Displacement of *Elodea canadensis* Michx by *Elodea nuttallii* (Planch.) H. St John in the British Isles

D. A. SIMPSON

The Herbarium, Royal Botanic Gardens, Kew, Surrey, TW9 3AE

ABSTRACT

Elodea nuttallii (Planch.) H. St John has spread rapidly since its introduction into the British Isles in 1966. A feature of its spread has been its displacement of *E. canadensis* Michx in places where the latter was well established. One possible reason is that *E. nuttallii* is able to achieve more rapid stem elongation, as well as produce a greater number of axillary stems over a given period of time, resulting in *E. canadensis* eventually being shaded out of a locality. Cultivation experiments suggested that stem elongation and axillary stem production was significantly ($P<0{\cdot}001$) greater in *E. nuttallii* under nutrient-poor and -rich conditions and a range of light intensities. Stem elongation in *E. nuttallii* appeared to be most rapid immediately after establishment, while in *E. canadensis* there was a gradual elongation as time progressed. These characteristics may lead to more rapid formation of a canopy of stems and leaves by *E. nuttallii* at or near the water surface, a factor which may help to bring about the eventual displacement of *E. canadensis* in many places.

INTRODUCTION

Elodea canadensis Michx and *E. nuttallii* (Planch.) H. St John are native to North America, but as adventive species they have become widely distributed around the British Isles. *E. canadensis* has long been established, but *E. nuttallii* was first recorded in 1966, since when it has spread rapidly. An interesting feature of its spread was its apparent displacement of *E. canadensis* in many localities where the latter species had been well established. This was observed by a number of workers (cf. Briggs 1977; Lund 1979; Simpson 1984) who noted that *E. nuttallii* more-or-less replaced *E. canadensis* over a period of one or two years, with only a few plants of the latter remaining after this time.

The speed of displacement initially led to suggestions that *E. nuttallii* was a phenotypic variant of *E. canadensis*, although this has been disproved (Simpson 1988). Nevertheless the displacement of *E. canadensis* appears to be continuing and, indeed, personal observations made in southern England over the past two years suggest that here, at least, *E. canadensis* is now much less common than *E. nuttallii*. However it should be noted that there are some sites where there seems to be little competition between the two species, and others where *E. canadensis* is still the only species present.

A number of incidental observations were also made on material of both species which had been planted at the same time in a nutrient-rich substrate in a large tank. Within three to four weeks of planting *E. nuttallii* had become well-established, producing many stems, whereas *E. canadensis* remained short and more or less decumbent with comparatively few stems being produced. *E. canadensis* remained in a similar condition throughout the growing season, while *E. nuttallii* continued to produce stems in quantity. One possible reason for the displacement of *E. canadensis* in natural habitats is that *E. nuttallii* is able to achieve more rapid stem elongation, as well as produce a greater number of axillary stems over a given period of time, with the result that *E. canadensis* may eventually be shaded out. To examine this in more detail, three cultivation experiments were carried out in which stem elongation and production of axillary stems were measured in both species under differing environmental conditions.

MATERIALS AND METHODS

Material was collected from the Lancaster-Kendal Canal, Burton-in-Kendal, Westmorland, v.c. 69 (*E. canadensis*) and R. Lune, Skerton, Lancaster, v.c. 60 (*E. nuttallii*) in August 1983. The three experiments, also carried out in August 1983, were as follows:

(i) 5 cm long apical stem sections of each species were planted in a 5 cm deep, nutrient-poor coarse sand/gravel mixture, which had been put into six 30 cm diameter, 40 cm deep polypropylene bins. 15 stem sections of each species were planted in each bin. The bins were placed in pairs in a glasshouse where supplementary illumination was provided by 20 Atlas 'Daylight' fluorescent tubes, giving a maximum light intensity of 250 μmol $m^{-2}s^{-1}$. The lights were set to give a 16 hour photoperiod and temperature was maintained at 22±5°C. Ten plants of each species were harvested on each date and immediately pressed. Stem length, together with the number of axillary stems produced by each plant, were recorded after 10, 20 and 30 days. Analyses of variance were carried out on species data for each harvesting date.

(ii) Plants were grown at four surface light intensity levels, 250 (high), 35 (medium), 2 (low) and 0 μmol $m^{-2}s^{-1}$. Otherwise, culture methods were similar to those in experiment (i). Ten plants of each species were grown at each light intensity. After 35 days stem length and the number of axillary stems per plant were recorded. Analyses of variance were carried out on stem length data between species at each light intensity.

(iii) Similar to experiment (ii) except the plants were grown in nutrient-rich river sediment.

RESULTS AND DISCUSSION

The results of experiment (i) are shown in Fig. 1. *E. canadensis* showed almost no stem elongation after ten days, and had grown to only about 7 cm after 30 days. Conversely, *E. nuttallii* showed a marked amount of stem elongation after ten days, when the mean stem length was 9·5 cm. By 20 days mean stem length was 12·5 cm, and this was followed by a further, although smaller increase after 30 days. The difference in stem length between the two species was highly significant ($P<0{\cdot}001$) on each sampling date. A similar rate of stem elongation in *E. nuttallii* was noted by Kunii (1982).

The results of experiments (ii) and (iii) are shown in Fig. 2 and Table 1. As expected, no plants

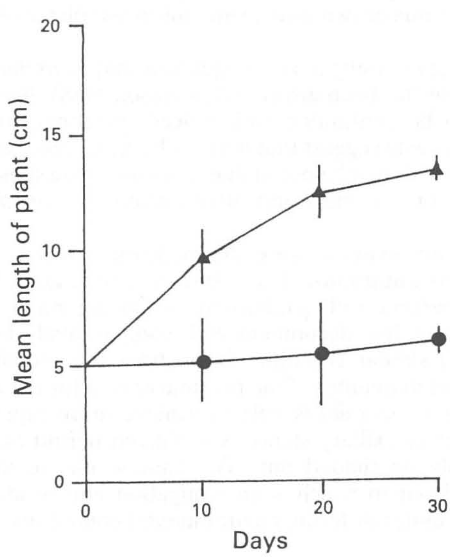

FIGURE 1. Growth of *Elodea canadensis* (●) and *E. nuttallii* (▲) under conditions of constant temperature, light intensity and photoperiod.

survived in total darkness. Otherwise both species demonstrated greater stem elongation in nutrient-rich substrate, and again, this was expected considering the impoverished nutrient regime provided by the coarse sand/gravel mixture. However in both experiments *E. nuttallii* showed significantly ($P<0{\cdot}001$) greater stem elongation than *E. canadensis* after 30 days at the two lower intensities. In material growing on nutrient-poor sand/gravel this difference was greatest at medium light intensity, but in plants growing on nutrient-rich river sediment it was greatest at high light intensity. The number of axillary stems per plant decreased in both species with decreasing light intensity in both substrate regimes. However at medium and high light intensities the number of branches was considerably higher in *E. nuttallii*, again in both substrate regimes.

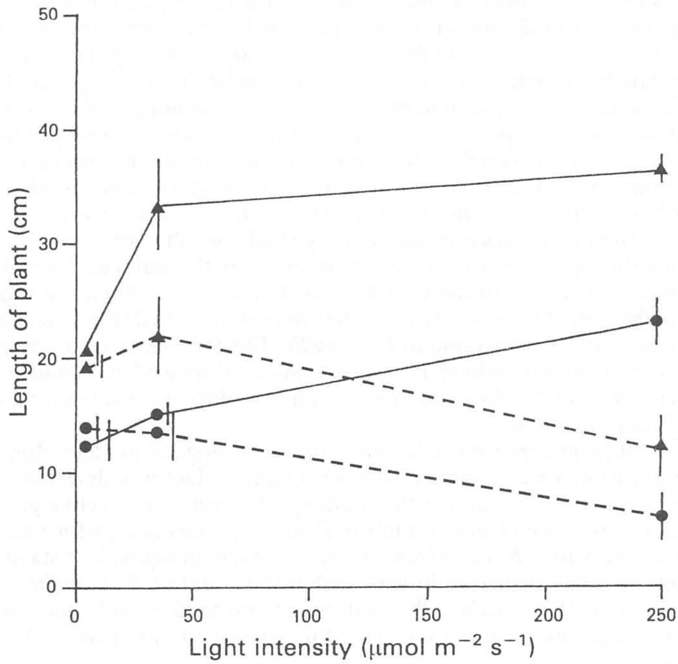

FIGURE 2. Growth of *Elodea canadensis* (●) and *E. nuttallii* (▲) after 30 days at differing light intensities in nutrient-poor (- -) and nutrient-rich (—) subtrates.

The data from experiment (i) also suggest that stem elongation in *E. nuttallii* is most rapid in the period immediately after establishment, while in *E. canadensis* there is only a gradual elongation as time progresses. As only nutrient-poor substrate was used in this experiment, it could be argued *E.*

TABLE 1. MEAN NUMBER OF AXILLARY STEMS PER PLANT ON *ELODEA CANADENSIS* MICHX AND *ELODEA NUTTALLII* (PLANCH.) H. ST JOHN AFTER 30 DAYS GROWTH ON NUTRIENT-POOR AND -RICH SUBSTRATES UNDER THREE DIFFERING LIGHT INTENSITIES

Substrate type	Light intensity	*E. canadensis* (mean±SE)	*E. nuttallii* (mean±SE)
Nutrient-poor	low	1·00±0·001	1·00±0·001
	medium	1·00±0·01	3·00±0·01
	high	1·00±0·001	5·00±0·01
Nutrient-rich	low	1·00±0·001	1·00±0·001
	medium	1·75±0·001	3·25±0·01
	high	8·75±0·02	11·00±0·01

canadensis might show more rapid stem elongation on nutrient-rich substrate. However experiment (iii) suggests that, even when nutrient-rich substrate is used, *E. nuttallii* is still capable of faster growth.

Although these experiments are by no means exhaustive, they do suggest that *E. nuttallii* has a greater rate of stem elongation and axillary stem production over a given period of time. One way in which these could be related to the displacement of *E. canadensis* is in the formation of a canopy. Canopy formation is of particular importance to submerged macrophytes which, because of the light attenuating properties of water, often grow in low light intensities. One of the main problems for such plants is to obtain sufficient light for photosynthesis, and to overcome this they concentrate photosynthetic tissue towards the water surface, as near as possible to the light (Barko & Smart 1981). In shallow water this results in the formation of a canopy at the water surface which is composed of a large number of densely crowded stems and leaves. Such a feature is characteristic of *Elodea* and related genera. An important feature of the canopy is that light levels below it are much reduced. This was amply demonstrated in *Hydrilla verticillata* (L.f.) Royle by Haller & Sutton (1975) who recorded a 95% reduction in light intensity under a canopy of this species. The effect of this would be to shade out other species present in the same habitat. Canopy production confers an obvious advantage as it severely restricts the competitive ability of other species (Haller & Sutton 1975; Titus & Adams 1979; Barko & Smart 1981). The implications of this are that if stem elongation and axillary stem production is more rapid in *E. nuttallii*, this species may produce a canopy more quickly than *E. canadensis* and thereby shade out the latter.

In deep water, aquatic plants are often unable to elongate to the water surface (Barko *et al.* 1982) and they do not produce a canopy of the type described above. Nevertheless a canopy may still be formed, although in this case it consists of longer, less densely crowded stems and leaves. Again, the formation of a canopy may be more rapid in *E. nuttallii*. This is supported by observations made in Mitchell Wyke Bay, Windermere where *E. nuttallii* rapidly displaced *E. canadensis* (Lund 1979), although both species grow at depths of up to 3 m or more and never reach more than 1·35 m below the water surface (Simpson 1983).

The results obtained from experiment (i) may also be analogous to stem elongation occurring early in the growing season, which might be another significant factor in determining the success of *E. nuttallii* over *E. canadensis*. Assuming that both species commence active growth at the same time, stem elongation may proceed more rapidly in *E. nuttallii*; thus canopy formation in this species is already well advanced before *E. canadensis* is able to reach an equivalent stage. As a result, *E. canadensis* may only be able to survive in gaps within the stand of *E. nuttallii*, or on its fringes, through the remainder of the season. Observations in the field would seem to fit in with this hypothesis, since *E. canadensis* is usually seen in this type of situation when the two species are growing in the same habitat.

Incidental observations were also made of the time taken for new roots to appear on the stem pieces. This was faster in *E. nuttallii*, and the first roots were usually seen about four days after planting. Those of *E. canadensis* took about 10–14 days to appear. In the British Isles both *Elodea* species spread by vegetative means. The stems are brittle and, when small pieces of stem break away from the parent plant, roots often form at the nodes, allowing the piece to establish itself as a new plant. Thus *E. nuttallii* may have a further advantage over *E. canadensis* in being able to establish itself faster by rooting more quickly.

It should be emphasised that the experiments described were of a fairly simple nature, and that measurements were made after only a short period of cultivation. Therefore it is conceivable that some of the differences may have occurred due to prevailing conditions in the original habitats. Nevertheless, although more detailed and lengthy work is needed to confirm the results, they do shed some light on the problem under discussion. The reasons why *E. nuttallii* seems to be more vigorous than *E. canadensis* in some habitats and not others also need to be determined and would be worthy of further investigation.

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