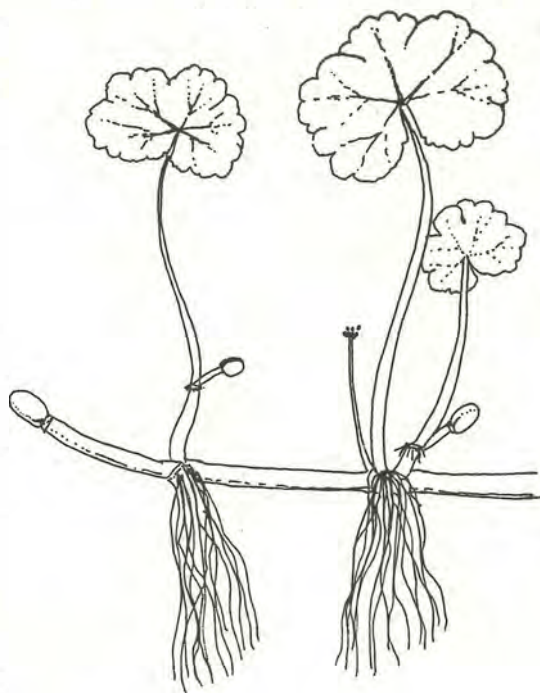


**Literature review of the Genus**  
***Hydrocotyle* L. (Apiaceae),**  
**with particular emphasis on**  
***Hydrocotyle ranunculoides* L.f.**



Swan River Trust  
Report No 18  
1994





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February 1994  
Report No 18

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## FOREWORD

*Hydrocotyle ranunculoides* has become a significant ecological problem for the Canning River environment. In an effort to gain a greater understanding of the ecology and biology of this aquatic weed, the Swan River Trust sponsored a summer project at the University of Western Australia to;

1. To review literature relating to the biology of the genus *Hydrocotyle* and to investigate seed viability and germination responses in the local weed species, *Hydrocotyle ranunculoides*.
2. Prepare a report on the results of the investigation as a basis for further studies into the control and/or eradication of *Hydrocotyle ranunculoides*.

This publication covers the review of literature relating to the biology of the genus *Hydrocotyle*. A further publication will contain information on seed germination and salinity tolerance.

## Author's Acknowledgements

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Maps in Appendices prepared by B Harrison

Cover Drawing by R Ruiz-Avila

## Disclaimer

The recommendations contained in this report reflect the opinion of the author and may not necessarily reflect the opinion of the Swan River Trust.



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## SUMMARY AND RECOMMENDATIONS.

A revision of the literature relating to the genus *Hydrocotyle* revealed that:

1. it is a widespread genus characterised by a rhizomatous creeping growth form, with many species occurring in aquatic or moist terrestrial habitats;
2. it is not known as a particularly weedy genus, but has been recorded as a weed in Chile (*H. ranunculoides*), Georgia USA (*H. ranunculoides*), Argentina (*H. bonariensis*), Brazil (*H. umbellata*) and Australia (*H. ranunculoides*, *H. bonariensis*, *H. laxiflora* and *H. tripartita*), although little information appears to be available on the management of these species;
3. *H. ranunculoides* has been recorded as a component of the vegetation in a number of cool water bodies occurring in either high altitude tropical lakes or low altitude coastal regions of the temperate zone. Within the limitations of these cool water bodies, this species appears to be a 'generalist' in its ecological responses;
3. *H. ranunculoides* is likely to proliferate in the Canning River due to its weedy plant characteristics and modifications of this water way by human activity. Weedy characteristics include (i) a flexible growth response, (ii) effective regeneration (e.g. vegetative propagation by fragmentation and possibly clonal integration), (iii) possibly high resistance to herbivory and (iv) a co-occurrence with other weed species, such as *Eichhornia crassipes*, *Salvinia molesta* and *Alternanthera aquaticum*. Modifications to the Canning River include the construction of the Kent Street Weir, which prevents upstream salt penetration during summer, and an increase in nutrient-rich urban drainage, particularly upstream of the weir due to reduced flushing to the ocean. The freshwater and high-nutrient conditions upstream of the weir, where *H. ranunculoides* largely occurs, are likely to favour the growth of this species;
4. *H. ranunculoides* is utilized in aquatic wastewater treatment systems, particularly in Florida. It is the weedy characteristics of *H. ranunculoides* (e.g. high productivity in high nutrient conditions, overwintering, effective vegetative propagation) which makes this species so suitable for use in such systems.

## RECOMMENDATIONS

Relatively little information appears to be available on the biology of *H. ranunculoides* or the genus as a whole. Specifically, the review highlights the need for an understanding of aspects of the biology of *H. ranunculoides* that includes the investigation of:

- (a) successional status;
- (b) the relative importance of asexual and sexual reproduction in contributing to population growth;
- (c) the possible occurrence of ecotypes within this species;
- (d) the effect of environmental parameters such as salinity, temperature and nutrients on the growth, survival and reproduction of *H. ranunculoides*.



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## 1. OVERVIEW

*Hydrocotyle ranunculoides* is a relatively recent weed of the Canning River of Western Australia. Extensive rhizomatous mats of this species have been known to reach from bank to bank in certain parts of the river, which may potentially undermine the value of the water body by interfering with water use. This species is currently controlled in the Canning River by a combination of chemical and physical techniques, which are successful in the short term, but result in further spread in the long term presumably due to reestablishment of fragmented segments after manual handling. Consequently, a further understanding of the species is required for effective long term management. The objective of this paper is to examine the literature relating to the genus *Hydrocotyle* to assist in gaining an understanding of *H. ranunculoides*.

The genus *Hydrocotyle* is a member of the large dicotyledon family, Apiaceae (Umbelliferae). It is a widespread genus of about 75 to 100 species characterised by a rhizomatous creeping growth form, with simple and usually inconspicuous umbels. Species mostly occur in moist habitats ranging from aquatic (seasonally submerged, floating or emergent) to moist terrestrial conditions. It is not regarded as a particularly weedy genus, but some species are regarded as weeds in Chile (*H. ranunculoides*), Argentina (*H. bonariensis*), Brazil (*H. umbellata*), and Australia (*H. ranunculoides*, *H. bonariensis*, *H. laxiflora* and *H. tripartita*).

Relatively little information is available on the autecology, synecology and management of *H. ranunculoides*. However, several weedy characteristics are apparent from other members of the genus and by the limited experimental work with *H. ranunculoides*. For instance, *H. ranunculoides* is known to have (i) a flexible growth response (e.g. overwintering behaviour and possibly morphological plasticity with respect to nutrients as shown by other creeping macrophytes); (ii) effective vegetative propagation by fragmentation and possibly clonal integration (the latter being displayed by *H. bonariensis* in a terrestrial sand dune environment); (iii) possibly high resistance to herbivory and (iv) a co-occurrence with other weed species, such as

*Eichhornia crassipes*, *Salvinia molesta* and *Alternanthera aquaticum*.

Reasons for the proliferation of this species in the Canning River may relate to (i) environmental factors, such as high nutrients, reduced salinity with the construction of the Kent Street Weir, suitable temperatures for rapid growth, and the absence of competitors and predators and diseases in this new habitat, and (ii) 'weedy' plant characteristics such as effective dispersal and recolonization (by vegetative propagation and perhaps seed germination), rapid growth, and the ability to tolerate a wide range of conditions (such as nutrients, light and temperature). Further studies of the biology and ecology of *H. ranunculoides* in the Canning River are required to achieve successful long-term control or eradication of this species.

## 2. INTRODUCTION

*Hydrocotyle ranunculoides* is an aquatic macrophyte that has invaded and proliferated to weed proportions in the Canning River Regional Park of Western Australia (Klemm *et al.*, 1993). The species was first observed in 1983, but its distribution was not extensive until early 1991 when it covered sections of the Canning River in large mats, reaching from bank to bank in some places, and occupying an estimated volume of 17,500 m<sup>3</sup>. Physical removal of *H. ranunculoides* in November 1991 was successful in the short term. However, the physical impact of removal resulted in a further spread of the weed and, by September 1992, the estimated volume within the Canning River Park had increased to 40,000 m<sup>3</sup>.

Spread of *H. ranunculoides* after its physical removal was thought to be facilitated primarily by vegetative propagation - small segments broken off from the large mats by manual handling are able to generate into new mats after being transported by the water to a new site. In the Canning River, the plant anchors to the bank at a depth of up to 15 cm, with the main bulk of the plant floating on the water. It has also been observed attached to overhanging branches and snags instead of to the river bank, although these mats tend to remain small.

Klemm *et al.* (1993) claim that the current



infestation of *H. ranunculoides* in the Canning River has the potential to undermine the value of the regional park, and further concerns that it may spread to other fresh water bodies were also expressed. Accordingly, this species was gazetted as a Class P1 (preventing importation, movement and trade of the plant) and Class P2 pest (plant requiring control and eradication) under the Agriculture and Related Resources Protection Act. Since this species is a common aquarium plant readily available throughout Western Australia, it is thought that *H. ranunculoides* first invaded the Canning River through the release of aquaria wastes into the system.

The distribution of *H. ranunculoides* appears to be limited by water salinity, largely occupying the freshwater region of the Canning River upstream of the Kent Street Weir, constructed to prevent the upstream penetration of salt during summer for agricultural purposes. The reduced salinity of the water above the weir has changed the vegetation in favour of freshwater fringing vegetation (Olsen and Skitmore, 1991). Furthermore, the combination of reduced flushing and nutrient rich urban drainage has made this section of the river more eutrophic. Earlier outbreaks of the freshwater weed, *Salvinia molesta*, were controlled by draining the weir to allow salt water to penetrate further upstream and by manual removal.

Currently, *H. ranunculoides* is controlled by a combination of chemical and physical control techniques (Klemm *et al.*, 1993). While this is successful in the short term, further understanding of the biology and ecology of this species is necessary to achieve long term management success. The objective of this review is to examine the literature relating to the genus *Hydrocotyle* in an attempt to increase an understanding of *H. ranunculoides*, and thereby to assist in devising effective management strategies for its control and eradication in the Canning River of Western Australia.

### 3. TAXONOMY

*Hydrocotyle* spp. are members of the Apiaceae (Umbelliferae), a large dicotyledon family of about 300 genera and 3000 species (Townsend, 1989). Flowers of the Apiaceae are always small and formed in a simple or compound umbel. The fruit consist of two symmetrical parts known as mericarps, each containing one seed, which separate at maturity.

Drude (1897) recognised three subfamilies within the Apiaceae according to their fruit and pollen characters: (i) Hydrocotyloideae, (ii) Saniculoideae and (iii) Apoideae. The subfamily Hydrocotyloideae is raised in rank by some authorities and treated as a separate family (Hickey and King, 1988). *Hydrocotyle* is the largest genus within the Hydrocotyloideae, consisting of about 75 (Muenscher, 1944; Cook, 1990) to 100 species (Ewart, 1930; Webb *et al.*, 1988; Johnson and Brooke, 1989). On the basis of fruit characters, *Hydrocotyle* is the most similar to the *Platysace*, *Centella*, *Xanthosia* and *Trachymene*, also of the Hydrocotyloideae (Tseng, 1967).

The name *Hydrocotyle* is derived from the Greek words *hydor* (water) and *kotyle* (a dish or plate), apparently alluding to the shape of the leaves, which are slightly depressed in the centre (Black, 1957). It is one of the few genera of the Apiaceae with entire leaves, most others possessing much divided pinnate leaves (Hickey and King, 1988). A distinguishing character of the genus is the presence of only one ovule in each mericarp (Tseng, 1967). In all other members of the Apiaceae examined, each mericarp contains two ovules, although the upper ovule always aborts.

*Hydrocotyle* is often regarded as a relatively primitive member of the Apiaceae, although it also possesses a number of apparently advanced characters (Rodriguez, 1971). For example, the laterally compressed fruit is regarded as a primitive feature while the creeping herbaceous habit and the absence of ventral bundles in the vascular system of the ovary and fruit are considered to be advanced features. *Hydrocotyle* is one of the few genera of the Apiaceae classified largely on the basis of leaf features (Constance and Dillon, 1990). A description of the genus by Cook (1990) is as follows:





*Stems floating or creeping; rooting at most nodes. Leaves distinctly stalked, simple or peltate or with basal sinus, orbicular to reniform, entire, toothed or lobed, stipules present. Umbels simple, sometimes proliferous, rarely an interrupted spike, axillary, usually inconspicuous. Fruit ovoid-ellipsoid to suborbicular, strongly flattened dorsally; mericarps with three subequal ribs; fruit wall a woody inner layer. Seasonally submerged to floating, emergent or terrestrial; entomophilous or perhaps autogamous; diaspores globose or somewhat flattened mericarps; probably dispersed in mud by water or perhaps by animals.*

Comprehensive monographs of the genus *Hydrocotyle* have been published by Richard (1820) and Eichler (1987a,b).

#### 4. GEOGRAPHIC DISTRIBUTION

*Hydrocotyle* is a widespread genus, occurring in tropical and temperate regions of both hemispheres (Hickey and King, 1988), and being particularly well represented in North and South America (Mathius, 1971). Fifty five species of *Hydrocotyle* occur in Australia, of which 24 occur in Western Australia and 11 in the Perth region (Marchant *et al.* 1987; Klemm *et al.* 1993). At least ten native and one naturalised *Hydrocotyle* species occur in New Zealand (Johnson and Brooke, 1989). Summaries of information found on the occurrence of *Hydrocotyle* species in Australasia and the rest of the world are contained in Appendices 1 and 2, respectively.

*Hydrocotyle* is not well known as a weed genus throughout the world. However, *H. umbellata* is regarded as an aquatic weed in south-western USA (Anderson, 1990) and *Hydrocotyle* spp. are listed amongst potential weeds in eastern and north-

central USA (Steward, 1990). Fernandez *et al.* (1990) compiled a survey of aquatic weeds in South America and noted that *H. bonariensis* (Argentina), *H. umbellata* (Brazil) and *H. ranunculoides* (Chile) were only cited once or twice in the survey, and that the importance of these species as weeds is difficult to assess and the extent of problems caused by them is unknown.

In Australia, *H. bonariensis*, *H. laxiflora* and *H. tripartita* are regarded as weeds in certain habitats (Auld and Medd, 1987). *H. bonariensis* is a native of South America and occurs mostly in maritime habitats along the New South Wales coast and around Adelaide. It is common on dunes and in wasteland, gardens and lawns grown on sandy soils. Both *H. laxiflora* and *H. tripartita* are native to Australia. These two species are also listed as Australian weeds by Swarbrick (1973). *H. laxiflora* (stinking pennywort) occurs throughout the Eastern States and is common in pastures and open grasslands, wasteland and woodland. In the dry sclerophyll forests of Victoria, it is a dominant understorey species, although it is not mentioned as being a weed in this habitat (Foreman and Walsh, 1993). This species occasionally persists in lawns and along the banks of streams (Auld and Medd, 1987). *H. tripartita* also occurs in eastern Australia, mostly in sheltered places on the banks of streams, and sometimes as a weed in lawns. This species has become naturalised in New Zealand (Webb *et al.*, 1988; Johnson and Brooke, 1989).

Within Australia, *Hydrocotyle ranunculoides* appears to occur only in the Canning River, Western Australia. *H. ranunculoides* is native to Europe (Marchant *et al.* 1987) and is included in the flora of America (Mathius 1936; Cook *et al.* 1974; Mason, 1957; Aulbach-Smith *et al.* (1990; Wijninja, 1989), Africa (Lock, 1973; Thompson, 1985; Agnew, 1974; Denny, 1973; Harper, 1992; Townsend, 1989; Gaudet, 1977) and Chile (Steubing *et al.*, 1980), although these references do not indicate whether *H. ranunculoides* is native, naturalised or a weed in these regions. *H. ranunculoides* is, however, stated as a weed of unknown proportions in Chile (Fernandez *et al.*, 1990) and a serious weed of northern South America (Mathius, 1936). A summary of the geographical distribution of *H. ranunculoides* is contained in Appendix 3.



## 5. ECOLOGY

### 5.1. Ecology of *Hydrocotyle ranunculoides*

It appears that there is little information available on the autecology of *H. ranunculoides*. However, an examination of the abiotic and biotic conditions occurring in habitats in which this species has been recorded may provide possible reasons for its proliferation in the Canning River environment. *Hydrocotyle ranunculoides* occurs in three intensively-studied high altitude tropical lakes: Lake Naivasha of Kenya, Lake Bunyonyi of southwest Uganda and Laguna de la Herrera of Colombia. It is also recorded as a dominant species of a Mehuin Brook of the temperate humid zone in Chile, and coastal USA.

#### 5.1.1. Tropical Zone Waterbodies

##### *Lake Naivasha, Kenya*

Lake Naivasha is a freshwater closed basin lake which occurs at an altitude of 1890 m above sea level (Harper, 1992). The lake occupies an area of approximately 140 km<sup>2</sup> (Harper, 1992) and has an average and maximum depth of 4 m and 7.6 m, respectively (Gaudet, 1977). The shoreline is gently sloping, which is ideal for the development of a wet mud flora (Gaudet, 1977), and consists of silts, clays and diatomites (Thompson and Dodson, 1963). Details of the lake's chemical properties are listed by Denny (1985), including a conductivity of 363  $\mu\text{s cm}^{-1}$ , pH of 8.8, alkalinity of 3.3 meq dm<sup>-3</sup>, and a sodium and chlorine concentration of 45 and 14 mg dm<sup>-3</sup>, respectively. Although no measurements were made, eutrophication of the lake may be occurring due to high agricultural production as the lake's edge (Gaudet, 1977).

The lake is characterised by a natural, unpredictable fluctuation in the water level, given the term 'drawdown'. A combination of the characteristic drawdown and the freshness of the water is thought to give rise to a high species richness of aquatic plants associated with succession on wet mud at the lake's edge (Harper, 1992). Gaudet (1977) documented the succession following a natural

drawdown in Lake Naivasha in November 1973. Initially, three zones could be identified: a composite zone (dominated by *Conyza* spp., closest to the dry land), sedge zone (dominated by *Cyperus papyrus*, *C. digitatus* and *C. immensus*), and a seedling zone (closest to the lake water). After reflooding, *Sphaeranthus* dominated the seedling zone and, by March 1975, the drawdown succession had progressed to a papyrus (*Cyperus papyrus*) fringe swamp.

The mature papyrus swamp community consisted of plant species occupying the swamp-land and swamp-lake interfaces, with very few species occurring within the papyrus stand. *H. ranunculoides* commonly occurred at the swamp-lake interface, occupying the swamp edge in shallow water (Gaudet, 1977). It is therefore apparent that *H. ranunculoides* formed part of the sub-climax community along the edges of Lake Naivasha. However, this does not necessarily indicate that *H. ranunculoides* is itself a late successional species, particularly since it was also common on recently exposed shore. An understanding of the position of *H. ranunculoides* in plant succession has implications for effective weed management in the Canning River of Western Australia. Many weed species are pioneer or opportunist species that are difficult to control because short-term programs provide the environment these plants are best able to colonise and exploit (Mitchell, 1980). For these species, allowing the habitat to develop naturally may be a more effective weed control strategy than weed removal (Wade, 1990). Provided that *H. ranunculoides* is shown to be consistently a late successional species in the Canning River environment, short-term weed control programs may possibly be more successful than for opportunistic weed species.

Lake Naivasha has been observed to undergo considerable changes in aquatic plant composition during the period of 1930 to 1988 (Harper, 1992). During the so-called 'normal-phase' of 1930 to 1975, species dominant outside the papyrus clumps were *Nymphaea caerulea* (water lilies) and *H. ranunculoides* together with the submerged species *Ceratophyllum demersum* and *Potamogeton* spp. (Beadle, 1932; Gaudet, 1977). By 1982 the submerged vegetation was completely eliminated from the lake (Harper, 1984). However, the



emergent *H. ranunculoides* was still common during this 'reduced phase' and was often seen colonising large floating *Salvinia molesta* mats, an introduced species that dominated the floating vegetation at this time. This floating community moved in rafts or islands of various sizes around the lake as a result of wind action, and covered about a quarter of the lake surface. Submerged vegetation has been progressively returning since 1984 and this return is coincident with a decline in crayfish population density (Harper, 1992). The persistence of *H. ranunculoides* during the 'reduced phase' of 1975 to 1983 suggests that, unlike the submerged species, it is not severely predated, if at all, by the introduced crayfish, *Procambarus clarkii*.

#### Lake Bunyonyi, Uganda

Lake Bunyonyi is another high altitude (1950 m above sea level) lake of Tropical East Africa (Denny, 1973). It has an open water surface of approximately 60 km<sup>2</sup> and an additional area of 21.7 km<sup>2</sup> that is covered with swamp vegetation. Lake Bunyonyi is a dammed valley lake and, unlike Lake Naivasha, has a steep-sloping shoreline and is comparatively deep, with a maximum depth of 40 m. Permanently anoxic conditions occur below 7-15 m, depending upon local weather conditions, and the epilimnion is nutrient-poor and low in phytoplankton (Denny, 1972). No obvious changes in the bottom substrate occur around the lake shores. The lake is relatively undisturbed, and artificial fertilizers have not been used in the cultivation of nearby land.

Two distinct communities occurred within and on the edges of the lake: (i) a steep, exposed shoreline community and (ii) a swamp community in the shallow sheltered bays and inflows (Denny, 1973). Wind and wave action characterises the steep, exposed shores. Only a narrow band of vegetation occurred in this region, dominated by an outer belt of the firmly rooted emergent species *Phragmites australis*, usually with an inner belt of *Cyperus papyrus*. Floating-leaved *Potamogeton* sp. and *Nymphaea caerulea* sometimes occurred outside the emergent species, and submerged species, including *Ceratophyllum demersum*, that grew down to 8 m depth. In the sheltered swamps, floating mats of *Cyperus papyrus* and *Cladium jamaicense* dominated.

Vegetation surveys were conducted on four representative swamp sites: Majera Bay, Sites A and B, Bugoroba Swamp and Gweru Bay (Denny, 1973). *H. ranunculoides* was listed as present at all sites excepting Majera Bay. The absence of *H. ranunculoides* from this site may be due to the conditions (abiotic and biotic) or to the chance event that dispersal did not occur to this area. However, a determination of causes is uncertain since this objective was not directly addressed in the study and no differences in conditions between Majera Bay and the other sites were identified.

At Sites A and B, *H. ranunculoides* was common on floating mats dominated by *Cladium jamaicense*. Other 'island' species included *Polygonum salicifolium*, *Pycnostachys coerulea* and the fern, *Thelypteris squamigera*. Excepting the presence of these floating mats at Sites A and B, the vegetation pattern was similar to Majera Bay.

Bugoroba Swamp was different in physical structure to the previously mentioned swamps of Lake Bunyonyi (Denny, 1973). It occupied a shallow bay (with the depth less than 3.5 m) that was considerably silted, with the entire bottom consisting of very soft anoxic mud. The dominant species of the swamp was *Cladium jamaicense* which formed large masses of floating vegetation as it did at swamp Sites A and B. A 100 m<sup>2</sup> quadrat taken within the swamp indicated that *H. ranunculoides* formed a part of this community, although its cover was regarded as insignificant. Present in slightly higher proportions was the related species, *Hydrocotyle mannii*.

*H. ranunculoides* was also scattered throughout the floating mats of *Cladium jamaicense* at the swamp/lake interface of Gweru Bay. The main inflows to the lake occurred at Gweru Bay. The rivers provided a gentle flow through the swamp and at the mouth oxygen readings indicated that the water was well oxygenated except immediately above the mud surface. *H. ranunculoides*, *Polygonum salicifolium*, *Thelypteris squamigera* and *Cyperus nudicaulis* were scattered amongst the *Cladium jamaicense* and *Cyperus papyrus* rhizomes of the floating mats. *Potamogeton x bunyonyiensis* and *Nymphaea caerulea* occurred around the outer fringes of the rafts, *Utricularia vulgaris* formed floating masses in the water around the rafts, and *Hydrilla verticillata* and *Ceratophyllum demersum* covered the bottom down to 5 m.



In addition to these specific sites at Lake Bunyonyi, the *Cladium*-dominated floating mat communities were a common feature of the lake as a whole. The vegetation was examined on one large mat floating in open water. The mat measured 75 m by 65 m and was composed of close mesh interwoven roots and rhizomes of *Cladium* which formed a raft up to 0.64 m thick. The upper layers of the mat were interspersed with dead and decaying organic detritus with little or no inorganic sediment, and oxidising conditions prevailed. In addition to *Cladium jamaicense*, *Thelypteris squamigera* was abundant while other swamp plants including *H. ranunculoides* and *Polygonum salicifolium* were common. Floating-leaved and submerged aquatic macrophytes occurred in pools between the mats, and included *Nymphaea caerulea*, *Potamogeton thunbergii*, *P. x bunyonyiensis*, *Lemna minor*, *Ceratophylla demersum* and *Utricularia vulgaris*. Attached to the outside of the raft were *Hydrilla verticillata* and *Chara* sp.

The commonest swamp plant in tropical East Africa is *Cyperus papyrus* (Carter, 1955), and Denny (1973) attributes its reduced abundance at Lake Bunyonyi to strong competition from other emergents, particularly *Cladium jamaicense* and *Phragmites australis*, at high altitude. *P. australis*, a pioneer species, appears to outcompete both *C. jamaicense* and *C. papyrus* in exposed sites. Presumably, *P. australis* is less successful in less exposed areas because it is in direct competition with *C. jamaicense* and *C. papyrus*.

The growth habits of *C. jamaicense* and *C. papyrus* are similar, both forming rhizomatous mats which grow out over the surface of the water, and fragment at their outermost fringes to form floating islands. Denny (1973) suggests that these two species could be direct competitors for swamp sites, with the greater susceptibility of *C. jamaicense* to fragmentation making it more likely to float off in the rafts which accumulate in windward bays. Interestingly, *H. ranunculoides* also occupies a similar niche to these two species, and it is therefore possible that its growth in the Lake Bunyonyi system was kept in check by the presence of competitors such as *C. jamaicense* and *C. papyrus*, both of which are absent from the Canning River environment.

### *Laguna de La Herrera, Colombia*

Laguna de La Herrera is a 2.9 km<sup>2</sup> lake that occurs on the high plain of Bogota, Colombia, at an altitude of approximately 2550 m (Wijninga *et al.*, 1989). It experiences a bimodal distribution of rain (occurring from April-June and from September-November), with a mean annual rainfall of 635 mm. Temperatures are cool, with a yearly average of 12.5°C and the occasional night frost. The lake is polluted primarily by detergents draining from nearby sloping pastures, and also by cattle dung and artificial fertilizers on nearby grasslands. Wijninga *et al.* (1989) conducted a detailed survey of the tropical mountain lake vegetation of Laguna de La Herrera because it is the last big natural lake on the high plain of Bogota, and therefore has conservation value.

Wijninga *et al.* (1989) recognised ten community types surrounding and within the lake (Table 1). These communities were classified as either terrestrial, helophytic or pleustophytic, a system not found to be employed by any other authors. Helophytes are defined by Cook (1990) as "essentially terrestrial plants whose photosynthetically active parts tolerate long periods of either floating or being submerged", as distinct from hydrophytes, which are defined as "plants physiologically bound to water, with at least part of the generative cycle occurring in or on the surface of the water". However, these definitions do not appear to be adopted by Wijninga *et al.* (1989), since they used the terms helophytes and hydrophytes interchangeably. Rather, it appears that in this study, helophytes are regarded as emergent or submerged plants. Furthermore, no definitions of pleustophytes were located in the literature, although these species appear to correlate to the free-floating aquatic plants of other classifications (e.g. Gaudet, 1977).

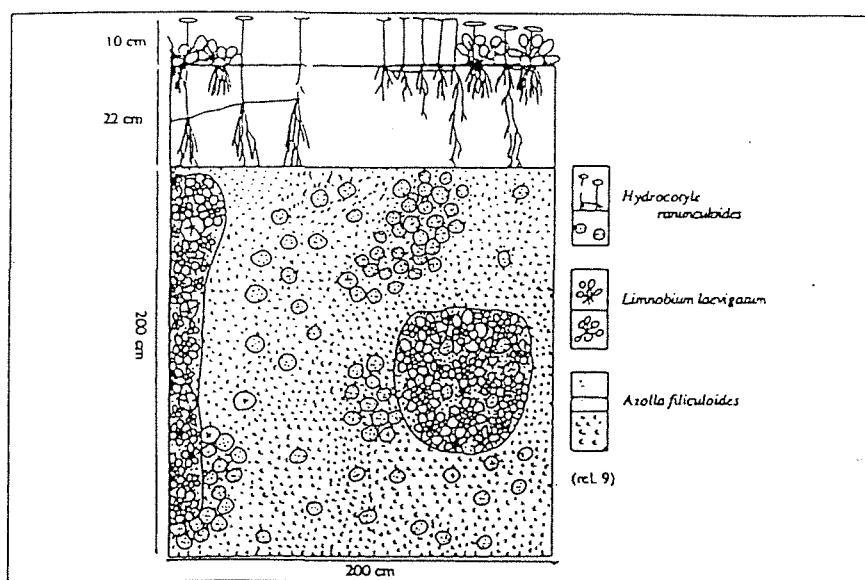


**Table 1.** Comparison of presence/absence of *Hydrocotyle ranunculoides*, mean ECC and mean pH at each of the community types recognised at the Laguna de la Herrera (Sabana de Bogota, Colombia) by Wijninga *et al.* (1989).

COMMUNITY	COMMUNITY TYPE	PRESENCE/ ABSENCE OF <i>H. ranunculoides</i>	MEAN ECC (u s)	MEAN p H
<i>Hydrocotyle ranunculoides</i>	helophytic	present (common, dominant)	106	6.0
<i>Polygonum punctatum</i>	helophytic	present (common)	187	6.2
<i>Rumex obtusifolius</i> / <i>Polygonum punctatum</i>	helophytic	present (common)	108	6.0
<i>Bidens laevis</i>	helophytic	present (moderate)	208	6.0
<i>Phytolacca bogotensis</i>	terrestrial	absent	-	-
<i>Scirpus californicus</i> / <i>Typha angustifolia</i>	helophytic	absent	130	6.0
<i>Scirpus californicus</i>	helophytic	absent	95	5.9
<i>Eichhornia crassipes</i>	pleustophytic	present (rare)	147	5.9
<i>Limnobium laevigatum</i>	pleustophytic	absent	104	5.9
<i>Azolla filliculoides</i> / <i>Lemna cf. miniscula</i>	pleustophytic	absent	249	6.1

In one of the community types, *H. ranunculoides* was the dominant species with a cover of 75% to 100% (Fig. 1). Associated hydrophytes were *Pennisetum clandestinum* and *Ludwigia peploides*, although both were rare with a low percentage cover. Of the pleustophytic representatives, *Azolla*

*filliculoides* was dominant with a moderate to high cover, while other species (including *Lemna cf. gibba*, *Limnobium laevigatum* and *Ricciocarpus natans*) were relatively rare. This community occupied shallow water of a depth ranging between -40 cm to +22 cm.



**Figure 1.** Quadrat (2 m<sup>2</sup>) of the *Hydrocotyle ranunculoides*-dominated community of the Laguna de la Herrera (Sabana de Bogota, Colombia). From Wijninga *et al.* (1989).



*H. ranunculoides* also occurred as an associate species in five of the other community types, that is the shallow communities of *Rumex obtusifolius*/*Polygonum pictatum* and *Polygonum pictatum*, and the deeper communities of *Bidens laevis*, *Eichhornia crassipes* and *Limnobium laevigatum*. The *Rumex obtusifolius* (dominant) and *Polygonum pictatum* (subdominant) community, of which *H. ranunculoides* was a part, occupied shallow waters of a depth between -80 cm and 10 cm. In the usually deeper conditions (5 cm to 60 cm) of the *Polygonum punctatum* community, *H. ranunculoides* was the associate species with other helophytes being less frequent. This community frequently occupied zones along marshy shores and was not found in the centre of the lake.

The *Bidens laevis* community occurred in the course of the Bojaca River, and was persistently the deepest part of the lake. *H. ranunculoides* was the associate species of this community, and displayed moderate cover. Of the other helophytic species, only *Ludwigia peploides* and *Rumex obtusifolius* were present, and had low cover. In obvious contrast to the other communities, the floating *Azolla filiculoides* layer was absent, perhaps due to the stronger water currents.

The pleustophytic communities of *Eichhornia crassipes* and *Limnobium laevigatum* supported only a very low cover of *H. ranunculoides*. Other helophytic species of very low cover that were present in the *Eichhornia crassipes* community included *Polygonum punctatum* and *Ludwigia peploides*, and associate pleustophytic species included *Azolla filiculoides*, *Lemna* cf. *gibba* and *Spriodela* spp. Other helophytic species were virtually absent from the *Limnobium laevigatum* community, while *Azolla filiculoides* and *Lemna* cf. *gibba* were common.

Communities in which *H. ranunculoides* was not recorded included the terrestrial *Phytoclasca bogotensis* community (situated above the waterline), the helophytic communities of *Scirpus californicus*/*Typha angustifolius* (average depth of 15 cm) and *Scirpus californicus* (depth of 40 to 50 cm), and the pleustophytic *Azolla filiculoides*/*Lemna* cf. *gibba* community (depth of 15 to 40 cm).

No marked differences in the measured environmental parameters were apparent between communities of the Laguna de La Herrera in which

*H. ranunculoides* was present or absent (Table 1). This species occupied both shallow swampy regions and deeper regions of greater flow velocity. Mean pH was relatively consistent between the communities and no difference in ECC was apparent. The communities in which *H. ranunculoides* occurred occupied a total of 64% of the lake, although its percentage cover was low in much of this area. The community in which it was dominant occupied only 1%, and it was common in communities occupying a total of 38% of the lake.

### 5.1.2. Temperate Zone Waterbodies

#### *Mehuín Brook, Chile*

The brook of Mehuín supports permanently flowing fresh water in the region of Valdivia, south Chile (Steubing *et al.*, 1980). It has a maximum depth of 40 cm, a mean pH of 6.2 (similar to the Laguna de La Herrera), gently sloping banks (5°C mean inclination), and a sand substrate. The area in which it occurs receives high precipitation (mean annual rainfall of 2372 mm) and low temperatures (yearly mean of 12.1°C). At the time of the study, aquatic ecosystems of the Valdivia region were oligotrophic, and without observable contamination. Mehuín Brook was totally covered with floating-benthic hydrophytes of which the dominant species were *H. ranunculoides* (70% cover) *Callitriche stagnalis* (20% cover) *Rorippa naturium-aquaticum* (5% cover) and *Mimulus luteus* (2% cover) (Steubing *et al.*, 1980).

#### *Marga-Marga Estero, Chile*

The distribution patterns of the aquatic and marsh flora along the Marga-Marga stream in central Chile were studied during the 1982 summer-autumn season (Palma *et al.*, 1987). *H. ranunculoides* together with *Elodea potamegeton* were the most abundant species. Distribution patterns of the species were interpreted in terms of substrate and physiochemical variables, particularly salinity and eutrophication of the water. Unfortunately, only the abstract is available in English and extraction of further information requires translation.

#### *Coastal United States of America*

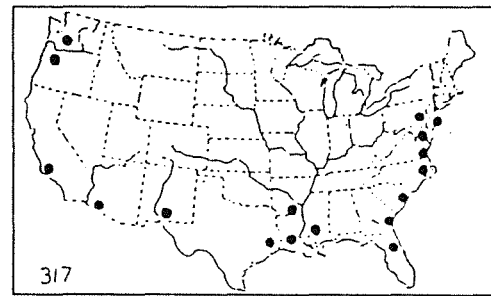
*H. ranunculoides* occurs mostly on sandy substrates in ponds, lakes and stream margins of

coastal USA (Fig. 2; Muenscher, 1944; Mason, 1957; Aulbach-Smith *et al.*, 1990). Unlike the high altitude lakes of the tropical zones, it is restricted to lower altitudes in temperate California (Mason, 1957). In South Carolina, *H. ranunculoides* forms large floating mats that can support other plants such as *Bidens* spp., *Polygonum densiflorum*, *Alternanthera aquaticum* and *Myriophyllum aquaticum* (Aulbach-Smith *et al.*, 1990), the latter two species being noxious weeds in Australia (Parsons and Cuthbertson, 1992). Extensive populations of *H. ranunculoides* have been reported in South Carolina, occurring from autumn to spring, but dying back during the summer after flowering in April and May (Aulbach-Smith *et al.*, 1990). This is in contrast to its growth pattern in the Canning River, where its maximal growth period is thought to occur during summer (Klemm *et al.*, 1993).

*H. ranunculoides* was reported as a potential problem weed species in Ebenezer Creek, Georgia (Newman and Thomaston, 1979). Ebenezer Creek is a tributary of the Savannah River, and is a long, narrow stream that drains large areas of low-lying river swamp land. At the time of the report, the creek was infested primarily with *Alternanthera philoxeroides*, until control measures (such as introduction of the alligator flea beetle, *Agasicles hygrophila*, and the application of Kuron herbicide) reduced its population to a few floating patches of leafless shoots and stems. However, the decrease in *Alternanthera philoxeroides* resulted in a considerable increase in the weeds *H. ranunculoides* and *Myriophyllum brasiliense*. Unfortunately, more recent reports on the status of *H. ranunculoides* in Ebenezer Creek could not be found.

### 5.1.3. Conclusion: Ecology of *H. ranunculoides*

Two distinct habitats can be recognised in which *H. ranunculoides* occurs: high altitude tropical lakes (of East Africa and South America) and low altitude coastal regions of the temperate zone (of USA and South America). This species has been observed attached to the banks of shallow pools, particularly in swampy regions, as well as in deeper water, often as part of a floating island community. It is present in both flowing water, such as river



**Figure 2.** Geographic distribution of *Hydrocotyle ranunculoides* in the USA. From Muenscher (1944).

outflows, and in sheltered swamps. It is able to establish itself off both steep (e.g. Lake Bunyonyi) and shallow banks (e.g. Lake Naivasha and Mehuin Brook). Gaudet (1977) claims that a gentle sloping shoreline is ideal for the development of a wet mud flora, although Klemm *et al.* (1993) observed that *H. ranunculoides* in the Canning River appears to establish itself less successfully where the bank has a gentler slope.

Similar pH occurred at the Laguna de La Herrera and Mehuin Brook, both of South America, while both pH and ECC was lower at the Laguna de La Herrera than the East African Lake Naivasha. In coastal USA and Mehuin Brook, Chile, a sandy substrate is regarded as important for growth and establishment.

In all the studies, *H. ranunculoides* was a common component of the aquatic flora, but it was not recorded as proliferating to weed status as it does in the Canning River. Invading populations of *H. ranunculoides* may proliferate in the Canning River due to (i) high nutrient availability, (ii) the absence of competitors, and (iii) the absence of herbivores. *H. ranunculoides* occupied both nutrient-enriched (e.g. Laguna de La Herrera, Lake Naivasha) and oligotrophic systems (e.g. Lake Bunyonyi, Mehuin Brook). Although it is difficult to compare the productivity of *H. ranunculoides* between systems from the information provided in the literature, it was perhaps the most prolific in the polluted Laguna de La Herrera, where it was dominant or codominant over much of the lake, and in the Marga-Marga Estero, where it was the most abundant species. This latter reference (Palma *et al.*, 1987) is likely to contain information on the effect of nutrients on the abundance of *H. ranunculoides*.



In the East African lakes, the growth of *H. ranunculoides* may be limited by competition with other species, particularly *Cladium jamaicense* and *Cyperus papyrus*, both of which occupy a similar niche and have a similar growth form to *H. ranunculoides*. Other species typically co-occurring with *H. ranunculoides* in these lakes include *Typha latifolia*, *Ceratophyllum demersum*, *Nymphaea caerulea*, *Hydrilla verticillata* and the introduced *Salvinia molesta*. Of these species, both *Hydrilla verticillata* and *Salvinia molesta* have both occurred in the Canning River. Common

genera of Lake Naivasha, Lake Bunyonyi and the Laguna de La Herrera include *Polygonum*, *Bidens*, *Rumex* and *Lemna*.

It is possible that the absence of *H. ranunculoides*-specific herbivores in the Canning River contributes to its proliferation in this environment. Prevalent faunal species in Lake Naivasha, Lake Bunyonyi and the Laguna de La Herrera are summarised in Table 2, although no mention was made in any of the studies of these species specifically consuming *H. ranunculoides*.

LOCATION	SPECIES	COMMON NAME	COMMENTS
Lake Naivasha (Gaudet, 1977)	<i>Myocastor coypus</i>	aquatic rodent	population explosion, known to eat <i>Nymphaea</i>
Lake Naivasha (Harper, 1992)	<i>Procambus clarkii</i>	crayfish	decline of submerged macrophytes attributed to introduction of crayfish
Lake Naivasha (Gaudet, 1977)		Hippopotamus	major grazers at night on drawdown flora, excepting <i>Polygonum</i> plants
Lake Naivasha (Gaudet, 1977)		Cattle	major grazers at day
Lake Bunyonyi (Denny, 1973)	<i>Biomphalaria</i> sp.	Bilharzia snail	prevalent on <i>Ceratophyllum demersum</i>
Lake Bunyonyi (Denny, 1973)	<i>Haplochromis</i> sp. and <i>Clarias carsonii</i>	fish	large numbers
Laguna de La Herrera (Wijininga et al., 1989)		cattle	observed feeding on water plants, esp. <i>Limnobium laevigatum</i>

**Table 2.** Summary of faunal species in freshwater habitats of *Hydrocotyle ranunculoides*.

## 5.2. Ecology of Other *Hydrocotyle* Species

Ecological studies of other *Hydrocotyle* species include those of the aquatic *H. verticillata*, the semi-aquatic *H. vulgaris*, and the terrestrial sand dune species, *H. novae-zeelandiae* and *H. bonariensis*.

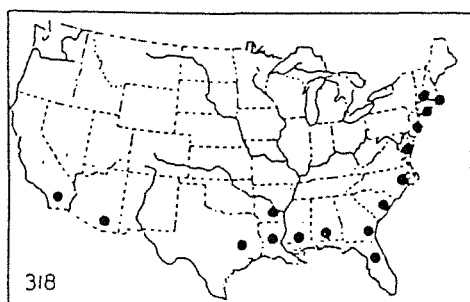
### 5.2.1. *Hydrocotyle verticillata*

*H. verticillata* is native to USA, occupying marshes

and shallow ponds along streams, particularly along the Atlantic and Gulf Coasts (Muenscher, 1944; Fig. 3). Rejmankova (1992) examined the growth strategies of this species, as well as four other emergent macrophytes, *Ludwigia peploides*, *Myriophyllum aquaticum*, *Nasturium officinale* and *Oenthe sarmentosa*, all of which commonly occur in nutrient rich pools, sloughs and irrigation and drainage canals throughout central and southern California. The author suggests that these species be classified as 'creeping emergents', as opposed to erect emergents (which include species



such as *Typha latifolia*, *Scirpus acutus* and *Phragmites australis*). Much study has been devoted to erect emergents, while information on creeping emergents is lacking.



**Figure 3.** Geographic distribution of *Hydrocotyle verticillata* in the USA. From Muenscher (1944).

Members of the creeping emergents group belong to unrelated taxa but they develop from very similar growth forms, probably as a response to a common environment (Rejmankova, 1992). The most characteristic feature of creeping emergents is their creeping mode of growth. They root in the substrate and send out long prostrate or ascending stems freely rooting and branching at nodes and often creating dense tangled mats. Adventitious roots, which develop on these long stems, are often without any direct contact with the substrate. From this description, it is apparent that *H. ranunculoides* could also be classified as a creeping emergent.

Rejmankova's (1992) study of five creeping emergents revealed that rapid growth, high nitrogen accumulation, allocation of most biomass and nitrogen into above-ground plant parts, and rapid decomposition were characteristic of each species in nutrient rich sites. Erect emergents, in contrast, have much higher standing crops, with a larger proportion of the biomass allocated to below ground rhizomes. *Ludwigia peploides* was able to grow for a prolonged period of time at high density without showing any signs of senescence, being attributed primarily to its high leaf area, which was suggested to be a characteristic of the creeping emergents in general. *H. verticillata* was particularly noted for its rapid rate of decomposition, with the half time of decomposition being 7 days. Rapid decomposition of creeping emergents was attributed to a low C:N ratio, generally around 10:1, compared with 20-30:1 in erect emergents (Rejmankova, 1991).

Rejmankova (1992) claims that creeping macrophytes, at least in the case of the study species, benefit from human impact on watercourses and lakes. It is suggested that the creeping macrophytes behave as typical stress tolerators, according to Grime's life history strategies (Grime, 1979). Most are able to survive periods of low groundwater levels as well as waterlogged conditions. Furthermore, in undisturbed nonpolluted habitats, these species are usually inconspicuous, but their behaviour changes substantially once they get established in fertile, nutrient-rich environments. Here they grow vigorously, developing extensive dense mats and showing typical traits characteristic of plants from fertile habitats: high relative growth rates and a rapid response to nutrient supply. If left undisturbed, the creeping emergents are usually slowly outcompeted by erect emergents. In contrast, creeping emergents are likely to outcompete erect emergents in disturbed habitats, typically from periodic dredging and water level fluctuations.

### 5.2.2 *Hydrocotyle vulgaris*

*H. vulgaris* is a wetland species with creeping rooted stems bearing leaves held aloft on long petioles (Grime *et al.*, 1988). It is largely restricted to unshaded mire, although plants rooted on ditch banks may extend into still aquatic habitats where the leaves become submerged. However, it persists only at positions along reservoir margins at the winter water level, suggesting an inability to exploit sites which are waterlogged throughout the year. As with most wetland species, its distribution is largely restricted to gentle slopes. It is mainly restricted to soils of pH 4.5 to 6.0, and is absent from calcareous soils. The latitudes at which it occurs are wide-ranging, but it is more abundant within the upland regions (up to 530 m) due to habitat destruction in lowland districts. The geographical distribution of this species is summarised in Appendix 2.

*H. vulgaris* tends to occur in local monocultures or in a turf with other species, particularly *Sphagnum* (Grime *et al.*, 1988). It has only been recorded from vegetation providing an almost continuous vegetation cover, although its



stoloniferous growth can facilitate its spread onto bare disturbed ground adjacent to established colonies. *H. vulgaris* only rarely occurs in shaded situations, where it may form an understory to species such as *Juncus effusus*. Canopy height is determined by the length of the petiole, with petiole length and leaf size decreasing in dry or grazed habitats. Marked changes in morphology are also associated with plants growing beside water; individuals rooted under water often have a disproportionately long petiole and lack the hairs present on the leaves of terrestrial forms (Sculthorpe, 1967).

*H. vulgaris* overwinters with minute leaves, resuming growth in late spring. This is followed by self-pollinated flowering in June to August, with seed being set from August to October (Grime *et al.*, 1988). Like *H. ranunculoides*, *H. vulgaris* regenerates vigorously by the creeping shoots which often form extensive patches. For both species, detached fragments root readily, and are probably important in the colonization of stream- and ditch-side sites following disturbance (Grime *et al.*, 1988; Klemm *et al.*, 1993). The fruits of *H. vulgaris*, which float and possibly adhere to the feet of birds (Ridley, 1930), may also play a role in colonizing more distant sites. However, Grime *et al.* (1988) claim that regeneration by seed is probably of infrequent occurrence since: (i) it appears to produce few flowers when growing amongst tall vegetation, (ii) no persistent seed bank has been detected, and (iii) seed germination in the laboratory has been unsuccessful, with seed dormancy breaking mechanisms requiring investigation.

### 5.2.3. *Hydrocotyle novae-zelandiae*

Sykes and Wilson (1990 a,b) investigated the ability of about thirty native and introduced New Zealand sand dune species to sand burial. Tolerance of sand deposition involves both the plant's ability to grow up through the sand and to survive darkness while it does so. In one experiment, plants were grown for 15 weeks under laboratory conditions in four different treatments: surface (S), burial to two-thirds plant height (0.66 H), fully buried (1.0 H) and full burial plus a further third of plant height (1.33 H) (Sykes and Wilson, 1990a). Measurements of total plant biomass,

shoot:root ratio and live leaf:live stem ratio at final harvest were used to analyse growth response.

Creeping herbs were generally tolerant of burial, growing to the surface from 1.33 H burial. The original plant parts mostly died, but survival was facilitated by the regrowth of small pieces of stolon. *H. novae-zelandiae*, a small creeping herb endemic to New Zealand, was the only species whose shoot:root ratio increased up to a burial depth of 1.33 H. For this species, there was a substantial decrease in total dry weight, with much of the original plant dying (Table 3). However, the plant was able to reach the surface via fine petiole extensions of one or two new leaves as well as slender adventitious rooting from the remaining stolon. This was reflected in the increased shoot:root ratio at the lowest depth (Table 3) and the higher leaf:stem ratio with partial burial. It was suggested that this regrowth from a 'bank' of dormant buds is important in situations of complete burial in the sand dune environment.

A second experiment examined the length of time the sand dune species survived complete darkness in a lightproof box (Sykes and Wilson, 1990b). Survival length ranged from 19 to 141 days, with *H. novae-zelandiae* being the longest survivor. The authors suggested that for many of the species, and *H. novae-zelandiae* in particular, etiolation assists in the progression of the buried plant to the sand surface. In the case of *H. novae-zelandiae*, the original aerial parts died in the dark, but etiolated leaves grew up from the stolons, some collapsing and others replacing them. In conclusion, the ability of *H. novae-zelandiae* to tolerate both burial and darkness appears to assist survival in a mobile sand dune environment.



**Table 3.** Comparison of total plant dry weight and shoot:root ratio of *Hydrocotyle novae-zelandiae* plants not buried (surface) or buried to various proportions of their height (H). Depths with the same letter are not significantly different ( $p < 0.05$ , data log-transformed). From Sykes and Wilson (1990a).

BURIAL DEPTH	TOTAL PLANT DRY WEIGHT (g)	SHOOT:ROOT (DRY WEIGHT)
Surface	6.90a	2.57 a
0.66 H	3.43 a	5.14 ab
1.33 H	0.08b	12.87 b

#### 5.2.4. *Hydrocotyle bonariensis*

*H. bonariensis* is a rhizomatous herb native to, and common in, coastal dune communities of the southeastern United States (Fig. 4; Evans, 1992). Its rhizomes grow linearly, with solitary leaves and roots being produced at regularly spaced nodes. A branch meristem occurs in the axil of the leaf at each node, and an inflorescence bud occurs opposite the leaf. Each node is regarded as a ramet since they are the smallest potential physiologically independent units that are capable of producing new clones when planted separately (Fig. 5). New ramets are generated vegetatively through the forward extension and lateral branching of rhizome meristems located in the leaf axils. In the field, rhizome connections between ramets can persist for up to three years, although within this time, severing of connections may occur as a result of trampling, grazing and exposure of rhizomes to extreme heat or cold (Evans, 1992).

The branched rhizome systems of *H. bonariensis* can be composed of over a thousand interconnected ramets covering over 100 square meters of the coastal dune environment (Evans, 1988). This environment is characterised by highly patchy and unpredictable light, nitrogen and water resource conditions. The patchiness of light in dune systems is generally associated with the presence of long-lived evergreen shrubs (spatial variation) and the accretion of sand over portions of the clone

(temporal variation). Portions of a clone also experience temporal variation in soil moisture availability as a result of small-scale erosional patterns on a dune slope (Evans, 1991). Variation in nitrogen availability is caused by a spatial array of decaying pockets of organic matter in the rapidly leached, nitrogen poor, dune soil. Abrupt changes in resource availability can occur within a meter in this environment, and low levels of each of these resources have been shown to limit plant growth in dune systems (Kachi and Hirose, 1983; Barbour *et al.*, 1985; Gibson, 1988).

In this type of environment, the most abundant plant species are usually clonal (Silander, 1985). Several studies (Evans, 1988; Evans, 1991; Evans, 1992) examine the possibility that the maintenance of physiological connections between *H. bonariensis* ramets allows a clone to integrate water, light and nitrogen in environments where these resources are patchy and that this integration may confer an adaptive advantage in the sand dune environment. Experiments were conducted in which *H. bonariensis* clones were grown across artificially created light, water and nitrogen gradients with and without ramet connections.

Evans (1988) demonstrated that acropetal translocation of nitrogen (old to young ramets) resulted in highly significant benefits to clones growing from areas of high nitrogen to areas of low nitrogen. Ramets responded to increased nitrogen availability, from either intracolonial translocation or immediate uptake from the soil, by producing primary, secondary and tertiary rhizome branches. In low nitrogen conditions, clones allocated a greater percentage of biomass to the main rhizome and very little to branching.

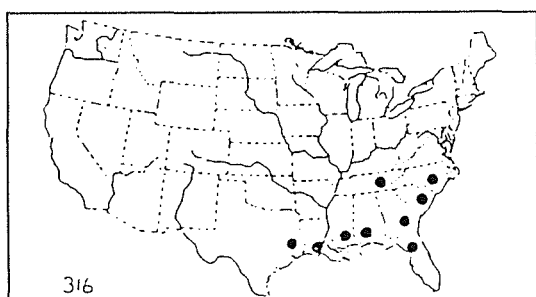
Evans (1991; 1992) demonstrated the basipetal movement (young to old) of water, nitrogen and photosynthates between two rhizome branch systems that interconnected hundreds of ramets within a clone. Ramet response to clonal integration was shown to be a function of an interaction of light, water and nitrogen conditions (Evans, 1991). In high light conditions, nitrogen transport was shown to be facilitated by the existence of a water gradient. When both nitrogen and water were limiting, the water potential gradient drove the movement of water and nitrogen to the deficient portion of the clone, whereas when nitrogen was the only limiting factor, nitrogen



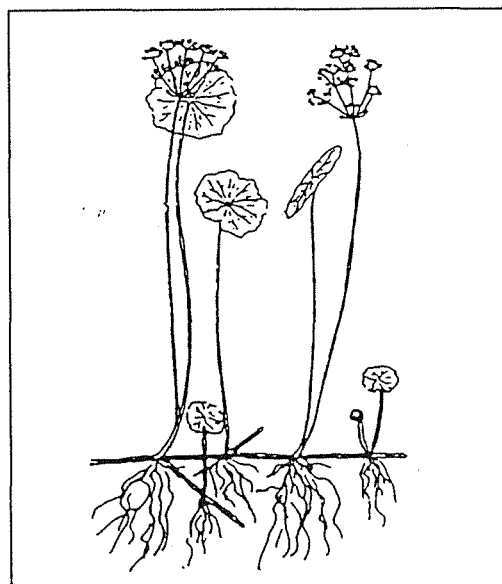
supply was limited to local uptake. However, this interaction between nitrogen and water did not occur in the presence of a light gradient. A combination of both a water and light gradient apparently resulted in less basipetal water movement than in high light alone, since there was probably less transpiration in the shade.

Translocation of water and nitrogen to portions of a clone deficient in these resources resulted in a significant net benefit to the clone in terms of fitness-related traits such as total biomass, ramet proliferation and seed production (Evans, 1991). Clonal integration facilitated an increase in reproduction (increase in inflorescence and seed production) under low nitrogen conditions (Evans, 1992). Severed ramets (i.e. those in which translocation from nonlimiting resources did not occur) responded to low soil moisture by increasing root production and decreasing sexual reproduction. However, ramets in local low water conditions that were connected to ramets in high water conditions showed an increase in clonal proliferation and sexual reproduction.

**Figure 4.** Geographic distribution of *Hydrocotyle bonariensis* in the USA. From Muenscher (1944).



The translocation of photosynthates across light gradients also allowed for sexual reproduction and clonal expansion in the shade, although this incurred a net cost to the clone in terms of ramet and seed production (Evans, 1991). Leaf characteristics such as internode distance and petiole height varied according to light intensity, but were not affected by local water and nitrogen conditions or resource integration (Evans, 1992). It was suggested that increased petiole height under low light conditions is critical for the placement of the blade above accreting sand or competing vegetation, while short, rigid petioles produced in the open dunes allow a leaf to endure persistent wind exposure.



**Figure 5.** Four ramets are located on the main rhizome segment of a *Hydrocotyle bonariensis* clone. The oldest ramet (on left) has a secondary branch with a newly established ramet. Ramets are centred around a node and consist of a leaf, roots, a branch meristem, rhizome and a potential inflorescence. From Evans (1992).

In addition, Evans and Whitney (1992) examined the benefits associated with clonal integration among interconnected ramets spanning a soil salinity gradient. While *H. bonariensis* does not typically grow in saline environments, it sometimes expands into salt marshes from adjacent dunes. In rhizome-severing experiments conducted under both field and laboratory conditions, *H. bonariensis* was shown to proliferate ramets under saline conditions, provided that these ramets were connected to other ramets growing in nonsaline conditions. Supporting ramets incurred no net cost in terms of biomass or ramet production, but there was an increased percentage allocation to roots and rhizomes. In contrast, ramets grown in saline conditions without the benefit of clonal integration showed high mortality and produced little or no net clonal growth.

Thus, it is apparent from the results of these studies that *H. bonariensis* clones are highly integrated with respect to water, nitrogen, photosynthates and salt. Clonal integration results in increased ramet proliferation which in turn increases the production of resource acquisition units (leaves and roots), resource transport and storage units (rhizomes) and sexual reproduction units (inflorescences), thereby



increasing total clonal fitness. This physiological integration of resources allows a clone to effectively utilize the temporally and spatially patchy resource conditions of its coastal dune environment.

### 5.2.5. Conclusion: Ecology of other *Hydrocotyle* Species

Ecological studies of *Hydrocotyle* species show the adaptation of particular species to their environment. The creeping aquatic macrophyte, *H. verticillata*, was suggested to display plastic behaviour according to the nutrient status of the water body. It is an inconspicuous component of the vegetation in nonpolluted waters, but flourishes with an increase in nutrient levels. This is also likely to be the case for *H. ranunculoides*, an aquatic species which also fits the description of a creeping emergent macrophyte. In a sand dune environment, survival of *H. novae-zelandiae* is assisted by its ability to tolerate darkness and burial by sand, while *H. bonariensis* is known to use clonal integration to facilitate survival in a patchy, unpredictable environment.

In terms of moisture, the habitat of *H. vulgaris* is intermediary, persisting in moist aquatic environments that are not waterlogged throughout the year. This is one of the few *Hydrocotyle* species in which germination studies appear to have been attempted. Seed germination is thought to be of limited importance to the regeneration of *H. vulgaris*, with vigorous vegetative propagation apparently being sufficient. Interestingly, Bell (1971) notes that the few genera of the Apiaceae with reduced umbels and inconspicuous flowers (including *Hydrocotyle*, *Centella* and *Lilaeopsis*) also have very effective methods of asexual reproduction, although no quantitative studies exist to confirm this possible correlation. Other somewhat scant information on seed germination relates to *H. ranunculoides*, with Townsend (1989) reporting that the fruit of *H. ranunculoides* become buried in the mud at maturity. While this may sometimes be the case, seed collected from upright stalks from the Canning River were shown to germinate at 25°C after 11 days (pers. observation).

## 6. GENETICS, USES AND CHEMICAL PROPERTIES

Fedorov (1974) summarised the chromosome numbers of 20 *Hydrocotyle* species, including *H. ranunculoides* which has a diploid chromosome number of 24 (Table 4). Moore (1971) noted that the genus *Hydrocotyle* displays a wide range of polyploids, up to 15-ploid, together with aneuploidy at all levels.

French (1971) lists a number of *Hydrocotyle* species which are used as food and medicinal resources, including *H. alchemilloides* (aromatic properties), *H. bonariensis* (used for skin diseases and toothache), *H. bupleurifolia* (astringent; used for diarrhoea), *H. moschata* (aromatic), *H. sibthorpioides* (leaves eaten, cough remedy), *H. umbellata* (used for liver and kidney ailments) and *H. vulgaris* (aperitive, detergent and a Danish home remedy for whooping cough). *H. asiatica* (syn. for *Centella asiatica*) is eaten by humans in Asian countries and has a number of medicinal uses in India, including use as a tonic, diuretic and skin disease treatment (French *et al.*, 1971). Cho and Kim (1988) report that this species produces biologically active triterpenoids that have possible therapeutical uses in ulcerations, extensive wounds and eczemas. Other useful species include *H. japonica*, used as a folk medicine in Korea (Cho and Kim, 1988); *H. sibthorpioides* and *H. maritima*, both having hemostatic and antitumor activities (Asakawa *et al.*, 1982); *H. tincture*, known for its healing activity in the treatment of wounds (Morisset *et al.*, 1987); and *H. podantha*, which has spasmolytic properties (Rao *et al.*, 1979).

Flavanols, rather than flavones, predominate in the less advanced genera of the Apiaceae, including *Hydrocotyle* (Harbourne, 1971). The authors suggest that the replacement of flavanol by flavone appear to have evolutionary significance within the Apiaceae family, and probably among the angiosperms generally. The flavanol glycoside Quercetin (3-Glucoside) is common within the Apiaceae, including in the leaves of *Hydrocotyle* species (Crowden *et al.*, 1969). Other chemical investigations have identified the flavanol glycoside,

hyperin, in *H. maritima* (Asakawa *et al.*, 1982); the flavanol glycoside, Quercetin 3-(6"-



caffeoylgalactoside) in *H. sibthorpiodes* (Shigematsu *et al.*, 1982); the flavanol isorhamnetin-3-O-beta-D-galactoside in *H. japonica* (Cho and Kim, 1988); *trans*-beta-farnesene as the major terpenoid constituent of *H. sibthorpiodes* and *H. maritima* (Asakawa *et al.*, 1982); the lignan, L-sesamin, in *H. sibthorpioides* (Ina *et al.*, 1987); the lineoleic-oleic-palmitic type of fatty acid composition in the seed oil of *H. asiatica* (syn. for *Centella asiatica*) (Suhail *et al.*, 1987); and Madecassis acid in both *H. asiatica* (syn. for *Centella asiatica*) and *H. vulgaris*, a triperpernoid compound thought to assist in defence against venous diseases, but absent in *H. ranunculoides* (Tomei *et al.*, 1989).

## 7. HERBICIDE APPLICATIONS

No information was found in the literature relating to an effective herbicide for the management of *Hydrocotyle ranunculoides*. However, *H. bonariensis*, a dominant weed in the rubber plantations of Bahia, was shown to be fairly effectively controlled by the application of glyphosate (Lima and Pereira, 1985). The order of herbicide efficiency based on the total weed dry weight (composed of *H. bonariensis* as well as other weed species) was (per hectare): 1.3 kg glyphosate > 1.5 kg oxyfluorfen + 0.2 kg paraquat > 2 kg diuron + hexazinone > 3 kg diuron + ametryn + 0.2 kg paraquat.

Trials on the North and South Islands of New Zealand indicated that the herbicide, clopyralid (Versatill™), was ineffective on the *Hydrocotyle* species that were present (Saville, 1987). Furthermore, the aquatic herbicide, Sonar™ (fluridone) was reported to kill many vascular submersed weeds (including *Hydrilla*, *Equisetum*, *Potamogeton*, *Cabomba*, *Najas*, *Egeria* and *Utricularia* spp.), but *Hydrocotyle* spp. were tolerant to the herbicide (Tarver, 1985). Other tolerant species included *Chara*, *Nitella*, *Pontederia cordata*, *Juncus effusus* and *Scirpus* spp.

## 8. HERBIVORY

Biological control is a favourable method of weed management in that it is likely to have the lowest

SPECIES	DIPLOID CHROMOSOME NO. (2n)
<i>H. acutifolia</i>	48
<i>H. asiatica</i>	18, 22
<i>H. benguetensis</i>	96
<i>H. bonariensis</i>	22
<i>H. chamaemorus</i>	72
<i>H. dichondroides</i>	22
<i>H. dissecta</i>	44
<i>H. javanica</i>	72, 96
<i>H. keelungensis</i>	24
<i>H. leucocephala</i>	32, 48
<i>H. mexicana</i>	32
<i>H. moschata</i>	about 36, 48
<i>H. novae-zeelandiae</i>	48
<i>H. poeppigii</i>	48
<i>H. ranunculoides</i>	24
<i>H. rotundifolia</i>	24
<i>H. setulosa</i>	48
<i>H. sibthorpioides</i>	24, 48, 64
<i>H. umbellata</i>	48?
<i>H. vulgaris</i>	96
<i>Hydrocotyle</i> sp. (unidentified)	about 160

**Table 4.** Diploid chromosome numbers of a number of *Hydrocotyle* species. From Federov (1974).

long-term environmental impact on the total ecosystem. *H. ranunculoides* has been included in at least two studies to determine its palatability to potential predators.

Firstly, *H. ranunculoides* was included in a study designed to test the host specificity of a small water weevil, *Neohydronomus pulchellus* (DeLoach *et al.*, 1976). The weevil was shown to be host specific, feeding almost entirely on water lettuce (*Pistia statiotes*, a serious aquatic pest in India, Ghana, Laos and Thailand), and not feeding on *H. ranunculoides* at all. Due to its demonstrated host



specificity, the water weevil was suggested as a possible biological control agent for water lettuce. Secondly, Santos *et al.* (1988) examined the attractiveness of extracts of macrophyte leaves to the snail *Biomphalaria tenagophila*. Amongst the macrophyte species examined, preference was in the order of: *Nasturium pumilum*, *Polygonum acre*, *Commelina* sp. = *Echinochloa crusgalli*. However, extracts from *Hydrocotyle ranunculoides* and *Heteranthera reniformis* were unattractive to the snail. It is therefore apparent that no suitable biological control agents for *H. ranunculoides* in the Canning River are evident from the available literature. In any case, a potential biological control agent must be very host specific to *H. ranunculoides*, with particular care taken to select an agent that does not eat native species and commercially important members of the Apiaceae, such as carrots.

Other *Hydrocotyle* species are known to serve as food sources. For instance, *H. asiatica* (syn. for *Centella asiatica*) is among the most popular traditional Malaysian vegetables, and Mansor (1988) outlines the nutritional contents of this species. Secondly, Rowell (1985) determined the diet of eleven Costa Rican species of the grasshopper genus *Rhachicreagra* by direct observation and by faecal analysis. Plant species of the Compositae were the principal component foodplant of many of the grasshopper species, although in montane habitats, *Hydrocotyle* species became important foodplants. *Hydrocotyle* was included in the natural diet of six grasshopper species. In summary, *Hydrocotyle* spp. were the principal foodplant of *R. dryomocnemensis*; both *Hydrocotyle* spp. and Compositae were the principal foodplants of *R. gracilis*; and *Hydrocotyle* spp., *H. mexicana* and *Iresine diffusa* (Amaranthaceae) were the principal foodplants of *R. obsidian*. *Hydrocotyle* comprised a minor component of the diet of *R. anchidiphalara*, *R. brachysphagicerca* and *R. melanota*.

In the Tidbinbilla Nature Reserve, Australian Capital Territory, the native *H. laxiflora* appeared to be eaten by the grey kangaroo, *Macropus giganteus* (Neave and Tanton, 1989). A large proportion of the Reserve was previously cleared to facilitate the grazing of sheep and cattle, and in 1971 the Reserve was declared a Public Park. *H. laxiflora* was absent from one of the study sites

(Maxwell's Paddock) in 1982-1983, but was present in a further sampling in 1986. A number of other new species were recorded, and this was thought to be related to the natural succession of plants after clearing. Interestingly, the establishment of *H. laxiflora* only occurred in treatments where the kangaroo was excluded, although the presence of the rabbit did not appear to affect establishment. Similarly, at another study site (Tidbinbilla River), the height of *H. laxiflora* had dramatically increased in plots where the kangaroos had been excluded, although no physical signs of grazing were evident. It therefore appears that the grey kangaroo feed on *H. laxiflora*, although direct evidence is required to confirm this suggestion.

In central Florida, the dipteran *Coquillettidia perturbans* infested a solid vegetation mat composed of *Hydrocotyle umbellata*, *Ludwigia octovalvis* and *Panicum* spp. (Slaff and Haefner, 1985). Unfortunately, only the abstract of this paper was available, and this did not indicate whether or not *H. umbellata* serves as a foodplant.

## 9. ECOPHYSIOLOGY

*H. ranunculoides*, among other typical southern USA wetland species, was analysed for its contribution of methane emissions to the atmosphere (Sebacher *et al.*, 1985). Methane is produced by anaerobic bacterial decomposition in the organic-rich sediments that support the hydrophyte root system. In this study, the rooted aquatic plants were shown to play an important gas exchange role in the carbon cycle between wetlands and the atmosphere. However, detectable levels of methane were not emitted by *H. ranunculoides*, *Alternanthera philoseroides* and *Lemna* sp., most likely because these species, being classified by the authors as free-floating, were not rooted in the anaerobic sediments during the experiment. However, other observations have shown that *H. ranunculoides* can be rooted to the sediment (Harper, 1992; Klemm *et al.*, 1993), and it is possible that under these conditions this species emits higher levels of methane.

*H. ranunculoides* was also included in a study comparing carbonic anhydrase (CA) levels and lacunar CO<sub>2</sub> concentration in a range of submerged,

floating and emergent aquatic macrophytes of the United States (Weaver and Wetzel, 1980). In this study, *H. ranunculoides* was classified as an emergent species. The results indicated an increase in the CA levels along the habitat gradient of submerged to floating to emergent growth forms, with *H. ranunculoides* displaying the highest CA activity of all the species (Fig. 6).

A direct relationship was found between CA activities and primary productivities of these plants over the habitat gradient: both productivity and CA activity was low in submerged and high in emergent plants. While a number of factors may be responsible for the low productivity of submerged plants (e.g. low light, excretion of dissolved organic compounds), low CA levels in

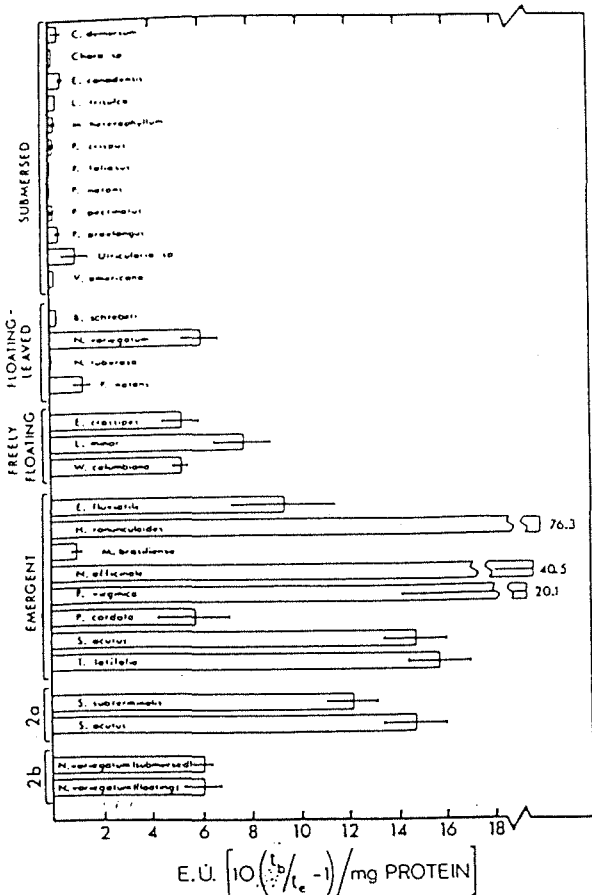
these plants may also contribute to low productivity. The results also indicated that the internal lacunar concentrations of emergents were generally lower than those of submerged plants. Submerged macrophytes may accumulate  $\text{CO}_2$  due to the slow diffusion of gas across the leaf surface in water, particularly in unstirred water where a boundary layer of gas lies immediately adjacent to the leaf surface. In contrast, gas diffusion into and out of the lacunar system of emergent plants is much more rapid because of their aerial growth form. Efficient gas diffusion is also likely to be facilitated by wide open stomata, since the soil in which emergents are rooted is usually saturated (Weaver and Wetzel, 1980).

It has been suggested that a possible function of CA is in the refixation of respired and photorespired  $\text{CO}_2$  in  $\text{C}_3$  plants in the same manner that phosphoenolpyruvate carboxylase scavenges and facilitates the refixation of  $\text{CO}_2$  in  $\text{C}_4$  plants (Everson and Slack, 1968). If so, CA is likely to be important in emergent macrophytes such as *H. ranunculoides*, but less important for submerged plants since their lacunar system may serve the same function of refixing respired and photorespired  $\text{CO}_2$  (Weaver and Wetzel, 1980).

In another ecophysiological study, both *H. bonariensis* and *H. umbellata* were shown to have adaptive physiological responses to their specific environment (Overdieck and Strain,

1981). Ramets were collected from three contrasting habitats on Shackleford Banks, a small barrier island off the central North Carolina coast of USA. One ecotype of *H. bonariensis* was collected from coastal sand dunes, and another ecotype of this species was collected from the deep shade of an evergreen maritime forest. The third type, *H. umbellata*, is found only in fresh or brackish water ponds. Like *H. ranunculoides*, this species is rooted to the bottom of the pond with its leaves extend 1-2 cm above the water surface.

Ramets were grown under controlled environmental conditions and measurements of net photosynthesis, transpiration and total leaf diffusion resistance were used to examine possible effects of atmospheric humidity on the three *Hydrocotyle* types. The results of the study indicated that increasing habitat dryness had large effects on gas exchange ( $\text{CO}_2$  and water vapour)



**Figure 6.** Carbonic anhydrase (CA) activities (EU  $\pm$  SE) of aquatic macrophytes grouped along habitat gradients. The emergent *Hydrocotyle ranunculoides* has the highest CA activity. 2a= CA comparison between *Scirpus subterminalis*, one of the few submerged species of this genus, and the emergent *S. acutus*. 2b= CA comparison between submerged and floating leaves of *Nuphar variegatum*. From Weaver and Wetzel (1980).





and on total diffusion resistance of the pond type, moderate effects on the forest type, and no significant effects on the dune type. It therefore appeared that the habitat gradient from wet to dry corresponded to a decrease in sensitivity to dry conditions.

## 10. WASTEWATER TREATMENT AND RESOURCE RECOVERY

The most intensive research into *Hydrocotyle* appears to be in relation to its use in aquatic systems for wastewater treatment and biomass harvesting for fuel production. Both *H. umbellata* and *H. ranunculoides* have been evaluated as potential beneficial species in such systems, although more emphasis has been given to *H. umbellata*. The benefits of these aquatic plant systems are two-fold: (i) wastewater treatment by aquatic plants offer low-cost, low-energy solutions to pollution control (Crites, 1979; Tchobanoglous and Culp, 1980; Whingham, 1982), and (ii) the conversion of plant material into methane through aerobic digestion is an economical use for the biomass by-product of the wastewater treatment systems (Wolverton and McDonald, 1981; Reddy and DeBusk, 1984).

Much of the research on this subject has been

conducted in Florida, although these systems are beginning to gain widespread use in other tropical or subtropical regions of the world. Aquatic macrophytes have been cultured in nutrient-rich waters of sewerage effluents, agricultural runoff and drainage effluents, runoff from cattle feedlots, methane digester effluents, and eutrophic lakes and streams (Reddy, 1984). It is anticipated that the importance of aquatic macrophyte systems in wastewater treatment and subsequent fuel production will continue to increase (Wolverton, 1987).

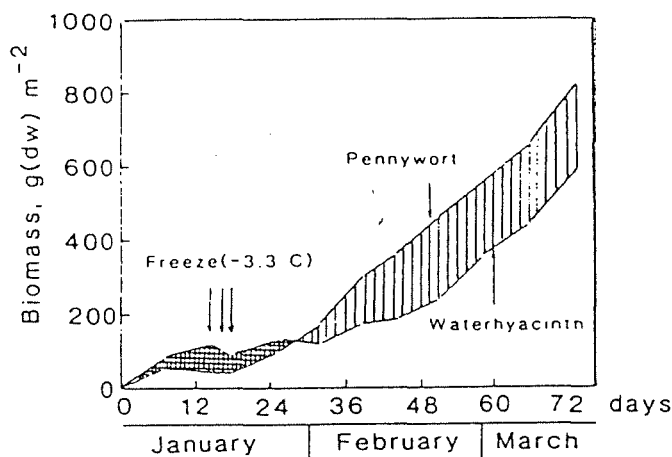
Most of the aquatic wastewater treatment and biomass energy systems have focused on *Eichhornia crassipes*, an obnoxious weed of many regions, including the United States. Its suitability in these systems relate to its high productivity and the ease with which it can be stocked and harvested due to its floating habit (DeBusk and Reddy, 1987). In order to optimize the efficiency of wastewater treatment and energy production systems, a continuous supply of biomass should occur. One of the shortcomings of the *E. crassipes* system in Florida is its lack of tolerance to low winter temperatures, which can retard growth and cause death (Reddy, 1984). This has prompted research into other potential species to use in waste treatment and resource recovery.

**Table 5.** Nitrogen and phosphorus uptake ( $\text{g m}^{-2} \text{d}^{-1}$ ) by the floating aquatic macrophytes, *Eichhornia crassipes* and *Hydrocotyle umbellata*, during summer and winter in central Florida. From DeBusk and Reddy (1987).

SPECIES	NITROGEN		PHOSPHORUS	
	Summer	Winter	Summer	Winter
<i>Eichhornia crassipes</i>	1.30	0.25	0.24	0.05
<i>Hydrocotyle umbellata</i>	0.37	0.37	0.09	0.08

*H. umbellata* has been widely accepted as a useful substitute for *E. crassipes* during cold winter months (Reddy, 1984; Reddy and DeBusk, 1984; Reddy and Tucker, 1985; Clough *et al.*, 1987; Reddy, 1988; Agami and Reddy, 1991). This species has been shown to play a significant role in removal of nutrients from polluted waters (Reddy, 1983; Reddy and Tucker, 1985). The

potential nitrogen and phosphorus removal rates of a *H. umbellata* system during winter were found to be  $321\text{-}645 \text{ mg N m}^{-2} \text{ day}^{-1}$  and  $103\text{-}106 \text{ mg P m}^{-2} \text{ day}^{-1}$  respectively (Reddy and Tucker, 1985). Reddy (1983) demonstrated that both *E. crassipes* and *H. umbellata* removed about 50% of the inorganic nitrogen in a eutrophic system over 4 days.



**Figure 7.** Biomass recovery rates of *Eichhornia crassipes* (waterhyacinth) and *Hydrocotyle umbellata* (pennywort) after a freeze in January 1982 (Florida) for three consecutive nights ( $-17^{\circ}\text{C}$ ,  $-3.3^{\circ}\text{C}$ , and  $-2.8^{\circ}\text{C}$ , respectively). From Reddy (1984).

During a Florida summer, both productivity and nutrient uptake of *E. crassipes* exceeds *H. umbellata* during the summer (Reddy and DeBusk, 1985). However, while nutrient uptake by *H. umbellata* remains relatively constant throughout the year, *E. crassipes* displays a sharp drop in nutrient assimilation during winter (Table 5). Furthermore, Reddy (1984) demonstrated that *H. umbellata* recovered much faster from a hard freeze over three consecutive nights than *E. crassipes*, resulting in significantly higher biomass yields (Fig. 7).

Interestingly, the standing crop of both species was shown to be greater when grown together than when grown in monoculture (Agami and Reddy, 1991). *H. umbellata* was able to coexist with the highly productive *E. crassipes* due to its elongated petioles (avoiding shading by *E. crassipes*) and its ability to outcompete *E. crassipes* during winter. It was claimed that the improved growth of *H. umbellata* in the presence of *E. crassipes* was due to the physical support provided by the *E. crassipes* plants. Thus, the results of this study suggest that the combined use of these two species in wastewater treatment and biomass production would be successful in providing year-round optimum performance.

In addition to plant productivity and nutrient

uptake, oxygen transport capacity is also an important design criteria for aquatic plant wastewater treatment and resource recovery systems (Reddy *et al.*, 1989). Aquatic plants transport oxygen from foliage to roots, resulting in an oxidised environment in the rooting zone (Armstrong, 1964). Rhizosphere oxidation has important implications in wastewater treatment since it detoxifies hydrogen sulphide and the reduced forms of iron and manganese, and activates biogeochemical processes such as the oxidation of soluble organic compounds and nitrification of  $\text{NH}_4$ -nitrogen (Reddy *et al.*, 1989).

Several studies have revealed that *H. umbellata* has a high oxygen transport capacity. Moorhead and Reddy (1988) measured oxygen transport by plants as the net change in dissolved oxygen with time, and demonstrated a greater transport rate by *H. umbellata* than *E. crassipes* ( $3.49$  and  $1.24$   $\text{g O}_2 \text{ kg}^{-1}$  dry root mass  $\text{h}^{-1}$ , respectively) under laboratory conditions. Reddy *et al.* (1989) measured oxygen transport rate as the oxygen consumed by the effluent (biological  $\text{O}_2$  demand, or  $\text{BOD}_5$ ), and also found a greater transport capacity by *H. umbellata* than *E. crassipes* ( $10.1$  and  $2.75$   $\text{mg O}_2 \text{ g}^{-1}$  plant dry wt, respectively) under laboratory conditions. Clough *et al.* (1987) measured percentage  $\text{BOD}_5$  removal by both species in outdoor tanks in Florida. Typical  $\text{BOD}_5$  reductions in the wastewater effluent varied from 70 to 90% during the study, with the highest  $\text{BOD}_5$  removal observed in tanks containing *H. umbellata* during both warm and cool seasons.

*H. umbellata* has also been successfully utilized in thin film systems for contaminant removal of polluted effluent (Dierberg *et al.*, 1987a,b). A thin film system consists of vascular plants grown in shallow raceways through which a thin layer of wastewater is passed. The plants develop a dense mat of roots which, together with the colonizing bacteria, reduce suspended solids and  $\text{BOD}_5$ . Dierberg *et al.* (1987a) showed that *H. umbellata* was able to substantially decrease the concentration of two common chlorinated compounds, 2,4-dichlorophenol and monochloramine, from secondary domestic effluent under long-term, continuous feeding conditions. The authors claimed that this system is superior to the use of chemical dechlorinating agents because it is cheaper and circumvents the deoxygenation of



water caused by dechlorinating agents.

In a similar thin film system, *H. umbellata* was shown to remove the heavy metals, copper and lead, at levels of 69% and 85%, respectively (Dierberg *et al.*, 1987b). However, the high copper loading proved to be ultimately toxic to the plants, and a subsequent decline in treatment efficiency occurred after one month's operation. The authors suggest that lower metal loadings to such thin-film systems are likely to enable greater heavy metal reductions by *H. umbellata*.

The results of such research into the use of aquatic macrophytes in wastewater treatment and resource recovery indicate that, while the productivity and nutrient uptake of *E. crassipes* is the greatest of all tested macrophytes under optimal growth conditions, *H. umbellata* is a useful substitute during the cooler months in *E. crassipes*-based systems. Production of both species is higher when they are grown together than in monoculture, and the inclusion of both species facilitates efficiency throughout the year. In addition to greater growth and nutrient uptake than *E. crassipes* during winter, *H. umbellata* was also shown to provide greater BOD<sub>5</sub> removal efficiency during both warm and cool seasons.

Less extensive work has been conducted on the potential use of *H. ranunculoides* as an aquatic macrophyte for wastewater treatment and resource recovery. Boyd and Bayne (1988) compared the efficacy of the use of *H. ranunculoides* and *E. crassipes* in the treatment of wastewater discharged from a livestock waste lagoon in Alabama. Initially, the study examined *E. crassipes* only, but after an incident of mass mortality due to an unknown cause, it was noticed that small quantities of *H. ranunculoides* that had invaded the tanks were not adversely affected. Consequently, this species was also included in a subsequent trial. In this second trial, both species were treated with the insecticide, Sevin, and both remained healthy throughout the growing season.

Maximum growth rate and standing crop was 0.009 lb ft<sup>-2</sup> day<sup>-1</sup> and 8.20 tonnes a<sup>-1</sup>, respectively, for *H. ranunculoides*, and 0.0084 lb ft<sup>-2</sup> day<sup>-1</sup> and 13.02 tonnes a<sup>-1</sup>, respectively, for *E. crassipes*. Both plants were found to be effective in removing pollutants from the water. Usually, concentrations of total ammonia nitrogen, phosphate, biological oxygen demand, chemical oxygen demand, organic

nitrogen and total suspended solids in the effluent was about half of that in the influent. However, effluent water still had appreciable levels of all measured variables except the amount of total suspended solids, nitrate and nitrite after passing through the aquatic plant treatment ponds. It was suggested that the effectiveness of these species may be improved by aeration, since anaerobic conditions were created by the extensive cover of both species in the treatment ponds.

*H. ranunculoides* was found to offer some advantages as a wastewater treatment species over *E. crassipes*. Firstly, *E. crassipes* is a serious weed species in the aquatic systems of Alabama, while *H. ranunculoides* is relatively uncommon in this region. Secondly, *E. crassipes* suffered winter kill while *H. ranunculoides* overwintered. In Alabama, perpetuation of natural stands of *E. crassipes* is dependent upon seed germination or reintroduction the following growing season (Dinges, 1982). Like *H. umbellata*, *H. ranunculoides* appears to be more cold tolerant, successfully overwintering during a winter when *E. crassipes* was killed (Boyd and Bayne, 1988). The use of an aquatic plant that does not require annual restocking, such as *H. ranunculoides*, is economically desirable.

Thirdly, *H. ranunculoides* showed less root diminution than *E. crassipes*. At the beginning of the study, the root length of *E. crassipes* exceeded that of *H. ranunculoides*, and by the end of the study, the reverse was true. Boyd and Bayne (1988) suggest that root mass maintenance by aquatic wastewater treatment plants is likely to be an important characteristic since the microscopic flora and fauna associated with the roots are important in the improvement of water quality.

A further benefit of *H. ranunculoides* related to its potential use as livestock food. While plant nutritive content of both *H. ranunculoides* and *E. crassipes* compared well with other common livestock forage plants, the former had a higher crude protein and digestibility than *E. crassipes* (Table 6). Crude protein, fat and ash values of both species were similar to previous findings by Wolverton and McDonald (1981).



**Table 6.** Comparison of nutritive variables (dry weight basis) of *Hydrocotyle ranunculoides* and *Eichhornia crassipes* grown in wastewater treatment ponds with common livestock forage plants. Unbracketed values are from Boyd and Bayne (1988), bracketed values are from Wolverton and McDonald (1981).

SPECIES	% CRUDE PROTEIN	% FAT	% ASH	% ACID DETERGENT FIBER	% DIGESTIBILITY
<i>Hydrocotyle ranunculoides</i>	24.2 (23.4)	1.7 (2.19)	18.3 (17.4)	29.4	69.3
<i>Eichhornia crassipes</i>	15.1 (14.7)	1.1 (1.59)	16.7 (11.1)	34.3	47.9
Alfalfa ( <i>Medicago sativa</i> )	18.9	3.0	10.6	35.0	55.4
Bahia grass ( <i>Paspalum notatum</i> )	8.2	2.1	6.4	41.0	-
Bermudagrass ( <i>Cynodon dactylon</i> )	6.0	2.3	6.6	38.0	56.7
Fescue ( <i>Festuca</i> spp.)	9.5	2.0	10.0	39.0	51.4

While *H. ranunculoides* may be more suitable than *E. crassipes* for wastewater treatment (Boyd and Bayne, 1988), *E. crassipes* appears more suitable for subsequent fuel (methane) production (Wolverton and McDonald, 1981). The efficient anaerobic digestion process of both species is likely to be facilitated by their low lignin content. However, the content of hemicellulose, which is regarded as more amenable to bacterial degradation than cellulose, was greater in *E. crassipes* than in *H. ranunculoides*. Furthermore, the maximum volume of methane production was greater for *E. crassipes* ( $0.198 \text{ m}^3 \text{ kg}^{-1}$  or  $3.17 \text{ ft}^3 \text{ lb}^{-1}$ ) than for *H. ranunculoides* ( $0.146 \text{ m}^3 \text{ kg}^{-1}$  or  $2.34 \text{ ft}^3 \text{ lb}^{-1}$ ). It is therefore apparent that, under the prevailing experimental conditions, *E. crassipes* is easier to digest anaerobically than *H. ranunculoides*, suggesting its greater suitability as an energy source.

## 11. CONCLUSION

Plants of the genus *Hydrocotyle* adopt a creeping habit, with many species being restricted to aquatic or moist terrestrial habitats. The geographic distribution of the genus is cosmopolitan, although

it is particularly well represented in North and South America. It is not recognised as a particularly weedy genus, but has been recorded as a weed in Chile (*H. ranunculoides*), Argentina (*H. bonariensis*), Brazil (*H. umbellata*), and Australia (*H. ranunculoides*, *H. bonariensis*, *H. laxiflora* and *H. tripartita*).

Weediness is determined by two major factors - the environment and aspects of the plant's life history (Mitchell and Bowmer, 1990). Important abiotic environmental factors include temperature, salinity and nutrient availability, while major biotic environmental factors include the presence of competitors, predators and diseases. In general, life history characteristics such as high reproductive rate, rapid growth, short life-span, multiple reproductive strategies, and effective dispersal mechanisms for propagules are associated with weediness. Physiological adaptations which may be of importance include an ability to withstand water and salt stress, and a wide tolerance to a range of temperatures and nutrient levels.

Relatively little information is available on the life history characteristics, ecology and management of *H. ranunculoides*. It is not a widely known

weed species, but does co-occur with other weed species, including *Eichhornia crassipes*, *Alternanthera philoxeroides*, *Myriophyllum brasiliense* and *Salvinia molesta*. It appears to have a flexible growth response, for example, it overwinters to avoid low temperature. It may also show morphological plasticity with respect to nutrients, being known to undergo rapid growth in the high-nutrient conditions of wastewater treatment systems and the Canning River of Western Australia. The rapid growth rates of other aquatic creeping emergent macrophytes (e.g. *H. verticillata*) under nutrient non-limiting conditions are thought to facilitate vigorous invasion, particularly in habitats disturbed by man. These creeping emergents are evidently inconspicuous in undisturbed habitats, but become weedy in eutrophic, disturbed habitats. Further research is required to determine whether the growth rate of *H. ranunculoides* also increases with an increase in nutrients as it is possible that the eutrophic condition of the Canning River is at least partly responsible for this species' prolific growth.

*H. ranunculoides* is capable of both sexual and asexual reproduction, although the contribution of seedlings to population growth appears to be currently unknown. Little other information is available on the seed biology of the genus except for *H. vulgaris* which, however, is still thought to depend primarily on vegetative propagation for regeneration. Indeed, the creeping rhizomatous growth form of *Hydrocotyle* species is an extremely effective method of propagation and may decrease the selection pressure for energy input into sexual reproduction. In the aquatic environment, small ramets detached from a *Hydrocotyle* mat are able to be transported by water to colonize another site (e.g. *H. ranunculoides*, *H. verticillata*, *H. vulgaris*). In the terrestrial sand dune environment, *H. bonariensis* is able to dominate a patchy environment by the transportation of resources (such as nutrients, photosynthates and water) from a part of the clone in nonlimiting conditions to a part of the clone in stressful conditions. It is possible that clonal integration also occurs within the extensive rhizomatous mats of *H. ranunculoides*. From a management perspective, clonal integration may assist in the efficient translocation of herbicides such that lower rates of application may be needed than supposed.

Few studies have been conducted which investigate the effect of abiotic and biotic environmental factors on the growth and survival of *Hydrocotyle* species. Physical and chemical limits on the survival of *H. ranunculoides* are difficult to determine from the literature. It is consistently a freshwater species, and is common in two distinct habitats, both of cool temperatures - high altitude tropical lakes and low altitude coastal regions of the temperate zone. Within these habitats, it attaches itself to a sandy or muddy substrate, or forms part of a floating island community. No preferences for water velocity, water depth, bank slope, pH or nutrients were apparent from the literature. This species therefore appears to be a 'generalist' in its ecological responses within the limits of cool fresh water bodies.

The absence of competitors and predators in the Canning River may also contribute to the success of *H. ranunculoides* in this environment. It was suggested that the growth of *H. ranunculoides* in East African lakes was limited by competition from other species of similar life form (e.g. *Cladium jamaicense* and *Cyperus papyrus*). Species of similar life form in direct competition with *H. ranunculoides* may be absent from the Canning River. *Centella asiatica* (syn. for *H. asiatica*) is morphologically similar to *H. ranunculoides*, being a rhizomatous plant which roots at the nodes. However, this species tends to occupy more terrestrial, rather than permanently aquatic, habitats of the Canning River. Limited experimental work on the palatability of *H. ranunculoides* suggests that it species may be rather resistant to herbivory. *Hydrocotyle* species which have been shown to be palatable to herbivores include (i) *H. asiatica* (syn. for *Centella asiatica*), which is a common salad vegetable in Asia, (ii) *H. mexicana*, which is a common component of a number of grasshopper species of the genus *Rhachicreagra* and (iii) *H. laxiflora*, which appears to be eaten by the grey kangaroo *Macropus giganteus*.

Despite the detrimental effect the extensive mats of *H. ranunculoides* are claimed to have on the Canning River environment (such as reduced oxygen levels, reduced recreational opportunities, increased erosion and exclusion of native aquatic plant species), this species has also been recognised for its beneficial characteristics. Both *H. ranunculoides* and *H. umbellata* have been shown



to effectively reduce the nutrient levels of polluted water, being particularly useful during the winter months when the otherwise highly productive *Eichhornia crassipes* is affected by low temperature. It is therefore noteworthy that *H. ranunculoides* may actually be beneficial to the Canning River environment with respect to its ability to reduce the nutrient concentrations of this eutrophic system, provided the accumulated biomass is removed from the system to prevent recycling of nutrients. The resulting biomass from aquatic plant wastewater systems can then be used as a cheap source of gaseous fuel (methane). Furthermore, *H. ranunculoides* has been shown to have high digestibility and greater nutritive content than typical livestock forage plants. Many other *Hydrocotyle* species are used by man as medicines and food sources.

In conclusion, *H. ranunculoides* appears to possess a number of typical weed characteristics, including high growth rates (probably in high nutrient conditions such as wastewater treatment systems, the Canning River and certain polluted water bodies such as the Laguna de la Herrera), effective vegetative propagation (fragmentation and possibly clonal integration), plasticity in growth response (e.g. overwintering) and possibly high resistance to herbivory. Further studies of the biology and ecology of *H. ranunculoides* in the Canning River are required to achieve successful long-term control or eradication of this species. In particular, information which is likely to assist in devising an effective management strategy include the determination of successional status, the relative importance of asexual and sexual reproduction on population growth, possible ecotypic variation (as shown by *H. bonariensis* ecotypes), and the effect of environmental parameters such as salinity, temperature and nutrients on growth, survival and reproduction of *H. ranunculoides*.



## 12. REFERENCES

- Agami, M., and K. R. Reddy. 1991. Interrelationships between *Eichhornia crassipes* and *Hydrocotyle umbellata*. *Aquatic Botany* 39: 147-157.
- Agnew, A. D. Q. 1974. *Upland Kenya Wildflowers: a flora of the ferns and herbaceous flowering plants of upland Kenya*. London: Oxford Univ. Press.
- Anderson, L. W. J. 1990. Aquatic weed problems and management in western United States and Canada. *Aquatic Weeds: the Ecology and Management of Nuisance Aquatic Vegetation*, A. H. Pieterse, and K. J. Murphy (eds.), pp 371-391. Oxford: Oxford Univ. Press.
- Anderson, L. C. 1983. *Hydrocotyle bowlesioides* in Georgia - new to United States. *Castanea* 48: 317.
- Armstrong, W. 1964. Oxygen diffusion from the roots of some British bog plants. *Nature* 204: 801-802.
- Asakawa, Y., R. Matsuda, and T. Takemoto. 1982. Mono- and sesquiterpenoids from *Hydrocotyle* and *Centella* species. *Phytochemistry* 10: 2590-2592.
- Aulbach-Smith, C. A., S. J. de Kozlowski, and L. A. Dyke. 1990. *Aquatic and Wetland Plants of South Carolina*. South Carolina Aquatic Plant Management Council.
- Auld, B. A., and R. W. Medd. 1987. *Weeds: an Illustrated Botanical Guide to the Weeds of Australia*. Melbourne: Inkata Press.
- Barbour, M. G., T. M. De Jong, and B. M. Pavlik. 1985. Marine beach and dune plant communities. *Physiological Ecology of North American Plant Communities*, B. F. Chabot, and H. A. Mooney (eds.), pp. 296-322. New York: Chapman and Hall.
- Beadle, I. C. 1932. The waters of some East African Lakes in relation to their flora and fauna. *J. Linn. Soc. Lond. Zool.* 38: 157-211. (Cited from Harper, 1992).
- Beadle, N. C. W., O. D. Evans, R. C. Carolin, and M. D. Tindale. 1982. *Flora of the Sydney Region*. NSW: Reed.
- Bell, C. R. 1971. Breeding systems and floral biology of the Umbelliferae or evidence for specialisation in unspecialised flowers. , V. H. Heywood (ed.), pp 93-108. London: Academic Press.
- Black, J. M. 1957. *Flora of South Australia*. Adelaide: Govt. Printer.
- Boyd, C. E., and D. R. Bayne. 1988. *Use of Water Hyacinths (Eichhornia crassipes) and Water Pennywort (Hydrocotyle ranunculoides) in Treatment of Poultry Wastewater*. Alabama: Dept. Fisheries and Allied Aquacultures, Auburn Univ.
- Burbidge, N. T., and M. Gray. 1970. *Flora of the Australian Capital Territory*. Canberra: Aust. Nat. Univ. Press.
- Carter, G. S. 1955. *The Papyrus Swamps of Uganda*. Cambridge: W. Heffer & Sons. (Cited from Denny, 1973).
- Cho, E. H., and I. H. Kim. 1988. Studies on the pharmaco-constituents of *Hydrocotyle japonica*. *Journal of the Pharmaceutical Society of Korea* 32: 281-286.
- Clough, K. S., T. A. DeBusk, and K. R. Reddy. 1987. Model water hyacinth and pennywort systems for the secondary treatment of domestic water. *Aquatic Plants for Water Treatment and Resource Recovery*, K. R. Reddy, and W. H. Smith (eds.), 775-781. Florida: Magnolia Publ.
- Constance, L., and M. O. Dillon. 1990. A new peltate *Hydrocotyle* (Umbelliferae) from Northern Peru. *Brittonia* 42: 257-259.



- Cook, C. D. K. 1990. *Aquatic Plant Book*. The Hague, Netherlands: SPB Academic.
- Cook, D. K., B. J. Gut, E. M. Rix, J. Schneller, and M. Seitz. 1974. *Water Plants of the World: a manual for the identification of the genera of freshwater macrophytes*. The Hague: Dr. W. Junk Publ.
- Costa, C. S. B., and U. Seeliger. 1988. Leaf demography of *Hydrocotyle bonariensis*, a rhizomatous perennial herb, in coastal dunes of Rio Grande do Sul, Brazil. *Revista Brasileira de Biologia* 48: 443-452.
- Crites, R. W. 1979. Economics of aquatic treatment systems. *Aquaculture Systems for Wastewater Treatment: Seminar Proceedings and Engineering Assessment*, R. Bastian, and S. Reed (eds.), pp 475-485. Washington, DC: USA Environmental Protection Agency.
- Crowden, R. K., J. B. Harbourne, and V. H. Heywood. 1969. Chemosystematics of the Umbelliferae: a general survey. *Phytochemistry* 8: 1963-1984.
- DeBusk, T. A., and K. R. Reddy. 1987. Wastewater treatment using floating aquatic macrophytes: contaminant removal processes and management strategies. *Aquatic Plants for Water Treatment and Resource Recovery*, K. R. Reddy, and W. H. Smith (eds.), pp. 643-656. Florida: Magnolia Publ.
- DeLoach, C. J., A. D. DeLoach, and H. A. Cordo. 1976. *Neohydronomus pulchellus*, a weevil attacking *Pistia stratiotes* in South America: biology and host specificity. *Annals of the Entomological Society of America* 69: 830-834.
- Denny, P. 1985. Submerged and floating-leaved aquatic macrophytes (euhydrophytes). *The Ecology and Management of African Wetland Vegetation*, P. Denny (ed.). Geobotany 6, The Netherlands: Junk.
- \_\_\_\_\_. 1973. Lakes of south-western Uganda. II. Vegetation studies on Lake Bunyonyi. *Freshwater Biology* 3: 123-135.
- \_\_\_\_\_. 1972. Lakes of south-western Uganda. 1. Physical and chemical studies on Lake Bunyonyi. *Freshwat. Biol.* 2: 143-158. (Cited from Denny, 1973).
- Dierberg, F. E., N. A. Goulet, and T. A. DeBusk. 1987a. Removal of two chlorinated compounds from secondary domestic effluent by a thin film technique. *J. Environ. Qual.* 16: 321-324.
- Dierberg, F. E., T. A. DeBusk, and N. A. Goulet. 1987b. Removal of copper and lead using a thin film technique. *Aquatic Plants for Water Treatment and Resource Recovery*, K. R. Reddy, and W. R. Smith (eds.). Florida: Magnolia Publ.
- Dinges, R. 1982. *Natural System for Water Pollution Control*. New York: Reinhold.
- Drude, O. 1897. Umbelliferae. *Die natuerlichen Pflanzenfamilien* 3: 63-150. (Cited from Tseng, 1967).
- Eichler, H. 1987a. Nomenclatural and bibliographical survey of *Hydrocotyle* L. (Apiaceae). Part I. *Feddes Repertorium* 98: 1-51.
- \_\_\_\_\_. 1987b. Nomenclatural and bibliographical survey of *Hydrocotyle* L. (Apiaceae). Part II. *Feddes Repertorium* 98: 145-196.
- Evans, J. P. 1992. The effect of local resource availability and clonal integration on ramet functional morphology in *Hydrocotyle bonariensis*. *Oecologia* 89: 265-276.
- \_\_\_\_\_. 1991. The effect of resource integration on fitness related traits in a clonal dune perennial, *Hydrocotyle bonariensis*. *Oecologia* 86: 268-275.
- \_\_\_\_\_. 1988. Nitrogen translocation in a clonal dune perennial, *Hydrocotyle bonariensis*. *Oecologia* 77: 64-68.





- Evans, J. P., and S. Whitney. 1992. Clonal integration across a salt gradient by a nonhalophyte, *Hydrocotyle bonariensis* (Apiaceae). *American Journal of Botany* 79: 1344-1347.
- Everson, R. G., and C. R. Slack. 1968. Distribution of carbonic anhydrase in relation to the C-4 pathway of photosynthesis. *Phytochemistry* 7: 581-584.
- Ewart, A. J. 1930. *Flora of Victoria*. Melbourne: Govt. Printer.
- Ewart, A. J., and O. B. Davies. 1917. *The Flora of the Northern Territory*. Darwin: McCarron & Bird.
- Fedorov, A. 1974. *Chromosome Numbers of Flowering Plants*. Koenigstein: Otto Koeltz Science.
- Fernandez, O. A., D. L. Sutton, V. H. Lallana, M. R. Sabbatini, and J. H. Iriogoyen. 1990. Aquatic weed problems and management in South and Central America. *Aquatic Weeds: the Ecology and Management of Nuisance Aquatic Vegetation*, A. H. Pieterse, and K. J. Murphy (eds.), pp 406-425. Oxford: Oxford Univ. Press.
- Foreman, D. B., and N. G. Walsh. 1993. *Flora of Victoria. Vol. 1: Introduction*. Melbourne: Inkata.
- French, D. H. 1971. Ethnobotany of the Umbelliferae. *The Biology and Chemistry of the Umbelliferae*, V. H. Heywood (ed.), pp. 385-412. London: Academic Press.
- Gaudet, J. J. 1977. Natural drawdown on Lake Naivasha, Kenya, and the formation of papyrus swamp. *Aquatic Botany* 3: 1-47.
- Gibson, D. J. 1988. The maintenance of plant and soil heterogeneity in dune grassland. *J. Ecol.* 76: 497-508.
- Godwin, H. 1984. *History of the British Flora*. Cambridge: Cambridge Univ. Press.
- Grime, J. P. 1979. *Plant Strategies and Vegetation Processes*. Chichester: Wiley.
- Grime, J. P., J. G. Hodgson, and R. Hunt. 1988. *Comparative Plant Ecology: a Functional Approach to Common British Species*. London: Unwin Hyman.
- Harbourne, J. B. 1971. Flavenoid and phenylpropanoid patterns in the Umbelliferae. *The Biology and Chemistry of the Umbelliferae*, V. H. Heywood (ed.), pp. 293-314. London: Academic Press.
- Harper, D. M. 1992. The ecological relationships of aquatic plants at Lake Naivasha, Kenya. *Hydrobiologia* 232: 65-71.
- \_\_\_\_\_. 1984. Recent changes in the ecology of Lake Naivasha, Kenya. *Verh. int. Ver. Theoret. Angewandlte Limnol.* 22: 1192-1197. (Cited from Harper, 1992).
- Hickey, M., and C. King. 1988. *One Hundred Families of Flowering Plants, 2nd ed.* Cambridge: Cambridge University Press.
- Ina, H., A. Asai, H. Iida, and T. Ushida. 1987. Chemical investigation of *Hydrocotyle sibthorpioides*. *Planta Medica* 53: 228.
- Jessop, J. 1981. *Flora of Central Australia*. Sydney: Reed.
- Johnson, P., and P. Brooke. 1989. *Wetland Plants in New Zealand*. Wellington: D.S.I.R.
- Kachi, N., and T. Hirose. 1983. Limiting nutrients for plant growth in coastal sand dune soils. *J. Ecol.* 71: 937-944.
- Kaplan, K. 1990. The sundew and marsh pennywort community in artificial ponds of lower Saxony and Westphalia (Germany). *Drosera* 90: 23-28.



- Klemm, V. V., N. L. Siemon, and R. J. Ruiz-Avila. 1993. *Hydrocotyle ranunculoides*: a control strategy for the Canning River Regional Park. Swan River Trust Report 6.
- Lima, A., and R. C. Pereira. 1985. Evaluation of herbicide efficiency in a mature rubber plantation in the south of Bahia. *Comuniado Tecnico No. 43*, Centro Nacional de Pesquisa de Seringueira e Dende.
- Linblad, R., and B. Staul. 1989. Notes on *Apium inudatum* (Apiaceae) *Baldellia ranunculoides* (Alismataceae) in Northern Halland, southwestern Sweden. *Svensk Botanisk Tidskrift* 83: 211-217.
- Lind, E. M., and M. E. S. Morrison. 1974. *East African Vegetation*. London: Longman.
- Lock, J. M. 1973. The aquatic vegetation of Lake George, Uganda. *Phytocoenologia* 1: 250-262.
- Mansor, P. 1988. Traditional salad vegetables of Malaysia. *Teknologi Sayur Sayuran* 4: 1-5.
- Marchant, N. G., J. R. Wheeler, B. L. Rye, E. M. Bennett, N. S. Lander, and T. D. Macfarlane. 1987. *Flora of the Perth Region. Part 1*. Perth: WA Herbarium.
- Mason, H. L. 1957. *A Flora of the Marshes of California*. Berkeley: University of California Press.
- Mathius, M. E. 1971. Systematic survey of New World Umbelliferae. *The Biology and Chemistry of the Umbelliferae*, V. H. Heywood (ed.), pp 13-30. London: Academic Press.
- \_\_\_\_\_. 1936. The genus *Hydrocotyle* in northern South America. *Brittonia* 2: 201-237.
- Mitchell, D. S. 1980. Aquatic weeds. *An Ecological Basis for Water Resource Management*, W. D. Williams (ed.), 81-89. Canberra: Australian National Univ. Press.
- Mitchell, D. S., and K. H. Bowmer. 1990. Aquatic weed problems and management in Australasia. *Aquatic Weeds: the Ecology and Management of Nuisance Aquatic Vegetation*, A. H. Pieterse and K. J. Murphy (eds.), pp 355-363. Oxford: Oxford Univ. Press.
- Monteferrante, F. J. 1987. Plant water relations of four coastal Louisiana dune and swale species. *Dissertation Abstracts International, B. Science and Engineering* 47: 9.
- Moore, D. M. 1971. Chromosome studies in the Umbelliferae. *The Biology and Chemistry of the Umbelliferae*, V. H. Heywood (ed.), pp. 233-255. London: Academic Press.
- Moorhead, K. K., and K. R. Reddy. 1988. Oxygen transport through selected aquatic macrophytes. *J. Environ. Qual.* 17: 138-172.
- Morisset, R., N. G. Cote, J. C. Panisset, L. Jemni, P. Camirand, and A. Brodeur. 1987. Evaluation of the healing activity of *Hydrocotyle tincture* in the treatment of wounds. *Phytother. Res.* 1 (117-121):
- Muenscher, W. C. 1944. *Aquatic Plants of the United States*. New York: Comstock Publ.
- Murata, G. 1973. New or interesting plants from Southeast Asia. I. *Hydrocotyle chiangdaoensis*. *Acta Phytotaxonom. Geobot.* 25: 97-106.
- Neave, H. M., and M. T. Tanton. 1989. The effects of grazing by kangaroos and rabbits on the vegetation and the habitat of other fauna in the Tidbinbilla Nature Reserve, Australian Capital Territory. *Australian Wildlife Research* 16: 337-351.
- Newman, M. J., and W. W. Thomaston. 1979. Aquatic weed control in Georgia. *Proc. South. Weed Sci. Soc.* 32: 271-279.
- Ohwi, J. 1965. *Flora of Japan*. Washington: Smithsonian Institute.
- Olsen, G., and E. Skitmore. 1991. *State of the Rivers of the South West Drainage Division*. Western Australian



Water Resources Council.

Overdieck, D., and B. R. Strain. 1981. Effects of atmospheric humidity on net photosynthesis, transpiration, and stomatal resistance: *Hydrocotyle umbellata* and *Hydrocotyle bonariensis*. *Int. J. Biometeor.* 25: 29-38.

Palma, B., C. San-Martin, M. Rosales, L. Zuniga, and C. Ramirez. 1987. Spatial distribution of the aquatic flora and marsh vegetation in the Marga-Marga Estero in central Chile. *Anales del Instituto de Ciencias del Mar Y Limnologia Universidad Nacional Autonoma de Mexico* 14: 125-132.

Parsons, W. T., and E. G. Cuthbertson. 1992. *Noxious Weeds of Australia*. Melbourne: Inkata Press.

Rao, M. N. A., G. K. Patnaik, and R. P. Rastogi. 1979. Spasmolytic principle of *Hydrocotyle podantha*. *Indian Drugs* 16: 185-187.

Reddy, K. R. 1988. Water hyacinth (*Eichhornia crassipes*) biomass cropping system. I. Production. *Methane from Biomass: a Systems Approach*, W. H. Smith, and J. R. Frank (eds.). London: Elsevier.

\_\_\_\_\_. 1984. Water hyacinth (*Eichhornia crassipes*) biomass production in Florida. *Biomass* 6: 167-181.

\_\_\_\_\_. 1983. Fate of nitrogen and phosphorus in a wastewater retention reservoir containing aquatic macrophytes. *J. Environ. Qual.* 12: 137-141.

Reddy, K. R., E. M. D'Angelo, and T. A. DeBusk. 1989. Oxygen transport through aquatic macrophytes: the role in wastewater treatment. *J. Environ. Qual.* 19: 261-267.

Reddy, K. R., and W. H. Smith. 1987. *Aquatic Plants for Water Treatment and Resource Recovery*. Florida: Magnolia Publ.

Reddy, K. R., and W. F. DeBusk. 1984. Growth characteristics of aquatic macrophytes cultured in nutrient-enriched water: I. Water Hyacinth, Water Lettuce and Pennywort. *Economic Botany* 38: 229-239.

Rejmankova, E. 1992. Ecology of creeping macrophytes with special reference to *Ludwigia peploides*. *Aquatic Botany* 43: 283-299.

\_\_\_\_\_. 1991. *Vegetation and Water Chemistry of Oso Flaco Lakes*. Report for State of California Dept. Parks and Recreation, Sacramento. (Cited from Rejmankova, 1992).

Richard, A. 1820. Monographie du Genre *Hydrocotyle*. *Ann. Sci. Phys.* 4: 145-225. (Cited from Mathius, 1936).

Ridley, H. N. 1930. *The Dispersal of Plants Throughout the World*. Ashford: Reeve. (Cited from Grime *et al.*, 1988).

Rodriguez, R. L. 1971. The relationships of the Umbellales. *The Biology and Chemistry of the Umbelliferae*, V. H. Heywood (ed.), pp 63-91. London: Academic Press.

Rodway, L. 1903. *The Tasmanian Flora*. Hobart: Govt. Printer.

Rowell, C. H. F. 1985. The feeding biology of a species-rich genus of rainforest grasshoppers (*Rhachicreagra*, Orthoptera, Acrididae). *Oecologia* 68: 87-98.

Santos, M. B. L., and J. R. de Freitas. 1988. Preference of *Biomphalaria tenagophila* among macrophytes and their periphytons determined through the degree of attractiveness. *Revista do Instituto de Medicina Tropical de Sao Paulo* 30: 264-269.

Saville, G. W. 1987. Turf weed control with clopyralid herbicide. *Proceedings of the New Zealand Weed and Pest Control Conference*,

Sculthorpe, C. D. 1967. *The Biology of Aquatic Vascular Plants*. London: Edward Arnold.



- Sebacher, D. I., R. C. Harriss, and K. B. Bartlett. 1985. Methane emissions to the atmosphere through aquatic plants. *J. Environ. Qual.* 14: 40-46.
- Shaffer, G. P., C. E. Sasser, J. G. Gosselink, and M. Rejmanek. 1992. Vegetation dynamics in the emerging Atchafalaya Delta, Louisiana, USA. *Journal of Ecology* 80: 677-687.
- Shevchic, V. L. 1986. New habitat of *Hydrocotyle vulgaris* (Apiaceae) in the European part of the USSR. *Bot. Zh.* 71: 1271-1277.
- Shigematsu, N., I. Kouno, and N. Kawano. 1982. Quercetin from *Hydrocotyle sibthorpioides*. *Phytochemistry* 21: 2156-2158.
- Silander, J. A. 1985. Microevolution in clonal plants. *The Population Biology and Evolution of Clonal Organisms*, J. B. G. Jackson, L. W. Buss, and R. E. Cook (eds.), pp. 107-152. Connecticut: Yale Univ. Press.
- Slaff, M., and J. D. Haefner. 1985. Seasonal and spatial distribution of *Mansonia dyari*, *Mansonia titillans* and *Coquillettidia perturbans* (Diptera: Culicidae) in the central Florida, USA, phosphate region. *Journal of Medical Entomology* 22: 624-629.
- Steubing, L., C. Ramirez, and M. Alberdi. 1980. Energy content of water- and bog-plant associations in the region of Valdivia (Chile). *Vegetatio* 43: 153-161.
- Steward, K. K. 1990. Aquatic weed problems and management in the eastern United States. *Aquatic Weeds: the Ecology and Management of Nuisance Aquatic Vegetation*, A. H. Pieterse, and K. J. Murphy (eds.), pp 391-405. Oxford: Oxford Univ. Press.
- Suhail, A., M. H. Ansari, M. Ahmad, and S. M. Osman. 1987. Studies on minor seed oils. XII. *Fett. Wissenschaft-Technologie* 89: 154-156.
- Swarbrick, J. T. 1973. *A Working List of Australian Weeds*. Lawes: QLD Ag. College. (Cited from Mitchell, 1978).
- Sykes, M. T., and J. B. Wilson. 1990a. An experimental investigation into the response of New Zealand sand dune species to different depths of burial by sand. *Acta Botanica Neerlandica* 39: 171-181.
- \_\_\_\_\_. 1990b. Dark tolerance in plants of dunes. *Functional Ecology* 4: 799-805.
- Tarver, D. P. 1985. Status report on Sonar as an aquatic herbicide. *Proceedings of the Southern Weed Society*,
- Tchobanglous, G., and G. Culp. 1980. Wetland systems for wastewater treatment: an engineering assessment. *Aquaculture Systems for Wastewater Treatment: an Engineering Assessment*, S. Reed, and R. Bastian (eds.), pp 13-42. Washington, DC: US Environmental Protection Agency.
- Thompson, A., and R. Dodson. 1963. Geology of the Naivasha Area. *Geological Survey of Kenya, Report No. 55*, Nairobi: Govt. Printer. (Cited from Gaudet, 1977).
- Thompson, K. 1985. Emergent plants of permanent and seasonally-flooded wetlands. *The Ecology and Management of African Wetland Vegetation*, P. Denny (ed.), pp. 43-107. The Netherlands: Junk.
- Tomei, P. E., C. L. Cioni, and I. Morelli. 1989. Geobotanical and phytochemical comments on the subject of *Hydrocotyle vulgaris*, *Hydrocotyle ranunculoides* and *Centella asiatica*. *Plantae Medicinales et Phytotherapie* 23: 38-45.
- Townsend, C. C. 1989. *Flora of Tropical East Africa: Umbelliferae*. Rotterdam: Balkema.



- 
- Tseng, C. C. 1967. Anatomical studies of flower and fruit in the Hydrocotyloideae (Umbelliferae). *Univ. Calif. Publ. Bot.* 42: 1-58.
- Wade, P. M. 1990. General biology and ecology of aquatic weeds. *Aquatic Weeds: the ecology and management of nuisance aquatic vegetation*, A. H. Pieterse, and K. J. Murphy (eds.). Oxford: Oxford Univ. Press.
- Wakefield, W. A. 1951. Notes on some Australian species of *Hydrocotyle*. *Victorian Naturalist* 68: 7-9.
- Weaver, C. I., and R. G. Wetzel. 1980. Carbonic anhydrase levels and internal lacunar carbon dioxide concentrations in aquatic macrophytes. *Aquatic Botany* 8: 173-186.
- Webb, C. J. New Zealand species of *Hydrocotyle* (Apiaceae) naturalised in Britain and Ireland. 18 93-95.
- Webb, C. J., and P. N. Johnson. 1982. *Hydrocotyle* (Umbelliferae) in New Zealand: a three-foliolate species. *New Zealand Journal of Botany* 20: 163-168.
- Webb, C. J., W. R. Sykes, and P. J. Garnock-Jones. 1988. *Flora of New Zealand. Vol. 14. Naturalised Pteridophytes, Gymnosperms, Dicotyledons*. Christchurch: D.S.I.R.
- Webb, D. H., and W. M. Dennis. 1981. Additions to the flora of Tennessee: *Najas gracillima*, *Cyperus difformis*, *Eleocharis tortilis*, *Hydrocotyle umbellata*. *Sida Contributions to Botany* 9: 184-185.
- Welsh, S. L., N. D. Atwood, S. Goodrich, and L. C. Higgins. 1987. *A Utah Flora*. Utah: Birmingham Young Univ.

Appendix 1. Occurrence of *Hydrocotyle* species in Australasia. (ACT=Australian Capital Territory; NSW=New South Wales; Vic=Victoria; SA=South Australia; QLD=Queensland; Tas=Tasmania; NT=Northern Territory; WA=Western Australia; NZ=New Zealand).

SPECIES	LOCATION	COMMENTS	REFERENCE
<i>H. acutiloba</i>	southern NSW & eastern Vic		Wakefield (1951)
	Sydney	widespread	Beadle <i>et al.</i> (1982)
<i>H. alata</i>	WA	winter-wet depressions	Marchant <i>et al.</i> (1987)
<i>H. asiatica</i>	Throughout Australia (incl. SA) & NZ; Asia; Africa; America	in or near water	Black (1957)
	Throughout NZ, Australia, & most warm parts of world	very common in swamps	Rodway (1903)
	Vic; Australasia	medicinal, narcotic	Ewart (1930)
<i>H. blepharocarpa</i>	WA	near-coastal sands & limestones	Marchant <i>et al.</i> (1987)
<i>H. bonariensis</i>	NSW & SA	maritime habitats; sandy soil lawns	Auld & Medd (1987)
	Sydney	sandy soils near beach; common; introd. from South America	Beadle <i>et al.</i> (1982)
	WA	naturalised in disturbed sandy soil at Bunbury; native to Nth & Sth America	Marchant <i>et al.</i> (1987)
<i>H. callicarpa</i>	Southern Australia		Rodway (1903)
	temperate Australia, incl. SA		Ewart (1930); Black (1957)
	WA; Vic; Tas; NSW	moist soil	Marchant <i>et al.</i> (1987)
<i>H. capillaris</i>	Tas; Vic; SA; WA		Rodway (1903)
	temperate Australia		Ewart (1930); Black (1957)
<i>H. comocarpa</i>	Kangaroo Is.		Black (1957)
<i>H. crassiuscula</i>	Kangaroo Is.		Black (1957)
<i>H. diantha</i>	SA; WA	wet soil	Black (1957)
	WA	sandy or granitic soils	Marchant <i>et al.</i> (1987)
<i>H. dissecta</i>	NZ	endemic; forest margins and river terraces	Webb <i>et al.</i> (1988)
<i>H. elongata</i>	NZ	endemic; wet areas of forest margins or clearings	Webb <i>et al.</i> (1988)
<i>H. geraniifolia</i>	Sydney	widespread; sheltered places	Beadle <i>et al.</i> (1982)
	Vic; NSW		Ewart (1930)
<i>H. grammatocarpa</i>	NT		Ewart & Davies (1917)
<i>H. heteromeria</i>	NZ	endemic; damp or shaded lawns	Johnson & Brook (1989)
	NZ	endemic; lawn weed; damp shady places	Webb <i>et al.</i> (1988)
<i>H. hirta</i>	Tas, Vic, NSW, SA, WA		Wakefield (1951)
	Tas; extra-tropical Australia	very common	Rodway (1903)
	Vic; temperate Australia; QLD	moist places	Ewart (1930); Black (1957)
<i>H. hispidula</i>	WA	sandy soils	Marchant <i>et al.</i> (1987)
<i>H. hydrophila</i>	NZ	endemic; lake, streams, swamp margins	Webb & Johnson (1982); Johnson & Brooke (1989); Webb <i>et al.</i> (1988)
<i>H. intertexta</i>	WA	endemic; King George's Sound & Pemberton	Wakefield (1951)

<i>H. laxiflora</i>	ACT; widespread in SE Australia & Tas	common in pastures, waste ground, woodland & dry forest	Burbidge & Gray (1970); Auld & Medd (1987)
	Vic	dominant understorey species of dry sclerophyll forest	Foreman & Walsh (1993)
	Vic; QLD; NSW; SA;	weed of damp pastures; foul smell	Ewart (1930); Black (1957); Willis <i>et al.</i> (1975); Beadle <i>et al.</i> (1982)
<i>H. lemnooides</i>	WA	apparently endemic to Perth region; swamps; rarely collected	Marchant <i>et al.</i> (1987)
<i>H. medicaginoides</i>	Vic; SA; WA		Ewart (1930); Black (1957)
<i>H. microphylla</i>	NZ	endemic; damp open or shady places; lawn weed in wetter areas	Johnson & Brook (1989); Webb <i>et al.</i> (1988)
<i>H. moschata</i>	NZ	endemic; forest margins & clearings; lawn weed	Webb <i>et al.</i> (1988)
<i>H. mucosa</i>	Tas, southern Vic, SA		Wakefield (1951)
<i>H. novae-zelandiae</i>	NZ	endemic; damp tussockland, grassland, sedge and swamp; sometimes submerged	Johnson & Brooke (1989); Webb <i>et al.</i> (1988)
<i>H. peduncularis</i>	ACT, QLD to Tas	wet ground under shrubs	Burbidge & Gray (1970)
	Sydney	widespread	Beadle <i>et al.</i> (1982)
	Tas, Vic, NSW, SA, QLD		Wakefield (1951)
<i>H. pilifera</i>	SA; WA		Black (1957)
	WA	moist soils	Marchant <i>et al.</i> (1987)
<i>H. plebeia</i>	SA; WA	in water	Black (1957)
<i>H. pterocarpa</i>	NZ	indigenous to NZ & Australia; swamps, lake margins & stream edges	Webb <i>et al.</i> (1988)
	Tas; Vic; SA		Rodway (1903)
	Vic; SA; Tas; NZ	in water	Ewart (1930); Black (1957)
<i>H. ranunculoides</i>	WA	naturalised in permanent fresh water streams; native to Europe	Marchant <i>et al.</i> (1987)
<i>H. rugulosa</i>	SA; WA		Black (1957)
<i>H. sulcata</i>	NZ	endemic; tussock grassland, swamps, lakes and stream edges	Webb & Johnson (1982); Johnson & Brooke (1989); Webb <i>et al.</i> (1988)
<i>H. tetragonocarpa</i>	WA	occurs on sands	Marchant <i>et al.</i> (1987)
<i>H. trachycarpa</i>	Central Australia		Jessop (1981)
<i>H. tripartita</i>	Eastern Australia	common in moist places	Rodway (1903); Black (1957)
	NZ	naturalised (Australian)	Webb & Johnson (1982); Johnson & Brooke (1989); Webb <i>et al.</i> (1988)
	QLD to Vic		Wakefield (1951)
	Sydney	widespread; margins of streams; sheltered places; lawn weed	Beadle <i>et al.</i> (1982)
	Vic; QLD; NSW; SA		Ewart (1930)
<i>H. vulgaris</i>	most of Australia, incl. SA; Europe; Africa	near water	Black (1957)
	Sydney	uncommon	Beadle <i>et al.</i> (1982)
	Vic; temperate Australia, except Tasmania	poisonous	Ewart (1930)

Appendix 2. The occurrence of *Hydrocotyle* species throughout the world.

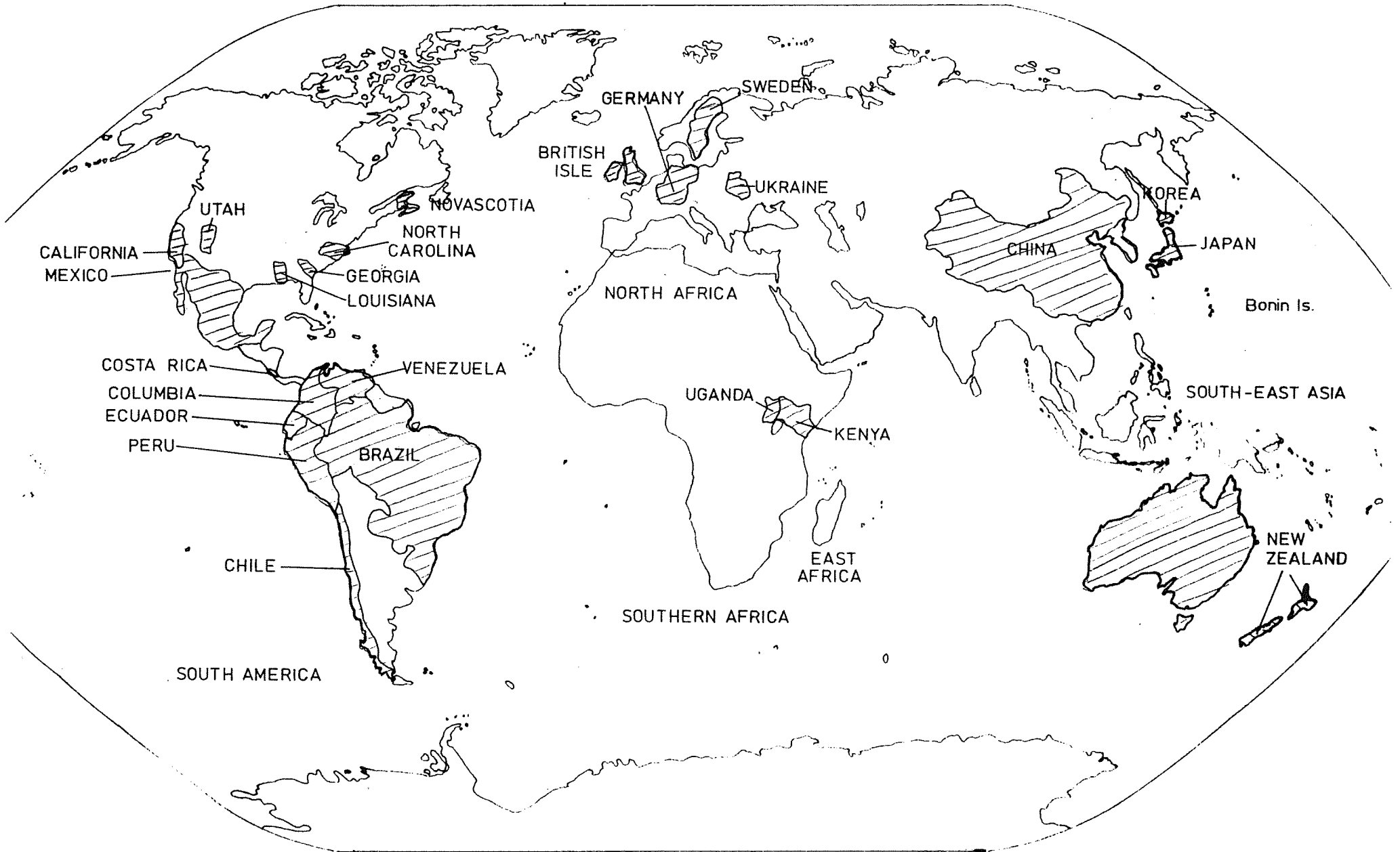
SPECIES	LOCATION	COMMENTS	REFERENCE
<i>H. aconitifolia</i>	Colombia; Venezuela		Constance & Dillon (1990)
	South America		Mathius (1936)
<i>H. acuminata</i>	South America		Mathius (1936)
<i>H. acutifolia</i>	South America		Mathius (1936)
<i>H. alchemilloides</i>	South America		Mathius (1936)
<i>H. boliviana</i>	South America		Mathius (1936)
<i>H. bonariensis</i>	Louisiana	coastal dunes	Monteferrante (1987)
	North Carolina (USA)	common coastal species	Evans (1988)
	Rio Grande do Sul, Brazil	dominant species of coastal sand dunes	Costa & Seeliger (1988)
	South America	irrigation ditch banks; along shaded stream banks; moist soil	Mathius (1936)
<i>H. bonplandii</i>	South America		Mathius (1936)
<i>H. bonplandii</i> var. <i>glabra</i>	South America		Mathius (1936)
<i>H. bonplandii</i> var. <i>hirtipes</i>	South America		Mathius (1936)
<i>H. bowlesiioides</i>	Georgia, USA; Costa Rica; Paraguay; Brazil	moist loamy soil under partial shade; similar to <i>H. sibthorpioides</i>	Anderson (1983)
<i>H. chiangdaoensis</i>	South-East Asia		Murata (1973)
<i>H. dahlgrenii</i>	South America	moist sandy banks	Mathius (1936)
<i>H. dichondroides</i>	Japan		Ohwi (1965)
<i>H. filipes</i>	South America		Mathius (1936)
<i>H. geranioides</i>	South America		Mathius (1936)
<i>H. globiflora</i>	Peru		Constance & Dillon (1990)
	South America		Mathius (1936)
<i>H. gracilis</i>	South America		Mathius (1936)
<i>H. grossulariaefolia</i>	South America		Mathius (1936)
<i>H. gunnerifolia</i>	South America		Mathius (1936)
<i>H. hederacea</i>	South America		Mathius (1936)
<i>H. heucheraefolia</i>	South America		Mathius (1936)
<i>H. hexagona</i>	Ecuador		Constance & Dillon (1990)
<i>H. hexagona</i>	South America		Mathius (1936)
<i>H. hirta</i>	Chile	emergent life form; associated with <i>Juncetum procerii</i>	Steubing <i>et al.</i> (1980).
<i>H. hitchcockii</i>	South America	moist ground	Mathius (1936)
<i>H. humboldtii</i>	Colombia; Ecuador; Peru		Constance & Dillon (1990)
	South America	ravines	Mathius (1936)
<i>H. incrassata</i>	South America		Mathius (1936)
<i>H. japonica</i>	Korea		Cho & Kim (1988)
<i>H. javanica</i>	Japan; Tropics of Asia	woods in low mountains	Ohwi (1965)



<i>H. langsdorf</i>	Brazil		Constance & Dillon (1990)
<i>H. lehmannii</i>	Columbia		Constance & Dillon (1990)
	South America		Mathius (1936)
<i>H. leucocephala</i>	South America		Mathius (1936)
<i>H. longipes</i>	South America		Mathius (1936)
<i>H. mannii</i>	East Africa	woodland, near mountain lakes	Lind & Morrison (1974)
	Uganda, tropical East Africa	occurs in swamp (1% cover) with <i>H. ranunculoides</i> (insignificant % cover)	Denny (1973)
	upland Kenya	quite common on the forest floor in & below the bamboo zone	Agnew (1974)
<i>H. maritima</i>	Japan; Korea; China; Bonins	lawns & roadsides in lowlands & hills; common	Ohwi (1965)
<i>H. mexicana</i>	South America		Mathius (1936)
<i>H. minutifolia</i>	South America		Mathius (1936)
<i>H. monticola</i>	upland Kenya	muddy & peaty stream banks in the upper forest levels into the alpine zone	Agnew (1974)
<i>H. multifida</i>	South America		Mathius (1936)
<i>H. palmata</i>	South America		Mathius (1936)
<i>H. pennellii</i>	South America	along stream in clearing	Mathius (1936)
<i>H. peruviana</i>	South America		Mathius (1936)
<i>H. pusilla</i>	South America		Mathius (1936)
<i>H. quinqueloba</i>	Brazil; Peru		Constance & Dillon (1990)
	South America		Mathius (1936)
<i>H. ramiflora</i>	Japan; Korea	lawns & sunny places in lowlands & low mountains	Ohwi (1965)
<i>H. rotundifolia</i>	South America	damp ground	Mathius (1936)
<i>H. sagasteguii</i>	Peru		Constance & Dillon (1990)
<i>H. sibthorpioides</i>	Japan; widely distributed in tropical & warm-temperate Asia	shaded places in the lowlands; common	Ohwi (1965)
	Japan	common weed	Shigematsu <i>et al.</i> (1982)
	Japan	medicinal	Ina <i>et al.</i> (1987)
<i>H. sphenoloba</i>	South America		Mathius (1936)
<i>H. tambalomaensis</i>	South America		Mathius (1936)

<i>H. tenerrima</i>	South America		Mathius (1936)
<i>H. umbellata</i>	Nova Scotia, Canada	rare, coastal plain	Roland (1991)
	South America	street gutters; pastures; edge of pools; meadows	Mathius (1936)
	Tennessee		Webb & Dennis (1981)
	throughout California, east to Atlantic, south to Mexico; southern Africa	edges of ponds, ditches, marshy ground	Mason (1957)
<i>H. urbaniana</i>	South America		Mathius (1936)
<i>H. venesuelensis</i>	South America		Mathius (1936)
<i>H. verticillata</i>	California	aquatic; commonly occur in irrigation and drainage canals	Rejmankova (1992)
	California; Atlantic states, Mexico, West Indies		Mason (1957)
	Utah	moist ground or in water in Washington Country; S. America north to Massachusetts & California	Welsh <i>et al.</i> (1987)
<i>H. verticillata var. racemosa</i>	South America		Mathius (1936)
<i>H. vestita</i>	South America		Mathius (1936)
<i>H. vulgaris</i>	British Isles		Godwin (1984)
	British Isles; W, C & S Europe northwards to Scandanavia & southwards to Portugal & Greese; N Africa; introduced to NZ		Grime <i>et al.</i> (1988)
	Europe		Tomei <i>et al.</i> (1989)
	Germany	codominant with <i>Drosera intermedia</i>	Kaplan (1990)
	Sweden	small pools near coast; sandy substrate	Lindblad & Stahl (1989)
	Ukraine		Zelenchuk (1987)
	USSR	endangered species	Shevchic (1986)
<i>H. yabei</i>	Japan	woods in hills & mountains	Ohwi (1965)
<i>H. yanghuangensis</i>	Ecuador		Constance & Dillon (1990)
	South America	woods, at base of rotten trunks	Mathius (1936)
<i>Hydrocotyle sp.</i>	Louisiana, USA	coastal deltaic wetlands	Shaffer <i>et al.</i> (1992)

DISTRIBUTION OF THE GENUS HYDROCOTYLE  
THROUGHOUT THE WORLD



Appendix 3. The occurrence of *Hydrocotyle ranunculoides* throughout the world.

LOCATION	COMMENTS	REFERENCE
Africa		Lock (1973); Thompson (1985)
California	shallow pools & muddy shores, lower altitudes	Mason (1957)
Central America		Cook <i>et al.</i> (1974)
Chile	one of dominant species (70% cover) of fresh, clear water brooklets, brooks and small rivers in the Central valley & pacific littoral region of south Chile	Steubing <i>et al.</i> (1980)
Chile (central)	codominant with <i>Elodea potamogeton</i>	Palma <i>et al.</i> (1987)
Colombia	a dominant species, up to 75-100% cover	Wijninga (1989)
Europe		Tomei <i>et al.</i> (1989)
Florida		Weaver & Wetzel (1980)
Georgia, USA	potential weed	Newman & Thomaston (1979)
Kenya (upland), East Africa	locally common in ponds & marshes, growing in water between the reeds	Agnew (1974)
Kenya, East Africa	a dominant water-edge species colonising the <i>Salvinia molesta</i> (weed) mats; floating community moving in rafts or islands due to wind action; covering about 25% of lake surface	Harper (1992)
Kenya, East Africa	occurs in shallow water & recently exposed shore of Lake Naivasha (tropical freshwater lake in closed basin)	Gaudet (1977)
northern South America	Pennsylvania & Washington south to southern South America at coastal & low elevations; common name: <i>Somberito de agua</i>	Mathius (1936)
South Carolina	restricted to coastal plain	Aulbach-Smith & de Kozlowski (date??)
Tropical East Africa	appears to be geocarpic, the peduncle bending over to push the fruits into the mud	Townsend (1989)
Uganda		Denny (1973)
USA	in ponds, lakes & margins of streams; mostly on sandy bottom. Atlantic coast; local in the South & westward. Distribution map provided	Muenscher (1944)

DISTRIBUTION OF HYDROCOTYLE RANUNCULOIDES  
THROUGHOUT THE WORLD

