Flowering phenology of invasive alien plant species compared to native species in three mediterranean-type ecosystems

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Fenología de floración de las especies de plantas exóticas invasoras en tres ecosistemas mediterráneos en comparación con las especies nativas.

Resumen

- *Antecedentes y Objetivos*: La fenología de floración es un componente esencial del éxito de las especies invasoras, ya que una elevada fecundidad incrementa su potencial invasor. Por tanto, estudiamos la relación existente entre los patrones de floración de las especies invasoras y nativas en tres regiones con clima mediterráneo: California, España y la Región Sudafricana de El Cabo
- *Métodos*: 227 pares de especies invasoras-nativas fueron utilizados
- *Resultados clave*: Las especies invasoras tienen diferentes patrones de floración en comparación con las especies nativas en las tres regiones. Las especies invasoras florecen antes, al mismo tiempo y después que las nativas en función del clima al que pertenezcan y de la proporción de los distintos tipos de climas que compongan la flora. Las especies invasoras que invaden al menos dos de las regiones estudiadas muestran el mismo patrón de floración, indicando que la fenología de floración es un rasgo conservativo. Las especies invasoras con rangos nativos templados florecen antes que las especies nativas, aquellas provenientes de clima mediterráneo al mismo tiempo mientras que las tropicales florecen más tardíamente. En California, donde la proporción de especies invasoras provenientes de clima mediterráneo es alta, el patrón de floración no difirió entre especies invasoras y nativas, mientras que en España como la proporción de especie de clima tropical es elevada, las especies invasoras florecieron más tarde que las nativas. Por ultimo, en la región sudafricana del

Cabo las especies invasoras florecieron antes que las nativas debido a que provenían de climas templados

- *Conclusiones*: Los patrones observados son debidos a la unión por factores humanos de especies con diferentes historias evolutivas en regiones climáticas diferentes. La severidad del principal filtro abiótico impuesto en la región invadida (sequía estival) no ha sido lo suficientemente fuerte (todavía) como para modificar el patrón de floración de las especies invasoras hacía el que las nativas muestran. Sin embargo, sí que determina la longitud total de la floración y el tipo de hábitat que invaden aquellas invasoras con floración estival. Los resultados sugieren diferentes implicaciones evolutivas entre las tres regiones.

Palabras clave: Invasiones biológicas, Fenología de floración, Inercia genética, Región Florística del Cabo, California, España, Ecosistemas Mediterráneos, Disponibilidad hídrica, Origen climático.

Abstract

- *Background and Aims* Flowering phenology is a potential important component of success of alien species, since elevated fecundity may enhance invasiveness. We studied the flowering patterns of invasive alien plant species and related natives in three regions with mediterranean-type climate: California, Spain and South Africa's Cape region.
- *Method* 227 invasive-native pairs were compared.
- *Key Results* Invasive alien plant species have different patterns of flowering phenology to native species in the three regions. Whether the alien species flower earlier, later, or at the same time as natives depends on the climatic regime in the native range of the aliens and the proportion of the invasive floras originating from different regions. Species invading at least two of the regions displayed the same flowering pattern, showing that flowering phenology is a conservative trait. Invasive species with native ranges in temperate climates flower earlier than natives, those from mediterranean-type climates at the same time, and species from tropical climates flower later. In California, where the proportion of invaders from the Mediterranean Basin is high, the flowering pattern did not differ between invasive and native species, whereas in Spain the high proportion of tropical species results in a later flowering than natives and the Cape region early flowering than natives was the result of a high proportion of temperate invaders.
- *Conclusions* Observed patterns are due to the human-induced sympatry of species with different evolutionary histories whose flowering phenology evolved under different climatic regimes. The severity of the main abiotic filters imposed by the invaded regions (e.g. summer drought) has not been strong enough (yet)

to shift the flowering pattern of invasive species to correspond with that of native relatives. It does, however, determine the length of the flowering season and the type of habitat invaded by summer-flowering aliens. Results suggest different implications for impacts at evolutionary time scales among the three regions.

Key words: biological invasions, flowering phenology, genetic inertia, Cape Floristic Region, California, Spain, Mediterranean-type ecosystems, water availability, climatic origin.

INTRODUCTION

The timing of sexual reproduction is a critically important determinant of plant reproductive success. Flowering at the optimum time ensures fecundity and good development of seeds and fruits (Mazer, 1987). Flowering phenology is mediated by the interaction of internal factors (Murfet, 1977; Putterill *et al.*, 2004) with external environmental signals such as temperature (Hollister *et al.*, 2005), day length (Imaizumi and Kay, 2006), or drought (Fox, 1990a). In general, plant species in their native ranges have coupled the sensitive flowering period to the optimal climatic conditions through natural selection, thus maximising their reproductive success. The main selective factors acting upon flowering phenology differ between ecosystems. In mediterranean-type ecosystems (MTEs), which occur in five widely separated regions of the world (Cowling *et al.*, 1996), summer drought and rainfall variability (Cowling *et al.*, 2005) modulate the flowering plant response. Drought is one of the most limiting factors for vegetative growth and flower development (Mitrakos, 1980; Roche *et al.*, 1997). Flowering is concentrated in spring and autumn in most native plants in MTEs, which can be interpreted with reference to avoidance of summer water-stress (Johnson, 1993; Orshan, 1989; Castro-Díez and Montserrat-Martí, 1998; Perez-Latorre and Cabezudo, 2002).

Rainfall variability plays an important role on the start and length of flowering phenology in these ecosystems. Less predictable regimes select for a largely plastic response of flowering start to cope with the uncertain moisture conditions of spring; this also occurs in other seasonally-dry ecosystems (Borchert *et al.*, 2004). Climate-change studies focused on responses of wide-ranging plant species occurring along latitudinal gradients corroborate the idea of high phenological plasticity in fluctuating environments (Arft *et al.*, 1999; Parmesan, 2006). However, phylogenetic and genetic inertia of flowering phenology imposes limits to this plasticity (Herrera, 1992; Rathcke and Lacey, 1985). Consequently, plasticity of flowering, measured as the length of temporal internal plant sensitivity to flower development, is a conservative trait, since it has a genetic base (Ausin *et al.*, 2005), and plant species may be unable to shift their timing of flowering when they are introduced into a new region.

Widespread introductions of plant species to areas outside their natural ranges gives us the opportunity to gain new insights on the importance of flowering phenology as a component of success of alien species in a new region, since enhanced fecundity appears to be an important trait associated with invasiveness (Pyšek and Richardson, 2007). To be a successful invader, introduced plants must first cope with the abiotic filters imposed by the new region and then reproduce (Richardson *et al.*, 2000); this requires them to flower at the appropriate time of year according to plant requirements. Flowering phenology has been shown to be fairly flexible in within-alien comparisons. For example, successful invaders generally display early flowering or long blooming periods (Goodwin *et al.*, 1999; Pyšek *et al.*, 2003), since the chance of acquiring improved fitness via effective pollination visits is increased. On the other hand, late, short flowering gives insufficient time for completion of the life cycle or results in a shorter time for pollination, reducing opportunities for fruit and seed development (Roche *et al.*, 1997). In the case of alien-native comparisons, many authors have found that invasive alien species flower earlier than natives (Cadotte and Lovett-Doust, 2001; Lake and Leishman, 2004). Others have found that alien species that flower later than natives are more abundant (Celesti-Grapow *et al.,* 2003; Lloret *et al.*, 2005). Exhibiting a different flowering pattern compared to native species may be more frequent in those alien species which have evolved under climatic conditions markedly different to that of the invaded region. This premise is based on the following argument: If plant species maintain their genetic inertia of timing of flowering when they are introduced in a new ecosystem, different flowering phenology between invasive and native species may occur as a direct result of different strategies of reproduction selected by evolution. On the contrary, invasive species with the same climatic conditions between their native range and the invaded ecosystems will not show any difference related to natives.

MTEs probably provide the best opportunity to test this hypothesis, since they have been severely affected by invasions of introduced (alien) plant species (Groves and di Castri, 1991). Many studies have sought reasons for differential success of different alien plant species in the different MTE regions (see Lloret *et al.*, 2005 for the Mediterranean Basin, Rejmánek, Randall, 1994 for California, Jimenez *et al.*, 2008 and Sax, 2002 for California and central Chile; and Richardson and Cowling 1992 and Richardson *et al.*, 1992 for the Cape region of South Africa). The fate of introduced species has clearly been influenced by many factors, including numerous inherent features of the different regions and differences in cultural links between the regions and colonial powers, which shaped the magnitude, timing and nature of early introductions and dissemination within regions. In addition, recent socio-economic developments and human-mediated modification of landscapes have also driven further introductions and their dissemination within the regions (Wilson *et al.*, 2007).

This paper examines the flowering phenology of invasive alien species in three different regions with mediterranean-type climate. We addressed the following questions: 1) Does the flowering phenology of invasive alien species differ from that of native species? 2) Are there differences between regions? 3) Is the flowering phenology of invasive alien species explained by the climate in their regions of origin?

MATERIALS AND METHODS

Climatic characteristic of selected regions

Three mediterranean-type ecosystems regions were selected to represent a gradient of summer drought and rainfall reliability severity among regions of the world with this climatic regime (Cowling *et al.*, 2005). The California region has the lowest summer precipitation (San Francisco (SF)= 4.9mm, San Diego (SD)= 4.8mm) and a high water deficit in this season (SF= -296.4mm, SD= -298.5mm), the Cape region has a relative high summer precipitation (Cape Town (CT)= 47mm, Port Elizabeth (PE)=110 mm) and the lowest water deficit (CT= -96.0mm, PE= -13.7mm) (Fig. 1). The Spanish mediterranean region falls somewhere in between these two regions, although with a remarkable variability in summer rainfall along latitudinal and coast-inland gradients. Water deficit was calculated as the difference between the precipitation and the potential evapotranspiration in each month. In this sense, potential evapotranspiration was calculated by the Jensen's method (Jensen *et al.*, 1990). This method is considered the most accurate from latitudes 0º to 60º. It takes into account latitude of the studied region, mean of the maximum and minimum temperatures, mean altitude and total irradiance considering the number of hours of sun. Climatic data for a 30-year period were used; for California and data for the Cape region were obtained from NOAA (1961-1990), and Spanish data were obtained from the national meteorological institute for the same period (INM 1971-2000).

Species selection and data compilation

To standardise between regions, our data set comprised introduced plant species that were clearly invasive (sensu Pyšek *et al*., 2004), with clear impact on the native ecosystems (transformer species, *sensu* Richardson *et al*., 2000). Three major sources were used to compile the lists of invaders: Invasive plants of the California's Wildlands (Bossard *et al.*, 2000), Atlas de las Plantas Alóctonas Invasoras en España (Sanz Elorza *et al.*, 2004) and The Complete Guide to Declared Weeds and Invaders in South Africa (Henderson, 2001). For California, all species listed by Bossard *et al.*, (2000) were included, since the criteria used by these authors for inclusion of species in their book match ours. For Spain, all listed species were selected, except those alien plants that are invasive only in the Canary Islands (non-mediterranean climate) and those that are *naturalized* but not *invasive sensu* (Pyšek *et al.*, 2004). For South Africa, all species listed by Henderson (2001) with mapped occurrence in the Cape Floristic Region were included. A total of 227 alien species were selected [**Supplementary information**].

Each of the selected species was coded for 7 characters (Table 1), using primarily information from the sources mentioned above. Climatic origin of the invasive species in their former native range was considered important since plants have a genetic inertia on flowering development due to climatic conditions under which they evolved (Herrera, 1992; Rathcke and Lacey, 1985). Four main habitats that are representative of invaded habitats across the regions were selected, as differences in timing of flowering are sometimes explained by habitat conditions rather than different flowering strategies (Thies and Kalko, 2004). Growth form was selected because environmental variables that affect flowering differ for woody and herbaceous plants (Arft *et al.*, 1999; Post and Stenseth, 1999). Pollination type was considered important because different flowering strategies have been documented for animal- and wind-pollinated plants (Rathcke and Lacey, 1985). Finally start, end and length of flowering phenology were also compiled.

To compare characters of invasive species with those of native plants having similar ecological requirements, we paired each invasive species with one closely related native species based on four criteria: (1) within each pair, the native must be recorded in the region where the alien species is invasive; (2) native and invasive alien species must share the same habitat type - to be potential competitors; (3) the two species must belong to the same growth form and pollination type and finally (4) the two species must belong to the same genus or family, to get phylogenetic independent contrasts (Ackerly, 2000). Native species with small range of distributions or under a threaten category were excluded. In the case of the fourth criteria mention above, this was only possible for the case of California and the Cape region, as in Spain, few species met the four conditions due to the big phylogenetic differences between invasive and native flora. Thus, phylogenetic relatedness was taken into account *a posteriori* in Spain. In this case, we collected total phylogenetic distances for each species through the angiosperm plant phylogenetic supertree described by Soltis *et al.*, (2000) and their modifications of Bremer *et al.*, (2003). Currently, these studies are the most highly resolved and strongly supported topology obtained for angiosperms. Next, we tested if the differences in the start and the end of flowering between invasive and native species were influenced by phylogenetic relationship between each pair species. ANCOVA analysis testing for differences in flowering time, demonstrated no phylogenetic effects on the results due to the native species selection for the ecological pairs construction (start of flowering: $F=0.23$ $p=0.632$, end of flowering: $F= 1.21$ $p=0.274$). In this sense, the phylogenetic relationship of the Spanish pairs was the covariable calculated as the mean of phylogenetic distance to the first common ancestor of both pair species.

Characteristics of Californian native species as well as their flowering phenology were collected based on the Online Interchange for California Floristics (2007), based the Jepson Manual Higher Plants of California (Hickman, 1993). For Spain, native plant characters were collated from the Iberian Flora (Castroviejo, 1986-2005). Unfortunately, accounts of some Spanish native species are yet to be published in the Iberian Flora. Characters for these species were compiled from regional floras such as Flora of Western Andalucia (Valdés *et al.*, 1987) and Flora of Catalonia (Bolòs and Vigo, 1984-2001). Because the information was obtained from three different sources, we tested differences in flowering onset and cessation in 31 species common among floras with a one-way ANOVA. No differences were found either in the start (F=7.7E-4, p=0.978) or in the end of flowering time (F=0.723, p=0.402). Finally, Goldblatt, Manning, (2000) provided us with the best reference on the required information for the native plants of the Cape region.

Statistical analyses

Chi-square tests were applied to test for differences between the exotic floras of the three regions in the spectra of climatic origin, life form and type of invaded habitat. An orthogonal general lineal model (GLM) for unbalanced designs was used to test for significant variables affecting differences in the start, end and length of flowering between native and invasive species. Categorical predictors were the invaded mediterranean regions plus those used to create invasive-native pairs (growth form, pollination type and invaded habitat). Pairwise Watson-William F-tests for dependent samples in circular statistic were performed to test for differences in flowering phenology between: 1) all invasive alien and native species pairs in the three regions; 2) those species pairs in each region where the alien invasive species shared the same climatic origin or pollination type; 3) those species pairs that are animal-pollinated and for which the invaders share the same climatic origin; and 4) differences in flowering phenology between invasive alien species present in at least in two different regions. These analyses were performed with the ORIANA package (Kovach Computing Services (Kovach, 1994). In all circular analyses, flowering phenology data followed a

Von Mises distribution (circular version of normal distribution) so no transformation was needed. T-tests for paired samples were performed to test for differences in the length of flowering between invasive alien and native species. SPSS 12.0 (SPSS, Inc) was used for non circular statistic analysis.

RESULTS

Characteristic of invaders

Invasive species in the three mediterranean-type ecosystems showed different patterns of climatic origin, growth form, and invaded habitats (Fig. 2). The invasive flora of California had the smallest proportion of tropical species and a high proportion of invaders with Mediterranean and temperate origin. Spain and the Cape region had almost the same proportion of Mediterranean invaders (around 15% of species). However, the alien flora of the Cape region showed a higher proportion of temperate species while in Spain tropical species were more abundant. Herbaceous plants were the principal growth form in the invasive floras of California and Spain, and disturbed areas had the highest percentages of invasive species. However, a higher proportion of the invasive flora in Cape region was made up of woody plants and invaded habitats were mostly natural shrubland. The proportion of climbers is similarly low in the three MTEs.

Differences in flowering phenology between invasive and native species

Differences in the start of flowering between invasive and native species were significantly influenced by the invaded region and by the interaction between region and pollination type (Table 2). These differences in the start were generally lower in California than Spain and the Cape region. In addition, wind-pollinated species had higher differences than animal-pollinated species in California, whereas in the Cape region the pattern was the opposite. Differences in the end of flowering were significantly influenced by the interaction between region and growth form (Table 2). In this sense, only invasive climbers in California had lower differences in the end of flowering compared to the invasive climbers in Spain and the Cape Region. Finally, differences in the length of flowering varied significantly depending of the invaded region, being shorter in California (Table 2 and Table 3).

Variation of flowering phenology of invasive species between regions

The flowering length of invaders was positively correlated with the climatic conditions of the three regions. Invasive species flower for longer periods where the summer precipitation is higher. Thus, invasive alien plants in the Cape region bloom over 5.2 months, in Spain over 4.8 months and in California 4.1 months on average. Overall, we found no differences in flowering length between invasive-native pairs, except in the Cape region where invasive species flower for longer than natives (Table 3). When considering the climatic origins of invasive species, only tropical plants showed different patterns between the invaded region and the length of flowering. In Spain, tropical invaders flowered over a shorter period than the natives, whereas invaders of tropical origin in the Cape region flowered for longer than the natives (Table 3).

For different regions, invasive species flowered earlier, later or at the same time as co-occurring natives. In California, the start and the end of the flowering period was similar for invasive alien and native species. However, when the comparison only included those pairs where the invasive had Mediterranean origin, invaders started flowering one month earlier and finished one month earlier than natives. By contrast, in Spain invasive species started and ended flowering later than native species. This result was true for those species pairs where the alien has either tropical or temperate origin, but not for the Mediterranean group (Table 3). Timing of flowering of tropical invasive species in Spain and California showed the same pattern. This suggests that a displacement of flowering phenology may also occur in the latter region. However, no significant differences were found, probably due to the small sample size. In the Cape region, invasive species flowered earlier than natives, due to the early onset of flowering of invaders of temperate origin (Table 3). Tropical species ended flowering later than their native pairs but no differences were found when the comparison was conducted with the full set of native species. Although native species showed a big variation in their spring onset of flowering, the flower development corresponded with those months with a mean temperature of 18ºC and with relatively low water deficits (Fig. 1, Table 3).

Finally, the 28 species that are invasive in at least two regions showed no displacement of flowering phenologies, either for the initiation ($F= 0.11$ $p=0.745$) or cessation of flowering ($F=0.22$ $p=0.638$). Overall these results suggest that the differences in flowering phenology of invasive species are due to the differences in climatic origin of invaders rather than the particular species composition of the invasive flora.

Animal-pollinated species and climatic origin

Animal-pollinated invasive species displayed the same pattern as for the entire invasive-native comparison (Table 3, Fig. 3). This means that in California they had the same flowering phenology as native species, in Spain they started and finished their flowering later, and in the Cape region they started their flowering earlier, while invasive and native species finished at the same time. When comparing between regions, different climatic origins of animal-pollinated invaders showed differences in the onset of flowering. In California, Mediterranean invaders started flowering earlier than temperate invaders (Julian day Mediterranean sps= 89, Julian day Temperate sps=127, $F=4.65$ $p<0.05$). In Spain, tropical invaders started later than temperate invaders but these differences were not significant (Julian day Temperate sps=132, Julian day Tropical sps=162, $F=3.56$ $p=0.065$). In the Cape region, tropical invasive species started significantly later than temperate ones (Julian day Temperate sps=233, Julian day Tropical sps=307, $F=20.65$ $p<0.001$) and also than Mediterranean ones (Julian day Mediterranean sps=232, Julian day Tropical sps=307, $F= 7.2$ $p<0.01$).

Invasive alien species had a different end of flowering in relation to their climatic origin. In California, tropical invaders finished flowering later than invaders from the Mediterranean (Julian day Mediterranean sps=181, Julian day Tropical sps=285, $F= 4.6$ $p<0.05$). In Spain, no differences between groups were found for the offset of flowering. Lastly, in the Cape region temperate invaders finished flowering earlier than tropical (Julian day Temperate sps=338, Julian day Tropical sps=76, $F=27.1$ $p<0.001$) or Mediterranean ones (Julian day Temperate sps=338, Julian day Mediterranean sps=72, $F=7.1$ $p<0.01$)

In summary, these differences suggest that a segregation of timing of flowering is occurring depending of the climatic origin of invasive species. Temperate invaders start flowering first, followed by the mediterranean invaders and then the tropical invaders.

DISCUSSION

The three mediterranean-climate regions dealt with here occur along a gradient of summer drought severity, and their invasive floras differ in terms of the proportion of growth forms, their climatic origins, and the habitats most invaded. Depending on the region selected, invasive species flowered earlier, later, or at the same time as natives. Thus, different flowering phenology pattern between groups is context dependent. It must to be taken into account that, for a different timing of flowering between invasive and native species, two events must co-occur: 1) a small proportion of invasive species have to belong to the same climatic origin as the invaded region, i.e. Mediterranean climate; and 2) Climatic and habitat conditions must minimise summer drought to allow invasive plants to survive. Related to the former premise, species tend to show a genetic inertia for the time of flowering because flowering phenology is an adaptive trait selected to avoid unfavourable climatic conditions in the regions where the plants evolved (Fox, 1990b; Herrera, 1992; Johnson, 1993). In this sense, invasive species maintain the same flowering phenology when they are introduced to regions with the same climatic characteristics. Twenty-eight invasive species shared between at least two regions showed the same flowering phenology in both invaded regions, providing support for this idea. In general, invasive species from the Mediterranean flowered predominantly in spring, whereas tropical invaders continued flowering further into summer. On the other hand, temperate aliens flowered in early spring (in the Cape region) or in summer (in Spain) depending on whether they are woody or herbaceous species.

Recent studies have highlighted the importance of studying historical factors (e.g. the links between regions and colonial powers or human-mediated modifications to landscapes) as these factors are thought to shape the composition and magnitude of introductions (Lockwood *et al.*, 2007; Wilson *et al.*, 2007). Such anthropogenic factors may also influence the biotic interactions between invasive and native species as can occur with animal-pollinated plants. For example, no difference was noted in flowering phenology between invasive and native species in California, because the proportion of invaders from the Mediterranean Basin is high. This is due to the California's historical links with Europe and especially with Spain as a colonial power (Bancroft, 1890). As both groups flower at the same time, they may compete for pollinators (Lopezaraiza-Mikel *et al.*, 2007). Competition for pollinators is thought to be an important form of disruption of plant-animal interactions caused by invasive species (Traveset and Richardson, 2006). However in the Cape region and in Spain flowering phenology of invaders was different to that of natives, since the proportion of invaders from mediterranean-climate regions is small. A high proportion of invaders of temperate and tropical origin in the Cape region are attributable to two events. From the 17th to the 19th century the current South Africa and thus the Cape region was a European colony. The influence and trade with countries such as The Netherlands and specially the United Kingdom increased the rate of deliberate introductions (Henderson, 2001). Temperate alien species were introduced from Europe or other European colonies such as Australia (e.g. *Hypericum perforatum* from Europe*, Acacia* species from Australia). On the other hand, more recently, tropical species (e.g. *Araujia sericifera, Passiflora caerulea*) have been also deliberately introduced for horticulture (Henderson, 2001). Although the introductions of alien species in both historical situations were for different reasons, the ecological result is convergent. Invasive species flower at a different time to the natives, filling an empty temporal niche. Flowering at a different time compared to natives may be an advantage for invasive species. It increases sexual fitness due to avoidance of pollen limitation and competition for pollinators with natives (Sargent and Ackerly, 2008). In contrast to the situation in the Cape region, most of invasive plants in Spain were introduced accidentally with the trade of plants for agricultural purposes (Lloret *et* *al.,* 2005). Tropical summer weeds invading croplands and disturbed areas highlight the importance of the Spanish past linked to their American colonies.

The reason for some invaders flowering in summer (the least favourable period for flower development in MTEs) is due to the type of habitat they invade. Disturbed areas are generally the most susceptible to invasion (Cadotte *et al.*, 2006; Lake and Leishman, 2004). Some disturbed habitats such as irrigated summer croplands and riparian habitats seldom experience water stress, allowing invasive plants to survive the summer drought in mediterranean-type climates (Lake and Leishman, 2004). The importance of disturbed areas as a microenvironment for avoiding abiotic filters of the invaded region depends of the severity of summer drought. In California and Spain, where summer drought is intense, most of the species on our lists invade disturbed areas. In the Cape region, however, where summer drought is relatively mild, invasive species seem less limited by drought and can invade natural areas (Fig. 2).

Climatic and habitat environmental conditions can also influence the growth form of invaders and thus the length of flowering phenology of invasive species (Castro-Diez *et al.*, 2003). For example, disturbed areas have the advantage of minimizing abiotic unfavourable conditions, but limit the type of growth form that can invade. Annuals and short-lived plants are better adapted to rapid changes and disturbance conditions of this type of habitat (Grime, 1974). These types of invaders which can complete their life cycles in a few months showed a short flowering period associated to their short-lived cycle. Mainly herbaceous invaders of tropical origin in Spain (e.g. *Datura stramonium*, *Xanthium strumarium*) illustrate this situation. They show significantly shorter flowering periods than natives (Table 1). On the other hand, tropical invaders in Cape region are mainly woody species that invade natural areas and flowering longer than natives (Table 1, Table 2 and Fig. 2).

Previous studies have shown that successful invaders generally display early flowering or long blooming periods (Goodwin *et al.*, 1999; Pyšek *et al.*, 2003). Also, in alien-native comparisons, many authors have found that invasive alien species flower early than natives (Cadotte and Lovett-Doust, 2001; Lake and Leishman, 2004). Those results suggest that invasive species capitalize on an early blooming strategy to increase their reproductive success since the chance to acquire improved fitness via effective pollination visits is also increased (Goodwin *et al.*, 1999; Pyšek *et al.*, 2003). This idea is supported by other authors who have found late, short flowering for pollination reduced opportunities for fruit and seed development of alien species (Roche *et al.*, 1997). However, our results show that early flowering is not the only reproductive strategy for successful invaders. They can also flower at the same time or later than native species and be successful. Therefore, the possible different flowering phenology is mainly a consequence of different nature, historical and human factors that drives the reproductive relationship between groups. If this argument is correct, the same alien plant flowering phenological pattern should be found in regions with homogenous environmental conditions and the same history of introductions. This seems to apply for regions within the Mediterranean Basin. Dominance of summer flowering among invasive species in Spain (Table 3) is in agreement with previous results found for Italy (Celesti-Grapow *et al.*, 2003) and Mediterranean Islands (Lloret *et al.*, 2005).

Most invasion ecology studies relate traits of alien species to their capacity to invade, with the overall aim of unravelling aspects of the invasion process and aiming to predict future invasions. However, not all the observed plants traits identified as being associated with invasiveness in aliens really confer invasiveness, since other causes often underlie the observed pattern. This seems to be the case with flowering phenology. Although several studies have founded a positive relationship between flowering phenology of aliens and their invasiveness potential (Goodwin *et al*., 1999; Cadotte and Lovett-Doust, 2001; Pyšek *et al*., 2003; Lake and Leishman, 2004), flowering phenology of invasive species and the possible differences relative to natives is only a consequence of different history of human-orchestrated introductions. The results of this study proved that under the same climatic conditions in three widely-separated regions, invasive alien species do not display a common flowering phenology pattern. Instead, they flower early, later or at the same time than native species depending on the climatic regime in the region where they evolved.

SUPPLEMENTARY INFORMATION

Checklist of the 227 plant species (alien-native comparisons) in the three mediterranean-type regions, California, Spain and the Cape region of South Africa. Flowering phenology of each species is recorded in months.

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Table captions

TABLE 1 List of characters for which data were scored and used in ecological pair construction and invasive-native comparisons.

Character	Character state
Climatic origin	Tropical, Temperate, Mediterranean type-ecosystems (MTE)
Habitat type	Disturbed areas, Coastal areas, Lakes & Rivers, Shrub &Woodland
Growth form	Woody, Herbaceous, Climber
Start, end & length of flowering of invasive and native species in the three MTEs	January to December (months) *
Pollination type	Animal, Wind

* Flowering times for the Cape region were transformed to the Northern Hemisphere calendar

TABLE 2 Results of a General Lineal Model (GLM) of the differences in the start, end and length of flowering phenology (dependent variables) between invasive and native species pairs, for region (California, Spain and the Cape region of South Africa), growth form, habitat invaded and pollination type as categorical predictors (see Table 1). Three and higher order interactions are not showed for clarity and because they were not significant. To perform this analysis, flowering times for the Cape region were transformed to the Northern Hemisphere calendar (i.e. January - July)

Variable	*Start of flowering*			*End of flowering*			*Length of flowering*		
	DF	F	p	DF	F	p	DF	F	p
Region (R)	2	5.233	< **0.01**	2	2.974	0.053	2	8.949	**<0.001**
Growth Form (GF)	2	1.998	0.138	2	0.144	0.866	2	1.422	0.244
Pollination Type (PT)	1	0.002	0.963	1	0.411	0.522	1	2.129	0.146
Habitat Type (HT)	3	0.93	0.427	3	0.359	0.783	3	0.166	0.919
R*GF	4	1.147	0.335	4	2.822	**<0.05**	4	0.701	0.592
R*PT	2	3.506	**<0.05**	2	2.99	0.052	2	0.187	0.83
GF*PT	2	0.647	0.525	2	0.299	0.742	2	0.85	0.429
R*HT	6	1.722	0.117	6	1.449	0.198	6	1.305	0.256
GF*HT	6	1.157	0.331	6	0.596	0.733	6	0.332	0.92
PT*HT	3	1.355	0.258	3	0.41	0.746	3	0.833	0.477

TABLE 3 Mean values of flowering phenology parameters between invasive and native plant species according to climatic origin and pollination-type in the three mediterranean-climate regions. Circular mean values were transformed to days of the year for easier interpretation. Watson-Williams F value and t-test value are also represented (p>0.05 ns, * p<0.05, ** p<0.01, *** p<0.001).

Parameters California		All species (n=78)	Tropical (n=3)	Temperate (n=45)	Mediterranean (n=30)	Animal pollinated (n=60)	Wind pollinated (n=18)
Start of flowering	Invasive	29 April	17 May	19 May	25 March	11 April	19 May
	Native	5 May	17 February	19 May	26 April	10 May	3 May
F-value, p		0.63 ns	0.64 ns	1.22E-04 ns	4.83*	2.44 ns	0.88 ns
End of flowering	Invasive	21 July	16 October	13 August	6 June	24 July	23 July
	Native	22 July	11 August	6 August	13 July	8 August	6 July
F-value, p		9.10E-4 ns	1.31 ns	0.13 ns	4.62*	0.73 ns	1.04 ns
Flowering length	Invasive	4.1	6.7	3.9	3.9	4.2	3.6
	Native	3.9	6.0	3.6	3.6	3.9	3.2
t-value, p		0.67 ns	0.36 ns	1.20 ns	0.67 ns	0.98 ns	1.27 ns
Parameters Spain		**All species (n=90)**	**Tropical (n=43)**	**Temperate (n=36)**	**Mediterranean (n=11)**	**Animal pollinated (n=67)**	**Wind pollinated (n=23)**
Start of flowering	Invasive	4 June	14 June	2 June	20 May	30 May	30 May
	Native	18 April	9 April	16 April	2 May	19 April	9 April
F-value, p		21.85***	27.82***	11.48***	0.42 ns	11.09***	11.63***
End of flowering	Invasive	28 September	2 October	8 October	5 September	27 September	28 September
	Native	4 September	3 September	2 September	7 September	18 August	24 September
F-value, p		3.72*	3.88*	4.42*	0.01 ns	4.02*	0.04 ns
Flowering	Invasive	4.8	4.7	4.8	5.5	4.8	4.6

length	Native	5.3	5.9	5.2	4.9	4.9	5.7
t-value, p		-1.47 ns	-2.53**	-0.93 ns	0.54 ns	-0.44 ns	-2.27*
Parameters Cape region		All species (n=73)	Tropical (n=28)	Temperate (n=33)	Mediterranean (n=12)	Animal pollinated (n=53)	Wind pollinated (n=20)
Start of flowering	Invasive	15 September	29 October	27 August	8 September	11 September	26 September
	Native	5 November	3 November	14 November	22 September	12 November	22 October
F-value, p		22.20***	0.05 ns	37.52***	1.56 ns	21.21***	2.53 ns
End of flowering	Invasive	25 January	4 April	10 December	9 February	25 January	22 January
	Native	13 January	26 January	5 February	8 March	15 January	5 January
F-value, p		0.51 ns	3.97*	1.26 ns	0.61 ns	0.33 ns	0.25 ns
Flowering length	Invasive	5.2	6.1	4.5	5.2	5.1	5.4
	Native	4.3	4.4	4.0	5.1	4.1	4.8
t-value, p		2.59**	2.96**	1.16 ns	0.86 ns	2.51*	0.86 ns

Figures captions

FIG. 1 Climatic characteristic of the three mediterranean-type ecosystems studied: a) California, b) Spain and c) the Cape region of South Africa. The three regions represent a gradient of summer-drought severity. California has the driest and the Cape region has the mildest summers. Climatic charts of two different localities in each region illustrate this gradient. Columns represent the precipitation; solid lines the temperature, and dashed line the water deficit in each month. Charts of the southern hemisphere localities (Cape region) have been modified to show drought between June and July for clearer comparison with northern-hemisphere localities.

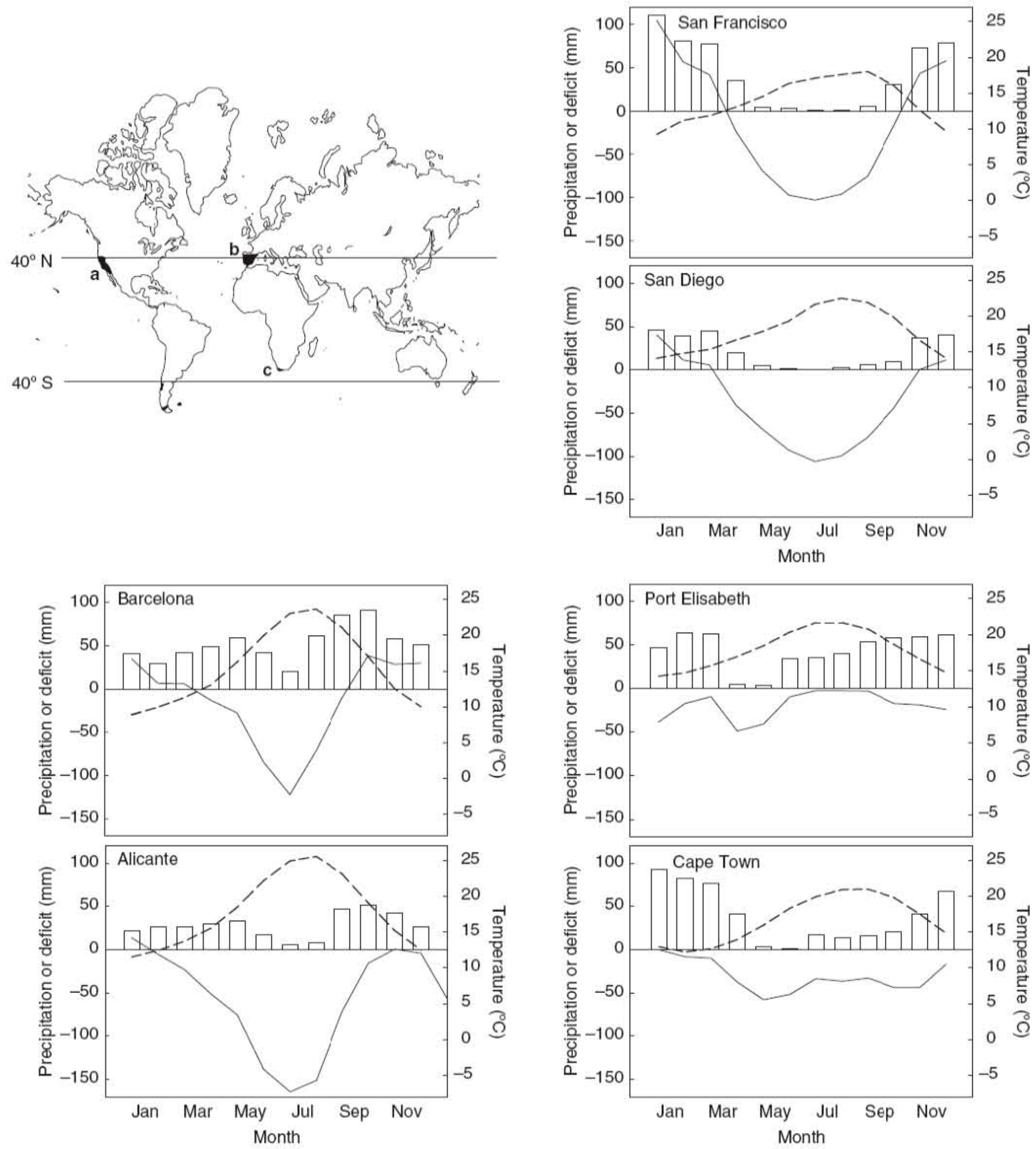

40° N
40° S
a
b
c
San Francisco
San Diego
Barcelona
Alicante
Port Elisabeth
Cape Town
Precipitation or deficit (mm)
Temperature (°C)
Jan
Mar
May
Jul
Sep
Nov
Month

FIG. 2 Proportions of invasive species according to their climatic origin, growth invaded ecosystem in the three mediterranean-climate regions.

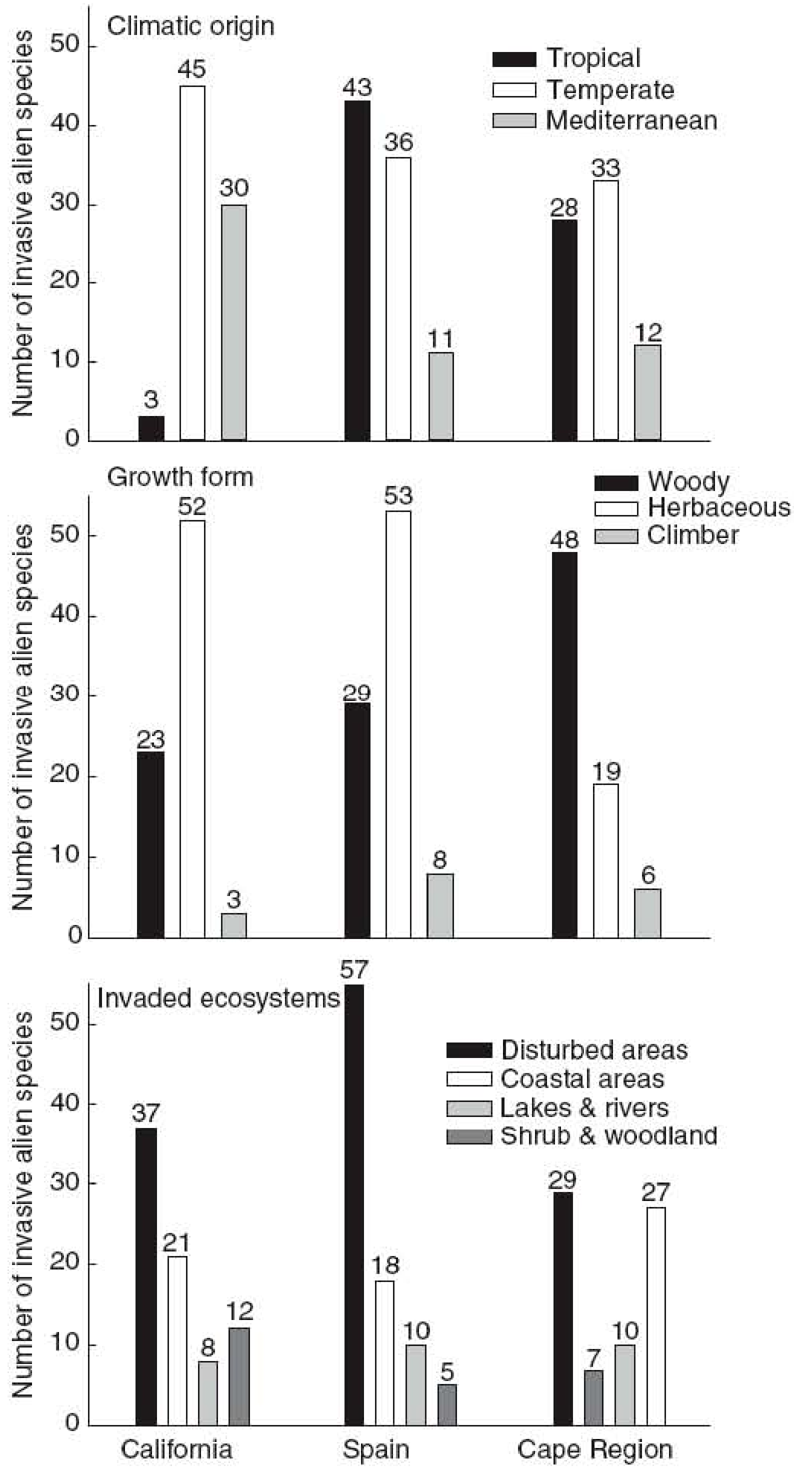
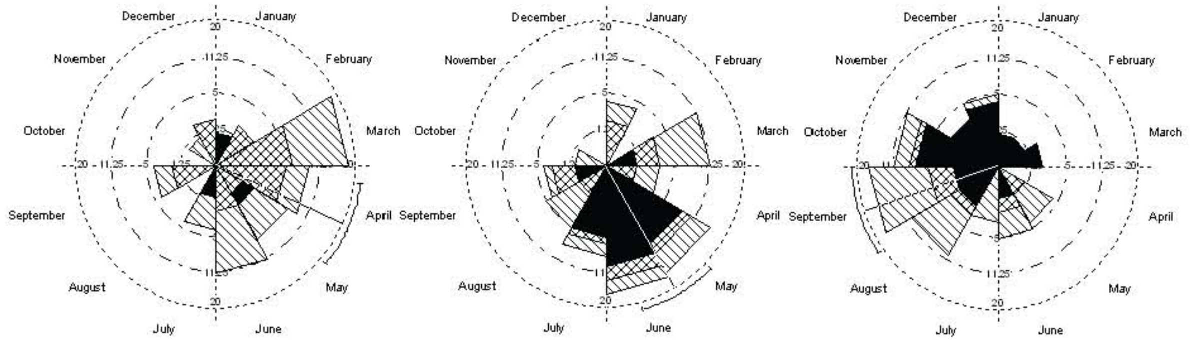
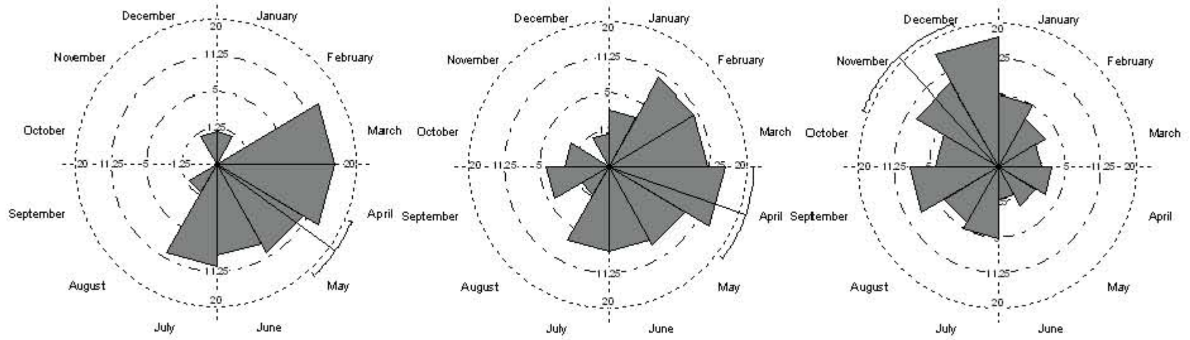


FIG. 3 Circular histograms for the start and the end of flowering in animal-pollinated invasive species and corresponding native species (see text). Triangles represent the number of species that flower in that month. Solid black areas indicate alien species of tropical; diagonal hatching indicates species with temperate origin, and cross-hatching shows species with Mediterranean origin. Native species are shown in grey. Mean and standard deviations are also shown.

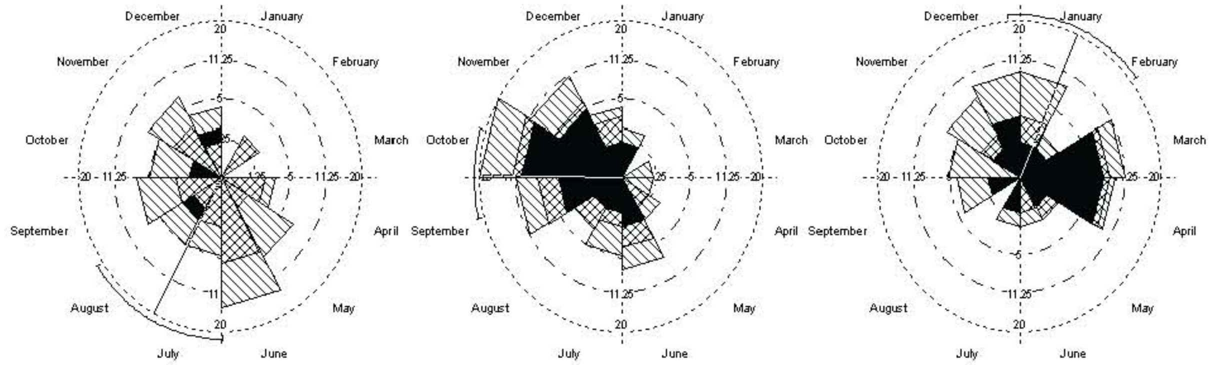
California Spain Cape Region



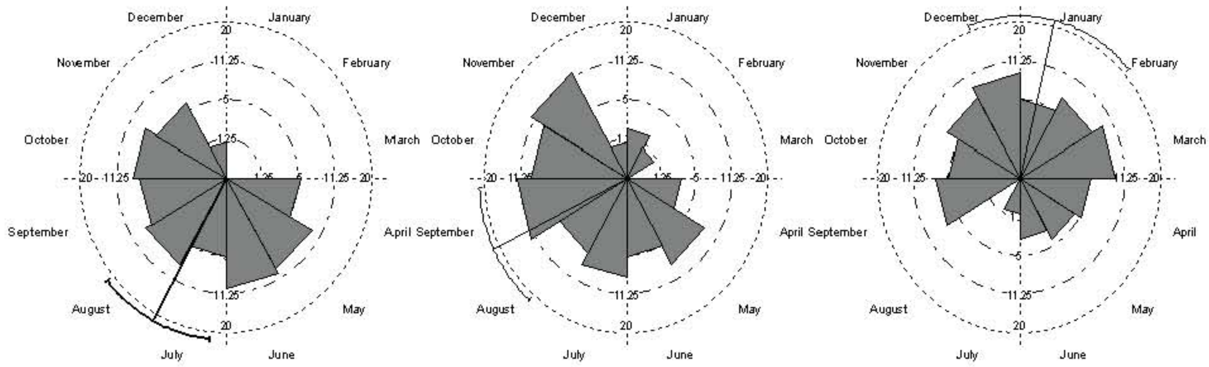
Start



California Spain Cape Region



End



SUPPLEMENTARY INFORMATION

Checklist of the 227 plant species (alien-native comparisons) in the three mediterranean-type regions, California, Spain and the Cape region of South Africa. Flowering phenology of each species is recorded in months.

Invasive Family/Species	Start of flowering	End of flowering	Native Family/Species	Start of flowering	End of flowering
		California			
Aizoaceae					
Aptenia cordifolia	Feb	Nov	**Nyctaginaceae**/ *Abronia latifolia*	May	Nov
Carpobrotus edulis	Sep	Nov	**Brassicaceae**/ *Cakile edentula*	Jun	Sep
Conicosia pugioniformis	Mar	Jun	**Asteraceae**/ *Agoseris apargioides*	Jul	Sep
Mesembryanthemum cristallinum	Apr	Sep	**Convolvulaceae**/ *Calystegia soldanella*	Apr	Jun
Anacardiaceae			**Anacardiaceae**		
Schinus molle	Sep	Nov	*Toxicodendron diversilobum*	Mar	May
Apiaceae			**Apiaceae**		
Conium maculatum	Apr	Jun	*Daucus pusillus*	Mar	Apr
Foeniculum vulgare	May	Nov	*Angelica tomentosa*	Jun	Jul
Apocynaceae			**Apocynaceae**		
Vinca major	Mar	Jun	*Cycladenia humilis*	May	Jun
Araliaceae			**Araliaceae**		
Hedera helix	Sep	Nov	*Aralia californica*	Jul	Jul
Asteraceae			**Asteraceae**		
Ageratina adenophora	Mar	Jun	*Ambrosia psilostachya*	Jul	Oct
Artotheca calendula	Mar	Jun	*Helianthus annuus*	Jul	Oct
Cardus pycnocephalus	Sep	Dec	*Cirsium scariosum*	Jun	Sep
Centaurea calcitrapa	Apr	Jun	*Cirsium cymosum*	Apr	Aug
Centaurea melitensis	Apr	Jun	*Cirsium quercetorum*	Apr	Aug
Centaurea solstitialis	Apr	Dec	*Madia sativa*	May	Oct
Cirsium arvense	Jun	Aug	*Cirsium douglasii*	Jun	Aug
Cirsium vulgare	Jun	Nov	*Stephanomeria virgata*	Jul	Oct
Cynara cardunculus	Apr	Jun	*Cirsium brevistylum*	Apr	Sep
Delairea odorata	Dec	Feb	*Cirsium occidentale*	Apr	Aug
Erechtites glomerata	Jul	Sep	*Conyza canadensis*	Jul	Nov
Erechtites minima	Jul	Sep	*Xanthium strumarium*	Aug	Oct
Helichrysum petiolare	Jul	Aug	*Baccharis pilularis*	Jul	Sep
Leucanthemum vulgare	May	Aug	*Erigeron divergens*	Jul	Nov
Senecio jacobaea	Jun	Sep	*Tanacetum camphoratum*	Jun	Sep
Brassicaceae			**Brassicaceae**		

Cardaria chalepensis	Mar	Jun	*Cardamine californica*	Mar	Apr
Cardaria draba	Mar	Jun	*Erysimum capitatum*	Mar	Apr
Lepidium latifolium	May	Jul	*Lepidium virginicum*	Mar	Nov
Brassica tournefortii	Dec	Feb	*Lepidium densiflorum*	Apr	May
Chenopodiaceae			**Chenopodiaceae**		
Atriplex semibaccata	Apr	Dec	*Atriplex leucophylla*	Jun	Dec
Bassia hyssopifolia	Jun	Oct	*Kochia californica*	Jul	Nov
Halogeton glomeratus	Jun	Oct	*Atriplex patula*	Jun	Nov
Eleagnaceae			**Eleagnaceae**		
Elaeagnus angustifolia	May	Jun	*Shepherdia argentea*	May	May
Euphorbiaceae			**Euphorbiaceae**		
Euphorbia esula	Apr	Jul	*Euphorbia crenulata*	Mar	Aug
Ricinus communis	Jan	Dec	*Bernardia myricifolia*	Dec	Aug
Fabaceae			**Fabaceae**		
Alhagi pseudalhagi	Jun	Aug	*Caesalpinia virgata*	Mar	May
Cytisus scoparius	Mar	Jun	*Lotus procumbens*	Apr	Jun
Cytisus striatus	Mar	May	*Senna armata*	Mar	Jul
Genista monspessulana	Mar	Jul	*Lupinus albifrons*	Mar	Jun
Retama monosperma	Feb	Apr	*Amorpha fruticosa*	May	Jul
Robinia pseudoacacia	May	Jun	*Prosopis glandulosa*	May	Oct
Spartium junceum	Mar	Apr	*Lotus procumbens*	Apr	Jun
Ulex europaea	Mar	May	*Lupinus arboreus*	Apr	Jun
Haloragaceae			**Haloragaceae**		
Myriophyllum aquaticum	Mar	Jun	*Myriophyllum hippurioides*	Jun	Sep
Myriophyllum spicatum	Mar	Jun	*Myriophyllum sibiricum*	Jun	Sep
Hydrocharitaceae					
Egeria densa			**Ranunculaceae**/ *Ranunculus aquatilis*	Apr	May
Hydrilla verticillata			**Hydrocharitaceae/** *Elodea canadensis*	Jun	Aug
Lamiaceae			**Lamiaceae**		
Menta pelugium	Jun	Nov	*Mentha arvensis*	Jul	Oct
Lythraceae			**Lythraceae**		
Lythrum salicaria	Jun	Sep	*Lythrum californicum*	May	Aug
Moraceae			**Ulmaceae**		
Ficus carica	Mar	Oct	*Celtis reticulata*	Jan	Apr
Myoporaceae			**Rutaceae**		
Myoporum laetum	Mar	May	*Ptelea crenulata*	Apr	May
Myrtaceae			**Hippocastanaceae**		
Eucalyptus globulus	Nov	Apr	*Aesculus californica*	May	Aug
Poaceae			**Poaceae**		
Ammophila arenaria			*Leymus mollis*	Apr	May
Arundo donax	Jun	Sep	*Phragmites australis*	Jun	Aug
Bromus madritensis	Feb	May	*Bromus vulgaris*	Apr	Jun
Bromus tectorum	Apr	Jun	*Bromus carinatus*	Mar	May
Cortaderia jubata	Jul	Sep	*Achnatherum coronatum*	Apr	Jun

Cortaderia selloana	Aug	Sep	*Sporobolus airoides*	Jun	Nov
Ehrharta calycina	Dec	Apr	*Panicum acuminatum*	Mar	Jun
Ehrharta erecta	Dec	Apr	*Eragrostis pectinacea*	Mar	Jun
Ehrharta longiflora	Dec	Apr	*Eragrostis mexicana*	Mar	Jun
Pennisetum setaceum	Jul	Oct	*Hordeum jubatum*	Apr	May
Phalaris aquatica	May	Jun	*Phalaris lemmonii*	Apr	May
Schismus arabicus	Mar	May	*Vulpia octoflora*	Apr	Jun
Schismus barbatus	Mar	May	*Phalaris californica*		
Spartina alterniflora	Jul	Sep	*Spartina foliosa*	Jun	Sep
Spartina anglica	Jul	Sep	*Deschampsia cespitosa*	Jul	Sep
Spartina densiflora	Jul	Sep	*Distichlis spicata*	Jun	Jun
Spartina patens	Jul	Oct	*Paspalum distichum*	Jul	Sep
Taeniatherum caput-medusae	May	May	*Elymus elymoides*	Apr	Jun
Pontederiaceae			**Nymphaeaceae**		
Eichhornia crassipes	Jul	Oct	*Nuphar lutea*	Apr	Oct
Rosaceae			**Rosaceae**		
Cotoneaster ssp	Jun	Sep	*Heteromeles arbutifolia*	Jun	Jul
Crataegus monogyna	Mar	Jun	*Crataegus douglasii*	May	Jun
Rubus discolor	May	Jul	*Rubus ursinus*	Mar	Jun
Scrophulariaceae					
Bellardia trixago	Apr	Jul	**Orobanchaceae**/ *Castilleja affinis*	Mar	Jun
Digitalis purpurea	Jun	Sep	**Scrophulariaceae**/ *Penstemon heterophyllus*	Mar	Jun
Verbascum thapsus	Jun	Oct	**Asteraceae**/ *Achillea millefolium*	May	Sep
Simbaroubaceae			**Aceraceae**		
Ailanthus altissima	May	Aug	*Acer macrophyllum*	Apr	May
Tamaricaceae			**Salicaceae**		
Tamarix chinensis	Mar	May	*Salix exigua*	Mar	Apr
Tamarix gallica	Mar	May	*Salix laevigata*	Apr	May
Tamarix parviflora	Mar	May	*Salix lucida*	Apr	May
Tamarix ramosissima	Mar	May	*Salix lutea*	Mar	May

Spain

Aceraceae			**Oleaceae**		
Acer negundo	Mar	Apr	*Fraxinus angustifolia*	Dec	Jan
Agavaceae			**Lamiaceae**		
Agave americana	Jul	Sep	*Rosmarinus officinalis*	Sep	May
Aizoaceae			**Apiaceae**		
Carpobrotus acinaciformis	Jan	Jun	*Crithmum maritimum*	May	Jul
Anacardiaceae			**Anacardiaceae**		
Schinus molle	May	Jun	*Pistacia lentiscus*	Mar	May
Apocynaceae			**Caryophyllaceae**		
Vinca diformis	Jan	Dec	*Silene latifolia*	Apr	Jul
Asclepiadaceae					

Gomphocarpus fruticosus	Jun	Aug	**Apocynaceae**/ *Nerium oleander*	May	Sep
Araujia sericifera	May	Sep	**Smilacaceae**/ *Smilax aspera*	Sep	Nov
Asclepias curassavica	May	Oct	**Lamiaceae**/ *Ballota hirsuta*	May	Jul
Asteraceae					
Achillea filipendulina	Jun	Oct	**Scrophulariaceae**/ *Verbascum pulverulentum*	May	Jul
Ambrosia artemisifolia	Jun	Nov	**Brassicaceae**/ *Cakile maritima*	Feb	Oct
Arctotheca calendula	Mar	Jun	**Polygonaceae**/ *Polygonum aviculare*	Apr	Oct
Artemisia verliotorum	Jul	Nov	**Asteraceae**/ *Artemisia vulgaris*	Jul	Nov
Baccharis halimifolia	Aug	Oct	**Chenopodiaceae**/ *Halimione portulacoides*	Aug	Nov
Bidens aurea	Sep	Jan	**Polygonaceae**/ *Polygonum hydropiper*	Jul	Oct
Bidens frondosa	Sep	Nov	**Polygonaceae**/ *Polygonum lapathifolium*	Jun	Nov
Bidens pilosa	Jul	Oct	**Brassicaceae**/ *Rorippa palustris*	Apr	Nov
Bidens subalternus	Aug	Nov	**Ranunculaceae**/ *Ranunculus sceleratus*	Mar	Oct
Conyza bonariensis	Mar	Sep	**Fabaceae**/ *Melilotus officinalis*	May	Nov
Conyza canadiensis	Jul	Nov	**Asteraceae**/ *Crepis vesicaria*	Feb	Jun
Conyza sumatrensis	Jul	Nov	**Polygonaceae**/ *Rumex pulcher*	Apr	Jul
Cotula coronopifolia	Mar	Aug	**Asteraceae**/ *Aster tripolium*	Oct	Nov
Helianthus tuberosus	Aug	Oct	**Asteraceae**/ *Calendula arvensis*	Jan	Dec
Senecio inaequidens	May	Oct	**Asteraceae**/ *Centaurea aspera*	Mar	Nov
Senecio mikanioides	Sep	Dec	**Rosaceae**/ *Rubus ulmifolius*	Jun	Aug
Xanthium spinosum	Jul	Oct	**Asteraceae**/ *Sonchus oleraceus*	Jan	Dec
Xanthium strumarium	Jul	Sep	**Asteraceae**/ *Sonchus asper*	Feb	Sep
Boraginaceae *Heliotropium crassavicum*	Jun	Oct	**Asteraceae**/ *Pulicaria dysenterica*	Jul	Oct
Brassicaceae *Isatis tinctoria*	Apr	Jul	**Brassicaceae** *Sisymbrium austriacum*	Apr	Aug
Buddlejaceae *Buddleja davidii*	Jun	Nov	**Cornaceae** *Cornus sanguinea*	May	Jul
Cactaceae					

Opuntia dilleni	Jun	Jul	**Rhamnaceae**/ *Rhamnus lycioides*	Mar	May
Opuntia ficus-indica	May	Jun	**Cistaceae**/ *Cistus albidus*	Feb	Jun
Caprifoliaceae					
Lonicera japonica	May	Sep	**Ranunculaceae**/ *Clematis vitalba*	Jun	Aug
Chenopodiaceae					
Achyranthes sicula	Mar	Jun	**Lamiaceae**/ *Marrubium vulgare*	Mar	Jul
Amaranthus blitoides	Apr	Dec	**Chenopodiaceae/** *Chenopodium murale*	Jan	Dec
Amaranthus hybridus	May	Dec	**Chenopodiaceae/** *Chenopodium vulvaria*	Apr	Oct
Amaranthus muricatus	Apr	Dec	**Malvaceae/** *Malva parviflora*	Mar	Aug
Amaranthus powelli	Jun	Nov	**Chenopodiaceae/** *Chenopodium opulifolium*	Mar	Nov
Amaranthus retroflexus	May	Dec	**Chenopodiaceae/** *Chenopodium album*	May	Nov
Amaranthus viridis	Apr	Dec	**Chenopodiaceae/** *Chenopodium chenopodioides*	Jul	Oct
Atriplex semibaccata	Sep	Oct	**Chenopodiaceae/** *Atriplex postrata*	Jul	Sep
Commelinaceae					
Tradescantia fluminensis	Mar	Sep	**Lamiaceae** *Glechoma hederacea*	Feb	Jun
Convolvulaceae					
Ipomoea acuminata	Jun	Nov	**Convolvulaceae/** *Calystegia sepium*	May	Sep
Ipomoea purpurea	Jun	Nov	**Rubiaceae/** *Galium aparine*	Mar	Jul
Ipomoea sagittata	Jun	Aug	**Ranunculaceae/** *Clematis flammula*	Apr	Aug
Cyperaceae			**Cyperaceae**		
Cyperus alternifolius	Jun	Sep	*Scirpus lacustris*	May	Jul
Elaeagnaceae			**Tamaricaceae**		
Elaeagnus angustifolia	May	Jul	*Tamarix canariensis*	Apr	Nov
Euphorbiaceae					
Chamaesyce polygonifolia	Jul	Nov	**Fabaceae**/ *Medicago littoralis*	Feb	Nov
Ricinus communis	May	Dec	**Solanaceae**/ *Lycium europaeum*	Sep	Oct
Fabaceae					
Acacia dealbata	Jan	Mar	**Betulaceae**/ *Betula alba*	Apr	May
Acacia longifolia	Mar	Jun	**Rosaceae/** *Pyrus cordata*	Apr	Jun
Acacia melanoxylon	Mar	Jun	**Rosaceae**/ *Malus communis*	Apr	Jun

Acacia saligna	Mar	May	**Fabaceae**/ *Ceratonia siliqua*	Sep	Jan
Gledistsia triacanthos	Mar	Jun	**Salicaceae/** *Populus alba*	Feb	Apr
Robinia pseudoacacia	Mar	Jul	**Ulmaceae**/ *Celtis australis*	Apr	May
Sophora japonica	Jun	Aug	**Ulmaceae**/ *Ulmus glabra*	Feb	Apr
Hydrocharitaceae			**Potamogetonaceae**		
Elodea canadensis	May	Aug	*Potamogeton densus*	Jul	Jul
Iridaceae			**Primulaceae**		
Tritonia x crocosmiflora	May	Aug	*Lysimachia nemorum*	Apr	Aug
Malvaceae			**Malvaceae**		
Abutilon theophrasti	Aug	Sep	*Malva neglecta*	Mar	Sep
Myrtaceae					
Eucalyptus camaldulensis	Jan	Dec	**Lauraceae**/ *Laurus nobilis*	Feb	Apr
Eucalyptus globulus	Oct	Jan	**Tiliaceae**/ *Tilia platyphyllos*	Jun	Sep
Nyctaginaceae			**Malvaceae**		
Mirabilis jalapa	Jun	Sep	*Malva sylvestris*	Jan	Oct
Onagraceae			**Apiaceae**		
Oenothera biennis	Jun	Sep	*Foeniculum vulgare*	Jun	Nov
Oenothera glazioviana	Jun	Sep	*Daucus carota*	Mar	Sep
Oxalidaceae			**Asteraceae**		
Oxalis pes-caprae	Sep	May	*Cirsium arvense*	Jun	Jul
Papaveraceae			**Papaveraceae**		
Eschscholzia californica	May	Oct	*Papaver rhoeas*	Feb	Sep
Passifloraceae			**Cannabaceae**		
Passiflora caerulea	Jun	Oct	*Humulus lupulus*	Jun	Sep
Poaceae					
Bromus wildenowi	May	Aug	**Poaceae**/ *Dactylis glomerata*	Mar	Jul
Cenchrus incertus	Jun	Sep	**Poaceae**/ *Lagurus ovatus*	Mar	Jul
Chloris gayana	Mar	Aug	**Poaceae**/ *Hyparrhenia hirta*	Jan	Dec
Echinochloa hispidula	Jul	Oct	**Cyperaceae**/ *Cyperus difformis*	Jun	Nov
Echinochloa oryzicola	Jul	Oct	**Cyperaceae/** *Scirpus mucronatus*	Jul	Sep
Echinochloa oryzoides	Jul	Oct	**Cyperaceae/** *Eleocharis palustris*	May	Aug
Eleusine indica	Jul	Oct	**Poaceae/** *Poa annua*	Jan	Jun
Paspalum dilatatum	Jul	Oct	**Cyperaceae/** *Scirpus holoschoenus*	May	Nov
Paspalum paspalodes	Jul	Sep	**Poaceae/** *Polypogon viridis*	Apr	Jun
Paspalum vaginatum	Jul	Sep	**Cyperaceae/**	Feb	Jun

			Carex divisa		
Sorghum halepense	May	Oct	**Poaceae/** *Piptatherum miliaceum*	Apr	Nov
Spartina patens	Jun	Sep	**Poaceae/** *Spartina maritima*	May	Jul
Stenotaphrum secundatum	Jul	Sep	**Poaceae/** *Cynodon dactylon*	Jan	Dec
Polygonaceae					
Fallopia baldschuanica	May	Oct	**Caprifoliaceae/** *Lonicera peryclimenum*	May	Aug
Reynoutria japonica	Aug	Sep	**Asteraceae/** *Eupatorium cannabinum*	Jul	Sep
Pontederiaceae			**Nymphaeaceae**		
Eichhornia crassipes	Mar	Jul	*Nymphaea alba*	Mar	Oct
Simaroubaceae			**Ulmaceae**		
Ailanthus altissima	May	Jul	*Ulmus minor*	Feb	Apr
Solanaceae					
Datura innoxia	May	Sep	**Boraginaceae/** *Heliotropium europaeum*	Mar	Nov
Datura stramonium	May	Nov	**Solanaceae**/ *Hyoscyamus albus*	Jan	May
Nicotiana glauca	Apr	Oct	**Celastraceae**/ *Maytenus senegalensis*	Jul	Sep
Solanum bonariense	Apr	Jul	**Solanaceae**/ *Solanum dulcamara*	Jul	Sep
Tropaeolaceae			**Urticaceae**		
Tropaeolum majus	May	Sep	*Urtica dioica*	Apr	Sep
Verbenaceae			**Verbenaceae**		
Lippia filiformis	Jun	Sep	*Verbena officinalis*	Jun	Oct
Zygophyllaceae			**Chenopodiaceae**		
Zygophyllum fabago	Jun	Aug	*Atriplex rosea*	Jul	Sep

Cape region

Agavaceae			**Asphodelaceae**		
Agave americana	Dec	Mar	*Aloe ferox*	May	Nov
Agave sisalana	Dec	Mar	*Aloe lineata*	Feb	Mar
Apocynaceae			**Apocynaceae**		
Araujia sericifera	Nov	Apr	*Cynachum obtusifolium*	Jan	Dec
Nerium oleander	Sep	Mar	*Carissa haematocarpa*	Jan	Apr
Araceae			**Potamogetonaceae**		
Pintia stratoites	Feb	May	*Potamogeton pectinatus*	Oct	Jan
Asteraceae			**Asteraceae**		
Ageratina adenophora	Aug	Dec	*Arctotheca calendula*	Jul	Nov
Cirsium vulgare	Sep	Apr	*Foveolina tenella*	Jun	Sep
Xanthium spinosum	Oct	Apr	*Senecio arenarius*	Jul	Sep
Xanthium strumarium	Oct	Apr	*Senecio elegans*	Sep	Nov

Boraginaceae			**Boraginaceae**		
Echium plantagineum	Sep	Mar	*Cynoglossum hispidum*	Oct	Nov
Brassicaceae			**Asteraceae**		
Rorippa nasturtium-aquaticum	Sep	Mar	*Cadiscus aquaticus*	Aug	Sep
Cactaceae			**Asphodelaceae**		
Pereskia aculeata	Mar	Jul	*Aloe lineata*	Feb	Mar
Cereus jamacaru	Nov	Jan	*Aloe plicatilis*	Aug	Oct
Opuntia ficus-indica	Oct	Dec	*Aloe africana*	Jul	Sep
Opuntia monocantha	Oct	Apr	*Aloe arborescens*	May	Jun
Cannaceae			**Iridaceae**		
Canna indica	Sep	Apr	*Chasmanthe aethiopica*	Apr	Jun
Cheponodiaceae			**Cheponodiaceae**		
Achyrantes aspera	Dec	Mar	*Pupalia lappacea*	Dec	Apr
Salsola kali	Sep	Nov	*Sericocoma avolans*	Jan	Apr
Atriplex nummularia	Sep	Jan	*Manochlamys albicans*	Sep	Jan
Clusiaceae			**Clusiaceae**		
Hypericum perforatum	Oct	Jan	*Hypericum lalandii*	Nov	Mar
Convolvulaceae			**Convolvulaceae**		
Convolvulus arvensis	Dec	Feb	*Convolvulus ulosepalus*	Dec	May
Ipomoea purpurea	Oct	Dec	*Convolvulus capensis*	Sep	Oct
Euphorbiaceae			**Euphorbiaceae**		
Ricinus communis	Jan	Dec	*Jatropha capensis*	Nov	Jan
Fabaceae			**Fabaceae**		
Alhagi maurorum	Oct	Nov	*Asphalatus rostrata*	Sep	Nov
Spartium junceum	Aug	Nov	*Lebeckia cytisoides*	Jul	Mar
			Polygalaceae/		
Prosopis glandulosa	Jun	Nov	*Muraltia heisteria*	Oct	Dec
Robinia pseudoacacia	Sep	Dec	*Psoralea floccosa*	Sep	Sep
Acacia cyclops	Oct	May	*Acacia caffra*	Dec	Mar
Acacia saligna	Aug	Oct	*Acacia karroo*	Nov	Dec
Lamiaceae			**Lamiaceae**		
Plectranthus comosus	Mar	Sep	*Plectranthus fruticosus*	Nov	Apr
Malvaceae			**Malvaceae**		
Lavatera arborea	Sep	Nov	*Abutilon sonneratianum*	Nov	Jan
Myoporaceae			**Asteraceae**		
Myoporum tenuifolium	Jul	Oct	*Brachylaena neriifolia*	Jan	Mar
Myrtaceae					
Eucalyptus camaldulensis	Sep	Jan	**Cunoniaceae**/ *Cuconia capensis*	Dec	Feb
Leptospermum laveigatum	Jul	Oct	**Cunoniaceae**/ *Platylophus trifoliatus*	Dec	Feb
Metrosideros excelsa	Sep	Jan	**Myrtaceae**/ *Metrosideros angustifolia*	Dec	Feb
Onagraceae			**Onagraceae**		
Oenothera biennis	Sep	Apr	*Epilobium capense*	Dec	Mar

Orobanchaceae			**Orobanchaceae**		
Orobanche minor	Aug	Nov	*Hyobanche sanguinea*	Aug	Oct
Passifloraceae			**Ranunculaceae**		
Passiflora caerulea	Aug	Mar	*Clematis brachiata*	Dec	May
Phytolaccaceae			**Aquifoliaceae**		
Phytolacca dioica	Sep	Dec	*Ilex mitis*	Sep	Dec
Pittosporaceae			**Pittosporaceae**		
Pittosporum undulatum	Aug	Sep	*Pittosporum viridiflorum*	Nov	Dec
Poaceae	Jan	Mar	**Poaceae**		
Arundo donax	Feb	Apr	*Phargmites australis*	Feb	May
Cortaderia selloana	Aug	Jan	*Miscanthus capensis*	Dec	May
Pennisetum clasdestinum	Nov	Jul	*Trachypogon spicatus*	Oct	May
Pennisetum setaceum	Sep	Dec	*Andropogon appendiculatus*	Oct	Apr
Aira cupaniana	Sep	Jan	*Ehrharta calycina*	Jul	Dec
Bromus diandrus	Jul	Nov	*Aristidia congesta*	Dec	May
Bromus pectinatus	Nov	May	*Aristidia adcensionis*	Dec	Sep
Chloris gayana	Jun	Jul	*Sporobolus africanus*	Oct	Apr
Chloris truncata	Nov	Jun	*Chaetobromus dregeanus*	Sep	Nov
Digitaria abyssinica	Oct	Dec	*Digitaria argyrograpta*	Nov	Mar
Hordeum murinum	Oct	Dec	*Hordeum capense*	Nov	Dec
Lolium perenne	Sep	Jan	*Pentachistis aspera*	Sep	Dec
Lolium rigidum	Sep	Jan	*Stipa capensis*	Aug	Nov
Phalaris minor	Jan	Dec	*Panicum repens*	Oct	Jun
Poa annua	Sep	Apr	*Poa bulbosa*	Aug	Oct
Polypogon monspeliensis	Sep	Jan	*Schismus pleuropogon*	Nov	Nov
Polypogon viridis	Jan	Mar	*Stenotaphrum secundatum*	Oct	Jan
Pontederiaceae			**Nymphaeaceae**		
Eichhornia crassipes	Nov	Apr	*Nymphaea nouchali*	Dec	Mar
Proteaceae			**Proteaceae**		
Hakea gibbosa	Jun	Sep	*Diastella divaricata*	Jan	Dec
Hakea drupacea	May	Jun	*Diastella thymelaeoides*	Aug	Nov
Hakea sericea	Jun	Oct	*Brabejum stellatifolium*	Dec	Jan
Rosaceae					
			Rosaceae/		
Pyracantha angustifolia	Sep	Dec	*Rubus rigidus*	Oct	Feb
			Rosaceae/		
Rubus fruticosus	Sep	Jan	*Rubus pinnatus*	Nov	Feb
			Kiggelariaceae/		
Eriobotria japonica	May	Jun	*Kiggelaria africana*	Feb	Jul
			Icacinaceae/		
Cotoneaster franchetii	Aug	Jan	*Cassinopsis ilicifolia*	Sep	Nov
Salicaceae			**Salicaceae**		
Salix babilonica	Aug	Oct	*Salix mucronata*	Sep	Oct
			Flacourtiaceae/		
Populus x canescens	Sep	Dec	*Scolopia mundii*	Nov	Dec
Solanaceae					

			Boragineaceae/		
Datura stramonium	Oct	Mar	*Trichodesma africanum*	Jul	Oct
			Celastraceae/		
Nicotiana glauca	Aug	Mar	*Maytenus oleoides*	Apr	Sep
			Solanaceae/		
Solanum mauritianum	May	Jul	*Solanum aculeastrum*	Mar	Oct
Solanum			**Solanaceae/**		
pseudocapsicum	Oct	Jan	*Solanum giganteum*	Dec	Apr
			Celastraceae/		
Nicotiana glauca	Aug	Mar	*Maytenus oleoides*	Apr	Sep
Verbenaceae			**Plumbaginaceae**		
Lantana camara	Sep	Apr	*Plumbago auriculata*	Dec	May