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Canary Island date palms, *Phoenix canariensis*, invading a remnant riverine eucalypt forest in south-eastern Australia: processes and patterns of recruitment

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Abstract: The recruitment processes and resulting distribution pattern of bird-dispersed Canary Island Date Palm, *Phoenix canariensis* (family Arecaceae) in a riverine forest setting are described. All palms on a near-urban peninsula of the Murrumbidgee River near Hay, New South Wales were GPS mapped and classified into height-dependent age categories. The distribution of the plants was examined spatially in relation to possible source palms and in relation to elevation with regard to flooding levels.

Successful recruitment is subject to a range of environmental parameters, primarily palatability to vectors and seedling mortality due to lack of moisture, frost or grazing by herbivores. If a seedling survives that critical period of the first 18 months, long-term success is (almost) guaranteed, unless catastrophic events (bushfires, prolonged flooding) intervene. Based on the findings, a conceptual model for the recruitment of *Phoenix canariensis* palms is provided. Even though the palms produce fruit for much of the year (March–December), the time window for successful recruitment is restricted to a period from August to mid-September with short shoulder periods on either side.

Keywords

Seed dispersal; Frugivory; invasive species; remnant vegetation; riparian forest; Murrumbidgee River

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Introduction

Phoenix canariensis H. Wildpret (family Arecaceae) (Rivera et al., 2013), the Canary Island Date Palm, is endemic to the Canary Islands (Lipnitz & Kretschmar, 1994; Sosa et al., 2016). It entered the nursery trade in the mid-1860s and soon found wide acceptance on a global scale, first as an indoor and warm-house plant, and soon after as a landscaping feature in private and public spaces (Spennemann, 2018d, 2019b; Zona, 2008). Today it is present in most parts of the world with a temperature or subtropical climate (Spennemann, 2018c). Introduced to Australia in the 1870- 1880 period (Spennemann, 2018b), the Canary Islands date palm proved hardy in much of temperate Australia and the public readily embraced these palms as exotic features for landscaping (Spennemann, 2018a).

Many horticultural plants escape their managed environments and become naturalised in areas of natural and remnant vegetation. In the Australasian setting, the date palm has been formally regarded as naturalised in New South Wales (Hosking, Conn, Lepschi, & Barker, 2007), South Australia (Brodie & Reynolds, 2012), south-eastern Queensland (Biosecurity Queensland, 2018), Victoria (Conn & Walsh, 1993), and Western Australia (Lohr & Keighery, 2016, p. 32), as well as Norfolk Island (Biosecurity Queensland, 2018) and New Zealand (Esler, 1987).

As very prolific seeders with a fleshy fruit that is readily dispersed by a range of volant and terrestrial vertebrate vectors, *Phoenix canariensis* palms have the potential to spread from their horticultural settings into managed agricultural production landscapes as well as into remnant bushland. It is referred to as a ‘nuisance plant’ (Ku-ring-gai Council, 2007, p. 20), ‘a garden escape taking up much time to control’ (in Dubbo, NSW: Gye & Thomas, 2007), a ‘species with huge potential as an invasive weed’ (Anonymous, 2016) or is even listed ‘among the ten worst environmental weeds’ (Landcare Echuca, 2009). Without demonstrated evidence, the date palm is listed as a weed plant that “has started to establish along waterways across the regions (NSW, Vic, SA, WA)” (F. J. Richardson, Richardson, & Shepherd, 2006, p. 13f; 2011, p. 19f). It has not been formally declared a prohibited or noxious weed in any of the Australian states.

Setting aside humans as the primary, long-distance dispersal agent (as ornamentals) (Spennemann, 2018b, 2018d; Zona, 2008), a range of volant and terrestrial vertebrate vectors are responsible for the palm dispersal (see review in Spennemann, 2019c). Given the size of the drupe (and seed), fruit bats (*Pteropus poliocephalus*) are a possible, but less common disperser in the Australian context (Spennemann, 2018e), whereas larger birds such as Pied Currawong (*Strepera graculina*) and Honeyeaters tend to disperse readily, but in the main only short-distance (to the closest perch) (Spennemann, in press). Starlings and crows tend to disperse over greater distances, but their effects have not been studied at any level of detail. Foxes (*Vulpes vulpes*) can transport seeds in their gastro-intestinal tract over greater distances (Spennemann, 2020). Their behaviour of territorial scent marking results in defecation on or near the same spots,

leading to the accumulation of scats (Spennemann, 2018f) and thus an increased chance of germination.

Juvenile *Phoenix canariensis* occur in the riverine Red gum forest in a lobate floodplain pocket or floodplain peninsula (henceforth ‘peninsula’) of the Murrumbidgee floodplain near Hay, in southwest NSW. As the river separates the peninsula from the mature source *Phoenix canariensis* in South Hay, terrestrial vectors such as Foxes can be ruled out limiting the vector range to volant species. This study examines the distribution of the self-seeded *Phoenix canariensis* in terms of their age structure as well as patterns of distribution, part of a wider research project (‘Palms in the Anthropocene’) to assess patterns of the establishment, naturalisation and adaptation of *Phoenix canariensis* and other horticulturally significant ornamental palms to urban, peri-urban, and rural landscapes.

Methods

Phoenix canariensis is a dioecious anemophilous plant that is solely propagated by seed (Barrow, 1998), with pollination occurring at distances in excess of 390 m (Saro, Robledo-Arnuncio, González-Pérez, & Sosa, 2014). The date palm readily and reliably sets fruit and seeds freely, annually producing between 5,000 and 30,000 obovoid drupes (‘dates’) (Djouab et al., 2016; Saro et al., 2014), that are a fleshy fruit with a small, single seed and small amount of fibrous pericarp. The drupes range from 15-30 mm in length, 12-17 mm in thickness and 2–5 g in mass (Djouab et al., 2016), of which the seed contributes less than 0.9–1.5 g. The drupes, which occur in hanging clusters, vary widely in their physical properties (shape, length, diameter, mass, colour) between individual palms. When ripe, they tend to attain a dark orange to red colour.

It reaches reproductive maturity and first flowers after six to seven years (in some locales between 8 to 10 years) (Borzi, 1912), which is the first time that a plant’s gender can be determined. In the southern hemisphere, date palm drupes ripen between March and June, with fruit often available to birds until late December (Spennemann, 2019d). Immediately following ripening, the germination rate of date palm seeds is very high (Noto & Romano, 1987). The seed requires temperatures between 25°C and 35°C (Chatty & Tissaoui, 1999) and germinates under natural conditions after 83-110 days. It shows its first two-leaved shoots at about one year of age. It is a slow-growing plant in early establishment, but once the foliage has increased to a full crown and the trunk has reached close to its standard diameter, the rate of growth begins to increase (unpublished data). The plant will then produce between 10 and 26 leaves annually, each with a life expectancy of 3–7 years (Sajdak, Velazquez-Marti, & Lopez-Cortes, 2014). Palm growth is also dependent on access to moisture, in particular during the juvenile period, as increased growth of leaves and ultimately crown development has a direct bearing on the production of chlorophyll and thus the growth potential of the palm. Unless affected by disease or pests, the plant can live for 200-300 years (Beech, 2017).

Study area

The study area is a peninsula in the floodplain of Murrumbidgee River near Hay, bounded by the river in the east, south and west, and by open farmland to the north (Figure 1). The surveyed area, a former Reserve for Travelling Stock and Camping, comprises the 19.3 ha Cemetery Bend Reserve (lot 7030 of DP 1,026,023) which is managed as public recreational space (Hay Shire Council, 2017). For the most part, the peninsula is covered by a remnant, tall open riverine woodland dominated by mature 20–25m tall River Red Gums (*Eucalyptus camaldulensis*) with a more open woodland in the north-eastern sector dominated by 10–15 m tall Black Box (*Eucalyptus largiflorens*) interspersed with River Red Gums. The understorey in both areas is very open to non-existent. In addition to the palms discussed here, two self-seeded Kurrajong (*Brachychiton populneus*), trees of 3 m and 5 m height were noted under River Red Gum perch trees as well as a large number of milk thistles (*Silybum marianum*) primarily in the south-eastern section of the peninsula. Except for the main access tracks, the ground was covered with dense leaf litter under the River Red Gums, while much bare soil was exposed in the black box woodland (due to vehicular traffic and recreational camping activities). The soil in the area is comprised of alluvial fine loamy sand.

The peninsula exhibits a depression in the north-west as well as ridges and swales as evidence of former channels. The depression, an ephemeral billabong, marked as ‘lagoon’ on early cadastral maps (Department of Lands, 1890; Surveyor General’s Office, 1882), is readily discernible on the contour map (Figure 3).

For deep rooting trees, the peninsula exhibits three moisture regimes, one close to the banks of the Murrumbidgee; one in the centre with an east to west groundwater flow, with additional variations depending on whether the trees are growing on the ridges or in the swales; and the third regime further inland at the neck of the peninsula. The water level of the Murrumbidgee River at Hay fluctuates between 0.4 m in dry summers and 8.5 m during spring floods, with a past-30-year average of 2.7 ± 1.2 m ($n=1459$ weeks) (Speer, 2018 [data set]). The section of the Murrumbidgee at Hay forms part of the Hay Weir Pool, with its level regulated by demand for water allocations (Page, Read, Frazier, & Mount, 2005). Despite regulation, in the past thirty years, six major flooding events (6.7 m at gauge) are on record (for 1989, 1990, 1991, 2010, 2012, and 2016) (Office of Water, 2014; Speer, 2018 [data set]).

In the 1990s the ‘Hay Trees on Plains’ Landcare Group secured a grant to systematically remove all “palm trees and olive trees from the riverbank areas of the Hay town area which included major removals in the Cemetery Bend area” (Reid, 2019a). While no documentary file evidence could be located, both approximate date and the nature of removal were confirmed by other sources. All observed *Phoenix canariensis* plants in the study area are therefore likely to have colonised in the past twenty years.

Source populations

South Hay has two source locations of *Phoenix canariensis* palms. Bishop’s Lodge (co-ords -34.518966, 144.848531), a National Trust-owned historic property with heritage-listed landscaped grounds (NSW Office of Environment and Heritage, 2018), now surrounded by residential, suburban development has *Phoenix canariensis* palms in the gardens planted in the first half of the 1930s. ‘Riverton’ a privately-owned 1890s homestead on the southern bank of the Murrumbidgee River (co-ords -34.517684, 144.855782), has two female and a male palms, planted in the gardens in 1987 (pers. comm. Summers, 2018).



Figure 1. The study area in relation to Hay and South Hay. The location of the palms at the Bishop’s Lodge (1) and Riverton (2) are marked with a star. The dashed red line outlines the extent of the study area. (Base image: Land and Property Information, 2013).

Field Survey Methods

The data were collected in December 2018. Given the open understorey, all *Phoenix canariensis* palms larger than 0.3 m high were easy to see. The palms and palm seedlings were mapped on site using ArcGIS with a non-differential GPS-enabled Toughbook 20 (Figure 2, Table 2). The accuracy of the GPS was tested at the start and the end survey, with a positioning error of less than 3 m. The height of the plants was estimated with a survey range rod in 0.5 m gradations.

An additional 11 Canary Island date palms were recorded in the suburban areas of Hay, especially in South Hay, drawing on aerial imagery with verification via Google StreetView. In most cases Google StreetView allowed to approximate the height of the palm. Large palms were classified as ‘female’ (readily recognisable by their orange infructescences) or ‘mature.’ While it is highly probable that mature palms without orange infructescences are likely to be male, they were conservatively classified as ‘mature’. The local landscaping also utilised *Washingtonia robusta* and in particular *Archontophoenix cunninghamia* and *Howea fosteriana*, the latter two species appear to be popular in housing developments from the 1980s onwards but no self-seeded specimens of either species were noted in the bushland setting.

Data analysis

Mapped *Phoenix canariensis* were classified into five size-dependent age groups (Table 1). Seedlings were those plants where the leaves were undivided (Figure 6), while juveniles and immature plants had fully developed pinnate leaves with a rachis and leaflets (Figure 7). The number of small seedlings with two to four leaves are likely to be underrepresented in the data as some may have escaped observation due to size. In the classification adopted here (Table 1), juvenile plants had thin leaves with a wide spacing of leaflets (Figure 6), while immature plants had numerous fully developed pinnate leaves. Classified as young were *Phoenix* with fully developed crowns and incipient trunk development where the gender was discernible, and which were, therefore, reproducing. The significance assessment of observed differences in frequencies and percentages used the Chi-squared test with n-1 correction of the MEDCALC comparison of proportions calculator (Campbell, 2007; MedCalc Software, 2018; J. T. E. Richardson, 2011).

Table 1. Age classes of the *Phoenix canariensis* observed in the Cemetery Bend reserve

Age Class	Status	Height bracket	Definition	Image	Frequency
Seedling		≤ 1 m	low plants with undivided leaves	Figure 6	16
Juvenile	Non-Reproducing	0.5–2 m	thin leaves with a wide spacing of leaflets	Figure 7	21
Immature		3–4 m	numerous fully pinnate leaves	Figure 8	39
Young	Reproducing	5–10 m	developed crowns, incipient trunk development, gender discernible	Figure 9	24
Mature		>10 m	developed crowns, well developed trunks		

River Gauge Data

The River gauge data draw on Speer (2018) (until end of June 2017) and on scans of the actual gauge logbooks (period from July 2017 to 31 December 2018) made available by the PID. Geographically, both gauges are in the same weir pool (Hay Weir pool) some 9.4 stream km apart and bracket the study area. The PID gauge (coordinates-34.495618, 144.875381), which covers the past 30 years, is located 5.6 stream km upstream of the apex of the Cemetery Bend peninsula, while the location of the town gauge is 3.8 stream km downstream of the apex of the Cemetery Bend peninsula. For a calculation of the depth of inundation at a given elevation, the available

gauge data were corrected. While the elevation of both gauges is known (town gauge 95.7 m mean sea level (MSL); PID gauge 95.9 m MSL), the zero level is only known for the town gauge (AWRC no. 410002; zero gauge at 81.49 m MSL) (Water NSW, 2018). Despite extensive research into files and institutional memory, the zero level for the gauge operated by the PID could not be ascertained (Bisset, 2019) and had to be estimated based on sample pairs for the two gauges. Setting aside the short runs of both end years, the readings on the PID gauge are on the average marginally lower than the town gauge (-0.04 ± 0.29 m, range -1.24 – 1.28 ; $n=731$ sample pairs). There is, however, a systematic difference between the period 1969–1974 where the annual averages of the town gauge are consistently lower (-0.16 ± 0.25 , range -1.11 – 1.05 , $n=317$) and the period 1975–1982 where the annual averages of the town gauge are consistently higher ($+0.07 \pm 0.29$, range -1.24 – 1.28 , $n=414$ sample pairs). For the purposes of this paper, an arbitrary zero level for the apex of the Cemetery Bend peninsula was established by adjusting the readings of the PID by $+0.038$ m (observed gauge differences 1975–1982 adjusted for stream kilometres).

Results and Discussion

In total 100 *Phoenix canariensis* palms and palm seedlings were mapped, four of which were self-seeded palms plotted on the left bank of the Murrumbidgee. Sizes ranged from 0.5 m seedling to 8 m high plants. Of young and mature trees ($n=24$), the majority were males, only six female plants noted. No sex-based spatial distribution pattern could be observed (Table 2). The distribution of self-seeded *Phoenix canariensis* on the peninsula appears clustered rather than evenly distributed, even though the canopy cover is quite uniform in density and height (Figure 2, Table 3).

Table 2. Size distribution of the *Phoenix canariensis* observed in the Cemetery Bend reserve

Height	seedling	immature	female	male	Total
0.5	16	15			31
1		13			13
1.5		6			6
2		1			1
2.5		2			2
3		2			2
4		20			20
4.5		1	2	2	5
5			1	2	3
6			3	10	13
7				2	2
8				2	2
Total	16	60	6	18	100

Table 3. Approximate size distribution of the palms in the Cemetery Bend reserve by elevation (in overall %)

elevation (m)	86.5	87.0	87.5	88.0	88.5	89.0	89.5	n
Seedling	—	—	—	21	14	36	29	14
Juvenile	3	—	8	18	23	41	8	39
Immature	13	4	9	26	35	9	4	23
Young	4	21	25	17	25	8	—	24
Mature	—	—	—	—	—	—	—	0
Total	5	6	11	20	25	25	8	100

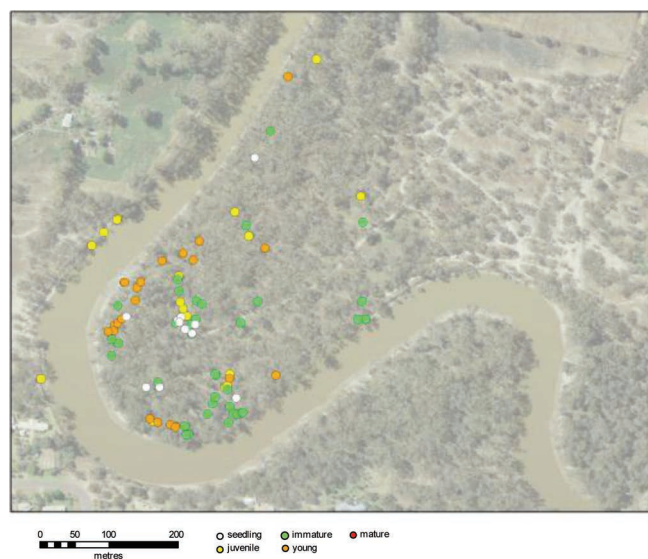


Figure 2. Distribution of self-seeded *Phoenix canariensis* on the peninsula of the in the Cemetery Bend reserve in relation to the primary vegetation pattern. (Base image: Land and Property Information, 2013).

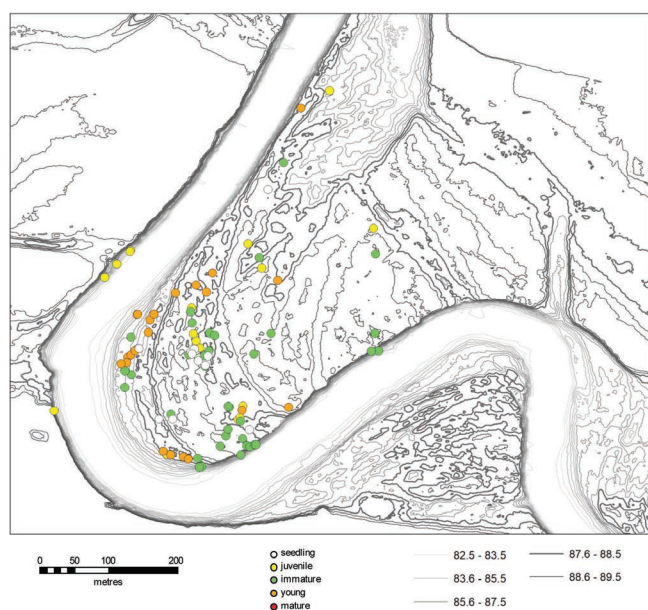


Figure 3. Distribution of self-seeded palms on peninsula in relation to micro contours

Aspects of recruitment—Vectors

The volant vectors recorded in Australia include Common Myna (*Sturnus [Acridotheres] tristis*), Australian Raven

(*Corvus coronoides*), Blue-faced Honeyeater (*Entomyzon cyanotis*), Pied Currawong (*Stepera graculina*), European Starling (*Sturnus vulgaris*) and the Eurasian Blackbird (*Turdus merula*) (Spennemann, 2019c). Vectors noted in the *Phoenix canariensis* at ‘Riverton’ homestead in South Hay were Pied Currawongs, Starlings, and Blue-faced Honeyeaters, as well as Eastern Koel (*Eudynamys orientalis*) and Little Raven (*Corvus mellori*) (Summers, 2018). The palms at Bishop’s Lodge (also South Hay) are frequented by European Starlings, House Sparrows, and Miners (*Manorina* spp.). Observed as feeding on drupes were Starlings and Miners (Reid, 2019b). Grey-headed flying-foxes (*Pteropus poliocephalus*) which are less likely vectors (Spennemann, 2018e), have not been observed at Hay.

As the study area is separated from all nearby mature seed *Phoenix canariensis* on the southern bank, only volant vectors need to be considered. While Red Foxes can traverse rivers by swimming, and do so during sub-adult dispersal when establishing new territories (Abbott, 2000; Trehwella & Harris, 1988), they do not tend to swim as part of their normal territorial behaviour (Larivière & Pasitschniak-Arts, 1996).

Based on a review of the effectiveness of various vertebrate vectors as seed dispersers of the date palm (Spennemann, 2019c), the primary vectors to be considered are Pied Currawongs, followed by Starlings and Blue-faced Honeyeaters. Currawongs consume multiple drupes and regurgitate these on favoured perches generating a narrow seed shadow that increases the successful germination enhanced by the processing of the drupe in the Currawong’s crop causing mechanical scarification significantly increasing the seed’s germination potential (Spennemann & Pike, 2019).

Pied Currawong tend to be seasonal vectors, favouring urban habitat and its resources of fruits and seeds of ornamental plants (commonly exotics) during winter (Anonymous, 1934; Bass, 1995; Platypus, 1939; Readshaw, 1968a, 1968b). As Binns (1940) noted for the riverine forest at Cobram, Pied Currawongs “appear to spend the night in the river timber, and soon after daylight they come gradually into the town. ... Towards nightfall they retire once again to the red gums. They spend the day scavenging the township, ... perch in the street palms (*Phoenix canariensis*), and gorge on the orange-coloured, ripe ‘dates.’ By this means the seeds are spread, and after the currawong visitation, seedling palms appear over a widespread area.”

Aspects of recruitment—Origin of the Seeds

The dispersal of invasive *Phoenix canariensis* on the peninsula appears to be associated with proximity to the source palms in South Hay and confined to the River Red Gum forest rather than the open woodland in the north-east of the area (Figure 2) though this may be merely an artefact of distance from the source palms. In the absence of genetic testing, the attribution of the self-seeded *Phoenix canariensis* offspring to source palms has to occur based on flight distances. *Phoenix canariensis* plants in urban Hay, are separated from the study site by several meanders and associated riverine vegetation and given the distances and the intermediate vegetation, can be discounted. There are two

sources of *Phoenix canariensis* in historic gardens in South Hay however, Bishop’s Lodge and ‘Riverton’ homestead. Other planted *Phoenix canariensis* in South Hay seem to be male and thus can be ruled out. The palms in the gardens of the Bishop’s Lodge (Figure 1) were planted in the first half of the 1930s (NSW Office of Environment and Heritage, 2018). One of these is a 16.7 m tall male (Figure S1), the other a ca 15.8 m tall female (Reid, 2019a). The distance from these to the closest self-seeded palms on the peninsula is about 700 m, with a 1150 m distance to the furthest palm. At ‘Riverton’ homestead, are two female and a male plant, planted in 1987 (pers. comm. Summers, 2018). The distance from these source palms to the closest self-seeded palm on the peninsula is about 350 m, with the furthest self-seeded palm being 720 m away. All distances are well within the standard flight range of the potential vectors.

The observed distribution of the *Phoenix canariensis* on the peninsula fits well with a concentric model centred on the Bishop’s Lodge gardens with numbers of self-seeded palms decreasing with increasing distance (Table 5). The only deviation is the 701-800 m bracket, but most of this area falls either in the channel of the Murrumbidgee or its sandy banks. All closer areas are in suburban housing areas, lacking suitable perch trees. The distribution does not fit a concentric model centred on Riverton, however, as the pattern is linear without the expected drop off as distance increases (Table 6). Furthermore, in the Riverton model the absence of palms in the open black box woodland cannot be unequivocally explained, unless the extensive exposure of barren ground underneath the River Red Gums and Black Box inhibits seedling establishment. The differential groundwater flow under the peninsula as opposed to the black box area will have little, if any, effect on seedling establishment as palms are shallow rooting.

Table 5. Approximate size distribution of the *Phoenix canariensis* (in %): Bishop’s Lodge distance (m) model (n=100)

Size	701–800	801–900	901–1000	1001–1100	1101–1200	Total
Seedling	—	8	5	1	—	14
Juvenile	2	9	8	2	1	23
Immature	1	24	8	4	2	39
Young	1	13	7	1	—	24
Mature	—	—	—	—	—	0
Total	4	54	28	8	3	100

Table 6. Approximate size distribution of the *Phoenix canariensis* (in %): Riverton distance (m) model (n=100)

Size	401–500	501–600	601–700	701–800	Total
Seedling	6	8	—	—	14
Juvenile	5	8	5	5	23
Immature	22	11	5	1	39
Young	4	4	14	2	24
Mature	—	—	—	—	0
Total	37	31	24	8	100

Aspects of recruitment—Lack of moisture

The River red gum forest on the peninsula indicates floodplain colluvium and groundwater flow, while the open Black box woodland is a remnant forest on the lowest river terrace. *Phoenix canariensis* are comparatively shallow rooting with the vast majority of roots penetrating less than 2 m (Hodel, 2009; Hodel, Pittenger, & Downer, 2005). In contrast, mature *Eucalyptus camaldulensis* can have root systems up to 10 m deep allowing access to groundwater flow (Davies, 1953). *Phoenix* seedlings require a stable moisture regime to succeed. In well-watered gardens and park settings, the ground under female palms is often covered with a dense mat of seedlings, not observed under palms in drier settings. In farmland settings, seedlings will successfully establish themselves in low, 0.1 - 0.4 m tall grass (unpubl. data), which seems to produce enough shade and moisture retention compared to totally open settings. While fluctuating environmental conditions may inhibit germination in the season of deposition, date palm seeds remain viable until the next moisture pulse, unless predated by rodents or insects (Spennemann, 2018f, 2019a).

As the distribution of self-seeded *Phoenix canariensis* on the peninsula appears clustered even though the canopy cover is quite uniform in density and height, other factors may be at play. Geomorphologically, the peninsula exhibits a ridge and swale system (Figure 3) which is likely to result in differential moisture conditions, which in turn may be reflected in the plant geography of the area. While the 1.5 m zone between 88.0 and 89.5 m MSL elevation contours accounts for 70% of *Phoenix canariensis* at Cemetery Bend (Table 3), the pattern is more complex once we consider the relative proportions within various age groups (Table 4). The lack of seedlings below 88 m is highly significant ($\chi^2= 26.508$; $P=<0.0001$), as is the low frequency of juvenile plants ($\chi^2= 49.034$; $P=<0.0001$) and immature plants ($\chi^2= 10.282$; $P= 0.0013$) at the same elevation. These differences are not carried through for the mature palms, however, where both areas are statistically identical ($\chi^2= 0.000$; $P=<1.00$). When the frequency of palms per contour interval is corrected for area (Table 7), the highest density of palms of all ages occurs at the 88 m contour. The fact that there is no spatial pattern or difference among the young, sexually reproductive palms counsels against a generalisation that palm seedlings have a greater chance of establishment on the higher, and drier ground. Rather, other factors must be at work.

Table 7. Approximate density of *Phoenix canariensis* per m² by contour area and age class

elevation (m)	86.5	87.0	87.5	88.0	88.5	89.0	89.5
Seedling	—	—	—	0.202	0.006	0.007	0.015
Juvenile	0.021	—	0.029	0.470	0.027	0.021	0.012
Immature	0.063	0.025	0.019	0.403	0.024	0.003	0.004
Young	0.021	0.127	0.058	0.269	0.018	0.003	—
Mature	—	—	—	—	—	—	—
Area (m ²)	4,789.7	3,950.4	10,351.8	1,488.1	33,758.3	76,617.0	25,865.5

Aspects of recruitment—Excessive of moisture

During the past 30 years the Murrumbidgee River has flooded in 1989, 1990, 1991, 2010, 2012, and 2016 (Office of Water, 2014). Using weekly gauge data the annual flooding frequencies of the various elevations can be computed (Table 8). The Murrumbidgee is a managed river system, primarily delivering water to agricultural irrigators with a reduced emphasis on environmental flows; the flooding events are no longer seasonal, but, determined by anthropogenic factors (Page et al., 2005). The flooding history explains the lack of smaller plants at lower elevations. Three flooding events occurred since the mid-1990s removal of the palms, 2010/11, 2012 and 2016 (Table 8). Of significance are both the duration of the flooding and the depth of inundation (Table 9–Table 11) and the concomitant responses of the *Phoenix canariensis* to the waterlogging.

While *Phoenix* palm is reputedly “resistant to temporary waterlogging caused by sudden rains” (CABI, 2017), there appears to be no studies of anaerobic stress on growth and survival. Extrapolating from other palm species, we can expect that prolonged root-level inundation will *inter alia* impact leaf gas exchange and the uptake of nitrogen and thus will cause stunted growth and reduced fruiting. Full, crown-level immersion for a multi-day period proves fatal, in particular for younger plants. Both the 2010/11 and 2016 floods were gradual build-ups of flood levels (Table 9, Table 11), while the 2012 event was a deep inundation with a sudden onset (Table 10). The 2016 flooding event was the most severe. It lasted for eight weeks (Table 11), with the lowest elevations (86.5 m and 87.0 m) inundated for all eight weeks, and the next two elevations (87.5 m and 88.0 m) inundated for seven and six weeks respectively.

Table 8. Flooding and climatic events (in weeks) 1988–2017

Year	Flooding events elevation (m)							Climatic events days <-2°C	
	86.5	87.0	87.5	88.0	88.5	89.0	89.5	total	2-day
1988	3	1							
1989	17	12	9	6	2	2	1		
1990	12	11	10	8	3				
1991	6	5	2	1	1	1			
1992	9	8	6	1					
1993	9	6	5	2					
1994								3	
1995	3	2	2					2	
1996	5	3	2						
1997								3	1
1998								2	1
1999									
2000									
2001								1	
2002									
2003									
2004									
2005									
2006								1	

Year	Flooding events elevation (m)							Climatic events days <-2°C	
	86.5	87.0	87.5	88.0	88.5	89.0	89.5	total	2-day
2007								3	
2008									
2009									
2010	7	4	3	2	2	1	1		
2011	1	1	1					1	
2012	4	4	3	3	3	3	3	2	1
2013									
2014								4	1
2015								2	
2016	8	8	7	6	5	4	3		
2017								17	5
2018								7	1
Total	84	65	50	29	16	11	8		

Table 9. Depth of inundation (in m) at the root level of *Phoenix canariensis* during the floods of 2010/11.

elevation (m)	86.5	87.0	87.5	88.0	88.5	89.0	89.5
28/10/2010							
4/11/2010	1.1–1.5	0.6–1.0	0.1–0.5				
11/11/2010	0.6–1.0	0.1–0.5					
18/11/2010							
25/11/2010							
2/12/2010	0.1–0.5						
9/12/2010	0.1–0.5						
16/12/2010	0.1–0.5						
23/12/2010	3.1–3.5	2.6–3.0	2.1–2.5	1.6–2.0	1.1–1.5	0.6–1.0	0.1–0.5
30/12/2010	2.1–2.5	1.6–2.0	1.1–1.5	0.6–1.0	0.1–0.5		
6/01/2011	1.1–1.5	0.6–1.0	0.1–0.5				
13/01/2011							

Table 10. Depth of inundation (in m) at the root level of *Phoenix canariensis* during the flood of 2012.

elevation (m)	86.5	87.0	87.5	88.0	88.5	89.0	89.5
9/03/2012							
16/03/2012	3.1–3.5	2.6–3.0	2.1–2.5	1.6–2.0	1.1–1.5	0.6–1.0	0.1–0.5
23/03/2012	3.1–3.5	2.6–3.0	2.1–2.5	1.6–2.0	1.1–1.5	0.6–1.0	0.1–0.5
30/03/2012	3.1–3.5	2.6–3.0	2.1–2.5	1.6–2.0	1.1–1.5	0.6–1.0	0.1–0.5
6/04/2012	0.6–1.0	0.1–0.5					
13/04/2012							

Table 11. Depth of inundation (in m) at the root level base of *Phoenix canariensis* during the flood of 2016

elevation (m)	86.5	87.0	87.5	88.0	88.5	89.0	89.5
15/09/2016							
22/09/2016	1.1–1.5	0.6–1.0	0.1–0.5				
27/09/2016	1.6–2.0	1.1–1.5	0.6–1.0	0.1–0.5			
4/10/2016	2.6–3.0	2.1–2.5	1.6–2.0	1.1–1.5	0.6–1.0	0.1–0.5	
11/10/2016	3.1–3.5	2.6–3.0	2.1–2.5	1.6–2.0	1.1–1.5	0.6–1.0	0.1–0.5
18/10/2016	3.1–3.5	2.6–3.0	2.1–2.5	1.6–2.0	1.1–1.5	0.6–1.0	0.1–0.5

elevation (m)	86.5	87.0	87.5	88.0	88.5	89.0	89.5
25/10/2016	3.1–3.5	2.6–3.0	2.1–2.5	1.6–2.0	1.1–1.5	0.6–1.0	0.1–0.5
31/10/2016	2.1–2.5	1.6–2.0	1.1–1.5	0.6–1.0	0.1–0.5		
7/11/2016	0.6–1.0	0.1–0.5					
14/11/2016							

Table 12. Duration of inundation (weeks) at various flooding events. Elevation < 88 m.

Age Class	Height	root-level inundation				crown-level inundation			
		2010	2010/11	2012	2016	2010	2010/11	2012	2016
Seedling	≤ 1m	2	6	4	8	—	3	4	8
Juvenile	0.5–2m	2	6	4	8	—	3	3	7
Immature	3–4m	2	6	4	8	—	1	3	3
Young	5–10m	2	6	4	8	—	—	—	—
Mature	>10m	2	6	4	8	—	—	—	—

Table 13. Duration of inundation (weeks) at various flooding events. Elevation ≥ 88 m.

Age Class	Height	root-level inundation				crown-level inundation			
		2010	2010/11	2012	2016	2010	2010/11	2012	2016
Seedling	≤ 1m	—	2	3	6	—	2	2	5
Juvenile	0.5–2m	—	2	3	6	—	2	2	4
Immature	3–4 m	—	2	3	6	—	—	—	—
Young	5–10m	—	2	3	6	—	—	—	—
Mature	>10m	—	2	3	6	—	—	—	—

Table 14. Approximation of the number of currently existing plants exposed to flooding events. Elevation < 88 m.

Age Class	Height	root-level inundation				crown-level inundation			
		2010	2010/11	2012	2016	2010	2010/11	2012	2016
Seedling	≤ 1m	—	—	—	—	—	—	—	—
Juvenile	0.5–2m	—	—	—	4	—	—	—	2
Immature	3–4 m	4	4	4	6	—	—	—	6
Young	5–10m	12	12	12	12	—	2	—	—
Mature	>10m	—	—	—	—	—	—	—	—

Table 15. Approximation of the number of currently existing plants exposed to flooding events. Elevation ≥ 88 m.

Age Class	Height	root-level inundation				crown-level inundation			
		2010	2010/11	2012	2016	2010	2010/11	2012	2016
Seedling	≤ 1m	—	—	—	—	—	—	—	—
Juvenile	0.5–2m	—	2	6	26	—	—	—	—
Immature	3–4 m	—	4	6	12	—	—	—	—
Young	5–10m	—	6	6	9	—	—	—	—
Mature	>10m	—	—	—	—	—	—	—	—

Based on the gauge levels during the inundation events we can calculate both the water depth and the duration of the inundation at various contours (Table 9–Table 11), and estimate the approximate duration of the *Phoenix canariensis* age classes at both root-level and crown level (i.e. fully submerged) (Table 12–Table 13). Using palm growth data estimates, it is clear that none of the palms presently growing at ≥ 88 m elevation were exposed to crown level inundation, but that 8 palms at ≤ 88 m elevation were fully submerged

during the 2016 event. Both immature and young plants at ≤ 88 m elevation were exposed to root-level inundation during all flooding events. The survey did not note any obvious dead juvenile plants. While dead seedlings would have decayed, evidence of dead multi-leafed juvenile or immature plants should persist for some time (see decayed *Washingtonia robusta* in Spennemann, 2018g). Following the flood pulses, however, we can expect increased germination of rehydrated *Phoenix canariensis* seed especially when embedded in a moist seed bed. Prolonged inundation (in excess of three months) of seeds of other palm species, however, inhibited germination (*Socratea exorrhiza* and *Oenocarpus bacaba*, Pacheco, 2001) with increased fungal attack a contributing factor (*Acrocomia aculeata*, Rubio Neto et al., 2012). The high number of juvenile palms at Hay can be attributed to the flooding event of 2016, which would have secured the establishment of seedlings derived from seeds deposited in 2015 and 2016. The low number of extant seedlings however, cannot be explained by water levels and flooding of any intensity, nor by the survey methodology.

Aspects of recruitment—Temperature

Death threshold temperatures for *Phoenix canariensis* appear to be -2°C for emerging seedlings, -7.5°C one year-old seedlings, -10.5°C for large parts of the leaves of mature trees and below -18°C for the entire plant (Doughty, Gill, & Blouin, 1994; Larcher & Winter, 1981; Rousseau, Monfort, & Ferry, 1999; Sakai & Larcher, 2012, p. 182; Troubelzkoï, 1880). The temperature regime for Hay ranges from -6.3°C in July to 47.9°C in January (period 1881–2018, Bureau of Meterology, 2019a, 2019b). While the recorded minimum temperatures do not affect one year-old seedlings, juvenile or young plants, temperatures do fall below the threshold for emerging seedlings. By and large, the number of frost days below - 2°C (Table 8) is limited to one to four days per year. Exceptions were 2017 with seventeen days and 2018 with seven days. These would have severely impacted on recruitment.

Even though the death threshold for emerging seedlings is -2°C, topographic micro-variations may have a local effect on mortality. The effect of low temperature is compounded when the temperature drops during consecutive days. This occurred in 2012, 2014, 2016 and especially in 2017 when there were five occasions of two days with minima below -2°C, including one for three consecutive days. Given the temperature data, we can assume a mass mortality of all emerging seedlings in June and July 2017—which explains the lack of larger seedlings during the survey.

Other constraining factors

Seedling establishment may also be limited by allelopathic action and predators. The allelopathic action of *Eucalyptus camaldulensis* in inhibiting seedling growth of other species is well documented (Ahmed, Hoque, & Hossain, 2008; del Moral & Muller, 1970; May & Ash, 1990) but the extent of this on *Phoenix*, or the relationship of the inhibitory action with the overall moisture regime are unclear.

Rats and mice will predate *Phoenix canariensis* seeds (Spennemann, 2018f) and will also feed on the emerging cotyledonary petiole as well as the radicle, if the seed is insufficiently buried. Some palm seedlings and juveniles showed evidence of grazing (Figure 6), presumably by kangaroos or rabbits (as stock have been excluded for the past 40 years). Western Grey Kangaroos (*Macropus fuliginosus*) have been documented as grazing on the leaves of commercial date palms (*Phoenix dactylifera*) in the Riverland of SA (Reilly & Reilly, 2014). Eastern Greys (*Macropus giganteus*) may be likely to feed on *Phoenix canariensis*. Rabbits (*Oryctolagus cuniculus*) will graze on *Phoenix canariensis* seedlings and, especially when combined with other herbivores, can disrupt and even terminate successful recruitment (Ludwig, Lavergne, & Sevathian, 2010; Maunder et al., 2002; Priddel, Carlile, & Wheeler, 2000). Rabbit grazing on seedlings tends to be much more severe during late summer when there is less alternative green feed available (Mutze, Bird, Cooke, & Henzell, 2008). Given the overall paucity of fresh green leaf matter among ground cover in the riverine forest, it can be surmised that rabbit predation of seedlings will be high.

Once the plant is past the seedling stage, the resilience of juvenile palms against grazing is assured. While the leaves can be bitten back to the rachis or even the petiole, the grazing does not impact the terminal growth bud (apical meristem) which is well protected by very sharp spines which break off

easily and embed themselves in body tissue (Adams, Timms, & Hanlon, 2000; Cahill & King, 1984; Cozen & Fonda, 1953), causing prolonged pain to a predator.

Towards a model

The previous observations can be combined into a conceptual model (Figure 4). There is a core period of viable seed availability (May to mid-October) flanked by low periods. Late season drupes have begun to dehydrate on the tree (*Tamr* stage) and thus are less palatable to vectors than mid-season drupes (Spennemann, in press). The early season seeds from prematurely picked (eaten) drupes are not as mature as mid- and late season drupes. This is carried through to the germination, with fewer early-season seeds germinating.

Periods of low rainfall will result in seedling mortality, reducing the number of first shoots that would appear the following year. Once shoots have emerged, they are at risk from grazing by herbivores, as well as frost. Consequently, in adverse conditions only a very small number of seedlings will develop into juveniles. Based on the model, the first 18 months are critical. If a seedling survives that period, long-term success is (almost) guaranteed, unless catastrophic events, such as bushfires or prolonged flooding intervene, which are outside the scope of this model.

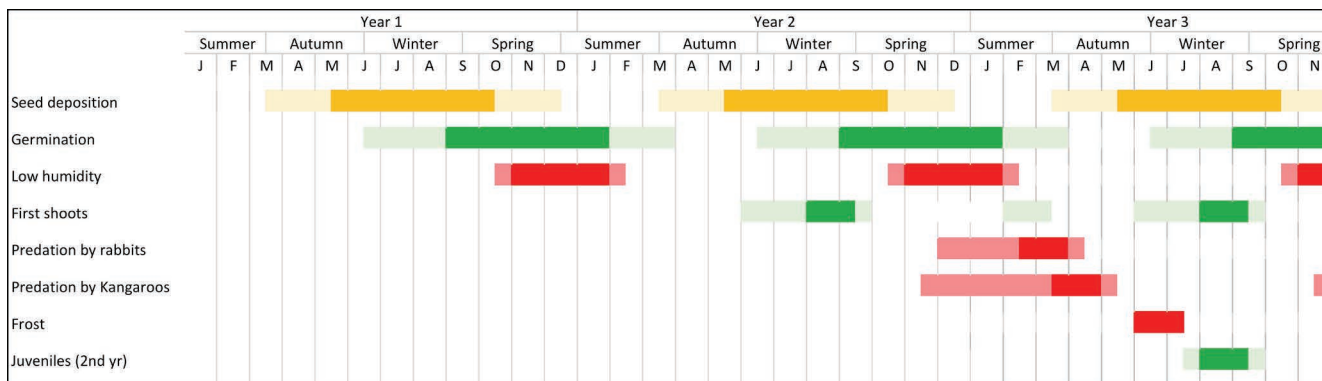


Figure 4. Conceptual model for the recruitment of *Phoenix canariensis* in the Murrumbidgee Floodplain (effects of floods excluded). Colours: Orange seeds; green seedlings and plants, red inhibitory factors.

Future Research

Phoenix canariensis palms are possibly quite widespread in the near-urban riverine forests in the Murray-Darling Basin. Though no formal assessment has been carried out, management plans and similar documents refer to several instances on the Lachlan (Lachlan CMA, 2008), Murray (Deniliquin–Barham: Harrington & Hale, 2011; Echuca: Landcare Echuca, 2009; Gunbower: North Central CMA, 2015) and Murrumbidgee floodplains (e.g. Ash & Verbeek, 2007; Wagga Wagga: Waratah Eco Works, 2017). The distribution of data points in available databases (e.g. ALA, 2019) is patchy and unsystematic and hinders an analysis of biogeographical, geomorphological and climatological factors that might circumscribe the preferred habitat of

self-seeded palms. There is a clear need for basic mapping and data collection, ideally driven by local Landcare Groups and the CMAs.

Lacking also are systematic studies that examine the establishment of the *Phoenix canariensis* in various ecological niches along the urban–remnant bushland landscape gradient (*i.e.* urban↔sub-urban↔peri-urban↔agricultural/remnant bushland). Clearly, there is an interrelationship between the spread of the plant and the connective potential of the vectors. While the spread of the *Phoenix canariensis* from urban/suburban environments into remnant bushland is clear, there is a dearth of knowledge on how the plant performs for onwards dispersal in these newly colonised areas. Will the plant continually spread

and expand its range, or is essentially confined to remnant bushland on the periphery of urban communities? There is also room for studies that empirically assess the survival of seedlings, through controlled watering as well as herbivore exclusion plots in riverine woodlands.



Figure 5. Vegetation pattern in the riverine forest at Hay.



Figure 6. Six-leaved, grazed seedling with evidence of grazing.



Figure 7. Seven-leaved, juvenile plant.



Figure 8. Two immature palms underneath perch trees.



Figure 9. Two young, reproductive palms.

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