Phenotypic plasticity of *Elodea nuttallii* (Planch.) H. St John and *Elodea canadensis* Michx in the British Isles

D. A. SIMPSON

Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB

ABSTRACT

Elodea nuttallii (Planch.) H. St John and *E. canadensis* Michx show a wide range of morphological variation, a feature which has caused many problems of identification. In the British Isles variation within the two species is entirely due to phenotypic plasticity. The features which most obviously demonstrate plasticity are leaf shape, leaf size, leaf posture, internode length and plant colour. Some of these have been incorrectly used in the past as diagnostic characters. The range of variation in these features is described. Field studies are reported which examine the variation of material in two different localities during the growing season, and cultivation experiments are described in which material from one genotype of each species was grown under a variety of environmental conditions. Possible factors influencing plasticity are discussed.

INTRODUCTION

Three species of the genus *Elodea* Michx occur in the British Isles, namely *E. canadensis* Michx, *E. nuttallii* (Planch.) H. St John and *E. callitrichoides* (Rich.) Casp. All are adventive in the British Isles and are native to the New World.

E. nuttallii and *E. canadensis* show a wide range of morphological variation, even though only a few genotypes of each species occur in the British Isles (Cook & Urmi-König 1985). This has caused many problems of identification, and such problems were particularly evident in Great Britain during the 1960s and 1970s, a period coinciding with the introduction and spread of *E. nuttallii*. This species, first reported from Oxford in 1966 (Simpson 1984), became widespread during the following ten years and its range of variation was great enough to suggest the possibility of two or even three new taxa being present. In addition some material could have been a hybrid between the two species. It was known that in America *E. canadensis* and *E. nuttallii* readily hybridize with each other (Ernst-Schwarzenbach 1945a, 1945b; Cook & Urmi-König 1985), a feature which probably accounts for some of the variation in American specimens (Cook & Urmi-König 1985), and could also have applied to British and Irish material. It was also suggested that material assigned to *E. nuttallii* was merely a phenotype of *E. canadensis* which had appeared as a response to changing environmental conditions, particularly the increasing eutrophication of water bodies (S. Haslam, pers. comm.; Harding 1979).

However, in my recent investigation of *Elodea* in the British Isles (Simpson 1983), it was concluded that *E. canadensis* and *E. nuttallii* are two distinct species, which cannot hybridize because only female plants are present. It was also shown that both species exhibit a wide range of phenotypic plasticity, which would explain the problems of identification. Aspects of phenotypic plasticity in Japanese material of *E. nuttallii* have been examined by Kunii (1982, 1984) who concentrated particularly on growth and phenology. In this paper I describe the range of phenotypic plasticity shown by British material of *E. nuttallii* and *E. canadensis*, with particular emphasis on features of taxonomic interest, such as leaf shape and size. I also report field and laboratory studies which were carried out (i) to demonstrate the range of phenotypic plasticity in the species in two localities over the growing season, (ii) to examine the effect of differing environmental conditions on their plasticity, and (iii) to determine whether the two species adopt a similar morphology under certain conditions. Possible factors which influence their plasticity are also discussed.

MATERIALS AND METHODS

INITIAL OBSERVATIONS

Before carrying out experimental work it was necessary to identify which parts of the plant were showing phenotypic variation. This was done by examining a range of living and herbarium material from a variety of different habitats. A full list of the latter is kept in LANC and a list of the herbaria consulted is given in Simpson (1986).

FIELD OBSERVATIONS

Field observations were made predominantly on *E. nuttallii*. The aim was to record the phenotypic plasticity of plants at four different depths on four dates during the growing season. Two contrasting sites were chosen, one in a shallow section of the R. Lune at Skerton, Lancaster, Lancs., v.c. 60, and the other in deeper water at Mitchell Wyke Bay, Windermere, Westmorland, v.c. 69. Whole plants were taken from 0·5–1 m depth in the R. Lune and 2–3 m depth in Mitchell Wyke Bay. Observations were made on the uppermost stems of these plants, which were gathered on 25 April, 15 June, 18 August and 23 September 1981. On 23 September, material of *E. canadensis* was collected for comparison. In this case the plants were taken from the Lancaster to Kendal canal at Burton-in-Kendal, Westmorland, v.c. 69, as well as from Mitchell Wyke Bay. Light intensity was measured at both sites in terms of quantum flux density. Measurements were made at the depths of the uppermost stems with a 'Lambda' quantum sensor adapted for underwater use. Light intensities received by the uppermost stems of the plants varied from nearly 100% of the surface intensity for plants at 0·5 m in the R. Lune and the Lancaster-Kendal Canal (i.e. the uppermost stems were at or near the surface), to only 8% for plants at 3 m depth in Windermere. In all cases ten plants from each depth were collected and pressed. Leaf shape, leaf posture and plant colour were noted. Measurements were made of leaf length, leaf width at the mid-point and internode length. Length and width of five cells in each leaf were also measured from plants at 0·5 m in the R. Lune, and at 2 and 3 m in Mitchell Wyke Bay. All leaf data were taken from the verticillate leaves only.

During the latter part of the fieldwork a simple transplant experiment was carried out, in which material was transferred from shallow to deep water. Ten stem apices each 10 cm long from one genotype of each species were planted in sand/gravel in plastic containers. One container of each species was then placed at 2, 3 and 4 m depths in Mitchell Wyke Bay and grown for 35 days between 18 August and 23 September 1981. The plants were obtained from c.0·5 m depth in the R. Lune (*E. nuttallii*) and the Lancaster-Kendal Canal, Burton-in-Kendal (*E. canadensis*). Plants growing at these localities were examined during the course of the experiment for comparison. The characters listed above were recorded from growth which had taken place during the 35 day period.

CULTIVATION EXPERIMENTS

Three simple laboratory experiments were carried out in which material representing one genotype of each species was subjected to a variety of environmental conditions. The apparatus for each experiment was similar, consisting of polypropylene bins filled with nutrient-poor sand/gravel or nutrient-rich river sediment and tap water. The experiments were as follows.

Plants of both species were grown for 35 days under low, medium or high light intensities (2, 35 and 250 μmol m^{-2} s^{-1}) in either sand/gravel or river sediment at c.19°C. Reduced light intensity was achieved by shading the bins with neutral density filters. Light intensities were chosen to reproduce, as near as possible, those in the two habitats during August and September.

E. nuttallii was grown for 30 days at high light intensity (250 μmol m^{-2}s^{-1}) in sand/gravel or river sediment at a raised water temperature of c.27°C.

Plants of both species were grown for 30 days in sand/gravel with different levels of water nutrient enrichment. This was achieved by adding 'Phostrogen' 10:10:27 N:P:K fertiliser in three different concentrations.

Ten stem apices 10 cm long were used in each treatment. These were obtained from the same source as material used in the transplant experiment. All observations were made on growth which had taken place during the course of the experiment. Again, material growing at the two sources was examined during the experiment for comparison. In the first two experiments observations

were made on the same characters as those examined in the field work. In the third experiment leaf shape, leaf apex shape, leaf width c.0·5 mm below the apex and plant colour were recorded. Leaf data were again taken from the verticillate leaves. Voucher material of all field and experimental work is in **LANC**.

<div align="center">RESULTS</div>

RANGE OF PHENOTYPIC PLASTICITY IN *E. CANADENSIS* AND *E. NUTTALLII*

Phenotypic plasticity in both species is seen in the vegetative parts of the plant. The characters which most obviously demonstrate plasticity are: leaf shape, leaf size, leaf posture, internode length and plant colour.

Leaf shape has often been used as a diagnostic character for separating *Elodea* species, although in many cases it has been inadequately described (cf. St John 1965). It is most variable in *E. canadensis*, in which the leaves range from ovate to linear-oblong and occasionally linear-lanceolate. In *E. nuttallii* the leaves are either linear or linear-lanceolate. Of particular taxonomic importance is the shape of the leaf apex, which is broadly acute to obtuse in *E. canadensis* and narrowly acute to acuminate in *E. nuttallii*. This discontinuity is an important character for separating the two species.

Leaf length and mid-point width are highly variable in both species. The greatest variation of leaf length is seen in *E. nuttallii*, in which the leaves may be up to 35 mm long. However, mid-point width varies most in *E. canadensis* (Table 1). In many cases the leaves of *E. nuttallii* are longer and narrower than those of *E. canadensis*, although there is a wide range of overlap between them. Such overlap makes these characters of little use in separating the two species. However, leaf size does yield one taxonomically important feature, namely the width of the leaf measured at a point c.0·5 mm below the apex. This is usually greater in *E. canadensis* and reflects differences shown by the shape of the leaf apex. It is the most reliable character for separating this species from *E. nuttallii*.

Six types of leaf posture may be recognised in *Elodea*, ranging from patent to strongly recurved (Simpson 1986). *E. canadensis* has only three of the types, its leaves being patent, slightly recurved or spreading. *E. nuttallii* has six types, the most frequent being those seen in *E. canadensis*. However in *E. nuttallii* at least some leaves are strongly recurved, with their apices touching the stem. This type of leaf posture is diagnostic for *E. nuttallii*.

In both species the internodes become shorter towards the apex. However internode length at any given point along the stem is highly variable, and this appears to be closely associated with variation in leaf size. Thus plants with the longest, narrowest leaves also have the longest internodes and vice-versa. The greatest range of variation is seen in *E. nuttallii*, which can have internodes up to 20 mm long (Table 1).

Plant colour has often been used as a diagnostic character, with *E. canadensis* being described as dark green and *E. nuttallii* as light green or greenish brown. However, colour variation bears little relation to species differences and seems to be dependent on light intensity and/or nutrient status of the water or substrate.

FIELD OBSERVATIONS

The morphology of *E. nuttallii* in the R. Lune was similar at both depths on 25 April, the plants having short, broad, strongly recurved, linear-lanceolate, mid- to dark green leaves and short internodes. As the season progressed the leaves adopted a spreading posture, together with an

TABLE 1. RANGE OF LEAF SIZE AND INTERNODE LENGTH IN *ELODEA CANADENSIS* AND *ELODEA NUTTALLII*

Character	*E. canadensis*	*E. nuttallii*
Leaf length (mm)	4.5–17.0	
Leaf mid-point width (mm)	1.4–5.6	
Internode length (mm)	0.5–9.1	

increase, followed later by a decrease, in leaf mid-point width (Figs 1 & 2). The internodes remained short.

In Windermere the seasonal pattern was different, particularly at 2 m. Plants from both 2 m and 3 m started off the season with a morphology similar to those in the R. Lune, but by 15 June there was an increase in leaf length and mid-point width. At 2 m there was a continued increase in leaf length, coupled with a decrease in mid-point width, so that by 18 August the plants had long, spreading, linear, light green leaves and long internodes. At the same time plants at 3 m adopted a morphology which was intermediate between that at the start of the season and the plants at 2 m as described above. The overall pattern was more or less the same on 23 September. None of the Windermere plants elongated sufficiently to reach the surface of the water.

The differences in external morphology were usually reflected by differences in leaf cell size (Table 2). The cells of plants from 0·5 and 1 m in the R. Lune were generally longer and broader than those of the 2 m plants from Windermere. In plants at 3 m there was no definite pattern in cell size, except that cell width was greater than in plants at 2 m.

E. canadensis showed a similar variation pattern to *E. nuttallii* on 23 September both in external morphology and cell size, although the range of variation was not as wide as in *E. nuttallii* (Fig. 2; Tables 2 & 3). The longest, narrowest leaved plants were again found at a depth of 2 m. Material from the canal was dark green, whilst that in Windermere was mid-green.

In the transplant experiment, the containers at 3 m were vandalised and no result was obtained. At 4 m none of the plants survived. This was probably due to their being below the lower depth limit for the growth of the two species. At 2 m a number of changes were noted (Fig. 3). At the start of the transplant experiment, material of *E. nuttallii* had short, broad, mostly recurved, mid-green leaves and short internodes. After 35 days the plants became similar to wild material at the same depth, having long, narrow, spreading, light green leaves. A similar transition to longer and somewhat narrower leaved material was also noted in *E. canadensis*, and again, the transplanted material became similar to wild material growing at the same depth. In *E. nuttallii* internode length showed little change, whereas in *E. canadensis* it was shorter on the new growth. It is likely that the experimental period was not long enough to allow the internodes to develop fully.

TABLE 2. CELL SIZE IN UPPER STEM LEAVES TAKEN FROM WHOLE PLANTS OF *ELODEA NUTTALLII* AND *ELODEA CANADENSIS* ON 23 SEPTEMBER 1981 (MEAN±S.E.)

Measurement (µm)	Depth of plant (m)		
	0.5	2.0	3.0
E. nuttallii			
Cell length	93.20±2.72	75.73±2.12	67.60±3.20
Cell width	36.80±0.80	26.40±0.56	35.20±0.50
E. canadensis			
Cell length	109.20±3.71	79.84±3.13	76.00±2.73
Cell width	46.88±0.76	15.10±0.45	38.80±1.47

TABLE 3. COMPARISON BETWEEN THREE MORPHOLOGICAL CHARACTERS OF *ELODEA CANADENSIS* ON 23 SEPTEMBER 1981 (MEAN±S.E.)

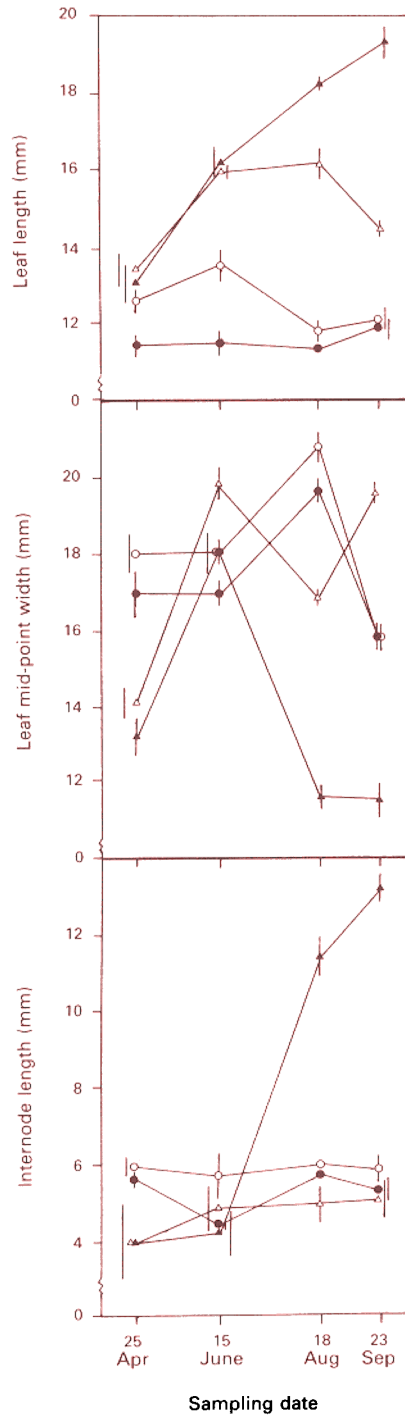|	Site and depth of plant (m)			
	Burton-in-Kendal		Windermere	
	0.5	1.0		3.0
Leaf length (mm)	7.8±0.1	8.0±0.1	14.1±0.4	6.8±0.1
Leaf mid-point width (mm)	2.9±0.03	2.0±0.03	2.0±0.06	3.3±0.1
Internode length (mm)	9.1±0.3	8.6±0.2	10.5±0.3	5.6±0.3

FIGURE 1. Variation in *E. nuttallii* of three morphological characters in relation to sampling date and depth. Points are means of 50 measurements. Bars indicate ± standard error. ● = 0·5 m R. Lune, ○ = 1 m R. Lune, ▲ = 2 m Mitchell Wyke Bay, △ = 3 m Mitchell Wyke Bay.
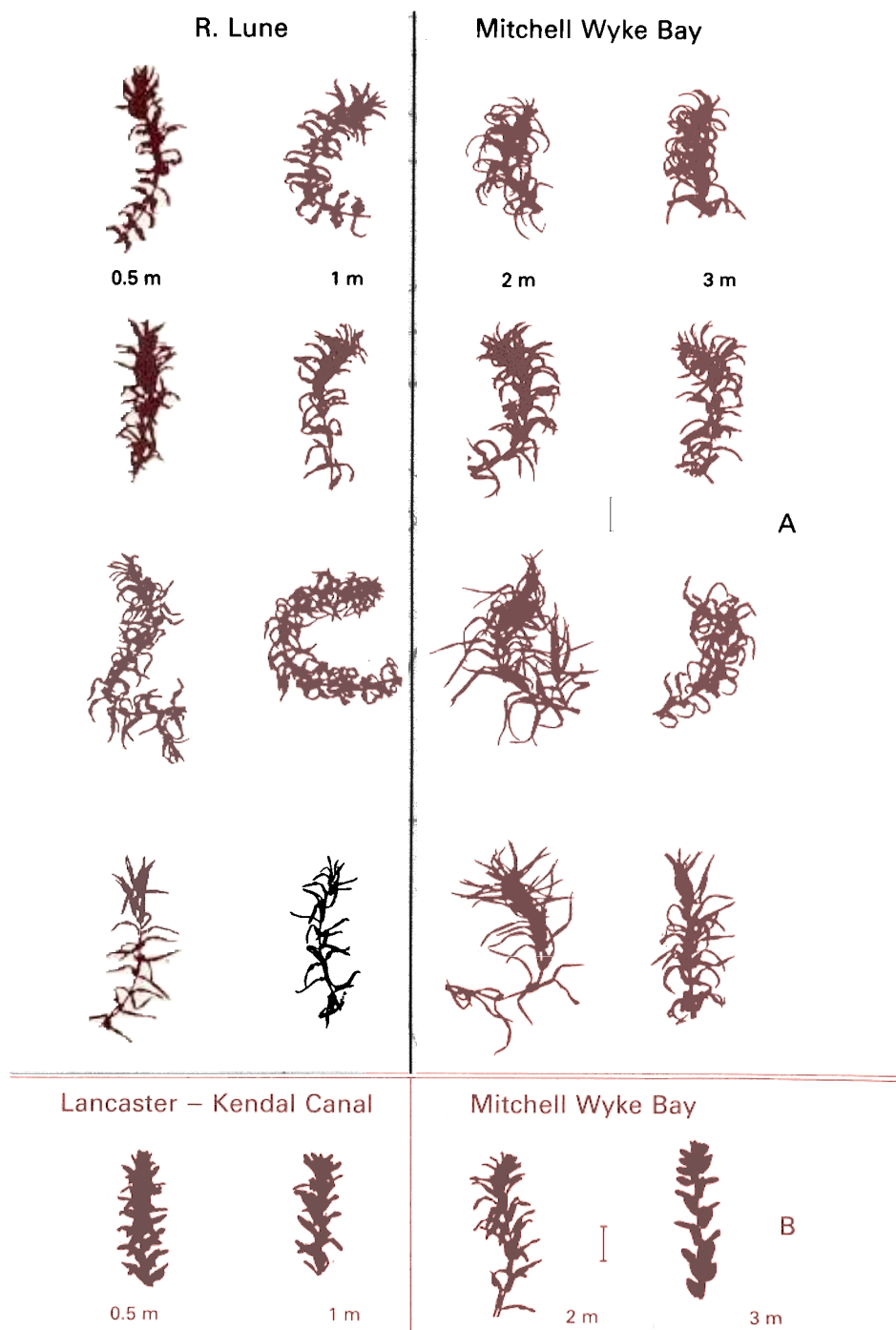
FIGURE 2. A: Silhouettes of upper stems from whole plants of *Elodea nuttallii* collected in relation to sampling date and depth; B: Silhouettes of upper stems from whole plants of *Elodea canadensis* collected on 23 September in relation to depth. Scale bar = 10 mm.
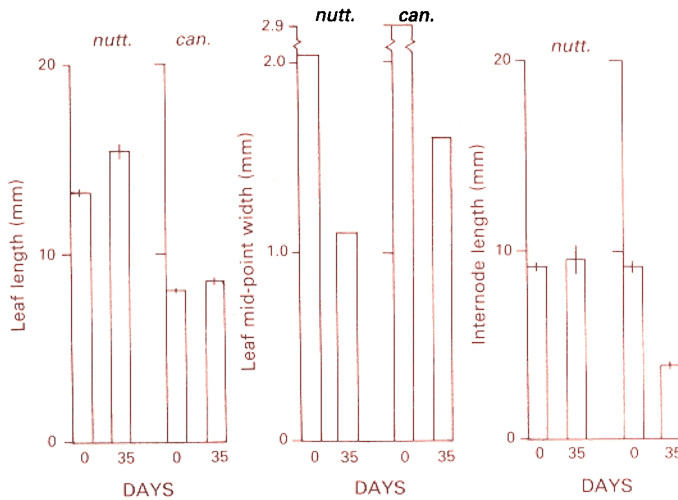
FIGURE 3. Changes in three morphological characters of *Elodea nuttallii* and *Elodea canadensis* 35 days after transplanting into Mitchell Wyke Bay. Columns are means of 20 measurements. Bars = ± standard error.

CULTIVATION EXPERIMENTS

At the start of all the cultivation experiments material of both species was identical in morphology to that at the beginning of the transplant experiment. After 35 days in nutrient-poor sand/gravel at 19°C, *E. nuttallii* showed an overall increase in leaf length, together with a decrease in mid-point width and internode length (Fig. 4). However, the overall variation pattern was similar to that seen in wild material on 18 August. In particular, material grown at the medium light intensity had similar characteristics to the plants at 2 m from Windermere, with long, narrow, spreading leaves. *E. canadensis* grown under the same conditions had a similar pattern of variation, with the most noticeable changes occurring at the middle light intensity. In this species the widest range of variation was noted in leaf mid-point width.

When grown in nutrient-rich river sediment, plants of both species under the low and medium light intensities showed a similar variation pattern to those grown in nutrient-poor sediment under equivalent lighting conditions. However, at high light intensity, light transmission below water level was reduced due to excessive phytoplankton growth. Plants grown under these conditions were similar to those at the medium light intensity.

Under conditions of raised water temperature, the responses shown by *E. nuttallii* varied with the type of substrate (Fig. 5). In both cases the plants developed linear, spreading leaves. However, plants in nutrient-poor substrate had shorter leaves and internodes. Incidental observations of *E. canadensis* under similar conditions indicated that it developed short and markedly narrow, linear-oblong or rarely linear-lanceolate leaves.

Plants grown in nutrient-poor sand/gravel at medium and high levels of water-nutrient enrichment showed some of the detrimental effects of such enrichment, including loss of leaves on the lower part of the stem. After 30 days the morphology of both species was similar to corresponding material grown under raised temperature and high light intensity conditions (Table 4). These forms developed at all levels of water-nutrient enrichment.

DISCUSSION

A wide range of phenotypic plasticity is characteristic of many aquatic taxa and this has caused numerous taxonomic difficulties within such groups. A notable example is that of *Ranunculus* L. subgen. *Batrachium* (DC.) A. Gray, in which Cook (1966) found a total of 302 possible names for the 17 species that he recognised. In *Elodea*, St John (1965) delimited 17 species of which ten were
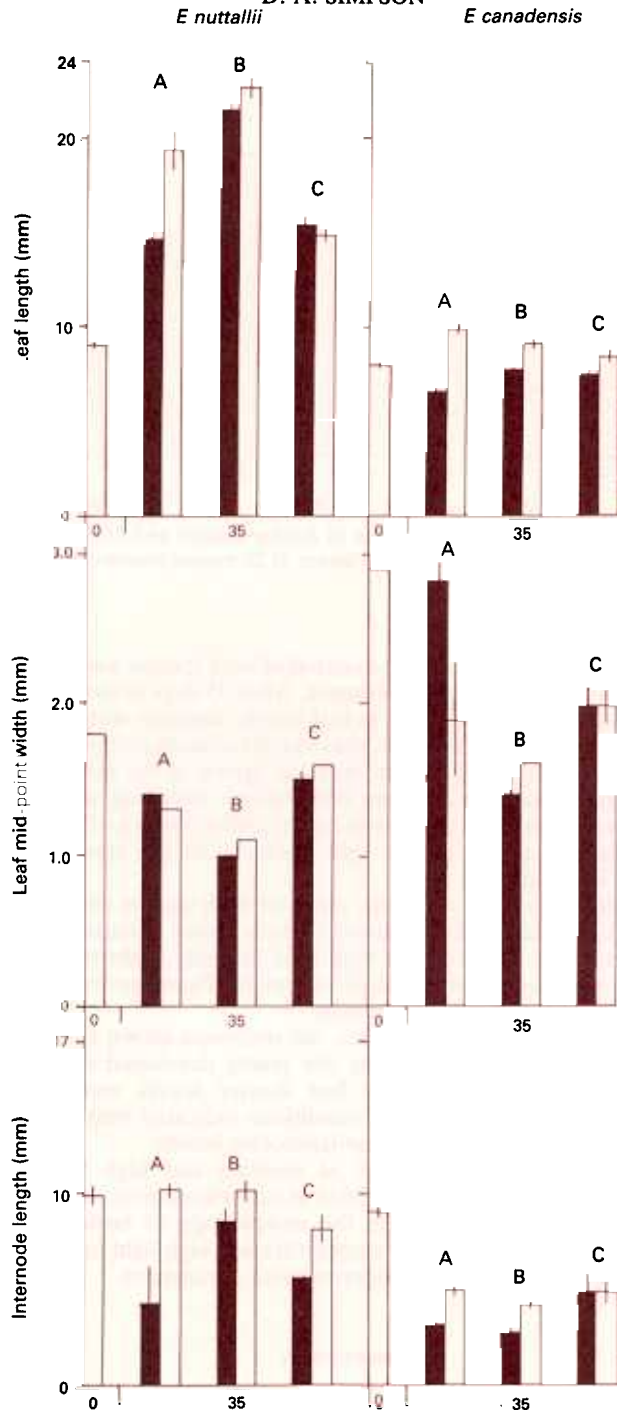
D. A. SIMPSON

FIGURE 4. Changes in three morphological characters of *Elodea nuttallii* and *Elodea canadensis* after 0 and 35 days growth in differing light intensities in nutrient-poor and -rich substrates. A: high light intensity; B: medium light intensity; C: low light intensity. Shaded columns = nutrient-poor substrate, unshaded columns = nutrient-rich substrate. Columns are means of 20 measurements. Bars = ± standard error.
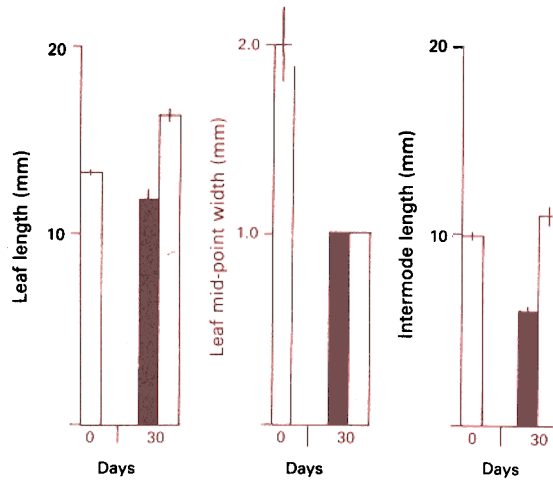
FIGURE 5. Changes in the morphology of *Elodea nuttallii* after 0 and 35 days growth at high light intensity at raised water temperature in nutrient-poor and -rich substrates. Shaded columns = nutrient-poor substrate, unshaded columns = nutrient-rich substrate. Columns are means of 20 measurements. Bars = ± standard error.

newly described. Unfortunately he based his work purely on herbarium material, which restricted his interpretation of the range of phenotypic plasticity. However, this is taken into account in the revision of Cook & Urmi-König (1985) who reduced the number of species to five.

From the present work it is apparent that *E. nuttallii* is the most variable of the species in the British Isles, particularly in leaf size and internode length. The variation is such that the two extremes of its morphological range have the appearance of distinct taxa, one with long, narrow, spreading leaves, the other with shorter, broader, strongly reflexed leaves. Narrow-leaved material, such as that seen in the Cumbrian lakes, is almost indistinguishable from *E. callitrichoides*, and microscopic characters, such as the length of the teeth on the leaf margins, are needed to separate them vegetatively. Furthermore, in the British Isles *E. nuttallii* has been confused with species in closely related genera, such as *Hydrilla verticillata* (L.f.) Royle and *Lagarosiphon major* (Ridley) Moss. Indeed for many years British and Irish material of the former was treated as being conspecific with *E. nuttallii* (Tutin 1962; Scannell & Webb 1976). However close observation shows that the two extremes of variation often occur on the same plant. These represent responses to environmental conditions which prevail during the growth of a given part of

TABLE 4. LEAF MORPHOLOGY OF *ELODEA NUTTALLII* AND *ELODEA CANADENSIS* AFTER 30 DAYS GROWTH AT THREE LEVELS OF WATER NUTRIENT ENRICHMENT (MEAN±S.E.)

		Concentration of added nutrient (mg/l)		
	Nutrient	Low	Medium	High
	N	0.025	0.05	0.10
	P	0.022	0.044	0.088
Character	K	0.055	0.11	0.22
E. nuttallii				
Leaf shape		linear	linear	linear
Leaf apex shape		acuminate	acuminate	acuminate
Leaf width 0.5 mm below apex (mm)		0.4±0.02	0.5±0.03	0.4±0.03
E. canadensis				
Leaf shape		linear-oblong	linear-oblong	linear-oblong
Leaf apex shape		broadly acute	broadly acute	broadly acute
Leaf width 0.5 mm below apex (mm)		1.1±0.03	1.0±0.04	1.0±0.03

the plant. Unfortunately such differences are rarely detected on herbarium specimens since only small sections of the plant are usually collected. This has undoubtedly emphasised the taxonomic difficulties associated with *E. nuttallii*, and indicates the need to have living material for identification wherever possible.

E. canadensis has a narrower range of variation than *E. nuttallii* except in leaf shape, and has not usually been confused with other species in related genera. Nevertheless, problems have sometimes arisen in distinguishing *E. nuttallii* from *E. canadensis*. In North America, where hybridization occurs, this would be expected. However in the British Isles, where hybridization cannot take place, such problems have come about because knowledge of the characters separating the two species was inadequate.

As indicated earlier, it has also been suggested that *E. nuttallii* is merely a phenotype of *E. canadensis*. In relation to this, three points should be made about the comparative variation of the two species and their distinctness under differing environments. Firstly, both species respond in a broadly similar manner to varying environmental conditions. This is exemplified by wild material from different depths late in the growing season. Thus in both species the leaves tend to be shorter and broader in shallow water, longer and narrower in deeper water and intermediate between these phenotypes at the deepest levels. The two species also show similar variation in leaf anatomy. Secondly, the wider range of plastic response shown by *E. nuttallii* is demonstrated in the field by the differences between this species and *E. canadensis* on 23 September, and experimentally by the variation they show in relation to light intensity. From this the third, and taxonomically important, point is that when the responses of the two species to each environmental factor are compared, both *E. canadensis* and *E. nuttallii* maintain distinct morphological facies. These facies are based on a combination of leaf shape, leaf apex shape and leaf width c.0·5 mm below the apex-tip (Table 5), and represent a clear morphological discontinuity between *E. canadensis* and *E. nuttallii*. There is, therefore, no justification for treating *E. nuttallii* as conspecific with *E. canadensis*.

Of the environmental factors influencing phenotypic plasticity of aquatic macrophytes, light is probably the most significant, particularly in terms of intensity. There is a sharp contrast in light intensity between shallow and deep water, and the underwater light climate is characteristically one of deep shade (Spence 1981, 1982). This has a marked effect on plasticity, and the adaptations of terrestrial plants to sun and shade conditions are well known. Similar adaptations are shown by aquatic macrophytes (Spence & Chrystal 1970a, b; Spence 1982). Temperature may also be important and, in common with light, varies according to the time of year and depth of water. It is also interactive with light, and responses to the two factors may be impossible to separate (Barko *et al*. 1982). Other factors which might have an influence include light quality, photoperiodism, nutrients and ontogenetic drift.

The limited amount of literature on factors influencing phenotypic plasticity in *Elodea* suggests that light, temperature, substrate and water nutrients are involved (Adams *et al*. 1971; Spence &

TABLE 5. COMPARISON OF LEAF WIDTHS 0.5 MM BELOW THE APEX OF *ELODEA NUTTALLII* AND *ELODEA CANADENSIS* UNDER VARYING ENVIRONMENTAL CONDITIONS (MEAN±S.E.)

	Mean width 0.5 mm below apex (mm)	
Environmental variable	*E. nuttallii*	*E. canadensis*
a. Depth (m) 23 September		
0.5	0.6±0.02	1.0±0.03
1.0	0.6±0.02	1.0±0.03
2.0	0.4±0.01	0.8±0.01
3.0	0.6±0.02	1.2±0.03
b. Differing light intensities, nutrient-poor substrate		
High	0.4±0.05	1.8±0.16
Medium	0.3±0.03	0.8±0.04
Low	0.5±0.03	0.9±0.02
c. Differing light intensities, nutrient-rich substrate		
High	0.3±0.04	1.0±0.03
Medium	0.2±0.02	0.8±0.01
Low	0.4±0.02	0.9±0.06

Dale 1978; Swann 1978; Barko et al. 1982). What might be deduced from previous and present work about their effect on plasticity in E. nuttallii and E. canadensis? Of the four factors, substrate probably has the least influence, although plants grown experimentally in nutrient-poor and nutrient-rich substrates do show slight variation. In the case of water nutrients, studies by Adams et al. (1971) of E. canadensis growing in a variety of habitats indicated that with increasing water nutrient enrichment, the species showed increases in leaf length and internode length, together with decreases in leaf mid-point width. Unfortunately no account was taken of variation in the light and temperature conditions of these habitats. In addition, the present work suggests that, when in cultivation under the same light and temperature regime, there is little response to water nutrient enrichment in either species. Although slight organic pollution of the water occurred at both sampling sites, comparison with equivalent pollution-free sites showed that a similar pattern of variation was taking place in both species during the growing season.

From both the literature and the present work it is clear that both species react markedly to varying light intensity and temperature. For example Spence & Dale (1978) noted a general increase in internode length of E. canadensis with increasing temperatures at low light intensities, whereas there is a decrease with increasing light intensities at all temperatures. Barko et al. (1982) indicated a similar relationship by showing that stem length increases with increasing temperature up to 28°C. Lawrence (1976) noted a decrease in leaf width in E. canadensis maintained at a mean temperature of 25·6°C, while Swann (1978) observed that E. canadensis plants in a static water tank growing in temperatures fluctuating between 22 and 30°C showed a 25% decrease in leaf length. Barko et al. (1982) concluded that E. canadensis is most responsive to differences in light when at optimum temperature levels and vice versa. In the present work, E. nuttallii and E. canadensis grown in the same substrate under differing light intensities at 19°C showed variation somewhat similar to that of wild plants in August and September, particularly in leaf shape and size. The light and temperature regimes in these experiments were designed, within the limits of the equipment available, to reproduce conditions equivalent to that of the sampling sites in late August or September. Therefore it is likely that the phenotypic plasticity shown by the two species is in response to variation in light and temperature.

The effects of these two factors might be as follows: except at the lowest light intensity, an interaction between the two factors produces longer, narrower leaves and longer internodes. At the highest light intensity, a high temperature (c.27°C and above) is required to produce the longer, narrower-leaved form, but as the light intensity decreases the optimum temperature similarly decreases. Such high temperatures are rarely experienced by plants in the British Isles. Therefore material receiving the highest light intensity will usually have short, broad, mid- or dark green leaves and short internodes. Where light intensity is reduced, ideal conditions will occur for the production of long, narrow, light green leaves and longer internodes. Thus the shorter, broader-leaved phenotype typically occurs when the plants are close to the water surface, whereas the long, narrow-leaved phenotype occurs in deeper water. The latter may also be present near the surface when light intensity is reduced due to shading or turbidity of the water.

The phenotypes described above demonstrate obvious adaptations to sun and shade conditions. However, a problem arises in relation to material growing at the lowest light intensities in deep water, such as that found at 3 m in Windermere. It appears that at the lowest light intensity, plants show characters which are intermediate between the short, broad-leaved and long, narrow-leaved phenotypes. This suggests that another environmental factor, not previously considered, might be involved. One such factor is pressure. It has been argued that pressure may limit the depth distribution of aquatic macrophytes (Gessner 1952), although this has been disputed (Bodkin et al. 1980; Spence 1982). However it is possible that morphological and anatomical adaptations might occur which combine extra rigidity with the need to maintain leaves capable of utilising low light intensity in an efficient manner. This may be worthy of further investigation.

REFERENCES

ADAMS, F. S., MACKENZIE, D. R., COLE, H., & PRICE, M. W. (1971). The influence of nutrient pollution levels upon element constitution and morphology of *Elodea canadensis* Rich. in Michx. *Environ. Pollut.*, **1**: 285–298.

BARKO, J. W., HARDIN, D. G. & MATTHEWS, M. S. (1982). Growth and morphology of submerged macrophytes in relation to light and temperature. *Can. J. Bot.*, **60**: 877–887.

BODKIN, P. C., POLUSZNY, V., & DALE, H. M. (1980). Light and pressure in two freshwater lakes and their influence on the growth, morphology and depth limits of *Hippuris vulgaris*. *Freshwater Biol.*, **10**: 545–552.

COOK, C. D. K. (1966). A monographic study of *Ranunculus* (L.) subgen. *Batrachium* (DC.) A. Gray. *Mitt. Bot. StSamml. Münch.*, **6**: 47–237.

COOK, C. D. K., & URMI-KÖNIG, K. (1985). A revision of the genus *Elodea* (Hydrocharitaceae). *Aquat. Bot.*, **21**: 111–156.

ERNST-SCHWARZENBACH, M. (1945a). Zur Blütenbiologie einiger Hydrocharitaceen. *Ber. schweiz. bot. Ges.*, **55**: 33–69.

ERNST-SCHWARZENBACH, M. (1945b). Kreuzungsversuche an Hydrocharitaceen. *Arch. Julius Klaus-Stift. Vererbforsch.*, **20**: 22–41.

GESSNER, F. (1952). Der Druck in seiner Bedeutung für das Wachstum submerser Wasserpflanzen. *Planta*, **40**: 391–397.

HARDING, J. P. C. (1979). River macrophytes of the Mersey and Ribble basins. *Tech. Rept. North-West Water Authority*, no. TS–BS–79–1.

KUNII, H. (1982). *Biology of* Elodea nuttallii *(Planch.) St John with special reference to its growth*. Ph.D thesis, Tokyo Metropolitan University.

KUNII, H. (1984). Seasonal growth and profile structure development of *Elodea nuttallii* (Planch.) St John in Pond Ojaga-Ike, Japan. *Aquat. Bot.*, **18**: 239–247.

LAWRENCE, D. K. (1976). Morphological variation of *Elodea* in western Massachusetts: field and laboratory studies. *Rhodora*, **78**: 739–749.

ST JOHN, H. (1965). Monograph of the genus *Elodea*: summary. *Rhodora*, **67**: 155–181.

SCANNELL, M. J. P. & WEBB, D. A. (1976). The identity of the Renvyle *Hydrilla*. *Ir. Nat. J.*, **18**: 327–331.

SIMPSON, D. A. (1983). *Experimental taxonomic studies of* Elodea Michx *in the British Isles*. Ph.D. thesis, University of Lancaster.

SIMPSON, D. A. (1984). A short history of the introduction and spread of *Elodea* in the British Isles. *Watsonia*, **15**: 1–9.

SIMPSON, D. A. (1986). Taxonomy of *Elodea* Michx in the British Isles. *Watsonia*, **16**: 1–14.

SPENCE, D. H. N. (1981). Light quality and plant responses underwater, in SMITH, H., ed. *Plants and the daylight spectrum*, pp. 245–275. London.

SPENCE, D. H. N. (1982). The zonation of plants in freshwater lakes. *Adv. Ecol. Res.*, **12**: 37–124.

SPENCE, D. H. N., & CHRYSTAL, J. (1970a). Photosynthesis and zonation of freshwater macrophytes, I: depth distribution and shade tolerance. *New Phytol.*, **69**: 205–215.

SPENCE, D. H. N. & CHRYSTAL, J. (1970b). Photosynthesis and zonation of freshwater macrophytes, II: adaptability of species to deep and shallow water. *New Phytol.*, **69**: 217–227.

SPENCE, D. H. N. & DALE, H. M. (1978). Variations in the shallow water form of *Potamogeton richardsonii* induced by environmental factors. *Freshwater Biol.*, **8**: 251–268.

SWANN, E. L. (1978). *Elodea canadensis* and *Elodea nuttallii*. *Trans. Norfolk and Norwich Nat. Soc.*, **24**: 183–192.

TUTIN, T. G. (1962). *Elodea* Michx, in CLAPHAM, A. R., TUTIN, T. G. & WARBURG, E. F. *Flora of the British Isles*, 2nd ed. pp. 937–938. Cambridge.