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Effects of light conditions and plant density on growth and reproductive biology of *Cascabela thevetia* (L.) Lippold

Faiz F. Bebawi[A,C], *Shane D. Campbell*[A] *and Robert J. Mayer*[B]

[A]Biosecurity Queensland, Department of Agriculture, Fisheries and Forestry, Tropical Weeds Research Centre, PO Box 187, Charters Towers, Qld 4820, Australia.
[B]Agri-Science Queensland, Department of Agriculture, Fisheries and Forestry, Maroochy Research Station, Mayers Road, Nambour, Qld 4560, Australia.
[C]Corresponding author. Email: Faiz.Bebawi@daff.qld.gov.au

Abstract. *Cascabela thevetia* (L.) Lippold (Apocynaceae) is an invasive woody weed that has formed large infestations at several locations in northern Australia. Understanding the reproductive biology of *C. thevetia* is vital to its management. This paper reports results of a shade house experiment that determined the effects of light conditions (100% or 30% of natural light) and plant densities (one, two, four or eight plants per plot) on the growth, time to flowering and seed formation, and monthly pod production of two *C. thevetia* biotypes (peach and yellow). Shaded plants were significantly larger when they reached reproductive maturity than plants grown under natural light. However, plants grown under natural light flowered earlier (268 days compared with 369 days) and produced 488 more pods per pot (a 5-fold increase) over 3 years. The yellow biotype was slightly taller at reproductive maturity but significantly taller and with significantly greater aboveground biomass at the end of the study. Both biotypes flowered at a similar time under natural light and low plant densities but the yellow biotype was quicker to seed (478 versus 498 days), produced significantly more pods (364 versus 203 pods) and more shoot growth (577 g versus 550 g) than the peach biotype over 3 years. Higher densities of *C. thevetia* tended to significantly reduce the shoot and root growth by 981 g and 714 g per plant across all light conditions and biotypes over 3 years and increase the time taken to flower by 140 days and produce seeds by 184 days. For land managers trying to prevent establishment of *C. thevetia* or to control seedling regrowth once initial infestations have been treated, this study indicates that young plants have the potential to flower and produce seeds within 268 and 353 days, respectively. However, with plant growth and reproduction most likely to be slower under field conditions, annual surveillance and control activities should be sufficient to find and treat plants before they produce seeds and replenish soil seed banks. The most at-risk part of the landscape may be open areas that receive maximum sunlight, particularly within riparian habitats where plants would consistently have more favourable soil moisture conditions.

Additional keywords: Captain Cook tree, flowering, height, seed formation, shoot and root biomass, yellow oleander.

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Introduction

Cascabela thevetia (L.) Lippold; syn. *Thevetia peruviana* (Pers.) K. Schum. (Apocynaceae) is native to Mexico, Central America, South America and the Antilles (Alvarado-Cárdenas and Ochoterena 2007). It has become naturalised in many parts of the world, including Australia, where it commonly exists as two biotypes based on its flower colour: peach and yellow. These same colours are described by Alvarado-Cárdenas and Ochoterena (2007) as orange and yellow. In Australia, it is commonly grown as a garden plant in warm areas, thriving in a variety of environments ranging from wet coastal regions to dry inland areas on soils ranging from sandy loam to black clay (Everist 1974).

The adult plant of *C. thevetia* is a shrub or tree capable of growing up to 10 m tall with milky sap (Everist 1974; Alvarado-Cárdenas and Ochoterena 2007). It spreads into new areas mainly through dispersal of seeds by animals and water (Fallen 1986; Ridley 1990). Livestock generally refuse to eat the plant under normal circumstances but have occasionally been observed grazing shoot tips and consuming fruit (F. Bebawi, pers. obs.).

Cascabela thevetia is most commonly known as 'yellow oleander' in Australia (Smith 2011), but is also frequently referred to as Captain Cook tree in Queensland (Department of Agriculture, Fisheries and Forestry 2013). It has been classified as Category 3 – Restricted Matter in Queensland under the *Biosecurity Act* (2014) based on economic, environmental and social reasons. Bebawi *et al*. (2002) ranked it as the thirteenth most important weed in the dry tropics of North Queensland in terms of its economic, environmental and social impact. It has

invaded natural areas and formed dense thickets along creek lines and floodplains particularly in Charters Towers, South Townsville, Will Creek, Two-mile Creek, Douglas River, Silver Valley, and the Cook Shire (Bebawi *et al*. 2002; Anonymous 2003; F. Bebawi, pers. obs.). It was also listed as a 'sleeper weed' in the wet tropics of North Queensland (Werren 2001). Further south, it has become naturalised on ex-pasture land near Rockhampton, on St Helena Island National Park near Brisbane and at Burleigh Heads (Csurhes and Edwards 1998). In the Northern Territory, it was identified as one of the major weeds threatening rangeland biodiversity (Grice and Martin 2005) and has been listed as a 'species of concern' (Cowie and Kerrigan 2007; Miller and Walduck 2011; Short *et al*. 2011). In Western Australia, it has become naturalised on creek lines at Coolan Island (Hussey *et al*. 1997). Anecdotally, individual infestations appear to comprise either the yellow or the peach biotype but not both.

Field observations by the authors across the sites in North Queensland revealed not only an absence of pasture species under the canopy of dense infestations of *C. thevetia* plants but also absence of any native vegetation and other ground cover species. Any loss to pasture production resulting from invasive weeds, such as *C. thevetia*, is expected to adversely impact the viability of grazing enterprises and the absence of any regeneration of native vegetation is expected to reduce biodiversity.

Several options, including mechanical and chemical techniques, are available for land managers to control *C. thevetia* (Department of Agriculture, Fisheries and Forestry 2013). It is particularly susceptible to fluroxypyr-based herbicides using foliar, basal bark or cut stump applications (McKenzie *et al*. 2010). Vitelli and Madigan (2011) also reported high mortality using the EZ-Ject herbicide system and suggested that, if registered for *C. thevetia*, it would be a good option in sensitive areas.

To date, limited research has been undertaken into the ecological aspects related to management of *C. thevetia* in Australia and there is a paucity of information from its range. One important ecological question that is often asked by land managers trying to control weeds is how long does it take young plants to reach reproductive maturity? This information provides an indication of how regularly control of regrowth will need to occur in order to minimise replenishment of the seed bank (Campbell and Grice 2000). There are many factors that may influence this such as prevailing environmental conditions, soil type, habitat, and inter- and intra-specific competition (Harper 1977). In the case of *C. thevetia*, differences between biotypes may also occur, as has been reported for other weeds such as parthenium (*Parthenium hysterophorus* L., Navie *et al*. 1996).

The primary objective of this study was to quantify how quickly young plants of *C. thevetia* could reach reproductive maturity under a range of conditions, while collecting related information on their growth and reproduction. To do this we tested the null hypothesis, that light conditions, plant density and biotype would not affect the growth (i.e. plant height, basal diameter, shoot and root biomass), time to flowering and seed formation, or pod production of plants of *C. thevetia*. The results of this study are discussed with reference to likely habitat preferences and the practical management of *C. thevetia*.

Materials and methods

Experiment design

A 2 × 4 × 2 factorial experiment was conducted at the Tropical Weeds Research Centre in Charters Towers (20°09′S, 146°26′E) between December 2007 and March 2011. It incorporated a split-split plot design with four replications. There were two light conditions (100% or 30% of natural light) assigned to the main plots, four planting densities (one, two, four and eight plants per pot) assigned to the subplots, and the two biotypes of *C. thevetia* (peach and yellow) were assigned to the sub-subplots.

Large pots (50 cm diameter × 40 cm depth with drainage holes in the bottoms) were placed on concrete slabs (4.5 wide × 13.5 m long), aligned perpendicular to the direction of the sun, and spaced 2.2 m apart to minimise shading. Each slab contained a replicate block. One end-quarter of each slab was randomly chosen to receive natural light, the middle half was left as a buffer, and the other end quarter-shaded using a metal structure (3.9 m wide × 3 m long × 2.5 m high) fully enclosed with 70% UV block forest green Coolaroo shadecloth manufactured by Gale Pacific Ltd, Braeside, Vic., Australia.

Within the shaded and natural light sections of each slab, eight large plastic pots filled with river loam soil were placed at an even distance from each other in four rows of two pots. Each row was then randomly assigned to one of the four designated densities and within rows each pot was planted with seeds of either peach or yellow *C. thevetia*. Seeds of the yellow biotype were collected from Townsville (130 km East North East of Charters Towers, 19°′34′S, 146°87′E) whereas seed of the peach biotype were collected from Mingela (56 km East North East of Charters Towers, 19°49′S, 146° 33′E). Seeds were sown into the pots at a depth of 1 cm on 25 December 2007 at double the required final density. Seedlings were then thinned to the required final density 3 weeks after emergence. Pots were watered daily until they were saturated and water drained out the bottom.

Measurements

Plants were monitored daily to record when flowering and fruiting first occurred in pots. Seed formation was indicated by the formation of a woody seed pod after flowers were shed. Once plants flowered, their height (cm) and basal diameter (mm) was measured and the plants were tagged to avoid double counting. All pods were removed at monthly intervals and recorded as total number of pods produced per pot. This procedure continued for each pot until the experiment finished on 23 March 2011. Weekly measurements of light intensity and air temperature at the soil surface of pots were also made. Light intensity was measured using a hand-held digital DSE Q-1400 Lux light meter (Dick Smith Electrical, Sydney, NSW, Australia), which was placed on the soil surface of pots. Lux data was subsequently converted to photon values using the Lighting Radiation Conversion system developed by Environmental Growth Chambers (Chagrin Falls, OH, USA). A Cole–Parmer scope and laser-sighting infrared thermometer (John Morris Scientific, Sydney, NSW, Australia) was used to record soil temperature on the soil surface.

At completion of the experiment, shoot dry weights (g) were determined by cutting plants at soil surface level and oven-drying

the vegetative material at 80°C for 48 h. Roots were sieved from the soil and oven-dried. Care was taken to remove all soil from the plant root system by placing the root system on top of an elevated stainless steel grid (~1 m^2; pore diameter, 8 mm) and applying water under pressure from a garden hose connected to the mains' water supply. To enhance drying of stem sections, they were cut into small pieces, ~40 cm in size.

Statistical analysis

Data were subjected to split-split plot ANOVA (the light factor split for the density factor split for the biotype factor). Analysis of counts data produced residuals, which were often skewed with unequal variance. In such cases a square-root transformation (of original counts plus 0.5) was applied before analysis. Back-transformed means were calculated and plotted in figures. GENSTAT was used for all statistical analyses (GENSTAT 8.1, VSN International, Hemel Hempstead, Hertfordshire, UK) and Fisher's protected least significant differences test was used to determine differences between treatments whenever analysis showed treatment effects to be statistically significant.

Results

Light and temperature conditions

Patterns of light intensity over the seasons (averaged over 3 years) varied considerably under the two light treatments (Table 1). There was slight variation under natural light, with levels lowest in May (1018 µmoles photons m^{-2} s^{-1}) and highest in October (2060 µmoles photons m^{-2} s^{-1}), while light under shade varied from 262 µmoles photons m^{-2} s^{-1} to 580 µmoles photons m^{-2} s^{-1} on monthly averages. Overall, light intensity reductions of 72% occurred under artificial shade compared with natural light. Soil surface temperatures were on average around 3.5°C cooler under shade (Table 1).

Plant height

A significant difference ($P < 0.01$) in plant height at flowering was observed between light conditions, among plant densities and between biotypes, but there were no significant interactions ($P < 0.05$) (Fig. 1). Irrespective of biotype and density, shaded plants were on average 111.0 cm taller at flowering than those growing under full sunlight. Increasing plant density from one to eight plants per pot adversely affected plant height at flowering. Plants at the highest density were significantly shorter averaging 138 cm, compared with those grown at the lowest density, which averaged 153 cm. Plants of the yellow biotype were significantly taller than the peach biotype when they reached the flowering stage, averaging 150.1 and 142.7 cm across all light conditions and plant densities, respectively.

Table 1. Monthly light intensity (µmoles photons m^{-2} s^{-1}) and monthly soil surface temperature (°C) under natural light and artificial shade, averaged between 2008 and 2010

Month	Soil temperature (°C)		Light intensity (µmoles photons m^{-2} s^{-1})	
	Light	Shade	Light	Shade
Jan.	37.4	33.6	1676.8	478.2
Feb.	35.8	32.8	1692.6	568.9
March	35.4	31.9	1671.6	471.3
April	33.6	29.6	1675.9	476.7
May	30.3	26.1	1018.1	262.2
June	27.8	24.5	1541.4	413.5
July	27.4	24.0	1205.5	282.9
Aug.	27.6	24.3	1427.7	370.4
Sept.	30.9	27.9	1413.2	380.1
Oct.	37.1	35.3	2060.6	572.7
Nov.	37.0	33.6	2021.3	580.1
Dec.	39.5	34.5	1706.5	510.4
Mean	33.3	29.8	1592.6	447.3

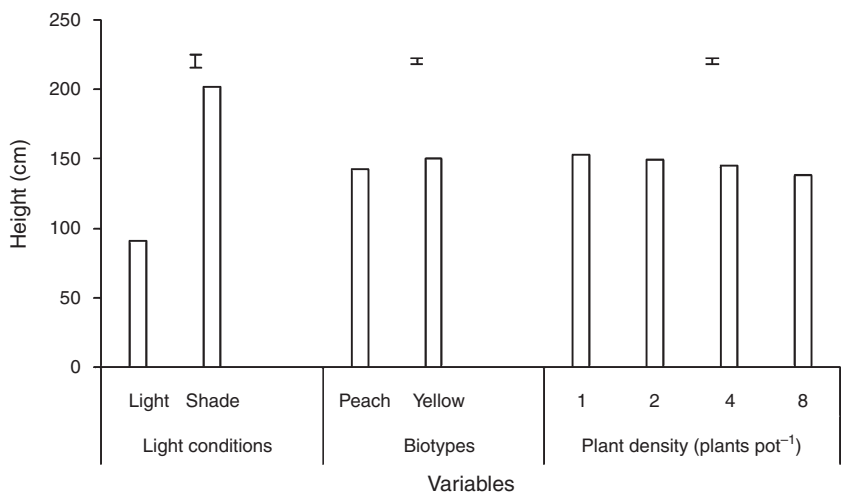

Fig. 1. Plant height at flowering as affected by two light conditions (light and shade) over all biotypes and plant density, biotypes (peach and yellow) over all light conditions and plant density, and four plant densities over all light conditions and biotypes. Vertical bars indicates the least significant difference at $P = 0.05$.

Basal diameter

As with plant height, significant differences ($P < 0.05$) in the basal diameter of plants at flowering were observed between light conditions, among plant densities and between biotypes, but there were no significant interactions ($P < 0.05$) (Fig. 2). Averaged across biotypes and density, plants grown under shaded conditions had larger basal diameters when they reached flowering than those exposed to full sunlight, averaging 27 and 22 mm, respectively. Similar to plant height, plants at flowering also had the largest basal diameter averaging 27 mm if grown at the lowest plant density with a gradual decline occurring thereafter with increasing plant density. In contrast to plant height, plants of the yellow biotype had significantly smaller basal diameters, averaging 21 mm at flowering, compared with the peach, which averaged 28 mm over all light conditions and plant densities.

Time to initial flowering and 100% flowering

Significant interactions ($P < 0.01$) were observed between light conditions, among plant densities and between biotypes in time to initial flowering and to 100% of plants flowering (Fig. 3). Averaged across biotypes, both initial flowering and time to 100% flowering occurred earlier under natural light at the two lowest plant densities, averaging 268 days from seed planting compared with 330 days at the highest density of eight plants per pot, respectively. Days to flowering increased significantly with increasing plant density under natural light.

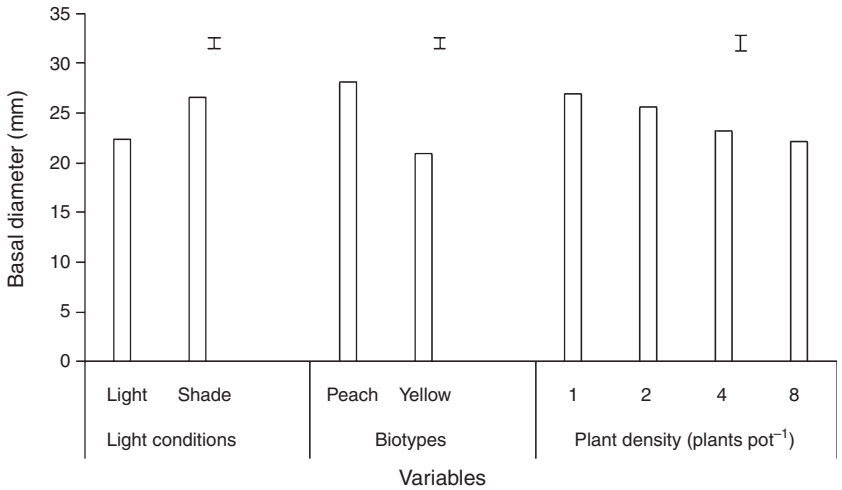

Fig. 2. Basal diameter at flowering as affected by light conditions (light and shade) over all biotypes and plant density, biotypes (peach and yellow) over all light conditions and plant density, and four plant densities over all light conditions and biotypes. Vertical bars indicates the least significant difference at $P = 0.05$.

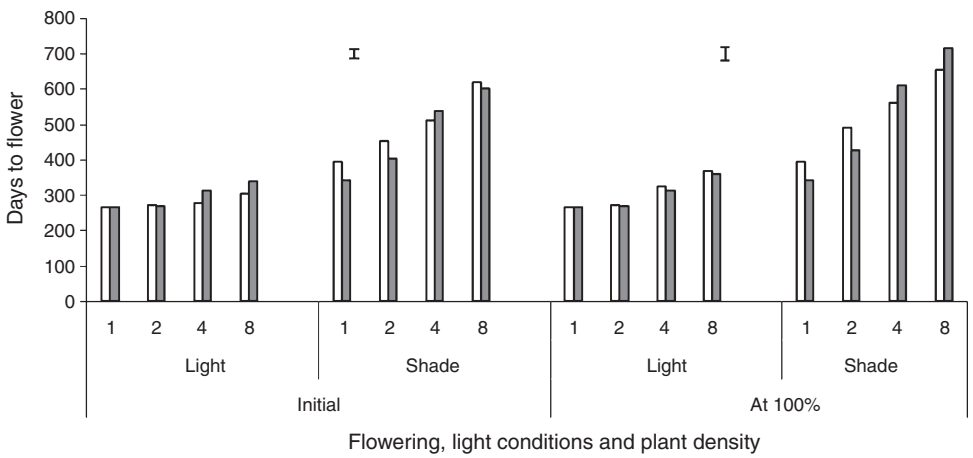

Fig. 3. Days to initial and 100 biotypes of plants of *C. thevetia* under two light conditions (light and shade) and at all four plant densities. The vertical bars indicate the least significant difference for time to initial and 100% flowering at $P = 0.05$. % of plants flowering of the peach (white bars) and yellow (grey bars).

Shading significantly ($P < 0.01$) increased flowering times of both biotypes, particularly as the density of plants increased. Irrespective of biotype, initial flowering was slowest under artificial shade at the highest plant density, averaging 620 days from seed planting. Time to 100% flowering was also slowest under similar conditions, but there was a significant difference ($P < 0.01$) between biotypes. The yellow biotype took longer to reach 100% flowering (715 days) than the peach biotype (655 days) at eight plants per pot. However, at one plant per pot, the peach biotype took longer (400 versus 340 days, Fig. 3). In other words, there was a significant ($P < 0.05$) interaction between plant density and biotype for time to 100% flowering but only under shade.

Time to seed formation

A significant interaction ($P < 0.01$) occurred between light conditions and plant density (Fig. 4) in the time plants took to produce seeds. There was also a significant difference ($P < 0.01$) between biotypes averaged across all light conditions and plant densities.

Plants exposed to natural light produced seeds quicker than shaded plants at all plant densities (Fig. 4). Under natural light there was no significant difference at the two lowest densities (average of 353 days from seed planting) but time to seeding increased significantly thereafter with increasing density. At a density of eight plants per pot, plants took 471 days to produce seeds. Under shade conditions, the time to seeding increased significantly with increasing density, from 448 days at the lowest density up to 687 days at the highest density. Plants of the yellow biotype produced seeds quicker than the peach biotype, averaging 478 and 498 days, respectively, across all light conditions and plant densities.

Pod production per pot

Besides variations in the time that plants started to produce pods under the light conditions imposed, there were also large variations in the quantity of pods produced both on a monthly basis and over the whole period of the experiment (Fig. 5). Plants of both biotypes were capable of producing pods all year round once they reached reproductive maturity, although there were some distinctive peak periods such as between November 2009 and January 2010. It is observed that pod production for both biotypes under both light conditions was significantly low in December 2010 compared with December 2009. There was a weak positive correlation between pod production and natural light condition ($r = 0.22$ and 0.29 for the peach and yellow biotypes, respectively), but slightly greater under shade compared with natural light ($r = 0.40$ and 0.43 for the peach and yellow biotypes, respectively). No correlation was detected between pod production and soil temperature under natural light whereas a weak positive correlation was detected under shade ($r = 0.24$ and 0.31 for the peach and yellow biotypes, respectively).

A significant light condition × biotype interaction ($P < 0.01$) was observed for total pod production of plants per pot over the study period (Fig. 6). Increasing plant densities did not significantly ($P > 0.05$) affect pod production per pot across all light conditions and biotypes.

Maximum pod production per pot was observed under natural light conditions where the yellow biotype produced significantly more pods (775 pods) than the peach biotype (371 pods) across all plant densities (Fig. 6). Under shaded conditions, pod production was low, averaging $\leq$96 pods per pot over the study period, and there was no significant difference between the yellow and peach biotypes (Fig. 6).

Shoot and root biomass at end of experiment

A significant interaction ($P < 0.01$) between light conditions and plant density was observed for shoot biomass (Fig. 7*a*). There was also a significant difference ($P < 0.01$) in shoot biomass between the two biotypes across all light conditions and plant densities.

Shaded plants had a larger shoot biomass than those grown under natural light at all plant densities, although increasing plant density caused a reduction in shoot biomass, with the difference between the two light conditions greatest at the lowest density

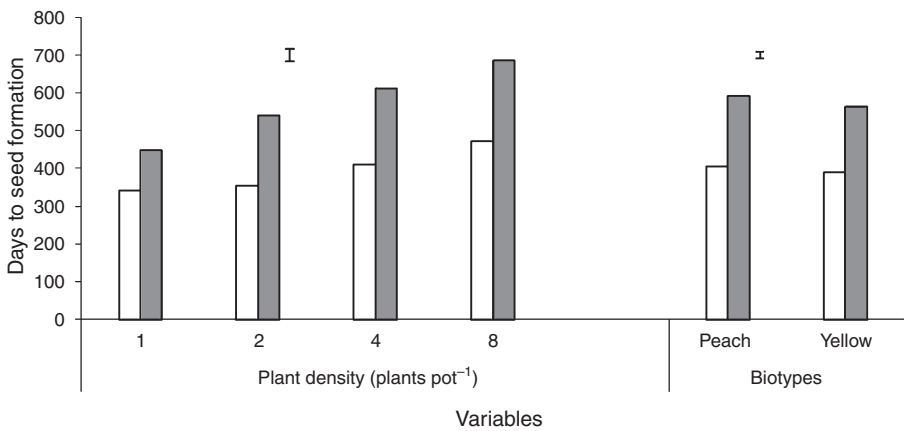

Fig. 4. Days to seed formation of plants of *C. thevetia* under two light conditions [light (white bars) and shade (grey bars)] and four plant densities over all biotypes and biotypes (peach and yellow) over all plant densities. The vertical bar indicates the least significant difference at $P = 0.05$.

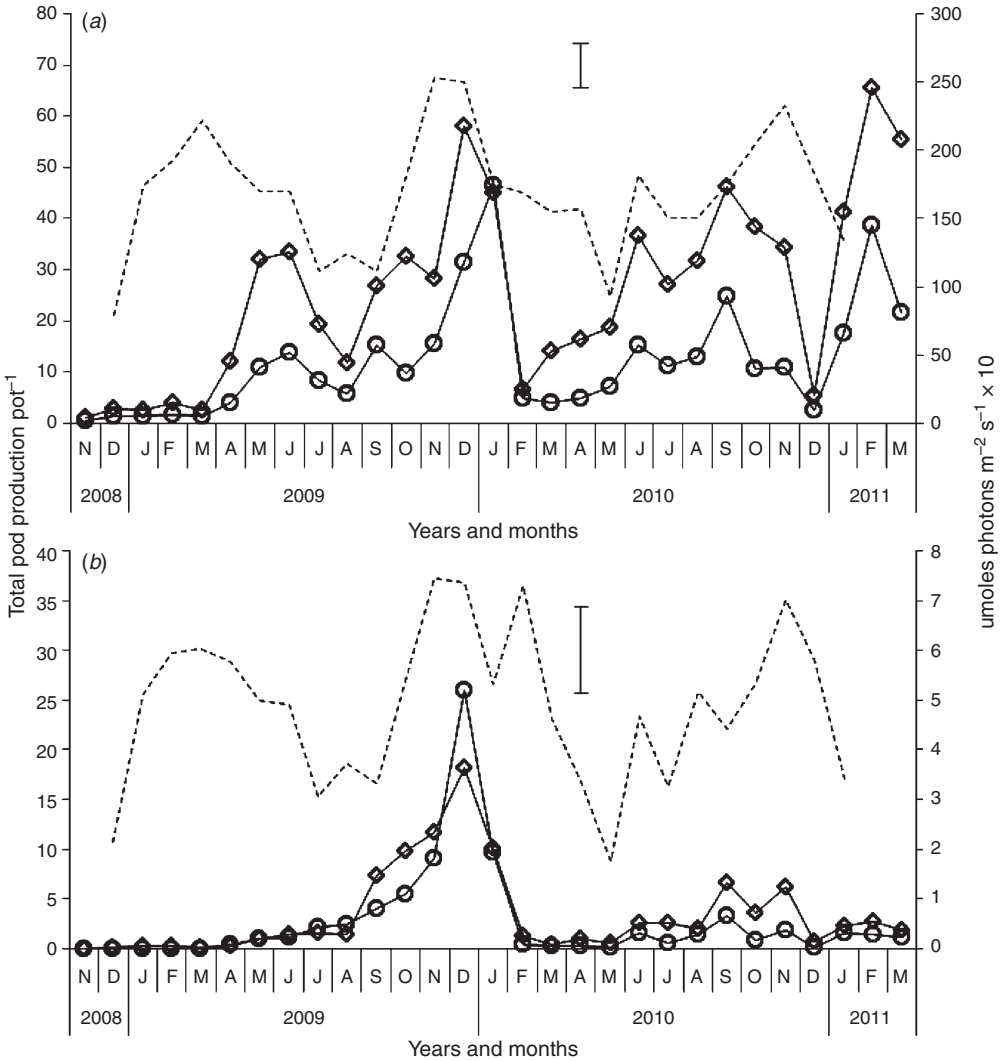

Fig. 5. Total monthly pod production per pot of the peach (circles) and yellow (diamonds) biotypes of *C. thevetia* under (*a*) light and (*b*) shade conditions over 3 years over all plant densities. The photons received are given as a dotted line. The vertical bar indicates the least significant difference at $P = 0.05$.

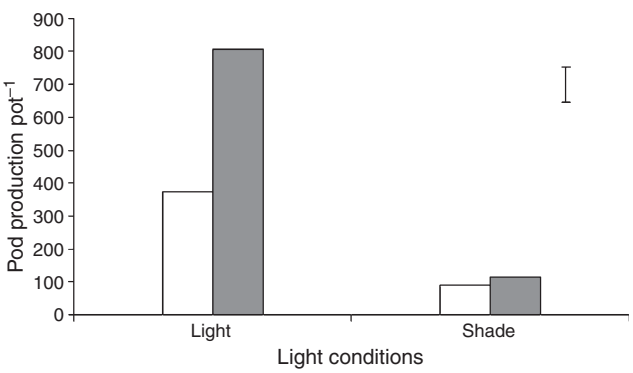

Fig. 6. Total pod production per pot as affected by light conditions (light and shade) and biotypes [peach (white bars) and yellow (grey bars)] over all plant densities over 3 years. Vertical bars indicate the least significant difference at $P = 0.05$.

and least at the highest density (Fig. 7*a*). Plants of the yellow biotype had greater shoot biomass than the peach biotype at the end of the study, averaging 577 and 550 g across all light conditions and plant densities, respectively.

For root biomass there was a significant difference ($P < 0.01$) between plant densities, but light conditions, biotypes and interactions were not significant. Root biomass decreased with increasing plant density, from a maximum of 837 g at a density of one plant per pot to a minimum of 123 g at a density of eight plants per pot (Fig. 7*b*).

The significant interaction ($P < 0.05$) in partitioning between shoot and root growth under the various treatments imposed resulted in differences between light conditions and density for the shoot proportion expressed as a percentage of total biomass (Fig. 8). A similar response was observed for both biotypes. Plants consistently allocated a greater proportion of biomass to shoot growth under shaded conditions compared with full

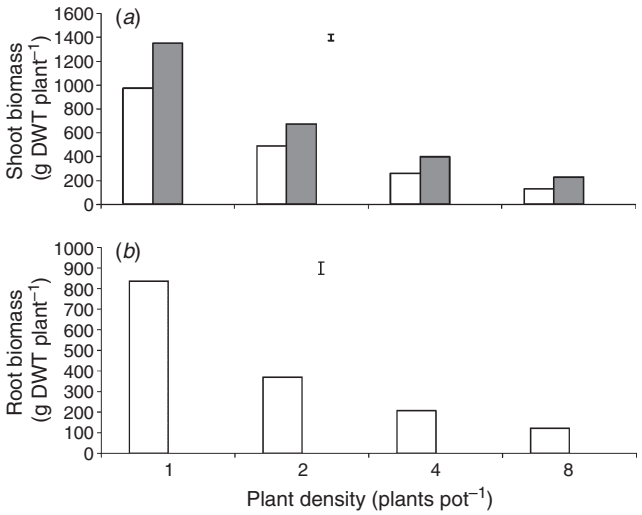

Fig. 7. Mean shoot biomass of plants of *C. thevetia* under (*a*) two light conditions [light (white bars and shade (grey bars)] and four plant densities averaged over all biotypes and (*b*) root biomass under four plant densities averaged over all light conditions and biotypes. The vertical bar indicates the least significant difference at $P = 0.05$.

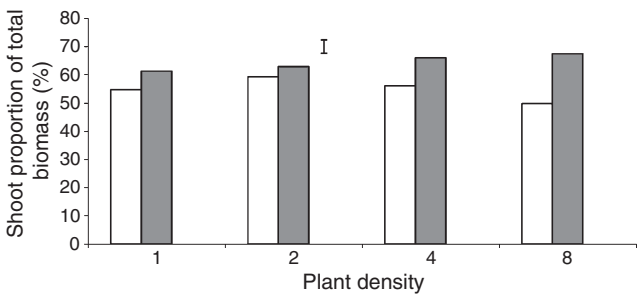

Fig. 8. Proportion of shoots in total biomass of plants of *C. thevetia* under two light conditions [light (white bars and shade (grey bars)] and four plant densities averaged over both biotypes. The vertical bar indicates the least significant difference at $P = 0.05$.

sunlight. There was no significant trend associated with increasing density under natural light, except at the highest density, which was significantly lower than at the other densities. Under shaded conditions, there was a gradual increase in the allocation of resources to shoot growth with increasing plant density (Fig. 8).

Discussion

Shading increased the stem height, basal diameter, shoot biomass and time to flowering and seed formation of *C. thevetia*, but it decreased pod production. Increasing plant density generally reduced the size of plants of *C. thevetia* (height, basal diameter, and shoot and root biomass), and increased the time to flowering and seed formation. The yellow biotype of *C. thevetia* had taller stems and greater shoot biomass than the peach biotype and produced seeds quicker. It also produced more pods under natural light conditions than the peach biotype.

Plant growth

In competition for light, some plants adjust their architecture to bring the leaves higher in the vegetation where more light is available than in the lower strata to power the process of photosynthesis that generates carbohydrates (assimilates) from atmospheric carbon dioxide and water (Devlin *et al*. 2003). The ability to compete for light when light energy becomes limiting is known as the shade avoidance syndrome (Forster *et al*. 2011). The syndrome is expressed as an increase in stem elongation and stem mass at the expense of root and leaf mass (Smith 1982; Schmitt and Wulff 1993; Dudley and Schmitt 1995; Franklin and Whitelam 2005). The response of young plants of *C. thevetia* to increased shading in this study in terms of stem elongation is consistent with the shade avoidance syndrome response observed for other plants such as *Quercus liaotungensis* Kiodz (Xing-fu *et al*. 2011) and *Lindera melissifolia* (Walt.) Blume. (Aleric and Kirkman 2005). It is also consistent with the optimal partitioning theory that plants facing limiting supplies, such as light, will shift biomass partitioning towards more shoot production and less root production (Mooney *et al*. 1985; Robinson 1986; Tilman 1988; Hilbert 1990). Increasing plant density of *C. thevetia* resulted in further increases in the ratio of shoot to root biomass under shaded conditions but not natural light. This suggests that, under shaded conditions, intra-specific competition was occurring for the limited light that was available to plants.

The differential response in plant growth observed between the two biotypes of *C. thevetia* is common for plants that have different biotypes or varieties, and has been reported previously for other invasive weeds in Australia, such as bellyache bush (*Jatropha gossypiifolia* L.) (Bebawi and Campbell 2004; Bebawi *et al*. 2009; Randall *et al*. 2009) and parthenium (Navie *et al*. 1996).

Reproduction

In the present study, the greater time taken for *C. thevetia* to flower and produce seeds under shaded conditions, over all plant densities and biotypes, may have been caused by the allocation/partitioning of carbon assimilates to stem elongation rather than to seed production. Casal (2013) indicated that a reduced generation of yield potential is a natural response that helps plants cope with the limited generation of photoassimilates under shade. However, some plants may respond differently and use strategies such as accelerated early flowering as a shade-avoidance response (Franklin 2008; Keuskamp *et al*. 2010). These differential responses to shading may be explained by variations among plants in growth rates, which are determined by differences in photosynthetic rates to balance resource limitation (Morgan and Smith 1979; Casal 2013). Apparently, high seed yield and high growth rate are not always compatible since plants must allocate resources in a way that balances conflicting needs (Schmitt *et al*. 1995). Casal and Smith (1989) also indicated that the reallocation strategy of resources towards vegetative growth may reduce the competitive success of an individual as well as lead to risk of lodging and mechanical injury. The distinctly low pod production for both biotypes under both light conditions observed in December 2010 compared with December 2009 may be attributed to any of three factors including below average

light radiation, flower production and/or population of pollinators in that particular year.

Increasing plant density of biotypes of *C. thevetia* delayed time to initial flowering and 100% flowering. Similar responses were reported for weedy biotypes of proso millet (*Panicum miliaceum* L.) (Warwick and Thompson 1987) and for bellyache bush (Bebawi *et al*. 2005). However, the different response of the peach and yellow biotype to increases in plant density under both natural light and artificial shade may reflect phenological and/or physiological differences between the two biotypes. For example, at the highest density of eight plants per plot under artificial shade, the peach biotype reached 100% flowering earlier than the yellow biotype (655 days versus 715 days) but at low plant densities the peach biotype was the slowest (500 days versus 420). In general, both wild and hybrid plants are more sensitive to changes in density. For example, greater density significantly delayed flowering in wild plants of radish (*Raphanus raphanistrum* L.) (Campbell and Snow 2007).

Differences between the two biotypes was also observed for seed production with the yellow biotype not only producing seeds faster than the peach biotype across all light conditions and plant densities, but also more of them under the most favourable growth conditions (i.e. natural light). According to Gilbert *et al*. (2001) and Weinig (2000), responsiveness to light irradiance can vary among species, among populations within species and within populations. The greater correlation values between pod production and light conditions under shade compared with natural light for both biotypes indicate that *C. thevetia* is more sensitive to shade than natural light, which may explain the significantly lower pod production under shade compared with natural light. The variability between biotypes in shade avoidance might reflect adaptation to local conditions. Changes in temperature are also known to exert a pronounced effect on the growth of plants and hence upon their productivity (Ong and Baker 1985). However, the weaker correlation between pod production and soil surface temperature under shade compared with nil correlation under natural light also suggests that pod production of *C. thevetia* is less sensitive to reductions in soil surface temperature in tropical environments.

Ecology and management implications

It is important to understand the biology and reproductive traits of a particular invasive species to effectively treat it. The findings of the present study found that plant growth and reproduction of *C. thevetia* is maximised under full sunlight conditions when soil moisture is non-limiting. This would suggest that open areas would be the most favourable locations for *C. thevetia* to grow and reproduce but personal observations indicate that dense infestations tend to form most frequently in riparian areas. While riparian habitats are often thought to have a high canopy cover associated with native species, in rangeland environments open patches or areas of light canopy cover occur and tend to be where *C. thevetia* is most frequently observed. Here plants would have access to the most favourable soil moisture conditions in the landscape and receive sufficient light for growth and reproduction. However, as *C. thevetia* increases in density, the development of young plants within infestations is likely to be restricted through intra-specific competition, particularly from mature parent plants.

The differences between biotypes in this study suggest that the yellow biotype of *C. thevetia* poses a greater risk than the peach biotype because it grows faster and reaches reproductive maturity earlier. However, it is important to note that moisture availability was non-limiting in this study and differential responses between biotypes could occur under natural rainfall conditions. Competition studies between the two biotypes under different moisture availability conditions would help determine which biotype is most competitive.

For land managers trying to prevent establishment of *C. thevetia* or to control seedling regrowth once initial infestations have been treated, this study indicates that young plants have the potential to flower and produce seeds within 268 and 353 days, respectively. However, with plant growth and reproduction most likely to be slower under field conditions, annual surveillance and control activities should be sufficient to find and treat plants before they produce seeds and replenish soil seed banks.

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References

Aleric, K. M., and Kirkman, L. K. (2005). Growth and photosynthetic responses of the federally endangered shrub, *Lindera melissifolia* (Lauraceae), to varied light environments. *American Journal of Botany* **92**, 682–689. doi:10.3732/ajb.92.4.682

Alvarado-Cárdenas, L. O., and Ochoterena, H. (2007). A phylogenetic analysis of the *Cascabela-Thevetia* species complex (Plumerieae, Apocynaceae) based on morphology. *Annals of the Missouri Botanical Garden* **94**, 298–323. doi:10.3417/0026-6493(2007)94[298:APAOTC]2.0.CO;2

Anonymous (2003). 'Declared Plants of Queensland, NRM Facts – Pest Species, PPI.' Land protection, the State of Queensland. (Department of Natural Resources and Mines: Brisbane, Qld.)

Bebawi, F. F., and Campbell, S. D. (2004). Interactions between meat ants (*Iridomyrmex spadius*) and bellyache bush (*Jatropha gossypiifolia*). *Australian Journal of Experimental Agriculture* **44**, 1157–1164. doi:10.1071/EA03194

Bebawi, F. F., Campbell, S. D., and Stanley, T. D. (2002). Priority lists for weed research in the wet- and dry-tropics of north Queensland. *Plant Protection Quarterly* **17**, 67–73.

Bebawi, F. F., Mayer, R. J., and Campbell, S. D. (2005). Flowering and capsule production of bellyache bush (*Jatropha gossypiifolia* L.). *Plant Protection Quarterly* **20**, 129–132.

Bebawi, F. F., Vitelli, J. S., Campbell, S. D., Vogler, W. D., Lockett, C. J., Grace, B. S., Lukitsch, B., and Heard, T. A. (2009). *Jatropha gossypiifolia* L. *In*: 'The Biology of Australian Weeds, Vol. 3'. (Ed. F. D. Panetta.) pp. 102–127. (R. G. and F. J. Richardson: Melbourne, Vic.)

Biosecurity Act (2014). Available at: www.legislation.qld.gov.au (accessed 19 July 2014).

Campbell, S. D., and Grice, A. C. (2000). Weed biology – a foundation for weed management. *Tropical Grasslands* **34**, 271–279.

Campbell, L. G., and Snow, A. A. (2007). Competition alters life history and increases the relative fecundity of crop-wild radish hybrids (*Raphanus* spp.). *New Phytologist* **173**, 648–660. doi:10.1111/j.1469-8137.2006.01941.x

Casal, J. J. (2013). Photoreceptor signalling networks in plant responses to shade. *Annual Review of Plant Biology* **64**, 403–427. doi:10.1146/annurev-arplant-050312-120221

Casal, J. J., and Smith, H. (1989). The function, action and adaptive significance of phytochrome in light-grown plants. *Plant, Cell & Environment* **12**, 855–862. doi:10.1111/j.1365-3040.1989.tb01966.x

Cowie, I., and Kerrigan, R. (2007). 'Introduced Flora of the Northern Territory.' (Department of Natural Resources, Environment, The Arts and Sport: Darwin, NT.)

Csurhes, S., and Edwards, R. (1998). 'Potential Environmental Weeds in Australia.' (National Weeds Program, Environment Australia: Canberra, ACT.)

Department of Agriculture, Fisheries and Forestry (2013). 'Fact Sheet – Captain Cook Tree.' (The State of Queensland, Department of Agriculture, Fisheries and Forestry, Queensland Government: Brisbane, Qld.)

Devlin, P. F., Yanovsky, M. J., and Kay, S. A. (2003). A genomic analysis of the shade avoidance response in *Arabidopsis*. *Plant Physiology* **133**, 1617–1629. doi:10.1104/pp.103.034397

Dudley, S. A., and Schmitt, J. (1995). Genetic differentiation in morphological responses to simulated foliage shade between populations of *Impatiens-Capensis* from open and woodland sites. *Functional Ecology* **9**, 655–666. doi:10.2307/2390158

Everist, S. L. (1974). 'Poisonous Plants of Australia.' (Angus and Robertson Publishers Pty Ltd: Sydney, NSW.)

Fallen, M. E. (1986). Floral structure in the Apocynaceae: morphological, functional and evolutionary aspects. *Botanische Jahrbucher Systematik* **106**, 245–286.

Forster, M. A., Ladd, B., and Bonser, S. P. (2011). Optimal allocation of resources in response to shading and neighbours in the heteroblastic species, *Acacia implexa*. *Annals of Botany* **107**, 219–228. doi:10.1093/aob/mcq228

Franklin, K. A. (2008). Shade avoidance. *New Phytologist* **179**, 930–944. doi:10.1111/j.1469-8137.2008.02507.x

Franklin, K. A., and Whitelam, G. C. (2005). Phytochromes and shade avoidance responses in plants. *Annals of Botany* **96**, 169–175. doi:10.1093/aob/mci165

Gilbert, I. R., Jarvis, P. G., and Smith, H. (2001). Proximity signal and shade avoidance differences between early and late successional trees. *Nature* **411**, 792–795. doi:10.1038/35081062

Grice, A. C., and Martin, T. G. (2005). 'The Management of Weeds and Their Impact on Biodiversity in the Rangelands.' (The CRC for Australian Weed Management and CSIRO Sustainable Ecosystems, Commonwealth of Australia: Canberra, ACT.)

Harper, J. L. (1977). 'Population Biology of Plants.' (Academic Press: London, UK.)

Hilbert, D. W. (1990). Optimization of plant root: shoot ratios and internal nitrogen concentration. *Annals of Botany* **66**, 91–99.

Hussey, B. M. J., Keighery, G. J., Dodd, J., Lloyd, S. G., and Cousens, R. D. (1997). 'Western Weeds: a Guide to the Weeds of Western Australia.' 2nd edn. (The Weeds Society of WA: Victoria Park, WA.)

Keuskamp, D. H., Sasidharan, R., and Pierik, R. (2010). Physiological regulation and functional significance of shade avoidance responses to neighbours. *Plant Signaling & Behavior* **5**, 655–662. doi:10.4161/psb.5.6.11401

McKenzie, J., Brazier, D., Owen, A., Vitelli, J., and Mayer, B. (2010). Stem injection: a control technique often overlooked for exotic woody weeds. *In*: 'Proceedings 17th Australasian Weeds Conference'. (Ed. S. M. Zydenbos.) pp. 459-461. (New Zealand Plant Protection Society: Christchurch.)

Miller, I. L., and Walduck, G. D. (2011). 'Weeds in Top End Gardens.' Agnote. (Biosecurity and Product Integrity, Northern Territory Government: Darwin, NT.)

Mooney, H. A., Bloom, A. J., and Chapin, F. S. III (1985). Resource limitation in plants, an economic analogy. *Annual Review of Ecology and Systematics* **16**, 363–392.

Morgan, D. C., and Smith, H. A. (1979). Systemic relationship between phytochrome controlled and species habitat, for plants grown in simulated natural radiation. *Planta* **145**, 253–258. doi:10.1007/BF00454449

Navie, S. C., McFadyen, R. E., Panetta, F. D., and Adkins, S. W. (1996). A comparison of the growth and phenology of two introduced biotypes of *parthenium hysterophorous*. *In*: 'Proceedings of the 11th Australian Weeds Conference'. (Ed. R. C. H. Shepherd.) pp. 313–316. (Weed Science Society of Victoria: Frankston, Vic..)

Ong, C. K., and Baker, R. H. (1985). Temperature and leaf growth. *In*: 'Control of Leaf Growth'. (Eds N. R. Baker, W. J. Davies and C. K. Ong.) pp. 175–199. (Cambridge University Press: Cambridge, UK.)

Randall, A., Campbell, S., Vogler, W., Bebawi, F., and Madigan, B. (2009). 'Bellyache Bush (*Jatropha gossypiifolia*) Management Manual – Current Control Options and Management Case Studies From Across Australia.' (Queensland Primary Industries and Fisheries, Department of Employment, Economic Development and Innovation: Brisbane, Qld.)

Ridley, H. N. (1990). 'The Dispersal of Plants throughout the World.' (L. Reeve & Co.: Kent, UK.)

Robinson, D. (1986). Compensatory changes in the partitioning of dry matter in relation to nitrogen uptake and optimal variations of growth. *Annals of Botany* **58**, 841–848.

Schmitt, J., and Wulff, R. D. (1993). Light spectral quality, phytochrome and plant competition. *Trends in Ecology & Evolution* **8**, 47–51. doi:10.1016/0169-5347(93)90157-K

Schmitt, J., McCormac, A. C., and Smith, H. (1995). A test of the adaptive plasticity hypothesis using transgenic and mutant plants disabled in phytochrome-mediated elongation responses to neighbours. *American Naturalist* **146**, 937–953. doi:10.1086/285832

Short, P. S., Albrecht, D. E., Cowie, I. D., and Stuckey, B. M. (2011). 'Checklist of the Vascular Plants of the Northern Territory.' Northern Territory Herbarium. (Department of Natural Resources, Environment, The Arts and Sport: Darwin, NT.)

Smith, H. (1982). Light quality, photoperception, and plant strategy. *Annual Review of Plant Physiology and Plant Molecular Biology* **33**, 481–518.

Smith, N. M. (2011). 'Weeds of Northern Australia: a Field Guide.' (Environment Centre: Darwin, NT.)

Tilman, D. (1988). 'Plant Strategies and the Dynamics and Structure of Plant Communities.' (Princeton University Press: Princeton, NJ.)

Vitelli, J., and Madigan, B. (2011). Evaluating the efficacy of the EZ-Ject herbicide system in Queensland, Australia. *The Rangeland Journal* **33**, 299–305. doi:10.1071/RJ11038

Warwick, S. I., and Thompson, B. K. (1987). Differential response to competition in weedy biotypes of proso millet. *Canadian Journal of Botany* **65**, 1403–1409. doi:10.1139/b87-194

Weinig, C. (2000). Differing selection in alternative competitive environments: shade-avoidance responses and germination time. *Evolution* **54**, 124–136. doi:10.1111/j.0014-3820.2000.tb00013.x

Werren, G. (2001). 'Environmental weeds of the Wet Tropics Bioregion: risk assessment and priority ranking.' Report prepared for the Wet Tropics Management Authority. (Rainforest CRC: Cairns, Qld.)

Xing-fu, Y., Jian-li, W., and Li-biao, Z. (2011). Effects of light intensity on *Quercus liaotungensis* seed germination and seedling growth. *Ying Yong Sheng Tai Xue Bao* **22**, 1682–1688.