Dispersal of the exotic coastal dune plants *Gladiolus gueinzii* and *Trachyandra divaricata* in Australia

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Gladiolus gueinzii (Iridaceae) and *Trachyandra divaricata* (Liliaceae s.l.) are South African dune plants naturalised in Australia. *Gladiolus gueinzii* has two modes of dispersal: winged seeds, and cormels that may float for up to seven months in seawater. Its Australian occurrences are restricted to New South Wales. It was first collected in 1950 near Newcastle and has spread 250 km to the north and 500 km to the south. From large distances between the early herbarium records it was inferred that buoyancy of the cormels enables *Gladiolus gueinzii* to establish at sites remote from existing populations. The climatic conditions of the area over which *Gladiolus gueinzii* presently occurs are broadly similar to those of the more humid part of its native range. Further spread may be restricted due to unfavourable thermal factors.

Trachyandra divaricata is a 'tumbleweed'. Wind dislodges and carries away the 'crowns' of tangled mature infructescences, in the process peppering their trails with innumerable small seeds. In the 1930s *Trachyandra divaricata* became established near Perth, Western Australia, while in 1940 it was also found near Karridale, 300 km further south. In the intervening area it has become a major weed in the dunes and has spread to paddocks inland, causing poisoning of livestock. *Trachyandra divaricata* has also turned up at several other outlying coastal locations as well as at an inland site. The distances involved are suggestive of dispersal by human agency, for instance through cars or boats. The Mediterranean and adjacent semi-arid climates of the south-west of Western Australia mirror a similar situation in southern Africa. Hence, the area appears to be well suited to *Trachyandra divaricata* and further spread can be expected.

In New South Wales *Trachyandra divaricata* was first found in 1968 at a dune rehabilitation site near Wollongong. It possibly came in as a contaminant of *Acacia saligna* planting stock from Western Australia. Since then it has become established at several other reclaimed areas, but has not spread much beyond such sites, possibly because of unfavourable climatic conditions. Nevertheless, in case aggressiveness takes a turn for the worse, it would appear desirable to eradicate occurrences in New South Wales while this is still achievable.

Introduction

Gladiolus gueinzii Kunze (family Iridaceae) and *Trachyandra divaricata* (Jacq.) Kunze (family Liliaceae s.l.: Asphodelaceae, Anthericaceae) are coastal species native to South Africa. The former occurs in the south-east, the latter in the south-west, with its range extending along the Namibian coast (Fig. 1). Their distributions overlap along the southern coastline, where *Gladiolus gueinzii* is more common on foredunes with a pioneer vegetation, *Trachyandra divaricata* on older, more densely vegetated dunes. After presumably accidental introduction into Australia, both species have become naturalised and have enlarged their range. In this paper the dispersal ecology and present Australian distribution of *Gladiolus gueinzii* and *Trachyandra divaricata* are analysed and the likelihood of further spread is discussed.

Methods

The data for this paper have been obtained during investigations of the dispersal ecology of strandplants. These investigations started in 1980 and although fieldwork has been predominantly carried out in south-eastern Australia, over the years a good many beaches have been visited elsewhere. Concurrently, experiments were began to test the buoyancy and viability of propagules of various strand- and foredune plants. No great sophistication was applied to these experiments, as there were only two basic questions to be answered: firstly, do propagules float and if so, for how long, and secondly, how long do they remain viable? Seeds, fruits and, in the case of *Gladiolus gueinzii*, cormels were put in jars with seawater and numbers remaining buoyant were regularly assessed. Viability was tested at the start of such experiments, as well as at intervals afterwards. During the earlier years the propagules were sown in a mixture of sand and perlite, but later they were placed on moist filter paper in petri dishes, which were either kept in a growth cabinet or at ambient room conditions. The viability of propagules stored in paper wrappers at, or at somewhat lower than, room temperature was tested as 'control'.

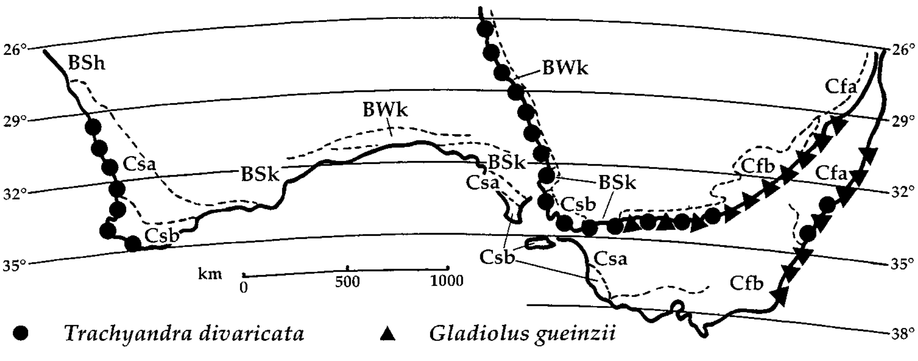

Fig. 1. The geographic distribution of *Gladiolus gueinzii* and *Trachyandra divaricata* in relation to climate. The maps of Africa and Australia south of 26°S have been overlaid for easy comparison of the climates of the coastal regions, which have been classified according to Köppen's scheme (after Schulze & McGee 1978 and Gentilli 1972, respectively). BS: semi-arid, and BW: arid climates with mean annual temperatures above (h) or below 18°C (k); Cs: 'Mediterranean' climates with winter rains and hot, dry summers (a) or long, mild summers (b); Cf: humid mild-winter climates with appreciable rainfall throughout the year, either with hot summers (a), or with mild summers (b).

Collection records for *Gladiolus gueinzii* and *Trachyandra divaricata* were acquired from all major Australian herbaria. These records were used to infer the mode of introduction and subsequent spread, based on the presumptions that the earliest collections would have been made in the general area of where the species first became naturalised and that this area served as the source of further dispersal. Also, if early collections are far apart, but close in time, this would indicate multiple introductions as is, for instance, the case with *Arctotheca populifolia* (Asteraceae; Heyligers 1983, 1998) and *Euphorbia paralias* (Euporbiaceae; Heyligers 1989, 1993). Analysis of the herbarium records of these and other introduced strandline and foredune species with buoyant propagules such as *Cakile edentula, Cakile maritima* (Brassicaceae) and *Hydrocotyle bonariensis* (Apiaceae; Heyligers 1996, 1998), has lead to the hypothesis that the dispersal of such species happens by making 'leaps' entrained in major current systems with subsequent filling in of the 'gaps' by means of largely wind-driven along-shore drift. The records of *Gladiolus gueinzii* provided another opportunity to test this proposition.

Information on occurrence in southern Africa has been exclusively obtained from the literature, especially from taxonomic treatments (Lewis et al. 1972, Obermeyer 1962, Goldblatt & Manning 1998) and from sources found in the comprehensive overview of the coastal vegetation by Lubke et al. (1997).

Nomenclature follows Harden (1990–1993) except for *Cotula turbinata* and *Tetragonia decumbens,* taxa not mentioned in Harden, for which Marchant et al. (1987) was used.

The plants

Gladiolus gueinzii is a small gladiolus with narrow, rather glaucous leaves, which are at best 60 cm long and not uncommonly about half that length (Fig. 2). Hence the plants are rather inconspicuous amongst the similarly grey-green *Spinifex sericeus* (Poaceae) vegetation of the foredunes. Plants grow from corms, which may be located 30 or 40 cm, or even deeper, under the surface. These corms are about 20–30 mm across and somewhat less in height. New corms develop on the top of older ones and thus three generations of corms may be found together, while at their base a mass of dark-brown tunic remnants indicates the demise of previous corms.

Usually, a 'corona' of cormels surrounds the sutures between corms. Cormels develop at the end of short stolons, which grow out from the corm bases (Fig. 2). According to Goldblatt and Manning (1998) cormels produced deep underground have thin, light-brown tunics, while those near the soil surface develop a dark-brown, thick, leathery or corky tunic. In my experience this is a phenomenon that is an expression of ageing rather than of depth under the surface. As cormels are easily dislodged, their number per corm or per plant is not easily assessed, but from a count of stolon remnants and judging from the numbers of cormels found during digging out a clump of plants, 16 cormels per corm, or 35 per plant are likely to be minimum estimates. Cormels may also form in the axils of the sheathing bases of the lower leaves if these nodes are under the surface. Most cormels appear to remain dormant, but some sprout *in situ*, thus forming a clump of plants around the 'parent' (Fig. 2).

The flowering stems are shorter than the leaves and carry one to five, about 3.5 cm long, mauve-pink flowers. The flowers open sequentially, starting with the lowest one, and usually only one flower is open at a time. Their attractively patterned nectar mark remains largely hidden from view, as the flowers hardly open out. Goldblatt and Manning (1998) report that *Gladiolus gueinzii* is self-compatible and autogamous, which is unusual in the genus. The main flowering season is from October till December, when some plants may produce a second generation of flowers on a short branch from the base of the inflorescence or on new stems (Fig. 2). The fruits ripen through the summer and the seeds are shed as soon as the capsules are ripe. The old flowering stems with the dry capsules remain standing for the rest of the year and often during the next season as well, thus providing a more obvious clue to the presence of the species than the living parts of the plants.

In contrast, *Trachyandra divaricata*, False Onion Weed or Strapweed (Hussey et al. 1997) is a conspicuous member of the vegetation. Its lax, narrow, bright-green, rather fleshy leaves spread out over the sand and may be up to one metre long (Fig. 3). Thus, older plants cover considerable areas and are strong competitors for space. They grow from a compact rhizome. To what extent this rhizome can cope with sand burial is not known. It grows upward and outward with stubby 'branches', about 2.0–3.5 cm thick as well as long, and is clothed in many, up to 17 mm long, brown, membranous bracts. Basal sections carry coarse roots covered by a felt-like pubescence of interlacing root hairs, which seem to be able to absorb water very quickly (Obermeyer 1962). In the middle sections roots gradually give way to leaves. Each new rhizome branch produces a -supposedly terminal- inflorescence.

The inflorescences are up to 0.7 m tall and more or less divaricately branched from about halfway. They carry pale-lilac flowers, about 1.5 cm across, which are very attractive to honeybees. Counts have given figures between 100 and 700 flowers per inflorescence. Fruit set is variable. The reasons for this are not immediately apparent; factors such as age of the plants and weather conditions may be implicated. The main flowering season is from mid-winter to late spring, but at least on the east coast of Australia flowering goes through a second season in autumn. There are only a few fruiting stems on a young plant, but older plants carry an impressive 'crown' of infructescences.

Dispersal mechanisms

Both species have adaptations for dispersal by wind and water. The seeds of *Gladiolus gueinzii* are winged, while *Trachyandra divaricata* is a tumbleweed: when ripe and dried-off, the 'crown' of fruiting stems is dislodged and carried away by wind (Fig. 3). In addition, the cormels of *Gladiolus gueinzii* and the dry infructescences of *Trachyandra divaricata* are buoyant in sea water.

The loculicidal capsules of *Gladiolus gueinzii* contain about 40 seeds per capsule. The globular seeds have a diameter of 3 mm and are surrounded by a 4 mm wide wing consisting of 'loose, large cells containing air pockets, which ensures lightness and

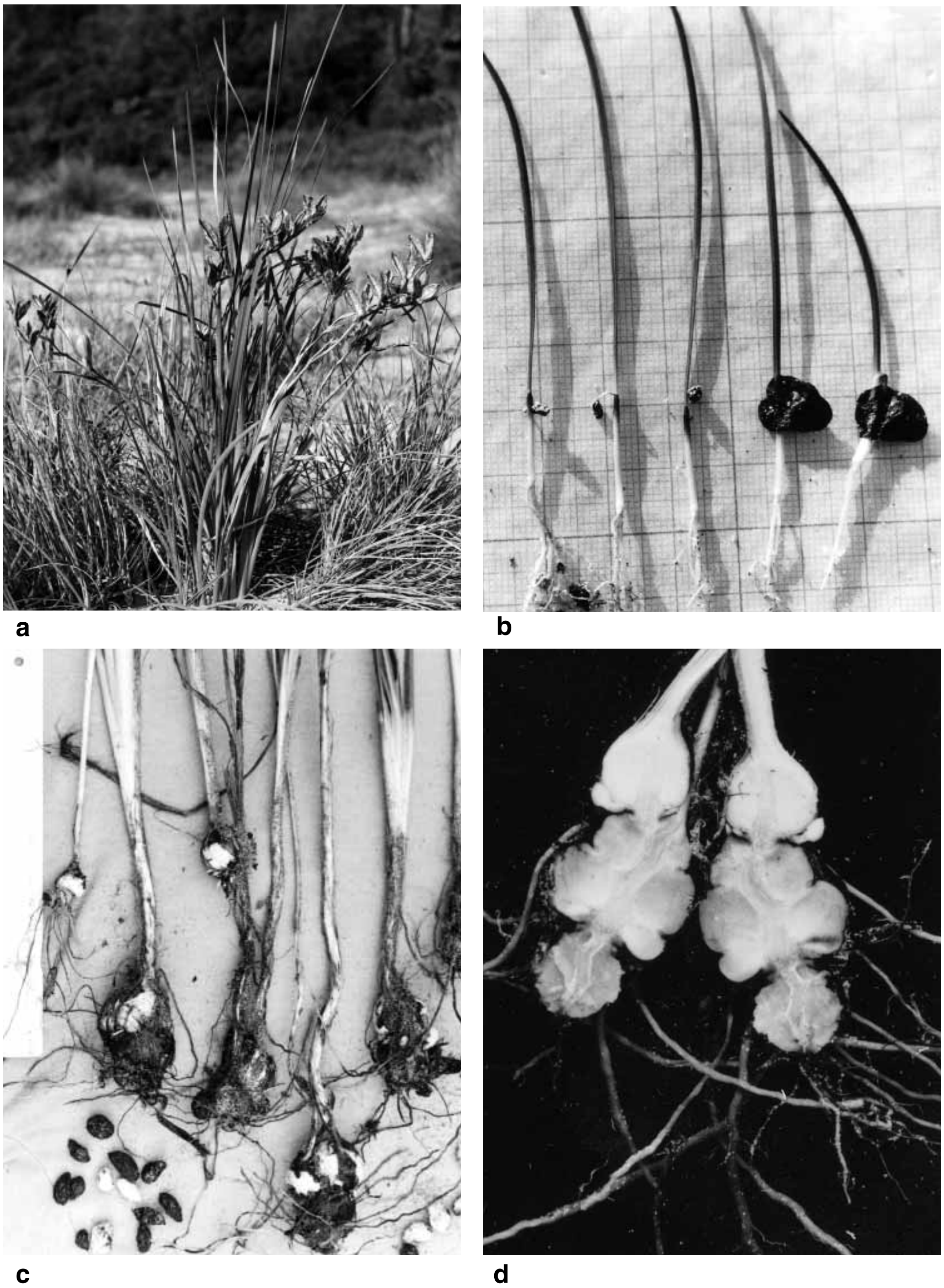

Fig. 2. *Gladiolus gueinzii*. **a**, clump of plants at Nelson Beach, NSW on 24 March 1991; the flowering stems are 40 cm tall; most capsules have shed their seeds; a late-season flowering stem points to the left from the clump centre; **b**, seedlings; the two seedlings at the right are still attached to the winged seed husks (the graph paper has 1 cm main divisions); **c**, underground part of a clump of which the stems have been teased apart showing staggering of corms and cormels which fell off during excavation (the ruler is 20 cm long); **d**, transverse cut through lower part of a stem showing three generations of corms and cormels being formed at the base of the top corm.

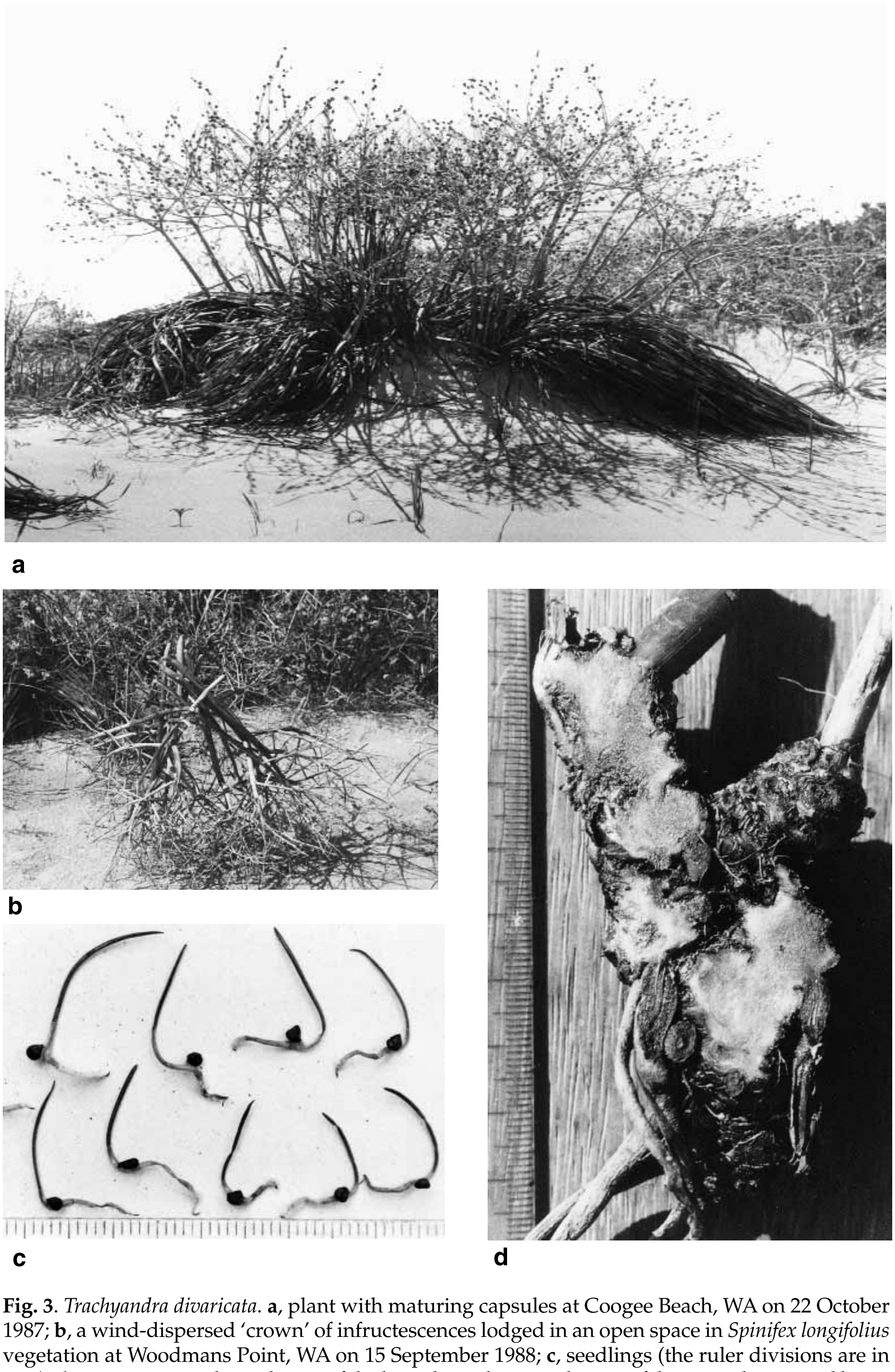

Fig. 3. *Trachyandra divaricata*. **a**, plant with maturing capsules at Coogee Beach, WA on 22 October 1987; **b**, a wind-dispersed 'crown' of infructescences lodged in an open space in *Spinifex longifolius* vegetation at Woodmans Point, WA on 15 September 1988; **c**, seedlings (the ruler divisions are in mm); **d**, transverse cut through part of the branching rhizome showing felt-covered roots and bases of two flowering stems; leaf-scars can be seen on the uncut branch (the ruler divisions are in mm).

wind dispersal' (Lewis et al. 1972; Fig. 2). With commonly only one or a few flowering stems per plant, seed production is in the order of 100 to 400 seeds per plant per year.

In comparison, the much-branched inflorescence of *Trachyandra divaricata* may develop 400 fruits and on average carries about half that number. Each fruit, also a loculicidal capsule, contains from three to 22, on average 11, seeds which are pyramidal in shape and about 2 mm across (Fig. 3). With an average production of about 2000 seeds the reproductive potential of a single infructescence is already an order of magnitude larger than that of a *Gladiolus gueinzii* plant. However, even young *Trachyandra divaricata* plants have a couple of inflorescences and this number increases with age. A clump 0.7 m in diameter may carry about 25 tangled fruiting stems which, dislodged and driven forth by the wind, may pepper their path with 50 000 seeds.

The buoyant cormels of *Gladiolus gueinzii* become vehicles for long-distance dispersal if they are dislodged by wave or wind erosion of foredunes or due to undercutting of sandspits by currents. In South Africa *Gladiolus gueinzii* cormels were found to float for three weeks (Muir 1937). However, in my two tests, each with 30 cormels, 15 stayed afloat for seven or more weeks, while some remained buoyant for longer than half a year (Fig. 4). After 16 months in seawater the cormels were still viable; most sprouted within seven weeks when the fibrous tunics were removed before planting, but it took more than half a year before cormels with intact tunics began to sprout. After 28 months in sea water viability of cormels had greatly declined: only one out of five 'peeled' cormels sprouted after about five months, and none of the cormels with intact tunics. However, five dry-stored cormels sprouted within three weeks when the tunics were removed, while three of the five cormels with intact tunics sprouted later, but within 25 weeks. The corollary of these tests is that cormels washed out to sea can be transported by currents to other beaches and are still capable of sprouting on arrival. Inhibition of sprouting when the tunic has stayed intact may be an advantage if in the meantime the cormel has a greater chance to become covered by sand.

The buoyancy of seeds was also tested. The small unadorned seeds of *Trachyandra divaricata* sank within minutes, but those of *Gladiolus gueinzii*, due to the air trapped in the wings, stayed afloat till the wings had become soaked. Of the 100 seeds tested, none stayed afloat for longer than a week. It would appear that water dispersal of *Gladiolus gueinzii* seed can only be of local significance and hence, it may be merely of theoretical interest that sunken seed remains viable for more than a year.

Dry *Trachyandra divaricata* infructescences are buoyant by virtue of their hollow stems and may stay afloat for several weeks. They sink once they have become waterlogged and the remaining air has been expelled. However, before a bunch of infructescences is blown out to sea, many seeds will already have dropped out, diminishing the colonisation potential of a stranded bunch. When kept in seawater, seeds are still marginally viable after eight months.

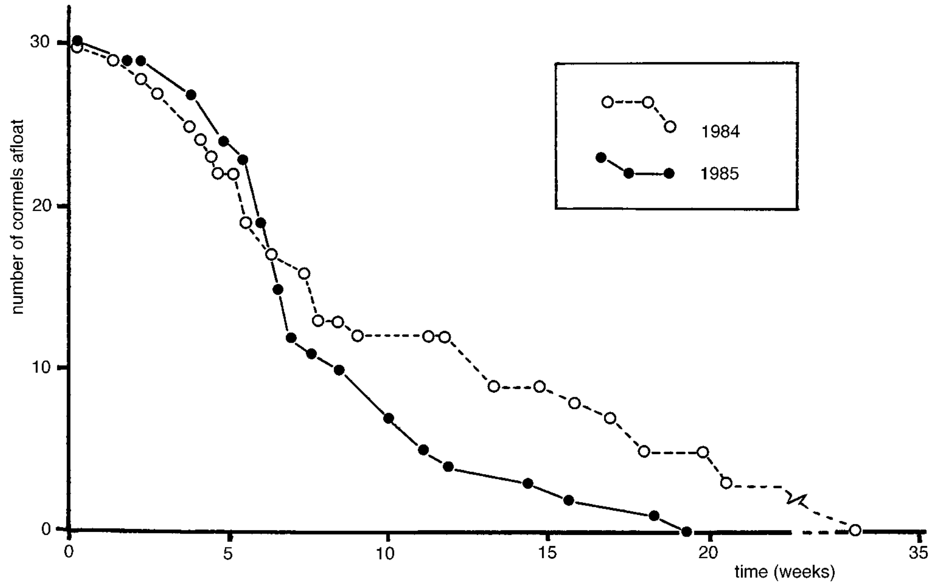

Fig. 4. Buoyancy of *Gladiolus gueinzii* cormels. Results from two tests; the first one was started on 30 September 1984, the second test one year later, each with 30 cormels of the same batch, which was collected on 26 August 1984 near Nowra, NSW. For the tests cormels were put and kept in jars with seawater at ambient room conditions.

A dispersal scenario for *Gladiolus gueinzii*

The Australian occurrences of *Gladiolus gueinzii* are confined to the coast of New South Wales (Fig. 5). The first collection was made in 1950 at Stockton, near Newcastle, a location rich in ballast plants, which include among others *Ursinia chrysanthemoides* and *Cotula turbinata* (Asteraceae), *Tetragonia decumbens* (Aizoaceae) and *Hebenstretia dentata* (Selaginaceae) from South Africa (Heyligers unpubl. obs.). Hence, introduction in dumped ballast appears to be the most likely explanation for *Gladiolus gueinzii*'s arrival on Australian shores. In the 1940s Mort (1949) made an extensive survey of the dune flora of New South Wales with a view to select species suitable for dune rehabilitation. In his enumeration of species he does not mention *Gladiolus gueinzii.* However, he could have missed it as especially non-flowering young plants are easily overlooked in the *Spinifex sericeus* vegetation of the dunes. Nevertheless, it is likely that the 1950 collection date is rather close to the actual date of introduction.

Soon afterwards, in 1953 and 1954, *Gladiolus gueinzii* was also collected at Palm Beach, on the southern peninsula at the entrance to Broken Bay north of Sydney and 90 km south-south-west of Stockton. Unless it was achieved by other means, then this occurrence at Palm Beach is an almost instantaneous demonstration of *Gladiolus gueinzii*'s capacity to disperse by ocean currents. As this species of *Gladiolus* is not available in the nursery trade (it is not listed by Bodkin 1986), and in England is only

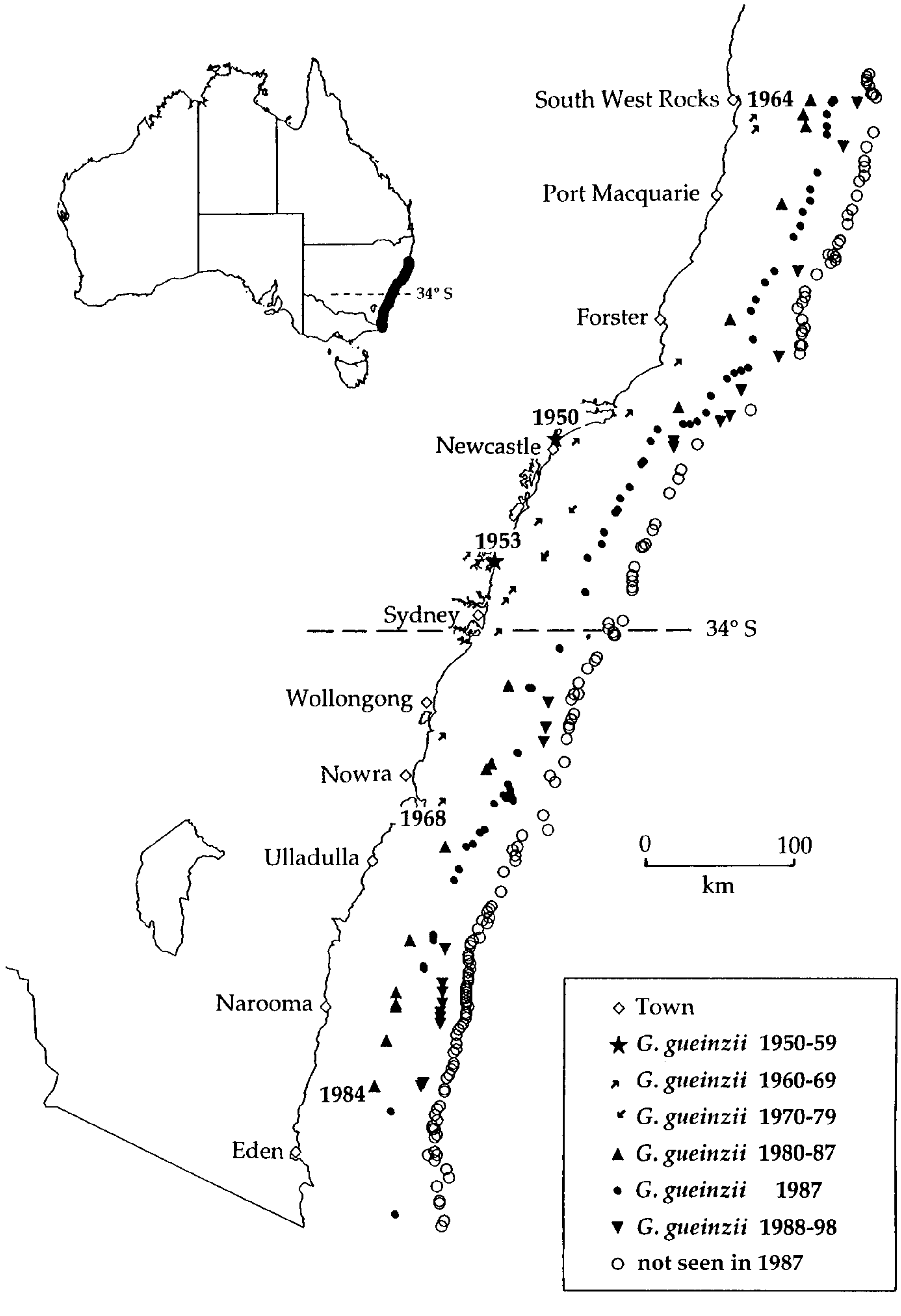

Fig. 5. Collection and observation sites of *Gladiolus gueinzii* in Australia. Sites have been grouped according to periods and these groups have been plotted in rows parallel to the coast. The pre-1980 data refer exclusively to herbarium records, while the 1987 data were gathered by P.J. Clarke during his transect surveys. Dates of collections or observations significant as an indication of the rate of spread have been added to some symbols.

grown by some people with a special interest in this genus (B. Matthews, Royal Botanic Gardens, Kew, pers. comm. 9 October 1987), dispersal by sea would appear to be the most likely explanation.

In 1964 and the following two years *Gladiolus gueinzii* was collected at several sites near South West Rocks, 240 km to the north-northeast of Stockton, while in 1968 at a similar distance in the opposite direction it was collected near Nowra (Fig. 5). In 1984, during my first inspection of Nelson Beach, between Narooma and Eden, I found a well-established population of *Gladiolus gueinzii*, which is another 210 km further south. A detailed transect survey of the vegetation of the coastal dunes in New South Wales in 1987 (Clarke 1989a, b) augments the rather sparse records and showed the widespread occurrence of *Gladiolus gueinzii* along the New South Wales coast south from South West Rocks. However, it is also worth pointing out that there are many dune areas where *Gladiolus gueinzii* is still absent.

The collated information shows that dispersal of *Gladiolus gueinzii* has been an efficient process to which both types of propagules have contributed: cormels in the first instance for dispersal from beach to beach, and seeds as well as cormels for spreading over the dunes backing these beaches. Why there is such an abrupt northern limit to the distribution is not clear. It could be that the local currents under influence of the eddies generated by the East Australian Current run in a counter direction. *Arctotheca populifolia* appears to have come to a dispersal standstill at the same 'barrier'. Hence it will be informative to watch the further northward spread of *Cakile maritima* from its present limit near Port Macquarie (pers. obs. March 1998). On the other hand, *Cakile edentula* and *Hydrocotyle bonariensis* appear to have successfully bypassed this barrier (Heyligers 1998), but it is possible that these species spread southward from southern Queensland, where both had become established by the late 1920s. In a later section the possibility will be discussed, that for *Gladiolus gueinzii* the barrier is a climatic one.

A dispersal scenario for *Trachyandra divaricata*

The first collection of *Trachyandra divaricata* in Australia was made in November 1912 at Coode Island, near Melbourne, a location at the time well-known for its ballast flora (Tovey 1911; Fig. 6). However, it did not persist, nor is there any evidence that it spread to neighbouring areas (Willis 1970).

In the 1930s *Trachyandra divaricata* became naturalised in the south-west of Western Australia. The earliest collection was made in 1932 at Cottesloe, a seaside suburb of Perth and a few kilometres north of Fremantle harbour; the next, in 1938, on the North Mole of that harbour (Fig. 6). Hence, the harbour facilities have most likely been the point of entry. In 1940 *Trachyandra divaricata* was also collected near Karridale, further to the south by about 300 km. As dispersability by currents appears to be limited, the most plausible explanation for bridging this distance in such a short time is that seeds had hitch-hiked on a car or boat, or on clothing or footwear. The role of these particular dispersal agents is often implied but seldom proven. A notable exception is the study by Wace (1977), who analysed the propagules found in the sludge of a car-wash in Canberra. One outcome was that these propagules were usually small and numerous; another, that grassy tumbleweeds were a conspicuous component at certain times of

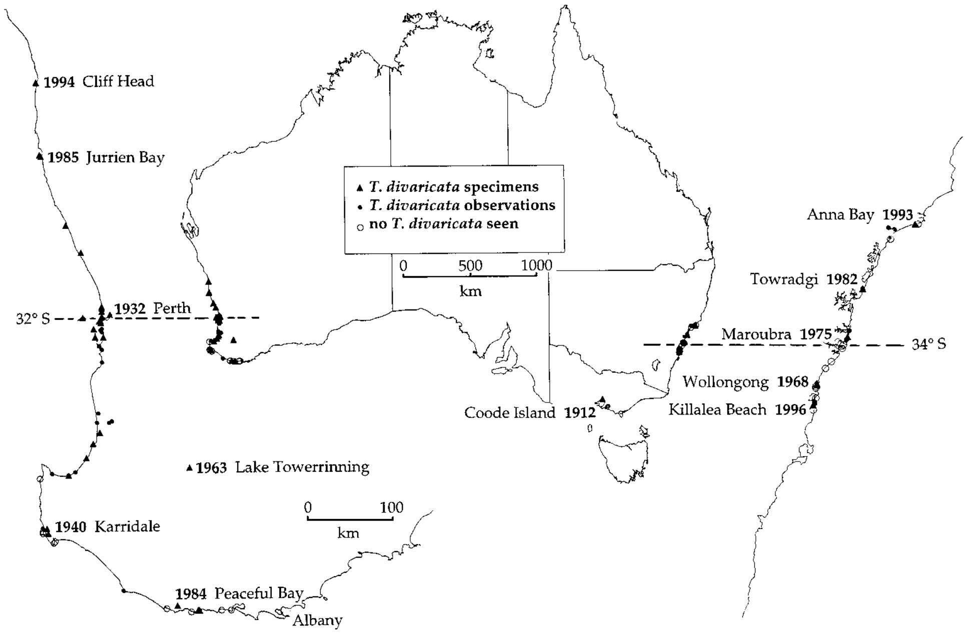

Fig. 6. The distribution of *Trachyandra divaricata* in Australia. The detailed coastline of south-western Western Australia has been centred on the latitude of Perth, that for central New South Wales on the latitude of Sydney. The annotations refer to the earliest dates for herbarium collections from the indicated locations.

the year. Whether the latter result is translatable to *Trachyandra divaricata* should not be too difficult to ascertain.

In the decades following the 1930s *Trachyandra divaricata* spread between Perth and Karridale and has become very common in the dunes. It has also invaded nearby pastoral country, where in times of fodder shortage it is grazed by stock, causing severe and irreversible toxicosis when eaten in quantity over several weeks (Huxtable et al. 1987). If the spread along the coast is mainly due to the 'tumbleweed' action of *Trachyandra divaricata*, a comparison is warranted between the efficiency of this mode of dispersal and that of the primarily sea-dispersed *Gladiolus gueinzii*: in about 50 years the former species 'filled in' a distance of 300 km, while the latter spread from a central focus over a range of 750 km.

In 1963 a collection of *Trachyandra divaricata* was made at Lake Towerrinning, 110 km inland from the coast as the crow flies, but only 25 km west of the nearest approach of the highway between Perth and Albany. In the 1980s *Trachyandra divaricata* was also collected at outlying coastal locations, namely at Jurien Bay, 200 km to the north of Perth, and at Peaceful Bay, 350 km south-south-east of Perth. During fieldwork in November 1988 I found it to be well established in the latter area, not just occurring in the foredunes, but also densely along some roads and vehicular tracks and scattered in the camping ground, where notwithstanding regular mowing it was coming into flower. The only other location along the coast between Albany and Karridale where I found *Trachyandra divaricata* was at Windy Harbour, 85 km west of Peaceful Bay, where a couple of plants were seen near the jetty. My presumption is that its journey to all these locations has been human-assisted. Jurien Bay is a fishing settlement, while the southern coastal locations are holiday destinations. Unless the situation during the intervening decade has rapidly changed, Hussey et al.'s (1997) statement that *Trachyandra divaricata* 'is widespread through the lower south-west from Jurien Bay to Albany, especially in interdunal beach heathland and roadsides on calcareous sandy soils' appears to be an overstatement of its present distribution.

Trachyandra divaricata has also been found on some of the smaller islands south-west of Perth: Carnac Island, Seal Island, Penguin Island and an unnamed island between the last two (Abbott & Black 1980). Although these islands do receive human visitation, given that the windblown infructescences may float for some weeks, it is also possible that *Trachyandra divaricata* arrived there as a component of flotsam.

Along the east coast of Australia *Trachyandra divaricata* was collected in 1968 at Fairy Meadow, north of Wollongong (Fig. 6). Since then it has been collected at, or reported from, several other locations along the Central Coast of New South Wales with Anna Bay, north-west of Newcastle, as the furthest location in northern direction and Killalea Beach, 30 km south of Wollongong, the furthest south. At most if not all of these sites dune restoration work has been carried out, often including planting of *Acacia saligna*, a species endemic to Western Australia. Therefore, it is likely that *Trachyandra divaricata* arrived as a contaminant of *Acacia saligna* seed or planting stock. Although some substantial populations have become established in the vicinity of these restoration sites, the 1987 dune vegetation survey of New South Wales (Clarke 1989a, b) has not come across occurrences elsewhere.

The likelihood of further spread

The climates of the coastal regions of southern Australia and southern Africa have a great deal in common (Fig. 1). Of the various climate classifications available, that of Köppen has been used, but other classifications, for instance the one devised by Walter and Leith (1967), would have given a similar pattern.

In southern Africa, *Gladiolus gueinzii* occurs from the humid warm climates with mild winters (Cfa, Cfb) in the south-east to the semi-arid conditions prevailing towards the western end of its range (BSk). In Australia, *Gladiolus gueinzii* is at this stage restricted to shores with Cfa and Cfb regimes which however have a less pronounced seasonal difference in rainfall than is the case in South Africa, where rainfall in winter is lower than in summer. Although it would appear from a comparison of the maps that there is no climatic barrier to *Gladiolus gueinzii* extending its range in New South Wales, the lesser seasonality of the rainfall may cause conditions to be unsuitable. Another possibility is that in both directions successful establishment is prevented by a temperature factor, especially in the south, where on average winter temperatures fall outside those experienced along the southern coastline of Africa. If that is the case, then *Gladiolus gueinzii* has about reached its limits in south-eastern Australia. However, an introduction into the more seasonal and drier areas along the southern coast of the continent could provide an opportunity for further colonisation.

Trachyandra divaricata occurs along the coasts of the south-western corner of the African continent (Fig. 1). It is a common and widespread dune plant in the Cape Town region, which has a Mediterranean climate (Csb), and the adjacent coasts, which are semi-arid (BSk). To the north *Trachyandra divaricata* is found also in the arid region of the Namib (BWk). Along the southern coast its distribution extends into the area with a marginal Cfb climate (mapped by Walter & Leith (1967) as transitional between Csb and Cfb). It reaches its eastern limit where summer rainfall markedly increases. In the south-western tip of Western Australia *Trachyandra divaricata* has found a close match with the climate prevailing in the Cape Town region, although winter rainfall is somewhat higher. The Mediterranean climate (Csa, Csb) extends along the coast northward as well as eastward, eventually giving way to much drier climates (BSh, BSk). Hence, climate-wise, there appears to be no impediment for *Trachyandra divaricata* to considerably enlarge its distribution in this corner of the continent.

In contrast to south-western West Australia, the Central Coast of New South Wales receives on average ample rain all year round. As this type of climate lies outside any regime that *Trachyandra divaricata* is subjected to in its native range, it is possible that this at least partly explains why in the more than 35 years since *Trachyandra divaricata* was first reported, it has not aggressively spread. Nevertheless, in case aggressiveness takes a turn for the worse, it would appear desirable to eradicate occurrences in New South Wales while this is still achievable.

Wetter and cooler conditions could also have contributed to the fact that *Trachyandra divaricata* did not spread from Coode Island. But as the island is a busy harbour facility, it is just as likely *Trachyandra divaricata* disappeared due to quite different causes.

Conclusion

I have outlined possible scenarios for the spread of *Gladiolus gueinzii* and *Trachyandra divaricata* along sections of the coast of southern Australia. The data for this were obtained from herbarium records and augmented with other information on location-specific occurrences. Both species are wind-dispersed, although the capacity of *Trachyandra divaricata* for this mode of dispersal is far superior to that of *Gladiolus gueinzii*. The reason for this is not only a much larger seed production, but also the fact that the entangled ripe infructescences function as tumbleweeds. However, to explain various disjointed occurrences satisfactorily, human-mediated transport was suggested to be another important factor in the spread of this species.

Gladiolus gueinzii forms cormels, which can stay afloat for many months if they have been washed out to sea. This provides a means for long-distance dispersal and appears to have been the main agent for its relatively rapid spread along the coast of New South Wales. The buoyancy of *Trachyandra divaricata* infructescences lasts at best for only a couple of weeks and as many seeds will have dropped out before the sea is reached, this mode of dispersal is presumed to be of only minor importance in this species.

At some stage each species was introduced at locations with climatic conditions favourable for their colonisation. *Gladiolus gueinzii* has so far remained within its 'natural' range and further spread may be curbed by conditions either too hot or too cold for its survival, but *Trachyandra divaricata* is likely to enlarge its range as there appear to be no climatic barriers to prevent this from happening. In contrast, where it has been found outside its 'natural' climatic bounds, it has either disappeared or only spread to a limited extent, which was, probably more often than not, solely due to fortuitous human assistance.

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