

Functional analysis of the newly established plants induced by nesting gulls on Riou archipelago (Marseille, France)

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Abstract – The recent population explosion of Yellow-legged gulls (*Larus cachinnans*), nesting on the Riou archipelago, off Marseille (France), has perturbed the flora and the vegetation of this site. The present study consists of a functional approach to the newly established plant species through an analysis of some of their vital attributes. Small islets appear to be more affected by floristic turnover than larger islands. In some cases, more than 50 % of the current flora was not present 35 years ago. The newly established taxa show special adaptations to the severe ecological pressure induced by gull colonies and to the characteristics of the Mediterranean climate. These plant species are mostly therophytes or hemicryptophytes and have a ruderal or a stress-tolerant strategy. Gulls' contribution to propagule dispersal from the continent appears to be very slight, dispersal by wind being the prevalent mode. © Elsevier, Paris

Disturbances / Mediterranean islands / SE France / floristic turnover / *Larus cachinnans* / life-history attributes / growth forms / dispersal / CSR strategy

1. INTRODUCTION

Insular systems have often been found to be very vulnerable to various disturbances, especially anthropogenic ones which frequently involve some spectacular ecological imbalances and first order invasions [1, 11, 34]. If these phenomena are particularly acute on islets due to the reduction of species diversity in communities and biotic interactions [26, 57], they can also affect large islands like Madagascar [19], the Réunion [36] or New Zealand [54].

The insularity enhances the fragility of these environments whose intrinsic resilience is largely restricted by biological simplicity and specificity [5], by reduced dispersal in island plant populations, and maybe by the rarity of redundant species [9, 12].

Islands often house large seabird colonies which benefit from the tranquility necessary to accomplish their nesting cycle. The perturbations induced by these colonies on vegetation has been studied on several islands, notably in Great Britain [17, 52] and Brittany [3, 4], but also in the southern hemisphere [15], especially subantarctic islands [e.g. 28, 48, 51]. However, very few works connected with this issue have consid-

ered the Mediterranean biota. Nevertheless, Gillham [18] studied the alteration of the breeding habitat by seabirds in the Mediterranean south-west Australian islands. Although the effects of colonial seabirds on the vegetation of the Mediterranean basin are sometimes mentioned [6, 7, 32, 42], they have not been thoroughly studied from the point of view of functional features.

Bird activities have several direct and indirect effects on vegetation [3, 18]. First, we can distinguish physical effects, such as trampling, sitting, digging, pulling-up; secondly, chemical effects due to guano manuring and bringing in nitrogenous, phosphorated and potassium compounds [17, 27, 48, 49, 50, 51]. Moreover, the degradation of the vegetation and the creation of stripped areas favours erosive phenomena on nesting sites, particularly under a Mediterranean bioclimate with violent rainfalls. The stripping can prove irreversible, inhibiting ecosystem resilience [23]. Lastly, changes in floristic composition, notably by the expansion of alien species and the disappearance of indigeneous species, can produce deep ecological disruptions within the original phytocenosis.

In spite of both its isolated location and its being part of the 'Conservatoire de l'espace littoral et des rivages lacustres', the Riou archipelago, which is of very high biological interest, is suffering from drastic perturbations directly explainable by its peri-urban situation. In fact, the establishment of a number of open-air refuse dumps on the outskirts of Marseille has resulted in a population explosion of Yellow-legged gulls (*Larus cachinnans*) on the Riou archipelago [56]. This gull species is an anthropophilous and opportunistic bird which has experienced a very strong demographic increase in most parts of the Mediterranean basin for some thirty years, particularly on the northern shore [47, 53, 58]. Showing a large dietary plasticity, this species efficiently exploits refuse and trawling discards [2, 10]. Such an easily reached daily food supply allows greater survival of immature birds and provides extra food for breeding adults, often resulting in population explosion [33].

Our original hypothesis was that the environmental perturbation caused by the gull population explosion is closely linked with the establishment of new plant species. This work represents a functional analysis of the ecological features of these newly established taxa, and we will particularly investigate the following points:

i) What proportion is made up by these new taxa in each islet's and island's plant diversity?

ii) Do these species show special adaptations (life strategies, growth forms, etc.) to the harsh living conditions induced by gull activities?

iii) Are the seeds of newly introduced taxa specifically adapted to gull-dispersal, making their immigration easier from the continent or from larger islands?

iv) Is the situation identical for all the islets and islands or does it vary from case to case? We will particularly examine the latter point with reference to island size.

v) What is different in the Mediterranean basin as compared to the Atlantic, Subantarctic and SW Australia ?

2. METHODS

2.1. Study area and data collection

This study has been conducted on the Riou archipelago, located to the south of the city of Marseille (south-east France) in the Mediterranean Sea. This uninhabited archipelago comprises four main islands (Riou, Maire, Jarre and Plane) each > 15 ha and four islets (Jarron, Tiboulén, Grand Congloué and Petit Congloué) < 3 ha; altogether, there are approximately 160 ha of emerged land (figure 1), with the highest point at 191 m. The climate on the archipelago is harsh: rainfall is about 350 mm.year⁻¹, there are more

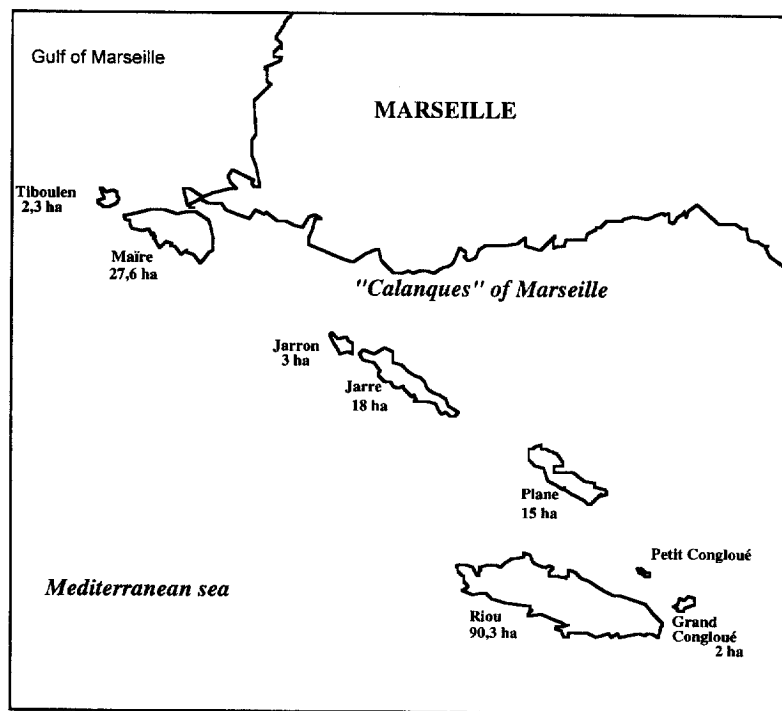


Figure 1. Map of the Riou archipelago (south-east France).

than 180 sunny days and 200 days of high wind per year, and diurnal variation in temperature is very high.

The notable studies of Knoerr [30, 31] provide a detailed plant species inventory for the archipelago. Made before seabird perturbation could have an effect on vegetation patterns, these inventories can be considered as a baseline reference state (when disturbance was very weak). When compared to the present state, they allow us to assess the ecological drift (i.e. floristic changes) which the vegetation has undergone in the last 35 years under gull pressure.

In 1995 and 1996, we drew up new plant inventories on every island in the archipelago. Plant nomenclature follows Kerguelen [29]. In this present study, the Petit Congloue islet has not been taken into account because Knoerr did not study this islet. Nevertheless, we must emphasize that all plant censuses are affected by sampling errors owing to the difficult topography and the relatively large dimensions of the four main islands. So, floristic turnover is rather a pseudo-turnover [40, 46].

2.2 Functional analysis

For each new taxon, two main life-history attributes have been considered: growth form and means of dispersal. Thus, growth forms are sometimes considered as functional types [13]. Additionally, we have analysed the data according to Grime's functional classification system [20–22] which is intermediate between the data-analysis approach and the determinist approach of functional types methods [41].

The Mediterranean Institute for Ecology and Paleoecology floristic databank [37], together with additional published data, were used to determine the value for the three attributes.

2.2.1. Growth forms

Following the classification of Raunkiaer [45] amended by Ellenberg and Mueller-Dombois [16], eight main categories have been considered: phanero-

phytes (Ph), chamaephytes (Ch), hemicryptophytes (H), biannual hemicryptophytes (Hb), geophytes (G), therophytes (Th), nanophanerophytes (NPh) and lianas (L).

2.2.2. Means of seed dispersal

Seed dispersal of the new species has been considered under five headings [55]: dispersal by wind, by animals (birds), by water, auto dispersal, and no special device dispersal. Only the prevalent mode of propagules dispersal has been taken into account. However, in order to thoroughly study dispersal by animals, we separate endozoochory from epizoochory.

2.2.3. The Grime CSR model

According to Grime [20–22], each plant species is associated with a strategy which can be defined by a combination of interspecific competition, disturbance and stress. Ruderal species (R), living in frequently disturbed habitats, show a high growth rate, a short life cycle and copious seed production. Competitive species (C) present high vegetative development, ecological plasticity and, sometimes, some allelopathic potential. Stress-tolerant species (S) can be encountered in harsh habitats characterized by very ephemeral and unpredictable resources. Moreover, four intermediate strategies have been taken into account: competitive-ruderal (CR), competitive-stress tolerant (CS), stress tolerant-ruderal (SR) species, and lastly the CSR strategy associated with a moderate environment. Plant characteristics taken into account for classification within the CSR model were, in particular, morphology of shoot, life-form, phenology, seed production and longevity of leaves [21, 38, 43].

3. RESULTS

3.1. Plant diversity

The severe pressure brought by gulls on the vegetation has led to the pronounced decline of some coastal plant communities and to the disappearance of some plant species (*table I*): from 21 % for Tiboulén, to 37 % for Plane, of the 1960 flora. Nevertheless, with

Table I. Number and part of the extinct 1960's plant species for each island and islet in the Riou archipelago. (Islands are placed according to decreasing area).

Islands	Number of taxa	%
Riou	51	26.7
Maïre	47	30.5
Jarre	30	25.9
Plane	30	36.6
Jarron	13	31.0
Tiboulén	8	21.1
Grand Congloue	8	25.8

Table II. Number and part of newly established plant species for each island and islet in the Riou archipelago.

Islands	Number of taxa	%
Riou	37	21.8
Maïre	23	19.5
Jarre	38	30.7
Plane	26	32.9
Jarron	32	52.5
Tiboulén	18	38.3
Grand Congloue	14	35.9

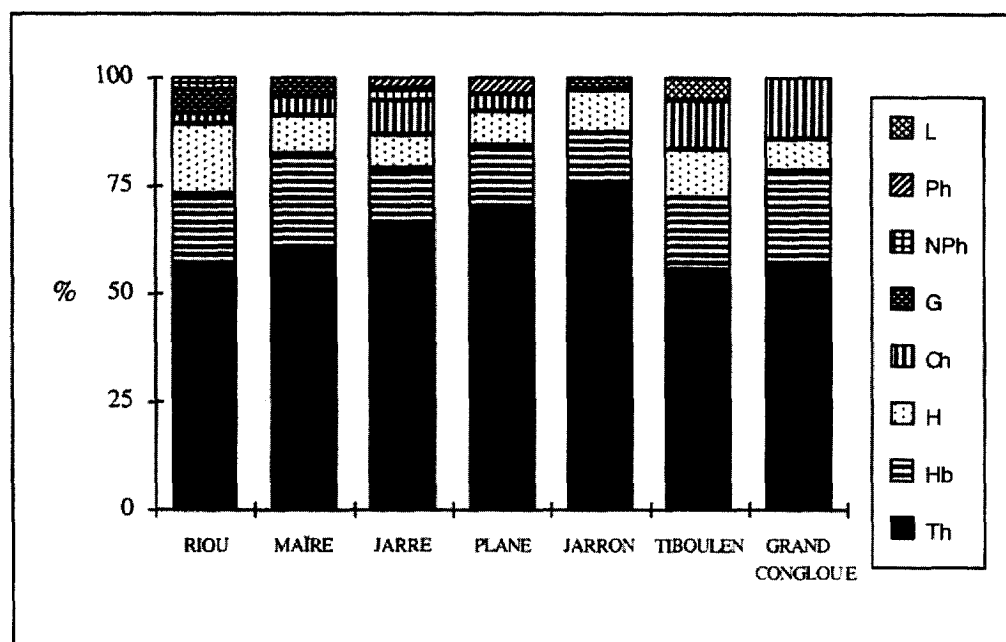


Figure 2. Distribution of growth forms within the newly established plant species. Th: therophytes; Hb: biannual hemicryptophytes; H: hemicryptophytes; Ch: chamaephytes; G: geophytes; NPh: nanophanerophytes; Ph: phanerophytes; L: lianas. (Islands are placed according to decreasing area).

regard to Knoerr's inventories, it also appeared that the number of newly established species sometimes exceeds the losses, leading to a species enrichment (unpubl. data). The proportion made up by the new taxa in the current plant diversity appreciably differs from one island to another (table II) and varies from 19.5 % (Maïre) to 52.5 % (Jarron). In other words, more than half of the current plant species on Jarron were not present 35 years ago on this island. It also appears that this proportion is generally higher on small than on large islands.

3.2. Growth forms

Whichever island is considered (figure 2), therophytes are largely dominant among the new plant species (53.6 to 75.0 %), versus other growth forms: biannual hemicryptophytes (12.5–21.7 %), hemicryptophytes (7.1–16.2 %) and chamaephytes (0–14.2 %). The remaining growth forms are always represented by less than 5 % of the total plant species. Also, growth form diversity is always higher on islands (5–6 growth forms) than on islets (4–5 growth forms).

3.3. Plant dispersal

Dispersal by wind is prevalent (50.0–65.6 %) when compared to other modes (figure 3): birds (13.0–27.8 %), no special device (8.1–28.6 %), water (0–13.5 %) and auto-dispersal (0–5.5 %). It is worth

noting that water is an important mean of dispersal only for the three largest islands.

We have subdivided dispersal by animals into endozoic (endo) and ectozoic (ecto) dispersal (table III). Ectozoic dispersal is weakly prevalent over endozoic dispersal (11.1 % and 7.8 % respectively). Nevertheless, endozoic dispersal prevails over ectozoic dispersal on larger islands (except Plane) in contrast to islets where the situation is reversed.

3.4. Grime CSR strategies

Figure 4 presents the distribution of the Grime strategies for the newly established plant species. With two exceptions (Riou and Jarre), the SR (stress tolerant/

Table III. Distribution of endozoic and ectozoic dispersal within the newly established plant species for each island and islet in the Riou archipelago.

Islands	% Endozoic	% Ectozoic
Riou	13.5	5.4
Maïre	8.7	4.4
Jarre	10.5	5.3
Plane	7.7	15.4
Jarron	3.1	9.4
Tiboulen	11.1	16.7
Grand Congloue	0	21.4

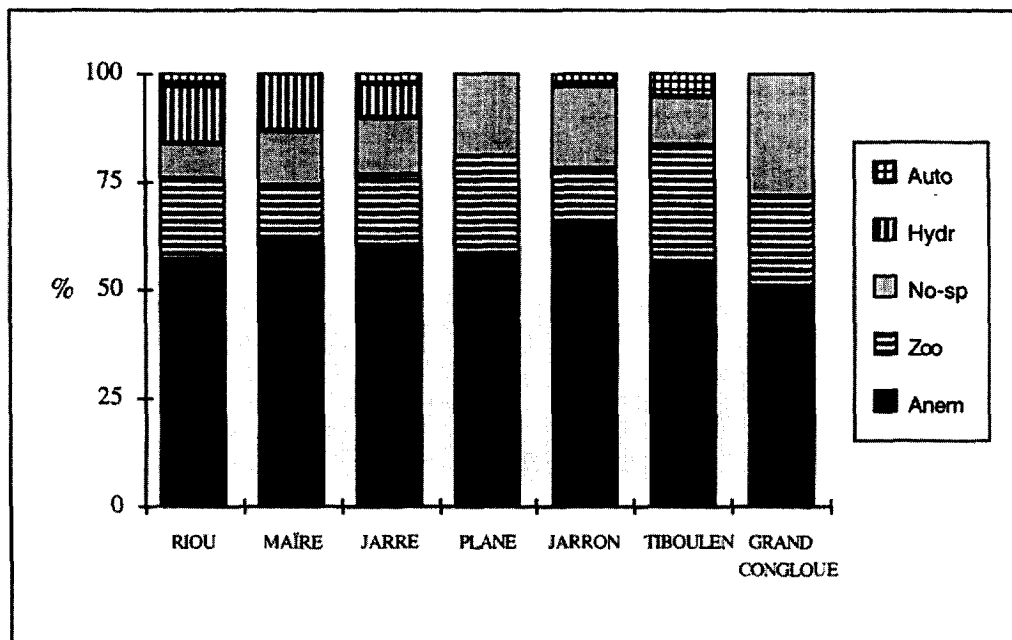


Figure 3. Distribution of principal means of dispersal within the newly established plant species. Anem: anemochory; Zoo: zoochory; No-sp: no special device; Hydr: hydrochory; Auto: autochory.

ruderal) intermediate strategy dominates (26.3 to 52.1 %). Then, in descending order of importance, the other strategies are R (21.9 to 40.5), S (5.6 to 18.4), CR (0 to 15.8) and SC (0 to 5.6). C and CSR strategies are not represented within the newly established taxa. The seven Grime strategies can be simplified in order to obtain only three main strategies: ruderal (R) strategy sensu lato (R+SR+CR), stress tolerance strategy (S) sensu lato (S+SR+SC), competition strategy (C) sensu lato (C+SC+CR). When this simplification is applied on the newly established taxa, it appears that, whichever island is considered, the R strategy sensu lato (76.3 to 88.9 %) largely rules over the S strategy (50 to 69.5 %).

4. DISCUSSION

Seabirds are the cause of an important deposition of guano and nest material [8, 25, 28] which often permits the establishment of a permanent vegetation on unvegetated rocky zones and cobble shores. Therefore, gulls colonies have heavier consequences on habitat heterogeneity and diversity on small islets (< 3 ha) compared to larger ones. Without them, these islets often allow only the presence of rock plants [37, 57]. By contrast, the original habitat diversity and the pres-

ence of disturbed areas on the largest islands mitigate the impact of such ornithogenic perturbations.

Monocarpic herbaceous species (therophytes and biannual hemicryptophytes) correspond to an adaptive strategy [14] related to stress induced by the unpredictability of the Mediterranean climate [24] and to harsh disturbances [21, 22]. These two growth forms are strongly represented among newly established species because of their resistance to the severe ecological conditions which dominate on this archipelago, notably the pressures induced by seabirds [25, 52]. According to Quézel et al. [44], therophytes are also the prevailing growth form of invasive plants in the entire Mediterranean basin.

Wind is the most important mean of dispersal for the newly established plants. This is probably due to the very windy character of the Marseille region which is often swept by a very strong north-westerly wind. This prevalent wind pattern often puts the archipelago leeward of the Marseille coastline (see figure 1). The slight contribution of Yellow-legged gulls to propagule dispersal differs from conclusions obtained with Ring-billed *Larus delawarensis* colonies in the Great Lakes region in Canada [25, 39] and is probably the result of different feeding habits. For example, *Larus cachinnans* is an exclusively flesh-eating bird whereas *Larus delawarensis* is omnivorous and consumes large num-

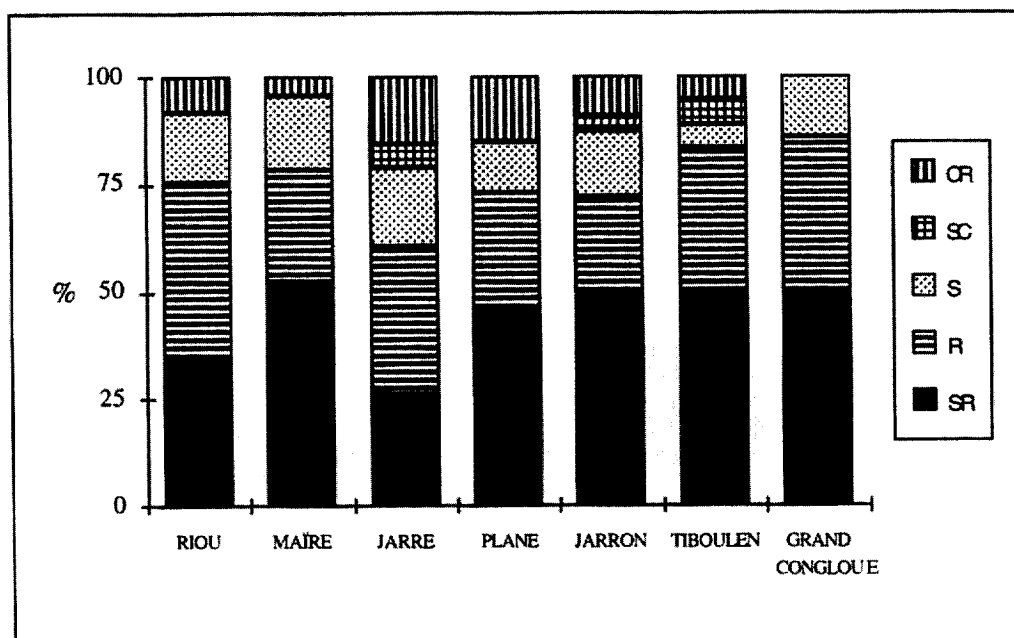


Figure 4. Distribution of demographic strategies within the newly established plant species. SR: stress-ruderal; R: ruderal; S: stress; SC: stress-competition; CR: competition-ruderal.

bers of seeds and fruits. Actually, the Yellow-legged gull is capable only of ectozoic dispersal. Thus, the endozoic dispersal is probably due to passerines which frequently visit the archipelago during their migration across the Mediterranean. The islands attracting passerines, which also are the largest in the archipelago (Riou, Jarre, Maïre), have a prevalent endozoic dispersal. It appears to be the other way round on islets where the rarity of passerines reduces the establishment of plants endozoically dispersed (Jarron, Tiboulen, Grand Congloue).

Very roughly, the distribution of the seven Grime demographic strategies follows similar patterns for each island, with a prevalence for the intermediate SR strategy (stress tolerance-ruderal). On this particular point, our results are in accord with Médail's [37] who studied 14 islands from Hyères archipelago, 80 km east of Riou. These results illustrate the two main components of the ecological pressure dominant in these insular systems: a constraining Mediterranean climate and the combination of various perturbations (gulls, polluted sea-sprays, etc.). Nevertheless, unlike the conclusions for Hyères archipelago drawn by Médail [37], the sensu lato stress strategy (S+SR+SC) does not prevail on Riou islands while sensu lato ruderal strategy (R + SR + CR) does. Thus, we can come to the conclusion that the ecological pressure dictated by gull activities has a more important influence on

Riou vegetation patterns than the bioclimatic features themselves. The prevalence of alien ruderal species in the nesting sites corresponds to what other authors have reported [8, 15, 52] and probably is a symptomatic manifestation of the strong environmental changes which have affected this archipelago recently.

This study illustrates the effect of island size on the functional patterns (notably the dispersal) and on the diversity of the newly established plant species. As a matter of fact, below a certain threshold-area, islets are subject to an important variability in their environmental conditions, which is able to destroy their phytocenosis. This phenomenon, sometimes called 'small-islands effect' [35], has already been shown for other French Mediterranean islands [37].

At present, the Yellow-legged gull population of the Riou archipelago, which reached 14 000 nesting pairs in 1995 (unpubl. data), represents 30 % of the entire French population of this species [58] making this site its most important French colony. The high nest density, which locally exceeds 250 pairs per ha, endangers the flora (16 protected species, some of which are of a high biogeographical interest, such as *Asplenium sagittatum*, *Galium minutulum*, *Stachys brachyclada* or *Teucrium polium* subsp. *purpurascens*). So we clearly need to tackle insular biogeography through a functional approach and not only through general specific

diversity concepts. Only such an integrated analysis can allow us to accurately perceive disfunction in insular flora and determine adequate management measures in terms of space-time levels for ecological intervention.

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Appendix

New species	Riou	Maïre	Jarre	Plane	Jarron	Tiboulén	Grand Congloue
<i>Allium acutiflorum</i>					X		
<i>Amaranthus albus</i>			X				
<i>Amaranthus deflexus</i>	X		X				
<i>Amaranthus retroflexus</i>	X						
<i>Anagallis arvensis</i>					X		
<i>Anthemis secundiramea</i>			X				
<i>Arenaria leptoclados</i>				X			
<i>Artemisia annua</i>			X				
<i>Arum cf. italicum</i>	X						
<i>Atriplex prostrata</i>					X		
<i>Avena barbata</i>					X		
<i>Beta vulgaris</i> subsp. <i>maritima</i>	X						
<i>Brachypodium retusum</i>					X		
<i>Brassica oleracea</i>	X						
<i>Bromus diandrus</i> subsp. <i>diandrus</i>			X				
<i>Bromus madritensis</i>					X	X	
<i>Bromus rubens</i>					X		
<i>Cakile maritima</i>		X					
<i>Camphorosma monspeliaca</i>		X	X				X
<i>Capsella rubella</i>		X	X	X			
<i>Cardaria draba</i>			X				
<i>Carduus tenuiflorus</i>				X	X		
<i>Catapodium maritimum</i>					X		
<i>Centaurea solstitialis</i>	X						
<i>Centranthus calcitrapa</i>		X					
<i>Cerastium semidecandrum</i>	X						
<i>Chenopodium murale</i>			X	X		X	
<i>Chenopodium rubrum</i>			X		X		
<i>Conyza</i> sp.				X			
<i>Crepis leontodontoides</i>	X						
<i>Crepis sancta</i> subsp. <i>nemausensis</i>	X	X					
<i>Dianthus sylvestris</i> subsp. <i>longicaulis</i>			X				
<i>Ecballium elaterium</i>	X						
<i>Echium vulgare</i> subsp. <i>pustulatum</i>							X
<i>Erica multiflora</i>			X				
<i>Erodium chium</i>					X		X
<i>Erodium cicutarium</i>		X	X		X	X	
<i>Erodium malacoides</i>			X				
<i>Eryngium campestre</i>	X						
<i>Foeniculum vulgare</i>	X						
<i>Frankenja hirsuta</i>				X	X	X	X
<i>Fumaria capreolata</i>	X			X			X
<i>Galium</i> gr. <i>lucidum</i>		X					
<i>Galium murale</i>	X		X				
<i>Geranium molle</i>				X	X	X	X
<i>Geranium rotundifolium</i>					X	X	
<i>Hedypnois rhagadioloides</i>		X					
<i>Heliotropium europaeum</i>			X	X			
<i>Hordeum murinum</i> subsp. <i>leporinum</i>				X	X	X	X
<i>Hornungia petraea</i>			X		X		
<i>Hymenolobus procumbens</i> subsp. <i>revelieri</i>				X	X		
<i>Hyoscyamus albus</i>		X		X		X	
<i>Hyoseris radiata</i>		X					
<i>Lactuca viminea</i> subsp. <i>ramossima</i>			X				
<i>Lactuca</i> cf. <i>virosa</i>			X				

Appendix. Continued.

New species	Riou	Maïre	Jarre	Plane	Jarron	Tiboulén	Grand Congloue
<i>Lagurus ovatus</i>					X		
<i>Lamium purpureum</i>	X						
<i>Limonium virgatum</i>			X				
<i>Lobularia maritima</i>						X	
<i>Lotus edulis</i>						X	
<i>Lycopersicon esculentum</i>	X		X				
<i>Malva neglecta</i>	X						
<i>Malva parviflora</i>	X						
<i>Malva sylvestris</i>	X	X	X				
<i>Medicago minima</i>				X			X
<i>Medicago polymorpha</i>				X			
<i>Nauplius aquaticus</i>		X	X				
<i>Nicotiana glauca</i>				X			
<i>Opuntia vulgaris</i>	X						
<i>Papaver rhoeas</i>	X		X	X			
<i>Parietaria judaica</i>					X		
<i>Picris echioides</i>					X		
<i>Plantago coronopus</i>	X					X	
<i>Plantago lanceolata</i>			X				
<i>Poa annua</i>	X		X	X			
<i>Poa infirma</i>	X						
<i>Poa trivialis</i>				X			
<i>Polycarpon tetraphyllum</i> subsp. <i>alsinifolium</i>			X				
<i>Polygonum aviculare</i> s.l.		X					
<i>Portulaca oleracea</i> s.l.	X	X	X	X	X	X	
<i>Raphanus raphanistrum</i>					X		
<i>Rapistrum rugosum</i> subsp. <i>orientale</i>	X		X		X		
<i>Reseda alba</i>	X						
<i>Rhamnus alaternus</i>			X				
<i>Sagina maritima</i>	X						
<i>Sedum caespitosum</i>	X	X	X	X	X		X
<i>Sedum litoreum</i> subsp. <i>litoreum</i>				X	X		
<i>Senecio vulgaris</i>	X						
<i>Silybum marianum</i>	X						
<i>Sisymbrium irio</i>			X		X		
<i>Smilax aspera</i>						X X	X
<i>Solanum nigrum</i> s.l.	X	X	X	X			
<i>Sonchus asper</i> subsp. <i>asper</i>						X	X
<i>Sonchus oleraceus</i>		X			X	X	X
<i>Sonchus tenerrimus</i>	X	X		X	X	X	X
<i>Spergularia bocconeii</i>	X						
<i>Stellaria media</i>		X			X		
<i>Stellaria pallida</i>	X		X				
<i>Suaeda splendens</i>		X	X	X			
<i>Suaeda vera</i>				X		X	X
<i>Teucrium flavum</i>			X				
<i>Umbelicus rupestris</i>	X	X					
<i>Urospermum picroides</i>		X	X		X		
<i>Urtica urens</i>			X	X			
<i>Veronica persica</i>	X						
<i>Vincetoxicum hirundinaria</i>		X			X		