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3

4 **Biological Flora of the British Isles: *Crassula helmsii***

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19 * Nomenclature of vascular plants follows Stace (2019) and, for non-British species, *Flora*

20 *Europaea*.

1 **Abstract**

- 2 1. This account presents information on all aspects of the biology of *Crassula helmsii* (Kirk)
3 Cockayne (New Zealand Pygmyweed, Australian Swamp Stonecrop) that are relevant to
4 understanding its ecological characteristics and behaviour. The main topics are presented within the
5 standard framework of the Biological Flora of the British Isles: distribution, habitat, communities,
6 responses to biotic factors, responses to environment, structure and physiology, phenology, floral
7 and seed characters, herbivores and disease, history, and conservation.
- 8 2. *Crassula helmsii* is an invasive aquatic macrophyte originating from Australia and New Zealand.
9 The first naturalised population was recorded in Britain in 1956. All British specimens appear to
10 represent a single lineage. DNA analysis indicates that British specimens originate from Australia.
- 11 3. *Crassula helmsii* is capable of growing in a wide range of lentic freshwater and riparian habitats. It
12 may grow as free floating, submerged, emergent or terrestrial forms. Morphology can differ
13 markedly on the same stem.
- 14 4. Flowers are produced, but with no known pollinators outside of its native range. Reproduction is
15 thought to be predominantly by asexual methods outside Australia and New Zealand, through stem
16 fragmentation and dispersal. Seed germination outside the native range appears to be very rare and
17 poorly understood.
- 18 5. *Crassula helmsii* has been and still is controlled by active management, because of fears that its
19 capacity to produce monocultures will lead to loss of biodiversity in the plant communities it
20 invades. Evidence for species losses due to colonisation by *C. helmsii* is rather anecdotal, although
21 suppression of native biomass through competition has been reported. No consistently effective
22 control procedures have been identified.

23

24 **KEYWORDS**

25 conservation, ecophysiology, geographical and altitudinal distribution, germination, management, non-
26 native invasive, reproductive biology

1 New Zealand Pygmyweed, Australian Stonecrop, Australian Swamp Stonecrop, Pygmyweed.

2 Crassulaceae. *Crassula helmsii* (Kirk) Cockayne is a succulent, glabrous, perennial, semi-aquatic,

3 herb with terrestrial, emergent, submerged and free-floating growth forms. Growth forms are not

4 mutually exclusive, with single specimens exhibiting multiple forms. Stems simple or branching

5 profusely at nodes to create overlapping growth and dense stands, rooting adventitiously at nodes.

6 Nodal spacing on stem shortest on terrestrial form, increasing with submergence / increased depth

7 in water column. Leaves in opposite pairs surrounded by a collar on the stem, connate at the base,

8 sessile, 2.3-7 mm long (4-10(-18) mm in Australia) x 0.7-1.6 mm wide (0.4-3 mm in Australia),

9 0.5-0.8 mm thick, narrowly lanceolate, oblong-lanceolate or elliptic lanceolate, flattened above and

10 strongly convex below, with apex rounded to an acute tip, margins entire, without conspicuous

11 venation. Leaf sheath 0.4-1 mm. Pedicels 2-8 mm, arising from upper leaf axils, not elongating at

12 fruiting, but recurving. Flowers solitary, star-like, 4-merous, 3-3.5 mm in diameter, bisexual. Petals

13 (3)4(6), 1.2-1.8 mm x 0.8-1 mm, broadly elliptic ovate, subacute, white or pink. Sepals 4, green, c.

14 half the length of petals, uniting in lower third, alternating with petals. Calyx lobes 1-1.5 mm x 0.5-

15 0.6 mm, triangular-ovate, acute or subacute, sepals narrowly ovate-oblong, obtuse to subacute.

16 Stamens 4, opposite the sepals, shorter than the petals, filaments slender, recurved; anthers small, 2-

17 celled, longitudinally dehiscent. Carpels 4, turgid, opposite to and shorter than the petals, free,

18 tapered to a truncated summit, styles short, \pm recurved, apical, with inconspicuous stigma. Each

19 carpel with a hypogynous, nectiferous scale similar in length to a young carpel, arising from its

20 base on the outer side; scales c. 0.7 mm, linear-oblongate, cuneately narrowed to the base.

21 Ovules c.8, not all developing, parietally attached on the inner angle of the carpel. Fruits consisting

22 of 4 smooth follicles, each c. 2mm long, splitting along the inner suture, tapered into the persistent

23 stylar beak, enclosing 3-5, elliptical, smooth seeds c. 0.5 mm long. Information compiled from

24 Laundon (1961), Aston, 1977, Vaughan (1978) Allan (1982), Swale & Belcher (1982), Dawson &

25 Warman (1987), Webb *et al.* (1988), Everett & Norris 1990, Dawson (1994), Toelken *et al.* (1996)

26 Preston & Croft (1997), Leach & Dawson (1999), Brunet (2002), Weber (2003), Smith (2015).

1 *Crassula helmsii* is a naturalised non-native species in the British Isles, probably resulting
2 from a single introduction before 1914; it is found exclusively within lentic waterbodies, where it
3 can become dominant, producing dense stands in ditches, scrapes, lakes and ponds (Dawson &
4 Warman, 1987, Brunet, 2002, Smith and Buckley, 2015), that can be continually wet or dry-out
5 temporarily during the summer.

6

7 **1 | GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION**

8 In the British Isles, *C. helmsii* is most abundant in England, with some preference towards the south
9 and east, which reflects its earliest colonisation patterns during the 20th century (Figure 1;
10 Braithwaite, Ellis & Preston, 2006). It is less abundant in Scotland and Wales, (Preston, 2002). It is
11 categorised as a lowland plant, with a maximum altitude of 345 m at Llyn Pendam, Cardiganshire
12 (Lockton, 2016). In Scotland, records are sparser and show some correlation with coastal areas and
13 loch edges at low altitudes (Figure 1), which is likely due to range expansion from its stronghold in
14 southern England. In its native range, it is present up to 900m in Victoria, Australia.

15 As a non-native, invasive species in Europe, the distribution of *Crassula helmsii* has been
16 monitored by the European and Mediterranean Plant Protection Organization (EPPO/OEPP). The
17 EPPO records the presence of *C. helmsii* in France, Belgium, Holland, Germany, Spain, Denmark,
18 Austria, Corsica, Ireland and Italy (Figure 2). It was previously recorded as being present in Russia
19 (EPPO, 2004), however a follow up study failed to locate it (EPPO, 2007). The first report of
20 naturalisation in Britain was in 1956 (Laundon, 1961). In continental Europe *C. helmsii*
21 introduction is more recent, with the first case reported from Belgium in 1982 (Dawson & Warman,
22 1987) and Holland in 1995 (Brouwer & den Hartog, 1996). It was first recorded in Germany in
23 1981, spreading to Hamburg, Hanover, Schleswig, Pfalzerwald and Westphalia (Leach & Dawson,
24 1999). *C. helmsii* is restricted to temperate regions of Europe (Sheppard *et al.*, 2006). It also occurs
25 as a non-native species in the USA in Washington, Florida and North Carolina – all east coast states
26 with similar temperate Köppen-Geiger climate zones (USDA, 2016). It is also noted as being

1 present in Minnesota and Wisconsin and noted as a high-risk species in the Great Lakes areas
2 (Gantz *et al.*, 2015).

3 Within its native range *Crassula helmsii* is distributed mainly in the south of Australasia, in
4 the states of New South Wales, Victoria, Tasmania, Western Australia and South Australia (Sainty
5 & Jacobs, 1981, Everett & Norris, 1990). In New Zealand it is present on the South Island from
6 41° to 42° 30' (Allan, 1982). It has also been reported from N.W. Nelson to Fiordland (Webb *et al.*,
7 1988) where it is considered sparse in its distribution (De Lange *et al.*, 2008).

8

9 **2 | HABITAT**

10 **2.1 | Climatic and topographical limitations**

11 The January mean temperature is 3.8°C in its British and Irish hectad distribution, with a July mean
12 temperature of 15.8°C (Hill *et al.*, 2004). Average annual precipitation in its British and Irish
13 hectad distribution is 826 mm (Hill *et al.*, 2004). In its native range, *Crassula helmsii* grows where
14 mean daily temperature ranges between 0 - 15°C in winter (May - Oct.) and 20 - 25°C in summer
15 (November - April) (Leach & Dawson, 1999). Leach & Dawson (2000) reported necessary rainfall
16 in its native range of 100 - 550 mm in summer and 220 - 300 mm in winter for the terrestrial form
17 (Leach & Dawson, 2000).

18 *Crassula helmsii* can be found in temporary lentic systems and remains viable but with
19 reduced vigour in years of low rainfall (Dawson & Warman, 1987). No apparent preference for
20 aspect is noted, with an ability to grow around the perimeter of waterbodies with consistent vigour.
21 Because of its low-growing nature, wind has little impact, although wind could be an agent for
22 distributing propagules across the surface of waterbodies. The multiple nodal branching of *C.*
23 *helmsii* enables the terrestrial form to knit into a loosely aggregated turf. This turf builds up a
24 damp, warm microclimate which may further stimulate growth (Smith, 2015).

25 *Crassula helmsii* is capable of surviving in shade, and is often found in woodland ponds and
26 other sites shaded by taller marginal growth (Smith, 2015). Wang *et al.* (2017) suggested that *C.*

1 *helmsii* had different climatic niches in its native and invasive ranges. However, an updated
2 classification of the Köppen-Geiger climate model shows the UK and most of North-west Europe to
3 be in the same climatic grouping (warm temperate, fully humid, warm summer) as the plant's
4 native range of south-eastern Australia and New Zealand (Kottek *et al.* 2006). The modelled impact
5 of climate change on distribution of *C. helmsii* in Ireland found no predicted change in the Irish
6 distribution of the plant up to 2080 (Kelly *et al.*, 2014). This single study suggests that climate
7 change alone would have little effect on the distribution of *C. helmsii* in the UK.

8

9 **2.2 | Substratum**

10 In Britain, *Crassula helmsii* is found on a range of substrata, including wet mud, shallow gravels,
11 sands and clays (Dawson, 1994; Child & Spencer-Jones, 1995). Initial colonisation is thought to
12 take place on bare ground, rather than in direct competition with natives (Smith, 2015, 2016). Sites
13 that are managed to include or create bare ground are therefore often rapidly colonised by *C.*
14 *helmsii*. Some lentic systems are also prone to rapid changes in the water level, and as such often
15 expose areas of bare sediments, which can be rapidly colonised.

16 The lowest pH recorded in pond systems colonized by *Crassula helmsii* was 5.7 in The
17 New Forest (Brunet, 2002) and 5.9 in Orlestone, Kent (Smith, 2015). Table 1 summarises water
18 chemistry measurements at the two sites. A reaction value of 6, given by Hill *et al.* (2004), indicates
19 growth on moderately acidic to weakly basic soils. Alkalinity was found not to be a factor for
20 invasion, with *C. helmsii* colonising sites ranging from 0.08 mEq l⁻¹ to 1 mEq l⁻¹ (Smith, 2015).

21 Laboratory studies have shown *C. helmsii* to tolerate high concentrations of copper (T.
22 Smith, unpublished), although it has not been found on copper-rich soils and sediments in the wild
23 (see section 6.5 for a full account its of copper tolerance and accumulation). *C. helmsii* is able to
24 grow in brackish water (Dean *et al.*, 2013) such as coastal marsh ditches on the north Kent coast of
25 up to 1.8 ppt salinity (Smith, 2015). In its native habitat it appears to favour more saline conditions

1 (Webb *et al.*, 1988). In New Zealand, *C. helmsii* colonises coastal rocks, cliffs and beaches (Allan,
2 1982, as well as lake margins, river margins, estuaries and salt marshes (Webb *et al.*, 1988).

3

4 **3 | COMMUNITIES**

5 As a non-native, *Crassula helmsii* is not characteristic of any British plant community but it has
6 been found in a variety of riparian and aquatic plant communities. It is categorised broadly as being
7 present in the NVC categories of ‘Standing Water and Rivers’ and ‘Rivers and Streams’ (Rodwell,
8 1995, Hill *et al.*, 2004). Community types in which it can be represented include *Nuphar lutea*
9 (A8), *Typha latifolia* swamp (S12b), *Typha latifolia* – *Alisma plantago-aquatica* swamp (S12c),
10 *Typha angustifolia* swamp (S13), *Sparganium erectum* swamp (S14c), *Glyceria fluitans* marginal
11 vegetation (S22a) and *Phragmites australis* – *Urtica dioica* (S26d) communities (Rodwell, 1995;
12 Smith, 2015).

13 *Crassula helmsii* is often found associated with *Phragmites australis*, growing amongst the
14 stems and creating an understorey layer (Dean, 2015). Dependent on the habitat, morphologically
15 similar species such as *Callitriche* spp., *Polytrichum* spp. and *Galium palustre* are frequently found
16 with it. Floating species, such as *Lemna* spp. and *Hydrocharis morsus-ranae*, may create sheltered
17 zones on the water’s surface and enhance fragment establishment of *C. helmsii* (Smith & Buckley,
18 2015). In its native range, it has been classified as an ARp (Amphibious fluctuation-responders
19 morphologically plastic) species (Nicol *et al.* 2003), as well as a submerged species, growing
20 alongside other ARp species and submerged species such as *Atriplex prostrata*, *Eleocharis acuta*
21 (R.Br.), *Thyridia repens* (R.Br.), *Aster subulatus* (Michx), *Typha domingensis* (Pers), *Althenia*
22 *australis* (F.Muell.) and *Nitella* sp. (see Nicol *et al.*, 2003; Table 4).

23

24 **4 | RESPONSE TO BIOTIC FACTORS**

25 The emergent form of the plant achieved maximum gas exchange under low light and low
26 temperature conditions (Hussner, 2009), and therefore would be expected to be tolerant of shading

1 by other plants. However, a negative correlation has been found overall in the field between
2 *Crassula helmsii* abundance and shade (Dean, 2015). Control measures, such as covering with
3 black plastic and removal by mechanical digger, are often ineffective in the long term. This is due
4 to the ability of the plant to survive long periods without light, fragmentation aiding its dispersal,
5 and possibly, the removal of native competition (Smith, 2015). Grazing pressure was found to
6 increase the abundance of *C. helmsii* in an experiment that tested livestock as a control mechanism
7 (Dean *et al.*, 2015). Brouwer *et al.* (2017) have shown that competition with *Littorella uniflora* and
8 *Hypericum elodes* reduced abundance of *C. helmsii* in laboratory trials, due to competition for
9 nutrients. *L. uniflora* had a significantly higher fresh weight than *C. helmsii*, which was thought to
10 be due to its larger root system and the competitive advantage this bestowed. Whilst competition
11 for nutrients with natives may occur in field settings (Smith, 2015), such competition has not been
12 demonstrated empirically.

13

14 **5 | RESPONSE TO ENVIRONMENT**

15 **5.1 | Gregariousness**

16 *Crassula helmsii* grows rapidly in a dense carpet on bare ground or sediment, as well as creating
17 dense floating mats. These can fragment from the terrestrial forms of growth, creating free floating
18 'islands' of plant material (Figure 3). This fragmentation can act as an efficient method of dispersal
19 (Smith, 2015). It is common to find *C. helmsii* as a dense stand on the margins of waterbodies,
20 extending along the water's edge. These stands may also grow onto the water surface, as well as
21 underwater, so it is difficult to distinguish cover below the water level because of the obscuring
22 effect of the emergent/surface form of the plant. Dawson and Warman (1987) found plant material
23 in spring and summer to be near the maximum for submerged and emergent growth forms, ranging
24 from 0.25 – 1.5 kg dry mass m⁻². These values were similar to those found in lakes in Germany,
25 where biomass was recorded as 1.1 kg dry mass m⁻² (Hussner, 2009). Growth is reduced with water

1 depth, and lower water levels in the summer were found to accelerate growth as the plant material
2 neared the water's surface (Dawson & Warman, 1987).

3

4 **5.2 | Performance in various habitats**

5 In Australia, *Crassula helmsii* is able to grow adjacent to flowing waters (Dawson & Warman,
6 1987). However, outside its native range the species is found in temporary and permanent lentic
7 systems, though slow flowing systems are noted as a possible habitat (Nault & Mikulyuk, 2011).

8 Dawson (1994) found that *C. helmsii* was able to grow in tank trials with water velocities
9 up to 0.3 m s^{-1} , and grew most vigorously in conditions of high nutrients and low alkalinity. *C.*
10 *helmsii* is thought to be present over a 'broad range' of nutrient conditions (Leech & Dawson,
11 2000). Dean (2015) found nitrate concentrations of $0 - 10.2 \text{ mg l}^{-1}$, ammonia concentrations of
12 $0.012 - 8.840 \text{ mg l}^{-1}$ and phosphorus concentrations of $0.129 - 1.962 \text{ mg l}^{-1}$ on invaded sites in
13 England. Smith (2015) recorded ranges of total organic nitrogen of $0.05 - 2.15 \text{ mg l}^{-1}$, ammonia of
14 $0.02 - 1.18 \text{ mg l}^{-1}$ and phosphate of $0 - 6.41 \text{ mg l}^{-1}$ on colonised sites in south-east England (Table
15 1). Smith (2015) found significantly less ($P < 0.05$) total organic nitrogen in invaded sites than
16 uninvaded ones in a study in south-east England. Whether this was a precursor to colonisation by *C.*
17 *helmsii* or a result of its presence was, however, unclear. Brunet (2002) noted the ability of *C.*
18 *helmsii* to take up large amounts of nutrients from a system, akin to that of *Lemna* spp.
19 (duckweeds). Brunet also suggested that high dissolved phosphorus concentrations could reduce
20 monoculture establishment, but not initial colonisation.

21

22 **5.3 | Effect of frost, drought, etc.**

23 *Crassula helmsii* can tolerate prolonged periods of freezing (Kirby, 1965), although it does die back
24 in winter (Figure 5; Smith, 2015). Dawson (1994) observed that shoots were able to survive for
25 several hours in ice and air temperatures of -7°C ; the stems became blackened but apical growth
26 remained viable. Kirby (1965) reported its ability to survive at several degrees below zero in pots

1 in glasshouse conditions. Although associated with water, *C. helmsii* seems well-adapted to
2 surviving prolonged spells of drought, often occurring in ponds and ditches that remain dry
3 throughout the summer. Dawson (1994) reported that tissues from plant material left to dry for 4
4 months remained viable for resumed growth.

5

6 | **STRUCTURE AND PHYSIOLOGY**

7 | **6.1 | Morphology**

8 The morphology of *Crassula helmsii* varies widely, with a number of environmentally influenced
9 growth forms. Branches are usually c.12- 16 cm long, slender and much branched (Aston, 1977)
10 with decumbent stems that ascend at the tips (Allan, 1982). It can form small to large, loose or
11 dense mats that are moss-like (Everett & Norris, 1990). Adventitious nodal rooting occurs below
12 prostrate stems (Aston, 1977; Webb *et al.*, 1988). In a monospecific stand, stems can intertwine to
13 form a loosely aggregated turf of up to 20 cm in height, and other species can be used as support to
14 enable a maximum stand height of approximately 45 cm (Dawson, 1994). The internode of the
15 terrestrial form is length is 2-5 mm. Poor anatomical structural support, likely due to its adaptations
16 for growth as an aquatic species, prevents *C. helmsii* from attaining unsupported heights in excess
17 of 2 -12 cm (Everett & Norris, 1990; Child & Spencer-Jones, 1995). Horizontal growth of up to 30
18 cm can be achieved either free floating in water or on the surface of the substratum (Dawson,
19 1994), but terrestrial forms rely on nodal rooting for the increase in length (Everett & Norris, 1990).
20 Free floating forms are often little branched, with no adventitious roots and larger leaves (Everett &
21 Norris, 1990). The submerged growth form, which can extend to 3 m or more, favours adventitious
22 root development over leaves, which are to 0.3-0.4 mm long (Dawson & Warman, 1987). The
23 internode length extends to 20-25 mm at the base of the stems, reducing to 15-20 mm towards the
24 apex. Diaz (2012) found that stem form can change between the short terrestrial form and the
25 longer submerged form within a month of changing water availability in tank trials. Figure 4 shows
26 the markedly different appearance of *C. helmsii* in its different growth forms.

1 Jones (2011) carried out a detailed study of the stems of *C. helmsii*, and reported details of
2 anatomy, including a uniseriate epidermis, the presence of stomata and air spaces within the cortex.
3 Leaves were shown to have hydathodes, but only on the abaxial surface, as well as air spaces in the
4 mesophyll, and vascular bundles scattered throughout. Amyloplasts, chloroplast and tannin-rich
5 cells were also found (Jones, 2011). Adaxial leaf stomatal density was 20 stomata mm⁻² on the
6 adaxial surface, and 13 stomata mm⁻² on the abaxial surface. The greater number on the adaxial
7 surface was thought to be due to *C. helmsii* being an aquatic species in or close to water, and so not
8 requiring water-saving adaptations (Jones, 2011).

9

10 **6.2 | Mycorrhiza**

11 No information on *C. helmsii* is currently available. The closely related *C. aquatica* has no
12 associated mycorrhiza (Harley & Harley, 1987). Another aquatic member of the genus, *C. natans*,
13 was found to form relationships with arbuscular mycorrhiza (Christiansen, 2017).

14

15 **6.3 | Perennation: reproduction**

16 *Crassula helmsii* is a perennial, evergreen forb (Dean, 2015), and is thought to reproduce in Britain
17 and Europe by asexual means only (Dawson & Warman, 1987). D'hondt *et al.* (2016) provided
18 evidence that reproduction from seed may potentially occur from whole fruiting flower heads in
19 Europe but there is as yet no evidence of it from individual seeds. Fragmentation and regrowth
20 therefore appears likely to be the main method of distribution outside of its native range. Root and
21 shoot regrowth from the nodes of stem sections have been observed (Figure 7), but not from leaves
22 (Hussner, 2009). However, regrowth from leaves is possible if they are supplied with synthetic
23 cytokinin BA, cytokinin 2iP and Zeatin (Kane *et al.*, 1993). Stem sections fragment easily where
24 the stem joins a node, resulting in widespread dispersal of nodal fragments. Nault and Mikulyuk
25 (2011) report water-based mechanisms as the dominant dispersal mechanism.

26

1 6.4 | Chromosomes

2 The chromosome number in the British material is $2n = 36$ (Stace, 2019). De Lange *et al.* (2008)
3 reported $2n = 42$ in Australia (Victoria) but $2n = 14$ in New Zealand (Westport, South Island).

4

5 6.5 | Physiological data

6 *C. helmsii* can fix carbon using crassulacean acid metabolism (CAM). CAM is also used by the
7 native *Crassula aquatica* (Newman & Raven, 1995; Preston & Croft, 1997). The use of CAM in
8 aquatic species is thought to enhance the uptake of dissolved inorganic carbon (DIC), in the form of
9 bicarbonate (HCO_3^-) when concentrations of CO_2 are low (Newman & Raven, 1995; Maberly &
10 Madsen, 2002). Newman and Raven (1995) investigated the effects of pH and irradiance on
11 photosynthesis in *C. helmsii*. They reported a marked diel fluctuation in titratable acidity, reflecting
12 changing levels of malic acid, as CO_2 was fixed at night and recycled during the day. The species
13 was, however, unable to use HCO_3^- for photosynthesis and showed generally low photosynthetic rates
14 when CO_2 was not limiting. Its photon flux density at photosynthetic light saturation was also low
15 for an aquatic macrophyte. They suggested that the advantage conferred on *C. helmsii* by CAM was
16 through an extension of the period of assimilation of dissolved inorganic carbon, resulting in a
17 reduction in the limitation on photosynthesis in aquatic environments by the very high diffusive
18 resistance to CO_2 .

19 Klavsen and Maberly (2009) found that the contribution by CAM to total daily photosynthesis
20 at a 0.5 m depth was 22% in April and 42% in July, while at 2.2 m the contribution was 18% in April
21 and 31% in July. The high values in July coincide with the most active growing period of *C. helmsii*.
22 This greater activity may have been due to the combined effects of increased light flux and raised
23 water and atmospheric temperatures, both of which are known to be limiting in terrestrial CAM plants
24 (Taybi *et al.*, 2002). Klavsen and Maberly (2010) investigated a range of light and CO_2 treatments
25 on the effects of CAM in *C. helmsii*. They found that CAM appeared to be an effective mechanism
26 for carbon assimilation at high light fluxes, but did not occur at low light. It was also found that the

1 contribution to the carbon budget was higher at low CO₂ levels in comparison to the plants exposed
2 to higher levels of CO₂. The amount of CO₂ taken up via CAM at night was 0.74 to 2.94 times the
3 amount of CO₂ lost in respiration (Klavnsen & Maberly, 2009). This could indicate that CAM acts to
4 enhance inorganic carbon uptake when it is in limited supply. Laboratory experiments demonstrated
5 a 13% greater contribution to the carbon budget by CAM in low CO₂ vs high CO₂ grown plants
6 (Klavnsen & Maberly, 2010). It is reported that *C. helmsii* is not limited to high alkaline (high DIC)
7 systems (Klavnsen & Maberly, 2010; Eward, 2014), which is reflected by its ability to colonise habitats
8 with a range of pH values. The ability of *C. helmsii* to maintain photosynthetic activity, even at
9 concentrations of CO₂ down to 3 mmol m⁻³, may act as a competitive tool against other macrophytes,
10 allowing it to exploit environments where other species may find DIC to be a limiting factor.

11 *Crassula helmsii* is a hyper-accumulator of copper, and can accumulate up to 9,000 ppm in
12 plant dry mass (Küpper *et al.*, 2009). Accumulation and compartmentalisation of the copper into the
13 shoots occurs, where it is held without causing harm towards the plant (Küpper *et al.*, 2009).
14 However, leaf and root regrowth is not observed in solutions which exceed 2 ppm copper (Smith,
15 2015). The process of accumulation is thought to be linked to CAM metabolism. Increased
16 presence of malate during CAM (Newman & Raven, 1995) acts as a copper ligand and may explain
17 its increase in the ability to accumulate copper (Newman & Raven, 1995; Küpper *et al.*, 2009). It
18 has been shown through diurnal cycles of pH, as well as carbon isotope discrimination ($\delta^{13}\text{C}$), that
19 pH extremes make *C. helmsii* more susceptible to copper toxicity (Küpper *et al.*, 2009). Whilst not
20 appearing to provide any competitive advantage to growth in Britain, this may be an evolutionary
21 response in its native range in Australasia, though information is lacking to support this.

22 Lead and zinc accumulation have also been shown to occur in *C. helmsii* (Zhang *et al.*,
23 2015). Out of 14 species tested, *C. helmsii* had the highest concentration of lead (35 µg/g) and zinc
24 (976 µg/g) in shoots. *C. helmsii* also exhibited a high level of tolerance when multiple metals were
25 used in the growth medium, showing the highest relative growth rate of the species tested over an
26 84-day period (Zhang *et al.*, 2015).

1 Experiments have shown that a reduction in growth when total concentrations of salts are
2 increased from 2-8 ppt. (Dean *et al.*, 2013). Field control attempts have shown that saltwater
3 inundation followed by natural allocthnous freshwater recharge to levels of up to 1.6 ppt is able to
4 support *C. helmsii* growth (J. Durnell, Unpublished Data). The highest salinity readings in brackish
5 ditch systems containing *C. helmsii* in south east England were approximately 1.8 ppt (Smith,
6 2015), and this would appear to be the upper threshold for successful growth in saline conditions.

7

8 **6.6 | Biochemical data**

9 No information.

10

11 **7 | PHENOLOGY**

12 Dieback of stems and leaves occurs in winter, but with little apparent change in root mass and
13 distribution (Figure 5; Smith, 2015). Mature plants remain viable despite this dieback, which
14 justifies the classification of *C. helmsii* as a perennial herb in Britain (Laundon, 1961). In the
15 British Isles it flowers in August and September (Clapham, Tutin, & Moore, 1987).

16

17 **8 | FLORAL AND SEED CHARACTERS**

18 **8.1 | Floral biology**

19 A pink corolla or bending of the petals (recurved or reflexed) are unusual variations (Swale &
20 Belcher, 1982). In its native range, Toelken (1981) noted that flowers were present all year as long
21 as water was available. Flowers are not produced below the water line, and if buds are present and
22 submerged due to water level changes, they are aborted (Diaz, 2012). Toelken (1981) describes the
23 flower of *C. helmsii* being a frondo-bracteose complex branching inflorescence, with the terminal
24 and lateral branches of the inflorescence tending to be monochasial. Toelken further describes a
25 high level of variability, with the arrangement of the complex branching consisting of several
26 dichasia at the apex, with branching at the base being reduced to a terminal dichasium, a binodal

1 botryoid, a triad or a single terminal flower when under extreme conditions. Figure 6 shows a
2 flower head, alongside mature seed heads for comparison (Richards, 1979). Whilst a fragrance to
3 the flowers has been noted (Dawson & Warman, 1987) no pollinators have been observed in
4 Britain. In its native range, *C. helmsii* has been shown to be visited by a number of hover-fly
5 (Syrphidae) species (Diaz, 2012). Pollen foraging has been observed, but due to the short distance
6 of movement of the flies, it is thought that the pollen flow will be geitonogamous, with minimal
7 cross-plant transport (Diaz, 2012).

8

9 **8.2 | Hybrids**

10 No hybrids have been found in Britain. There little geographical overlap between *C. helmsii* and its
11 congener *C. aquatica*. Webb, Sykes & Garnock-Jones (1988) suggested that *C. helmsii* may be a
12 departure state of *Crassula moschata* in New Zealand, due to the similarity in proportions but with
13 *C. helmsii* having smaller leaves and flowers.

14

15 **8.3 | Seed production and dispersal**

16 Each carpel contains 3 - 5 seeds (Allan, 1982) which are c. 0.5 mm in length (Webb, Sykes, &
17 Garnock-Jones, 1988). Seeds are produced in plants both in the native range as well as Britain
18 (Aston, 1977; Dawson, 1994). Seeds were found to float initially, but tended to sink over time,
19 which provides evidence of a possible dispersal mechanism (Dawson & Warman, 1987). Sampling
20 of the riparian soils allowed recovered split seed cases, but no evidence of germination was
21 discovered.

22 In its native range, it has been shown that *C. helmsii* can be dispersed by fallow deer (*Dama*
23 *dama*) and grey kangaroo (*Macropus giganteus*) through examination of scats (Claridge *et al.*,
24 2016). Wildfowl and livestock, such as highland cattle and New Forest ponies, are considered
25 suitable vectors for fragmented stem and node sections of *C. helmsii* in Britain (Denys *et al.*, 2014;
26 Ewald, 2014; Smith, 2015). Endozochorus distribution was investigated using geese that were

1 encouraged to consume *C. helmsii* (Denys *et al.*, 2014). Droppings from the birds were used as an
2 inoculum in growth trials, but it was concluded that the only plantlet to be produced came from an
3 undigested fragment and not a seed. This appears to suggest that seed dispersal in this manner is an
4 unlikely concern for species spread.

5

6 **8.4 | Viability of seeds: germination**

7 Germination was achieved *in vitro* from Tasmanian stock, under the conditions of 22 °C for 10 hours
8 in the light, 10 °C for 14 hours in the dark. Radicle emergence was first observed after 8 days, with
9 a 100% germination rate when seeds had been sterilised before inoculation onto water agar. Dawson
10 (1994) had noted the difficulties in achieving germination from British seed, and speculated that it
11 did not germinate because of unknown requirements for pre-treatments, as well as the difficulty of
12 excluding nodal fragments from collected samples. Denys *et al.* (2014) reported successful
13 germination but they used whole flower heads containing seeds, rather than direct seed sowing,
14 because of the difficulties in handling the tiny seeds. This method may have included nodes, from
15 which roots and stems readily develop. A similar experiment investigating germination potential of
16 seeds was conducted on samples collected across north-western Europe (D'hondt *et al.*, 2016). Again,
17 flower heads were used rather than individual seeds, and they were cold-stratified before sowing in
18 sand. Germination was examined under conditions of a 14h light / 10h dark regime at 18 °C and
19 12 °C, for a 128-day study period. A total of 222 seedlings was obtained from 7009 flower heads.
20 They found most of the populations studied had <25% germination but one population had just over
21 70% and one time point of another population that was sampled at different times of the year had
22 similarly high germination. To date, this remains the most exhaustive attempt at germination of non-
23 native seed stock, but rigorous experiments with individual seeds are still required.

24 D'hondt *et al.* (2016) also examined winter survival of seeds, by burying flower heads and
25 seeds in soils that were exposed to a Belgian winter. Microscopic analysis of the samples found them
26 to retain near-perfect condition, with only minor discolouration of the seeds resulting from the

1 treatment. Nicol *et al.* (2003) incubated sediments collected from a southern Australian wetland
2 complex containing *C. helmsii* plants. After a 22-week study period, seedling emergence was low
3 and it was considered a rare species from the assemblage collected. Nicol and Ward (2010) conducted
4 a germination test using the seedling emergence method for soil samples collected from lagoons in
5 South Australia. They found that of all the aquatic species tested, *C. helmsii* took the longest to
6 germinate (16 weeks, though possibly exaggerated by difficulties in seeing them) and only present in
7 low numbers. Differences in salinity appeared not to be significant, but prolonged inundation was a
8 factor. The apparent difficulties in germination that the species exhibits in its native range may be
9 why germination has not been detected in Britain, and thus why seed is unlikely to have been a major
10 factor in its spread.

11

12 **8.5 | Seedling morphology**

13 Figure 8 shows a scanning electron micrograph of a seed (Denys *et al.*, 2014). Germination and
14 seedling development over a period of 48 days is shown in Figure 9.

15

16 **9 | HERBIVORY AND DISEASE**

17 **9.1 | Animal feeders or parasites**

18 Deegan *et al.* (2008) found that *C. helmsii* was eaten by both Amphipoda and Trichoptera as
19 primary consumers in water bodies in South Australia. Other invertebrates that consume *C. helmsii*
20 include a weevil of the *Steriphus* genus (Varia, 2013), and *Hydrellia perplexa*, a leaf-mining fly
21 with an aquatic larval stage that shows host specificity to *C. helmsii* (CABI, 2016). The mite
22 *Aculus crassulae* has also been found feeding on the terrestrial and emergent forms of *C. helmsii*
23 Fallow deer (*Dama* L.) and grey kangaroo (*Macropus giganteus* Shaw) also consume *C. helmsii* to
24 some extent Claridge *et al.* (2016). Outside its native range, no known herbivory exists beyond
25 generalist grazing by livestock if present. Highland Cattle (*Bos taurus* L.) and Konik Pony (*Equus*
26 *ferus* f. *caballus* L.) have been observed occasionally grazing *C. helmsii* (T. Smith, pers. obs.).

1 Grass carp *Ctenopharyngodon idella* Valenciennes have been suggested as a potential biological
 2 control, but only in garden ponds due to their generalist feeding behaviour. Denys *et al.* (2014)
 3 found that geese could be induced to feed on *C. helmsii*. Warren (2008) observed Egyptian Geese
 4 (*Alopochen aegyptiaca* Linnaeus L.) feeding exclusively on *C. helmsii* for 30 minutes.

5

6 **9.2 | Plant parasites**

7 No parasites known in Britain or native range.

8

9 **9.3 | Plant diseases**

10 No diseases are known in Britain. Two fungal ascomycete pathogens have been identified from
 11 Australia and New Zealand during the search for a potential biological control agent. A *Cercospora*
 12 sp. (Ascomycota, Capnodiales) was shown to attack the leaves of *C. helmsii*, and a *Colletotrichum*
 13 sp. (Ascomycota, Glomerellales) was shown to attack the stem, leading to the collapse of the plant
 14 (Varia, 2013). The *Colletotrichum* sp. was initially considered as a possible biological control agent
 15 (CABI, 2016).

16

17 **10 | HISTORY**

18 *Crassula helmsii* was originally described as *Tillaea verticillaris* Hooker and subsequently as
 19 *Bulliarda recurva* Hooker, *Tillaea recurva* in Flora Tasmaniae Hooker, as *Tillaea helmsii* in the
 20 Student's Flora of New Zealand (Kirk, 1899), and as *Crassula recurva* in Dansk Botanisk Arkiv
 21 (Dansk Botanisk Forening, 1918). It continued to be referred to as *T. recurva* by Lousley (1957,
 22 1961). Laundon (1961) renamed the species *Crassula helmsii* in 1961 in line with its similarities to
 23 other Australasian *Crassula* species. (Laundon, 1961) provides a full history of synonyms of *C.*
 24 *helmsii*, as well as closely related species from its native range.

25 The first recorded presence of *C. helmsii* in the British Isles is a second-hand account of an
 26 introduction at 'Perry's Hardy Plant Nursery' in Middlesex before the First World War, although

1 the specific introduction date and a more detailed source beyond “Australia” is unreported (Swale
2 & Belcher, 1982). Neglect of the nursery tanks during the First World War, allowed *C. helmsii* to
3 become abundant, ‘choking out’ the *Nymphaea* species that were likely to have been the
4 ornamentals under cultivation (Swale & Belcher, 1982).

5 *Crassula helmsii* was first found naturalised in Greensted, Essex, in 1956 (Laundon,
6 1961), followed by a report from the University of Southampton in an artificial pond in 1957
7 (Lousley, 1957). The source of the plant at Greensted was thought to be either artificial planting or
8 through naturalisation from surrounding vegetation (Lousley, 1957; Laundon 1961). The source of
9 the plant at Southampton was reported as Perry’s Nursery (Laundon, 1961). This was followed by
10 reports across the country as identification by naturalists of a new species began (Bowman, 1977;
11 Hall, 1978; Vaughan, 1978; Clement, 1979; Cockerill, 1979; Richards, 1979; Byfield, 1984).
12 Between 1987 and 2004 *C. helmsii* showed a relative increase in distribution on a tetrad scale of
13 78% ($\pm 25\%$) (Braithwaite, Ellis & Preston, 2006). Analysis of the records held by The Botanical
14 Society of Britain and Ireland (BSBI, 2019) of southern British vice counties shows a continual rise
15 in the number of monads in which *C. helmsii* has been recorded since its introduction in the 1950s
16 (Table 2). Caution should be taken with these records however, as it is likely that some increases
17 can be explained over the last decade by an increase in surveyor effort, due to the wider attention
18 that *C. helmsii* has gained.

19 Dawson (1994) studied UK plant samples and seven enzyme systems, collected widely across
20 its British distribution. The results indicated only one lineage of *C. helmsii* present within the UK,
21 with no apparent polymorphism within the population. Dawson also studied the genetic differences
22 from the native range of *C. helmsii* (Dawson, 1994). This study looked at 34 separate sites and 11
23 separate enzyme systems. Of the 11 studied, differences were found only between the two enzyme
24 systems malate dehydrogenase and malic enzyme. This geographically separated the plant specimens
25 between the Northern Tablelands and New South Wales from other Australian plant specimens. The

1 genetic study indicated that the most likely source of the British strain was the River Murray area;
2 however, this particular river system drains approximately half of the Australian continent.

3 De Lange *et al.* (2008) investigated the genetic differences between *C. helmsii* from Australia
4 and New Zealand, which showed different chromosome numbers ($2n = 42$ in Australia (Victoria) but
5 $2n = 14$ in New Zealand (Westport, South Island)). Toelken (1981) discussed a variant from Mount
6 Arapiles and from Tasmania, where the leaf apices were cuspidate to acuminate and young flowers
7 were almost sessile, but these variants were morphologically similar enough to be classified as *C.*
8 *helmsii*.

9

10 **11 | CONSERVATION**

11 **11.1 | Impact on native species**

12 The main conservation concern is the impact of invasive *Crassula helmsii* on native species and
13 ecosystems. Reduced abundance of *Nymphaea* spp. (Swale & Belcher, 1982) and *Elodea* spp.
14 (Cockerill, 1979), following invasion of waterbodies by *C. helmsii* has been reported. Dawson &
15 Warman (1987) described the elimination of unnamed species due to *C. helmsii* dominance in
16 managed pond systems in Dorset, England. *Ludwigia palustris* (and *Galium constrictum* have been
17 shown to be affected (Dawson & Warman, 1987; Leach & Dawson, 1999). Hussner (2009)
18 described macrophyte species losses due to *C. helmsii* from lakes in Germany. Sims and Sims
19 (2016) described how *C. helmsii* had formed a dominant monoculture and excluded other
20 submerged native aquatic plants in two ponds at Mile Cross Marsh in Norwich, England. Watson
21 (2001) names *C. helmsii* as a significant risk to *Damasonium alsima*. Pilkington (2016) expresses
22 concern over the impact that *C. helmsii* could have on the liverwort *Riccia canaliculata*
23 (Channelled Crystalwort). Anecdotal occurrences of species loss are also reported (Dawson &
24 Warman, 1987; Leach & Dawson, 1999) but as stated by Lockton (2016) many of the reported
25 losses are inaccurate or anecdotal, rather than resulting from strict surveying protocols.

1 No studies comparing status before invasion with that after invasion have been carried out
2 to date. Some studies have shown that *C. helmsii* is not significantly linked to macrophyte species
3 loss. Dean (2015) studied the co-existence of *C. helmsii* with *Phragmites australis* and found the
4 two species had similar impacts on native species. Langdon (2004) found no evidence of species
5 loss or germination suppression of native species in field systems investigated in north-west
6 England, but did find germination suppression during tank trials. The impact on native aquatic
7 macrophyte biomass in the New Forest was estimated as a loss of 6% of native species (biomass)
8 for every 10% increase of *C. helmsii* biomass (Ewald, 2014). The few experimental studies carried
9 out have thus far found no significant impact on the diversity of macroinvertebrate species at sites
10 invaded by *C. helmsii* (Ewald, 2014; Smith, 2015; Smith & Buckley, 2015), when compared with
11 non-invaded sites. Diaz (2012) noted that dense cover of *C. helmsii* which restricts light
12 penetration and depletes CO₂ could affect both submerged plant, aquatic invertebrate and fish
13 populations. Dawson & Warman (1987) also suggested that *C. helmsii* could lead to widespread
14 species losses through the creation of monocultures and interspecific competition.

15

16 **11.2 | Control**

17 Much of the literature on *C. helmsii* is devoted to its control, and reviews of overall effectiveness of
18 these measures have been carried out (Alridge *et al.*, 2017; van der Loop *et al.*, 2018). Previous
19 attempts to control *C. helmsii* include application of chemical herbicides (Dawson & Henville,
20 1991; Spencer-Jones, 1994; Child & Spencer-Jones, 1995; Dawson, 1996; Leach & Dawson, 1999;
21 Gomes, 2005), hydrogen peroxide (Dawson & Henville, 1991; Dawson, 1996; Leach & Dawson,
22 1999), liquid nitrogen (Leach & Dawson, 1999), hot foam (Bridge, 2005) and flame throwers
23 (Leach & Dawson 1999). All of these control attempts were found to have varying degrees of
24 success in the short term, but minimal long-term impact on *C. helmsii* populations. Due to the
25 submerged growth form of *C. helmsii*, control attempts often only affected the emergent or
26 terrestrial form, leaving a source of propagules that was readily able to colonise any newly create

1 bare ground. Shading has been used, either by covering with black plastic (Leach & Dawson, 1999;
2 Wilton-Jones, 2005) or by colouring the water (Newman, unpublished). These two methods are
3 better able to kill the submerged growth forms, but are often unable to kill off the terrestrial forms.
4 The black plastic method often results in forcing the growth towards the light (edge of the plastic,
5 and subsequently outside of the control perimeter), whilst the coloured dyes have no effect on the
6 terrestrial or emergent forms.

7 Sea water inundation has been used to increase the salinity of waterbodies, thereby leading
8 to necrosis of *C. helmsii* tissue (Charlton *et al.*, 2010; Dean *et al.*, 2013). This method relies on
9 coastal proximity, and the ability for sea water to be both pumped into the waterbodies containing
10 *C. helmsii* and be retained there for a sufficient period of time to causes death of the plants. Dean *et*
11 *al.* (2013) demonstrated that a range of salinities between 2 and 8 ppt were effective at killing *C.*
12 *helmsii*. Physical removal (Dawson & Warman, 1987) is used extensively in Germany (Hussner,
13 2009) but is highly labour intensive and can be expensive. Management by selective removal rather
14 than killing all plant species is potentially beneficial as it has been shown that growth of *C. helmsii*
15 is reduced when native plant species are present to compete for nutrients (Brouwer *et al.*, 2017).
16 Anderson *et al.* (2015) investigated desiccation as a control method, in an attempt to stop the spread
17 of reproductive propagules. They found that when left to air dry as a control treatment, *C. helmsii*
18 took longer than 100 days to reach a 90% mortality rate.

19 Sims and Sims (2016) describe a procedure of draining ponds colonised by *C. helmsii*,
20 applying herbicide, excavating new ponds and using this material to fill in the previous ponds. No
21 colonisation was found from either the new ponds or filled in ponds after 3 years. Whilst this
22 method may be applicable in some situations, the size of the ponds, economic investment it would
23 require and the potential for wide-scale loss of other species would make this method very limited
24 in its applications and so unlikely to be utilised as a wide scale control method.

25 Shannon *et al.* (2018) described a method of cleaning equipment and footwear, using hot
26 water, as an additional step in improving biosecurity between sites. They found that whilst it is an

1 effective measure, the required temperatures of greater than 50°C for a period of 15 minutes would
2 limit uptake in field situations, leaving it only viable as a laboratory-based protocol. In field
3 situations, the equipment required to conduct this measure of sanitation would be both expensive
4 and impractical. Gassman *et al.* (2006) postulated that *C. helmsii* is likely to be a prime target for
5 biological control, and proposed genus-specific chrysomelid and curculionid beetles as potential
6 agents. The discovery of the previously unknown mite species *Aculus crassulae* may provide a
7 possible agent for selective control of *C. helmsii* (Knihinicki *et al.*, 2018). *A. crassulae* is currently
8 undergoing field trials at selected sites in the UK, after a pest risk analysis was conducted and a
9 release licence was granted for the trial (CABI, 2019).

10 Morphologically similar species to *C. helmsii*, such as *Callitriche spp.*, *Polytrichum spp.*
11 and *Galium palustre* are frequently found alongside *C. helmsii* (Smith & Buckley, 2015). This can
12 lead to misidentification and inappropriate management decision being made. Reviews of control
13 procedures by Delbart *et al.* (2013) and Smith (2015), showed that whilst chemical control is often
14 favoured (due to ease of use and economic benefits) it is rarely successful, and more labour-
15 intensive, selective, methods are more effective. The conclusions from these studies indicate that
16 few control methods can consistently successfully eradicate *C. helmsii*, with recolonization often
17 occurring rapidly from residual propagules and bare earth being left after management. Van der
18 Loop *et al.* (2018) found that of all the control attempts they studied, only 8% of methods had both
19 short term and long-term success – these were mechanical digging, mechanical sod-cutting and
20 removal by hand. These methods are only applicable as small scale control procedures, due to
21 economic limitation and impacts on non-target species. Van der Loop *et al.* (2018) prescribe the
22 prerequisites for eradication as small-sized infestation, presence in isolated systems, and the growth
23 form being terrestrial and not aquatic. The difficulty of *C. helmsii* control has led to control
24 management being abandoned on many sites (personal observation). As early as 2011, Delbart *et al.*
25 (2011) stated that control could not be achieved in Belgium, and thus management should accept
26 this and look to work alongside the species. The biological control may present itself as a viable

1 option in the future, but as yet is still awaiting full-scale release (CABI, 2019). Diaz (2012)
2 provides a detailed overview of the challenges facing control of *C. helmsii*. Control is often sought
3 without assessing the ecological benefits of removal of *C. helmsii* and the impact that control would
4 have not just on the target species but also on those native species (not just macrophytes) that would
5 be damaged by the control procedures. Consideration of whether *C. helmsii* is the driver of change
6 or a passenger species benefitting from change should be considered and investigated before any
7 management is conducted (Diaz, 2012).

8 The impacts of management have been studied in relation to the effects on the composition
9 of soil seed banks (Smith, 2015, 2016). A reduction in the native seed bank diversity was found as
10 a result of active management of *C. helmsii*, such as mechanical excavation, chemical spraying, and
11 artificial shading), when compared with either no management or physical removal by hand of *C.*
12 *helmsii*. This was possibly due to either stripping of native seed-containing topsoil or direct removal
13 of native seed-producing vegetation that was lost as a side effect of mechanical control (Smith,
14 2015).

15 Economic impacts were considered by Nault and Mikulyuk (2011), who discussed the loss
16 of recreational and aesthetic value to waterfront property values and a potential decline in tourism
17 including boating, fishing, swimming, water skiing, canoeing and kayaking. The dense mats may
18 also have safety implications, because the dense monocultures may appear to indicate solid ground
19 when they could be the floating form of growth (Sheppard *et al.*, 2006).

20

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3

4

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3 Table 1. Chemical and macronutrient concentrations in the water at *Crassula helmsii* sites, reported
4 in two separate studies. Total numbers of sites surveyed are given in parentheses. (-) represents
5 missing data
6

| | | pH | Conductivity (ppt) | Na (mg l ⁻¹) | K (mg l ⁻¹) | Total Organic Nitrogen (mg l ⁻¹) | Ammonia (mg l ⁻¹) | Phosphate (mg l ⁻¹) |
|---------------------------|---------|--------------|-----------------------|-----------------------------|----------------------------|---|----------------------------------|------------------------------------|
| Smith (2015) | Highest | 9.50 | 1.891 | 1198.98 | 123.36 | 2.15 | 1.18 | 6.41 |
| South-east England | Lowest | 5.90 | 0.087 | 0 | 0 | 0.05 | 0.02 | 0 |
| | Average | 7.72 (59) | 0.484 (59) | 251.24 (61) | 25.62 (61) | 0.66 (59) | 0.28 (59) | 0.47 (59) |
| | | | | | | | | |
| Brunet (2002) | Highest | 7.92 | 0.189 | (-) | 0.16 | 1.829 | (-) | 0.53 |
| | Lowest | 4.29 | 0.0189 | (-) | 8.56 | 0.208 | (-) | 0.003 |
| New Forest, Hampshire. | Average | 6.74 (28) | 0.101 (28) | (-) | 2.70 (26) | 0.41 (21) | (-) | 0.079 (24) |

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1 Table 2. Vice-county records of *Crassula helmsii* for its distribution in monads (1 x 1 km squares)
 2 in the southern vice-counties of Britain. Data sourced from the Botanical Society of Britain and
 3 Ireland distribution database (BSBI, 2019)
 4

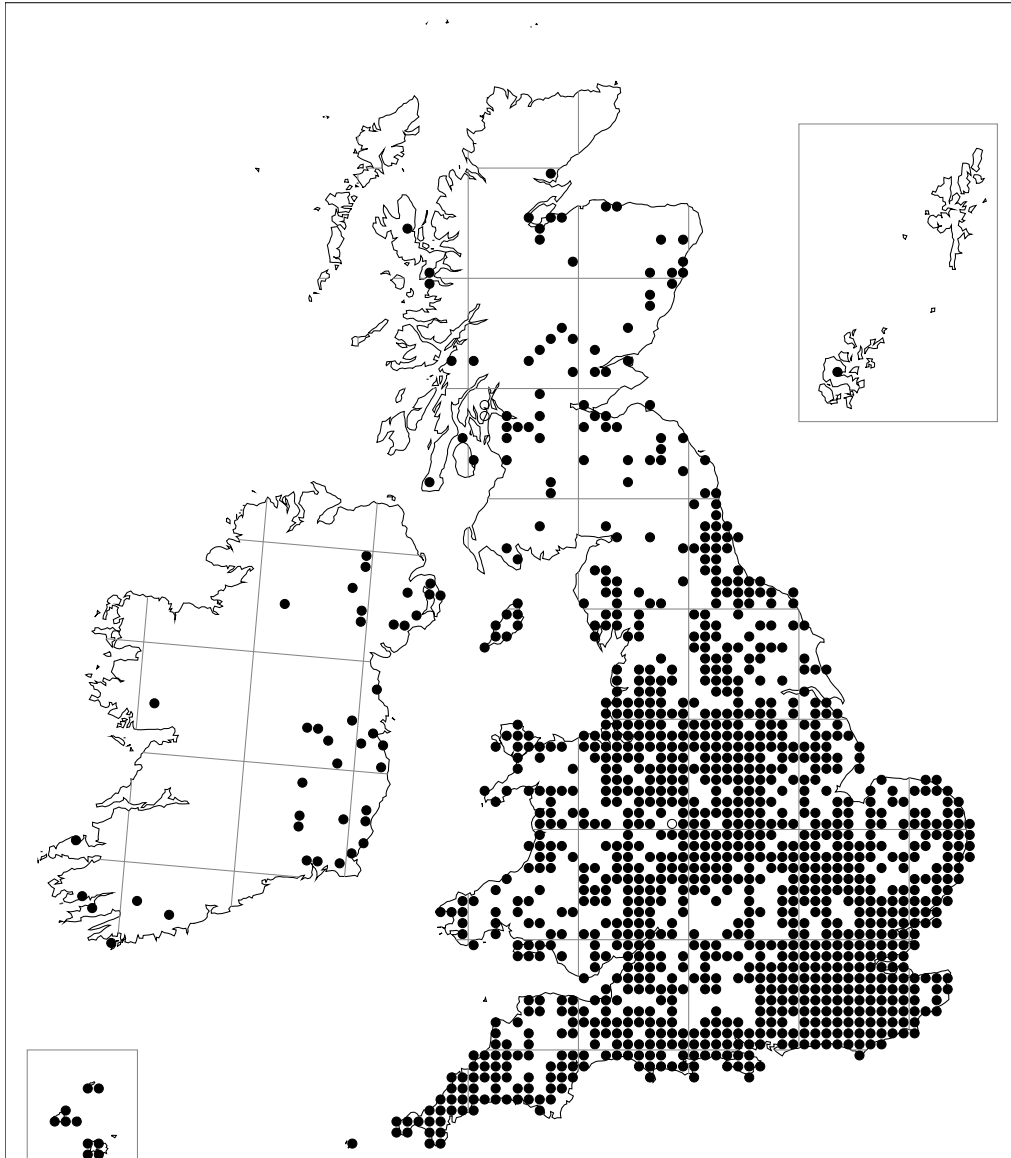
| Vice County | 1950- 1969 | 1970- 1986 | 1987- 1999 | 2000- 2009 | 2010- 2019 | Total |
|-----------------------------|---------------|---------------|---------------|---------------|---------------|-------|
| West Cornwall (with Scilly) | 0 | 2 | 8 | 30 | 37 | 62 |
| East Cornwall | 0 | 2 | 10 | 21 | 57 | 79 |
| South Devon | 0 | 6 | 18 | 24 | 21 | 55 |
| North Devon | 0 | 1 | 8 | 5 | 16 | 27 |
| South Somerset | 0 | 2 | 7 | 15 | 21 | 34 |
| North Somerset | 0 | 0 | 4 | 5 | 12 | 21 |
| North Wiltshire | 0 | 3 | 3 | 7 | 8 | 19 |
| South Wiltshire | 0 | 2 | 3 | 7 | 12 | 20 |
| Dorset | 1 | 5 | 24 | 10 | 31 | 62 |
| Isle of Wight | 1 | 5 | 7 | 11 | 10 | 24 |
| South Hampshire | 0 | 13 | 63 | 91 | 104 | 173 |
| North Hampshire | 2 | 4 | 25 | 29 | 46 | 69 |
| West Sussex | 0 | 2 | 3 | 16 | 11 | 28 |
| East Sussex | 3 | 8 | 14 | 49 | 9 | 75 |
| East Kent | 1 | 0 | 5 | 2 | 57 | 62 |
| West Kent | 1 | 1 | 6 | 2 | 51 | 58 |
| Surrey | 1 | 13 | 84 | 67 | 139 | 211 |
| South Essex | 2 | 14 | 37 | 31 | 46 | 100 |
| North Essex | 1 | 7 | 42 | 23 | 48 | 105 |
| Hertfordshire | 0 | 5 | 19 | 9 | 6 | 29 |
| Middlesex | 0 | 3 | 14 | 36 | 3 | 49 |
| Berkshire | 0 | 5 | 14 | 5 | 12 | 30 |
| Oxfordshire | 0 | 2 | 2 | 9 | 22 | 31 |
| Buckinghamshire | 0 | 4 | 9 | 14 | 0 | 25 |

| | | | | | | |
|----------------|----|-----|-----|-----|-----|------|
| East Suffolk | 0 | 4 | 15 | 12 | 10 | 35 |
| West Suffolk | 0 | 1 | 2 | 8 | 5 | 14 |
| East Norfolk | 0 | 1 | 2 | 20 | 9 | 24 |
| West Norfolk | 0 | 0 | 3 | 8 | 13 | 20 |
| Cambridgeshire | 0 | 3 | 12 | 29 | 76 | 101 |
| Bedfordshire | 0 | 0 | 10 | 7 | 11 | 25 |
| Total | 13 | 118 | 473 | 602 | 903 | 1667 |

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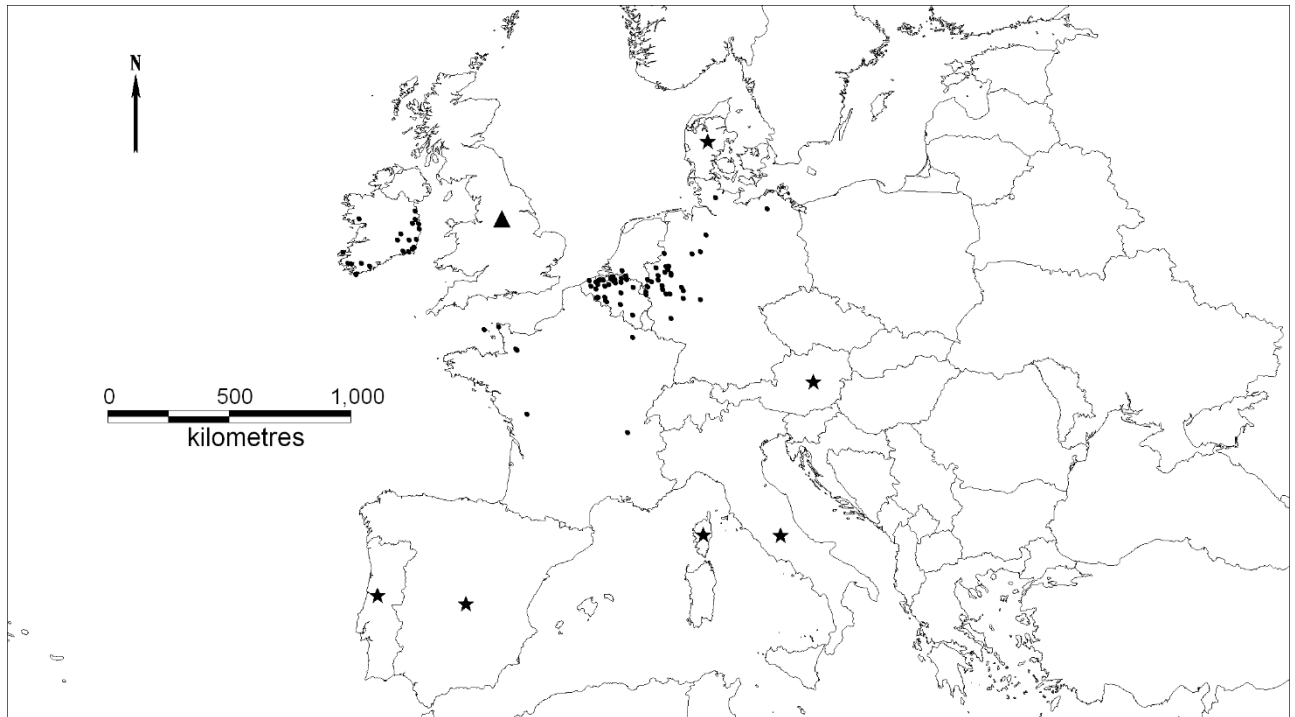
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3 **FIGURE 1** The distribution of *Crassula helmsii* in the British Isles. Each dot represents at least one
 4 record in a 10-km square of the National Grid. (●) non-native 1970 onwards; (○) non-native pre-
 5 1970. Mapped by Colin Harrower, Biological Records Centre, Centre for Ecology and Hydrology,
 6 mainly from records collected by members of the Botanical Society of Britain and Ireland, using Dr
 7 A. Morton's DMAP software.

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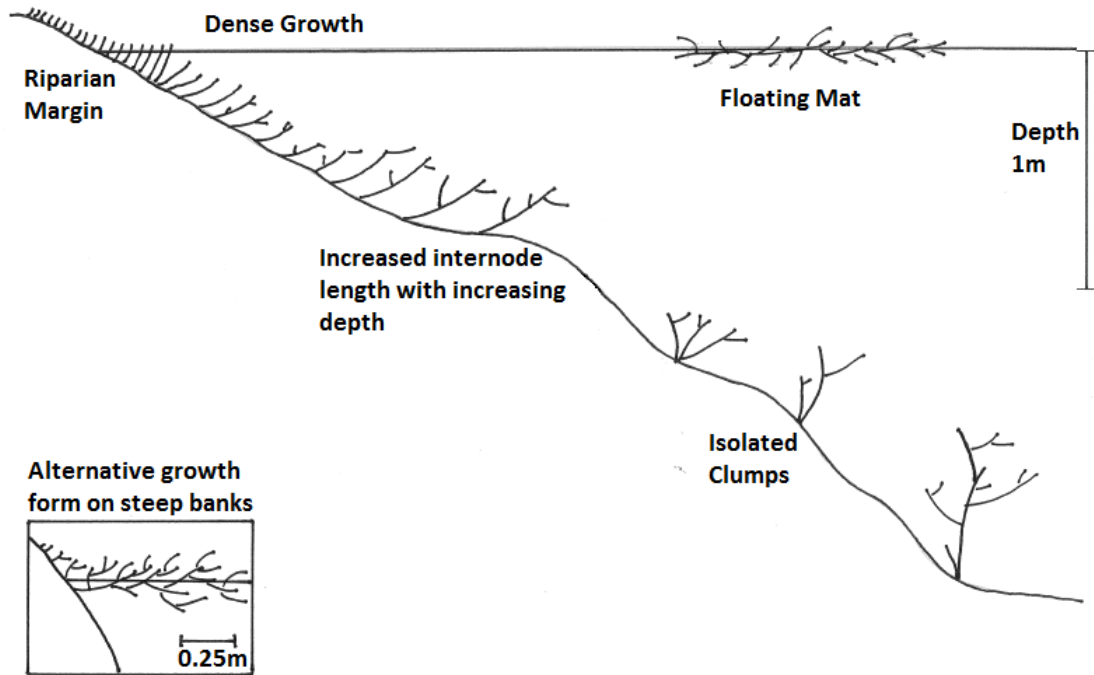
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2 **FIGURE 2** The distribution of *Crassula helmsii* in Europe in (Adapted from Jalas *et al.*, 1999;
3 Hussner, 2007; Delbart *et al.*, 2011; and the EPPO Global Database). Small circles represent actual
4 locations, stars represent a country in which *C. helmsii* has been reported as present but with no
5 detailed location, and the triangle represents where Figure 1 gives more more detailed information.

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3 **FIGURE 3** Different growth forms of *Crassula helmsii* in their natural settings (adapted from
4 Dawson & Warman, 1987).
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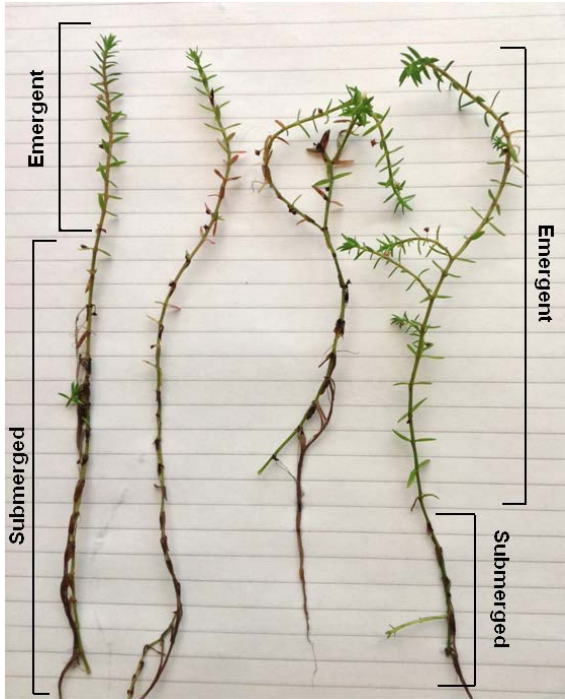
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FIGURE 4 The variation in morphology of *Crassula helmsii* on the same stem.

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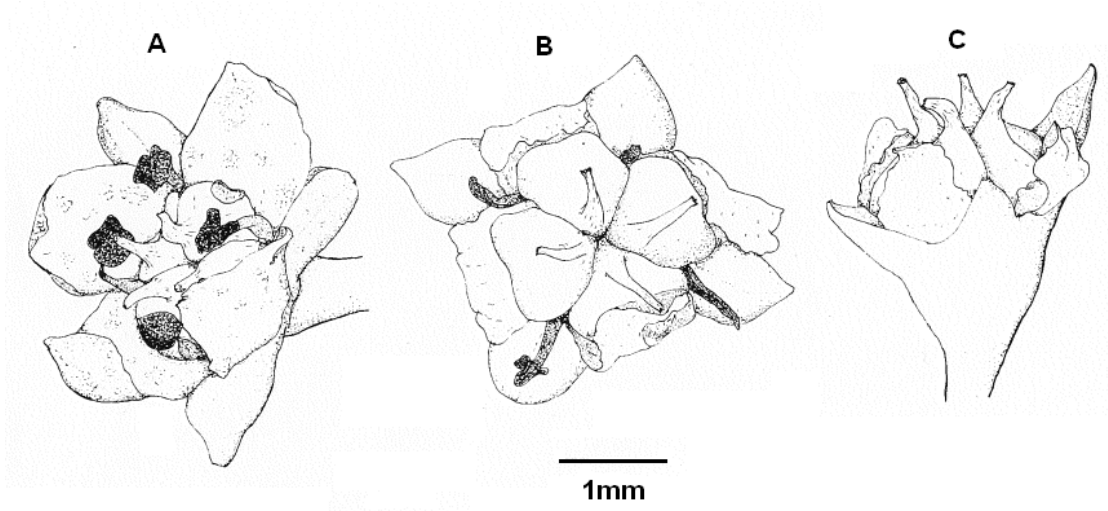


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4 **FIGURE 5** *Crassula helmsii* in the same pond in summer (left) and winter (right) within the Blean
5 Woodland complex in Kent (Grid reference TR112601).

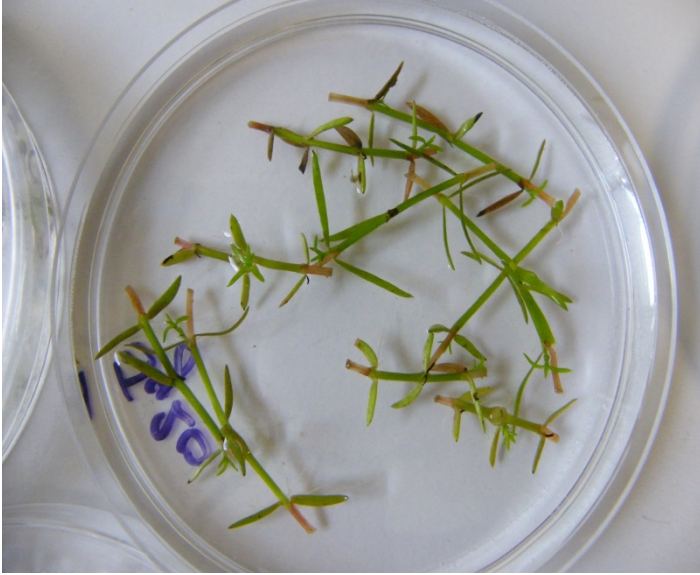
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FIGURE 6 Drawings of the flower (A) and seed head (B & C) of *C. helmsii*, published by the BSBI, to aid identification when the species was newly establishing in the British Isles (Richards, 1979).

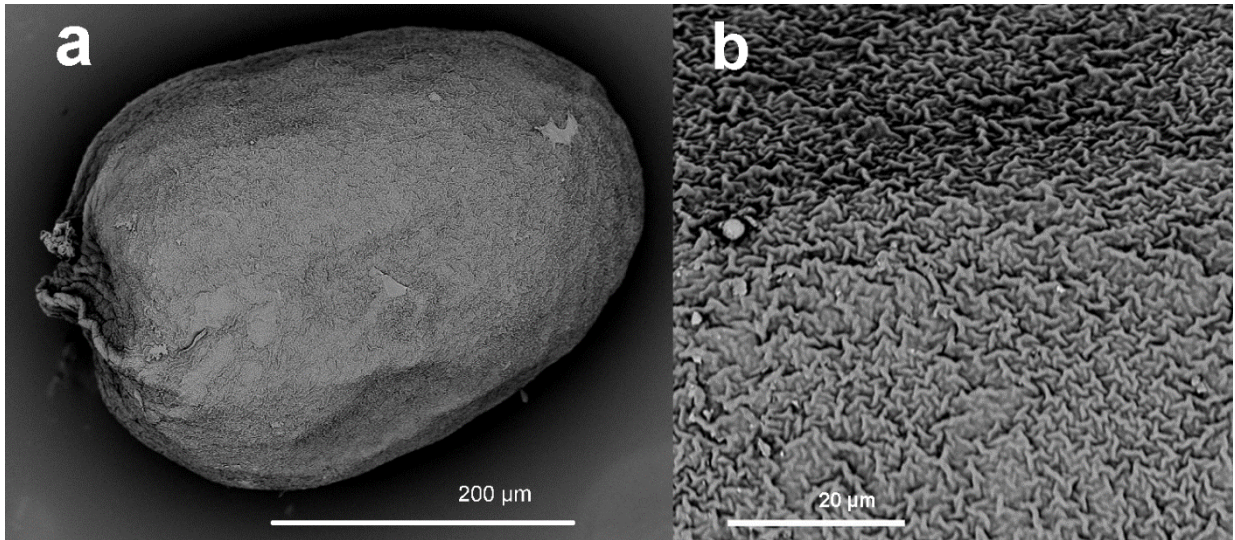
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FIGURE 7 Re-growth of *Crassula helmsii* from 3-node sections *in vitro*, showing new shoot growth.

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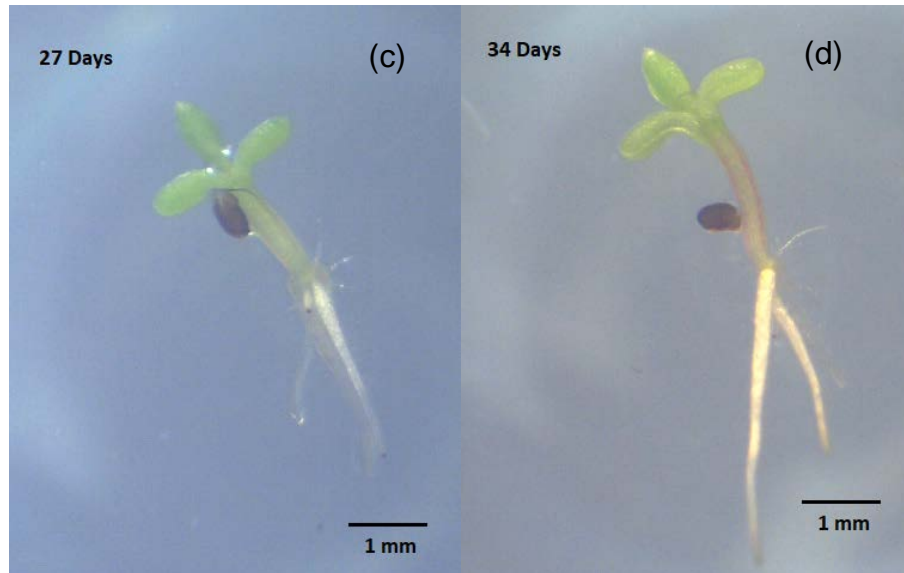


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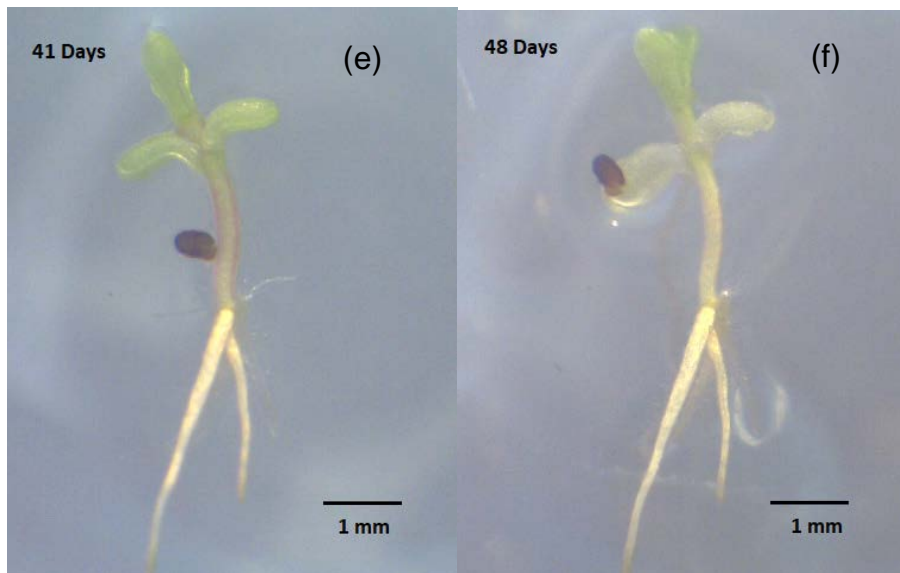
FIGURE 8 Scanning electron micrographs of (a) an individual seed of *Crassula helmsii* and (b) the sculpturing of the seed surface (from Denys *et al.*, 2014).



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1 **FIGURE 9** Seedlings of *Crassula helmsii* photographed at (a) 13, (b) 20, (c) 27, (d) 34, (e) 41 and
2 (f) 48 days from imbibition. Seeds/seedlings were incubated at a temperature regime of 25/10 °C
3 (10h light/14h dark). Seeds from Tasmania were supplied from the Millennium Seed Bank, Kew,
4 by permission of the Royal Tasmanian Botanical Gardens, Australia.
5

1 Graphical Abstract

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4 *Crassula helmsii* is an invasive, non-native aquatic macrophyte from Australasia that has naturalised in
5 Britain. There is concern about its rapid spread, because its dense stands were perceived to cause species
6 loss by competitive exclusion. This is reflected in the novel range of control methods that have been tried,
7 but ultimately without success. Evidence for native diversity losses is rather anecdotal, and as control is
8 often unattainable and can lead to greater impact than the invader itself, control has become less
9 widely adopted.

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