

160 populations, except if otherwise stated, was conducted randomly according to the following

161 described method: sampling was initiated at a random tree or location within the sampled stand.

162   Afterwards the direction of movement (north, east, south or west) as well as the steps taken

163   between the samples was determined from a random numbers table. After the steps taken were

164   completed, the nearest tree was sampled or sampling plot laid out. This was repeated at every site

165   for each of the studied species.

166   Visual vs. actual pod estimates

167   Pods and galls were visually estimated on seven to fifteen pod bearing trees for each species at

168   each site. The visual estimates ranged between 1 to 2500 pods / galls per tree. Afterwards, these

169   trees were felled, their pods and galls harvested and each pod and gall counted. These data were

170   used to establish relationships between visual estimated pod / gall loads and actual counted pod /

171   gall loads (Fig. S1). This sampling was done at four sites for *A. saligna* during both sampled

172   seasons. For *A. pycnantha* this sampling was conducted at five and three sites during 2012 and

173   2013 respectively. This same procedure was repeated for *A. longifolia* at one site, during 2013

174   when an additional 15 trees were sampled (total = 30 trees) to increase the range in tree size

175   sampled. The average stem diameters at breast height (DBH) of the sampled trees for *A.*

176   *longifolia*, *A. pycnantha* and *A. saligna* were 22.1 mm (6.1 to 49.7 mm), 31 mm (5.1 to 93 mm)

177   and 23.2 mm (1 to 86 mm) respectively.

178   Proportion aborted, predated and surviving seeds per tree

179   The proportion of seeds lost to abortion and predation was determined at five sites for *A.*

180   *pycnantha* and *A. saligna* during 2012 and 2013. Assessments were also conducted at five sites

181   for *A. longifolia* and three sites for *A. mearnsii* during 2013. Investigations of seed fate (abortion,

182   predation or surviving) commenced when pods of the studied Australian *Acacia* were mature

183   (Auld & Myerscough, 1986) during November / December (Milton, 1982). Mature or ripe pods

184   were defined as pods that were hardened and had started to open, but still contained all their

185   seeds.

186   Thirty pods from 8 to 30 fruiting trees (13.9 trees on average) were sampled at each site (thus

187   representing 65 and 67 trees for *A. saligna* and *A. pycnantha* respectively during 2012 and 71,

188   66, 75 and 45 trees for *A. saligna*, *A. pycnantha*, *A. longifolia* and *A. mearnsii* respectively

189   during 2013). Trees were divided into a top, middle and lower section based on tree size. Within

190   each section ten pods were sampled indiscriminately (Impson et al., 2004). If fewer than ten pods

191   were available within a section, those pods were collected within the other sections. All pods

192   were collected if a tree had fewer than 30 pods. Pods were opened, the seeds per pod counted and

193   each seed classified into one of the following three categories: aborted (under-developed and

194   shrivelled seeds), predated (seeds with holes or frass remains), and surviving (fully developed

195   seeds, no visual damage and no disintegration when pressed) (Brown, Enright & Miller, 2003).

196   Seeds assessed as aborted and surviving, however, may contain holes, due to damage caused by

197   insects, not visible without the use of a microscope. Therefore, seeds evaluated as aborted and

198   surviving were separately bulked for each species during 2013. Depending on availability, a

199   subsample of 180 to maximum of 3600 seeds from each bulked seed pool was taken. Each seed

200   was inspected underneath a microscope for insect damage. If aborted seeds had insect damage

201   they were reclassified as predated. These data were used to calculate the proportion of aborted

202   seeds, visually classified as potentially predated, that were in fact predated (see supplementary

203   information for all calculations). Surviving seeds with insect damage were evaluated as

204   potentially predated as they were not necessarily non-viable.

205   Surviving seeds with insect damage (34 to maximum of 180 seeds) were subjected to

206   germination (viability) experiments (see below). This was repeated for each species. Only seeds

207   that did not germinate were determined to be predated. These data were used to calculate the

208   proportion of surviving seeds, visually classified as potentially predated, that were in fact

209   predated. From these data the proportion of seeds initially assessed as aborted and surviving that

210   were predated was determined. Furthermore, these data were used to accurately calculate the

211   proportion of surviving, aborted and predated seeds for each tree. From this data the average

212   proportion of surviving, aborted and predated seeds for the studied species were calculated for

213   the respective reproductive seasons investigated. The average seeds per pod for each species

214   were also determined.

215   Effect of seed abortion and predation on seed survival

216   The number of pods per tree was visually estimated on the same trees from which the

217   abovementioned 30 pods were harvested. These visual pod estimates were made before the pods

218   were collected, and were done in the same manner as described above. The relationships

219   established between visual pod estimations and actual counted pods were used to estimate the

220   pods for each tree from their visual pod estimates. The pod estimates, average seeds per pod and

221   the proportion of aborted, predated and surviving seeds per tree were used to estimate the total

222   seeds produced, aborted, predated and surviving for each of the sampled trees. These data were

223   used to assess the effect of seed crop size, seed predation and abortion on seed survival.

224   Surviving seeds per tree and per square meter

225   *Surviving seeds per reproductive tree*

226   The seed rain m^{-2} beneath the canopies of individual reproductive trees was determined. During

227   2012, this was assessed at five sites for *A. pycnantha* and *A. saligna* (10 sites) and during 2013 at

228   four sites each for *A. longifolia*, *A. pycnantha* and *A. saligna* (12 sites).

229   Three seed traps were placed beneath the canopy of 25 pod bearing trees (75 traps), at each site.

230   Plastic cups (990 ml) with a diameter of 10.5 cm were sunk into the soil at similar distances from

231   the tree trunk, at angles of approximately 120° from each other. The distance of traps from the

232   tree trunk was dependant on tree canopy size. Traps were placed approximately ¾ of the distance

233   from the tree trunk towards the edge of its canopy as seed rain size remains constant underneath

234   the canopy of Australian *Acacia* trees (Marchante, Freitas & Hoffmann, 2010). Seed traps were

235   placed in position before seed fall of the investigated species commenced (October / November)

236   and were retrieved after seed fall had stopped (December to March) (Milton, 1982). The seeds

237   within each retrieved trap were counted. As there was some overlap between the canopies of the

238   trees, the number of seeds collected in each trap was divided by the average number of fruiting

239   trees within a radius of 1.5 m from the seed traps (see below). Afterwards the average seeds per

240   cup for each tree were calculated. These data were used to calculate the average seed rain m^{-2}

241   beneath the canopy of each tree. In addition, mean canopy diameter (mean of two measurements

242   at right angles to each other) and DBH of the selected trees were measured.

243   The surviving seeds of each tree (i.e. seeds that were not lost to abortion and predation) were

244   determined by multiplying its estimated canopy area with its estimated seed rain m^{-2}. Canopy

245   area (m^{-2}) for each tree was calculated using the area formula for a circle ($A = \pi r^2$, $r = mean$

246   *canopy diameter / 2*). These data were used to establish whether a relationship between the seeds

247   surviving per tree and DBH exists. Such a relationship would serve as an approximation of the

248   relationship between the seeds surviving per tree and time, as stem diameter is a proxy of tree

249   age (Spooner et al., 2004). In order to assess the average seeds surviving per tree at different time

250   steps, the stem diameter of each studied species was divided into different size classes and the

251   average seeds surviving per tree for each class calculated.

252 *Australian Acacia seed rain m^{-2}*

253 The seed rain m^{-2} within Australian *Acacia* stands was determined at four sites each for *A.*

254 *longifolia*, *A. pycnantha* and *A. saligna* during 2013 (total of 12 sites). To assess the seed rain

255 (m^{-2}) thirty seed traps, as described above, were randomly sunk into the soil throughout the

256 investigated Australian *Acacia* stands. Traps were placed out and retrieved during the same time

257 as stated for the previous experiment. After retrieval, the seeds in each trap were counted. At

258 each sampling point, the trees within a circle (1.5 m radius), with the seed trap as midpoint were

259 counted (Strydom et al., 2017). If the canopy of trees not inside the circle crossed the seed trap,

260 these trees were also counted (Strydom et al., 2017). It was also noted whether each counted tree

261 had pods. The DBH of all trees whose canopies intersected the sampling point was measured,

262 because the largest proportion of Australian *Acacia* seed fall directly beneath their canopy

263 (Milton & Hall, 1981; Marchante, Freitas & Hoffmann, 2010). It was also noted whether the

264 stems of these trees fell within or outside the circle. The DBH of up to three additional trees

265 within the circle was measured if the DBH of all the trees in the circle was not already measured

266 (Strydom et al., 2017). These data were used to calculate tree density, the proportion of fruiting

267 trees, average fruiting trees within 1.5 m of seed traps and average stem diameter. Furthermore,

268 it was used to determine whether relationships between tree density and the seed rain m^{-2} or

269 between tree size and the seed rain m^{-2} exist. In order to approximate the seed rain m^{-2} over time,

270 the average stem diameter of each studied species was divided into different size classes and the

271 average seed rain m^{-2} for each class calculated.

272 Seed viability

273 A sample of 100 seeds assessed as surviving was taken from the seed pool of each species at

274 each site. The seed coats of these seeds were chipped at the distal end and 25 placed in each of

275   four petri-dishes containing two filter paper discs moistened with 10 ml water (Pieterse &

276   Cairns, 1986a). Petri-dishes were placed in plastic bags to prevent moisture loss (Pieterse &

277   Cairns, 1986a) and incubated at 25 ˚C in the dark (Hendry & Van Staden, 1982). After 3 days,

278   seeds were checked for germination and thereafter daily for two weeks. Germination was

279   assumed if the radicle was at least 1 mm long (Holmes, 1988).

280   Seed Germination / Decay

281   Seven hundred and fifty seeds, from the surviving seed pool (seeds were bulked for each site) of

282   *A. pycnantha* and *A. saligna* at three sites, were selected for seed burial trials during 2012. The

283   same quantity of seeds were collected and used for *A. mearnsii* and *A. longifolia* at three and one

284   site respectively. Shade net (75 %) was used to make 5×5 cm packets in which 30 seeds were

285   placed (25 packets per site). The packets were buried five centimetres deep and one meter apart,

286   along five transects (one meter apart), at each site were the seeds were collected. The packets

287   were buried during June 2013 and left for a year, after which they were retrieved. The collected

288   packets were opened and the remaining seeds in each packet counted. Furthermore, initial

289   dormancy of seeds at the collected sites was also determined before burial. To asses this, an

290   additional one hundred seeds were selected from the surviving seed pool of *A. pycnantha* and *A.*

291   *saligna*, while the same quantity of seeds was collected at the *A. mearnsii* and *A. longifolia* sites.

292   The same procedure as described above for viability testing was followed, except seeds were not

293   chipped at their distal ends. The seeds that germinated were used to calculate the proportion of

294   initially non-dormant seeds.

295   Biological control and gall-forming agent presence

296   The gall-forming biological control agents of the studied species were released 25 to 30 years

297   ago and are present wherever their host plants occur within South Africa (Olckers & Hill, 1999;

298   Dorchin, Cramer & Hoffmann, 2006; Impson et al., 2011). Since their establishment across their

299   hosts' distribution range in South Africa, sufficient time has passed for these agents to have

300   visual and quantifiable impact on the populations of their hosts (Dennill, 1985; Dennill, 1987;

301   Morris, 1997; Hoffmann et al., 2002; Wood & Morris, 2007). In order to assess the impact of

302   these agents on seed rain and therefore seed survival over time, a chronosequence was

303   established. This was achieved through using stem diameter as a proxy of tree age (Spooner et

304   al., 2004). The relationship between average seed rain m^{-2} and stem diameter and therefore time

305   was determined through the use of quantile regression (see below). To estimate the average seed

306   survival of the studied species under the average impact of their gall-forming biological control

307   agents over time, average seed rain (m^{-2}) for tree size classes was established. This was achieved

308   by dividing the trees into different tree size classes based on DBH and then calculating the

309   average seed rain m^{-2} for each tree size class. The average seed rain m^{-2} for each size class or

310   time step also includes the influence of other limiting factors (e.g. water availability, nutrient

311   availability, competition etc.). Furthermore, this measurement also takes into account the average

312   time taken for agents to establish (locate, survive and reproduce) within populations as well as

313   their average annual accrual rates after disturbance events (Strydom et al., 2017). This

314   measurement therefore represents an estimate of seed survival over time under the established

315   dynamics between the gall-forming biological control agents and their invasive Australian

316   *Acacia* hosts. This same methodology has been used to determine the impact of gall-forming

317   biological control agents on the seed banks of invasive Australian *Acacia* over time (Strydom et

318   al., 2017).

319   At the studied sites, the presence of gall-forming biological control agents was also determined.

320   If gall structures were located on trees within the investigated populations, the gall-forming

321   control agents of the studied species were assessed as present (Strydom et al., 2017).

322   Statistical analyses

323   Generalised linear mixed models (GLMMs) were fitted to the seed fate (surviving, predated and

324   aborted seeds per tree) data to establish whether seed predation and abortion significantly affects

325   seed survival. GLMMs were also used to determine whether the surviving seeds produced per

326   tree (SST) and the seed rain m^{-2} were significantly related to tree and stand characteristics

327   respectively. Quantile regressions were then employed to assess the relationship between the

328   SST and stem diameter and seed rain m^{-2} and average stem diameter. All statistical analyses were

329   conducted in R 3.1.3 (R Core Team, 2015).

330   *Generalised linear mixed models*

331   GLMMs were used as the response variables in all the fitted models were count data and random

332   effects were present (Bolker et al., 2009). Models with a log link function and a negative

333   binomial error distribution were fitted to the data. A negative binomial error distribution was

334   used to account for overdispersion (Grueber et al., 2011). The explanatory variables were

335   standardised to remove the effect of scale on the parameter estimates (Grueber et al., 2011).

336   Furthermore, maximum likelihood estimation was used to obtain model parameters (Johnson &

337   Omland, 2004).

338   After assembling the maximal model (model containing all explanatory variables) (see Table 1),

339   a submodel set was generated from which a 95 % confidence model set was obtained (Grueber et

340   al., 2011). Models were compared through the use of information theoretic (I-T) model

341   procedures based on Akaike's information criterion (AIC) (Burnham, Anderson & Huyvaert,

342   2011). The model second order AIC value, the AICc, was used to select the best model. If the

343   best model had a corrected Akaike weight (AICcWt) of less than 0.9, model averaging was

344   considered. Model averaging was conducted on the 95 % model confidence set to obtain

345   parameter estimates, parameter confidence intervals and relative parameter importance (Grueber

346   et al., 2011).

347   *Quantile regression*

348   The set of five hierarchical models proposed by Huisman, Olff & Fresco, (1993) was used to

349   determine the response curve of the SST and seed rain m^{-2} to stem diameter and average stem

350   diameter respectively over the sampled environmental gradient. This was done for *A. longifolia*,

351   *A. pycnantha* and *A. saligna*. These models were used as they are appropriate to discover non-

352   linear response curves along environmental gradients (Oksanen & Minchin, 2002).

353   The highest order model, from which four lower order models can be derived, is defined by

354   Huisman, Olff & Fresco, (1993) as follows:

355
$$y \;=\; M \; \frac{1}{1 \;+\; e^{a\,+\,bx}} \; \frac{1}{1 \;+\; e^{c\,-\,dx}}$$

356   where y is the response variable, x the explanatory variable, *a*, *b*, *c* and *d* are the parameters to be

357   approximated and *M* a constant, which refers to the maximal attainable value for y. The value of

358   *M* was set by determining the highest recorded number of seeds per tree or seed rain m^{-2} of each

359   species. All five models were fitted to the data using quantile regression models at the 95$^{\text{th}}$

360   percentile. Afterwards the best fitting model was selected according to the AIC value. These

361   procedures were done in the same manner as described in Strydom et al., (2017).

Results

363   Gall-forming biological control agent presence

364   The gall agents of *A. longifolia* (*Trichilogaster acaciaelongifoliae*), *A. pycnantha* (*T.*

365   *signiventris*) and *A. saligna* (*Uromycladium tepperianum*) were present at all the sampled sites.

366   However, for *A. mearnsii*, its gall agent (*Dasineura rubiformis*) was only present at one of the

367   three sampled sites, viz. Rivendale.

368   Surviving seeds per tree

369   Many surviving seeds (i.e. not aborted or predated) were produced by the reproductive trees of

370   the studied Australian *Acacia* (Table 2) irrespective of the seeds lost to predation and abortion

371   (Table 3). This was confirmed by the seeds surviving per tree not being significantly related to

372   seed predation or abortion in the fitted GLMMs (Table 4, 5). However, the seeds surviving per

373   tree were significantly and positively related to seed crop size (Table 4, 5) and were also

374   significantly positively related to stem diameter (Table 6). Therefore, the surviving seeds per tree

375   increased with tree size and by inference, with tree age (Figs. 1A-1F). This relationship indicates

376   that more seeds survive as seed crop size increases. The highest numbers of recorded surviving

377   seeds produced by a tree were 35 865, 17 729 and 14 007 seeds for *A. longifolia*, *A. pycnantha*

378   and *A. saligna* respectively. The viability of the surviving seeds of all the studied species was

379   high. On average the seed viability of *A. longifolia*, *A. mearnsii*, *A. pycnantha* and *A. saligna* was

380   97.1 % (94.7 to 100 %), 98.5 % (97 to 99 %), 96.6 % (93.4 to 98.5 %) and 97.8 % (95 to 99 %)

381   respectively.

382   Seed rain

383 The abundance of seeds produced by reproductive trees led to many seeds surviving per m^{-2} as

384 shown by the seed rain of the studied Australian *Acacia* (Figs. 2A-2F). The seed rain m^{-2} of the

385 investigated Australian *Acacia* was found to be significantly related to average stem diameter

386 (Table 7, 8). Across all species, the seed rain m^{-2} increased with stem diameter until a maximal

387 point was reached after which the seed rain m^{-2} decreased with a further increase in stem

388 diameter (Figs. 2A-C). The average seed rain m^{-2}, for stem diameter classes of the studied

389 species (Figs. 2D-F), generally followed the same trend of increase and decline with an increase

390 in stem diameter class size as described above for their associated quantile regressions (Figs. 2A-

391 C). The seed rain m^{-2} of *A. pycnantha*, *A. saligna*, and *A. longifolia* is at a maximum when

392 average stem diameter for these species are 39 mm, 44 mm and 171 mm (Figs. 2A-C). At the

393 maximum point with stem diameter as the explanatory variable, the seed rain m^{-2} covered by *A.*

394 *pycnantha*, *A. saligna* and *A. longifolia* was estimated to be 1477 seeds m^{-2}, 6095 seeds m^{-2}, and

395 4800 seeds m^{-2} respectively.

396 Proportion of seeds persisting for one year or more

397 Seeds were retrieved successfully at nine of the ten sites as one of the *A. mearnsii* sites was

398 mechanically cleared during the duration of the experiment. *Acacia longifolia* lost the highest

399 proportion of its produced seeds after a year's burial (78 %), followed by *A. mearnsii* (77 %), *A.*

400 *saligna* (65 %) and finally *A. pycnantha* (58 %) (Table S2).

401 **Discussion**

402 Despite the presence of seed-reducing agents in the pre-dispersal phase, seed production and

403 seed survival of Australian *Acacia* remain high, confirming the patterns described for seed bank

404 accumulation by Strydom et al. (2017). The annual seed production and seed banks are therefore

405   larger than required to re-establish seedling densities as well as mature stand densities after

406   disturbance events (Strydom et al., 2017). Therefore, it is argued that the population dynamics of

407   the investigated Australian *Acacia* are likely unaffected by the released seed-reducing biological

408   control agents in South Africa.

409   The current study confirmed the prediction of seed bank studies (Strydom, 2012; Strydom et al.,

410   2017), that many seeds are still produced, survive (despite the presences of seed-reducing

411   biological control agents) and are constantly lost (to either germination or decay) from the seed

412   bank. Many seeds, not lost to seed abortion or predation, were produced by individual

413   reproductive trees of all the studied Australian *Acacia*. This translated into the investigated

414   Australian *Acacia* producing many seeds m^{-2}. However, a large proportion of these seeds is lost

415   to either germination or decay within the first year. This illustrates that continual seed production

416   is required to maintain the seed banks of these species and that current seed banks of the

417   investigated species are not the consequence of seed input before the release of their associated

418   gall-forming biological control agents. This conclusion is further supported by the relationship

419   between the seed rain and stem diameter mirroring the relationship between the seed bank and

420   stem diameter of the investigated Australian *Acacia* as established by Strydom et al. (2017).

421   Based on the seed bank (Strydom et al., 2017) and seed rain developmental curves, management

422   programs should focus on removing populations during the seedling phase. This will prevent the

423   accumulation of large seed banks and will ensure the management of the fewer individuals over

424   time (Strydom et al., 2017).

425   Stem diameter, and consequently tree age (as stem diameter is a proxy of tree age) (Spooner et

426   al., 2004), was an important determinant of reproductive capacity of invasive Australian *Acacia*,

427   both on an individual tree and population level. Therefore, when comparing seed production of

428   individual trees or populations, within and between species, it is important to consider tree size.

429   Therefore, our findings cannot be compared to that of many previous studies on Australian

430   *Acacia* (Milton & Hall, 1981; Weiss, 1983; Auld, 1986; Pieterse & Cairns, 1988; Holmes, 1990;

431   Brown, Enright & Miller, 2003), as tree size or stand age was not reported. The only studied

432   species for which comparative data of this nature are available is *A. saligna* (Wood & Morris,

433   2007; Strydom, 2012).

434   Despite Wood & Morris (2007) suggesting the opposite, there is no clear proof that the seed rain

435   m^{-2} of *A. saligna* has declined in the presence of the gall rust fungus, *U. tepperianum*. Wood &

436   Morris (2007) estimated seed rain m^{-2} during 1989 and 2004. However, the tree density

437   estimations of 1989 used in their calculations may not have been representative of the

438   investigated sites (tree densities of other sites or from 1991 were used) (Morris, 1997; Wood &

439   Morris, 2007). Therefore, only the data of 2004 can be used for comparative purposes.

440   Furthermore, the proportion of seeds lost to abortion and predation was not taken into account in

441   their calculations. Consequently, Wood & Morris (2007) estimated the seeds produced m^{-2} and

442   not the seeds surviving m^{-2}, i.e. the seed rain m^{-2}. Despite this, our study's seed rain estimate of

443   *A. saligna* (1514 seeds m^{-2}, stem diameter = 41.5 mm) was higher than the total seed production

444   estimate of Wood & Morris (2007) during 2004 (1429 seeds m^{-2}, stem diameter 41.6 mm).

445   Moreover, the seed rain m^{-2} estimate of *A. saligna* for our study is similar to seed production

446   measured in sites of similar type and tree size by Strydom (2012).

447   The survival of seeds produced by invasive Australian *Acacia* was not significantly influenced

448   by seed predation, with seed crop size being the only significant factor influencing the quantity

449   of surviving seeds. This indicates that the studied species satiate their seed predators. This is

450   expected given that Australian *Acacia* in their native environments have also been shown to

451   satiate seed predators (Auld, 1986; Auld & Myerscough, 1986), while seed satiation as a defence

452   mechanism has also been shown for other legumes and plant species (Janzen, 1969, 1971; Kelly

453   & Stork, 2002). The recorded seed predation levels may be caused by indigenous (Holmes &

454   Rebelo, 1988; Pieterse, 1998) and / or introduced insect agents (Impson et al., 2011). It is

455   therefore concluded that the introduced *Melanterius* spp. of the studied Australian *Acacia* does

456   not have a significant impact on the seed survival within the investigated *Acacia* populations.

457   This contradicts previous claims about the effectiveness of the released seed-feeding weevils

458   (Olckers & Hill, 1999; Impson et al., 2011).

459   Predation estimates in the absence of other population dynamic parameters are misleading and of

460   little value (Janzen, 1971; Gourlay & Martin, 1991; Kriticos et al., 1999). This is as high levels

461   of predation may not have significant impact on population dynamics (Andersen, 1989). We

462   found this to be the case in our study. This is concerning as previous studies (except Donnelly &

463   Hoffmann, 2004) or reviews (Olckers & Hill, 1999; Impson, Moran & Hoffmann, 2004; Impson

464   et al., 2011) expressed weevil damage as percentages without measuring or indicating seed

465   production on either a tree or population level. Furthermore, the percentage damage caused by

466   weevils, as quantified by previous studies (Donnelly & Hoffmann, 2004; Impson, Moran &

467   Hoffmann, 2004), was expressed without considering seed abortion. This was based on the

468   assumption that aborted seeds have no bearing on the potential seeds that may be lost to seed

469   feeding weevils belonging to the genus *Melanterius* (Auld & Myerscough, 1986). However,

470   Peguero, Bonal & Espelta (2014) have shown that seed abortion may influence the seeds of

471   invasive *A. pennatula* lost to predation in South America. Moreover, the total seeds lost to

472   predation will be over- or underestimated if seed abortion is not taken into account.

473 The lack of impact of *Melanterius* spp. on seed survival may be explained by their absence at the

474 studied sites. However, adult weevils were often observed at the studied locations for all species,

475 except within populations of *A. saligna* (personal obs.). Especially for *M. ventralis* this

476 explanation, for its lack of impact on seed production, is unlikely. *Melanterius ventralis* was

477 released during 1985 (Impson et al., 2011), and has since established and increased in abundance

478 throughout its host's distribution range (Impson & Moran, 2003; Olckers & Hill, 1999), and has

479 had its impact assessed as extensive (Impson et al., 2011). Impson et al., (2011) have stated that

480 there is no doubt that *M. ventralis* has contributed to the overall decline in the extent and

481 abundance of *A. longifolia*. In contrast, the data presented here suggest that *M. ventralis* is

482 having no measurable impact on the seed survival of *A. longifolia*.

483 Despite the presence of released biological control agents, seed banks remained large and viable

484 (Strydom et al., 2017). Before and after the seed rain, seed bank size of invasive Australian

485 *Acacia* (*A. longifolia*, *A. pycnantha* and *A. saligna*) was estimated to be approximately 1017 to

486 17261 seeds m^{-2} and 2023 to 17569 seeds m^{-2} respectively. Seed banks of similar size have been

487 shown to give rise to seedling densities of 19 to 1200 seedlings m^{-2} after disturbance events

488 under a wide range of environmental conditions (Milton & Hall, 1981; Pieterse & Cairns, 1986b;

489 Holmes, Dennill & Moll, 1987; Pieterse & Cairns, 1987; Holmes 1988; Jasson 2005; Merrett

490 2013). Holmes & Cowling (1997) indicated that as few as 10 Australian *Acacia* seedlings m^{-2} are

491 able to form a closed canopy. These seedling densities will eventually self-thin to form mature

492 stands, with closed canopies, of 0.52 trees m^{-2} (Milton & Siegfried, 1981). Therefore, this

493 provides further evidence that the released biological control agents are having no significant

494 impact on the population dynamics of their host plants. Current data suggests that Australian

495   *Acacia* in their invaded ranges in South Africa are not seed limited. Consequently, the

496   conclusions of Strydom et al. (2017) are supported by our study.

497   Historical and current distribution and abundance data of the studied plants confirm the findings

498   of the current investigation. The current distribution ranges (Henderson 1998; Henderson 2007)

499   of investigated plants includes their historic distribution ranges before the release of their

500   associated biological control agents (Stirton et al., 1978). Since the release of the biological

501   control agents of the studied plants, the area occupied by these plants has also increased over

502   time (Henderon & Wilson, 2017). This increase in extent could only have been the consequence

503   of less dense stands becoming denser or trees establishing in previously unoccupied locations.

504   Both these conditions require the production of seeds as these plants do not reproduce

505   vegetatively (Stirton et al., 1978). This shows that despite the impact of the released biological

506   control agents, enough seeds are produced to establish new and replace existing populations. The

507   distribution and abundance data (Henderson 1998; Henderson 2007; Henderson & Wilson 2017)

508   further suggest that the findings of the current investigation in dense monospecific stands are

509   also relevant to less dense stands.

510   Moran et al. (2003), Impson et al. (2004) and Zimmermann et al. (2004) have all stated that the

511   real benefits of the seed reducing agents are realised for management through the apparent

512   reduction in seed numbers, leading to fewer seedlings having to be managed over time, and

513   therefore a decrease in potential management costs. However, there is no quantitative proof that

514   current seed predation levels are leading to decreased seed bank sizes and consequently fewer

515   seedlings. On the contrary, Australian *Acacia* appear not to be seed limited and current seed

516   production and seed banks are several orders of magnitude larger than that required to re-

517   establish Australian *Acacia* populations after disturbance events (e.g. clearing). The increase in

518   the area occupied by these plants has also occurred in the presence of continual removal of fire

519   wood (Kull et al. 2011), a national scale clearing program that has been operating for more than

520   a decade (van Wilgen et al. 2012) and land use change. We conclude that the released biological

521   control agents are not exerting any significant control with no apparent benefit for clearing

522   operations.

523   **Conclusion**

524   Seed production and seed survival of invasive Australian *Acacia* in South Africa are still high.

525   Furthermore, based on seed production and seed bank data the released biological control agents

526   are exerting no significant impact on the population dynamics of their Australian *Acacia* hosts.

527   The released seed-reducing agents also have no benefit for clearing operations. The failure of

528   these agents is not surprising as evidence from other studies suggests that Australian *Acacia*

529   which are mass seeders are poor candidates for biological control through the use of seed-

530   reducing insects. This study supports the conclusion by Kriticos et al. (1999) that the population

531   dynamics of invasive plants should be conducted before biological control agents are released.

532   Furthermore, tree size is an important predictor of seed production and survival. The seed banks

533   of Australian *Acacia* also mirror their seed production. Consequently, management should be

534   done during the seedling phase to prevent the accumulation of seed banks of these invasive alien

535   plants.

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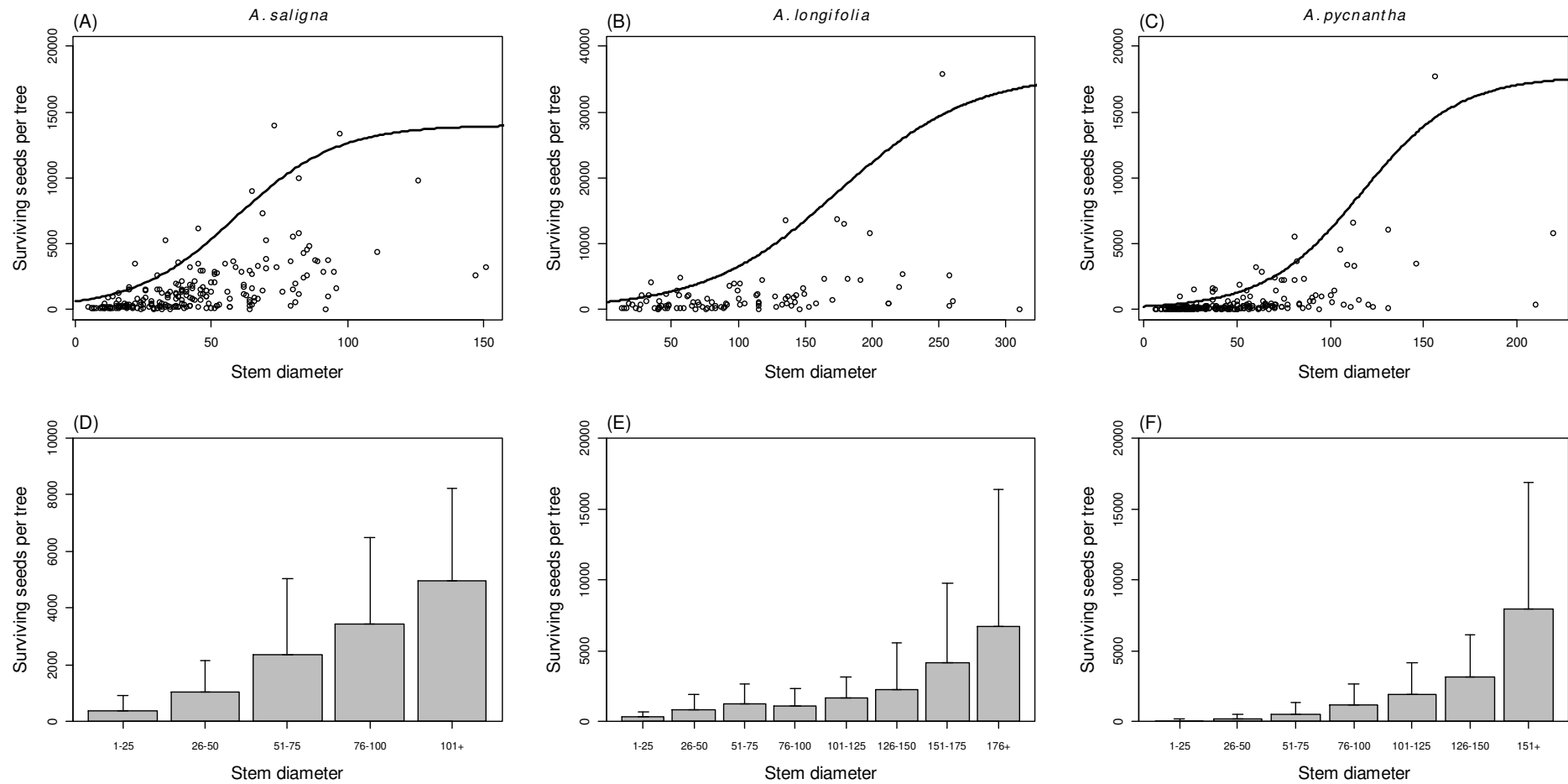
Australian *Acacia* seed survival for reproductive trees relative to tree size.

(A-C) The response of seeds surviving per reproductive tree to stem diameter, estimated by 95 % quantile regressions, of *A. saligna*, *A. longifolia* and *A. pycnantha*. (D-F) The average seeds surviving per reproductive tree (+SD) for stem diameter classes of three Australian *Acacia* in the Western Cape of South Africa.

Australian *Acacia* seed rain m^{-2} relative to average tree size measured within investigated area.

(A-C) The response of seed rain m^{-2} to average stem diameter, estimated by 95 % quantile regressions, of *A. saligna, A. longifolia* and *A. pycnantha*. (D-F) The seed rain m^{-2} (+SD) for stem diameter classes of three Australian *Acacia* in the Western Cape of South Africa.

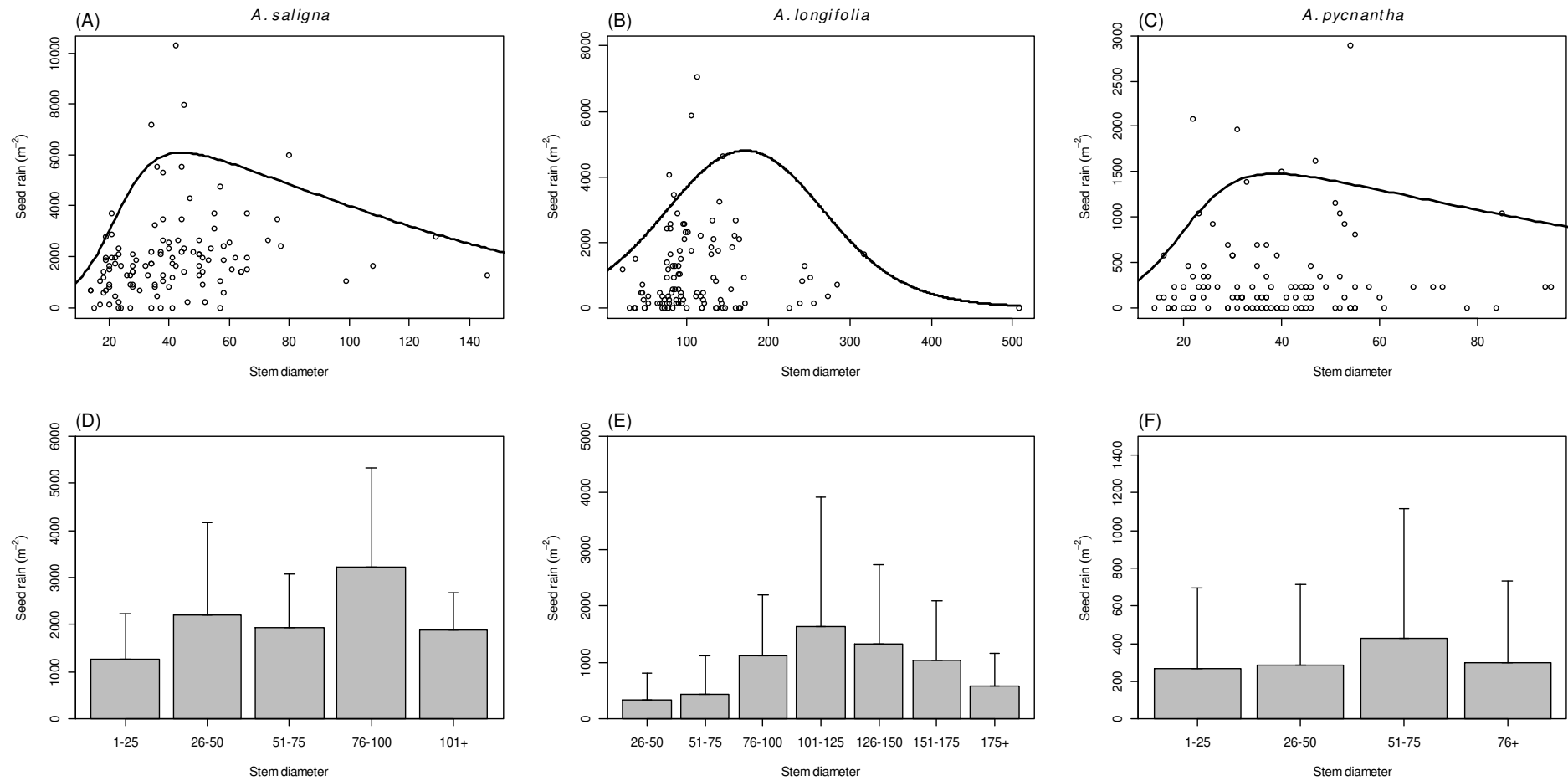
(A) *A. saligna*

(B) *A. longifolia*

(C) *A. pycnantha*

(D)

(E)

(F)

Maximal models (models containing all explanatory variables) used in analyses .

Response variable	Explanatory variables	Random Effects
Seeds surviving tree^{-1}	Seed crop size of tree + seeds aborted per tree + seeds predated per tree + species	Site and Year
Seeds surviving tree^{-1}	Stem diameter + species	Site and Year
Seeds surviving m^{-2}	Average stem diameter + tree density + species	Site

Average surviving seeds per reproductive tree (±SE) as well as the seed rain m^{-2} (±SE) of three Australian *Acacia* during 2012 and 2013 in the Western Cape of South Africa.

Species	Surviving seeds per tree		Seeds rain (m^{-2})
	2012	**2013**	**2013**
A. saligna	1454 (190)	1574 (229)	1942 (153)
A. pycnantha	460 (96)	107 (20)	307 (45)
A. longifolia	nm	2154 (439)	1006 (120)

nm – not measured

Proportion of aborted, predated and surviving seeds per reproductive tree of four
Australian *Acacia* during 2012 and 2013 in the Western Cape of South Africa.

Values in parenthesis indicate the standard error.

Species	% Aborted		% Predated		% Surviving	
	2012	2013	2012	2013	2012	2013
A. saligna	29.6 (1.9)	23.6 (1.7)	5.6 (1.5)	16.0 (2.9)	64.8 (2.6)	60.4 (3.6)
A. pycnantha	22.7 (1.4)	20.4 (1.3)	24.6 (1.8)	22.6 (1.6)	52.7 (2.7)	57.0 (2.0)
A. longifolia	nm	21.3 (1.2)	nm	39.1 (1.9)	nm	39.6 (2.0)
A. mearnsii	nm	30.6 (3.2)	nm	41.9 (2.2)	nm	27.5 (2.3)

nm – not measured

Results of model averaging over the fitted models with surviving seeds per tree as response variables for each studied species.

The effect of each parameter on the response variable is shown.

Parameters	Estimate	Standard error	p-value	Confidence interval	Relative importance
Intercept	7.53	0.24	< 0.001	(7.05 , 8.01)	
Crop size	1.65	0.27	< 0.001	(1.12 , 2.17)	1
Seeds predated	-0.07	0.15	0.669	(-0.64 , 0.20)	0.30
Seeds aborted	-0.03	0.13	0.830	(-0.58 , 0.36)	0.25
A. pycnantha	0.01	0.15	0.922	(-0.82 , 1.27)	0.06
A. saligna	0.02	0.16	0.915	(-0.85 , 1.37)	0.06

Best candidate models (95% model confidence set) predicting the surviving seeds per tree.

Model AICc values, model weights (ω_i), cumulative model weights (acc ω_i) and Laplace approximations (LL) is shown. Model averaging was conducted over the candidate models to obtain parameter estimates, parameter confidence intervals and relative parameter importance. Model averaging results shown in Table 4.

Model	k	AICc	Δ_i	ω_i	Acc ω_i	LL
Crop size	6	6376.99	0.00	0.46	0.46	-3182.37
Crop size + seeds predated	7	6378.49	1.50	0.22	0.68	-3182.08
Crop size + seeds aborted	7	6378.98	2.00	0.17	0.85	-3182.33
Crop size + seeds predated + seeds aborted	8	6380.40	3.41	0.08	0.93	-3181.99
Crop size + species	8	6380.93	3.49	0.06	0.99	-3182.26

Response of viable seeds per tree to stem diameter.

Data analysed with a generalized linear mixed model fit by the Laplace approximation with a negative binomial error distribution.

Fixed effect	Estimate ± SE	t-value	p-value
Intercept	6.44 ± 0.82	7.89	< 0.001
Stem diameter	0.92 ± 0.09	10.35	< 0.001
A. pycnantha	0.09 ± 0.91	0.10	0.918
A. saligna	0.63 ± 0.87	0.72	0.470

Model AIC value: 7682.7, Model deviance: 7666.7, Random effects:

Site, StDev = 0.53, Year, StDev = 0.95, Site factor: 14

Results of model averaging over the fitted models with seed rain m^{-2} as response variables for each studied species.

The effect of each parameter on the response variable is shown.

Parameters	Estimate	Standard error	p -value	Confidence interval	Relative importance
Intercept	6.27	0.38	< 0.001	(5.52 , 7.02)	
Average stem diameter	0.35	0.12	0.003	(0.12 , 0.57)	1
Tree density	0.01	0.05	0.831	(-0.14 , 0.22)	0.28
A. pycnantha	-0.62	0.54	0.253	(-1.68 , 0.44)	1
A. saligna	1.42	0.54	0.009	(0.36 , 2.47)	1

Best candidate models (95 % model confidence set) predicting seed rain m^{-2}.

Model AICc values, model weights (ω_i), cumulative model weights (acc ω_i) and Laplace approximations (LL) is shown. Model averaging was conducted over the candidate models to obtain parameter estimates, parameter confidence intervals and relative parameter importance. Model averaging results shown in Table 7.

Model	k	AICc	Δ_i	ω_i	Acc ω_i	LL
Stem diameter + species	6	5006.54	0.00	0.72	0.72	-2497.14
Stem diameter + tree density + species	7	5008.43	1.90	0.28	1	-2497.05