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The Potential Global Distribution of Tall Buttercup (*Ranunculus acris* ssp. *acris*): Opposing Effects of Irrigation and Climate Change

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Tall buttercup, a native of central and northern Europe, has become naturalized in the United States and Canada, and in South Africa, Tasmania and New Zealand. In Canada and New Zealand it has become an economically significant weed in cattle-grazed pastures. In this study we develop a CLIMEX model for tall buttercup and use it to project the weed's potential distribution under current and future climates and in the presence and absence of irrigation. There was close concordance between the model's projection of suitable climate and recorded observations of the species. The projection was highly sensitive to irrigation; the area of potentially suitable land globally increasing by 30% (from 34 to 45 million km^2) under current climate when a "top-up" irrigation regime (rainfall topped up 4 mm d^{-1} on irrigable land), was included in the model. Most of the area that becomes suitable under irrigation is located in central Asia and central North America. By contrast, climate change is projected to have the opposite effect; the potential global distribution diminishing by 18% (from 34 to 28 million km^2). This range contraction was the net result of a northward expansion in the northern limit for the species in Canada and the Russian Federation, and a relatively larger increase in the land area becoming unsuitable mainly in central Asia and south eastern United States.

Nomenclature: Tall buttercup, *Ranunculus acris* L. ssp. *acris*.

Key words: Animal health, climate change, CLIMEX, giant buttercup, meadow buttercup, tall buttercup, weed invasion.

Process-based niche models provide a means of defining the potential spatial extent and hence potential economic impact of a weed invasion. These models are based on the widely-accepted principle that climate is the key determinant of plant distribution. Process-based niche models such as CLIMEX have been widely used to project the potential distribution of plants under current and future climate (Bourdôt et al. 2010a; Bourdôt et al. 2010b; Kriticos et al. 2004; Kriticos et al. 2010; Potter et al. 2009; Watt et al. 2010). However, such analyses are not sufficient for species that require an understanding of how multiple anthropogenic factors, such as climate change and irrigation, may impact the distribution.

Ranunculus acris L. is a weed of old pasture and hay meadows in Europe (Harper and Sagar 1953b). Like other members of the genus, it produces the glycoside ranunculin which through enzymatic breakdown after inadvertent ingestion by grazing animals, forms protoanemonin (Harper and Sagar 1953b). This vesicant causes blistering of the lips and tongue and intestinal disorders in grazing animals (Connor 1977). It also causes *R. acris* and its associated pasture plants to be avoided by dairy cattle and other grazing animals, thereby reducing the stock carrying capacity of the pasture (Bourdôt et al. 2003; Harper 1957). Quoting from Harper (1957), *R. acris* "tends to spread in heavily grazed communities" and, "with the possible exceptions of montane grasslands and stages in succession of fen, the communities in which *R. acris* is found are determined by man or by introduced animals…[its] abundance in pastures and meadows is an index of the age of the pasture."

Ranunculus acris is a highly variable species common throughout its native range in central and northern Europe (Coles 1971). All infraspecific taxa in the complex are linked by intermediate forms; the most widespread and variable of these is *R. acris* ssp. *acris* L. (giant buttercup, meadow buttercup, tall buttercup). This subspecies varies clinally from west to east across Europe in stem and petiole hair characteristics, size of achenes and petals, and degree of dissection of leaves (Coles 1971), and several geographically or ecologically-based varieties are recognized (Coles 1971).

Ranunculus acris has spread beyond its native range in Europe to naturalize in other Northern hemisphere countries from the Arctic Archipelago Svalbard (74°N) to Morocco (35°N) and tropical Ethiopia (Abysinnia) (Hegi 1982). It has naturalized also in most upper continental states of the United States, in southern territories of Canada, as far north as the Aleutian Islands and Newfoundland, and as far south as northern New Mexico and Georgia (Editorial Committee 1997). In the Southern hemisphere it has naturalized in the Cape of South Africa, in Tasmania (Australia) and in New Zealand (Webb et al. 1988).

Judging from these known global occurrences of *R. acris*, anthropogenically modified environments, particularly irrigated or high-rainfall heavily-grazed pasture lands, roadsides, banks of rivers and drainage ditches, appear most vulnerable to invasion. It is in pastures that *R. acris* can be very damaging economically as is illustrated by an analysis conducted in dairy pastures in New Zealand (Bourdôt and Saville 2010). Here the species, referable to ssp. *acris* (Webb et al. 1988), occurs in 6 of 17 dairy farming regions (Bourdôt and Saville 2010), causing an annual revenue loss to dairy farmers equating to 2.6% of the national value of exported milk solids (Bourdôt et al. 2003). Economic losses for other parts of its invaded range have not been published although concern has been expressed about the spread and economic consequences of *R. acris* in Canada (Alec McClay, personal communication) and its rapid spread in North America has been noted (Coles 1971).

Given (a) the potential economic impact of *R. acris* in dairy pastures globally, (b) global increases in the extent of irrigated land (United National Environmental Programme 2012) enabling dairy farming to expand into arid regions (Fraser 2011), and (c) climate change (Olesen and Bindi 2002), *R.*

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acris makes an ideal test case for an analysis that combines irrigation and natural climatic conditions in a simulation of the potential distribution of a weed. Here we test three hypotheses regarding the global invasion of *R. acris*: (1) the species has not yet fully occupied its climatic potential distribution; (2) irrigation increases its potential distribution; and (3) projected climatic changes decrease its potential distribution.

To test these hypotheses we use CLIMEX (Sutherst et al. 2007) to identify climatic constraints on the current rain-fed (nonirrigated) distribution of *R. acris*. We fit the model to the occurrences of *R. acris* ssp. *acris* and its varieties as these are the most common forms of the species in the invaded range in Canada (Alec McClay, personal communication), United States (Reveal 2012) and New Zealand (Webb et al. 1988). The model is then used to project the potential global distribution of the species for both irrigated and rain-fed scenarios under current climate and under future (2070) climate for the rain-fed scenario. We did not attempt to explore the interaction of climate change and irrigation because there are no reliable models of land-use change to support this analysis.

Materials and Methods

CLIMEX. CLIMEX is a dynamic modeling system (Sutherst et al. 2007) that integrates the weekly responses of a population to climate using a series of annual indices. It uses an annual Growth Index to describe the potential for population growth as a function of soil moisture and temperature during favorable conditions, and up to eight Stress Indices (cold, wet, hot, dry, cold–wet, cold–dry, hot–wet and hot–dry) to simulate the population survival under unfavorable conditions. The model also includes a mechanism for defining the minimum thermal accumulation (number of degree days, PDD) during the growing season that is necessary for population persistence.

The growth and stress indices are calculated weekly and then combined into an overall annual index of climatic suitability, the Ecoclimatic Index (EI), that ranges from 0 for locations at which the species is not able to persist to 100 for locations that are optimal for the species (Sutherst et al. 2007). When the required PDD value is not reached at a particular location, the EI at that location is set to zero. In this study EI is classified into four classes of climatic suitability for *R. acris*: unsuitable ($EI = 0$), marginal ($EI = 1$ to 5), suitable ($EI = 6$ to 20) and optimal ($EI > 20$).

Current Distribution of *R. acris* ssp. *acris*. The current global distribution of *R. acris* ssp. *acris* was determined from published records of its occurrence. This was achieved by searching the Global Biodiversity Information Facility (GBIF 2009) and CAB Abstracts using the search term "*Ranunculus acris*". The coordinates, country and locality names for each of the records from GBIF were saved to an Excel spreadsheet. The same information for records from CAB Abstracts, ascertained after reading the relevant articles, flora and other sources, was added manually to the spreadsheet. Additional records were created in the spreadsheet for New Zealand based on personal observations by the authors. Additional records were also provided for Canada by Isabelle Simard (Ministère du Dévelopment durable, de l'Environnement et des Parcs, Québec), Alec McClay (McClay Ecoscience, Alberta), Sean Blaney (Atlantic Canada Conservation Data Centre, New Brunswick), Cheryl Heming (Invasive Species Council of Manitoba) and Julia Leeson (Agriculture and Agri-Food Canada, Saskatoon). Before using the data for model development, "cleaning" was necessary. To this end, records that where duplicates (based on coordinates), outliers with locality descriptions not consistent with the coordinates, and those with coordinates of lower precision than the climate data sets used in the modeling, were excluded.

Table 1. Occurrence records for *Ranunculus acris* (as determined from published literature, GBIF and personal communications) by geographical area and taxonomic classification. Only the *R. acris* ssp. *acris* records were used to fit (Europe), verify (United States) and validate (New Zealand) the CLIMEX model (Table 2).

	Ranunculus acris ssp. *acris*[a]	*Ranunculus acris*
Africa	0	0
Antarctica	0	0
Australia	0	1
Asia	0	17
Europe	941	27,891
New Zealand	83	0
Canada	0	1,625
United States (including Bermuda)	67	684
South Georgia & South Sandwich Islands	0	2
South America	0	0
Total records	1,091	30,220

[a] The taxon *Ranunculus acris* ssp. *acris* modeled in this study was assumed to be represented by the records named: *R. acris acris*; *R. acris* spp *acris*; *R. acris* L. var. Typicus G.Beck (ITIS 2010); *R. acris* ssp *acris* var. pumilus Wahlenb (Coles 1971); R. *acris* subsp. *acris*; *R. acris* var. *acris*; *Ranunculus acris* subsp. *acris* L.; *Ranunculus acris acris* L.; *Ranunculus acris* L. *acris*; *Ranunculus acris* L. ssp. *acris*; *Ranunculus acris* L. spp. *acris* – Ranun acr. acr; *Ranunculus acris* subsp. *acris*; *Ranunculus acris* ssp. ssp *acris*; *Ranunculus acris* var. *acris*.

The records of *R. acris* retrieved by the searches were documented under a variety of named subspecies, varieties and synonyms. Only the records classified as *R. acris* ssp. *acris*, a variety within this subspecies, a recognized synonym, or occurring in New Zealand [where all material is referable to ssp. *acris* (Webb et al. 1988)] (Table 1, Figure 1a) were used to fit, verify or validate the CLIMEX model. The records named only at the species level (Table 1, Figure 1b), of which many in Europe are likely to be ssp. *acris* given the wide distribution of this taxon (Coles 1971) were retained for model verification.

Fitting the CLIMEX Parameters. The CliMond 10′ spatial resolution climate dataset, (Kriticos et al. 2012) was used within CLIMEX for fitting the parameters. We used this dataset to infer the climatic requirements of *R. acris* ssp. *acris* from its known occurrences in the native and introduced ranges in Europe ($n = 941$ records) (Table 1). The model was fitted by iteratively changing the parameter values from the default "temperate" model (Sutherst et al. 2007) until the projected distribution of suitable climate ($EI \geq 1$) closely corresponded to the 941 records for *R. acris* ssp. *acris* in Europe (Figure 1a). In a second (verification) step the model's projected distribution of $EI \geq 1$ was compared with the occurrences of *R. acris* ssp. *acris* in the United States ($n = 67$, Table 1). Minor adjustments to Heat Stress and the Temperature Index parameters were made during this step.

Stress indices, which scale between 0 and infinity (0 = no stress and values of 100 or greater = lethal conditions), were

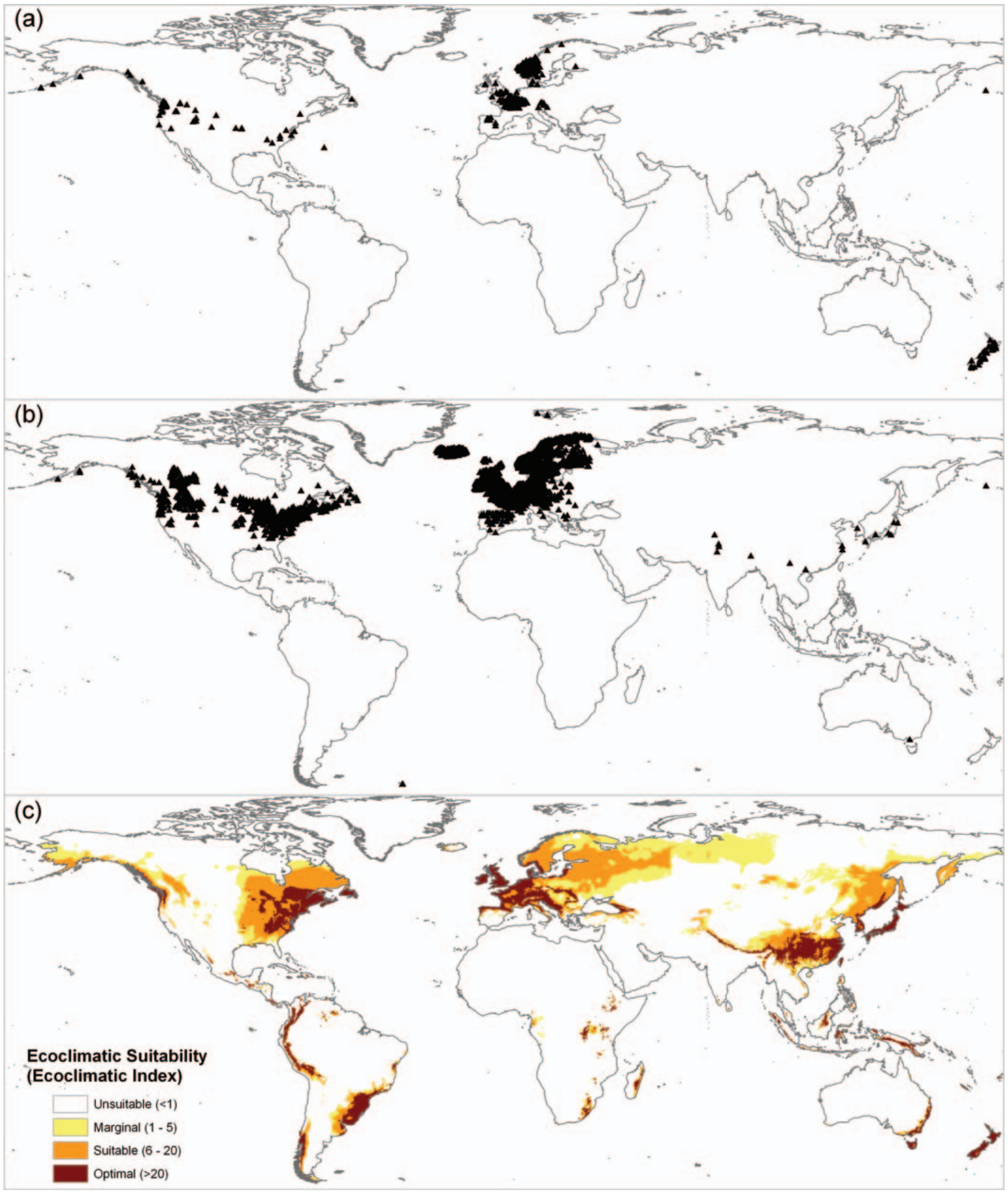

Figure 1. World map showing (a) the occurrences of tall buttercup *Ranunculus acris* recorded as *R. acris* ssp. *acris*, (b) the occurrences recorded as *R. acris* and (c) the global distribution of land climatically suitable for *R. acris* ssp. *acris* (under current climate) as modeled using CLIMEX (parameters in Table 2). The occurrences (a, b) were determined from GIBF, published literature and personal observations and communications.

initially adjusted so that stresses largely constrained the population to its present observed distribution limits in the native range in Europe. Several different mechanisms of cold stress and thermal accumulation were investigated (by adjusting parameter values) to find the mechanisms that best aligned with the observed range boundaries in Europe (Figure 1a). Next, the Growth Indices, which scale between 0 and 100 (0 = no growth, and 100 = perfect growing conditions year round), were adjusted iteratively so that the projected climate suitability patterns most closely matched the observed occurrence patterns in Europe. The parameter values chosen (for the Stress and Growth Indices) (Table 2) were also informed using experimental data on seed germination in response to soil moisture (Harper and Sagar 1953a), photosynthesis response to temperature (Mamushina and Zubkova 1996), growth response to temperature (Cooper 2004) and our own observations of the soil moisture and temperature conditions which appear to favor this species in New Zealand.

Cold Stress and Thermal Accumulation. In its native range in Europe, *R. acris* ssp. *acris* survives in many places that experience severe and frequent frosts. To model this range limit, the cold stress temperature threshold (TTCS) was reduced from 8 C (in the temperate model) to −1.0 C and the cold stress accumulation rate (THCS) was increased slightly to −0.00015 wk^{-1}. These parameters allowed the modeled suitable climate to extend further northward (than the standard temperate model allowed) to include the occurrences of the species in southwestern Norway (Figure 1a). In addition, the length of the growing season in the model, defined by the amount of thermal accumulation, was set at the temperate model default of 600 degree days (PDD)

Table 2. Parameters fitted to define the Growth and Stress Indices and the length of the growing season (thermal accumulation requirement) for *Ranunuclus acris* ssp. *acris* in the CLIMEX model.

Index	Parameter	Value	Units[a]
Temperature	DV0 = lower threshold	−1	°C
	DV1 = lower optimum temperature	16	°C
	DV2 = upper optimum temperature	20	°C
	DV3 = upper threshold	28	°C
Moisture	SM0 = lower soil moisture threshold	0.5	
	SM1 = lower optimum soil moisture	0.9	
	SM2 = upper optimum soil moisture	1.5	
	SM3 = upper soil moisture threshold	2.5	
Cold Stress	TTCS = temperature threshold	−1	°C
	THCS = stress accumulation rate	−0.00015	week^{-1}
Heat Stress	TTHS = temperature threshold	28	°C
	THHS = stress accumulation rate	0.001	week^{-1}
Dry Stress	SMDS = threshold soil moisture	0.5	
	HDS = stress accumulation rate	−0.03	week^{-1}
Length of growing season	PDD = degree-day threshold (minimum annual total no. degree-days above a weekly average of −1.0 °C (DV0) needed for population persistence)	600	°C Days

[a] Soil moisture parameters are quantified as a dimensionless index of soil moisture availability (e.g. a 0.5 indicates a soil moisture level that is 50% of field capacity).

above a weekly average of −1.0 C (Table 2). This represents the minimum annual heat accumulation limit for reproduction and persistence.

Heat Stress. The heat stress threshold (TTHS) was set at 28 C [the temperate model default value for the upper temperature limit for growth (DV3)] and the heat stress accumulation rate (THHS) was reduced from the default level to 0.001 wk^{-1}. These values allowed the model to include the occurrences in the southeastern states of the United States, and together with those for Dry Stress (below), those in northern Spain (Figure 1a).

Dry Stress. Previous research shows that *R. acris* ssp. *acris* is poorly tolerant of drought (Sarukhán 1974; Sarukhán and Harper 1973). To enable the model to represent this, the dry stress threshold (SMDS) was set at 0.5 (above permanent wilting point) and the dry stress accumulation rate (HDS) was set at −0.03 (considerably higher than the temperate model default value). These parameter values, along with those for Heat Stress, allowed the model to include the occurrences in northern Spain (Figure 1a) but constrained the south-eastern boundary of the model, reducing the modeled climatically suitable area in regions of Eastern Europe where there are few occurrences of the species (Figure 1a).

Temperature Index. The lower (DV0) and upper (DV3) temperature limit parameter values were set at −1 and 28 C to match the cold and heat stress thresholds respectively. The lower and upper optimum temperatures (DV1 and DV2) were set to 16 and 20 C, respectively, in accord with commonly recorded patterns for a range of temperate herbaceous plants (Kawanabe 1968).

Moisture Index. To maintain consistency with the dry stress threshold the lower soil moisture threshold (SM0) was set to 0.5. The lower (SM1) and upper (SM2) optimums for soil moisture were set to respective values of 0.9 and 1.5 so that high Moisture Index (MI) values occurred where *R. acris* ssp. *acris* has been observed growing profusely in Europe (Sarukhán 1974; Sarukhán and Harper 1973). The upper soil moisture threshold (SM3) was set to 2.5 to reflect the species' tolerance of wet soils.

Model Verification and Validation. In the verification step, the initial model based on the European records was projected onto the United States. This model did not project as suitable, areas in the southeast of the United States where there are several occurrences of the species. After minor adjustments to the Heat Stress and Temperature Index, most of these occurrences were modeled as suitable. The occurrences remaining outside the model (United States, $n = 7$; Spain, $n = 5$) were found, using Google Earth and by checking data sources, to be on either irrigated or riparian land, providing an acceptable explanation for them not being modeled as suitable.

The verified CLIMEX model was validated against the naturalized occurrences of *R. acris* ssp. *acris* in New Zealand ($n = 83$, Table 1). All occurrences in New Zealand were modeled as having suitable climate in the absence of irrigation ($EI > 1$). The model projections in other regions were examined and subjected to a reasonability test based on knowledge of climate geography (Köppen 1936) and the distribution of similar species.

These model verification and validation results provide confidence that the final model (Table 2) is an adequate representation of the climatic responses of *R. acris* ssp. *acris* and that its projection beyond the fitting, verification and validation ranges (Figure 1c & 2), provides realistic estimates of the locations and areas of land globally that are climatically suitable for the species and hence potentially susceptible to invasion.

Climate Change Scenarios. Four climate change scenarios were used as meteorological input for the validated CLIMEX model to project future potential distributions of *R. acris*. These scenarios were developed from two Global Climate Models (GCMs), each run using two standard emission scenarios. The latter represented medium (A1B) and high (A2) emissions and were drawn from the set of standardized emissions scenarios (IPCC 2007). The GCM climate data

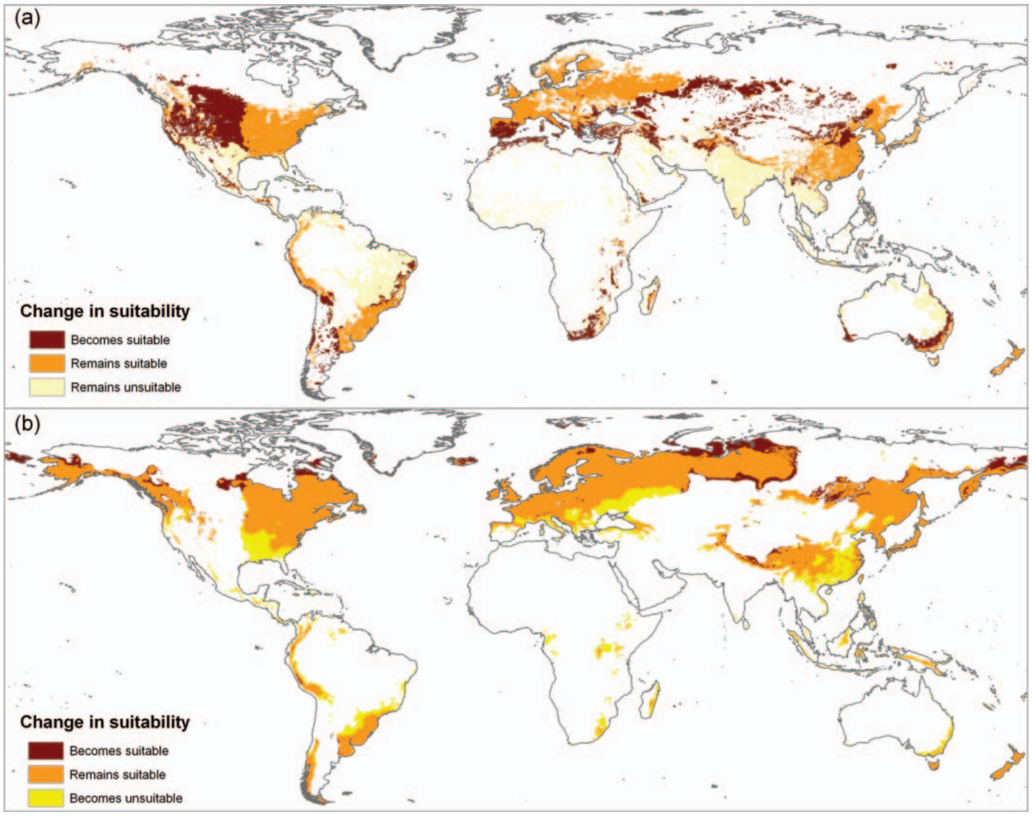

Figure 2. Change in climate suitability for *Ranunculus acris* ssp. *acris*, as affected by irrigation (natural rainfall topped up to 4 mm d^{-1} from early spring until mid autumn on irrigable land) and future climate (using the CSIRO Mark 3.0 model run with the A1B emission scenario). The maps show (a) the effect of irrigation under current climate restricted to irrigable land, and (b) the effect of future climate without irrigation. Shown in (a) are regions that become suitable (EI ≥ 1, dark brown), remain suitable (EI ≥ 1, orange) or remain unsuitable (EI = 0, yellow), and in (b) regions that become suitable (EI ≥ 1, dark brown), remain suitable (EI ≥ 1, orange) or become unsuitable (EI = 0, light orange). Please note, the total extent of the land that is climatically suitable under irrigation is equal to the area suitable (Marginal + Suitable + Optimal) in Figure 1c plus the area that becomes suitable in (2a). Similarly, the total extent of the land that is climatically suitable under climate change is equal to the area suitable in Figure 1c plus the area that becomes suitable minus the area that becomes unsuitable (2b).

were obtained from the World Climate Research Programme's "Coupled Model Intercomparison Project" phase 3 multi-model dataset (Meehl et al. 2007). Two GCMs with relatively small horizontal grid spacing and the requisite climatic variables at a monthly temporal resolution appropriate for CLIMEX were chosen: CSIRO Mark 3.0 (CSIRO, Australia) and MIROC-H (Centre for Climate Research, Japan). The climate data from these GCMs were pattern-scaled to develop individual change scenarios for 2070 relative to the base climatology (Whetton et al. 2005). The two models covered the following range of global warming expected with a doubling of the 1990 atmospheric CO_2 concentrations: CSIRO Mark 3.0 (3.07 C); MIROC-H (4.3 C). The climate variables required by CLIMEX (monthly averages of daily minimum and maximum temperature, relative humidity at 0900 and 1500 hours and monthly rainfall total) were extracted or estimated from the GCM data using techniques described in Stephens et al. (2007).

Irrigation Scenario. Irrigation was simulated in the final CLIMEX model under current climate by topping-up natural rainfall to 4 mm d^{-1} (from September 1 to April 30 in the Southern hemisphere) based on irrigation regimes on dairy farms in the Canterbury region of New Zealand (Grant Edwards, Professor of Dairying, Lincoln University, *pers. com.*). Projection of the "irrigated" CLIMEX model and estimation of land areas (next section) were restricted to land equipped for irrigation as defined by the Global Map of Irrigation Areas (GMIA) (Siebert et al. 2007). The GMIA data (percentage of land irrigable in 5′ [0.0833 decimal degrees] grid cells) was aggregated into 10′ cells by taking the means of the data in 4 (2 by 2) adjacent 5′ cells. These aggregated GMIA cells were then joined spatially with the CLIMEX 10′ grid cells so that the aggregated GMIA data was associated with its corresponding CLIMEX model output data.

Estimating the Size of the Land Areas of Suitable Climate Projected by the Parameterised CLIMEX Model. The land areas projected to have a climate suitable for *R. acris* ssp. *acris* (EI ≥ 1) were quantified for Africa, Asia, North America, South America, Europe, Australia and New Zealand for each of the five rain-fed climate scenarios (Current Climate, CSIRO Mark 3.0 with A1B emissions, CSIRO Mark 3.0 with A2 emissions, MIROC-H with A1B emissions, MIROC-H with A2 emissions), and for the irrigated scenario (Current Climate with irrigation). The areas of land suitable were quantified by reprojecting the EI output from the CLIMEX model into a "Behrmann equal area cylindrical" projection. This equal-area projection was used because it is suitable for thematic and distribution mapping on a worldwide scale (ESRI 1994) and because the areas calculated closely correspond to those in The Times Atlas of the World (Times Book Group Ltd 2007).

Results and Discussion

Current Distribution. The records of occurrences of *R. acris* ssp. *acris* reveal that this form of the species, within its native range in Europe, occurs mainly within the wetter temperate, continental and subarctic climates in Western Europe, southern U.K. and Scandinavia (Figure 1a). In North America, the naturalized distribution spans climatic zones from subtropical regions in the south, to subarctic, temperate and continental regions in the north (Figure 1a). *Ranunculus acris* ssp. *acris* has also been recorded sporadically within dry-land areas in New Mexico, central areas in the United States and in the Mediterranean regions of Spain (Figure 1a).

The distribution of the species documented at the species level (as *R. acris*) essentially mimics that of *R. acris* ssp. *acris* (Figure 1b cf. 1a), but the distribution extends further north and south in Europe, notably including Iceland and Svalbard in the north and southern Spain and Morocco in the south. It also includes Canada and Asia (China, Japan) in the northern hemisphere and Tasmania and the South Georgia and South Sandwich Islands in the southern hemisphere (Figure 1b). This wider distribution of the species when considered at the species level is partly attributable to the several subspecies and varieties recognized in Europe, the latter being separated on geographical and ecological characteristics (Coles 1971). It is also, we suppose, partly attributable to difficulty in assigning specimens to a particular subspecific taxonomic rank. It means that our model (Table 2), fitted strictly to the *R. acris* ssp. *acris* records (Table 1), may tend to underestimate the breadth of the climatic tolerance of this subspecies and hence also its potential global distribution. For example, none of the geo-coded records obtained in this study placed *R. acris* ssp. *acris* in Iceland, the Faroe Islands (in the North Atlantic sea) or in Scotland (Figure 1a), yet it is known to occur, as var. *villosus*, in these places (Coles 1971).

Potential Distribution under Current Climate. Under current climate (and without irrigation), the modeled potential distribution of *R. acris* ssp. *acris* shows a close fit to the observations for this form of the species (Figure 1c cf. 1a) and its preference for areas with high soil moisture levels (Table 2). Within Europe, the modeled potential range encompassed 936 (99.5%) of the 941 observations. Only five observations (all in central Spain) remained outside of the model's projection. Closer examination of these five observations using Google Earth revealed that they occur in irrigated situations, explaining their occurrence in apparently unsuitable conditions.

The modeled climatically-suitable area extends beyond the observed occurrences of *R. acris* ssp. *acris* into Eastern Europe, the Balkans, southern France and areas surrounding the Black Sea indicating that these areas may be climatically suitable. The CLIMEX Match Climates model (results not shown), was used to assess the climate similarity of the regions of Eurasia with cold continental climates that are apparently suitable but contained no occurrence records (e.g., Moscva, Russia) with continental locations in the United States for which there are occurrence records. The close similarity of these climates indicates that these cold continental parts of Eurasia, are indeed climatically suitable for *R. acris* ssp. *acris*, and that the species may either already occur there and be unreported, or it may be competitively excluded [e.g., by other conspecifics that are present in this region (Figure 1b)].

In North America, there was close concordance between modeled climate suitability and the *R. acris* ssp. *acris* observations within regions of high soil moisture in the northwest and southeast of the continent (Figure 1c cf. 1a). The observations of *R. acris* ssp. *acris* within drier central regions of the United States are modeled as having an unsuitable climate. However, as in Spain, all of these observations appear to occur within irrigated areas, hence explaining the lack of fit of the natural rainfall scenario model in these areas.

In New Zealand, all observations of *R. acris* ssp. *acris* occur in areas projected as climatically suitable by the rain-fed scenario model (Figure 1c cf. 1a; see Supplemental Figure 1 for a more detailed map). The model indicates that virtually the entire land area of New Zealand is currently climatically suitable for *R. acris* ssp. *acris* (Figure 1c). When compared with the current distribution, the model reveals that there may be considerable scope for range expansion in this country (Supplemental Figure 1).

The modeled potential distribution for *R. acris* ssp. *acris* revealed several regions throughout the world that are currently climatically suitable but where this form of the species has not been recorded (Figure 1c cf. Figure 1a). These include southeastern China, Japan, South Korea the south-eastern coast of Australia, Tasmania, Uruguay, southeastern Brazil, northeastern Argentina, Chile, Indonesia, Ethiopia, Uganda, South Africa and eastern Madagascar (Figure 1c). The species, recorded as *R. acris*, is present however in China, Japan, South Korea and Tasmania (Figure 1b) and it is probable that these records refer to *R. acris* ssp. *acris*, given that it appears to be the invasive form of the species in other parts of the world: Canada (Alec McClay, personal communication), United States (Reveal 2012), and New Zealand (Webb et al. 1988). In that case, the good fit of the model to these records may provide an additional validation of the model.

The model fitted to the *R. acris* ssp. *acris* occurrences (Table 2) also shows good concordance with the observations for the species documented at the species level (as *R. acris*) (Figure 1c cf. 1a). In the native range in Europe, almost all of 27,891 records (Table 1) are fitted by the model with the exception of Iceland and Spain, where approximately 50% are not fitted. Similarly in the invaded ranges in Asia, United States and Australia, almost all records are fitted, while in Canada most of the 1,625 records (Table 1) are also fitted apart from some in north central Alberta and Saskatchewan. Assuming that these records represent the range of subspecies and varieties recognizable within *R. acris* (Coles 1971), this close fit of the ssp. *acris* model implies that the subspecies and varieties within have rather similar climatic responses. This seems plausible and does not conflict with the morphological and geographical/ecological bases for separating, respectively, the subspecies and varieties (Coles 1971). While the lack of fit to 50% of the *R. acris* observations in Iceland, some of which could be ssp. *acris* (Coles 1971), implies that *R. acris* ssp. *acris* may tolerate a wider range of climatic conditions than defined in the model (Table 2), the lack of any geo-coded records for Iceland identified as *R. acris* ssp. *acris* precludes testing of this possibility. Because of this taxonomic uncertainty, our model for *R. acris* ssp. *acris* may, therefore, underestimate the cold climate limits for this subspecies.

The occurrence records show the core distribution of *R. acris* ssp. *acris* to be continental and temperate climates (Figure 1a),

Table 3. Projected land area (millions km^2) climatically suitable (EI ≥ 1) for *Ranunculus acris* ssp. *acris* under the rain-fed (natural rainfall under current climate), irrigation (natural rainfall topped up to 4 mm d^{-1} from early spring until mid autumn on irrigable land under current climate), and climate-change (using the CSIRO Mark 3.0 model run with the A1B emission scenario) scenarios. Percentage changes caused by irrigation and climate change relative to the rain-fed scenario are also shown. These irrigation and climate-change effects are illustrated spatially in Figure 2a, and b, respectively.

		Land area projected to be climatically suitable (EI ≥ 1)			Change in suitable area	
Geographical area	Total land area	Rain-fed	Irrigation	Climate change	Irrigation	Climate change
	million km^2				%	
Africa	29.88	1.08	1.97	0.22	82	−79
Asia	44.47	12.44	15.65	10.99	26	−12
Australia	7.67	0.39	0.91	0.16	130	−60
Europe	9.84	7.94	9.12	6.52	15	−18
New Zealand	0.26	0.26	0.26	0.26	0	0
North America	24.13	8.70	12.21	7.66	40	−12
Oceania	0.13	0.08	0.08	0.04	1	−50
South America	17.68	3.37	4.36	2.09	30	−38
World (excluding Antarctica)	134.06	34.25	44.56	27.96	30	−18

with model projections showing extension from these areas into climates ranging from subarctic to subtropical (Figure 1c). The species' tolerance of the low temperatures typical of subarctic to temperate climates is reflected in the CLIMEX model parameter values that show that cold stress accumulates at a low rate from a relatively low threshold value (Table 2). The other major defining feature of the climatic range is the sensitivity of *R. acris* ssp. *acris* to water availability. In the natural environment the species does not occur in desert or arid environments. A high threshold for soil moisture stress in the model (Table 2) was used to exclude the model's projection, i.e., the potential distribution, from these areas.

Irrigation and Climate Change. The projections from the simulations using the CLIMEX model (Table 2) of the land that may be climatically suitable for *R. acris* ssp. *acris* under current and future climate are quantified in terms of areal extent (Table 3) and illustrated spatially (Figure 2b). All four future climate scenarios gave remarkably similar projections and we have selected only those from the CSIRO model using the A1B emission scenario to illustrate the climate change effect (Table 3, Figure 2b).

Globally, 34 million km^2 of land may be climatically suitable for *R. acris* ssp. *acris* in the absence of irrigation under the current climate, constituting about a quarter of the total world land area (Table 3). Most of this suitable land (85%) is confined to the northern hemisphere: Asia (12 million km^2), North America (9 million km^2) and Europe (8 million km^2). The irrigation scenario used in the model, under current climate, increased the area of climatically suitable land globally (by 30%) to 45 m km^2 (Table 3). By contrast, the climate change scenario reduced the area of climatically suitable land (by 18%) to 28 million km^2.

It is apparent that most of the expansion in suitable area with irrigation occurs within central Asia and the central and northern areas of North America (Table 3, Figure 2a). By contrast, within the native range in Europe, increases in suitable area under irrigation are relatively modest (1.2 million km^2 or 6.5% increase) with most of this expansion occurring within Spain (Figure 2a). Other regions in which irrigation allows land to become climatically suitable include the southern coastal hinterland of Australia, high altitude regions in Africa and regions bordering its southern and northern coastline, central and northern Chile and Patagonia (Figure 2a). Because New Zealand is suitable throughout under the natural rain-fed scenario, there was no change in the land area climatically suitable under the irrigation scenario (Supplemental Figure 2). Nevertheless, irrigation substantially increases the degree of suitability throughout the dry eastern parts of both the North and South Islands of New Zealand as revealed by significant increases in the Ecoclimatic Index in these regions (Supplemental Figure 3).

Under the future climate scenario most of the (relatively small) reduction in suitable area occurs within Asia, North America and Europe through northward shifts in both the southern and northern limits of climate suitability (Table 3). The northward shift in the southern limit is particularly prominent in North America where the southeastern states of the United States become climatically unsuitable because of heat and dry stress (Figure 2b). This shift is also prominent in Eastern Europe and Asia (see Supplemental Figures 4 and 5 for detailed global maps of heat and dry stress under current and future climate). By contrast, in the southern hemisphere, the reductions in the land area climatically suitable for *R. acris* ssp. *acris* occur almost solely because of contractions through the southward shift of the northern limit of suitable climate. In these southern continents there is no increase in suitable area through a southward shift in the southern limit although some high-altitude areas in Chile and Peru become suitable (Figure 2b). New Zealand, in contrast to all other geographical areas, exhibits no change in the area of land that is climatically suitable under future climate (Table 3, Figure 2b).

Climate change had relatively little effect on the potential distribution of the species. As climate change effects on potential distribution are mainly mediated through global warming, this lack of sensitivity is attributable to the relatively wide tolerance of the species to air temperature. The greatest change in potential distribution occurred within currently subtropical regions, where temperatures under climate change shift above the species' temperature tolerances. Previous research shows far greater distributional change under climate change for species with narrower temperature tolerance (Kriticos et al. 2010; Potter et al. 2009; Watt et al. 2011).

In contrast to climate change, irrigation had a far greater influence on the potential distribution of *R. acris* ssp. *acris*. Although there is little comparative research, this type of response is most probably atypical and attributable to the extreme sensitivity of the species to dry stress. In one of few comparative studies, the potential distribution of *Abutilon theophrasti* Medik. (velvet leaf), a species with similar limiting and optimal soil moisture requirements to those of *R. acris* ssp. *acris*, is also greatly increased (in California) by irrigation (Holt and Boose 2000). Compared with the Dry Stress threshold of 0.5 necessary in the *R. acris* ssp. *acris* model, values for this parameter in CLIMEX models of other plants typically range from 0.1 for species adapted to seasonally-dry climates (Bourdôt et al. 2010b; Holt and Boose 2000; Potter et al. 2009) to 0.3 for some hydrophilic plants (Watt et al. 2009).

The strong influence of irrigation on the potential distribution of *R. acris* ssp. *acris* could have substantial economic implications. Climate change combined with increases in the global human population, are likely to result in reductions in current productive agricultural area and a greater demand for products from this diminished land area. Such demand may drive conversion of marginal land to intensive agriculture, including irrigation. Within New Zealand such conversions are already taking place driven by international demand for dairy products, highlighting the potential of future invasion by *R. acris* ssp. *acris* into areas that were previously not climatically suitable. Given the high financial returns obtained from irrigated land, invasion of these areas is likely to have a disproportionately high economic cost (Bourdôt and Saville 2010; Bourdôt et al. 2003).

Summary. The potential distribution maps presented in this study could be used to formulate broad strategic control plans to mitigate the further spread of *R. acris* ssp. *acris*. Specifically, the maps presented here could be used to (1) classify areas for different types of management for the weed, (2) support strategic control initiatives designed to prevent the spread of the weed into unoccupied areas and (3) identify areas of increasing invasion threat, allowing relatively inexpensive preventative management to be applied to minimize future impacts of the weed. This study highlights the utility of process-based niche models in identifying possible threats from high impact weed species under multiple anthropogenic influences. This type of knowledge is valuable in the planning and allocation of often-scarce resources to most effectively control high impact weeds. Without the synoptic view of the invasion and the assets at risk, there is a strong potential for regional pest management to be parochial, and, consequently, less effective at all scales.

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