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Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in Australia

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Summary

1. *Acacia nilotica* is a spinescent woody legume that has become highly invasive in several parts of the world, including Australia where it has been declared a weed of national significance. Understanding the likely potential distribution of this notorious plant under current and future climate scenarios will enable policy makers and land managers to prepare appropriate strategies to manage the invasion.

2. CLIMEX was used to synthesize available information from diverse sources to model the invasion potential of *A. nilotica* and gain insights into the climatic factors limiting its range expansion. The model identified areas at risk of further invasion so that early preventative or ameliorative measures could be undertaken in a timely manner.

3. The potential distribution of *A. nilotica* in Australia under current climatic conditions is vast, and far greater than the current distribution.

4. Global climate change is likely to increase markedly the potential distribution of *A. nilotica* in Australia, significantly increasing the area at risk of invasion. The factors of most importance are the expected increases in water-use efficiency of *A. nilotica* due to increased atmospheric CO_2 concentrations, allowing it to invade more xeric sites further inland, and increased temperatures, allowing it to complete its reproductive life cycle further southward (poleward).

5. *Synthesis and applications.* Simple paddock quarantine procedures may provide a means of limiting the range of *A. nilotica* within its potential distribution under current, as well as future, climate scenarios. The projected increased growth potential of *A. nilotica* throughout its current range suggests that if future management patterns result in seed pods lying unconsumed on the ground, heightened vigilance may be required to identify and eradicate new invasion foci arising from flood dispersal. The increased growth potential may also result in an alteration of the economic balance, in favour of harvesting *A. nilotica* for agroforestry or local bioenergy projects. A crucial component in containing this invasion will be raising public awareness of the invasion threat posed by *A. nilotica*, its identification and suitable control techniques.

Key-words: biological invasions, CLIMEX, global change, modelling.

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Introduction

Alterations in atmospheric chemistry and changes in climate have long been recognized as major components of global change. More recently, biotic invasions have been added to the list of important factors driving global change (Mack *et al.* 2000). Managers of biological invasions require a synoptic view of invasions as early as possible so that impact risks can be assessed and suitable long-term large-scale strategies can be formulated in a timely manner. In common with other aspects of global change, biological invasions can be likened to large, uncontrolled experiments. Hence, many questions regarding their behaviour are *trans*-scientific in the sense that they cannot be answered directly by science using traditional hypothesis-testing

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methods (Weinberg 1972). The early synoptic view of invasions can therefore only be gained using modelling tools that synthesize available information relevant to decision-makers' needs (Rastetter 1996). CLIMEX (Sutherst *et al.* 1999) is a modelling package that enables users to predict the climatic potential distribution of organisms based primarily on their current distribution. In CLIMEX, using the compare locations function, selected climate response functions for growth and stress are manually adjusted until a satisfactory agreement is reached between the predicted and known distribution of the modelled organism in the native range and any introduced ranges besides those for which the prediction is needed (Kriticos & Randall 2001). There are many climate-based packages designed to predict potential distribution. Most of these packages have been reviewed by Kriticos & Randall (2001). CLIMEX was the most suitable climate modelling package for undertaking this analysis because it can support model-fitting to a global plant distribution, it includes a climate change scenario mechanism, and it provides an insight into the plant's ecological response to climate (Kriticos & Randall 2001).

Prickly acacia *Acacia nilotica* (L.) Delile (Fabaceae) ssp. *indica* (Benth) Brenan (Hannan-Jones 1999) was introduced into Australia in the 1890s for shade, fodder and ornamental purposes (Bolton 1989). In its native range there are nine subspecies of *A. nilotica* distributed in an arc from northern South Africa to the north and east across to eastern India (Hill 1940).

In Australia, *A. nilotica* was well established in Queensland in the Bowen and Rockhampton districts by 1926, and was being actively promoted as a source of shade and forage for sheep while being noted as a problem in cattle country (Pollock 1926). The plant was not declared noxious under the Rural Land Protection Act until 9 March 1957. By this time, it had spread throughout much of central and western Queensland, providing nascent foci for further invasions. *Acacia nilotica* reduces pasture production, increases mustering times and costs, increases soil erosion, impedes stock access to water, and increases water loss through transpiration (Mackey 1997). A comparison between published works by Bolton & James (1985) and March (2000) indicated that *A. nilotica* continues to expand its range actively, and infill gaps in its distribution. A previous analysis of climate using BIOCLIM (Carter 1989), and derived using only Australian occurrence records, indicated that much of northern Australia was at risk of invasion. For an exotic species that is actively expanding its range, the use of only Australian (exotic) occurrence records probably underestimated the potential distribution of *A. nilotica* under current climatic conditions because the model would not be trained on the full range of climate to which the plant is adapted. None the less, this analysis helped fuel efforts by the Queensland government to confine *A. nilotica* to the northern Mitchell grasslands of Queensland, aiming to ensure that the remainder of Australia remains free of this weed (Mackey 1996).

The primary means of dispersal of *A. nilotica* beyond a livestock paddock boundary is through consumption and subsequent defecation of seeds by livestock, i.e. endozoochory (Tiver *et al.* 2000). In the absence of any quarantine strategy to ensure that livestock void *A. nilotica* seeds before being moved from infested paddocks (Mackey 1996), this plant will continue to invade beyond the Mitchell grasslands to other climatically suitable areas. This gives cause for concern under current climate conditions.

Climate change is likely to alter the potential distribution of *A. nilotica* compared with the present. By knowing the direction of change and the relative sensitivity of the potential distribution of *A. nilotica* to different climate change scenarios, we can assess the likely changes in the invasion risk posed by this species.

This study used the CLIMEX software package (Sutherst *et al.* 1999) to develop a model of the climate responses of *A. nilotica* ssp. *indica* based upon its naturalized distribution outside Australia to: (i) project the potential distribution and relative abundance of *A. nilotica* throughout Australia under current climate conditions based upon its global distribution with respect to climate; (ii) assess the sensitivity of this distribution to climate change; and (iii) examine the potential for human cultural systems to adapt to the invasion threat. The modelled potential distribution was then validated using the complete naturalized distribution including Australia. The climate response model was then run with a series of climate change scenarios to assess the sensitivity of the potential distribution to alterations in climate.

Methodology

CLIMEX

The CLIMEX model comprises two conceptual parts. The generic modelling technology includes the model framework, algorithms, software and climate database, and the species model includes a set of parameters that describe the climatic preferences of the species (Sutherst *et al.* 1999). CLIMEX is based on the observation that the distribution of plants and poikilothermal animals is primarily determined by climate (Andrewartha & Birch 1954; Woodward 1987). It uses an annual growth index (GI_A) to describe the potential for population growth during favourable climate conditions, and four stress indices (cold, wet, hot and dry) to describe the probability that the population can survive unfavourable conditions. Interactive stress effects (e.g. cold–dry) can also be included if necessary. The growth and stress indices are calculated weekly, and combined into an overall annual index of climatic suitability, the ecoclimatic index (EI), scaled from 0 to 100. CLIMEX also includes a mechanism for defining the minimum amount of thermal accumulation (number of degree-days)

Fig. 1. Countries where *A. nilotica* ssp. indica is found (light shading is native distribution, dark shading indicates introduced range). Adapted from Brenan & Greenway (1949), Brenan (1983), Fagg (1992), Khan (1970), R. Randall (personal communication), Sahni (1966).

during the growing season that is necessary for population persistence (PDD). This allows estimation of the ability of the plant to develop seed pods fully at each location.

Each stress or growth function included in a model is in effect a hypothesized mechanism that describes the population response to a particular climatic factor. CLIMEX draws from the published literature to provide a range of response types concerning the climatic responses of poikilothermal organisms. When choosing a mechanism we can consider the physiology of the organism and test the geographical response surface against all we know about the ecology of the organism. The geographical response surface for each stress or growth mechanism has a characteristic shape. This can be compared visually with the range boundaries for the species after due consideration is given to factors that might alter the climate response, such as land use or the existence of favourable microsites.

CLIMEX for Windows 1·1 includes a database of 675 meteorological stations throughout Australia, containing monthly averages for rainfall, daily minimum and maximum air temperature and relative humidity at 09:00 and 15:00 (Sutherst *et al.* 1999). CLIMEX uses these variables to drive a weekly time-step, single-bucket, soil moisture model adapted from Fitzpatrick & Nix (1969). In CLIMEX, soil moisture values are calculated in terms of the proportion of plant-available soil moisture in the effective rooting zone. The climate stations are located irregularly across Australia, with marked biases toward the coastal fringes and eastern mountain ranges, and the records are of variable quality. In order to overcome the spatial limitations of the supplied meteorological database, a 0·5-degree regular grid of long-term average climate surface variables was generated for Australia using ESOCLIM (Hutchinson *et al.* 2002). This grid was imported into CLIMEX and used in place of the standard Australian meteorological database.

For global projections, a 0·5-degree regular grid of long-term average climate surface variables for the entire terrestrial area of the globe was developed from a data set supplied by the Climate Research Unit (New, Hulme & Jones 1999). In order to use this grid in CLIMEX it was necessary to estimate 09:00 and 15:00 relative humidity surfaces from supplied temperature and vapour surfaces, using a technique described by Unwin (1980; A. Bourne, CSIRO Entomology, personal communication). The size of the global terrestrial climate database (62 483 points) made it necessary to use a Unix version of CLIMEX rather than the commercial CLIMEX for Windows package for global model runs. To visualize the results, CLIMEX output was 'loose-coupled' to a geographical information system (GIS) to create thematic maps.

PRESENT DISTRIBUTION OF *A. NILOTICA*

World-wide

The global distribution of *A. nilotica* ssp. *nilotica* was ascertained from a wide variety of sources, including Brenan & Greenway (1949), Sahni (1966), Brenan (1983), Fagg (1992) and R. Randall (Western Australian Department of Agriculture, personal communication). Sinha (1971) notes that *A. nilotica* has been naturalized in Jamaica and other Caribbean islands, but gives no indication as to whether it is *A. nilotica* ssp. *indica* that is being discussed. The global distribution of *A. nilotica* is primarily tropical (Figs 1 and 2), although it extends into equatorial and subtropical climatic regions.

The island of Java is climatically suitable for *A. nilotica* (Suharti, Santoso & Nazif 1987) and, according to

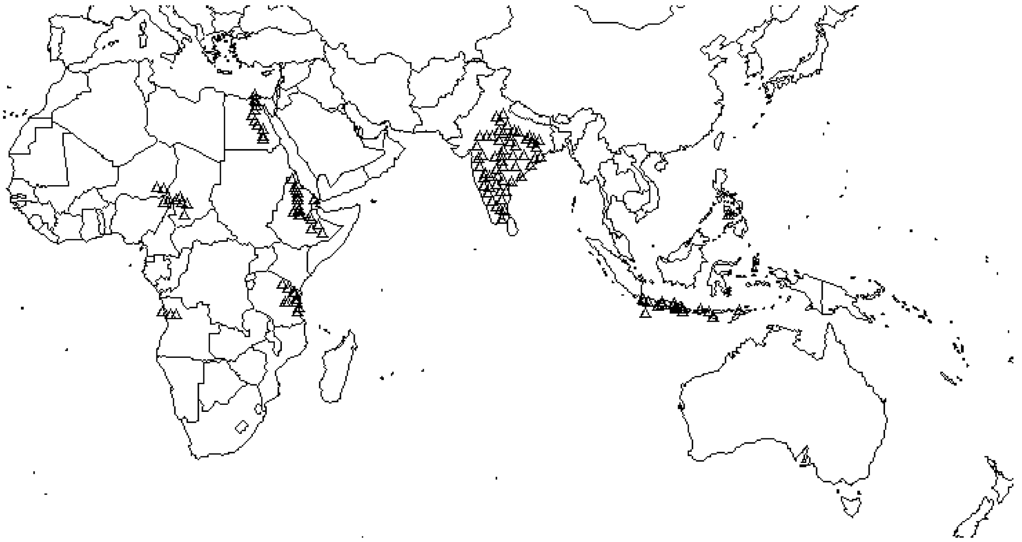

Fig. 2. Point locations of meteorological stations outside Australia climatically suitable for *A. nilotica* ssp. *indica* establishment (R. Randall, Department of Agriculture, Western Australia, personal communication).

R. Randall (Department of Agriculture, Western Australia, personal communication), the drier Indonesian islands to the east of Java are also climatically suitable for *A. nilotica* (Fig. 2). The close proximity of Sumatra to Java suggests that there should have been many opportunities for colonization. The lack of occurrence records, however, suggests that the island of Sumatra may be too wet for *A. nilotica*.

Australia

The present distribution of *A. nilotica* in Australia was gauged from several sources, including Bolton & James (1985), J.O. Carter (Queensland Department of Natural Resources, unpublished data), Queensland Herbarium database (Herbrecs, unpublished data) and Northern Territory Herbarium and DPIF (Department of Primary Industries and Fisheries) databases (K. Sanford-Readhead, personal communication).

Acacia nilotica is present in much of Queensland, in isolated pockets of the Northern Territory, New South Wales, and at one location in South Australia (Fig. 3).

PHENOLOGY AND ENVIRONMENT

In southern Sudan (northern hemisphere), *A. nilotica* flowers irregularly but usually from June to September, with podding occurring between January and May (Khan 1970). There is extensive leaf abscission in *A. nilotica* between April and May, with refoliation occurring between May and August (Khan 1970). This corresponds to exfoliation in the latter part of the dry season, with subsequent refoliation at the onset of the wet season. Where plant growth appears to be influenced by moisture availability, temperature affects flowering and fruiting (Khan 1970). Carter & Cowan (1988) and Carter, Jones & Cowan (1991) claim that in Queensland *A. nilotica* flowers from 'March to June with ripe pods being produced from November to January', although the flowering period can be extended in more xeric sites. This corresponds to flowering during the onset of the dry season and subsequent pod production during the early wet season. Work by CSIRO's Division of Tropical Agriculture shows that in a transect from Julia Creek (20°42′S 141°47′E) to Bowen (20°28′S 147°7′E) in north Queensland, *A. nilotica* flowered over a prolonged period from early February to late September in 1996 (M. Nicholas, unpublished data). In each case, the plant produces pods around the expected time of onset of the wet season at each site.

INFLUENCE OF CLIMATIC FACTORS ON DISTRIBUTION

Rainfall

Acacia nilotica has a wide tolerance for rainfall. It has been found in areas receiving less than 230 mm year^{-1} and in areas receiving more than 1500 mm year^{-1} (Carter, Jones & Cowan 1991; Fagg 1992; Carter & Cowan 1993).

At the Tropical Weeds Research Centre (TWRC, Queensland Department of Natural Resources, Charters Towers, Australia), a pot experiment was used to examine seed germination with different soil types and moisture regimes. Adding moisture at a rate of 8 mm day^{-1} above natural rainfall suppressed germination rates. Pots with additional moisture gave germination rates of 40%, compared with 60% for pots without additional moisture (Anonymous 1996). However, seedling growth of *A. nilotica* increased with increases in available moisture during the first 4 months post-germination (Anonymous 1996). Thus, high moisture and/or heavy soil conditions appear to suppress seed germination but enhance seedling survival and growth.

Rainfall strongly affects leaf production and fall (Carter, Jones & Cowan 1991) and hence plant growth:

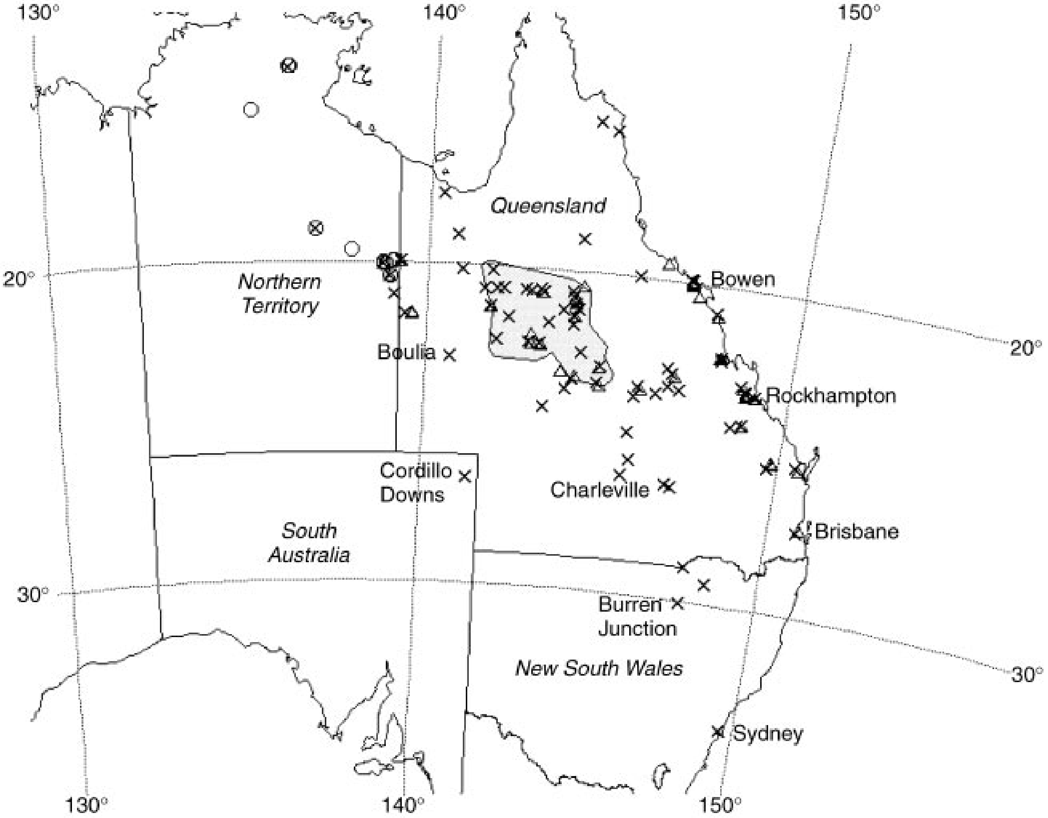

Fig. 3. Occurrence records of *A. nilotica* in Australia. J.O. Carter (unpublished data) (crosses), Queensland Herbarium (triangles), Northern Territory Herbarium and Department of Primary Industries and Fisheries (circles), and Bolton & James (1985) (shaded).

when leaves are absent or sparse, there is little plant growth and plants are presumed to be suffering drought stress.

Temperature

Acacia nilotica is reported to be intolerant of frost (Carter, Jones & Cowan 1991) and Fagg (1992) reports that the plant is frost tender when young. It grows in areas where the mean monthly temperature of the coldest month is 16 °C (Gupta 1970 cited in Carter, Jones & Cowan 1991) and it can withstand temperatures up to 50 °C (Fagg 1992; Adjers & Hadi 1993).

Carter, Jones & Cowan (1991) assume that seed pod production is an energy-demanding process. This indicates that a minimum threshold thermal accumulation each year (degree-days) may be necessary for seed production. The factors that govern the most poleward (southward) extent of this species may therefore be the length of the annual growing season and the moderate frost intolerance noted above.

Photoperiod

The flowering pattern of *A. nilotica* in north Queensland noted previously did not commence below a photoperiod of 12·7 h daylength. However, it appears that photoperiod is not limiting in areas otherwise climatically suitable, as it was possible to create a model with a good fit without employing a light index.

FITTING PARAMETERS

The parameters used in the CLIMEX model for *A. nilotica* are summarized in Table 1. The role and meaning of these parameters are fully described in Sutherst *et al.* (1999), and their values are discussed below. It should be noted that the meteorological data used in this model represent long-term monthly averages, not daily values. This means that it is not possible to compare directly values derived using the model with instantaneous values derived through direct observations. This applies mostly to parameters relating to maximum and minimum temperatures and to soil moisture.

The climatic requirements of *A. nilotica* were derived by fitting the predicted distribution to the known distribution outside Australia (Brenan 1983; R. Randall, Western Australian Department of Agriculture, personal communication) and then comparing the predicted and known distributions within Australia. Because of the paucity of climatic stations in the region of the border between Nepal and India, and the more comprehensive distribution records available for Australia, it was necessary to fit the thermal accumulation parameter to the Australian distribution records in northern New South Wales and south-eastern Queensland, and

Table 1. CLIMEX parameter values used for *A. nilotica* derived from climatic data associated with the known distribution outside Australia. Parameter mnemonics taken from Sutherst *et al.* (1999)

Index	Parameter	Value*
Temperature	DV0 = lower threshold	18 °C
	DV1 = lower optimum temperature	25 °C
	DV2 = upper optimum temperature	37 °C
	DV3 = upper threshold	45 °C
	PDD = degree-day threshold (minimum annual total number of degree-days above 18 °C (DV0) needed for population persistence	1200 °C days
Moisture	SM0 = lower soil moisture threshold	0·045
	SM1 = lower optimum soil moisture	0·2
	SM2 = upper optimum soil moisture	1·2
	SM3 = upper soil moisture threshold	1·5
Cold stress	TTCS = temperature threshold	2·5 °C
	THCS = stress accumulation rate	0·2 week^{-1}
Heat stress	TTHS = temperature threshold	45 °C
	THHS = stress accumulation rate	0·05 week^{-1}
Dry stress	SMDS = threshold soil moisture	0·045
	HDS = stress accumulation rate	0·025 week^{-1}
Wet stress	SMWS = threshold soil moisture	1·5
	HWS = stress accumulation rate	0·02 week^{-1}

*Values without units are dimensionless proportions.

then compare the results with the northern Indian distribution records (see Thermal accumulation below).

Stress indices

In CLIMEX, stress indices indicate negative population growth potential and vary between 0 and ∞, where a value of 100 or greater indicates lethal conditions. When threshold conditions are exceeded, stresses accumulate on a compounding weekly basis. The thresholds and accumulation rates are user-defined parameters.

Cold stress. The reported frost intolerance of *A. nilotica* (Fagg 1992), suggested that a cold stress temperature model might be appropriate. A threshold value of 2·5 °C for TTCS (Table 1) and an accumulation rate of 0·2 week^{-1} for THCS resulted in a cold stress value for Kathmandu (27°42′N 85°18′E) of 114 (lethal). This does not affect the potential distribution of the species in areas that are cool for long periods but do not suffer from intense frosts. A monthly average value of 2·8 °C for the minimum temperature in the long-term monthly average climate database correlates well with the 14th percentile value of 0 °C (Bureau of Meteorology 1975). According to the Bureau of Meteorology (1975) overnight minimum temperatures would be expected to fall below the 14th percentile level of monthly values on average once per week. A threshold cold stress value of 2·5 °C therefore corresponds to frosts occurring more than once per week.

This cold stress function does not affect noticeably the potential distribution of *A. nilotica* under current climatic conditions because the lethal frosts occur in areas that are already unsuitable due to an inadequate thermal accumulation. None the less, cold stress is included because it accords with the noted behaviour of the species in relation to frost and may influence the future potential distribution under climate change scenarios.

Heat stress. Fagg (1992) notes that *A. nilotica* can tolerate temperatures of up to 50 °C. Setting the heat stress threshold long-term average (TTHS) to 45 °C would include days when the maximum temperature approaches or exceeds 50 °C. Using these parameters there is no apparent heat stress in Australia or India. Two locations in Africa (Araouane 18°54′N 3°35′E in Mali and Reggan 26°46′N 0°09′E in Algeria) and one in Pakistan (Jacobabad 28°15′N 68°29′E) show a small degree of heat stress under the current climatic conditions.

Dry stress. The dry stress threshold (SMDS) was set at the same level as SM0, using the rationale that moisture-related stresses begin at the same soil moisture levels as population growth ceases.

Wet stress (waterlogging). The wettest places colonized by *A. nilotica* are in some parts of Indonesia. The wet stress threshold was set to equal SM3, and the wet stress accumulation rate was adjusted so as to prevent *A. nilotica* from persisting in conditions wetter than these Indonesian sites (P. Pheloung, personal communication). In Australia, the effect of this stress is to make a small area around Innisfail (17°31′S 146°03′E) in northern Queensland climatically unsuitable.

Growth index

The growth indices indicate how favourable each location is for population growth, and are scaled from 0 to 100. The temperature and moisture indices are combined multiplicatively to give the growth index GI_A, which is also scaled from 0 to 100. The growth index for a site is set to zero if the minimum requirement for thermal accumulation is not met.

Temperature index. The minimum (DV0) and maximum (DV3) threshold temperatures for development were established from the overseas distribution of the plant. The minimum threshold for population growth, DV0, was set to 18 °C, slightly above the minimum threshold temperature for germination (13 °C) noted by Carter, Jones & Cowan (1991). The minimum temperature for maximum growth rates (DV1) was set to 25 °C and the upper temperature threshold for maximum growth rates (DV2) was set to 37 °C. These values accord with the experimental results of Mahmoud *et al.* (1981) on growth rates of *A. nilotica* seedlings, and more generally the temperature response curves adopted by Fitzpatrick & Nix (1970) for tropical legumes. The maximum threshold for population growth (DV3) was set to 45 °C, the same value as the heat stress threshold.

Thermal accumulation. The distributions of plants can be limited in cool environments by the length of the growing season or by lethal low temperatures and frost. According to J.O. Carter (personal communication) there was a specimen of *A. nilotica* growing in the Sydney Botanical Gardens (33°51′S, 151°12′E). It had not been noted to set fruit but nevertheless was able to survive the winters unharmed. It was not possible using a threshold temperature model for cold stress alone to make Sydney suitable for physiological growth, but not reproduction, without producing results that conflict with the known performance of this species elsewhere. In contrast, a combination of the cold stress and degree-day models produced results that are consistent with the known growth and survival of this species throughout its recorded range in Australia.

The minimum amount of thermal accumulation necessary to complete a life cycle (PDD) was set to 1200 degree-days above DV0 (18 °C), based initially upon distribution records for northern New South Wales and south-eastern Queensland. The growth index predicts that this species will be able to grow throughout the tropics and well into the eastern temperate regions of Australia. Significantly, however, the plant is not predicted to be able to experience enough thermal energy to be able to reproduce successfully south of Burren Junction (30°5′S, 148°58′E). Therefore, while the plant is predicted to be able to grow to the south-east of Burren Junction, it is unlikely to be able to persist there indefinitely due to an inability to complete the life cycle.

The length of the growing season is calculated from the PDD and DV0 parameters. PDD is the number of degree-days of thermal accumulation above DV0 required by a species to complete one generation. For a perennial plant, this means the minimum annual amount of heat accumulation required for seed production. If this amount of heat is not available, the plant cannot reproduce. The value of PDD (1200 degree-days above 18 °C) was originally derived from the Australian distribution of *A. nilotica* (Fig. 3), ignoring the record at Sydney. The modelled distribution of *A. nilotica* in northern India and Nepal using the PDD parameters derived from the southern Australian distribution accorded with the known distribution, and validated the fitted parameter.

The sensitivity of the model to alterations in the value of PDD was also examined. It was determined that 1218 degree-days above DV0 was the total amount of thermal accumulation available at Kathmandu, a location known to be unsuitable for *A. nilotica*. Kathmandu would be unsuitable for a species requiring more than 1218 degree-days above 18 °C. Using these parameters (PDD = 1218 degree days) the potential distribution shifts a considerable distance southward into northern India, but makes no noticeable difference to the predicted Australian distribution. The difference in model behaviour between the two different regions is due to the different spacing of the climate stations and the altitude gradients. The retention of the original value for PDD of 1200 degree-days is therefore conservative. In the Australian context, this parameter is also insensitive.

Moisture index. Acacia nilotica is facultatively deciduous (Carter, Jones & Cowan 1991; Fagg 1992), allowing the plant to reduce its transpiration rate dramatically in times of moisture deficit. Accordingly, the lower threshold for soil moisture (SM0) was set as low as possible (0·045) whilst enabling populations to occur at Salalah (17°02′N 54°10′E, Oman), the driest location at which *A. nilotica* has been noted outside of Australia. SM1 (the lower threshold for optimum moisture conditions) was set low enough that sufficient growth could be made from low-magnitude rain events. SM2 and SM3 were set to account for the presence of *A. nilotica* in very high rainfall areas, such as Indonesia.

FUTURE CLIMATE

After the CLIMEX parameters were fitted under the present climate averages, six climate scenarios were chosen to reflect the range of possible future climatic conditions in the mid-to-late 21st century supported by the Intergovernmental Panel on Climate Change (1997) (Table 2). There is little doubt that global average daily temperatures will 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.

When using climate data sets that include relative humidity values to indicate atmospheric evaporative potential, CLIMEX estimates the evapotranspiration losses as a function of temperature and relative humidity. When temperatures increase and relative humidity values remain constant, the calculated evapotranspiration rates increase. We assume that the relationship between temperature and evapotranspiration rates for

Table 2. Selected climate change scenarios used in CLIMEX analyses

Temperature	Rainfall	E_t
+2 °C	+10%	0·8
		0·6
		0·4
	−10%	0·8
		0·6
		0·4

E_t is the proportion of class A pan evaporation lost through evapotranspiration.

a given value of relative humidity remains constant in climate change scenarios.

There is considerable uncertainty surrounding the likely effect of climate change upon rainfall in Australia. To account for this uncertainty, rainfall is either increased or decreased by 10%. There is evidence that increased CO_2 concentrations 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. While it is not possible within the present version of CLIMEX to simulate directly an increase in water-use efficiency (WUE), by reducing the evapotranspiration coefficient E_t (proportion of class-A pan evaporation that is lost from the soil profile as evapotranspiration) the rate of soil moisture depletion is decreased. This has the effect of potentially extending the growth period, with the net effect that the plant is able to increase its annual growth rate. The default value of 0·8 for E_t used in CLIMEX was reduced in steps of 0·2 to account for a range of potential increases in plant water-use efficiency. The value of 0·4 for E_t is considered excessive, although Farquhar (1997) states that a doubling of CO_2 concentration 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, more realistic, scenarios.

Results

CURRENT CLIMATE

The areas estimated to be climatically suitable for *A. nilotica* under current climatic conditions are illustrated for the world (Fig. 4) and Australia (Fig. 5). It is apparent that the potential distribution of this species includes all mainland states of Australia except Victoria. The current distribution of *A. nilotica* is fully consistent with the projected Ecoclimatic Index (Fig. 5).

The southern boundary of the potential distribution is due to a combination of lack of degree-days, cold stress (frost) and dry stress. The occurrence records in northern New South Wales (near Burren Junction) and South Australia (Cordillo Downs) accord well with the predicted south-eastern limit of potential distribution. The limit set by an inadequate length of growing season extends north, encircling Brisbane and some isolated pockets to the south and south-west of Rockhampton (Fig. 5). These isolated pockets are also apparent in the temperature and growth indices. According to this model, a small area south of Cooktown is predicted to be too wet for *A. nilotica*.

CLIMATE CHANGE SENSITIVITY

Climate suitability

The overall impact of predicted climate change upon the potential distribution of *A. nilotica* in Australia will be to increase the climatically suitable range poleward (south) and inland (west) (Fig. 6). The area of highly suitable habitat extends further north, south and west under the scenarios of higher precipitation and increased WUE (Fig. 6e–g). All scenarios show a poleward increase in range in response to rising temperature.

When simulated conditions also include decreased precipitation and no increase in WUE (Fig. 6b) there is a slight contraction of the highly suitable habitat towards the eastern coast compared with present climatic conditions. However, even moderate reductions in evapotranspiration (E_t) to simulate increases in WUE (Fig. 6c–d) compensate for the 10% reduction in precipitation. The marked effect of increasing WUE upon the projected distribution of different habitat suitability zones demonstrates that the model is particularly sensitive to this parameter. The uncertainty that this introduces to the analysis suggests that studies of the effect of increased CO_2 concentration on the WUE of *A. nilotica* at the stand level may be warranted.

Growth index

The distribution of the growth index for *A. nilotica* (Fig. 7) indicates the relative growth potential in the absence of climatic stresses and minimum thermal accumulation requirements. The area of highest growth potential under current climatic conditions is centred near Rockhampton, and extends in a coastal arc from the northern part of Western Australia clockwise across and down to mid-New South Wales (Fig. 7a). A comparison of the ecoclimatic index (Fig. 6) and the growth index (Fig. 7) shows that the area in which the plant can grow far exceeds the area in which it can persist and reproduce.

The expected increases in temperature, rainfall and WUE associated with climate change result in a large-scale expansion of the areas with highest GI_A. The areas of moderate to low GI_A increase toward the centre of the continent. These findings are reflected in the two components of GI_A: the moisture index and the temperature index.

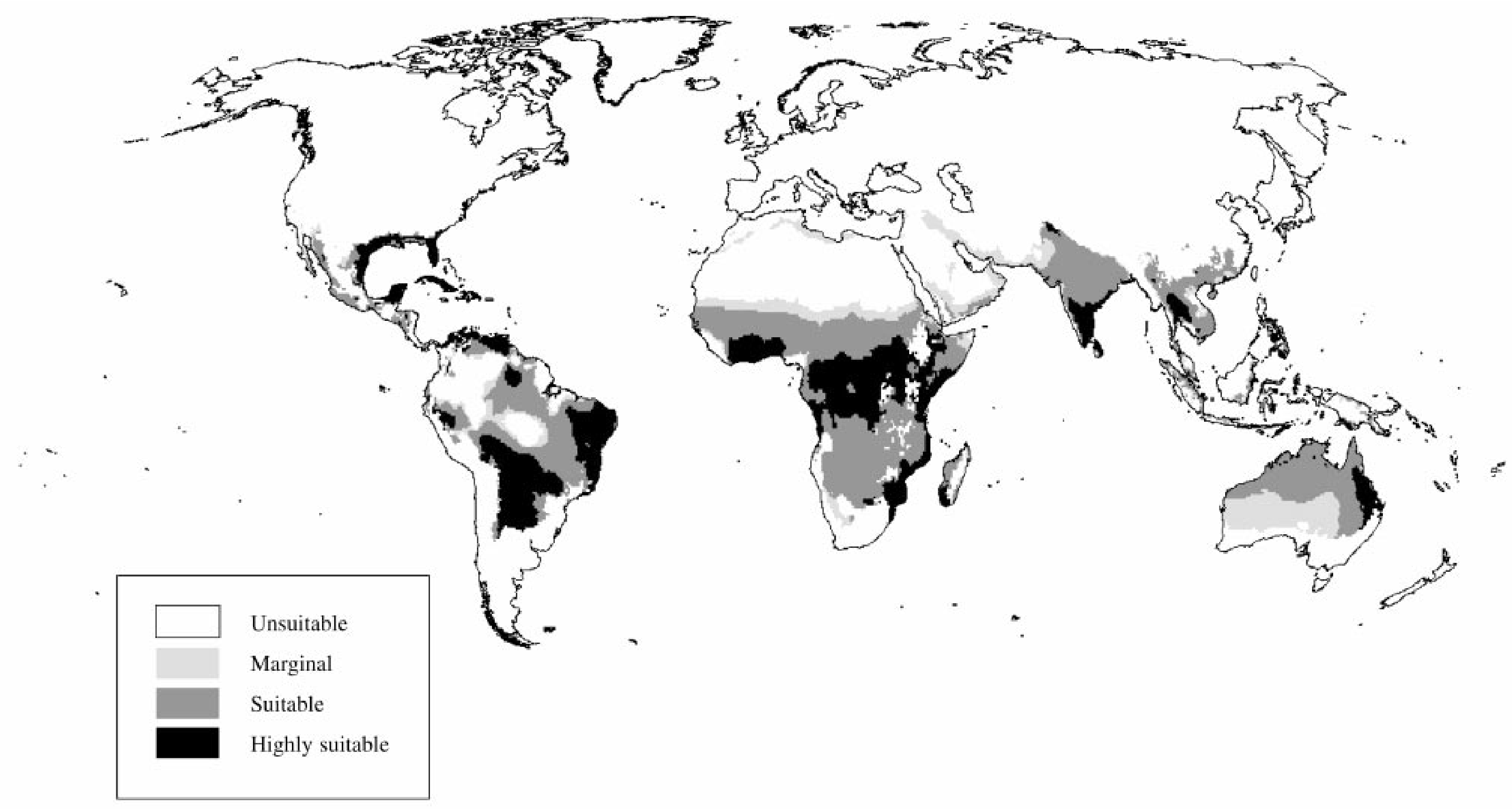

Fig. 4. World map showing climate suitability for *A. nilotica* under current climate modelled using CLIMEX.

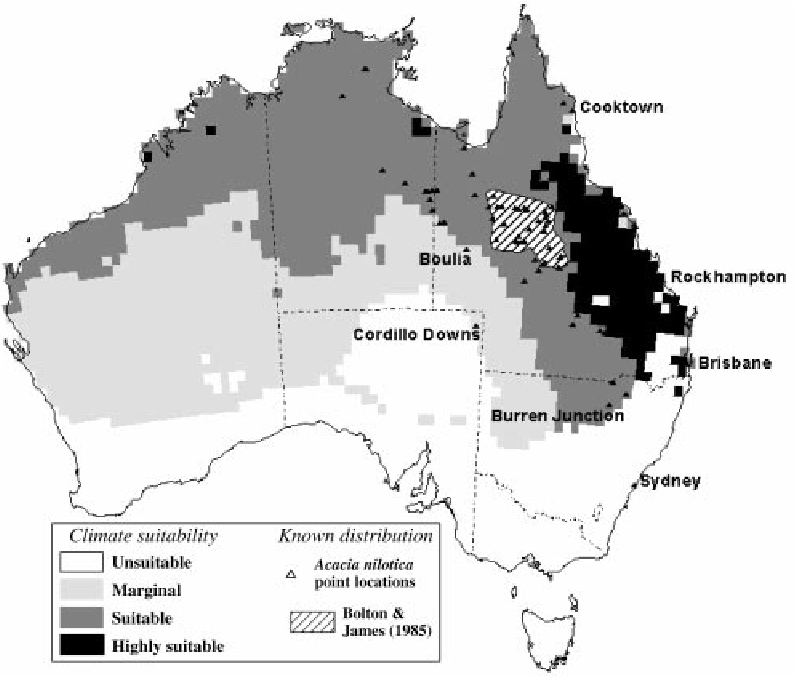

Fig. 5. Current and modelled potential distribution of *A. nilotica* under current climate conditions.

Cold stress

Cold stress due to frost intolerance is restricted to the southern highlands of the Great Dividing Range. The area of this unsuitable zone is considerably reduced by a 2 °C increase in global temperatures.

Thermal accumulation

The area that receives sufficient heat for seed pod development is increased by about 200 km 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 temperatures are still insufficient to support population persistence of *A. nilotica*.

Dry stress

Dry stress is increased by reductions in precipitation compared with current conditions. However, as with the moisture index and thus the growth index, moderate increases in WUE can compensate for the reduction in precipitation. Any increase in precipitation or WUE reduces the area in which *A. nilotica* would suffer even moderate dry stress.

Wet stress

There appears to be a small amount of wet stress in northern Australia under current climatic conditions. There is little impact of predicted climate change on the distribution of this stress. The combination of slight increases in wet stress and a coincident reduction in the moisture index are enough to reduce the climatic suitability of small patches of northern Australia under each of the scenarios that include a 10% precipitation increase. This effect is also apparent in the highest WUE and 10% precipitation reduction scenario.

Discussion

As far as we are aware, our study represents the first assessment of the sensitivity of the potential distribution of an invasive plant to predicted climate change. The results identify areas of Australia that will be vulnerable to invasion by *A. nilotica* as a consequence of climate change unless adequate control measures prevent further dispersal. This information can be used to alert public administrators and land managers to the invasion threat posed by this plant. The area at risk of invasion by *A. nilotica* under current climate conditions greatly exceeds the current distribution, with ‘suitable’ to ‘highly suitable’ habitat covering more than one-third of Australia (Fig. 5). Climate change as predicted will most probably increase the area at risk of invasion, most noticeably in New South Wales and the moderately productive coastal zones of Western Australia (Fig. 6). The large potential for further invasion under both current and future climates justifies concerns that this plant is a weed of national significance.

The modelled potential distribution exceeds that of Carter (1989), reinforcing the value of including the global distribution of a taxa in analyses of invasion potential (Kriticos & Randall 2001).

NON-CLIMATIC DISTRIBUTION FACTORS

Being climate based, the CLIMEX model ignores non-climatic factors that also determine habitat suitability for a particular species.

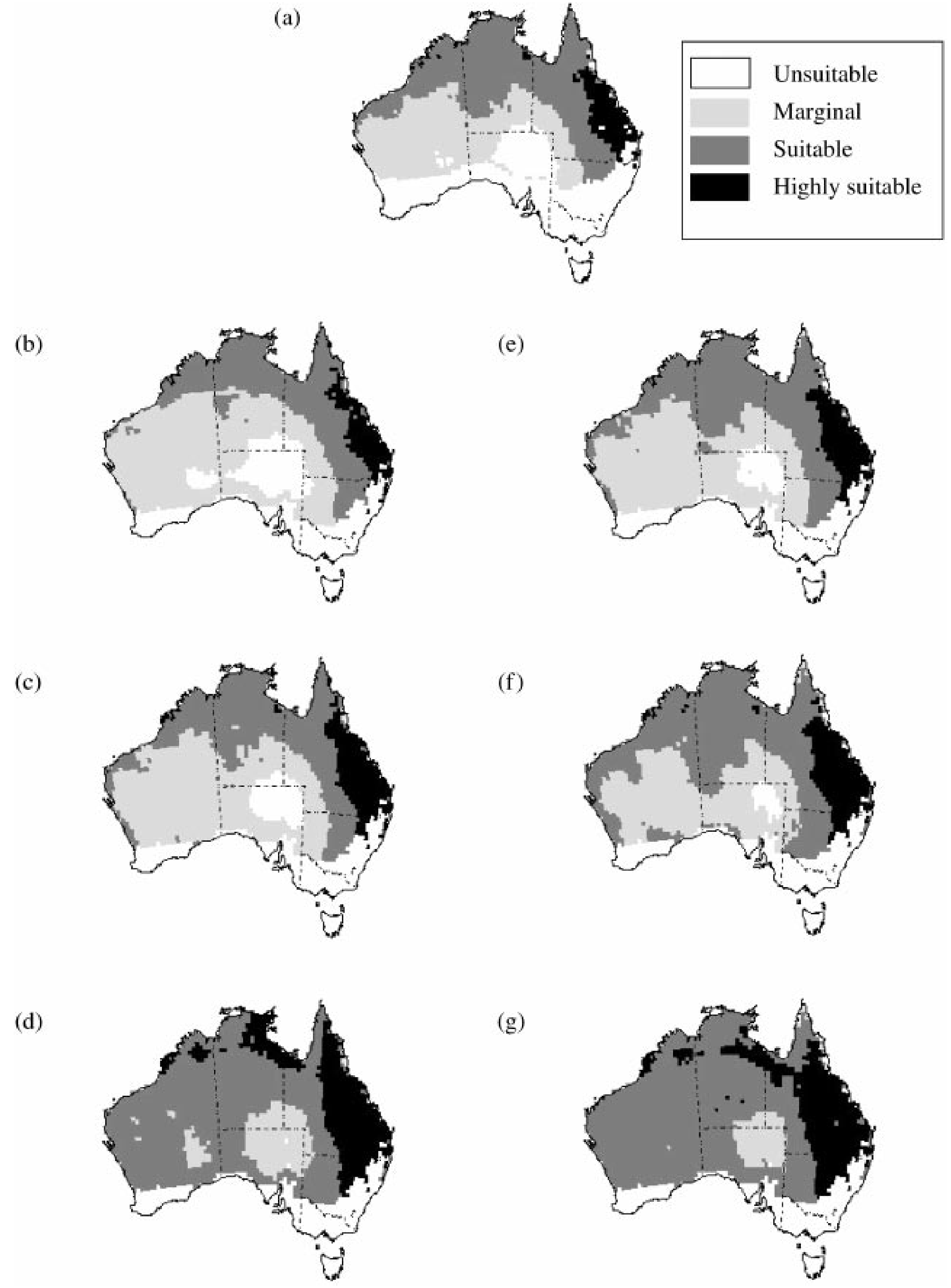

Fig. 6. CLIMEX climate suitability (ecoclimatic index, EI) for *A. nilotica* under different climate scenarios. (a) Current climate; (b) +2 °C, −10% rainfall, $E_t = 0{\cdot}8$; (c) +2 °C, −10% rainfall, $E_t = 0{\cdot}6$; (d) +2 °C, −10% rainfall, $E_t = 0{\cdot}4$; (e) +2 °C, +10% rainfall, $E_t = 0{\cdot}8$; (f) +2 °C, +10% rainfall, $E_t = 0{\cdot}6$; (g) +2 °C, +10% rainfall, $E_t = 0{\cdot}4$.

Local hydrology

Landlocked drainage channels, such as the Diamantina River (26°00′S 139°21′E), may carry water into regions that have extremely low, long-term average rainfall. With little topographic relief, this water can take a long period to drain or evaporate, providing enough moisture for germination and subsequent seedling establishment of a perennial plant. The plants might then persist until another such flooding event stimulates seed production and germination. This would allow populations to persist in locations such as Hungerford in southern Queensland (28°59′S 144°24′) that would otherwise be climatically unsuitable or marginally suitable.

Soil type

Acacia nilotica is often found growing on clay-rich soils, but may also grow on sandy loam soils under

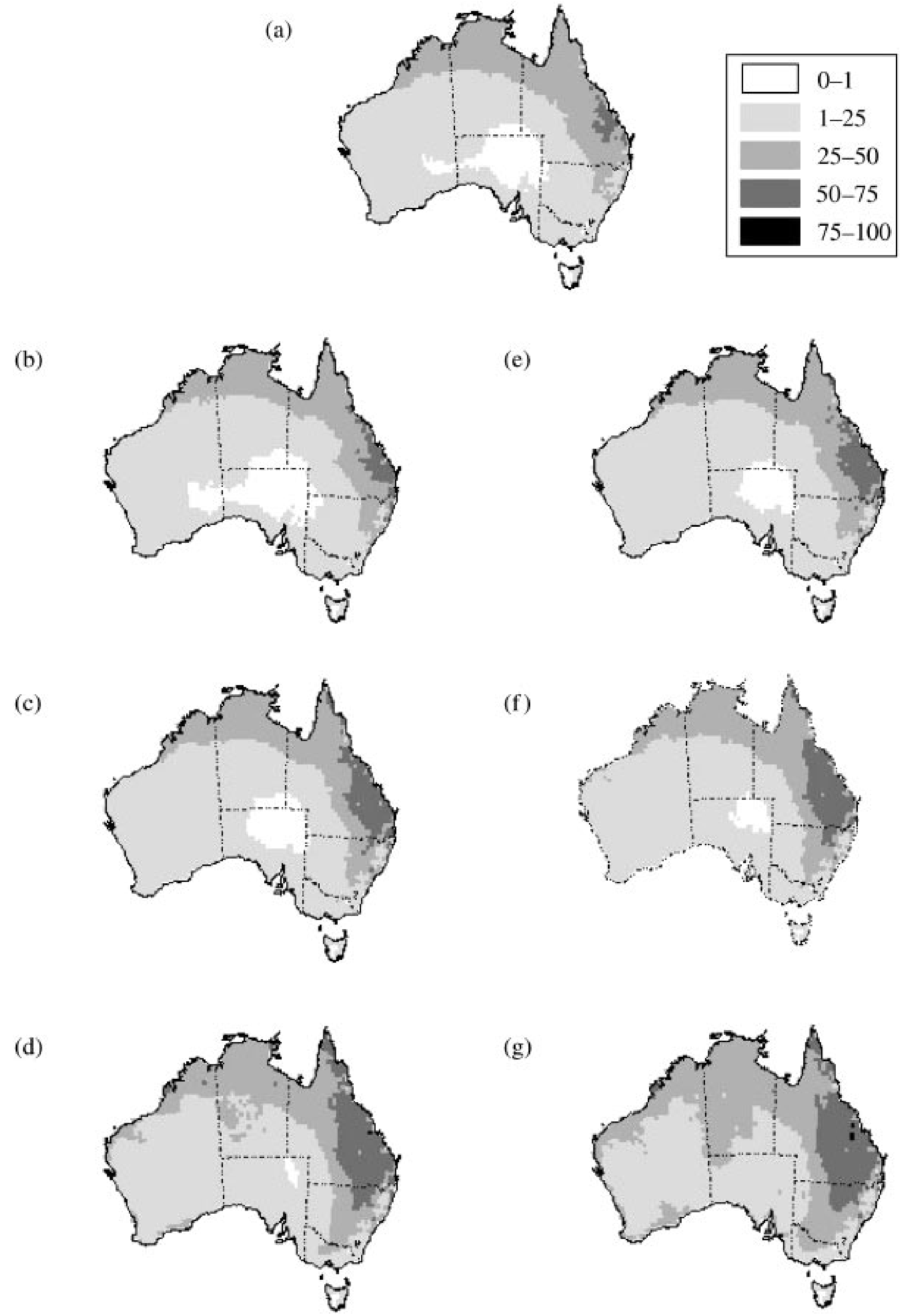

Fig. 7. CLIMEX growth index (GI_A) for *A. nilotica* in Australia. The climate change scenarios are the same as those for Fig. 6.

higher rainfall conditions (Carter, Jones & Cowan 1991). In a seedling establishment study, too few *A. nilotica* seedlings established in sand to permit a meaningful study, even with additional rainfall (Anonymous 1996). Thus, very sandy soils (principal profile form UC1, National Resource Information Centre 1991) will probably be unsuitable for *A. nilotica* establishment; CLIMEX, however, could not eliminate these areas from the analysis.

Gut passage through cattle, and to a lesser extent sheep, markedly increases seed germination rates for *A. nilotica* (Harvey 1981). Without livestock dispersal it is unlikely that *A. nilotica* will actively invade and establish in new areas (Tiver *et al.* 2000).

Land use and disturbance regime

Land use can influence the likelihood of *A. nilotica* invasion. As *A. nilotica* can take 5 years to mature (J.R. Brown, unpublished data), any disturbance that destroys juveniles every 5 years or less would prevent widespread recruitment. The effectiveness of fires in preventing recruitment will depend upon their frequency and intensity. Tillage-based agriculture should prevent *A. nilotica* invasion.

Undisturbed remnant native shrublands, woodlands and forests may limit invasion by *A. nilotica*, due to the reported shade intolerance of the species (Miller 1996), and the lack of sheep or cattle grazing (Tiver *et al.* 2000).

RESPONSES TO CLIMATE CHANGE

It is clear from CLIMEX that predicted climate change will greatly increase the area at risk of invasion by *A. nilotica* compared with current climatic conditions (Fig. 6). However, vulnerability to invasion by *A. nilotica* is a function of both the sensitivity of the system and our ability to manage the weed with respect to new suitable areas (Tol, Fankhauser & Smith 1998).

The frequency with which *A. nilotica* is dispersed by livestock across paddock boundaries remains unknown. Kot, Lewis & van den Driessche (1996) and Clark *et al.* (1998) have highlighted the risks of very low frequency long-distance dispersal events for rapid plant migration. A high priority should therefore be placed upon the early identification and eradication of any outlying populations of *A. nilotica* (Moody & Mack 1988). Outlying unknown inland populations of *A. nilotica* in marginal xeric sites may rapidly increase in numbers in the future. Simple paddock quarantine procedures that allow livestock to void weed seeds in controlled situations prior to transport from infected properties could ensure that *A. nilotica* never reaches its potential distribution under current climatic conditions, nor the expanded range afforded by expected climate changes. A lack of sufficient heat accumulation means populations of *A. nilotica* in northern New South Wales may not currently be considered a problem because they seldom, if ever, produce viable seed pods. However, climate change may alter this, increasing the weed's reproductive potential.

The increased growth potential of *A. nilotica* within its current range under future climate scenarios suggests that pastoral production costs and *A. nilotica* seed production in many currently infested areas could rise. If the increased seed production results in seed pods lying unconsumed on the ground, then extra vigilance may be necessary to control seedlings resulting from flood dispersal. The invasion significance of seeds dispersed into the immediate vicinity of the parent plant is likely to be minimal due to periodic intense asymmetric competition (Kriticos *et al.* 1999).

Agroforestry

Thompson (1992) reported that while *A. nilotica* is technically suitable for wood-chipping using modern techniques, an analysis concluded that it was uneconomical to harvest the plant commercially. Increases in the growth rates of *A. nilotica* with predicted climate change could alter the balance in favour of some form of economic harvesting, significantly reducing the cost of mechanical control of mature trees. Likewise, increased growth potential could also offer the opportunity of mixing pastoral and agroforestry activities on the same land, mitigating the effects of increasing CO_2 concentrations, or fuelling local bioenergy projects.

Those areas projected to be marginally unsuitable climatically for *A. nilotica* within Queensland and northern New South Wales under current climatic conditions could test the validity of this model. Deliberate planting of scarified seeds and seedlings within these areas should use livestock-proof exclosures to prevent spread beyond the experimental area.

The large potential for further spread and increased mitigation costs under both current and expected future climate conditions, and the relative ease of preventing further spread, means that this biological invasion may be containable. A crucial element in this response strategy will be adequate public education about the threat posed by *A. nilotica*, its identification and control techniques.

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