



Morphological Variation in Populations of *Ranunculus repens* from the Temporary Limestone Lakes (Turloughs) in the West of Ireland

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An unusual form of *Ranunculus repens* L. occurs in turlough basins (temporary lakes) in the West of Ireland. It is characterized by more highly-dissected and glabrous leaves than the more typical broad-leaved form. Leaf dissection of both forms was quantified using seed-derived plants which were cultivated in standard conditions. Leaves of both forms showed heteroblastic development and became increasingly dissected with each successively produced leaf until the adult leaf shape was attained around leaf 8. The dissection index of adult leaves was genetically based and had a high heritability. Changes in leaf dissection were recorded across a relatively deep, undulating turlough basin. The most dissected leaf form was found deep within the basin among a highly specialized species-poor community which was subjected to the most prolonged period of inundation. An intermediate-leaved form occurred higher up the sides of the basin in a damp grassland community, where the period of inundation was more transient. A broad-leaved form occurred around the upper fringes of the basin among a dry pastureland community. The intermediate-leaved form may have resulted from gene flow between the broad- and dissected-leaved populations, or may have evolved a distinct leaf shape adapted to the prevailing conditions at that point within the basin. © 2000 Annals of Botany Company

Key words: *Ranunculus repens* L., turloughs, leaf shape, heritability, ontogeny, population biology.

INTRODUCTION

Population studies on the pattern of variation in many plant species have revealed the existence of localized populations each adapted to the particular environmental conditions of their habitat (e.g. Turesson, 1922b; Bradshaw, 1960, 1991; McNeilly, 1968; Kik *et al.*, 1990; Geber *et al.*, 1992). Turesson (1922a) coined the term 'ecotype' to define an ecological subunit that arose as a result of a genotypical response to a particular habitat. If a species encounters a mosaic of habitats while expanding its range, the selective influences of each habitat act in turn upon the whole available pool of genetic variation (Jain and Bradshaw, 1966). Populations can continue to diverge in response to high selection pressures in spite of gene exchange between them (McNeilly, 1968; McNeilly and Antonovics, 1968). The amount of gene flow permissible between closely adjacent divergent populations without arresting or reversing divergence is dependent on the magnitude of the selective pressures maintaining population divergence (Jain and Bradshaw, 1966; Bradshaw, 1991).

Turloughs are temporary water bodies that occupy depressions in karstic areas, where limestone basins become inundated with ground water in the absence of an over-ground outflow (Coxon, 1986). These basins may form what appear to be extensive lakes during periods of high water table following prolonged rainfall, but in the driest seasons there is often no permanent surface water. The water levels may fluctuate rapidly by charging and discharging through subterranean water conduits, known

as swallow holes. The plant populations that occur in turlough basins are exposed to extremely different environmental conditions to those from the surrounding area, mainly due to the unpredictable fluctuations in water depth. The fact that the environment is a dominating factor in determining population differentiation suggests the potential for the evolutionary divergence of turlough plant populations.

Ranunculus repens is one of the many plant species that flourishes in turlough basins. The populations occurring within the influence of the groundwater are morphologically distinct from those in the surrounding pastureland. The most distinctive feature of turlough *R. repens* populations is leaf morphology, which is glabrous and more highly-dissected than the typical form (Lynn, 1998). Narrower, more dissected leaves are a characteristic of many submerged macrophytes as higher surface to volume ratios counteract some of the diffusive limitations on aquatic photosynthesis (Givinish, 1979; Smith and Walker, 1980).

R. repens has a wide geographical distribution and also a wide ecological amplitude (Harper, 1957). This species may have the ability to exhibit a broad tolerance to different environmental conditions. Alternatively, specialized populations may evolve in particular environments. This paper quantifies the morphological differences in leaf characteristics between turlough and more typical populations of *R. repens*, and determines whether this variation has a genetic or environmental basis. Changes in leaf morphology across a turlough/pastureland boundary were also investigated, and the ecological and evolutionary implications of leaf dissection of the turlough form of *R. repens* explored.

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MATERIALS AND METHODS

Plant collection and propagation

Seeds were collected from the locations listed in Table 1. The seeds were germinated in a growth room (14 h day, PAR 60–100 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 25°C day, 22°C night) on moist filter paper in glass Petri dishes. Seedlings were transferred to an equal part sand:peat:loam compost which was enriched with 3.5 g l^{-1} Osmocote Plus (Sierra Chemical Company, USA) slow release fertilizer.

Measurement of leaf shape

An index of dissection can be obtained by calculating the ratio of the perimeter of an outline to the square root of its area; this value was standardized so that a circle has a value of 1.0 (Kincaid and Schneider, 1983)

$$d = \frac{p}{2\sqrt{(a\pi)}}$$

where d is the dissection index, p is the perimeter and a is the area. This dimensionless number gives a simple measure of the degree to which an outline is more complex than a circle. Typically, the dissection index of an entire leaf is slightly larger than 1, and the more deeply lobed or dissected the leaf the larger the value (Kincaid and Schneider, 1983). Traced leaf outlines were scanned using a flat-bed Apple scanner and analysed by image analysis (NIH Image version 1.56) which converted the scanned drawing to a bitmap image and calculated the area and perimeter of the resulting image.

Leaf dissection ontogeny of ruderal and turlough populations

Populations: Dodder bank (ruderal), Lough Gealáin (turlough).

Individuals were raised from seed and grown in growth room conditions as outlined above.

Fully expanded successive leaves (leaves 1–10, 13, 16 and 19) produced from single shoot apices were removed and leaf dissection analysed in eight plants per population. Slopes of the association between perimeter and $\sqrt{\text{area}}$ were obtained for the individual populations to determine whether there was a developmental deviation from a 1:1 ratio, following the methods outlined in Hammond (1941). The association between the perimeter and $\sqrt{\text{area}}$ was assessed using the Pearson Product-moment Correlation Coefficient. Developmental differences were analysed by comparing the regression slopes of the association between perimeter and $\sqrt{\text{area}}$, with $\sqrt{\text{area}}$ assigned as the continuous independent variable. Changes in leaf dissection with age were also determined for both populations.

Heritability of leaf dissection index in ruderal and turlough populations

Seeds were collected from separate mothers in the wild; the pollen source was unknown. Plants were raised as described previously. Fully expanded leaves older than leaf

TABLE 1. Location details for the seed-derived populations of *Ranunculus repens*

Population	Grid reference	Habitat-type
Dodder	O 150 297	Ruderal
Bull Island	O 230 370	Ruderal
Lough Gealáin	R 317 938	Turlough
Hawkhill	M 411 025	Turlough
Cooloorta	R 337 979	Turlough

10 were chosen for dissection analysis in five part-sibs per family and five families per population from all populations listed in Table 1. Plants were arranged in a single fully randomized block. The Natural Progenies Design (Lawrence, 1984) was used to estimate the narrow sense heritability (t) of dissection index:

$$t = \frac{(\delta_1 - \delta_2)/r}{(\delta_1 - \delta_2)/r + \delta_2}$$

where δ_1 is the mean square between families, the additive genetic component; δ_2 is the mean square within families, the environmental component; and r is the number of sibs.

As the progeny were part-sibs, t lies between full and quarter narrow sense heritability ($ht_n > t > 0.25ht_n$) due to the unknown pollen source.

The association between the perimeter and $\sqrt{\text{area}}$ was assessed using the Pearson Product-moment Correlation Coefficient. Regression slopes of the association between perimeter and $\sqrt{\text{area}}$ were compared for habitat types with $\sqrt{\text{area}}$ as the continuous independent variable. Differences in leaf dissection between populations were analysed using a one-way ANOVA. Populations were also assigned to their habitat type, and differences between leaf dissection were analysed using nested ANOVA with populations nested within habitat type.

Hair cover in ruderal and turlough populations

Populations: Dodder bank (ruderal), Lough Gealáin (turlough).

Individuals were raised from seed and grown in growth room conditions as outlined above.

Leaf material was sampled from fully expanded rosette leaves. Fresh leaves were plunged into liquid nitrogen and then quickly placed onto the pre-cooled stage (approx. –60°C) of an Edwards ETD4 freeze drier. The stage area was evacuated using a rotary pump, and the temperature slowly raised to ambient over a period of 24 h. The freeze dried samples were removed and individually mounted onto 10 mm aluminium specimen stubs using carbon cement. The samples were placed in an Emscope SC500 gold sputter coater and coated with a very thin layer of gold to give them a conducting surface. The mounted samples were viewed under a scanning electron microscope (Leica/Cambridge S – 360).

Changes in leaf dissection along a turlough gradient

In June 1997, leaf dissection was assessed in six leaves sampled from plants within 13 1 m² quadrats located at intervals up and over the side of a turlough basin (Turlough na gCoileáin, Grid M 282 046) and into surrounding pasture. Quadrats were not chosen randomly as an attempt was made to include all aspects of the turlough habitat including depth changes and features such as swallow holes. The elevation at each quadrat was measured relative to a temporary bench mark on the basin floor using a level (WILD NAC-O). The values of the dissection index for the individual leaves were simultaneously plotted with elevation.

The vegetation of the transect consisted of a dry pastureland community above the influence of the high water mark at the highest elevation; this included species such as *Bellis perennis* and *Plantago lanceolata* (Lynn, 1998). This community was replaced by a diverse damp grassland community around the unpredictable margins of the high water mark and included *Filipendula ulmaria* and *Trifolium repens*. A species-poor community occupied the lower levels of the transect which fell deep within the turlough basin and which was subjected to a relatively predictable flooding regime. This area was dominated by *Ranunculus repens*, *Agrostis stolonifera* and *Potentilla anserina*, and all occurred throughout the transect suggesting a broad tolerance to changing water regimes. Quadrats 6 and 9 fell on swallow holes which were dominated by loose rock and the black moss *Cinclidotus fontinalis*.

RESULTS

Leaf dissection ontogeny of ruderal and turlough populations

Visually, the turlough leaves had more deeply cut lobes than the ruderal population (Fig. 1), which was evident from the first leaf produced. The development of the terminal and the two lateral leaflets resulted from a series of leaves with increasingly deeper incisions. This development occurred earlier in the turlough (leaf 3) than in the ruderal population (leaf 5). The leaflets became increasingly more deeply lobed in both populations until leaf 8, after which the amount of lobing was consistent between successive leaves.

The perimeter of both populations increased with leaf number until leaf 8 (Fig. 2A), and there was a slight drop in perimeter which then levelled off in the successive leaves that were measured. The turlough population had a slightly smaller perimeter than the ruderal population for all leaf numbers. A similar change in area was observed for both populations except that the turlough population had a considerably smaller area than the ruderal after leaf 2 (Fig. 2B).

The associations between perimeter and $\sqrt{\text{area}}$ of both populations are presented in Fig. 2C. Perimeter and $\sqrt{\text{area}}$ were highly positively correlated for the first 19 leaves produced by both populations (Table 2). The relationship between perimeter and $\sqrt{\text{area}}$ differed between populations: the turlough population had a significantly greater slope than the ruderal population (19.57 and 13.83,

respectively, $P > 0.0001$) indicating that the perimeter was relatively greater in the turlough population than the ruderal population for a given $\sqrt{\text{area}}$.

The dissection index increased in both populations until leaf 8 where it levelled off, although a very slight increase was still apparent in the turlough population (Fig. 2D). The higher dissection index in the turlough population was evident from leaf 2.

Heritability of leaf dissection index in turlough and ruderal populations

The association between perimeter and $\sqrt{\text{area}}$ is presented in Fig. 3. The correlations between perimeter and $\sqrt{\text{area}}$ for the individual populations and for the populations pooled into habitat type are presented in Table 3. The two variables were highly positively correlated in all cases. The turlough populations had a considerably higher perimeter relative to $\sqrt{\text{area}}$ than the ruderal populations; this is reflected in the significantly higher slope in the pooled data for the turlough than the ruderal populations (Table 4; $P < 0.001$).

When the dissection index was pooled into habitat type (Table 4), the turlough populations had a significantly higher ($P < 0.05$) dissection index than the ruderal populations. The turlough populations had a significantly higher dissection index than the ruderal populations (Fig. 3B; $P < 0.0001$) despite the Cooloorta turlough population having a slightly lower dissection index than the Lough Gealáin and Hawhill turlough populations (Table 5).

TABLE 2. Pearson Product-moment Correlation Coefficient for the association of perimeter with $\sqrt{\text{area}}$ for a turlough (Lough Gealáin) and ruderal (Dodder) population of *Ranunculus repens*

Population	Coefficient	d.f.
Ruderal	0.954***	94
Turlough	0.917***	98

*** $P < 0.001$.

TABLE 3. Pearson Product-moment Correlation Coefficient for the association between perimeter and $\sqrt{\text{area}}$ of the individual turlough (Lough Gealáin, Hawhill and Cooloorta) and ruderal (Dodder and Bull Island) populations and the pooled data for the populations pooled into habitat type

Habitat type	Coefficient	<i>n</i>	Population	Coefficient	<i>n</i>
Turlough	0.850***	64	Lough Gealáin	0.914***	25
			Hawhill	0.887***	25
			Cooloorta	0.874***	14
Ruderal	0.922***	45	Dodder	0.951***	25
			Bull Island	0.904***	20

*** $P < 0.001$.

n, Sample size.

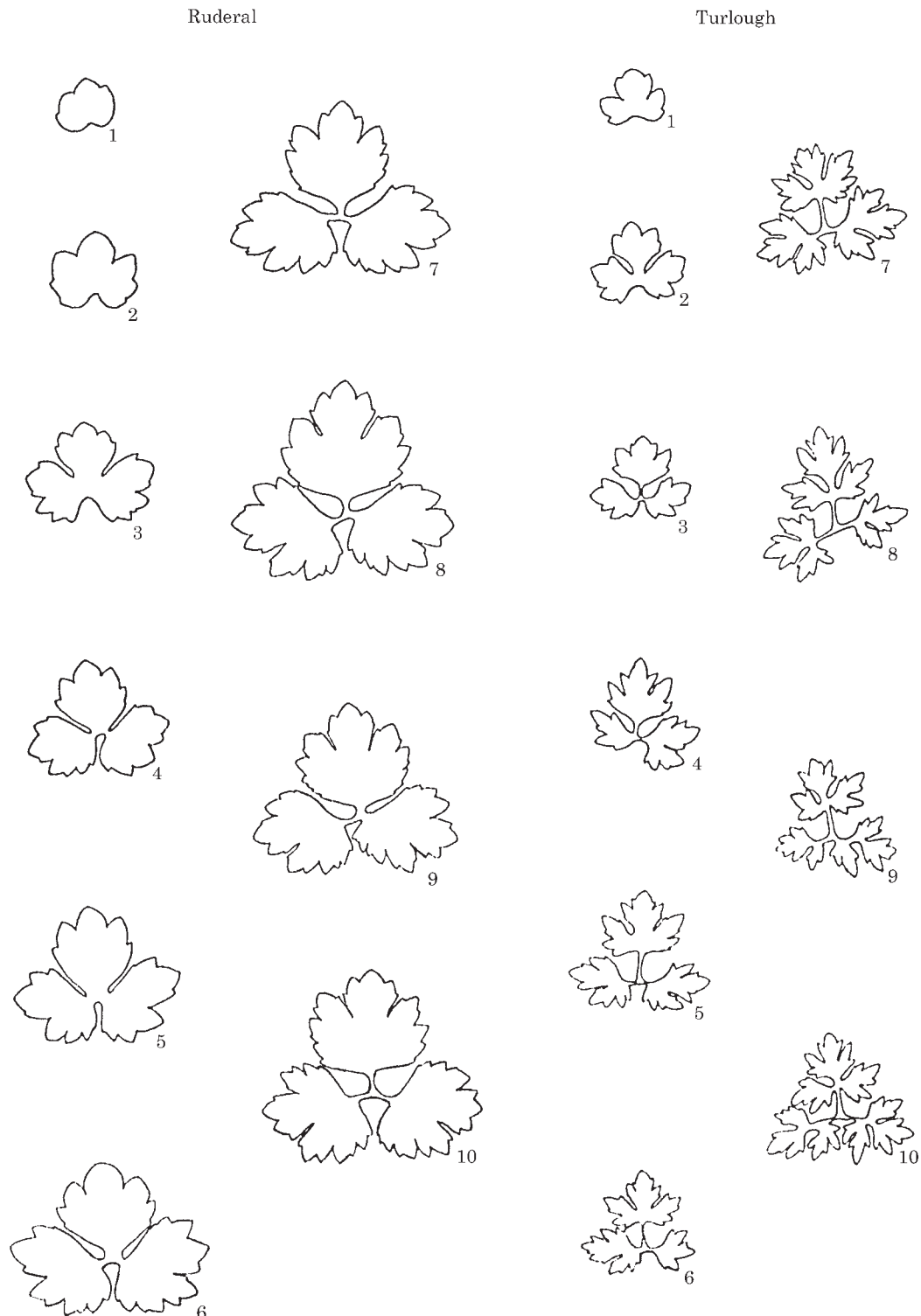


FIG. 1. Leaf outlines of a ruderal (Dodder) and turlough (Lough Gealáin) population of *Ranunculus repens*. Populations were grown from seed in growth room conditions. Linear dimension reduced by 50 %.

The narrow sense heritability estimate (t) for the heritability of leaf dissection in the above five populations was 0.72 i.e. 72 % of the additive genetic variation occurred between families and 28 % within families.

Hair cover in ruderal and turlough populations

The most striking difference between the two populations was the presence of trichomes; these appeared on both the upper and lower surface of leaves of the ruderal population

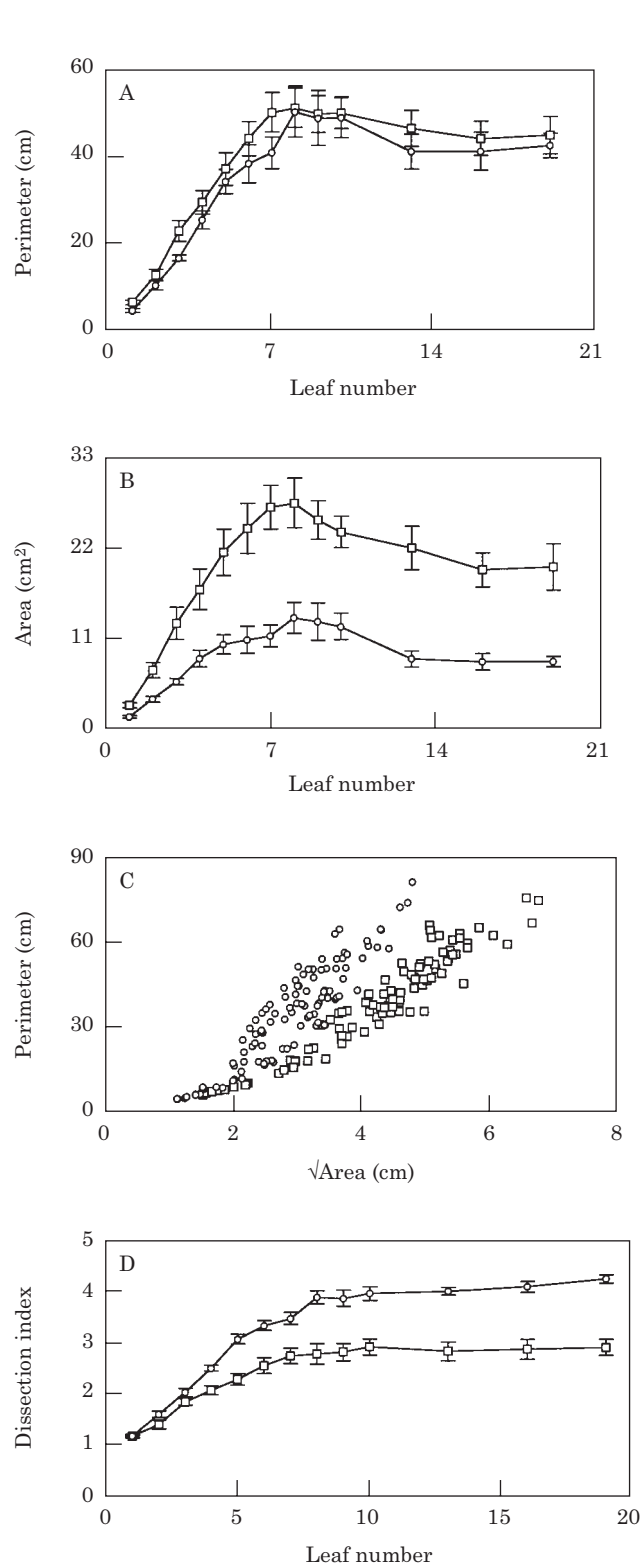


FIG. 2. A and B, Changes in perimeter and area with leaf number (in order of production) in a turlough (Lough Gealáin) (○) and ruderal (Dodder) (□) population of *Ranunculus repens*. Values are means of eight replicates. Error bars represent the standard errors of the means. C, The association between $\sqrt{\text{area}}$ and perimeter in the populations shown in A and B. D, Changes in dissection index with leaf number, populations, sample size and error bars as in A and B.

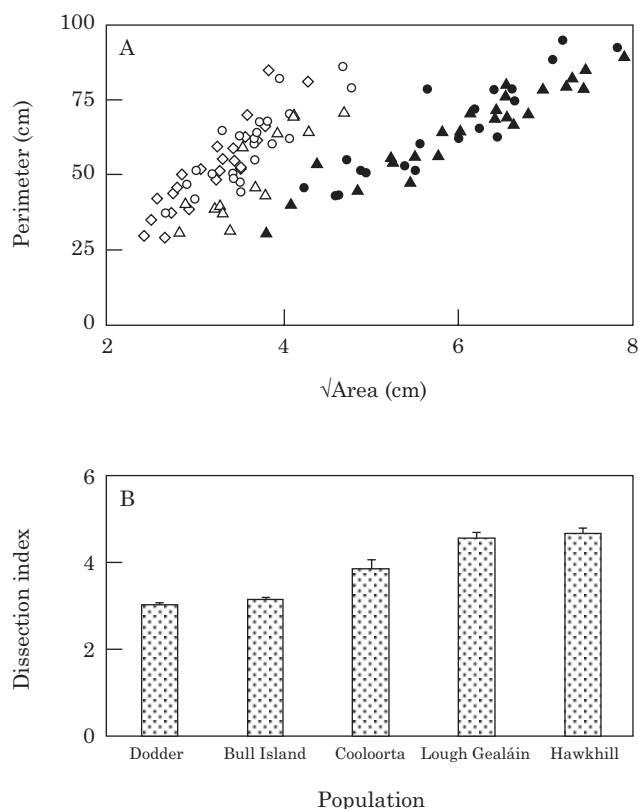


FIG. 3. A, The relationship between the perimeter and $\sqrt{\text{area}}$ in turlough [Cooloorta (△), Lough Gealáin (◇) and Hawkhill (○)] and ruderal [Dodder (▲) and Bull Island (●)] populations of *Ranunculus repens*. B, Dissection index values for the above populations. Values are the means of 25 replicates for Dodder, Hawkhill and Lough Gealáin, 20 for Bull Island and 14 from Cooloorta. Error bars represent the standard errors of the means.

TABLE 4. Dissection index means (\pm s.e.) pooled for habitat type of ruderal (Bull Island and Dodder) and turlough (Lough Gealáin, Hawkhill and Cooloorta) populations of *Ranunculus repens*

Habitat type	Dissection index	Slope	n
Ruderal	3.07 \pm 0.05	13.68	45
Turlough	4.45 \pm 0.09	22.64	64

The slopes were derived from the association between perimeter and $\sqrt{\text{area}}$.

TABLE 5. Bonferroni post hoc summary of the dissection index for the populations and their associated sample sizes displayed in Fig. 3B

Population comparisons	P value	Population comparisons	P value
Cooloorta–Hawkhill	ns	Hawkhill–Dodder	***
Cooloorta–Dodder	***	Hawkhill–Lough Gealáin	ns
Cooloorta–Bull Island	***	Dodder–Bull Island	ns
Cooloorta–Lough Gealáin	ns	Dodder–Lough Gealáin	***
Hawkhill–Bull Island	***	Bull Island–Lough Gealáin	***

***, $P < 0.001$; ns, $P > 0.05$.

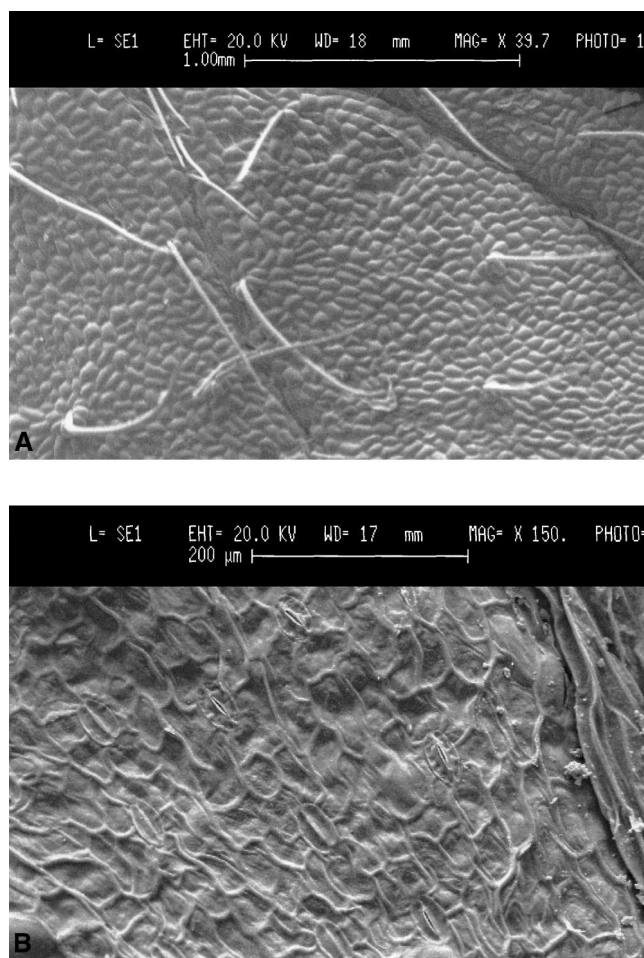


FIG. 4. Scanning electron micrographs of the leaf surfaces of a ruderal (A, Dodder) and turlough (B, Lough Gealain) population of *Ranunculus repens*. Populations were grown from seed in growth room conditions.

(Fig. 4), but were restricted to the tips of leaves of the turlough population, and an amorphous wax coating was evident across both surfaces in this population. The micrographs (Fig. 4) are presented at different magnifications: the lower magnification was applied to the leaf surface of the ruderal population (Fig. 4A) to give an indication of the density of trichomes. As no characteristics were visible at this magnification in the turlough population the magnification was increased (Fig. 4B) to show the presence of the epicuticular waxes which were not obvious at this magnification in the ruderal population.

Changes in leaf dissection along a turlough gradient

The turlough basin sloped downwards for the first six quadrats and then undulated across the basin floor (Fig. 5). The dissection index of the plants sampled in quadrats 1–4 was lower than that of leaves sampled over the rest of the basin (Fig. 5). Leaves from quadrats 5, 7, 8 and 12 had a dissection index intermediate between the leaves sampled in quadrats 1–4 and the leaves from quadrats 6, 9, 10 and 11. When these samples were pooled into the types described

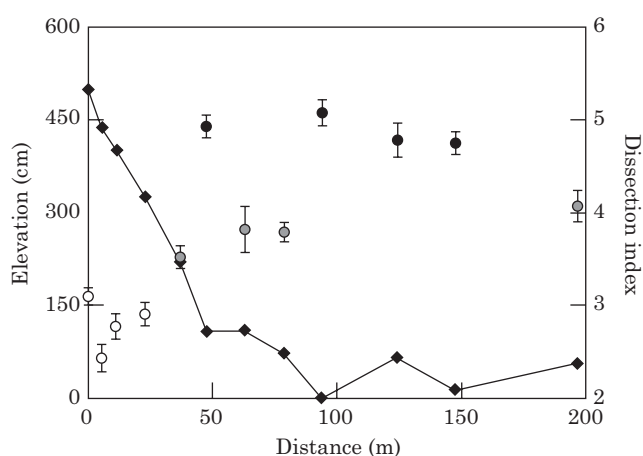


FIG. 5. Changes in the elevation and dissection index of *Ranunculus repens* across a turlough basin. Values for the dissection index are the means of six replicates. Error bars represent the standard errors of the means. ○, Broad-leaved; ●, dissected-leaved; ◆, Elevation.

TABLE 6. Pooled means for broad-, intermediate- and dissected-leaved samples of *Ranunculus repens* that were taken across a turlough basin

Leaf type	Mean \pm s.e.	<i>n</i>
Broad-leaved	2.80 \pm 0.09	24
Intermediate-leaved	3.88 \pm 0.08	23
Dissected-leaved	4.88 \pm 0.07	24

The types were pooled subjectively based on the quadrat means displayed in Fig. 5. *n*, Sample size.

(i.e. broad, intermediate and the more dissected leaves) each individual type was significantly different from the other two types (Bonferroni *post hoc* test $P < 0.0001$, see Table 6 for the type means).

DISCUSSION

Both visual and quantitative results demonstrated that the Lough Gealain turlough population had a more dissected leaf shape than the Dodder ruderal population, and these differences were manifested in cultivation. This difference in dissection was visually evident from the first leaf to be produced, although the difference was too subtle to be detected quantitatively. These differences were due to both populations having similar leaf perimeters, but the turlough population had much smaller leaf areas, therefore the perimeter was much higher relative to area in the turlough population.

Leaves of both populations became increasingly more dissected as the leaflets developed and were subtended on intralaminar petioles, which occurred earlier in the turlough population. The lamina also became more deeply cut with each successively produced leaf in both populations. However, there was a point (leaf 8) at which the change in dissection of the leaves levelled off, suggesting the attainment of an adult mature leaf shape. At this point the area,

perimeter and dissection index plateaued indicating that the leaves had reached their maximum size and developed their adult shape. These parameters are a function of the conditions under which they were produced, as factors such as nutrients (Marino *et al.*, 1997) and light (Dengler, 1980) are known to change leaf dimensions.

Leaves of both populations showed a heteroblastic development of leaf shape i.e. juvenile and adult leaf shapes were strikingly different (Ashby, 1948). Heteroblastic development of leaf shape is common in many plant species and is well documented (e.g. Richards, 1983; McLellan, 1993). Attempts have been made to link changes in the relative timing of development, or heterochrony, with evolutionary changes in morphology which is currently thought to be more complex than simple paedomorphic evolution in several cases (Jones, 1992, 1993). It is possible that the turlough population has, to some extent, speeded up leaf development resulting in the production of a smaller leaf than the ruderal population with a relatively longer perimeter to area relationship.

The mature leaves of three turlough populations all had a consistently more dissected leaf shape than the two ruderal populations. The dissection index was highly heritable in the populations examined, with a narrow sense heritability estimate of 0.72. The possibility of the inflation of the estimate by maternal effects and the effects of dominance cannot be ignored, particularly as the mating system was unknown. Preliminary evidence obtained from reciprocal crosses of a turlough and ruderal population yielded progeny that were somewhat intermediate between the parent types with a slight tendency to resemble the paternal population (Lynn, 1998). A high estimate of narrow sense heritability indicates that the level of leaf dissection of an individual will be passed directly to its offspring and therefore it is susceptible to the moulding influences of natural selection (Stearns, 1993).

Although the density of hair cover of the progeny derived from the heritability investigation was not quantified, the populations could be arbitrarily classified into ruderal populations which all possessed a dense covering of trichomes and turlough populations that were all glabrous except for a few long hairs at the tips of the lobes. These few long hairs may be important for streamlining when the leaves are submerged, particularly in flowing water in the vicinity of swallow holes. A covering of hairs in submerged conditions could be detrimental as it encourages the attachment of algae. The presence of amorphous epicuticular waxes on the surface of the turlough population may act as a waterproofing mechanism in the turlough habitat and may also occlude the stomata to prevent water entry as evident in *Nuphar polysepalum* (Brewer and Smith, 1995).

Changes in the dissection index of leaves of *Ranunculus repens* across the turlough/pastureland boundary reflect changes in the vegetation communities. The broad-leaved form occurred in the dry grassland community, a highly dissected form occurred in the wet grassland community, and an intermediate-leaved form occurred in the damp grassland community. It appears therefore that leaf dissection varies according to susceptibility to inundation.

The absence of any overlap between the areas suggests that high selection pressures are operating against a particular form in a particular area. As the leaves were sampled *in situ*, it is difficult to separate confounding environmental effects from genetic effects. However, recent studies have shown that the differences between the three levels of dissection taken from a transect in a different turlough site are retained under cultivated conditions (Lynn and Waldren, unpubl. res.).

The following theories are proposed to explain the differences in leaf dissection observed within the turlough basin. (1) Increasing leaf dissection has evolved as a response to increasing susceptibility to inundation. (2) The intermediate level of dissection is a result of an earlier production of the less-dissected summer leaves due to an earlier subsidence of water from these plants. (3) The intermediate level of dissection is more phenotypically flexible due to the more unpredictable environment where it occurs. (4) The intermediate level of dissection is a result of gene flow from the nearby broad-leaved populations.

The first theory may explain the evolution of the morphologically distinct turlough populations: directional selection may have produced populations with different optima adapted to the different microsites. However, the assumption must be made that in broad-leaved populations certain genotypes are more tolerant to submergence, or alternatively, a low percentage of more-dissected morphotypes exist in these populations. The only pioneering plants to survive the advancement into the turlough basin are likely to have been those that were more tolerant to submergence, or those that already possessed the features that proved to be adaptive in the submerged environment. The plants that would be at a selective advantage under the submerged conditions would be those that had the ability to plastically respond to submergence by producing a more dissected leaf shape. The genotypes that would have survived in areas of more prolonged submergence would be the ones that had the ability to produce the most dissected leaf shape.

The second theory assumes phenological differences between plants that grow in different parts of the turlough basin as a result of the timing of emergence following subsidence. Hintikka (1975) and Cole (1977) commented on the production of a more dissected leaf of *Ranunculus repens* early in the growing season. Clearly it would be a disadvantage to the turlough population to develop a less dissected leaf unless the possibility of summer flooding was eliminated. Another theory of the evolution of the more dissected leaf arises from these differences between early summer and winter leaves: genotypes more tolerant to submergence may have retained the more dissected early summer leaves all year round.

The third theory assumes that the intermediate-leaved population produces a less dissected leaf shape following subsidence or, alternatively, a more dissected leaf following submergence. Cook and Johnson (1968) reported a greater difference in submerged and aerial leaf shape in populations of *Ranunculus flammula* that occur in more unpredictable

habitats than populations from predictable habitats, i.e. from either terrestrial or aquatic habitats.

The fourth gene flow theory has two main problems: firstly, unlike the Park Grass Experiments (Snaydon, 1970; Davies and Snaydon, 1973a, b, c), gene flow is enormously restricted by heavy grazing, resulting in few flowers surviving to set seed. This factor, together with the low recruitment of seedlings of *R. repens* to a population (Sarukhán and Harper, 1973; Lovett Doust, 1981), would severely limit gene flow. However, these factors do not rule out gene flow effects ever having occurred as land usage may have changed in the past. Secondly, the presence of the potential hybrid population appears to have the ability to outcompete the dissected form in the more unpredictable areas. Studies by Briggs (1962) on the *Ranunculus lappaceus* group did, however, report that hybrids between types were restricted to narrow strips of habitat between the parents where neither of the parent populations occurred.

Adaptation to particular environmental conditions can occur over a relatively short space of time (McNeilly, 1968; McNeilly and Antonovics, 1968; Snaydon, 1970; Davies and Snaydon, 1973a, b, c), providing genes of an adaptive nature are present in the founding population. Without this variation the population will not be able to evolve under the influence of natural selection (Bradshaw, 1991). More dissected forms of *R. repens* have been observed in habitats not likely to experience submergence, such as in a fallow field (Riddelsdell, 1916) and in more cultivated areas of a forest ecosystem (Hintikka, 1975). Therefore, genetic variation for this characteristic appears to be present in ruderal populations of *Ranunculus repens*. Baker (1965) commented that highly successful weeds are likely to have been selected for a general purpose genotype which provides each individual plant with pre-adaptation to a range of environments.

In conclusion, selection pressures which are in operation within the turlough basin have resulted in the evolution of a dissected-leaved form of *Ranunculus repens*. Increased dissection is related to the increased susceptibility to submergence; therefore it can be assumed that the dissected-leaved form is an adaptive trait that enhances survival in the unpredictable environment of the turlough habitat.

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