Review

The Biology of Australian Weeds 31. *Oxalis pes-caprae* L.

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Name

Oxalis, derived from the Greek *oxys* meaning sour or sharp tasting, is a Greco-Latin word used for certain plants with acidic sap. Linnaeus (1753) narrowed its use as a generic name to include only plants we now know as members of the family Oxalidaceae. Although it was first described as *O. pes-caprae* L., Thunberg (1781), cited by Symon (1961) and Michael (1964), named the species *O. cernua* Thunb.; *cernua* referring to the night time drooping, or nodding movements associated with the foliage and flowers (Clarke 1934). Because *cernua* was so widely accepted, this name was preferred until Salter (1939) had the original name re-established. The name *pes-caprae* comes from the Latin *pes* meaning foot and *caprae* of a goat, suggesting that the shape of the leaf is like a goat's foot (Parsons and Cuthbertson 1992). Oxalidaceae is a small family of eight genera containing some 900 species of mostly herbs with fleshy rootstocks and an acid taste (Parsons and Cuthbertson 1992).

There are many common names for *O. pes-caprae* L. Soursob or soursobs are the main common names in Australia (Clarke 1934), while in South Africa it is referred to as geelsuring, oxalis, sorrel and yellow sorrel (Parsons and Cuthbertson 1992). These authors also list buttercup oxalis as a common name in the UK and USA and cape cowslip for the UK. Sourgrass, Bermuda buttercup and cape sorrel are also mentioned by Howes (1974).

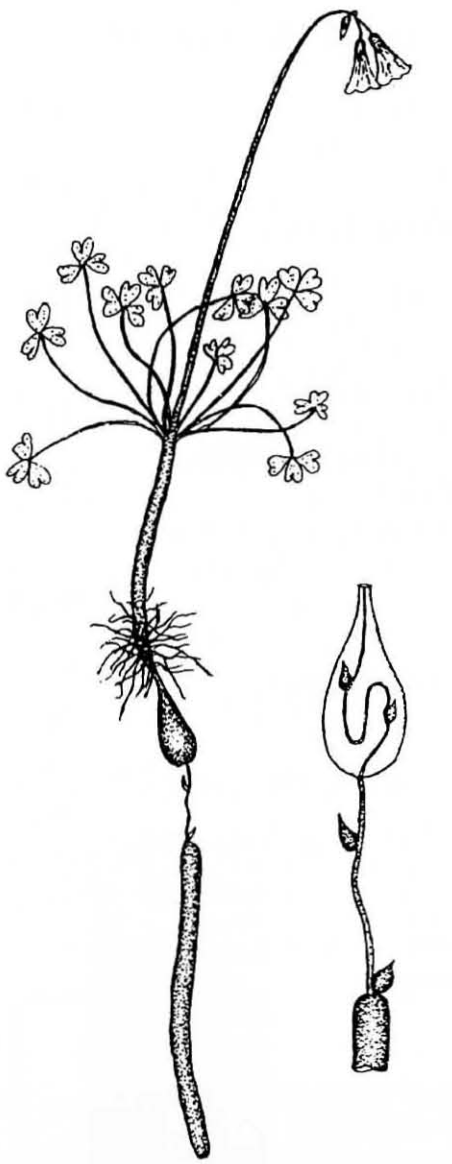

Figure 1. Mature *Oxalis pes-caprae* showing bulbs along the thread from parent bulb to contractile organs (from Peirce 1973).

Description

Detailed descriptions of *Oxalis pes-caprae* have been given by Clarke (1934), Salter (1944), Meadly (1955), Michael (1958), Parsons (1973), Peirce (1981, 1983), Lander (1987) and Parsons and Cuthbertson (1992).

The following description is adapted from Clarke (1934): '... an almost glabrous perennial, with an annual vertical subterranean stem 2–8 mm thick at ground level but tapering below into a fine thread-like extension which connects to the parent bulb. The whitish, mostly unbranched stem has numerous hair-like adventitious roots and one to several bulbs in the axils of scale leaves. Often below the bulb is a fusiform translucent structure formed by the tuberization of one of the secondary roots.

At ground level the stem produces leaves which consist of a short, flattened leaf base, a long, cylindrical petiole up to 13 cm long, and three terminal digitate leaflets. Leaflets are obcordate, two-lobed, 1–4 cm broad, often marked with small purple spots. Flowers are yellow, drooping, 3–16 in umbels on long radical peduncles. Sepals 6 mm long have two orange calli at their tips; petals 25 mm long; inner stamens longer, each with a staminodial appendage towards the base. Capsule oblong-acuminate, rarely maturing in Australia. Flowering takes place during June–October'. The plant is illustrated in Figure 1.

Salter (1944) described *O. pes-caprae* in South Africa as a variable species. Michael (1964), after studying many of the infestations through the southern states of Australia, also concluded that considerable variation existed within Australia. He identified major differences in markings on the sepals, size and colouring of the petals as well as differences in shape and markings on the leaflets. More recently, Peirce (1973) expanded the number of variations of leaflets illustrated by Michael (1964) from six to 13. Most of these were made from collections around the older town sites and the Perth metropolitan region of Western Australia.

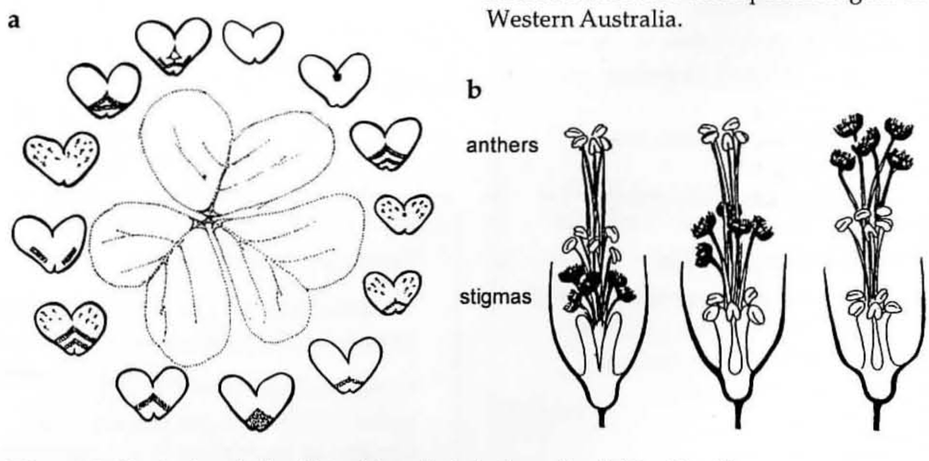

Figure 2. Variation in leaflets (a) and style-lengths (b) in *Oxalis pes-caprae* (from Peirce 1973).

According to Michael (1964) the infestations in South Australia and eastern Australia are of one stable 'variety', although some few years later Alcock (1968) described variants from the Eyre Peninsula. In Western Australia, clonal infestations are quite common in agricultural areas (Michael 1964, Peirce 1973). Including agricultural infestations, some 33 variants have been recognised in Western Australia (Peirce 1973). The main leaflet markings are presented in Figure 2a.

Within the bulb-forming *Oxalis* species, *O. pes-caprae* belongs to the group having outer bulb scales for protection and inner scales for food storage. Of the yellow flowered species having flowers borne in false umbels, *O. pes-caprae* can be distinguished by: (1) presence of crowded bracts at the base of the umbel of flowers, (2) stalked flowers, (3) a relatively robust habit of growth, (4) rounded (not flattened) leaf stalks, and (5) the presence of a few hairs on the underside of the leaflets (Clarke 1934).

Flowers of *O. pes-caprae* are tristylic and described as short, mid and long styled (Figure 2b), depending on the position of the stigmas relative to the two whorls of anthers (Michael 1964).

According to Michael (1964) the short styled plant with flecked leaflets, most common in Australia and the Mediterranean, is a pentaploid ($5n = 35$). Other varieties in South Africa (Marks 1956) and Australia (N. Marchant unpublished data) have been identified as tetraploids ($4n = 28$).

Baker (1965) also suggested the possibility of existence of a hexaploid ($6n = 42$) which may have crossed with a tetraploid to form the pentaploid. Although many tetraploids of different style lengths exist, it is thought that the pentaploid as described by Clarke (1934), Meadly (1955) and Parsons and Cuthbertson (1992), is present only as short-styled plants (Michael 1964).

There are various keys for identifying the species of *Oxalis* in Australia (Black 1948, Symon 1961, Michael 1965c, Thompson 1982, Jessop and Toelken 1986, Lander 1987, Conn and Richards 1994).

History

Detailed accounts of the origin and spread of *O. pes-caprae* have been given by Clarke (1934), Michael (1964) and Parsons and Cuthbertson (1992). *O. pes-caprae* is of South African origin (Salter 1944), and was deliberately introduced to England in the mid 18th century as an ornamental plant (Clarke 1934). Records suggest that it was cultivated from as early as 1757 and by the 1790s was listed in catalogues of garden plants in Europe (Clarke 1934). Today the weed is widespread through many countries including India, Morocco, Portugal, New Zealand, Spain and USA (Holm *et al.* 1979). According to Galil (1968) the spread into the Mediterranean was from the early introductions into England and western Europe. From there *O. pes-caprae* gradually moved eastwards and was introduced into Israel in the late 19th century. The plant is now a well established weed in North Africa (Algiers) (Ducellier 1914), Greece–Crete (Damanakis 1976, Protopapadakis 1985, Damanakis and Markaki 1990), and Sardinia (Leoni and Nieddu 1985). Introduction into Malta occurred about 1810 (Brandes 1991). According to Magnifico (1984) *O. pes-caprae* is only a 'new' weed of importance in Italy. An account of the spread in the Mediterranean is given by Marshall (1987).

As in England, Europe and the Mediterranean, it is probable *O. pes-caprae* was deliberately introduced into Australia as an ornamental garden plant. The history of the common pentaploid variety and the many tetraploids in Australia is well documented by Michael (1964). He found considerable evidence to suggest that, because many garden catalogues contained illustrations of *O. pes-caprae*, or at least a mention of its availability, the introduction in most cases would have been intentional. The Hackney Nursery in Adelaide, established by a former employee of the Loddiges Nursery at Hackney in London, listed *O. pes-caprae* under the previous name *O. cernua* in 1845 (Michael 1964). By the 1860s it was recognised as a weed of cereals (Clarke 1934). *O. cernua* was included in a list of plants grown by Sir William MacArthur at Camden, New South Wales. Ewart (1907) mentions that *O. pes-caprae* was widespread in Victoria, leading Michael (1964) to conclude that the weed must have been introduced considerably earlier than 1885, when it was first recorded in the National Herbarium of Victoria. Records show that *O. pes-caprae* was recorded in Tasmania in 1865 and Queensland in 1875 (Michael 1964).

In Western Australia both deliberate and unintentional introductions may have occurred (Michael 1964). While visiting the original farming property of James Drummond, who farmed in Western Australia in the early 1840s and was known to have had dealings with Loddiges Nursery in London, Michael (1964) found the pentaploid variety of *O. pes-caprae* growing around old fruit trees and ornamentals. The presence of seeds or bulbs in soil surrounding rootstocks was probably the main method of entry of the tetraploid varieties (Michael 1964, Peirce 1973, 1983). All stylar forms are present in South Africa (Salter 1944), and since many of the vine and fruit rootstocks introduced into Western Australia came from Mediterranean countries (Battye 1913), there is a strong possibility that *O. pes-caprae* entered as a soil contaminant. Due to the demand for fruit during the gold rush of the 1880s, more fruiting material was obtained from eastern Australia (Battye 1913), hence the possibility that more *O. pes-caprae*, in particular the pentaploid variety, was introduced. The results of these separate introductions are still visible today throughout the Swan Valley vineyards and a few agricultural infestations, where distinct variants are present on neighbouring properties.

Distribution

Australia

Oxalis pes-caprae is present in all States and Territories of Australia (Michael 1958, Parsons and Cuthbertson 1992) (Figure 3). In New South Wales the common pentaploid clone is present in southern coastal towns, south-west slopes and the Riverina area (Michael 1964). The distribution for Victoria has been given by D.N. McKenzie (personal communication), Parsons (1973) and Parsons and Cuthbertson (1992). *O. pes-caprae* occurs throughout that State, with large infestations present in the Wimmera and southern Mallee wheatlands.

The main infestations in South Australia are on the Adelaide Plains, Yorke and Eyre Peninsulas (Symon 1961, Alcock 1968, R.J. Carter personal communication, M.J. Catt personal communication). Stride (1960) suggested that dense infestations could cover between 6500 and 10 500 km^2. More recently R.J. Carter (personal communication) indicated that surveys in 1985 showed about 8000 km^2 of the Eyre Peninsula and west coast of that State to be infested.

Michael (1964) found many variants of *O. pes-caprae* around old town sites in the south-west of Western Australia, including paddock infestations of a tetraploid along the Avon Valley near York. A more recent distribution was given by Peirce (1983), showing infestations of the pentaploid variety along the Moore, Greenough, Avon and Dale rivers. Further infestations are present in cereal and sheep areas at Bruce Rock 200 km east of Perth, and Wagin 240 km south-east of Perth.

Oxalis pes-caprae occurs in Tasmania (Hyde-Wyatt and Morris 1975), Queensland (Everist 1959) and at Alice Springs in the Northern Territory (Chippendale 1964), but is much more restricted than in other States.

Outside Australia

Both the tetraploid and pentaploid *O. pes-caprae* are native to South Africa (Salter 1944). Baker (1965) suggests that tetraploids have limited establishment in North Africa, India and Australia, while the pentaploid is found in Europe, Mediterranean countries, Africa, Australia, Eastern Asia, South America, and western North America. From Ducellier's (1914)

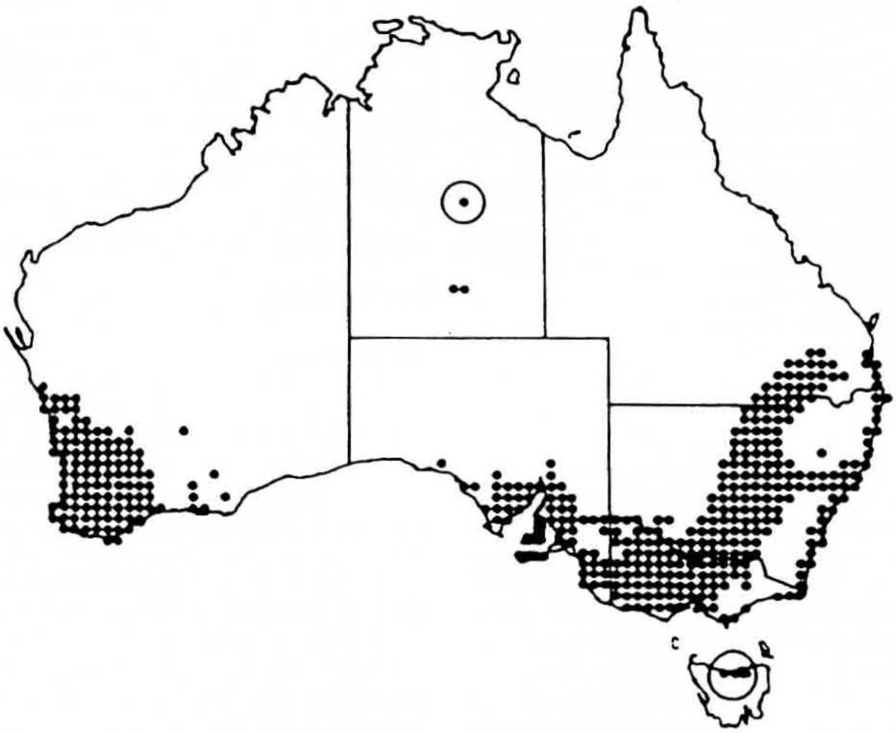

Figure 3. Distribution of *Oxalis pes-caprae* in Australia (from Parsons and Cuthbertson 1992).

description the pentaploid is common in North Africa, Spain, France, Italy, Greece, Asia Minor, the Canary Islands and the Isles of Madeira. Galil (1968) indicates that the pentaploid is widespread on the coastal and inland valleys of Israel. The world distribution is also given by Marshall (1987).

Habitat

Climatic requirements

The weediness of *O. pes-caprae* is mainly associated with Mediterranean-type climates, i.e. dominant winter rainfall and dry summers, but the plant grows from areas of sub-humid and semi-arid warm temperate to sub-tropical regions (Parsons and Cuthbertson 1992). The absence of severe frosts is also important (Clarke 1934, Michael 1958, Parsons and Cuthbertson 1992). Ducellier (1914) found *O. pes-caprae* favoured the milder Mediterranean climates associated with the coastal areas of Algeria. In Australia it is found where the average annual rainfall exceeds 330 mm (Catt 1972). Peirce (1979) showed that the rate of bulb sprouting (in the absence of moisture) was very sensitive to summer temperatures. Soil temperatures above 30°C and below 10°C reduced sprouting to less than 20% for two tetraploid and one common pentaploid variety (compared to 60–80% for bulbs stored at 20°C) and delayed sprouting by 13 and 20 days at 10 and 30°C respectively. The tetraploids were more sensitive to the lower temperatures.

Substratum

Henslow (1910) observed *O. pes-caprae* growing on range of soils varying from infertile to 'rich'. According to Parsons and Cuthbertson (1992), *O. pes-caprae* is found mainly on fertile, heavy soils that are well drained. Galil (1968) indicates that in Israel the plant is found growing on a wide range of soils. In South Australia the weed is present on fairly fertile mallee red sandy loams in the lower Murray Basin (Williams 1970), and on the lateritic podsols, solodized solonetz and red-brown earths in the lower and eastern Eyre Peninsula (Bicknell 1970). On the upper Eyre Peninsula *O. pes-caprae* is present on light brown sands that are about 60 cm deep and overlying clay (Holden 1970). In the upper north (Mowatt 1970), lower north (Michelmore 1970) and Yorke Peninsula of South Australia (Webber and Matz 1970), *O. pes-caprae* grows on the mallee loams and red-brown earth soils. Catt (1972) concluded that in South Australia there appeared to be no restriction on the type of soil where *O. pes-caprae* would grow.

Plant associations

In most of the Mediterranean region *O. pes-caprae* is mainly associated with olive, citrus or vineyards (Ducellier 1914, Damanakis 1976, Paspatis 1985, Protopapadakis 1985, Brandes 1991). In the USA *O. pes-caprae* is also associated with citrus orchards, but in addition is present in other crops such as artichokes (Hildreth and Agamalian 1985) and narcissus (Smith and Treaster 1990).

In Australia there is a common association with orchards (Michael 1958, Parsons and Cuthbertson 1992) but in addition there are significant infestations in cereal crops in South Australia (Michael 1958, Catt 1972, and Blowes 1984), Victoria (McKenzie 1973, Mahoney 1982b, Lane 1984, Parsons and Cuthbertson 1992) and Western Australia (Meadly 1955, Michael 1958, Peirce 1973). The presence of *O. pes-caprae* in cereals has also been mentioned in South Africa by Biljon *et al.* (1988).

Where *O. pes-caprae* is present in agricultural situations, adjacent domestic gardens are also usually infested (Ducellier 1914, Symon 1961). Cultivation appears to be a common link with most *O. pes-caprae* infestations. However there are infestations in non-cultivated olive groves (Leoni and Nieddu 1985) and pastures (Michael 1964).

Growth and development

Morphology

The elongated shape and tough nature of the coats surrounding the bulbs and bulbils make them less prone to damage by crushing during cultivation (Galil 1968). A contractile root forms soon after sprouting by the enlargement of one of the roots arising at the base of a bulb or bulbil. It has the dual purpose of water and nutrient storage and assisting in bulbil dispersal (Thoday 1926). This structure is common to a number of *Oxalis* species (Rimbach 1895, Rohde 1928, Jackson 1960, Chawdhry and Sagar 1974a). Ducellier (1914) gives an account of these structures on *O. pes-caprae*, but more thorough treatments and illustrations of contractile roots and their function in *O. pes-caprae* are given by Clarke (1934) and Galil (1968).

The distance and angle at which the new bulbs are moved down and away from the parent plant are controlled by the depth of the parent bulb, the moisture status of the soil and resistance the soil offers to the contractile tubers pulling the bulbs away from the parent plant (Galil 1968). Parent bulbs close to the surface tend to form contractile tubers which pull the new bulbs vertically into the soil, while parent bulbs at 15–20 cm depth in the soil tend to form contractile tubers that are horizontal to the parent bulb, hence moving the new bulbs away, up to 47 cm, from the parent plant when contraction is complete (Galil 1968). In studies undertaken by Pütz (1994) measurements were taken to quantify the pulling forces exerted by the contractile tubers.

Under situations of high soil moisture, other contractile roots are formed immediately below the crown of the plant at the soil surface (Hyde-Wyatt and Morris 1975, Peirce 1983). These structures may serve mainly for water and nutrient storage because as there are several formed radially

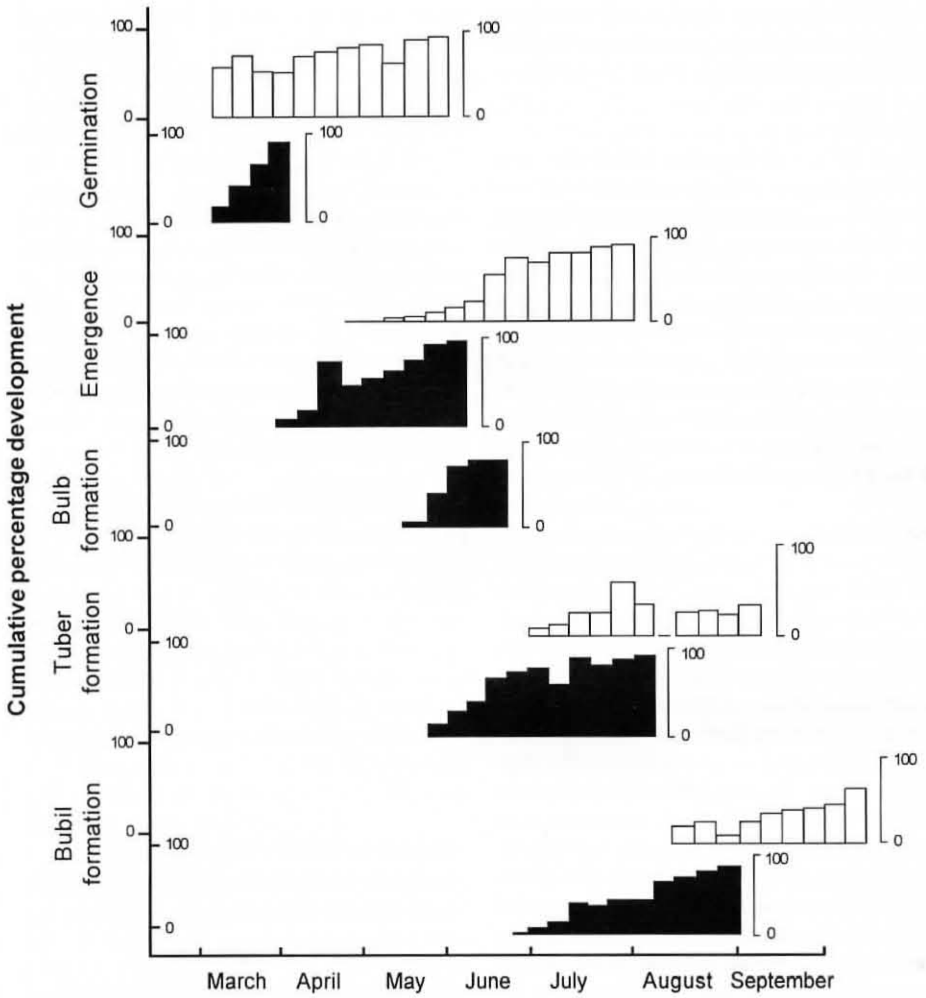

Figure 4. Development of *Oxalis pes-caprae* in Victoria; □ 1976, ■ 1977 (from Mahoney 1982b).

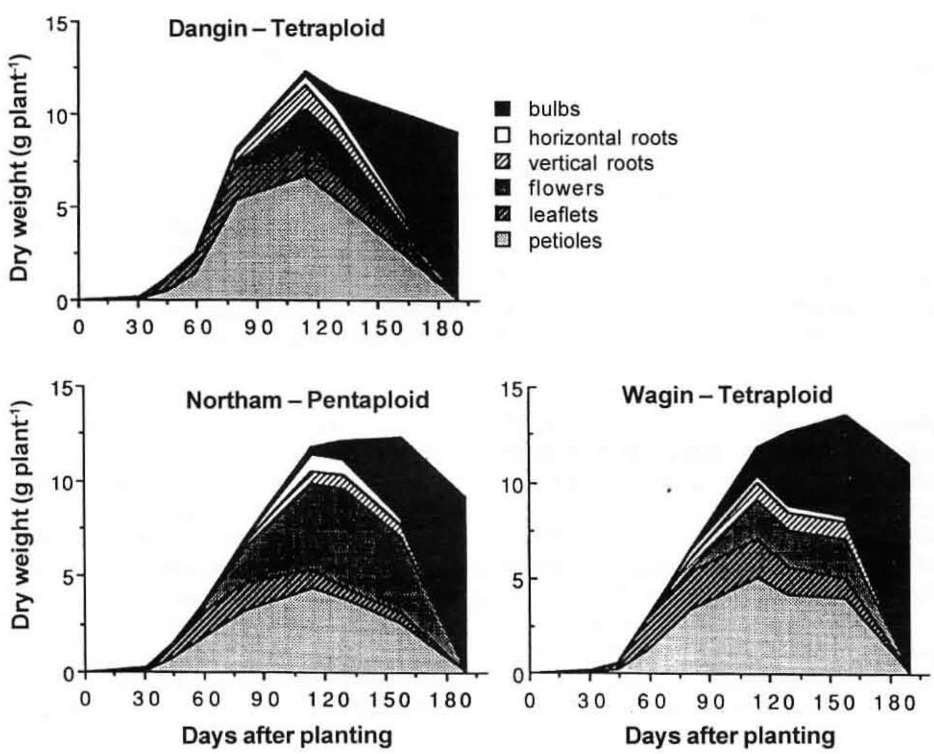

Figure 5. Initiation and dry weights of various organs of three variants of *Oxalis pes-caprae* from Western Australia (from Peirce 1983).

around the crown on each plant, any contraction would be at opposing angles. Sometimes there are bulbs associated with these surface contractile organs. If the roots were to break away from the stem, contraction might aid bulb dispersal (Peirce 1983).

Perennation

Oxalis pes-caprae, although giving the appearance of an annual plant because it dies back at the end of each growing season, is considered a perennial because it produces bulbs (Clarke 1934).

Physiology

Oxalis pes-caprae is extremely sensitive to light, the flowers responding by opening and following the sun's path and closing as the light intensity decreases (Clarke 1934). Movable joints (pulvini) located at the bases of stalks of flowers, leaves and the junctions of leaflets effect this and other movements.

The plant appears suited to either full sun or shade conditions (Galil 1968), although Clarke (1934) suggests these conditions lead to marked differences in the morphological appearance of plants.

Other species of *Oxalis* have been shown to vary in height, leaflet width, chlorophyll content, and seed production depending on light intensities (Packham and Willis 1977). Growth differences in height (leaf petiole length) and size of leaves has been illustrated, but not measured, in *O. pes-caprae* by Clarke (1934).

Growth rates of various parts of a pentaploid *O. pes-caprae* are given by Michael (1965a). In addition to the pentaploid, growth of two tetraploids from infestations in Western Australia was described by Peirce (1983). Compared to the tetraploids, the pentaploid variant made much more growth during the first 60 days after sprouting. The tetraploids then made considerably more leaf growth and produced more bulbs. Lane (1984) indicated that numbers and dry weights of leaflets of the pentaploid were strongly related to size of bulb from which the plants developed. Flower production is also higher in the pentaploid (Peirce 1983).

From limited studies, Clarke (1934) found that the levels of total oxalates in leaves decreased from 29–25% as the age of the plant increased through June–August and suggested that this was due to the increasing intensity and duration of light. Similar trends have been reported by others but the high values quoted appear to be questionable. Oxalate levels of about one third of those presented above were given by Hickinbotham and Bennett (1931), the former author supervising the analysis quoted by Clarke (1934). Michael (1965a) also showed a similar trend of decreasing percentage oxalate as age of the plant increased in the same pentaploid as studied by Clarke (1934), the levels being in the order of 10% declining to about 6% in the same period. Peirce (1983) carried out similar analyses on the common pentaploid and two tetraploids from Western Australia. Similar trends were found, with declining total oxalate from 6–8% (39 days), to 3–5% (59 days), rising to 8–10% (80 days after planting) and then declining rapidly with age. There was also a noticeable difference between variants of *O. pes-caprae*, with one of the tetraploids having a much higher oxalate content.

Some attempts had been made in Australia to analyse for crude protein, fat, carbohydrate, fibre, ash and oxalic acid (Hickinbotham and Bennett 1931). Similar studies have been carried out in the Mediterranean by Maymone *et al.* (1960), cited in Michael (1965a) and Biondo and Socini (1960).

Phenology
Growth and development studies of the pentaploid in Australia reported by Michael (1965a) identified three stages during the life cycle where changes in oxalate metabolism/transport corresponded to distinct growth stages. These were:

i. at the time of old bulb exhaustion (day 39–53) when there is a slowing in rate of oxalate production relative to dry weight. Leaflet oxalate is at its lowest during this time;
ii. at the beginning of development of bulbs and flowers, when there is a decrease in oxalate content while tuber development is increasing. By day 76 petiole oxalate is at its lowest;
iii. at the onset of senescence where there is a significant decrease in total oxalate.

Chawdhry and Sagar (1973), using autoradiography, identified 10 developmental stages in relation to the distribution of assimilates from radioactive carbon dioxide fed to aerial parts of the plant.

When plants were grown under uniform growth conditions in a glasshouse, Lane (1984) found a development timetable similar to that proposed by Michael (1958). Moisture availability influenced time of emergence (Mahoney 1982b), as did bulb size and depth of bulb placement (Lane 1984). Mahoney (1982b) studied undisturbed populations of the short styled pentaploid over two years in the Victorian mallee and concluded that although bulb germination commenced about the same time during early March in both years, emergence, bulb exhaustion, tuber formation, new bulb formation, flowering and senescence varied greatly in time of initiation and rate of development (Figure 4). Time and incidence of frosts and rainfall as well as the amount of the latter were the main influences. The phenology for three clones of *O. pes-caprae* in Western Australia indicates that there are marked differences in the initiation of various organs, particularly between the pentaploid and tetraploids (Peirce 1983) (Figure 5).

Mycorrhiza
There is limited documented evidence of the existence of an association of *O. pes-caprae* with mycorrhizae. Infection of *O. pes-caprae* by vesicular-arbuscular mycorrhizal spores, mainly *Acaulospora laevis* Gerd. and Trappe, was shown to be low by Smith (1984). Another *Oxalis* species, *O. corniculata* L., was shown to have 93% of root segments colonized by vesicular-arbuscular mycorrhizae mainly from the *Glomus* genus (Saif and Iffat (1976) cited by Lovett Doust *et al.* 1985).

Reproduction

Floral biology
The trimorphic arrangement of flowers is common within the genus *Oxalis* (Clarke 1934). According to Ornduff (1964), in tristylous species, plants of three kinds exist: plants having flowers with long styles and anthers at two levels below the stigmas; plants having mid-styled flowers with one set of anthers above and another below the stigmas; and plants with short-styled flowers with two levels of anthers above the stigmas. Tristyly is associated with mechanisms of cross pollination by bees and butterflies (Clarke 1934). Pollen from anthers on another flower, at the same level as the stigmas, is required before seed formation can take place (Symon 1961). However, Ornduff (1964, 1972) suggests that while the most productive crosses occur with this arrangement, less productive crosses can occur with pollen from anthers at different levels to the stigmas. The expression of tristyly in *O. pes-caprae* (Figure 2b) is not well documented, but for other *Oxalis* species, Ornduff (1964, 1972) suggests that tristyly is controlled by two unlinked loci.

Seed production and dispersal
Seed production by the pentaploid *O. pes-caprae* in Australia is uncommon (Clarke 1934, Michael 1964), while tetraploids will seed freely, providing plants having different style lengths are present (Michael 1964). Dehiscence of seed capsules is through loculicidal slits on the abaxial sides of the carpels, when a turgid aril everts and ruptures (Robertson 1975 cited by Lovett Doust *et al.* 1985). The force of ejection can scatter seeds up to 2 m from the parent plant (Lovett Doust *et al.* 1985).

There is no record of other agents dispersing the seed of *O. pes-caprae* in Australia. In other species of *Oxalis* it is common for some rodents to utilize the seeds in their diets, but no testing has been done to assess the viability of seeds after passage through the rodent's digestive tract (Lovett Doust *et al.* 1985).

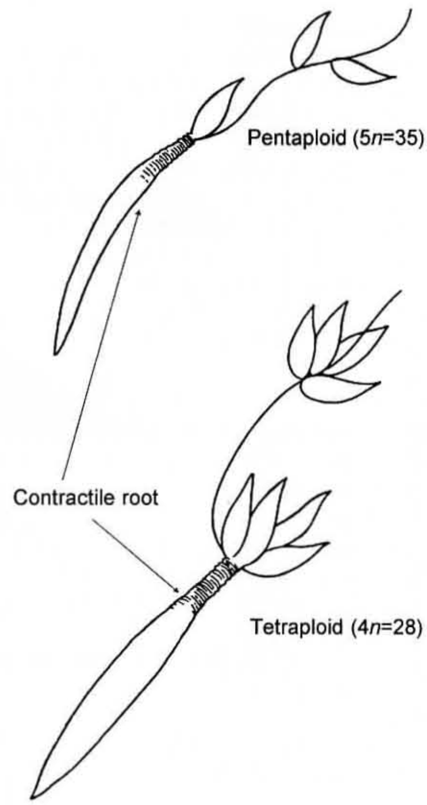

Figure 6. Variation between two variants in bulb formation on tuber and thread (from Peirce 1983).

Physiology of seeds and germination
There have been limited observations, probably due to the low frequency of crossing in Australia, on the seeds of *O. pes-caprae*. Seeds collected in the field or from plants housed in glasshouses in Western Australia appear to have little dormancy and germinate readily under cool moist conditions (J. Peirce unpublished data). Seedlings were often detected on the damp cement floors under tables supporting *O. pes-caprae* plants. Seeds stored for more than 12 months at room temperature failed to germinate when tested (J. Peirce unpublished data).

Vegetative reproduction
Although seed formation is important where clones of different style length grow in close proximity, the major method of reproduction in *O. pes-caprae* is from the production of bulbs (Clarke 1934, Galil 1968, Michael 1965b, Catt 1972, Peirce 1983, Lane 1984). Bulbs are produced on tubers and along the rhizomes. Their initiation usually commences between 80 and 114 days after the parent bulbs have sprouted under artificial conditions (Michael 1965a, Peirce 1983), and between mid-June and mid-August (105–150 days) under field conditions (Mahoney 1982b).

Mahoney (1982b) recorded bulb production of 20 per plant on small parent plants and up to 50 from large healthy plants. Average values of 10 per plant were recorded in Israel, with up to 30–40 per plant under warm winter conditions (Galil 1968). Under glasshouse conditions bulb production varied from an average of 19 per plant for the pentaploid, to 28–34 per plant for two tetraploid variants of *O. pes-caprae* from Western Australia (Peirce 1983). The higher value recorded for one of the tetraploids was mainly due to the multiple number of bulbs formed at each of the bud scales on the tuber and along the rhizome, compared to only single bulbs arising at similar positions for the other variants (Figure 6). Lane (1984) recorded average bulb numbers of about 11 per plant under glasshouse conditions in Victoria.

Dispersal of the bulbs can be localized due to the action of the contractile roots drawing the bulbs at an angle away from the plant, as illustrated by Clarke (1934) and Galil (1968). In addition, bulbs are transported in mud, and because they are light, Clarke (1934) considers that wind plays a major role. Bulbs float on water so this would also be significant, particularly in Western Australia where *O. pes-caprae* is associated with some major rivers and drainage systems (Peirce 1973).

Cultivation, particularly using tined implements, has been responsible for dragging plant fragments which are capable of regenerating and producing bulbs (Parsons and Cuthbertson 1992). Intentional propagation in home gardens or in soil nursery stock has aided dispersal, particularly where orchards and farm house sites were abandoned and came under cultivation. Birds have also been implicated in moving bulbs (Parsons and Cuthbertson 1992).

Hybrids

The presence of hybrids in field infestations is uncommon. However, around town sites there are often different style lengths present within an infestation and free seeding plants produce a range of variation (Michael 1964). This author reported that double-flowered varieties occur in South Africa and the Mediterranean regions and that variation is more obvious in South Africa. According to Michael (1964), hybrids of crosses between the pentaploid and tetraploids have occurred at Albany in Western Australia. Alcock (1968) recorded the presence of all three style lengths on the Eyre Peninsula in South Australia and his illustrations of the variation of petal, sepal and leaflet markings as well as seed capsules would indicate that considerable crossing has occurred. Some 33 variants were noted in a survey conducted in Western Australia (Peirce 1973).

Population dynamics

Despite its competitiveness, particularly in cereal crops (Clarke 1934, Michael 1965, Catt 1972, Peirce 1973, Mahoney 1982a, Lane 1984), *O. pes-caprae* is sensitive to the presence of other plants (Peirce 1983). Bulb production and weight in both tetraploid and pentaploid varieties were reduced by a factor of five when plants were grown in the presence of wheat and annual ryegrass (*Lolium rigidum* Gaudin). Bulb production of a tetraploid variety also decreased between 38 and 67% under field conditions in the presence various cultivars of subterranean clover (*Trifolium subterraneum* L.) (Peirce 1976). Measurements taken from an ungrazed pasture showed that the density of *O. pes-caprae* decreased from 890 to 560 plants m^{-2} in successive years (J. Peirce unpublished data).

The period over which growth occurs varies according to the availability of moisture (Lane 1984). Bulbs appear to become non-dormant over summer and sprout as temperatures fall, irrespective of the presence of moisture (Peirce 1978). In field situations this gives *O. pes-caprae* a competitive advantage over annual species as it is usually the first to appear after the break of the season. However the rate of emergence in any one season can vary between sites (Table 1). Emergence appeared to be strongly influenced by depth and friability of soils; shallow hard setting soils used for cereal production showed only about half the emergence in May compared to deep friable soils used for horticulture. Although no measurements of bulb sizes were taken it is thought that smaller bulbs were formed in the hard setting soils and after sprouting took considerably longer to reach the surface. Chawdhry and Sagar (1974b) indicated that bulb weight and numbers could be influenced by defoliation, and that the regular removal of top growth would prevent bulb formation.

Table 1. Emergence of *Oxalis pes-caprae* over time at three sites in Western Australia (J. Peirce unpublished results).

Site	Plants m^{-2} May	Plants m^{-2} July	Depth of deepest bulb (cm)
Northam (cereals)	750	2200	15
Swan Valley (vineyard)	1310	1490	>25
Chittering Valley (citrus orchard)	1220	1970	>25

Importance

Detrimental

Vigorous infestations of *O. pes-caprae* cause significant yield losses in cereal crops in Australia (Clarke 1934, Michael 1964, Catt 1972, McKenzie 1973, Peirce 1978, 1983). In vineyards in Australia (Stride 1960) and Greece (Paspatis 1985) its presence interferes with the growing of cover crops used to improve soil fertility. In Greece *O. pes-caprae* is considered the country's ninth most important weed as its presence under olive trees prevents the common practice of hand gathering of fruits from the ground (Damanikis 1976). Delfosse (1990) considered *O. pes-caprae* as a weed of 'sporadic' or 'geographically' limited importance to the dried fruit industry of Australia.

In addition to its competitiveness in cereal crops *O. pes-caprae* also dominates many pastures and because of its high oxalate content, is linked to stock deaths by oxalate poisoning, especially sheep (Bull 1929, Hickinbotham and Bennett 1931, Clark 1934, Gardner and Bennetts 1956, Dodson 1959, Everist 1959, Stride 1960, Gardiner and Royce 1963, Michael 1965a, Healy 1967, McIntosh 1972). Stock deaths have also been reported as well as poor meat and milk production in Sardinia due to the presence of *O. pes-caprae* in pastures (Leoni and Nieddu 1985).

The fodder value of *O. pes-caprae* is very low compared to other recognised green crops or mixed pastures. Hickinbotham and Bennett (1931) found that the plant had, in addition to the oxalate problems, high water content and low crude protein, fat, carbohydrate, fibre, ash and starch equivalent.

Oxalis pes-caprae is not known to host diseases that affect crops. However, Lovett Doust *et al.* (1985) reported that *O. stricta* L., *O. corniculata* L., *O. dillenii* Jacq. ssp. *dillenii* and *O. dillenii* Jacq. ssp. *filipes* (Small) Eiten hosted the maize rusts *Puccinia sorghi* Schw. and *P. polysora* Underw., sorghum rust *P. purpurea* Che. and Andropogon rust *P. andropogonis* Schw.

Beneficial

Oxalis pes-caprae is not usually regarded as a weed by orchardists/winegrowers in Australia, as its vigorous root system helps break up heavy soils, allowing aeration and moisture movement (Peirce 1973, Parsons and Cuthbertson 1992). The processes describing how the contractile roots and bulbs form these channels and the forces that are exerted are described by Pütz (1994) and Pütz *et al.* (1995). In addition, because the top growth dries off as summer approaches, the area beneath trees and vines is weed free and accessible during harvest. Paspatis (1985) made the same observation for southern Greece, claiming *O. pes-caprae* inhibited tenacious weeds such as *Parietaria* sp., *Amaranthus* spp. and *Chenopodium* spp. Apiarists believe the plant is also of some value to their industry (Parsons and Cuthbertson 1992).

Legislation

Victoria, Western Australia, South Australia, and Tasmania currently have legislation in place for *O. pes-caprae*. In Victoria it is a proclaimed noxious weed for the whole of the State except the Melbourne metropolitan area (Parsons and Cuthbertson 1992). More recently D. Lane (personal communication) has indicated that under a new act, The Catchment and Lands Protection Act, the list of noxious weeds will be reviewed and placed under four categories: I. Statewide prohibited, II. regionally prohibited, III. regionally controlled and IV. restricted. *O. pes-caprae* is assigned to the regionally controlled category in Horsham, Portland, Colac, Geelong, Central Gippsland and Melbourne regions. However, D. Lane (personal communication) suggests that in light of the availability of chemicals for control, *O. pes-caprae* will have a limited status as a noxious weed.

Western Australia lists *O. pes-caprae* under three categories according to its agricultural importance: P1 (prevention of introduction), P3 (requiring populations of plants to be reduced, using control measures) for the region of Cunderdin (160 km east of Perth) and P4 (containment preventing movement of the weed outside existing infestation boundaries) for the remainder of the State.

According to R. Carter (personal communication) it took some 25 years to gain a recommendation for the declaration of *O. pes-caprae* in South Australia. It was first proposed in 1940, but declaration was rejected because it was widely distributed and there were no control measures. After reports that it was possible to gain reasonable control and that *O. pes-caprae* had not reached its ecological limits, the Noxious Weeds Advisory Committee agreed to the proclamation in 1965 under the third schedule of the Weeds Act 1956–63 for a portion of the State, which included the South East and the Eyre Peninsula. It was subsequently proclaimed under the Pest Plants Act 1975 and the Animal and Plant Control (Agriculture and other purposes) Act 1986. The latter Act under section 52(2) restricts movement of the plant as a contaminant of soil and produce on public roads, sale of the plant, and produce/goods/soils carrying the plant (section 54(1)(2)) for the whole of the State. For part of the State, including the South East and the Eyre Peninsula and also any land used for extraction or removal of soil, loam, sand, gravel, the landholder is required under Section 57(2) to destroy the plant and inhibit its propagation as far as is reasonably achievable. Control boards can recoup the cost of control on roads under Section 60 from adjoining landholders.

Oxalis pes-caprae is declared a Secondary Noxious Weed under the Plant Protection Act 1994 for Tasmania (A. Harradine personal communication). Under this legislation, inspectors can prescribe control measures they consider appropriate.

Weed management

Herbicides

One of the earliest attempts at control of *O. pes-caprae* by chemicals was mentioned by Clarke (1934), who suggested the use of sodium chlorate. Despite the dangerous properties of the chemical, its use to kill the tops of *O. pes-caprae* was supported by Neal-Smith (1938). Bulb formation was suppressed by the soil fumigant sodium-N-methyldithiocarbamate when applied at the late post-emergence stage of growth (Marinos 1958). Some success in reducing the competitiveness of *O. pes-caprae* growing in a cereal crop by using 2,4-diclorophenoxy acetic acid was reported by Meadly (1955). Reduced bulb production and plant size was obtained using 2.2 kg a.i. ha^{-1} of fenoprop (2,4,5-trichlorophenoxy propionic acid) (Michael 1965c). The substituted urea herbicides linuron and diuron gave more permanent reductions in bulb numbers and at the same time worthwhile cereal yield increases in South Australia (Catt 1972) and Western Australia (Peirce 1978). Non selective control of *O. pes-caprae* has been achieved using 3-amino-1,2,4-triazole (Anon. 1961). Parsons and Cuthbertson (1992) mention paraquat and diaquat as being effective. Good control of *O. pes-caprae* became possible under many situations with the introduction of glyphosate (Mahoney 1982a, Peirce 1983, Blowes 1984, Parsons and Cuthbertson 1992). Mahoney (1982a) found that reductions in densities between 52–94% could be obtained in a cereal crop when glyphosate was applied at 0.54 kg a.i. ha^{-1} as a fallow treatment between June and August in the year prior to cropping. However, she found that this level of control was not accompanied by a cereal yield increase, and the optimum timing for the application varied considerably between experimental sites.

The introduction in the 1980s of the sulfonyl urea group of herbicides, namely chlorsulfuron at 12–15 g a.i. ha^{-1}, was so effective against *O. pes-caprae*, that it is now virtually eliminated as a problem weed in cereals in Australia (Peirce 1983, 1985, Parsons and Cuthbertson 1992). More recently another member of this group of compounds, metsulfuron methyl at 3 g a.i. ha^{-1}, has also been recommended for *O. pes-caprae* control in cereals (wheat and barley) (Peirce 1990). In South Africa triasulfuron at 10 g a.i. ha^{-1} gave 80% control of *O. pes-caprae* in wheat and barley (Biljon *et al.* 1988), but in Australia it is registered as giving suppression only (Parsons 1992). In Southern California control of *O. pes-caprae* was achieved with pre- and post-emergent applications of oxyfluorfen in globe artichokes (*Cynara scolymus* L.) (Hildreth and Agamalian 1985). Paspatis (1985) found that in addition to oxyfluorfen, mixtures with simazine, glyphosate, chlorthiamid and dichlobenil also gave good control of *O. pes-caprae* in vineyards in Southern Greece. This supports earlier work conducted in the same region by Damanakis (1976). The herbicides napropamide, oryzalin, prodiamine and isoxaben + oryzalin have all shown activity on *O. pes-caprae* (Smith and Treaster 1990).

Tables summarizing the various herbicides having activity on *O. pes-caprae*, prior to the introduction of the sulfonyl urea compounds, are given by Marshall (1987).

Other treatments

The use of cultivation followed by grazing from pigs or turkeys to consume the bulbs and tubers was suggested by Clarke (1934) after observing successes in the Gawler River area in South Australia. Clarke (1934) also recognised the value of cultivation and sowing a wheat crop, providing the crop was established early (April) so that it could compete with *O. pes-caprae* and prevent it from flowering. The timing of cultivation was also important; density of *O. pes-caprae* could be reduced by delaying seeding while several cultivations were undertaken.

Michael (1965b) quantified the levels of bulb reduction possible after cultivation treatments on the common pentaploid *O. pes-caprae* in South Australia (Table 2).

Table 2. Numbers and dry weights of bulbs in uncultivated and cultivated areas (from Michael 1965b).

	Bulbs m^{-2}	Total bulb dry wt (kg ha^{-1})	Mean bulb dry wt (g)
Stubble paddocks			
Uncultivated	5790	7220	0.13
Cultivated	2370	900	0.04
Pasture paddock			
Uncultivated	4830	2860	0.06
Cultivated	630	150	0.02

A single cultivation at the time food reserves in the parent bulb were exhausted was not entirely successful and a further cultivation was required later in the season to kill plants regenerating from stems and crowns of plants injured by the first cultivation. Mahoney (1982a) in field studies and Lane (1984) in glasshouse studies verified the ability of the plant to recover after a single cultivation and thus the necessity to use multiple cultivations. Other problems relating to soil types and conditions have been detailed by Catt (1972).

Michael *et al.* (1962) indicated that *O. pes-caprae* was susceptible to competition from dense legume pastures. Peirce (1976) measured the reduction of bulb numbers under various cultivars of subterranean clovers established in dense infestations of a tetraploid variant of *O. pes-caprae*. The percentage reduction of bulbs ranged from 67% (cv. Geraldton) and 60% (cv. Dwalganup) to around 38% in the presence of Clare and Dinninup cultivars. Under glasshouse conditions, annual ryegrass and wheat (cv. Gamenya) reduced bulb production by 77% (Peirce 1983).

Overgrazing of pastures can result in a significant shift of botanical composition, favouring *O. pes-caprae* (Carter 1995). A study conducted at the Waite Institute in South Australia indicated that at sheep stocking levels of 7.4–14.8 ha^{-1}, *O. pes-caprae* contributed only 0.8% of the sward, but when stocking levels were raised to 22.2 ha^{-1}, the *O. pes-caprae* content increased to 16.6%.

Natural enemies

Kluge and Claassens (1990) identified the noctuid moth, *Klugeana philoxalis* Geertsema, as a potential biological control agent. The egg, larval and pupal stages lasted 4–7, 22 days and up to 36 weeks respectively. Although larval feeding was not limited to *O. pes-caprae*, but extended also to other species within the genus *Oxalis*, *K. philoxalis* was still considered a likely candidate for biological control. Another noctuid moth, *K. swartlandensis* sp. nov., was also identified for potential activity on *O. pes-caprae* in South Africa (Geertsema 1990).

Parasitism of *O. pes-caprae* by *Orobanche* sp. was noticed in vineyards, citrus orchards and olive groves in Crete and may have potential for integrated control programs (Paspatis 1985).

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