



Climate change and biotic invasions: a case history of a tropical woody vine[★]

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Abstract

The impacts of climate change in the potential distribution and relative abundance of a C₃ shrubby vine, *Cryptostegia grandiflora*, were investigated using the CLIMEX modelling package. Based upon its current naturalised distribution, *C. grandiflora* appears to occupy only a small fraction of its potential distribution in Australia under current climatic conditions; mostly in apparently sub-optimal habitat. The potential distribution of *C. grandiflora* is sensitive towards changes in climate and atmospheric chemistry in the expected range of this century, particularly those that result in increased temperature and water use efficiency. Climate change is likely to increase the potential distribution and abundance of the plant, further increasing the area at risk of invasion, and threatening the viability of current control strategies markedly. By identifying areas at risk of invasion, and vulnerabilities of control strategies, this analysis demonstrates the utility of climate models for providing information suitable to help formulate large-scale, long-term strategic plans for controlling biotic invasions. The effects of climate change upon the potential distribution of *C. grandiflora* are sufficiently great that strategic control plans for biotic invasions should routinely include their consideration. Whilst the effect of climate change upon the efficacy of introduced biological control agents remain unknown, their possible effect in the potential distribution of *C. grandiflora* will likely depend not only upon their effects on the population dynamics of *C. grandiflora*, but also on the gradient of climatic suitability adjacent to each segment of the range boundary.

Abbreviations: GCM – global climate model; WUE – water use efficiency

Introduction

Those charged with managing biotic invasions require a synoptic view of the invasions in order to formulate the large-scale, long-term control

strategies called for by Mack et al. (2000). The ideal synoptic view would include the potential distribution and abundance of the organism so that the cultural and native ecosystems at risk of invasion can be assessed in terms of their vulnerability and potential for cultural adaptation to the invasion threat (e.g., establishing quarantine procedures or modifying agricultural production

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systems so as to disadvantage the biotic invader or minimise its impacts). Such knowledge can affect the set of nations, agencies, industries and individuals concerned with managing the invasion, and their respective levels of interest in controlling the invasion; those who perceive they are unlikely to be directly and strongly affected may have little interest in contributing resources to resist the invasion.

Paradoxically, the best time to act against an invader is at the earliest stages of invasion, when the least is known about its invasion potential in its new range (Moody and Mack 1988; Mack et al. 2000). Land managers confronted with a biotic invasion do not have the luxury of waiting for the results of unambiguous tests of the invasive potential of an organism such as waiting for the invasion velocity to approach zero as the potential range becomes fully-occupied. Questions regarding the potential distribution and abundance of an invader are therefore 'trans-scientific' insofar as they cannot be directly answered by science. In such cases it is desirable to employ modelling tools to synthesise indirect scientific information to provide the requisite synoptic view in a timely manner (Rastetter 1996). CLIMEX (Sutherst et al. 1999) is a modelling tool designed to explore the potential distribution and relative abundance of species, and is well suited to the task of assessing the invasion potential of exotic organisms (Kriticos and Randall 2001).

The large scale of some biotic invasions, their impacts and the lack of effective policies to prevent or control them, has prompted their addition to the list of major factors that constitute global change (Mack et al. 2000). This list includes other factors such as changes in land use, atmospheric composition, biogeochemistry, and climate. Whilst the potential for biotic invasions to influence other global change factors is now being recognised (Mack et al. 2000), little detailed attention has been paid to the potential for climate change to affect the rate or potential extent of biotic invasions on a geographic scale. Paleogeographic analyses have demonstrated that species' range can change dramatically in response to changes in climate such as those associated with the Pleistocene–Holocene transition (Cole 1982; Davis et al. 1986; Hengeveld 1990). More recent historical examples demonstrate how rapidly some biotic invasions can proceed (Roberts 1989; Hengeveld 1989; van den

Bosch et al. 1992). In the context of an active biotic invasion, changes in climate may significantly alter the area at risk of invasion (potential range) and the spatial pattern of abundance of the invader. Where climate change results in an expansion of the potential range of an invasive organism compared with that under current climate, the set of agencies that are concerned with managing the invasion may also expand as the regions for which the additional agencies are responsible for pest management that comes under greater risk of invasion. Likewise, cultural adaptation techniques and strategies based on the estimated potential distribution under current climate may be rendered less effective under climate change.

In order to explore the effects of climate change on the potential distribution of an invasive organism, it is perhaps best to start with an organism that has a widespread, well known, and climate limited distribution, i.e., not a cosmopolitan distribution. A good knowledge of the current native and introduced distribution is necessary in order to formulate and validate a reliable climate model under current climatic conditions. A widespread distribution means that there are likely to be several different climatic mechanisms limiting the organisms' distribution that each could be affected by climate change (Brown et al. 1996), and makes for a more interesting analysis.

Cryptostegia grandiflora Roxb. ex R. Br. (Asclepiadaceae) was introduced to Australia, prior to 1875, as a garden ornamental in several mining towns of north Queensland (Parsons and Cuthbertson 1992). The plant spread rapidly, and by the early 1900s had established large populations near the towns of Charters Towers (20°04' S 146°19' E), Chillagoe (17°08' S 144°34' E), Georgetown (18°15' S 143°31' E), and Rockhampton (23°23' S 150°34' E) (Parsons and Cuthbertson 1992; Mackey 1996). It continued to spread and now occurs throughout most of Queensland. In moist regions, it can form extensive infestations, smothering native vegetation. At xeric southern and western locations, it is generally found in isolated clumps in moist microsites, or as a deliberately cultivated plant.

Cryptostegia grandiflora has attained prominent weed status due to its ability to form dense monospecific stands, especially in riparian habitats. The presumed resulting reduction in native plant

biodiversity has raised concern from a conservation perspective. The dense infestations of *C. grandiflora* also cause reductions in domestic livestock production by restricting access to the relatively productive riparian habitat in semi-arid regions. There are also concerns about the potential for stock poisoning because *C. grandiflora* contains glycosides with toxic effects on cardiac systems (Mackey 1996). Previous analyses of the potential distribution of *C. grandiflora* under current climatic conditions indicate that it has not yet invaded all of the climatically suitable areas of Australia (Chippendale 1991; Kriticos 1996). The magnitude of the perceived threat posed by *C. grandiflora* has resulted in it being listed as one of Australia's Weeds of National Significance (Anonymous 1997).

The Queensland Government has developed a strategic response to the threat posed by *C. grandiflora* to northern Australia (Mackey 1996). Generally, this involves a campaign of chemical eradication of the plant to the south and west of a defined strategic control line, and the introduction of biological control agents to reduce the potential invasiveness and impact of the plant. This strategy is based upon the results of climate modelling analyses using current climate scenarios (Chippendale 1991; Mackey 1996). From a policy perspective, it is worth considering the likely effect of climate change upon the potential distribution of *C. grandiflora* to understand the expected future areas at risk of invasion and the likely sustainability of the current strategy.

In this paper, we seek to explore the impact of climate change on the potential distribution of *C. grandiflora* (ignoring issues regarding the rate of spread of the plant). The first step in assessing the likely impacts of climate change on *C. grandiflora* is to compare its potential distribution and relative abundance under current climatic conditions with the potential distribution under future climate conditions (Parry and Carter 1998). The difference between these scenarios indicate the potential biophysical impacts of climate change on the distribution and relative abundance of this species. This constitutes the 'sensitivity' to climate change. However, it is unrealistic to ignore the potential effects of human cultural adaptation strategies when assessing the impacts of climate change (Parry and Carter 1998).

The aims of this analysis are to: (1) estimate the potential distribution and relative abundance of *C. grandiflora* under current climatic conditions, (2) assess the sensitivity of these factors to expected climate changes in Australia, and (3) examine the scope for human cultural adaptation to the effects of climate change.

Methodology

An earlier climate change analysis (Kriticos 1996) that employed a set of regional climate change surfaces generated from the CSIRO Division of Atmospheric Research Global Climate Model (GCM) was abandoned in favour of a sensitivity analysis following an examination of sequential sets of GCM output (Climate Impact Group 1992, 1996). The two sets of climate change projections contrasted strongly enough to raise doubts as to whether the state of climate change science was sufficiently mature to currently support reliable regional scale climate projections.

This analysis used CLIMEX version 1.1 for Windows (Sutherst et al. 1999) to model the potential distribution and relative abundance of *C. grandiflora* under current climate. Using the standard meteorological database supplied with CLIMEX, we investigated the mechanisms that limit the range of *C. grandiflora*, and derived parameters for population growth and stress functions based upon its geographic distribution outside Australia. The derived population response parameters were first used to project the potential distribution of *C. grandiflora* under current climatic conditions. This distribution was visually compared with the known distribution (including Australia) to check the goodness-of-fit of the model and to assess the invasion threat posed by the plant under current climate. This comparison was achieved by running the model with the enhanced world 0.5° climate grid (New et al. 1999) and the Australian 0.5° grid created using ESOCIM (Hutchinson et al. n.d.). The population response parameters were then employed in a series of model runs where the climate surfaces were modified using greenhouse scenarios within CLIMEX to reflect the range of conditions expected to occur during the mid-to-late 21st century. The results were then mapped using a corresponding regular 0.5° polygon lattice clipped to

a global coastline. By using the greenhouse scenarios within CLIMEX, we are implicitly assuming that the effects of climate change will be uniform across the climate surface. The GCM research results suggest that in reality, the climate response to global warming will vary on a regional scale in terms of both magnitude and direction of change (CSIRO Division of Atmospheric Research 1988).

Present distribution of *C. grandiflora*

The four sources of information on the bioclimatic preferences of *C. grandiflora* that are useful for predicting its performance in Australia are its published distribution in the country of origin, Madagascar; published data on its worldwide distribution; its current distribution in Australia and a small amount of published information on the ecophysiology of *C. grandiflora*. Of these sources of information, the native range of an organism is normally the most important for CLIMEX analyses. By comparing the range, relative abundance and phenology of the organism with climate response surfaces, it is possible to directly infer population responses to climate variables, as opposed to short-term responses to weather sequences (Sutherst et al. 1999).

The native range of an organism is assumed to include climatically suitable areas within any geographic dispersal barriers (e.g., sea) and areas of biotic exclusion (e.g., competitive exclusion). Including distribution records from exotic ranges in an analysis provides an opportunity to identify additional suitable climatic conditions that are not represented in the native range due to dispersal barriers or biotic exclusion, and often markedly increases the predicted climatically suitable range (Kriticos and Randall 2001).

Due to its coarse geographic scale, the world distribution by country can only be used for a crude verification of the model. Ideally, the Australian distribution would be used only to validate the model. However, because of the lack of knowledge of the climate preferences of *C. grandiflora* to some climate variables, it was necessary to include consideration of the Australian distribution of the plant in building the model.

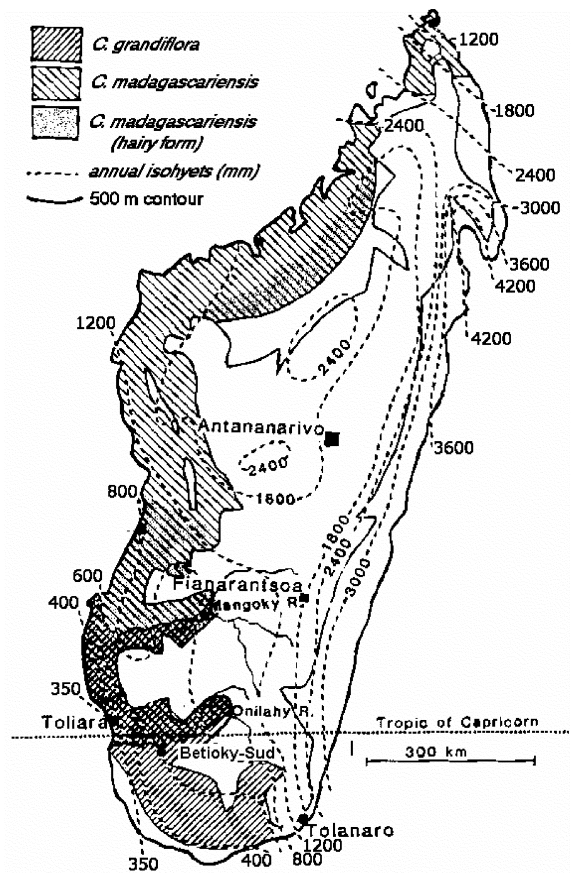


Figure 1. The distribution of *C. grandiflora* and *C. madagascariensis* in Madagascar (McFadyen and Harvey 1990).

Madagascar

The distribution of *C. grandiflora* in its country of origin, Madagascar (Figure 1) has been described by McFadyen and Harvey (1990), based on a work by Marohasy and McFadyen (unpublished data). The climate within the natural range of *C. grandiflora* is characteristically dry tropical with a highly pronounced summer bias in rainfall. The climatic conditions at Betsioky-Sud, near the centre of the *C. grandiflora* distribution in Madagascar, are typical (Figure 2).

Madagascar is a relatively small landmass, with a limited amount of climatic variation, where *C. grandiflora* may not be able to fully express its climatic preferences. This potential limitation is most likely to be significant in the ability of *C. grandiflora* to survive drier climates than are

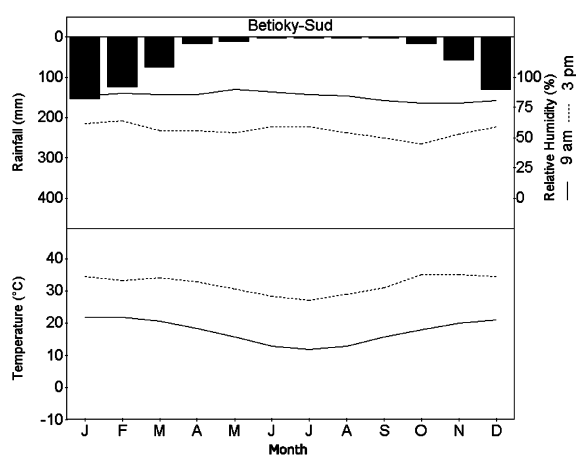


Figure 2. Climate summary for Betioky-Sud, Madagascar. Data extracted from CLIMEX.

present in Madagascar because it is this end of the climatic gradient that is limited by the ocean shore.

The existence of the congeneric *Cryptostegia madagascariensis* Decne. within the wetter, northern range of *C. grandiflora* (Figure 1) provides a further complication to the analysis. In Madagascar, there is a distinct north–south rainfall gradient along the western coast. Based upon their overlapping ranges, close genetic relationship and occupancy of otherwise similar habitats, *C. madagascariensis* may outcompete *C. grandiflora* in the north of the island. In the absence of this competition, *C. grandiflora* might persist in moist conditions than it has been noted occupying in Madagascar.

Worldwide

The global distribution of *C. grandiflora* (Figure 3), ascertained from Jenkins (1944) and Tomley (1995), is primarily tropical, but extends into equatorial and sub-tropical climatic regions, including areas that are both wetter, and drier than those found in Madagascar.

Australia

The information on the distribution of *C. grandiflora* in Australia (Figure 4) was determined from the PestInfo project (Queensland Department of Natural Resources). Of note are the scattered infestations in the southwest of Queensland. This area is subject to moderately large annual (5.2–35.7 °C) and diurnal temperature ranges, and on average,

receives very little rain (<300 mm per annum). However, the averaging process masks the extremely varying nature of the rainfall, which includes rare but major flooding events.

Ecology of *C. grandiflora*

C. grandiflora occurs naturally in arid areas wherever there is an abundance of water (Knight 1944; Curtis and Blondeau 1946; Siddiqui and Mathur 1946; Sen 1968 cited in Tomley 1995). This apparent contradiction is explained by the plant's life strategy. *C. grandiflora* appears to have some characteristics of each of Grime's (1979) ruderal, stress tolerator and competitor plant strategies. This adaptive strategy is apparent in its high seed production, its ability to quickly take advantage of a small amount of moisture for germination and subsequent development of a taproot, its successful capture of light, and its facultatively deciduous capability (Grice 1996; Brown et al. 1998). The tap root and an ability to store starch during favourable growing conditions enable established plants to tolerate a great deal of drought and cold stress (Dale 1980; Harvey, unpublished results cited in Tomley 1995).

Stress tolerance is associated with harsh environments where biotic competition may be less important than abiotic processes. There is some suggestion that *C. grandiflora* may be a poor competitor under warm, moist conditions. Beckett et al. (1934 cited in Tomley 1995) claimed that *C. grandiflora* is shade intolerant, and Polhamus et al. (1934 cited in Tomley 1995) found that "shading of plants slowed growth, and under natural conditions the species is limited to open areas and the margins of forested areas". Brown et al. (1998) conducted a competition experiment between seedlings of *C. grandiflora* and established grass swards. The fact that *C. grandiflora* seedlings could germinate, emerge through dense foliage, and survive for more than 90 days across a wide variety of competitive environments suggests that it is not competition from the herbaceous layer alone that would limit its establishment. Thus, whilst *C. grandiflora* is capable of growing very well in hot, moist conditions, it may not be able to invade undisturbed moist tropical communities without a suitable disturbance regime that creates gaps in the tree canopy layer.

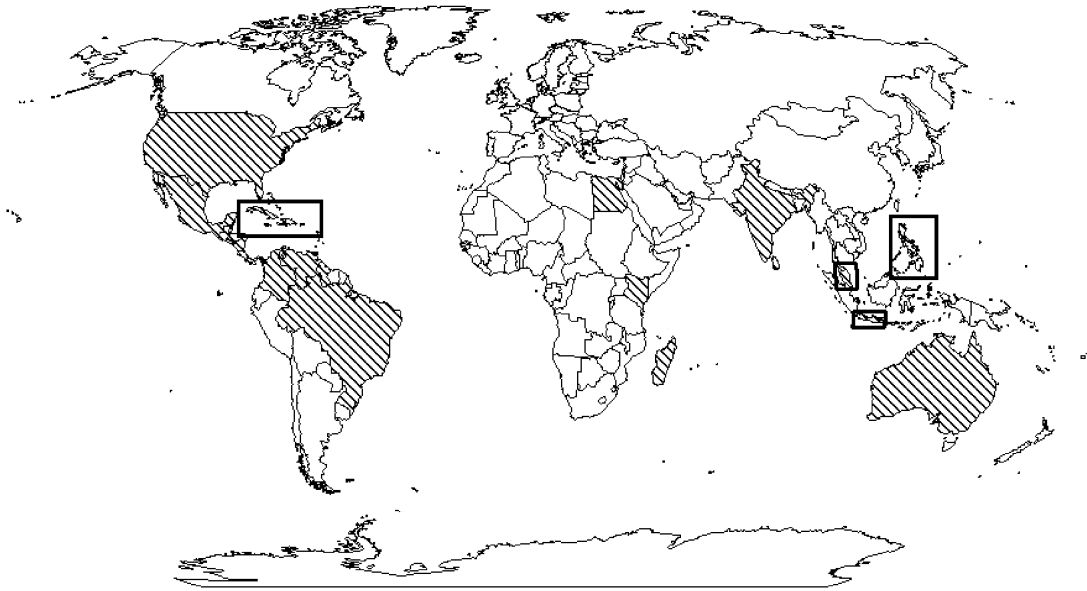


Figure 3. Worldwide distribution of *C. grandiflora* according to Jenkins (1944) and Tomley (1995). The shaded areas indicate countries with *C. grandiflora* and not actual territory occupied by this species. Rectangles contain small countries where *C. grandiflora* is present.

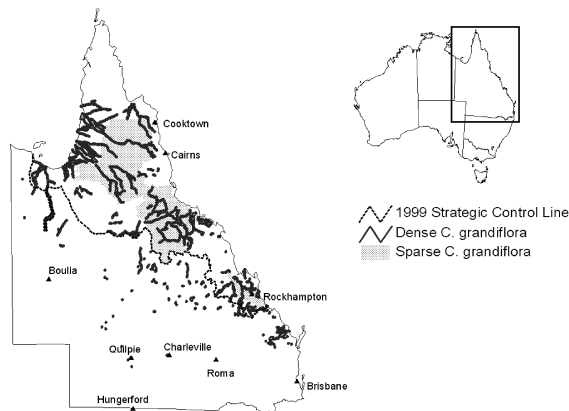


Figure 4. Australian distribution of *C. grandiflora* (adapted from Queensland Department of Natural Resources, PestInfo database 1999).

Some authors maintain that *C. grandiflora* is frost sensitive (Bonner and Galston 1947). However, Polhamus et al. (1934) claimed that -6.7°C is the lower limit for growth, whereas Trumbell (1942 cited in Caltabiano 1972) claimed that -7.8°C is the lower limit for growth. Considering that this plant is of tropical origin, the veracity of these claims must be questioned. Chippendale (1991) states that *C. grandiflora* has existed in Gatton, to the west of Brisbane, for many years, and that Gatton receives

a great deal of frost. He also states that this patch of *C. grandiflora* is confined to a creek. The microclimatic effects of the creek may have protected this patch from significant frost damage. In this model, we assume that *C. grandiflora* is frost sensitive, but that it can tolerate the climatic conditions found at Gatton.

Fitting parameters

The overall goal of the modelling exercise in this study was to fit parameters for CLIMEX climate response functions to the native distribution of *C. grandiflora*. In order to achieve this, stress functions were adjusted so that the cold, dry, heat, and wet stresses largely constrained the population from expanding beyond its present distribution limits in areas where it has had an opportunity to fully expand its range. Each of the model parameters was adjusted until maps of the stress indices compared favourably with the known distribution of the organism in its native and introduced range outside Australia. Several mechanisms of cold stress and thermal accumulation in the range of temperatures suitable for growth were investigated. Those mechanisms that provided the best fit

Table 1. CLIMEX parameter values used for *C. grandiflora*. Parameter mnemonics taken from Sutherst et al. (1999).

Index	Parameter	Value
Temperature	DV0 = lower threshold	15
	DV1 = lower optimum temperature	25
	DV2 = upper optimum temperature	37
	DV3 = upper threshold	43
	PDD = degree-day threshold (minimum annual total number of degree-days above 15 °C (DV0) needed for population persistence)	1985
Moisture	SM0 = lower soil moisture threshold	0.1
	SM1 = lower optimum soil moisture	0.3
	SM2 = upper optimum soil moisture	1
	SM3 = upper soil moisture threshold	1.3
Cold stress	TTCS = temperature threshold	2.5
	THCS = stress accumulation rate	0.2
Heat stress	TTHS = temperature threshold	43
	THHS = stress accumulation rate	0.25
Dry stress	SMDS = threshold soil moisture	0.1
	HDS = stress accumulation rate	0.0025
Wet stress	SMWS = threshold soil moisture	1.35
	HWS = stress accumulation rate	0.017

to the known distribution of *C. grandiflora* were retained (Table 1).

After the stress indices were fitted, the growth indices were adjusted in a similar iterative process, taking into account physiological growth data (see below). Wherever possible, the parameters were derived from the distribution of *C. grandiflora* in Madagascar. However, the density of weather recording stations on Madagascar is low ($\approx 22,000$ km² per station), and most of the stations are located on the coastal margin of the island. The climate database therefore provides little information on the climatic gradients within the island. Madagascar also lacks the extreme xeric conditions such as those found in central Australia. This meant that some parameters had to be inferred from physiological information, and some from knowledge of the plant's distribution in Australia. While this means that the model could not be properly validated using the Australian distribution of the plant, it is likely that the model is more accurate than one created without the use of Australian data

(Kriticos and Randall 2001). The known world distribution by country was also used as a coarse, but independent source of model validation.

There are no reports on the effect of photoperiod on growth or reproductive phenology, and a satisfactory model fit was obtained without the use of any photoperiod indices.

Stress indices

The stress indices are scaled from 0 to 100, with 0 indicating no stress and 100 indicating lethal conditions.

Cold stress. The cold stress function was used to simulate a susceptibility to frost damage. According to the Department of Science and Consumer Affairs (1975), a value of 2.5 °C for the long-term monthly average for daily minimum temperature includes a significant number of frost days per week. Accordingly, the temperature threshold at which cold stress starts to accumulate (TTCS) was set at 2.5 °C, and the weekly stress accumulation rate (THCS) was set at 0.2 °C per week below the threshold (Table 1). The resulting global pattern of modelled cold stress for *C. grandiflora* indicates that most high altitude regions are unsuitable for *C. grandiflora* due to excessive cold temperatures.

Heat stress. Heat stress is likely to accumulate rapidly as temperatures exceed approximately 45 °C, the temperature at which unprotected proteins start to denature (Larcher 1975). The heat stress threshold (TTHS) was set at 43 °C (Table 1), to account for the moderate effect of the long term averaging process used to create climate variables from weather sequences. Few locations in the world experience such conditions. It is included here for completeness, and because of the possibility that increasing temperatures accompanying climate change could significantly increase the area where heat stress could become a significant factor limiting the distribution of *C. grandiflora*.

Dry stress. The dry stress threshold (SMDS) was set at 0.1, a figure that equates to 10% of plant available soil moisture. This value was selected because it is close to the limit at which plants can extract moisture from the soil (Daubenmire 1974).

This value was also selected because at higher threshold levels, *C. grandiflora* is projected to be unable to persist at Hungerford or Boulia, from where it has been reported (Figure 4). Both locations have an average annual rainfall of approximately 260 mm and average modelled soil moisture levels never exceed 0.1. The rate of stress accumulation was adjusted such that Boulia and Hungerford were barely suitable for the plant (Table 1). The resulting global pattern of modelled dry stress for *C. grandiflora* coincides with areas noted for their extreme aridity.

Wet stress. Curtis (1946) states that the growth of *C. grandiflora* is severely retarded by high rainfall. Accordingly, the wet stress threshold (SMWS) was set at 1.35 and the stress accumulation rate (HWS) was set at 0.017 (Table 1). Using these values, *C. grandiflora* is projected to be unable to persist at the wet coastal sites in eastern Madagascar that McFadyen and Harvey (1990) described as unsuitable. *C. grandiflora* is found in the drier south western corner of Madagascar; north of the Tropic of Capricorn and it is progressively replaced by its congener, *C. madagascariensis*. This replacement coincides with an increase in precipitation and soil moisture availability. The model parameters were adjusted so that wet stress progressively increased as conditions became wetter than those found at the edge of its native range. Records of occurrence of *C. grandiflora* in Cooktown (Figure 4) provided a basis for limiting the rate of wet stress accumulation. The resulting global pattern of modelled wet stress for *C. grandiflora* includes the wet tropical regions of the world and some relatively small wet temperate areas in western North and South America.

Growth indices

The growth indices are scaled from 0 to 100, with a value of 0 indicating no growth, and 100 indicating that optimal growing conditions prevail throughout the year.

Temperature index. The temperature index was adjusted so that the upper limit for growth (DV3) coincides with the heat stress threshold. Noting that *C. grandiflora* defoliates during winter in Charters Towers (Mackey 1996), the lower limit (DV0) was set to 15 °C (Table 1). This value is

slightly higher than the long-term winter daily minimum of around 12 °C at Charters Towers. However, plant growth is likely to cease at a higher temperature than that which triggers defoliation. The upper and lower optimum temperature parameters (DV1 and DV2) were adjusted to biologically realistic values for tropical C₃ plants (Fitzpatrick and Nix 1970). The resulting global distribution of temperature index indicates that the temperature conditions favourable for plant growth are very widely distributed.

Thermal accumulation. *C. grandiflora* produces large seedpods. Because pods are created using a series of biochemical reactions, this is presumably an energy-demanding process. That is, the development of pods requires energy to proceed, and so its procession can be modelled as a function of thermal time through the accumulation of degree-days. Further evidence lies in the fact that previous models (Chippendale 1991; Kriticos 1996) did not employ a thermal accumulation mechanism in CLIMEX, and were unable to satisfactorily model the potential distribution of this plant. The threshold minimum heat accumulation parameter (PDD) was adjusted upward until the conditions at the three climate stations in the central highlands of Madagascar (Antananarivo, Antsirabe, and Fianarantsoa) became too cool for *C. grandiflora* (1540 degree-days above 15 °C). According to McFadyen and Harvey (1990), *C. grandiflora* is restricted to below 500 m elevation in Madagascar. An unrealistically high heat requirement (2590 degree-days above 15 °C) is needed to eliminate *C. grandiflora* from the remaining climate stations higher than 500 m above sea level (a.s.l.) (Ihosal, 800 m a.s.l. and Betroka, 795 m a.s.l.). This threshold value would prevent *C. grandiflora* from persisting in many coastal Queensland sites where it has been noted growing and reproducing. The true threshold annual heat requirement for *C. grandiflora* should lie somewhere between these two extremes. The threshold chosen for the model was 1985 degree-days. This value is the maximum heat requirement that would still enable *C. grandiflora* to persist in Gatton, and reflects the fact that Gatton appears to be climatically marginal for *C. grandiflora* (G.J. Harvey, pers. comm.). The effect of the uncertainty of this parameter upon the predicted potential distribution in Australia is rela-

tively minor, ranging 400 km along a narrow coastal belt of northern New South Wales from Taree (152°29' E, 31°53' S) to the Queensland border.

The modelled thermal accumulation threshold restricts the distribution within the area of temperature index values favourable for growth. The poleward boundaries of this threshold have a shape that is easily distinguished from other indicators of cold stress such as threshold temperatures or number of frost days.

Moisture index. The moisture index was adjusted to maximise the growth potential between the two moisture stress thresholds, whilst still maintaining a plausible range between the minimum level for growth (SM0) and the lower bound for optimum growth (SM1), and between the maximum level for growth (SM3) and the upper bound for optimum growth (SM2). The global distribution of the modelled moisture index indicates that whilst the soil moisture conditions conducive to growth are very extensive, they do not coincide closely with the distribution of thermal conditions most conducive to growth.

Climate change scenarios

After the CLIMEX parameters were fitted under the present climate averages, seven climate scenarios were chosen to reflect the range of possible future climatic conditions in the mid-to-late 21st century supported by the IPCC (Table 2). Global average daily temperatures are likely to rise in the order of 2 °C sometime during this period (Houghton et al. 1995; Climate Impact Group 1996). Therefore, all of the climate change scenarios include a 2 °C increase in daily minimum and maximum temperatures. There is much greater uncertainty surrounding the effect of climate change upon rainfall. To account for this uncertainty, rainfall is altered in the range $\pm 10\%$. There is considerable evidence that increased (CO_2) can lead to increased plant growth and a reduction in water use (Morison 1993; Farquhar 1997). The effect of this may be to reduce the rate at which soil moisture is depleted, prolonging the growth period in seasonally dry climates. Alternatively, the soil moisture could be depleted at a similar rate, but the plant community could produce more biomass per unit of water transpired. It is

Table 2. Selected climate change scenarios used in CLIMEX analyses. E_t is the evapotranspiration rate expressed as the proportion of class A pan evaporation.

Scenario number	Temperature	Rainfall	E_t
1	+2 °C	+10%	0.8
2			0.6
3			0.4
4		-10%	0.8
5			0.6
6			0.4
7		No change	0.6

not possible within the present version of CLIMEX to directly simulate an increase in plant water use efficiency (WUE). However, by reducing the evapotranspiration coefficient E_t (constant proportion of class-A pan evaporation that is actually lost to evapotranspiration), the rate of simulated soil moisture depletion is decreased. This potentially extends the simulated growth period, with the net effect that the plant is able to increase its annual growth. Whilst the net effect of increased plant WUE at the stand level is equivocal, this mechanism adequately simulates the necessary effects. The default value of 0.8 for E_t was reduced in steps of 0.2 to account for a range of potential increase in plant WUE. The value of 0.4 for E_t is considered extreme, though Farquhar (1997) states that a doubling of (CO_2) can act like a doubling of rainfall if all other constraints to growth are removed. This value is included to provide an extreme context for the other scenarios.

The first six scenarios in Table 2 are used to explore the sensitivity of the range of *C. grandiflora* in some detail within Australia; where there is abundant, detailed information on the current distribution, and for which there is ample scope for climate change to modify range boundaries without encountering geographic dispersal barriers such as marine coastlines. The seventh scenario is included to provide a mid-range indication of the sensitivity of the potential distribution to climate change on a global scale.

Model assumptions

Genetic homogeneity

It is assumed that *C. grandiflora* is genetically homogeneous with respect to its response to

climatic factors. According to Knight (1944), *C. grandiflora* introduced to Haiti is entirely pollinated by insects. However, Blake (1942, cited in Tomley 1995) finds no evidence of insect pollination of *C. grandiflora* in Australia, suggesting that in Australia at least, it self-pollinates. The lack of out-crossing opportunities afforded by insect pollination may ensure that a high degree of genetic homogeneity is maintained in the Australian population, as adapted genotypes are likely to be rapidly fixed and multiplied (Stebbins 1957; Allard 1965). As there is no indication to the contrary in the literature, the assumption of genetic homogeneity with respect to the climate response of *C. grandiflora* seems valid.

Climate is the primary determinant of potential distribution

The CLIMEX model assumes that the long-term average climate is a major factor controlling the distribution of plants and poikilothermal animals. Whether the predicted distributions exceed the actual distribution of an organism depends largely upon how range outliers are classified. Generally, the climatic range will include areas that are otherwise unsuitable due to non-climatic factors.

The main problems with this assumption have to do with microclimatic factors that enable a species to survive unfavourable conditions, or favourable microsites that enable it to grow when the macroclimate would indicate otherwise. For example, local hydrographic effects could concentrate rainfall runoff, perhaps increasing soil moisture availability above critical thresholds. Another important factor influencing the ability of a plant to persist at a given site is soils. The soil type (particularly the moisture holding capacity) has a large bearing upon the ability of a terrestrial plant to access moisture, especially during summer when evaporation rates may be high. Other edaphic properties such as pH and nutrient status can also affect the ability of a plant to persist.

Translating ecophysiological information into CLIMEX is problematic. CLIMEX uses long-term monthly averages of maximum and minimum temperature and rainfall. This smooths out much of the weekly and daily variation in the temperature and rainfall extremes, and makes it difficult to predict precise borders for phenomena such as frost tolerance.

Results

Caution is required when interpreting the results of the bioclimatic analysis presented below. Whilst the predicted climatic suitability is based upon the best available knowledge, there is also a considerable amount of uncertainty regarding this species' tolerance to some climatic factors. Additionally, the projection is based upon long-term average climate data, which introduces complications and uncertainties to the modelling process. Finally, climate surfaces used in the analysis are a spatial interpolation of long-term climate data, thereby introducing additional uncertainty.

Current climate

The fitted potential global distribution of *C. grandiflora* is characteristically tropical, extending into sub-tropical, semi-arid and equatorial areas (Figure 5). It compares favourably with the known distribution of the plant by country from published sources, correctly predicting suitable habitat for all known occurrences of the plant at the country level of resolution (Figure 3). This indicates that the predicted distribution is probably not too restricted.

The predicted bioclimatic limits to *C. grandiflora* distribution in its country of origin, Madagascar, are presented in Figure 6. All known sites where *C. grandiflora* had naturalised were used in the parameter-fitting exercise. It is noteworthy that this has resulted in the predicted bioclimatic limits of *C. grandiflora* in Madagascar exceeding its known natural distribution in that country. Logically, there are three possible reasons for this: (1) the existence of non-climatic factors restricting its distribution in Madagascar (e.g., dispersal barriers, soil types, cultural (disturbance regimes), microclimate, competition, or pests or pathogens), (2) genetic drift of exported sub-populations, or (3) incorrect model formulation.

The short period since introduction into Australia and the apparent absence of strong selective forces suggest that the second reason is unlikely. The strong agreement between the model and the known distribution of the plant elsewhere suggests that the model formulation is reasonable. Each new climate to which the plant was introduced provides a test of the model's

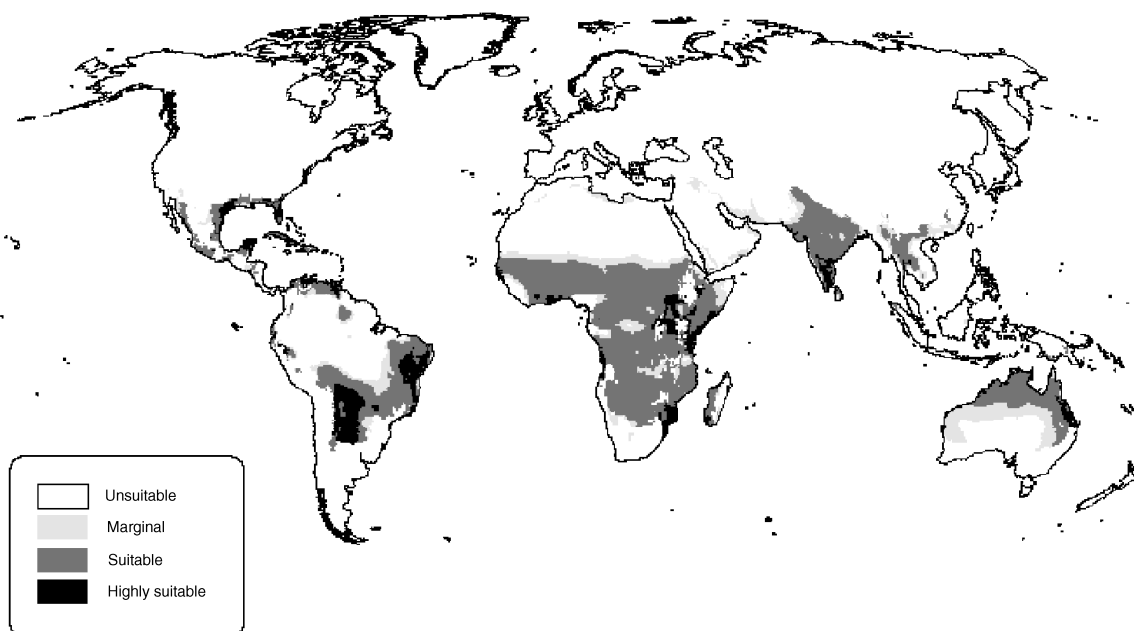


Figure 5. World map showing climatic suitability (ecoclimatic index) for *C. grandiflora* modelled using CLIMEX.

validity. A successful establishment without cultural assistance in an area predicted to be climatically unsuitable would invalidate the model provided it was not in unrepresentative microclimatic conditions. A failure to establish in an area predicted to be suitable, however, would require consideration of whether the failure to establish was due to a lack of adequate opportunity before it could be concluded that the model was invalid; i.e., whether establishment failure was due to environmental stochasticity, small numbers of disseminules etc. or whether the climate was genuinely unsuitable for long-term population persistence. It is most likely that non-climatic factors, such as competitive exclusion, explain the discrepancy between the observed and the predicted distributions in Madagascar. The fact that *C. grandiflora* does occur in an area predicted to be climatically favourable in Madagascar, but outside of its recorded distribution, gives some credence to this assertion. J. Marohasy (pers. comm.) has noted *C. grandiflora* growing in Tolanaro in the southeast of Madagascar (Figure 1). Tolanaro is outside of the known natural distribution, and in an area previously considered too wet for *C. grandiflora* (Curtis 1946; Chippendale 1991). The possibility

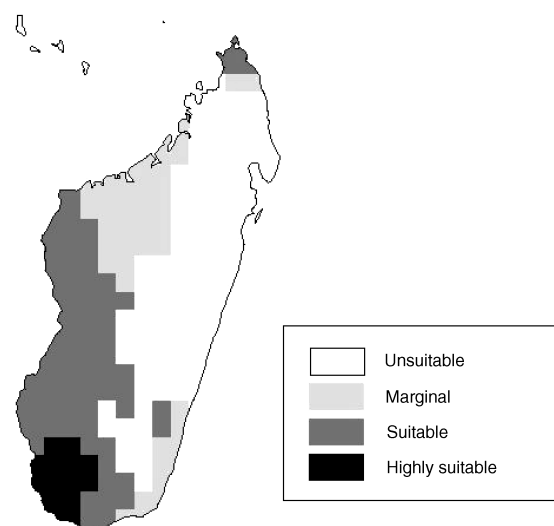


Figure 6. Climatic suitability (ecoclimatic index) for *C. grandiflora* in Madagascar modelled using CLIMEX.

that moderate to high amounts of rainfall do not directly limit *C. grandiflora* is supported by studies by Symontowne (1943) and J.R. Brown (CSIRO, pers. comm.). The natural distribution could be limited by indirect effects of higher rainfall, such

as added seedling competition for light in established undisturbed forests, or the added virulence of pathogens. The existence of the congener *C. madagascariensis* in Madagascar, with its overlapping range may also be restricting the range of *C. grandiflora* to less than its climatic limits through competitive exclusion in that region.

The predicted potential distribution of *C. grandiflora* in Australia is presented in Figure 7. This differs somewhat from a previous analysis by Chippendale (1991, Figure 4.14), primarily in the extension of the southern and south-western borders. Chippendale (1991) inferred his boundaries based on assumptions of frost intolerance and a requirement for a minimum of 300 mm of annual precipitation (Figure 8). These assumptions are challenged by the discovery of several healthy specimens in the frost-prone Quilpie Shire, and in the towns of Charleville and Roma. Specimens have also been discovered in the arid towns of Boulia near the central western border of Queensland, and in Hungerford on the southern border of Queensland. The specimen at Boulia has not been observed to produce viable seed and has not spread (D. Akers, Queensland Department of Natural Resources, personal communication). The specimen at Hungerford was in the Paroo River prior to being destroyed. The average annual precipitation at Hungerford is very low (<250 mm) and non-seasonal. However, the Paroo River floods periodically during rains in the northern part of the catchment. It is likely that these large, infrequent floods may have allowed *C. grandiflora* to germinate and survive despite the adverse long-term climatic conditions.

In order to model the bioclimatic limits of *C. grandiflora*, it was necessary to take into account the performance of the plant in these marginal climates. Based upon information provided by field staff of the Queensland Department of Natural Resources, it was decided that Boulia represented the most arid conditions in which *C. grandiflora* might occur adventitiously. In such climates, its distribution will be restricted to riparian and other, more mesic microhabitats. In these sub-marginal areas, it is likely that this plant will not take on excessively weedy characteristics, posing little threat to conservation or production values. The existence of *C. grandiflora* at Hungerford is most likely due to a combination of

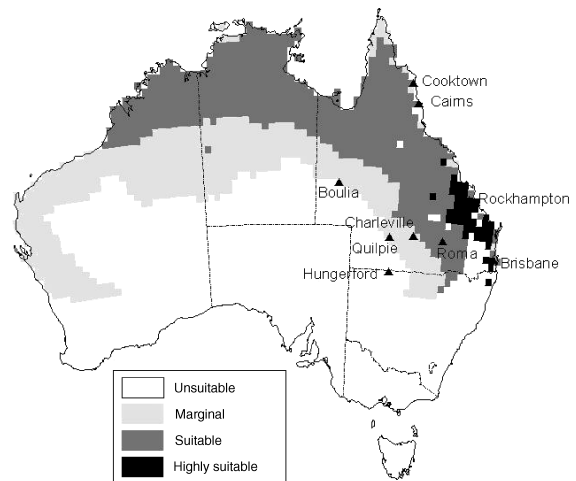


Figure 7. CLIMEX Climatic suitability (ecoclimatic index) for *C. grandiflora* in Australia under current climate.

cultural and other non-climatic effects. Whilst the plant can survive there, it is unlikely that it could significantly expand its population due to an inability to complete its lifecycle.

The specimens of *C. grandiflora* found in Quilpie Shire and in the towns of Charleville and Roma were vigorous and were obviously more suited to the climate than the plant at Hungerford. These vines have given rise to sporadic recruitment in years of milder or wetter than average conditions, or where there was disturbance (B. Toms, pers. comm.). Whilst these vines were restricted to more mesic sites such as creek banks, it is noteworthy that these sites are of disproportionate ecological importance in these xeric regions. The threat that this organism poses in these regions, whilst low in spatial terms, may still be significant from a conservation and agricultural production perspective.

The predicted performance of *C. grandiflora* in Australia indicates that it may become more of a problem in the coastal region around Rockhampton (23° S, Figure 4), and further south. Early distribution maps of *C. grandiflora* (e.g., Caltabiano 1972) indicated that the most extensive and intensive infestations were north of around Bowen (148° 10' E, 20° 00' S). The area infested by 1990 extended much further south and included particularly bad infestations around Rockhampton (Hynes et al. 1992). This indicates that whilst the plant may initially have been spread

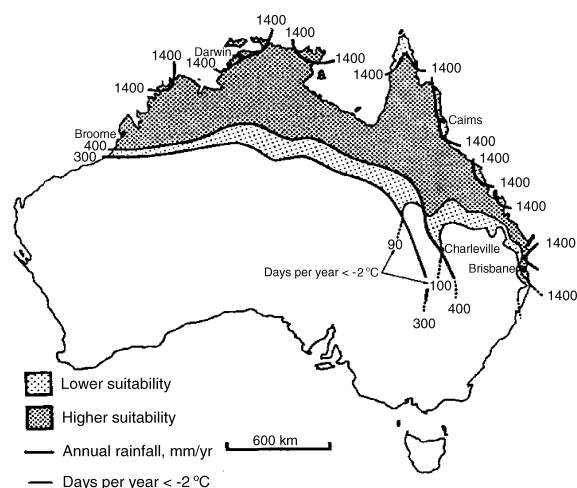


Figure 8. Modelled climate suitability of *C. grandiflora* according to Chippendale (1991).

further north, it has the potential to become more of a pest further south. Further evidence for this claim lies in the fact that Rockhampton lies on the Tropic of Capricorn (23° S), the same latitude as the middle of the natural distribution of *C. grandiflora* in Madagascar (Figure 1).

Climate change sensitivity

The impacts of climate change are assessed here in terms of the relative sensitivity of the potential distribution to a set of conditions that represent the range of IPCC scenarios. Thus, the results should not be viewed as predictions, but rather as projections, based on the stated assumptions about the plant's climatic preferences and the chosen climate scenarios. In interpreting these results, it must be remembered that the climate change scenarios are being applied evenly across the current long-term average climate surfaces. The real effects of climate change are likely to vary considerably on a regional basis (CSIRO Division of Atmospheric Research 1988). In particular, the effects of climate change upon precipitation are likely to vary in both direction and magnitude.

Australia

The overall impact of climate change upon the distribution of *C. grandiflora* in Australia will be

to increase its range poleward (south) and inland (west), potentially invading all mainland states except Victoria (Figure 9). The area of 'highly suitable' habitat extends further northward and westward under the wetter and more water-use efficient scenarios (Figures 9E–G). This signals that the southern margins of the Wet Tropics World Heritage Area and the northern section of the Great Dividing Range may come under more intense invasion pressure from *C. grandiflora* in the future.

The potential distribution of *C. grandiflora* is very sensitive to alterations in WUE due to increasing $[\text{CO}_2]$. All scenarios show a poleward increase in range. Compared with present climatic conditions, increasing temperatures with decreasing rainfall, and no increase in WUE (Figure 9B) results in a contraction of the highly suitable habitat towards the coast around Rockhampton. Increase in WUE (Figures 9B–G) has a very large effect on the distribution of different habitat suitability zones, increasing the range towards the arid interior of Australia.

The distribution of the growth index for *C. grandiflora* indicates where it can grow in the absence of climatic stresses and minimum thermal accumulation requirements for population persistence. In Australia, the zone of highest growth potential under current conditions is centred near Rockhampton. It increases in a predominantly southerly, and westward direction as temperatures, rainfall and WUE increase. Under these climate scenarios, there is an increase in the growth potential in the centre of the continent. These findings are reflected in the two components of the growth index, the moisture index and the temperature index.

Cold stress due to frost intolerance is restricted to the southern highlands of the Great Dividing Range. The area of this zone is slightly reduced by a 2°C increase in global temperatures. The area that receives sufficient heat for pod development is increased in a poleward direction. The change is fairly uniform along the southern boundary of the threshold, except for the highlands of the Great Dividing Range where frost occurrence also prevents the plant from persisting.

There appears to be a small amount of wet stress in northern Australia under current climatic conditions. There is little impact of climate change on the

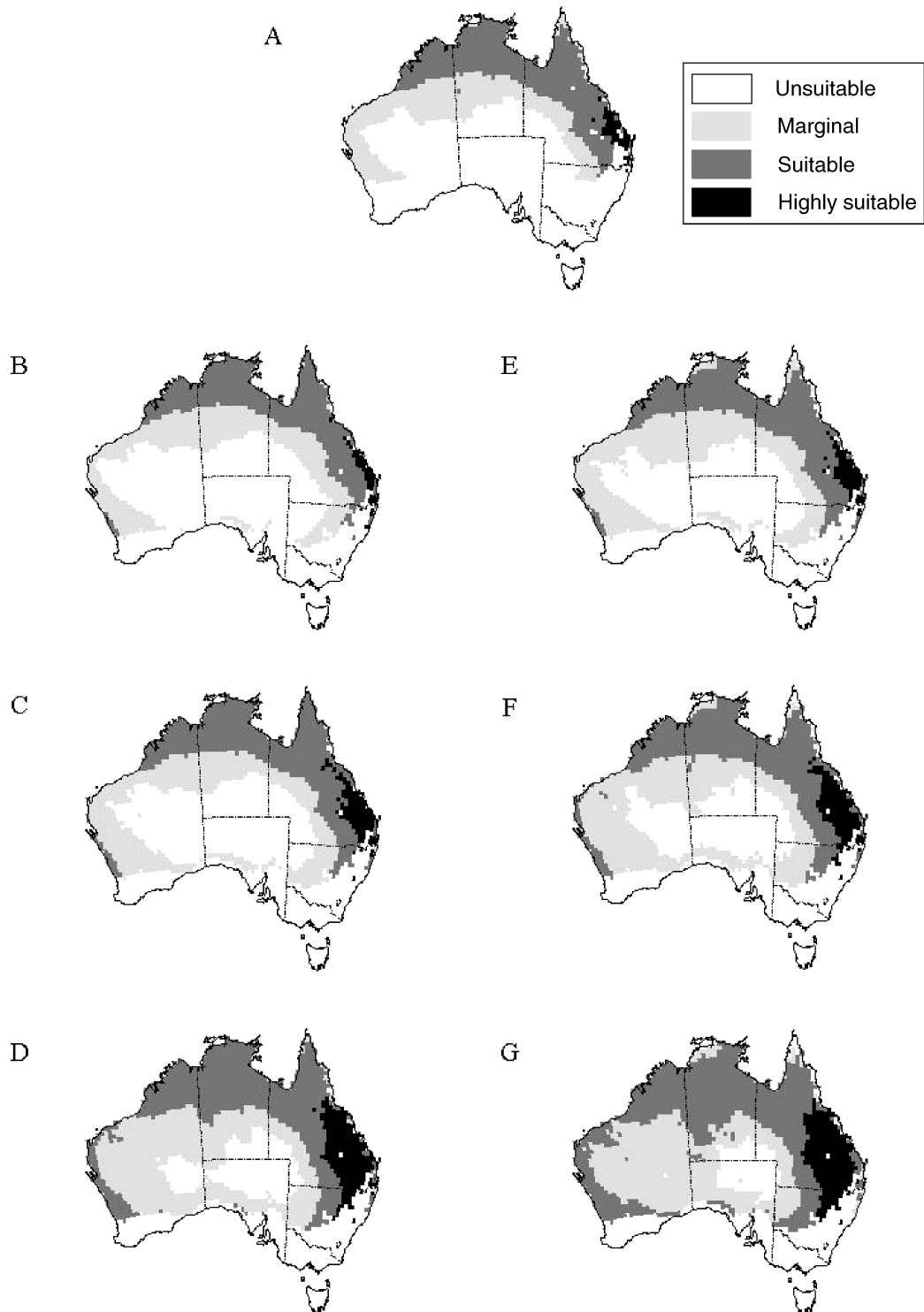


Figure 9. Modelled CLIMEX climate suitability (ecoclimatic index) for *C. grandiflora* under different climate scenarios. (A) current climate; (B) +2 °C, -10% rainfall, $E_t = 0.8$; (C) +2 °C, -10% rainfall, $E_t = 0.6$; (D) +2 °C, -10% rainfall, $E_t = 0.4$; (E) +2 °C, +10% rainfall, $E_t = 0.8$; (F) +2 °C, +10% rainfall, $E_t = 0.6$; (G) +2 °C, +10% rainfall, $E_t = 0.4$.

distribution of this stress. The combination of slight increase in wet stress and a coincident reduction in the moisture index is enough to reduce the climatic suitability of small patches of northern Australia under each of the scenarios that include a 10% precipitation increase. A similar result was found for the scenario with the highest WUE and reduced precipitation.

Under current climate conditions, intense dry stress in combination with low moisture availability for growth appears to limit the area within central Australia that is suitable for invasion by *C. grandiflora*. The effect of climate change is to cause this region of high dry stress to contract markedly in all cases except for the two driest scenarios. In the wettest scenario, *C. grandiflora* would not suffer intense dry stress anywhere in Australia.

Worldwide

A comparison of Figures 5 and 10 indicates that the results of the climate change simulations in Australia are reflected in the global pattern of change in the potential distribution of *C. grandiflora*, with an increase in range towards the poles, and towards more xeric regions. Globally, the areas of greatest increase in the eco-

climatic index as a result of climate change are in the southeastern seaboard regions of the United States of America, southern Brazil, northern Argentina, central and southern Africa, a thin band along the southern Mediterranean coastline, eastern India and southern China.

Discussion

It is apparent from this analysis that *C. grandiflora* occupies only a small portion of its potential range under current climatic conditions. Projected climatic changes may expand this potential range even further. The large proportion of the potential range currently unoccupied, and the high costs of invasion impact and control (Chippendale 1991; Mackey 1996) may justify the implementation of strategic containment and biological control programs against *C. grandiflora*, without reference to climate change. In Australia, a strategic control line (Figure 4) to protect some of the threatened, but as yet uninvaded habitat is attractive as it can focus scarce control resources on those regions that offer the greatest strategic benefits. It must be recognised, however, that depending upon their

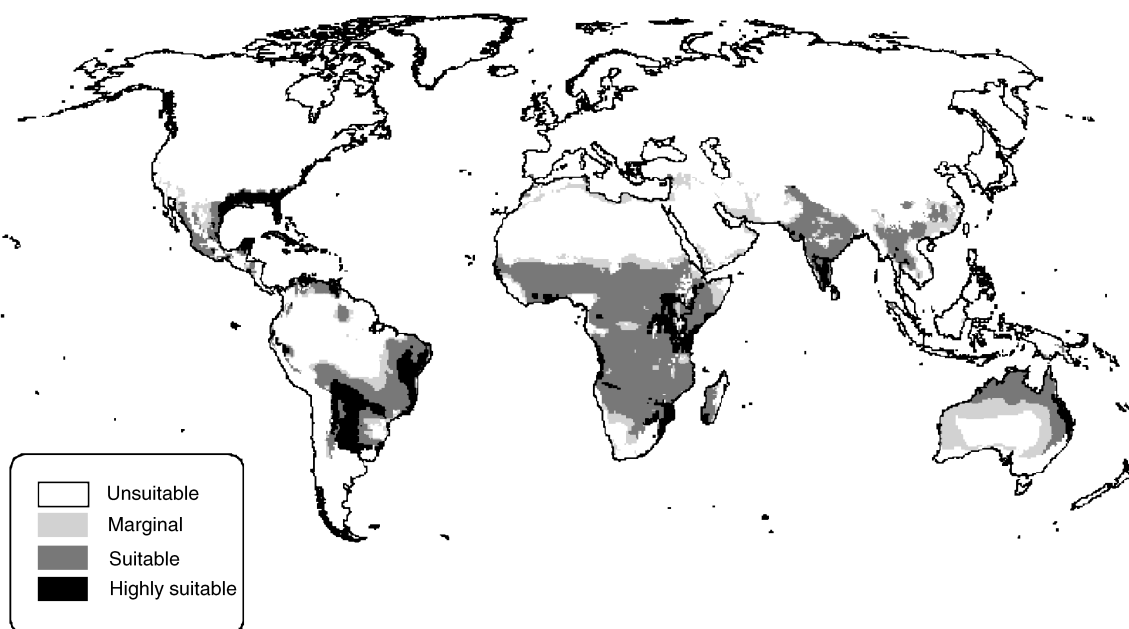


Figure 10. World map showing climatic suitability (ecoclimatic index) for *C. grandiflora* modelled using CLIMEX with a climate change scenario with 2 °C increase in temperature, no change in rainfall and an E_t value of 0.6.

location, climate change could place more invasion pressure on such strategic control lines. That is, climate change may increase the suitability of habitat for *C. grandiflora* in areas adjacent to the strategic control line. This will likely increase the number of disseminules and their probability of successfully establishing (Dale 1980). It is unclear whether the requisite levels of surveillance and control necessary to maintain this line can be marshalled effectively in the relatively sparsely populated regions of rural Queensland through which this containment line runs (Figure 4).

Efforts that reduce the rate of seed production, particularly near the periphery of the range of an invading plant, may significantly reduce the invasion velocity (Hoffmann and Moran 1998). Two biological control agents have been introduced to Australia in an effort to control *C. grandiflora*: a rust fungus *Maravalia cyptostegiae* and a leaf-feeding moth *Euclasta whalleyi* (Pyralidae) (Mackey 1996). Whilst neither agent appears to kill the plant, it is hoped that they will reduce the fecundity of *C. grandiflora*, and hence its invasion velocity, perhaps reducing the invasion pressure on the strategic control line (i.e., likelihood of establishment adjacent to the control line). To our knowledge, no analyses have been published on the potential distribution of these agents under current climatic conditions, or the likely impacts of climate change on these agents. It therefore remains unclear as to what level of control they are likely to exert upon *C. grandiflora* under future climate scenarios.

Climatic conditions are thought to determine the ultimate potential distribution of a plant (Woodward 1987). Interactions with biological control agents may affect the density and distribution of a species within that range, but may not significantly reduce its potential range. Two strands of argument support this notion. First, as Carter and Prince (1981, 1988) showed, epidemic dynamics can be used to explain species' distribution limits. Using the terminology of Carter and Prince, biotic population factors such as biological control interactions will possibly reduce the infection rate (plant fecundity or disseminule production) and the number of infective sites (adult plants). These biotic factors would tend to reduce the density and fecundity of plants near the distribution limits. However, in the absence of competitive exclusion, it is abiotic factors such as

climate and disturbance pattern that determine the number of susceptible sites and their susceptibility (i.e., habitat suitability).

The second supporting argument comes from predator-prey interactions, which dictate that as the plant density decreases, the density of the agent should decrease, and in turn, the agents' effects on the plant population should also diminish. The successful introduction of a biological control agent should result in a reduction of the dynamic equilibrium population level of the control target (White 1997). However, it is unlikely to lead to widespread population extinction, and the ultimate distribution limits may remain largely unaffected by biological control agents.

The outcome of the interplay between the biotic and abiotic factors in terms of the potential geographic range of the plant will be sensitive to the gradient of habitat suitability near the range margin. If the gradient is shallow as in the region of marginally suitable habitat for *C. grandiflora* in south-western Queensland (Figure 7), then there is scope for the control agents to reduce the plants density and fecundity below critical levels for population persistence across large areas. Conversely, abrupt range boundaries such as those in south-west China (Figure 5) and south-eastern Queensland (Figure 7) would require major impacts upon population processes to modify the range boundary, and would still be unlikely to shift the potential range markedly.

The close agreement between the predicted and Australian distribution under current climate provides some degree of model validation. However, comprehensive validation would require a network of study sites arranged along the periphery of the predicted distribution, straddling the boundary. Seeds and plants of *C. grandiflora* would need to be carefully observed through time to ascertain that the plant was capable of completing its life-cycle at each site. Such validation exercises could be expensive and time consuming for a perennial plant in a marginal environment where the opportunities for recruitment might occur very infrequently. Under such circumstances, this form of validation is likely to be of academic interest rather than serve any practical use.

The apparent conflict between the amount of heat accumulation necessary for reproduction in Gattton and that necessary to limit *C. grandiflora*

to below the 500 m contour in Madagascar may warrant investigation.

Conclusion

Even without the possibility of climate change there is potential for *C. grandiflora* to become an even more problematic weed in more mesic regions. On a regional scale, climate change may increase the area of suitable habitat further poleward and inland. It is also likely that on a local scale, the increase in the carbon fertilisation effect and WUE will enable *C. grandiflora* to invade further away from mesic sites such as natural drainage channels in xeric regions as upland plants grow better and become more fecund, fuelling greater invasion potential from these upland foci. This makes the early detection and treatment of outlying populations of prime importance. Whilst climate change may markedly increase the potential distribution of *C. grandiflora*, this effect may be less than the potential for expansion under current climatic conditions.

The increased potential for invasion because of climate change reinforces the status of this plant in Australia as a weed of national significance. It also indicates that a concerted effort should be made to contain the spread of *C. grandiflora* and prevent it invading new jurisdictions. Measures should therefore be taken to alert the public, the horticulture industries and weed professionals in those threatened regions about the increased potential for invasion by *C. grandiflora* as a result of climate change, the costs of invasion, and techniques to identify and eradicate outliers that could become foci for further invasion (Mack et al. 2000).

The potential effects of climate change on the potential distribution and abundance of *C. grandiflora* presented here highlight the desirability of considering the effects of altered climate and atmospheric chemistry when undertaking risk assessments for biotic invaders.

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