

ON THE ECOLOGY OF *COTULA CORONOPIFOLIA* L. AND *RANUNCULUS SCELERATUS* L.

I. GEOGRAPHIC DISTRIBUTION, HABITAT, AND FIELD OBSERVATIONS

J. VAN DER TOORN

Instituut voor Oecologisch Onderzoek, Kemperbergerweg 67, 6816 RM Arnhem

SUMMARY

The literature on the geographic distribution and the habitat of *Cotula coronopifolia* L. and *Ranunculus sceleratus* L. is reviewed, and observations on the population development of these species during their colonization of Zuid Flevoland, a new polder in The Netherlands, are reported. A discussion is also given of some ecological characteristics indicating that *C. coronopifolia*, a neophyte in Europe and introduced from southern Africa, is less adapted to its habitat than *R. sceleratus*, which explains the ephemeral behaviour of the former species.

I. INTRODUCTION

The genus *Cotula* (Compositae) comprises usually low-creeping species with small and predominantly yellow heads composed of tubular flowers. The approximately 80 species are distributed mainly over the southern hemisphere. *Cotula coronopifolia* presumably originated from South Africa, and was spread by man along the coasts of the Atlantic and Pacific oceans.

In N.W. Europe, where the species was introduced as early as 1739, colonization resulted in a sparse distribution. Nevertheless, it can be considered a neophyte, because of its occurrence in natural plant communities (SUKOPP 1962). This situation raises several questions, for instance: how could this subtropical species spread and maintain itself as a neophyte under the adverse climatic conditions of N.W. Europe? And what is the reason for its sparse distribution pattern compared to other neophytes?

As stated by HARPER (1965), "The biology of unsuccessful aliens is important in understanding the equipment of success". *Cotula coronopifolia* seems particularly interesting in this context, because it is difficult to reconcile its being a neophyte with its history as a not wholly successful colonist. For this reason we decided, when this species was found in 1972 in Zuid Flevoland, a recently reclaimed polder in the IJsselmeer (fig. 1A), to follow the further course of its colonization in this area. The studies were supplemented with experiments concerning its germination, seed longevity, life cycle, and seed dispersal. In these experiments *Ranunculus sceleratus* was used as a reference species. *R. sceleratus* is

native in Europe and can be considered a well-adapted species. It is – at least partially – comparable with *C. coronopifolia* as to life cycle and habitat, because in Western Europe both species are annual pioneers of bare, wet, and nutrient-rich mud. This was the case in Zuid Flevoland, where the population development during the colonization stage was followed. However, direct comparison between the two species was not possible in this area, because their colonization did not occur simultaneously.

In this paper the field observations are described, and a short review of the literature on the geographic distribution and the habitat is given. The experiments will be reported in subsequent papers (VAN DER TOORN & TEN HOVE; in prep.).

2. METHODS

The fields observations were restricted to the Zuid Flevoland area. At the start (in 1968), the soil of this polder consisted of mud with large amounts of mineral nitrogen (VAN SCHREVEN 1965) and small amounts of sodium chloride (c. 1 g NaCl per litre soil moisture).

The colonization by *C. coronopifolia* (to be further referred to as *Cotula*) took place, a few years after reclamation, in the marsh area called Oostvaardersplassen (figs. 1A and 3). In this area there was no drainage of rain water, and as a result shallow pools (with depths to about 0.5 m) formed and a natural vegetation arose (consisting chiefly of *Phragmites australis* and *Typha* spp.). In 1972, *Cotula* appeared in a zone bordering these pools. Its further spread over the whole area was followed between 1973 and 1976 (see fig. 3).

Seed output was estimated by repeated sampling of marked plants (10 individuals). During each sampling the ripe fruiting heads were counted, clipped

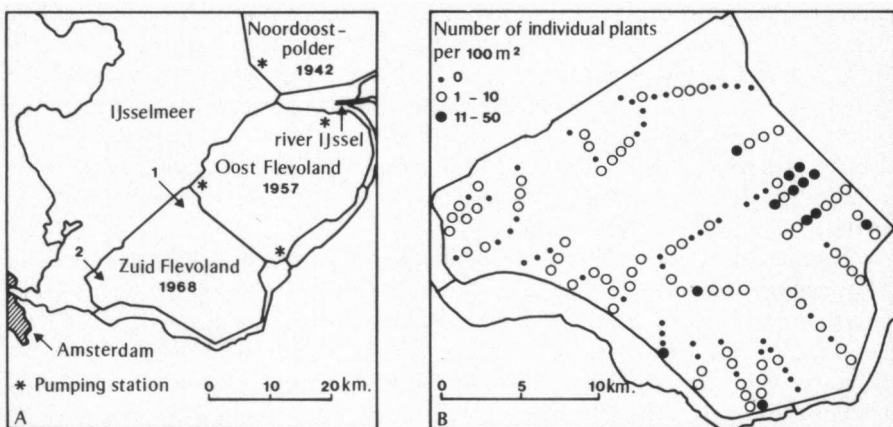


Fig. 1. A. Location of polders in the IJsselmeer area, with year of reclamation and study areas for *Cotula coronopifolia* (1) and *Ranunculus sceleratus* (2). B. Distribution of *Ranunculus sceleratus* in Zuid Flevoland, summer 1968.

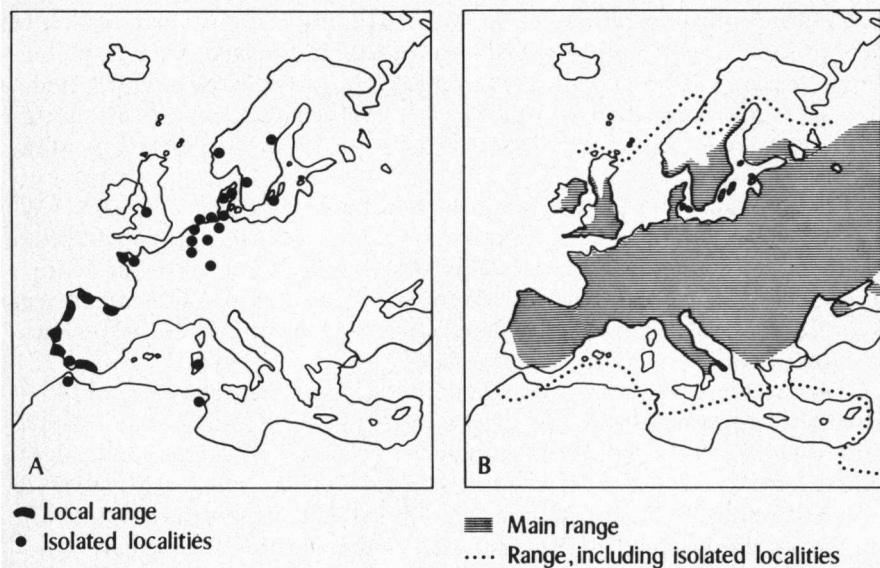


Fig. 2. Distribution of *Cotula coronopifolia* (A) and *Ranunculus sceleratus* ssp. *sceleratus* (B) in Europe, according to HULTÉN (1950, 1971). Information on *C. coronopifolia* from other sources has been incorporated.

off, and collected (one per plant), to determine the number of achenes (these achenes, like those of *R. sceleratus*, will be referred to here as seeds).

The colonization of *R. sceleratus* was followed during the first few years after reclamation in 4 relevées, each measuring 25 m². The study area was not the same as that used for *Cotula* (see fig. 1A). The distance between the relevées was 200 m. The density of adult *R. sceleratus* plants and the percentage cover accounted for by the various species was determined twice a year (table 2). Seed output was estimated in the same way as for *Cotula*, but with only a single sampling at the end of the ripening period.

The distribution of first-generation plants of *R. sceleratus* over the entire Zuid Flevoland area (fig. 1B) was investigated during the summer of 1968. All individual plants – both juvenile and adult – were counted in 100 m² quadrats situated in a number of transects.

3. GEOGRAPHIC DISTRIBUTION

According to HULTÉN (1950, 1971), *Cotula* is common in the southern hemisphere (Cape Province, St. Helena, Australia, New Zealand, and the southern part of South America) and is spreading, although not rapidly, along the coasts of both the North Atlantic and North Pacific oceans.

The distribution in Europe is given in fig. 2A, from which it can be seen that the species occurs along large parts of the Spanish and Portuguese coasts, whereas in

N.W. Europe the populations are more isolated. Populations north of France seem to show a more ephemeral behaviour, e.g., in England (CLAPHAM et al. 1962), Germany (RUNGE 1968), and Denmark (HANSEN & PEDERSEN 1959, 1968), than the southern populations, which have a stable character or are still spreading (CORILLION & LOLLIEROU 1956; MARCHIONI 1972; DE MARTIS & MARCHIONI 1975).

In 1739 the species was found for the first time in Europe near Emden in N.W. Germany, and the latter area and Denmark were colonized during the eighteenth and nineteenth centuries (HANSEN & PEDERSEN 1959). Presumably, further colonization of Europe took place from there. After about 1850, *Cotula* declined in N.W. Europe. In Brittany *Cotula* is mainly found in vegetation types belonging to the estuaries of the rivers Weser and Elbe).

In The Netherlands, *Cotula* was found in the period between 1835 and 1839 around Amsterdam (KOPS & VAN DER TRAPPEN 1846) and later as a wool alien in Tilburg (1938, 1941, and 1956, according to the *Rijksherbarium* in Leiden). Recently, the species was reported from the Zuid Flevoland polder (MENNEMA & VAN OOSTSTROOM 1973), the Dollard area (MENNEMA & VAN OOSTSTROOM 1977), and the Lauwerszee polder (1977; personal communication W. Joenje).

Ranunculus sceleratus s. lat. is, according to HULTÉN (1971), common in large parts of Europe, Asia, and North America. Outside this range the species occurs (probably introduced by man) in parts of Africa, India, China, New Zealand, Australia, and Tasmania. In Europe mainly the subspecies *sceleratus* is found (fig. 2B); only in the most northern areas (round the White Sea and in northern Siberia) is the ssp. *reptabundus* found.

From fig. 2 and the foregoing it can be concluded that: (1) the European range of *Cotula* falls within that of *R. sceleratus* ssp. *sceleratus* (further to be referred to as *Ranunculus*), but that of the latter extends somewhat farther northward; (2) *Cotula* is, unlike *Ranunculus*, found mainly in coastal areas; and (3) both species have been spread by man over large parts of the world.

4. HABITAT

In New Zealand *Cotula* is found on high spots in salt marshes in the contact zone between salt and fresh water (CHAPMAN 1960). This environment also holds for N.W. Europe. In Brittany *Cotula* is mainly found in vegetation types belonging to the alliance *Armerion maritimae*; class *Asteretea tripolii* (CORILLION & LOLLIEROU 1956). Along the coast of N.W. Germany *Cotula* is found in various types of vegetation such as the *Agrostis stolonifera*-*Potentilla anserina* association, class *Plantaginetea maioris* (RUNGE 1968), and the *Vaucheria-Deschampsia wibeliana* association (RAABE 1975). In N.W. Germany the optimum of *Cotula* lies in a vegetation of *Puccinellia distans* and *Spergularia salina* (E. W. Raabe, personal communication). This vegetation is related to the *Puccinellietum distantis* (class *Asteretea tripolii*). According to BEEFTINK (1965), this is a pioneer vegetation on grazed and disturbed sites in salt marshes and occurs optimally in the α -mesohaline zone of estuaries. It is also found on irregularly inundated

beach planes with fresh to brackish stagnating water.

According to HEGI (1928), *Cotula* also occurs on inland sites, mostly in moist and anthropogenic places (cattle tracks, fields grazed by geese, and near manure heaps). TÜXEN (1950) considers *Cotula* to be a regional character species of the *Rumex crispus-Alopecurus geniculatus* association (class *Plantaginetea maioris*), a pioneer vegetation on sand and clay soils which are inundated during the winter and spring. Such places occur mainly in river beds.

In Zuid Flevoland *Cotula* was found together with *Senecio congestus*, *Rumex maritimus*, *R. palustris*, and *Ranunculus sceleratus*, which are – according to

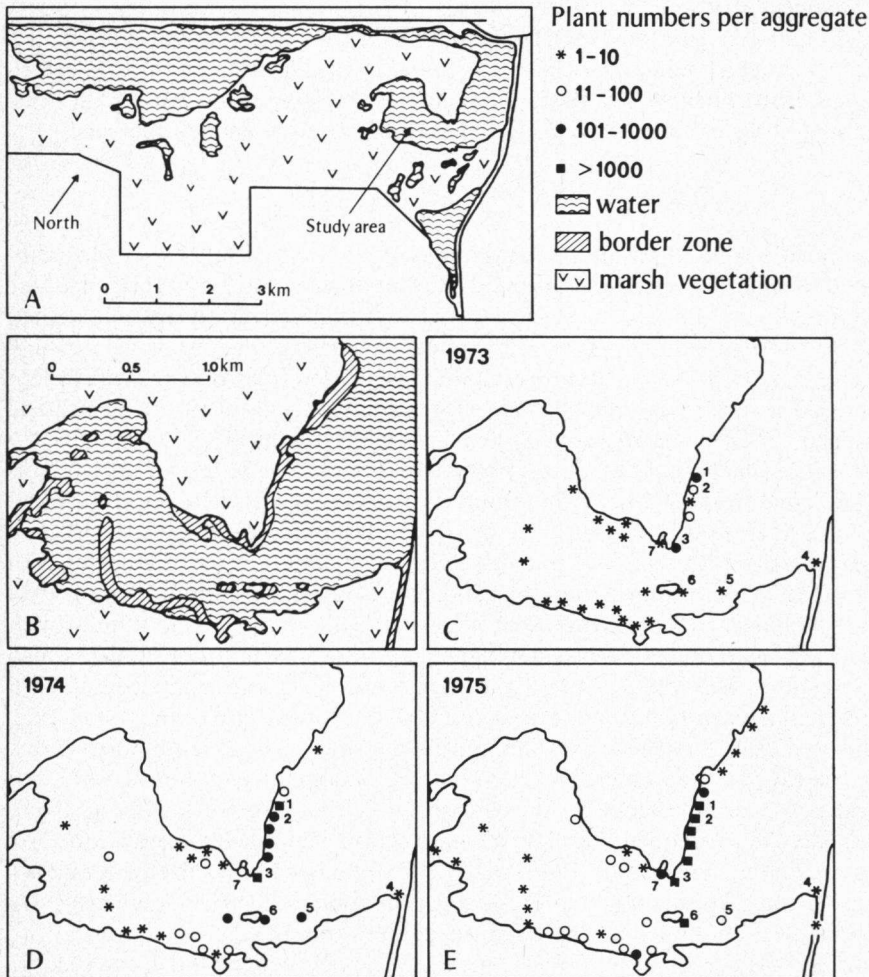


Fig. 3. A. Map of the Oostvaardersplassen area in which the study area is situated. B. Potential growing sites for *Cotula coronopifolia* (border zone). C-E. Distribution of *C. coronopifolia* in 1973, 1974, and 1975.

TÜXEN (1950) – character species of the *Rumicetum maritimi* (class *Bidentetea tripartitae*), which is a pioneer vegetation on periodically exposed border zones with moist nitrogen- and nutrient-rich mud occurring beside fresh-water pools and ditches.

From all this it can be concluded that *Cotula* is to be found on damp and open sand and clay soils which are inundated during most of the winter. Such places occur in both fresh- and brackish-water habitats. The species has a rather broad ecological range, comprising vegetation types of at least three phytocenological classes. The latter represent more or less natural plant communities, which confirms SUKOPP's (1962) conclusion that *Cotula* is a neophyte in N.W. Europe.

Ranunculus is – as character species of the *Rumicetum maritimi* – found predominantly in nutrient-rich fresh-water habitats. However, it also penetrates slightly brackish milieus, because it is found in the above-mentioned *Puccinellietum distantis* (BEEFTINK 1965). Both species therefore show substantial overlapping of their ecological ranges, and they can often be found together.

5. FIELD OBSERVATIONS

The border zone in the Zuid Flevoland polder colonized by *Cotula* was inundated during the winter and spring. In the summer months a vegetation arose of annual and biennial species with a low plant cover (usually less than 50%). In 1972 *Cotula* plants were found in a few places, growing in small aggregates. Each of the latter presumably originated from one or more parent plants. The surface covered by most of these aggregates gradually increased, and reached a mean value of about 2500 m² per aggregate in 1975.

Data on the population development are given in *fig. 3C-E* and *table 1*. It is evident that from 1973 to 1975 the number of aggregates as well as the total plant number increased, but there was considerable difference in growth between aggregates (*fig. 4*). This was due mainly to the position of the aggregates with respect to the prevailing southwest wind. More or less constant growth (in 1974 and 1975) occurred on sheltered sites (aggregates 1 and 2), whereas no growth occurred on more exposed sites (aggregate 4 and from 1975 onwards also aggregate 5). The decline in population density found in some aggregates in 1975 and in all aggregates in 1976, was caused by an artificial rise of the water level. This change was made to control botulism, which was killing many water birds. The elevation of the water level was relatively small in the autumn of 1974, but large in the autumn of 1975. At this higher water level the sites of *Cotula* were inundated more frequently and for a longer period, which led to considerable soil erosion and mud transport. Presumably, many seeds were washed away and became covered by soil, which prevented germination. After 1976, the new water regimen was continued and *Cotula* disappeared from the area.

Data on the seed output (*table 1*) indicate that between years there were large differences which showed correlation with germination time. On damp sites *Cotula* plants formed mats composed of creeping and rooting stems from which several flower stems arose. Early-germinating plants possess long creeping stems

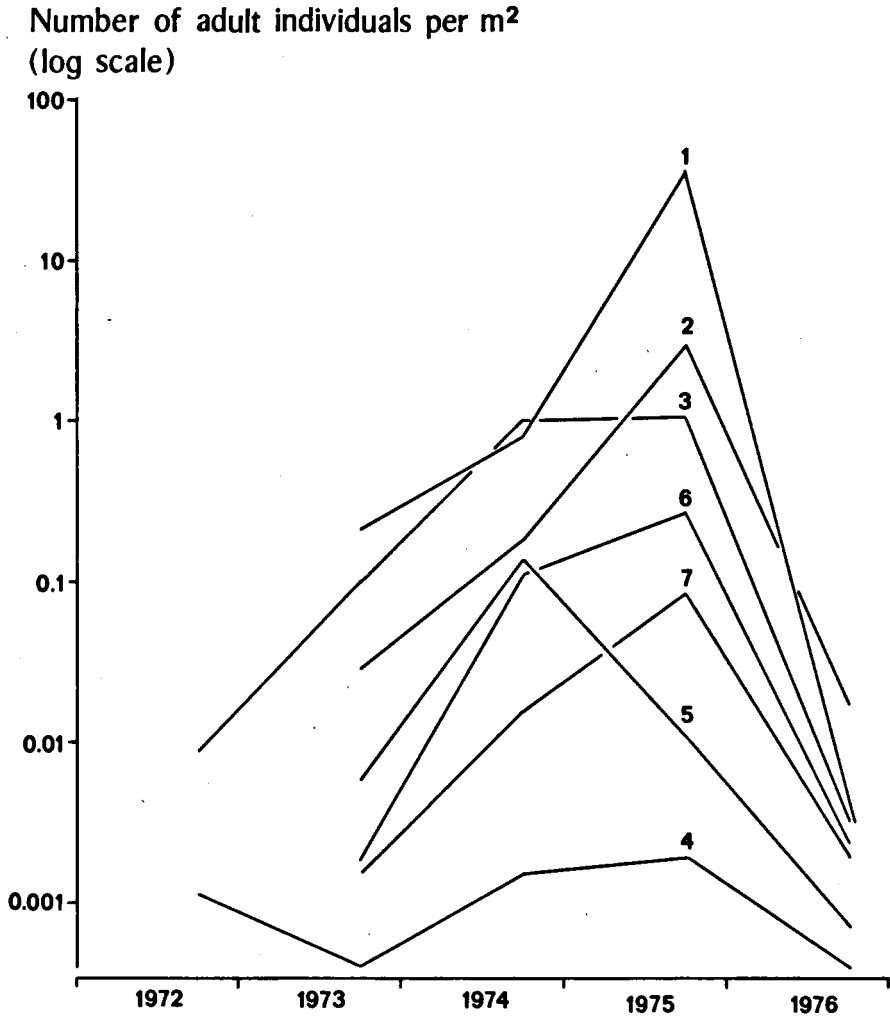


Fig. 4. Population development of *Cotula coronopifolia* in aggregates 1 to 7; Oostvaardersplassen area (for location, see fig. 3C-E).

and many flower heads. This was the case in 1974, when plants reached a diameter of about 60 cm (c. 35 cm in 1973 and 1975). In 1976 germination took place very late and gave rise only to small plants with almost no flowers or seeds.

From these findings it may be concluded that *Cotula* showed a rapid and almost exponential population growth during a period of several years. The mean multiplication factor (ratio of the plant number in year $n + 1$ to that in year n) ranges from 8 (1973–1974) to 15 (1974–1975). Only a very small proportion of the seeds gave rise to adult plants, i.e., 0.06 and 0.03 %, respectively, in the indicated years.

	1972	1973	1974	1975	1976
Number of seedling aggregates in area	ca. 7	25	30	38	—
Number of adult individuals in area ($\times 1000$)	<0.1	1	8	116	<0.2
Number of seeds per plant ($\times 1000$)*	—	13.3	50.2	20.9	nil
Period of germination	—	mid-June	mid-April	early-June	mid-July
Distance of dispersal (m): westward	—	—	350	350	—
northward	—	—	450	450	—

	1968		1969		1970		1971	
	15-7	20-9	13-6	8-9	18-6	22-9	27-5	7-10
Number of adult individuals per m ²		0.13	6.9	0.79	2.8			
Number of seeds per plant (× 1000)*		c. 500	560	2	nil			
Percentage cover by:								
<i>R. sceleratus</i> (including juvenile individuals)	< 1	1	15	1	1	< 1	1	
<i>Phragmites australis</i>	1	1	10	50	80	90	90	90
Other species	1	5	20	20	10	5	10	5

*Seed output estimated on 20-9-1968 from plant height

species (table 2). These species, which comprised chiefly *Senecio congestus*, and – in lesser amounts – *Atriplex hastata*, *Chenopodium rubrum*, and *Rumex maritimus*, reached their greatest development in 1969.

From the above it is clear that *Ranunculus* only showed a rapid population development during the first two years. In this period a 53-fold multiplication was found. This higher value, as compared to *Cotula*, was attained mainly by the very high seed output. A lower proportion (0.01 %) of the seeds produced adult plants. It was observed that seeds were spread by shallow rain-water pools formed during the autumn and winter. The water in these pools was blown over long distances by strong winds. Seeds were often washed into soil cracks; and were also concentrated locally, which resulted in high seedling densities.

Some indications on seed dispersal can be drawn from fig. 1B, which shows the distribution of first-generation plants over the whole polder area. Because germination conditions were favourable in the spring of 1968, it is likely that this distribution is a measure of the quantity of viable seeds present in the soil when the polder became dry. The homogeneous pattern (unlike that of other species; see VAN DER TOORN et al. 1969) indicates that the seeds had been dispersed (presumably by water) over large distances. These seeds came from two sources: (1) the coast of the mainland, and (2) the pumping stations of neighbouring reclamations, which means that the dispersal distance was at least 12 km.

6. DISCUSSION

A number of ecologically important characteristics for which *Cotula* and *Ranunculus* show both correspondence and divergence, will be discussed, viz., (1) life form, (2) pollination type, (3) seed output, and (4) seed dispersal.

6.1. Life form

Cotula behaves in the greenhouse as a perennial plant, and this is presumably also the case under subtropical conditions. In N.W. Europe the species behaves as a summer annual, since it dies in the first autumn frost. The life span (i.e., the minimal life-cycle period from seed to the next seed stage) is about two months (VAN DER TOORN & TEN HOVE in prep. b).

Ranunculus possesses two life forms (unlike *Cotula*), behaving as a summer annual and also as a winter annual. According to BAKKER (1966), it has a life span of about two months with the possibility of two generations per year. Because of their short life span, both species can be considered ephemerals (*sensu* BAKKER 1966).

6.2. Pollination type

Cotula populations from New Zealand are capable of self-fertilization (EDGAR 1958; LLOYD 1972). This is also the case in The Netherlands, since isolated plants produced good seeds in the laboratory. The same was found for *Ranunculus*. Cross-fertilization by wind or insects seems possible. Visiting by insects has been reported for *Cotula* (EDGAR 1958) and *Ranunculus* (CLAPHAM et al. 1962).

6.3. Seed output

The seed output of *Cotula* in Zuid Flevoland (20,000–50,000 seeds per plant), is high compared to that of other species of open and muddy habitats (SALISBURY 1942), but that of *Ranunculus* (maximum c. 500,000 per plant) is even higher. This very high seed output of *Ranunculus* (SALISBURY, 1942, reports a mean value of 26,600 and a maximum of 45,000) may in all likelihood be attributed to the favourable growth conditions prevailing during the first year after reclamation of these IJsselmeer polders (compare BAKKER 1960). When *Cotula* was first observed in 1972 the conditions were presumable less suitable for this species, because it appeared in a later period and in a more closed vegetation. Under favourable conditions both species show a high and almost equal seed output (VAN DER TOORN & TEN HOVE in prep. b).

6.4. Seed dispersal

Both species can be dispersed by water. Field observations indicate that this mode of dispersal is more efficient for *Ranunculus* than for *Cotula*, which is consistent with the results of experiments on the ability of seeds to float. Most *Cotula* seeds float for only a short period (less than 10 minutes), but most *Ranunculus* seeds for at least an hour or more (VAN DER TOORN & TEN HOVE in prep. b).

Several authors suppose that *Cotula* is spread by geese, because the plant grows in habitats frequented by these birds. In Zuid Flevoland *Cotula* fruitheads are incidentally eaten by birds, probably the Greylag Goose (*Anser anser* L.). Therefore, the viability of seeds was assessed after passage through the intestine of this species, and a high percentage of the seeds proved to be viable after a passage of 7–15 hours (VAN DER TOORN & TEN HOVE in prep. b). Thus, dispersal by birds seems possible, but there are indications that it rarely occurs. Although in the 1973–1975 period the Oostvaardersplassen area was frequented by many geese (DUBBELDAM 1978) flying between the various marshes and lakes, *Cotula* spread in only a limited area. On these grounds, water seems to be the most probable and most common dispersal agent within this area. Nevertheless, birds may be important for long-distance transport. It is not unlikely that *Cotula* was originally introduced into the Zuid Flevoland area by geese. At that time (c. 1970), the nearest and most important growing sites were in the Elbe estuary at a distance of about 300 km. Geese visiting these sites can cover such distance in a few hours on their way south. Transport of *Cotula* by man seems unlikely, because at the time in question the relevant area was dangerous to walk on and was rarely entered.

Colonizing species of open habitats often possess the following combination of characteristics (HARPER 1977): (1) short life span, (2) capacity for self-fertilization, (3) high seed output, and (4) efficient seed dispersal. These conditions hold for *Ranunculus*, but only the first three for *Cotula*. As a result, *Cotula* can show a rapid increase in numbers, but the species is limited in its dispersibility. Experiments showed that *Cotula* (in contrast to *Ranunculus*) germinates in the autumn and winter, which leads to a high seedling mortality by frost. Under

winter conditions *Cotula* seeds can only survive when covered by soil or water, but in this state, unlike *Ranunculus*, their longevity is limited (VAN DER TOORN & TEN HOVE in prep. a, and 1976). Consequently, the chances of local extinction of *Cotula* are high and the species can maintain itself only in particular habitats.

ACKNOWLEDGEMENTS

The author wishes to acknowledge with gratitude the stimulating discussions with the late Prof. D. Bakker. He is also greatly indebted to Prof. W. H. van Dobben (Wageningen), Prof. H. Sukopp (Berlin), Prof. E. W. Raabe (Kiel), Dr. D. König (Kiel), Ing. F. Mang (Hamburg), and Ir. R. J. de Glopper (Lelystad) for advice and valuable help, to the directors of the IJsselmeer Polders Authority for all of the facilities they provided, and to Mr. J. Mooi, Mr. H. J. ten Hove, Miss C. H. Dolleman, Mr. C. 't Hooft, and Mr. W. Verholt for technical assistance.

REFERENCES

- BAKKER, D. (1960): *Senecio congestus* in the Lake Yssel polders. *Acta Bot. Neerl.* **9**: 235–259.
- (1966): On life forms of hapaxants in the Dutch flora. *Wentia* **15**: 13–24.
- BEEFTINK, W. G. (1965): *De zoutvegetatie van ZW-Nederland beschouwd in Europees verband*. Thesis, Wageningen.
- CHAPMAN, V. J. (1960): *Salt marshes and salt deserts of the world*. London.
- CLAPMAN, A. R., T. G. TUTIN & E. F. WARBURG (1962): *Flora of the British Isles*. Cambridge.
- CORILLION, R. & CH. LOLLIEROU (1956): Sur l'extension récente et les caractères des végétations à *Cotula coronopifolia* L. (Composées) des rives du Trieux. *Bull. Soc. scient. de Bretagne*, **31**: 102–106.
- DUBBELDAM, W. (1978): De Grauwe gans anser in Flevoland in 1972–1975. *Limosa* **51**: 6–30.
- EDGAR, E. (1958): Studies in New Zealand *Cotulas*; I. Floret types and natural groupings of the species. *Trans. Soc. N.Z.* **85**: 357–377.
- HANSEN, A. & A. PEDERSEN (1959): Firkløft's (*Cotula coronopifolia* L.) forekomst i Danmark. *Flora og Fauna* **65**: 73–77.
- (1968): Nyt om *Cotula coronopifolia* L., Firkløft, i NV-Jylland. *Flora og Fauna* **74**: 37, 40.
- HARPER, J. L. (1965): Establishment, Aggression, and Cohabitation in Weedy Species. In: H. G. BAKER & G. L. STEBBINS (ed.): *The Genetics of Colonizing Species*. New York, London.
- (1977): *Population Biology of plants*. London, New York, San Francisco.
- HEGI, G. (1928): *Illustrierte Flora von Mittel-Europa*, Band VI: 622–626. München.
- HULTÉN, E. (1950): *Atlas of the distribution of vascular plants in NW Europe*. Stockholm.
- (1971): *The circumpolar plants II*: 182, 300. Stockholm.
- KOPS, J. & J. E. VAN DER TRAPPEN (1846): *Flora Batava IX*: 658, Amsterdam.
- LLOYD, D. G. (1972): Breeding systems in *Cotula* L. (Compositae, Anthemideae); I. The array of monoclinal and diclinal systems. *New Phytol.* **71**: 1181–1194.
- MARCHIONI, A. (1972): Sulla presenza in Sardegna di *Cotula coronopifolia* L. *Annali Bot.* **29**: 179–182.
- MARTIS, B. DE & A. MARCHIONI, (1975): Distribution of *Cotula coronopifolia* L. in Sardinia. *Boll. Soc. Sarda Sci. nat.* **15** (9): 63–72.
- MENNEMA, J. & S. J. VAN OOSTSTROOM (1973): Nieuwe vondsten van zeldzame planten in Nederland, hoofdzakelijk in 1972. *Gorteria* **6**: 181–198.
- (1977): Nieuwe vondsten van zeldzame planten in Nederland, hoofdzakelijk in 1976. *Gorteria* **8**: 219–240.
- RAABE, E. W. (1975): Die *Vaucheria-Deschampsia wibeliana*-Gesellschaft. *Kieler Notizen* **7**: 94–96.
- RUNGE, F. (1968): Die Laugenblume auf Langeoog. *Natur, Kultur und Jagd* **20**: 141–142.
- SALISBURY, E. J. (1942): *The Reproductive Capacity of Plants*. London.
- SCHREVEN, D. A. VAN (1965): Stikstofomzettingen in jonge IJsselmeerpoldergronden. *Van Zee tot Land* **41**: 1–74.

- SUKOPP, H. (1962): Neophyten in natürlichen Pflanzengesellschaften Mitteleuropas. *Ber. dt. bot. Ges.* **75**: 193–205.
- TOORN, J. VAN DER, M. BRANDSMA, W. B. BATES & M. G. PENNY (1969): De vegetatie van Zuidelijk Flevoland in 1968. *De Levende Natuur* **72**: 56–61.
- & H. J. TEN HOVE (1976): Germination experiments with *Cotula coronopifolia* and *Ranunculus sceleratus*. *Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., 2e Reeks*, **67**: 126–130.
- & — (in prep. a): On the ecology of *Cotula coronopifolia* L. and *Ranunculus sceleratus* L.; II. Experiments on germination and seed longevity.
- & — (in prep. b): On the ecology of *Cotula coronopifolia* L. and *Ranunculus sceleratus* L.; III. Experiments on life cycle and seed dispersal.
- TÜXEN, R. (1950): Grundriss einer Systematik der nitrophilen Unkrautgesellschaften in der Eurosi-birischen Region Europas. *Mitt. flor.-soz. Arb-Gemein. N.F.* **2**: 94–175.