The effect of growing season length and water level fluctuations on growth and survival of two rare and at risk Atlantic Coastal Plain flora species, *Coreopsis rosea* and *Hydrocotyle umbellata*

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Abstract: This study examined variables that may be limiting rare species of Nova Scotia's Coastal Plain flora to determine why they have not expanded to other lakeshores, including dam reservoirs with appropriate slope and substrate, and to determine how reservoir management could improve habitat quality. A transplant experiment was conducted to examine whether variables related to growing season (establishment time, position on shoreline, and water-level fluctuation) were limiting two at-risk species, *Coreopsis rosea* Nutt. (Pink Tickseed) and *Hydrocotyle umbellata* L. (Water-pennywort). Establishment time as well as timing and duration of flooding were found to limit both species. Unseasonable flooding and later establishment had similar effects in reducing biomass. The contribution of time spent above water to the final biomass was 2–3.4 times greater than time spent below water. At reservoirs, earlier spring draw down would reduce flood stress, while opening the dam during periods of high precipitation would avoid plant damage due to unseasonable flooding. Exposure of the lower shoreline for 49–71 d or greater would benefit *H. umbellata*, and exposure of the upper shoreline for 100–112 d or greater would benefit *C. rosea*. To conserve current habitat, we must also minimize disturbances to watersheds affecting natural fluctuations of occupied lakes.

Key words: conservation of biodiversity, artificially altered water level regimes, flooding, Atlantic Coastal Plain flora, *Coreopsis rosea*, *Hydrocotyle umbellata*, rare plant limitations.

Résumé : Les auteurs ont examiné les variables qui peuvent limiter les espèces rares de la flore de la plaine côtière de la Nouvelle-Écosse, afin de déterminer pourquoi elles ne se sont pas étendues à d'autres rives lacustres, y compris des réservoirs endigués possédant le substrat et la pente appropriés, et comment l'aménagement des réservoirs pourrait en améliorer la qualité de l'habitat. Ils ont effectué des transplantations expérimentales, afin d'examiner si des variables saisonnières (date d'établissement, position sur la grève, et fluctuation du niveau de l'eau) limitent deux espèces à risque, le *Coreopsis rosea* Nutt. (coréopsis rose) et l'*Hydrocotyle umbellata* L. (hydrocotyle à ombelle). On constate que le moment de la mise en place, ainsi que le moment et la durée d'immersion limitent les deux espèces. Des submersions hors saison et une mise en place tardive ont des effets comparables sur la réduction de la biomasse. La contribution à la biomasse finale, pour la durée passée hors de l'eau, est 2–3,4 fois plus importante que pour la durée sous l'eau. Sur les réservoirs, un abaissement hâtif du niveau de l'eau réduirait le stress de la submersion, alors que l'ouverture des vannes, au cours des périodes de fortes précipitations, préviendrait les dommages dus aux immersions hors saison. Une exposition de la rive inférieure de 49–71 jours ou plus, serait bénéfique pour le *H. umbellata*, et une exposition de la rive supérieure de 100–112 jours ou plus, favoriserait le *C. rosea*. Afin de conserver l'habitat actuel, il faut également minimiser les perturbations aux bassins versants qui affectent les fluctuations naturelles des lacs occupés.

Mots-clés : conservation de la biodiversité, altération artificielle des régimes de niveaux des eaux, immersion, flore de la plaine côtière de l'Atlantique, *Coreopsis rosea*, *Hydrocotyle umbellata*, limitations de plantes rares.

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Introduction

The Atlantic Coastal Plain flora (ACPF) is a taxonomically unrelated group of species that primarily occupy oligotrophic wetland habitats (including seasonal ponds, lake shores, peatlands, wet flatwoods, and some river shores) in the Atlantic Coastal Plain physiographic region, which extends along the coast from Texas to Cape Cod (Rawinski and Price 1994). Disjunct populations of certain species of the ACPF exist in the Great Lakes region (Reznicek 1994) and in southwestern Nova Scotia (Fernald 1921). The Nova Scotia disjunct populations of the flora are the northern-most occurrences for 66 of the Coastal Plain species (Sweeney and Ogilvie 1993). This study focuses on the environmental limitations faced by the rare elements of the ACPF in Nova

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Scotia, and in particular on lakes in the Tusket River watershed in southwestern Nova Scotia.

Throughout its range, the ACPF is facing increasing threats. The eastern seaboard is among the most densely populated areas in North America; habitat loss to urbanization and eutrophication has lead to a deterioration of the status of the Coastal Plain flora throughout its main range (Wisheu and Keddy 1989; Keddy 1994; Schneider 1994; Sorrie 1994; Sutter and Kral 1994). In comparison, Nova Scotia has relatively undisturbed habitat for these species (Sweeney and Ogilvie 1993), but even here damming, cottage development, associated shoreline alteration, and all terrain vehicle (ATV) use pose significant and ongoing threats to the flora and habitat integrity (Boates et al. 2005). Dams are of particular concern, as their placement often coincides with the large watershed lakes at the end of catchments that support higher numbers of rare elements of the flora (Hill and Keddy 1992). Morris et al. (2002) estimated that half of the most important shorelines on large watershed lakes in Nova Scotia have been lost as Coastal Plain flora habitat to development and damming.

Natural water-level fluctuations play an important role in maintaining species richness (Dynesius and Nilsson 1994) and habitat (Keddy 1991), and establishing zonation patterns within lakes and vertically on shorelines (Wisheu and Keddy 1989, Keddy 1984). Water-level fluctuations in wetlands play a similar role to that of fire in forests in that they destroy vegetation, and allow regeneration from seed (Keddy 1991). At more moderate levels of water fluctuation, only certain species such as shrubs (Wisheu and Keddy 1994) may be destroyed or excluded, as woody species are particularly sensitive to flooding (Kozlowski 1984). The exclusion of terrestrial species such as shrubs by periodic flooding is important, as they would otherwise out-compete the slow-growing Coastal Plain flora (Keddy 1989; Wisheu and Keddy 1994). Stabilization of water fluctuations by damming simplifies the shoreline, allowing shrubs to encroach into and replace the marsh and wet meadow portion of the shoreline that the flora requires to persist (Keddy 1991).

When a hydroelectric station was installed on the Tusket River in 1929, two types of dammed lakes were created, a head-water lake and several reservoir lakes. The head-water lake levels are kept constant to keep a steady flow of water through the turbines at the station. To achieve this, dams at reservoir lakes farther upstream are occasionally opened to add water to the head-water lakes. Because of the stabilization of water levels at the headpond lake, that shoreline no longer supports rare elements of the Coastal Plain flora (Keddy and Keddy 1983). Vaughan and Gavels Lakes, which now form one large head-water lake along with King's Lake, used to support populations of three and five rare Coastal Plain species, respectively; these species are now considered to be extirpated from those sites, as they have not been seen there since before 1925 (Keddy and Keddy 1983). The loss of this habitat is significant. For example, it represented the reduction of the number of total sites in Canada occupied by *Coreopsis rosea* Nutt. (Pink Tickseed) from 11 to 8 (Keddy and Keddy 1983; Keddy 1985; Newell 1998).

Other areas in the watershed, including reservoir lakes, appear appropriate for colonization by rare elements of the Coastal Plain flora, as shorelines there appear to be of the appropriate substrate type and slope, and water levels do fluctuate. The mechanisms restricting the rare elements of the ACPF from expanding their range to occupy these areas are poorly understood (Hazel 2004). Greater understanding of the variables that limit the rare elements of the ACPF could help to better understand the dynamics of present populations, and thereby better manage and maintain them, potentially moving toward restoring numbers of the rarest species through habitat restoration, creation, and maintenance.

Given that the Atlantic Coastal Plain flora is at the northern-most edge of its range in Nova Scotia (Sweeney and Ogilvie 1993), length of growing season may be important in limiting the growth and survival of Coastal Plain flora species and in controlling their distribution in Nova Scotia. If the rare elements of the flora in Nova Scotia are already at the limit of their climatic tolerance, a change in hydrologic regime affecting growing-season length could hamper their growth and survival. Work by Hill et al. (1998) in southwestern Nova Scotia suggests that the length of the growing season there may be drastically shorter at dam reservoir lakes, because the lake levels are kept artificially high through the spring and summer. This assumes that growth below water is insignificant in these species.

The main objective of this experiment was to test the effect of growing-season length on rare elements of the Coastal Plain flora along a vertical shoreline gradient under field conditions. A secondary objective was to determine to what extent these species are capable of growing under flooded conditions. There were three treatments: transplanting at different dates, transplanting at different shoreline depths, and transplanting at lakes with different hydrologic regimes. Together, the treatments in this experiment should determine if the length of growing season is the primary explanation for differences in the success of these species at different lakes and at different depths along the shoreline.

This research was done with the approval of the Atlantic Coastal Plain flora recovery team and touched on three of the five areas in the recovery plan: information concerning the rarer species of the ACPF, management of the ACPF, and stewardship (Vasseur et al. 2002). More specifically, the research addressed knowledge gaps in what is limiting these species and aimed to provide information and tools to allow the team to effectively manage populations and promote industry stewardship on dam reservoirs.

Material and methods

Study species

The species chosen for the transplant experiments were *C. rosea* (nationally endangered and globally rare) and *Hydrocotyle umbellata* L. (Water-Pennywort) (nationally endangered and nationally rare) (Keddy and Keddy 1983; Wilson 1984; Newell 1998, 1999). *Coreopsis rosea* is only found in a few sites all of which are in North America, and those that are in Canada are under threat, while *H. umbellata* is more common farther south, but is quite rare in Canada as it is only found at three sites, all of which are in Nova Scotia and under threat. *Coreopsis rosea* is found on the mid- to upper shoreline, while *H. umbellata* is

restricted to low-shoreline positions, and these species accordingly differ in the length of time they are exposed to a terrestrial environment (Hazel 2004). These species were selected among the flora because of their provincial and national significance, their contrasting shoreline positions, and the availability of transplant material. Given that these are rare species, care was taken to utilize material that had already been taken from the field for other projects, and thus reduce impact by reducing the amount of material being removed from natural populations. This work was done under permit (pursuant to section 14 (1)(a) of the Nova Scotia Endangered Species Act (1998) and section 16 of the Nova Scotia Special Places Protection Act (1989).

Study sites

Study sites were chosen from lakes within the Tusket River system in southwestern Nova Scotia, near the town of Yarmouth. Although some of the Coastal Plain species are present at other locations in southwestern Nova Scotia, the Tusket River watershed has the highest species richness of Coastal Plain flora in Atlantic Canada, and is the only place where the two study species are found together.

The three lakes chosen have common elements of the flora but have different catchment areas and, consequently, different hydrologic regimes. The catchment areas of the three lakes chosen are 107 000, 33 500, and 1700 ha and surface areas of 194, 645, and 347 ha, for Wilson's, Raynard's, and Kempt-Back lakes, respectively. Wilson's Lake was chosen as the control lake, as it is the only lake in southwestern Nova Scotia that supports natural populations of both *H. umbellata* and *C. rosea*. Wilson's Lake is undammed and has the highest species richness and diversity of rare elements (seven species) of the Coastal Plain flora in Nova Scotia (Hill et al. 1998). The other two lakes were chosen from the same watershed, as close as possible to Wilson's Lake, to keep substrate and climate consistent. Raynard's Lake is a reservoir with a dam, which is periodically opened to allow more water to flow into Lake Vaughan, the Tusket Falls power generating station's headpond. It was chosen because models based on catchment area (Hill et al. 1998) predict that it should support five or six rare species, but is reported as not supporting any of the rare elements of the flora. Kempt-Back Lake was chosen as it is known to support two rare species, despite having a relatively small catchment area and being a dam reservoir. Water levels were allowed to drop sooner in the spring at this reservoir lake than at others, and it was suggested by Hill et al. (1998) that this may be the reason that it supported rare species. Once the study began, it was discovered that the lake was no longer being managed by Nova Scotia Power as a reservoir lake, and that the weir that had previously been used to regulate water flows had been boarded up, keeping water levels uniformly high (J. Gavels, personal communication 2004).

Sites within each lake were chosen on the basis of known habitat preferences for ACPF. These plants are known to inhabit gently sloping, rocky to sandy, exposed shorelines with little competition from shrubs (Keddy and Wisheu 1989; Wisheu et al. 1994). Three sites satisfying these criteria were chosen at each of the study lakes. Sites were selected along the eastern to southeastern shores of the lakes to keep sunlight, wind, and wave exposure consistent (aspects of 82° to 139°). Individual sites on a given lake were at least 100 m apart.

Transplantion procedure

Standardized transplant plugs were prepared from *H. umbellata* and *C. rosea* maintained at the Harriet Irving Botanical Garden at Acadia University. This material was collected as vegetative slips for *H. umbellata* and seeds for *C. rosea* in the fall of 2000 from Wilson's Lake within the Tusket River Reserve, then propagated and maintained until 2004 at the gardens. Transplants were prepared from vegetative portions of this stock material on 28–29 April 2004 for *C. rosea* and on 4–5 May 2004 for *H. umbellata* through a process of cleaning, cutting, and treating the vegetative slip for any potential pests. For *H. umbellata*, this consisted of a 4 cm length of rhizome with one node and one leaf with a diameter of 1–1.5 cm. To ensure root length was consistent among slips, roots were trimmed to a maximum length of 1 cm. For *C. rosea*, the slips consisted of a 2 cm length of rhizome with one ramet that was 3–5 cm in height. Roots were trimmed to a maximum length of 3 cm. Once cut, the aboveground portions of transplants were dipped in a 1:50 dilution of Safer's insecticidal soap to kill any pests if present. Plant material was then planted in a mixture of 2 parts peat-based potting soil to 3 parts sand. Plug-cell size for the transplants was 4 cm × 4 cm × 5.5 cm deep for *H. umbellata*, and 4.5 cm × 5.5 cm × 5.5 cm deep for *C. rosea*.

Once prepared, the transplants were placed in growth chambers for a period of 7 weeks. The initial conditions were set at 80% humidity, 15 °C day and 10 °C night temperatures, with 8 h of light at 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$, to recreate late summer conditions. These conditions were maintained for 1 week, after which the temperatures were dropped to 12 °C during the day and 7 °C at night, followed by 10 °C during the day and 5 °C at night the following week. After 3 weeks, root production was judged insufficient to produce successful outdoor transplants, so the conditions in the growth chambers were increased to 20 °C during the day and 15 °C at night, with 12 h of light at 680 $\mu mol \cdot m^{-2} \cdot s^{-1}$ to stimulate more vigorous growth. These conditions were maintained for 3 weeks, followed by 1 week cool down to harden off the plants at 12 °C during the day and 7 °C at night, with the same light conditions. On average *C. rosea* transplants had 2.7 ramets averaging 1.5 cm tall each, a total of 13.8 leaves, and a root network along the periphery of the planting cell securing the soil, while *H. umbellata* transplants were on average 1.0 cm tall, had 6.8 leaves, and had a noticeable root network along the periphery of the planting cell. At that point transplants were randomly divided into three groups for three transplant dates to look at the effect of a delayed start to the growing season. Two groups were placed in a cold chamber at 4 °C and 80% humidity with no light, to arrest development, while the remaining group was immediately transplanted to the field. Plants kept in the cold chamber were checked daily and watered as needed to keep the soil moist. Plant growth and (or) senescence in the cold-chamber was negligible, and these plants were indistinguishable from the first group of plants at time of transplantation.

The initial (week 0) transplants were planted on 26–28 June

2004, the second session transplants (week 4) were planted 21–23 July 2004, and the third session transplants (week 8) were planted 18–20 August 2004. The first planting coincided with the time these plants are normally exposed by receding water levels on Wilson's Lake (Hazel 2004). According to Hazel (2004), upper shoreline plants at Raynard's Lake reservoir can experience a 4-week delay in exposure, while lower shoreline plants experience up to a 70 d delay. Plantings were done at 4 and 8 weeks after the original planting to capture most of this range.

Two replicate transects were planted at each site per transplant session. Transects were placed at 90° to the shoreline. Along the transects, transplants were placed at equivalent depths relative to the high water mark, so that the timing of exposure of plants would be the same across sites at a given lake as water levels dropped. The high water mark was assessed as the average shrub line at the middle experimental site; depths below the high water mark were established using a string level and a metre stick. *Coreopsis rosea* was planted at 30, 40, 50, 60, and 70 cm below the high water mark, and *H. umbellata* was planted at 50, 60, 70, 80, and 85 cm below the high water mark based on work by Hazel (2004), where she inventoried the shoreline and described the elevation range of these two species. In total, there were two replicate transplants per transplanting session at each of the five planting depths at each site and three sites per lake. In all there were 90 plants per species at each lake; a total of 540 transplants for this experiment.

To prevent confusion of transplants with natural plants of the same species at Wilson's Lake, a 15 cm tall, 10 cm diameter plastic tube was first installed with the top flush to the ground. The plastic tubes were installed immediately prior to transplantation by removing a spadefull of soil, inserting the tube and the transplant into the hole, and then sliding the spade's contents into the hole ensuring that the transplant was not damaged in the process. The soil was pressed firmly around the tube and transplant to ensure that the tube and transplant were well secured. Any plant material was removed from the soil before the transplant was inserted, though in all cases the vegetation density was very low. The same procedure was followed at the other two lakes with the exception that the plastic tubes were not inserted into the hole, as there were no reports of natural plants of either of the two study species at these lakes.

Measurements

The transplants were visited at 2-week intervals from planting until 27 November 2004, then from the beginning of April 2005 when the ice broke up, until the end of August when the transplants were harvested. At each visit, height of water level was determined. Growth at the end of the first season (17 September 2004) was assessed as leaf number for *C. rosea* and as leaf number times maximum leaf width for *H. umbellata*. Flowering was recorded through the two summers and first fall. Survival was noted every 2 weeks through the spring, two summers, and first fall. At the end of the experiment the transplants were harvested (10–24 August 2005), washed, and separated into leaf, stem, and belowground components, and oven dried for 48 h at 100 °C before weighing.

Data analysis

All statistical analyses were performed using SAS for Windows version 9.1 (SAS Institute Inc., Cary, N.C.). Analysis of variance (GLM procedure) was used to determine if planting time (week), vertical position on the shoreline, lake, or their interactions had a significant effect on natural log transformed size indices or final biomass. Week planted, depth along the shoreline, and lake were all treated as fixed factors. Because of a storm between 1 September and 17 September 2004 that killed the majority of plants at Kempt-Back Lake, we could not include that lake in these analyses. However, for comparison we include mean values (±SE) for Kempt-Back Lake in our tables and figures where they are available. Survival analyses were done with categorical models (CATMOD procedure) in SAS. The survival of the transplants was examined in seasonal periods (period 1, 26 June – 31 August 2004; period 2, 1 September – 27 November 2004; period 3, 28 November 2004 – 11 July 2005; period 4, 11 July – 18 August 2005) so that the timing and causes of mortality could more easily be assessed. The effect of depth and planting time on survival of a transplant through to the end of a period was assessed by lake. The effect of week planted, vertical position on the shoreline, lake, and their interactions on flower number was assessed with a generalized linear model (GENMOD procedure), as these count data followed a Poisson distribution.

Multiple regression models (STEPWISE procedure) were used to summarize the effects of growing-season length and exposure time on the growth of the two species, and to assess the relative importance of above- versus below-water growth. The number of days plants were above or below water within the growing season across the 2 years of the experiment was determined for each individual based upon measurements of water-level height and position of the plant on the shoreline. If the position of the plant on the shoreline was below the water line, the plant was considered below water. The length of the growing season was taken to be 1 May to 30 September for *H. umbellata* and 15 April to 15 October for *C. rosea*. These dates were chosen based upon observations of plant growth in the field and preliminary modelling exercises, where we varied the limits of the growing season. The dependent variable in the regression was final biomass at the end of the experiment, and the number of days plants were above and the number of days plants were below water were the two independent variables. Separate analyses were conducted for each species. In the case of *C. rosea*, days above or below water were corrected for differences in temperature over the growing season by assuming a Q_{10} of 2.0 and using daily mean temperatures reported for Yarmouth, Nova Scotia (23 km southwest of the study site) (www.climate.weatheroffice.ec.gc.ca/climateData/dailydata_e.html). A similar correction was applied to the *H. umbellata* data, but it did not improve the fit of the model, and so the uncorrected data were used in the final analysis. Data from the three transplantation dates, the three lakes, and the five vertical positions on the

shoreline were combined for this analysis, providing a wide range of growing-season lengths and exposure times.

Results

Water levels

Water-level fluctuation magnitude and frequency varied among the lakes. Wilson's Lake water levels were lower in the spring and much of the two summers than the other lakes, with the exception of a flood in July 2004 that was much more dramatic at Wilson's Lake than at the others (Fig. 1). This flood at Wilson's Lake occurred at the end of July 2004; water levels rose sharply between 21 July 2004 and 24 July 2004, reaching the shrub line, and then receded as precipitation waned and were back at more regular levels by 2 August 2004 (Fig. 1). Raynard's Lake levels were high in the spring of both years and very low in the fall of 2004. Water levels at Kempt-Back Lake were high through both years; the maximum drop was only to 30 cm below the high water mark during the summers, unlike the other lakes where levels dropped much lower (Fig. 1).

Survival

Survival was very high for both species (80%–100%) through all periods over the 2 years in all the treatments, with the exception of high mortality in the fall of 2004 at Kempt-Back Lake, where only 16%–62% of *H. umbellata* and 30%–36% of *C. rosea* survived depending on the week of planting. Week of planting had a significant effect on the survival of *H. umbellata* at Kempt-Back Lake in the fall of 2004 (p = 0.0014); earlier transplants had better survival (62% survival for week 0 transplants, 56% for week 4 transplants, and 16% survival for week 8 transplants).

Plant size at the end of the first growing season

At the end of the first growing season in 2004, *H. umbellata* transplants exhibited a slightly different pattern of growth at each lake depending upon depth and week planted (Table 1). However in general, plants were larger at Raynard's Lake than at Wilson's Lake at the end of the first year (Fig. 2). The *H. umbellata* transplants at Raynard's Lake were similar in size with the exception of the week 0 transplants at 60 and 70 cm below the high water mark, which were smaller than the rest. At Wilson's Lake, there was a slight tendency for size to decrease with depth; the week 0 *H. umbellata* plants at 80 cm below the high water mark were exceptionally small. In comparison with plants higher on the shoreline, these plants had fewer but larger diameter leaves and longer petioles. Among those few plants that survived at Kempt-Back Lake, size was highly variable.

Coreopsis rosea transplant size at the end of 2004 exhibited a different pattern at each lake depending upon transplantation date (Table 2). The week 0 *C. rosea* transplants were smaller than the week 4 transplants at Wilson's Lake (Fig. 3), contrary to the pattern we saw at the other lakes, where the earlier transplants were larger than the later ones. Transplants also had a different size based on their depth on the shoreline (Fig. 3); generally, transplants lower on the shoreline were smaller, with fewer leaves, often greater internode spacing, and thicker stems.

Plant size at the end of the second growing season

For *H. umbellata*, lake, depth, and week planted all had an impact on biomass at the end of the second growing season (Table 1). The effects of both lake and depth varied depending upon the week of transplantation. The first planting (week 0) of *H. umbellata* at Wilson's Lake did much better in terms of total and belowground biomass than the other plantings at that and other lakes (Fig. 4). Other than the difference in week 0 plants, the Wilson's and Raynard's Lake transplants were not significantly different in size, and transplants at Wilson's and Raynard's Lake were larger than those at Kempt-Back Lake for all dates. Total and belowground biomass of week 0 transplants were much more noticeably affected by depth on the shoreline than the later two plantings, although all transplant dates showed a pattern of greater biomass (total and belowground) higher on the shoreline (Fig. 5). The week planted affected the aboveground to belowground biomass ratio of *H. umbellata* (Table 1); the latest planting (week 8) had a lower aboveground to belowground biomass ratio: 0.82 ± 0.06 for week 0, 0.79 ± 0.06 for week 4, and 0.62 ± 0.05 for week 8. Depth of planting also had an effect on the ratio of aboveground to belowground biomass for *H. umbellata*; the 50 to 70 cm depths were smaller than the 80 and 85 cm depth ratios (0.54 ± 0.07 to 0.63 ± 0.07 for 50–70 cm, and 1.01 ± 0.07 to 0.97 ± 0.07 for 80–85 cm depths). The ratio of aboveground to belowground biomass was also affected by lake, with higher ratios at Raynard's (0.94 ± 0.05) and Kempt-Back Lake (0.91 ± 0.13) than at Wilson's Lake (0.54 ± 0.05).

For *C. rosea*, the results of the final harvest were similar to those observed at the end of the first season of growth. Lake, week, and depth all affected performance, and the effect of lake varied depending upon week of transplantation (Table 2). The first planting (week 0) of *C. rosea* at Raynard's Lake (Fig. 4) did much better in terms of total, aboveground, and belowground biomass than the other plantings and other lakes (Fig. 4). The earlier plantings were still larger than the later ones by the end of the second growing season at Raynard's Lake; however, there was little difference between the week 0, 4, and 8 plantings at Kempt-Back Lake (Fig. 4). The week 0 transplants at Wilson's Lake were still smaller than the week 4 plants, and were as small as the week 8 plants in aboveground, belowground, and total biomass. There were no differences between Raynard's and Wilson's Lakes *C. rosea* transplants for week 4 and 8 plantings (Fig. 4). The Wilson's and Raynard's Lake transplants were much larger than those at Kempt-Back Lake in total, aboveground, and belowground biomass for all three plantings. There were differences among lakes in the ratio of leaf to stem biomass for *C. rosea* (Table 2); *C. rosea* transplants at Wilson's Lake (0.42 ± 0.05) had a higher leaf to stem ratio than at Kempt-Back Lake (0.34 ± 0.05) and Raynard's Lake (0.28 ± 0.05). There was a linear relationship between depth and total, aboveground, and belowground biomass; *C. rosea* plants higher on the shoreline were larger, particularly below ground, than those lower on the shoreline (Fig. 6).

Coreopsis rosea flowering

Only *C. rosea* produced flowers during this experiment,

Fig. 1. Water levels at each lake relative to the high water mark.

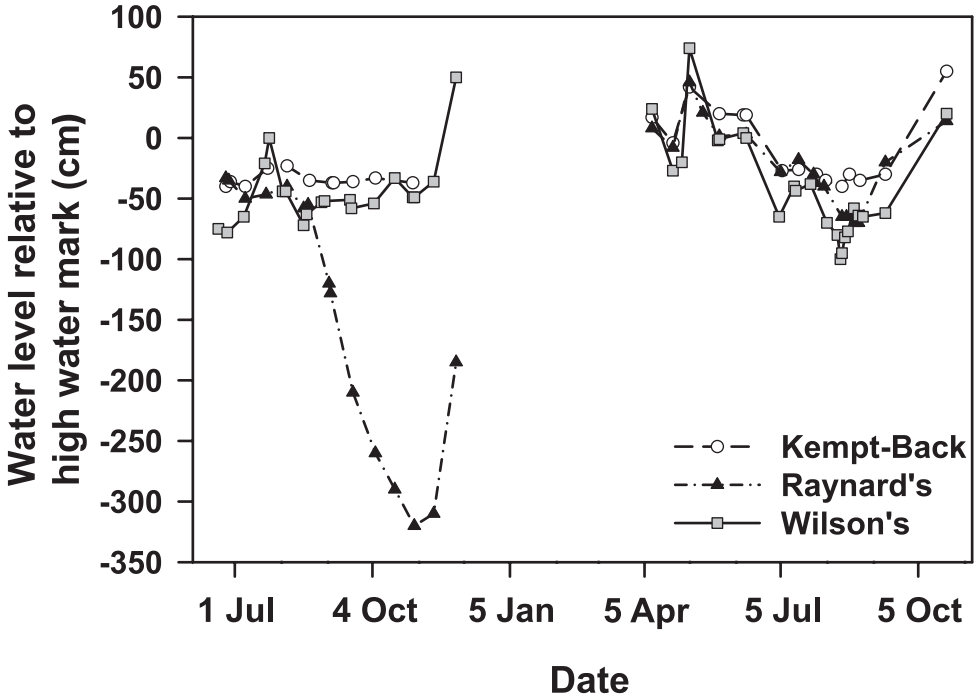


Table 1. Sums of squares for analyses of *Hydrocotyle umbellata* size at the end of the first growing season (17 September 2004), and biomass measures at the end of the second growing season (10–24 August 2006); analyses only include Raynard's and Wilson's lakes.

	Year 1	Year 2			
Variable	Size index[a]	Total biomass	Aboveground biomass	Belowground biomass	Aboveground/belowground biomass ratio
Lake	27.31**	0.023**	0.0004	0.017**	5.88**
Depth	8.76**	0.090**	0.0077**	0.048**	6.38**
Week	4.51*	0.038**	0.0056**	0.015**	1.23*
Lake × week	2.20	0.039**	0.0061**	0.015**	0.73
Lake × depth	3.82	0.005	0.0020	0.001	0.28
Week × depth	4.12	0.030*	0.0032	0.015*	2.11
Lake × week × depth	9.09*	0.008	0.0015	0.004	1.56
Error SS	69.39	0.21	0.037	0.08	18.78
Total SS	128.92	0.43	0.063	0.19	35.91
r^2	0.46	0.52	0.42	0.56	0.48

Note: *, $p < 0.05$; **, $p < 0.01$.

[a]*Hydrocotyle umbellata* size index was ln(number of leaves × maximum diameter).

and only in the second year of the experiment. The flowering of *C. rosea* in the second growing season was greater for week 0 plants (1.60 ± 0.22 flowers per plant) than week 4 (0.93 ± 0.21), and week 8 plants (1.06 ± 0.21). *Coreopsis rosea* flowered more at Raynard's Lake (1.62 ± 0.17 flowers per plant) than at Wilson's Lake (0.77 ± 0.18), and in turn more than at Kempt-Back Lake (0.06 ± 0.32). *Coreopsis rosea* had more flowers higher on the shoreline (2.43 ± 0.29 flowers per transplant at 30 cm and 2.26 ± 0.27 at 40 cm, versus 0.86 ± 0.28 to 0.12 ± 0.28 flowers per transplant at 50–70 cm below the high water mark).

Summary model

The number of days that *H. umbellata* spent above water in 2004 was greatest at Raynard's Lake (mean of 39.3 with a range of 35–49), followed by Wilson's Lake (14.5, 0–71), and least at Kempt-Back Lake (0, 0–0). In 2005, the lake with the most days above water for *H. umbellata* (only until the harvest in August) changed to Wilson's Lake (16.6, 4–35), from Raynard's Lake (5, 0–15); Kempt-Back Lake still had the smallest number of days above water (0, 0–0).

The same pattern was true for *C. rosea*. *Coreopsis rosea* spent the most days above water in 2004 at Raynard's Lake (67.9, 53–112) followed by Wilson's (45.7, 0–100), then Kempt-Back (13.7, 0–85). In 2005, the lake with greatest number of days above water also changed for *C. rosea* to Wilson's Lake (37.6, 15–61), from Raynard's Lake (14, 0–

Fig. 2. Effect of week planted, lake, and depth on *H. umbellata* size index (ln(number of leaves × maximum leaf diameter)) on 17 September 2004 (mean ± 1 SE).

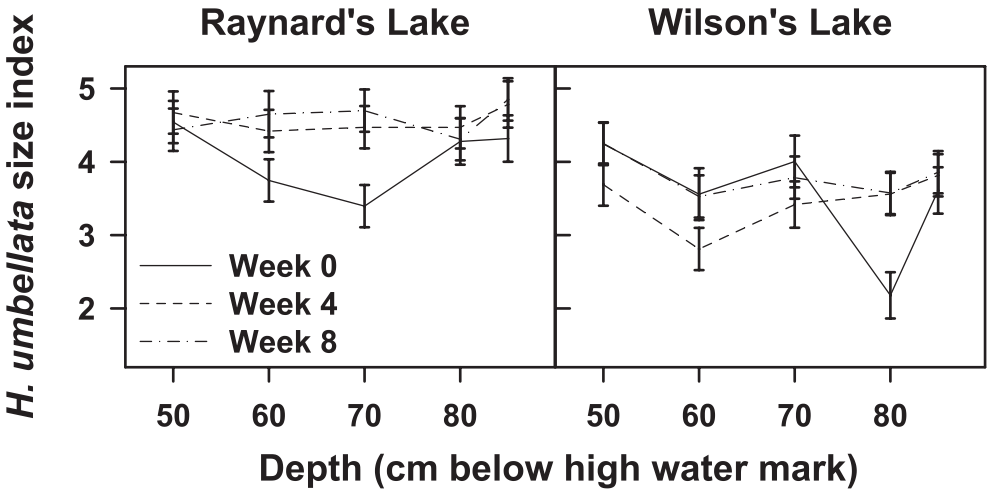


Table 2. Sums of squares for analyses of *Coreopsis rosea* growth at the end of the first growing season (17 September 2004), and biomass measures at the end of the second growing season (10–24 August 2006); analyses only include Raynard's and Wilson's lakes.

	Year 1	Year 2				
Variable	Size index[a]	Total biomass	Aboveground biomass	Belowground biomass	Aboveground/ belowground biomass ratio	Leaf/stem biomass ratio
Lake	1.92**	19.13**	6.60**	3.43**	1.98	0.83*
Depth	3.24*	23.22**	2.36**	10.08**	16.61	0.78
Week	15.40**	13.94**	1.81**	5.61**	2.78	0.10
Lake × week	9.00**	14.28**	2.69**	4.28**	26.23	0.16
Lake × depth	1.88	2.25	0.78	1.05	51.86	0.68
Week × depth	1.13	4.71	0.73	2.59	70.00	1.79
Lake × week × depth	2.71	3.10	0.57	1.29	49.90	2.04
Error SS	36.60	89.25	19.23	32.51	1201.80	25.72
Total SS	71.16	163.92	34.29	58.22	1431.62	31.81
r^2	0.49	0.46	0.44	0.44	0.16	0.19

Note: * $p < 0.05$, ** $p < 0.01$.

[a]*Coreopsis rosea* size index was ln(number of leaves).

26); Kempt-Back remained the lake with the fewest days above water (4.6, 0–23).

The best fit model of final biomass of *H. umbellata*, as judged by r^2, used the number of days above and below water from 1 May to 30 September (r^2 = 0.21, Table 3). The parameter estimates for time above and time below water were both positive, indicating both contributed positively to the final biomass of *H. umbellata*. The parameter estimate for time above water for *H. umbellata* was 3.4 times greater than the estimate for time below water, indicating that time above water contributes much more to final biomass than time below water. The partial r^2 value for time above water for *H. umbellata* was 0.19, compared with 0.02 for time below (Table 3), also indicating the importance of days spent above water, despite the greater total number of days spent below water at most sites.

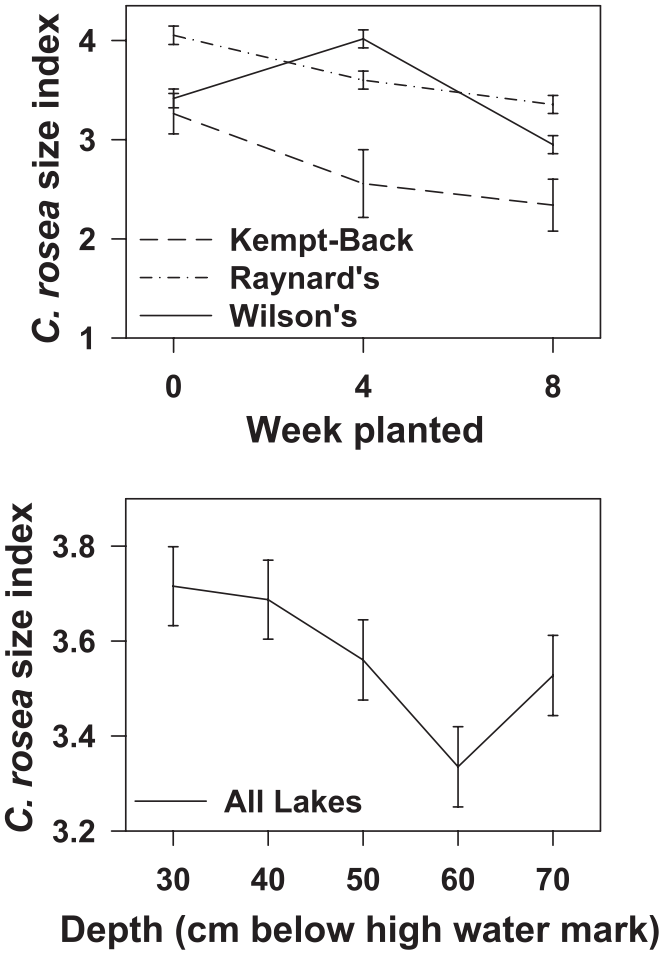
The best fit model of final biomass of *C. rosea*, as judged by r^2, used the number of days above and below water from 15 April to 15 October calibrated for daily temperature using a Q_{10} of 2.0 (r^2 = 0.29, Table 3). The parameter estimates for time above and time below water were both positive, indicating both contributed positively to the final biomass of *C. rosea*. The parameter estimate for time above water for *C. rosea* was 1.9 times greater than the estimate for time below water, indicating that time above water contributes much more to final biomass than time below water, but that it might be slightly less important for *C. rosea* than for *H. umbellata*. The partial r^2 value for time above water for *C. rosea* was 0.23, compared with 0.06 for time below (Table 3), which again emphasizes the importance of days above water.

Discussion

Water-level fluctuation

Each of the lakes had a different water fluctuation regime based on whether or not it was dammed and where it was in the watershed. Wilson's and Raynard's Lake are both low in the watershed and have the potential for high water-level fluctuations; however, Raynard's Lake is dammed, and

Fig. 3. Effect of week planted at each lake, and depth on *C. rosea* size index (ln(number of leaves) on 17 September 2004 (mean ± 1 SE).



flooding is controlled. Raynard's Lake levels did not drop as quickly as Wilson's Lake in both years of the study (Fig. 1), because the dam was kept closed in the spring. Raynard's Lake did not have a flood peak in July 2004 (Fig. 1), because the power company opened the dam during the period of heavy precipitation. Raynard's Lake also had a dramatic drop in water levels in the fall of 2004 (Fig. 1); water levels at Raynard's reservoir were much lower in the fall of 2004 than at Wilson's Lake, because the dam at Raynard's Lake was kept open during that period allowing water levels to drop over 3 m (Fig. 1). Kempt-Back is high in the watershed, and so receives smaller amounts of runoff and has smaller flood peaks. There is a weir on Kempt-Back, which prior to 2001 was opened periodically to supply water to the hydro station headpond (J. Gavels, personal communication, 2004). At some point since 2001 but before 2004, the dam at Kempt-Back Lake was boarded up, causing water levels there to become stable and high (J. Gavels, personal communication, 2004).

Growing-season length

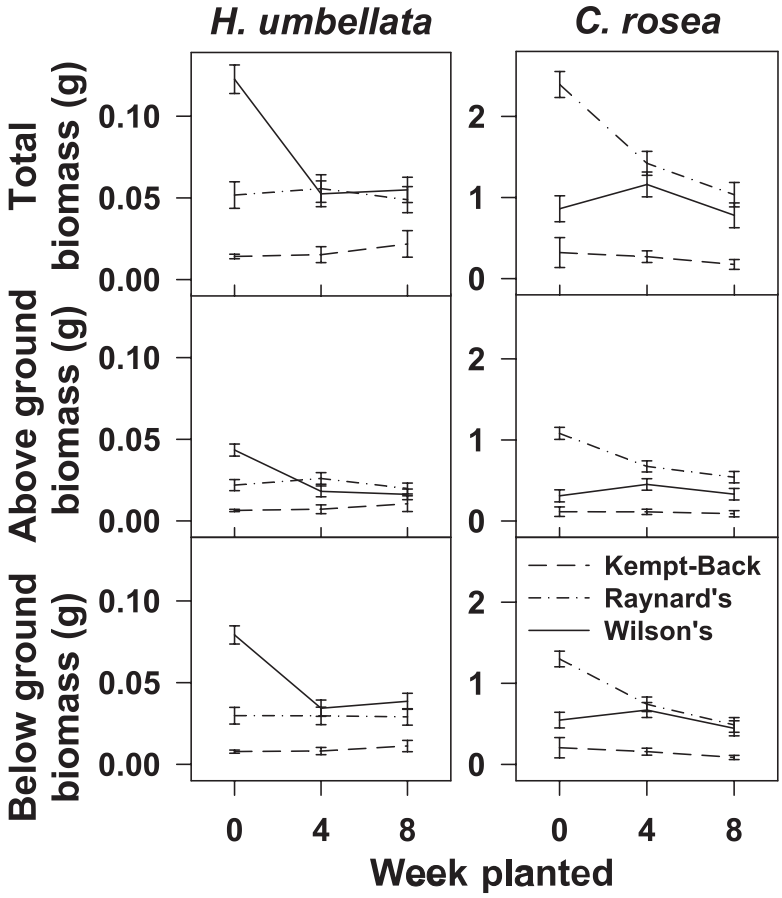
The actual growing season observed for *H. umbellata* and *C. rosea* was much longer than expected. No previous studies have documented active growth in these species prior to shoreline exposure in late June. We observed the first growth for both species in early April while they were still under water. These species are truly amphibious and are capable of growing under aquatic as well as terrestrial conditions. However, growth of both species was much better under terrestrial conditions, as seen in our biomass models for both species, where the contribution of a day above water was two to three times that of a day spent below water to the final biomass (Table 3). It was clear from the poor growth and survival of transplants at Kempt-Back Lake (Figs. 3 and 4) that at least some time above water is necessary for success. This is supported by Keddy (1985) findings that *C. rosea* is extirpated from head water lakes where water levels are kept constantly high. Plants grown under constant flooding, as was seen at Kempt-Back Lake (Fig. 1), may survive in the short term, but are likely susceptible to damage from wave wash, as we saw in the fall of 2004 with transplants at Kempt-Back Lake. These transplants grown solely under aquatic conditions at Kempt-Back Lake were small (Figs. 3 and 4) and likely, poorly rooted.

Using the contrasting regimes at the three lakes and the growth of plants there, we can make rough predictions of the number of days above water required by each species. *Hydrocotyle umbellata* growth was best at Wilson's Lake, where they experienced up to 71 d above water from 1 May to 30 September, worst at Kempt-Back Lake, where they experienced no days above water, and intermediate at Raynard's Lake, where they experienced at most 49 d above water. Growth for *C. rosea* was best at Raynard's Lake, where they experienced up to 112 d above water from 15 April to 15 October, worst at Kempt-Back Lake where they experienced at most 85 d above water in the uppermost position, and no days above water at the other four positions, and intermediate at Wilson's Lake, where they experienced at most 100 d above water. Thus we can suggest that management of lakes to ensure exposure of the lower shoreline for 49–71 d, or greater, would benefit *H. umbellata*, and exposure of the upper shoreline for 100–112 d, or greater would benefit *C. rosea*.

Also, given that *C. rosea* biomass was best explained with the temperature-adjusted model of days above and below water (Table 3), the benefit of the days above water would be greatest if they were in July or August when daily mean temperatures are greater, as this species' growth appears to be temperature sensitive. This temperature sensitivity of *C. rosea* is not surprising given these species are of southern origins, with the main range of *C. rosea* extending as far south as South Carolina (Keddy and Keddy 1983; Newell 1998) and that of *H. umbellata* extending into Mexico (Wilson 1984; Newell 1999). *Hydrocotyle umbellata* appears not to have been as sensitive to daily average temperature during the growing season; this may be due to the buffering capacity of water and shorter growing season. *Hydrocotyle umbellata* was below water for most of the growing season (Fig. 1), and thus would not have experienced as broad a range of temperatures, and also had a shorter growing season, and thus would not have experienced the colder temperatures in April and October.

Our results suggest that rapid fluctuations between terrestrial and aquatic conditions during the growing season are likely detrimental, at least for *C. rosea*. Wilson's Lake expe-

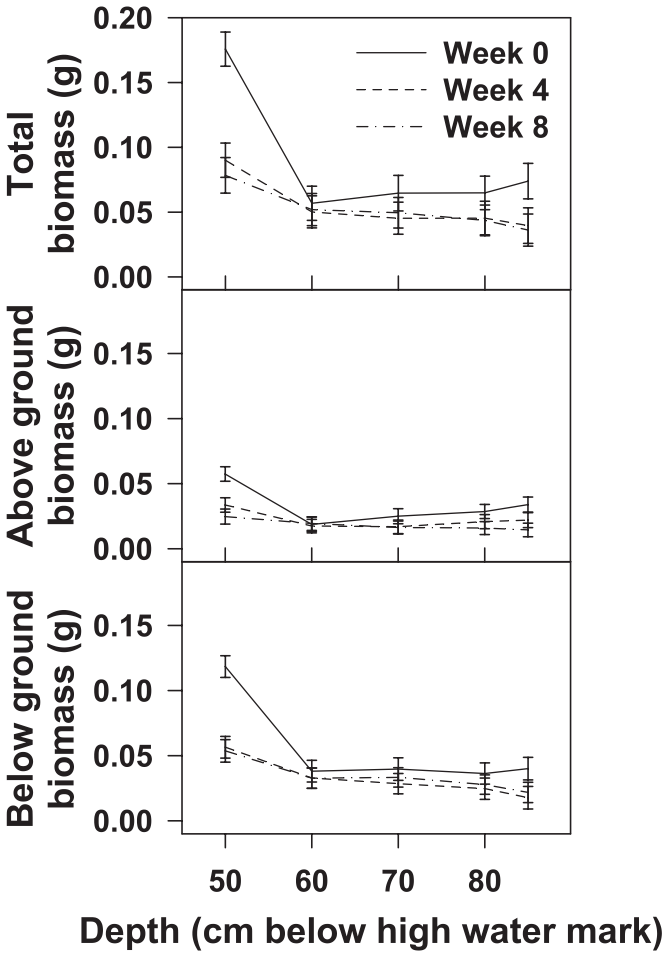
Fig. 4. Total, aboveground, and belowground biomass (means ± 1 SE) of *Hydrocotyle umbellata* and *C. rosea* at the end of the 2-year experiment, by week planted and lake.



rienced a flood peak early in the 2004 growing season shortly after the first set of transplants were put out (Fig. 1). Raynard's and Kempt-Back Lake levels were only marginally affected by the rain event that triggered the flood at Wilson's Lake (Fig. 1) as the Raynard's Lake dam was open during that period, and Kempt-Back is higher in the watershed and on a smaller branch of the drainage area, and so, subject to much smaller flood peaks. The week 0 transplants of *C. rosea* at Wilson's Lake were apparently damaged by the flood, as they did not grow as quickly or as much as the week 4 transplants that were set out after the flood receded, a pattern that was not observed on the other two lakes (Fig. 3). The following summer, the week 0 transplants on Wilson's Lake were as small as the week 8 transplants with similar final aboveground, belowground, and total biomass (Fig. 4). The similar size of the week 0 and week 8 *C. rosea* transplants 1 year after the flood suggests that the damage caused by that flood was roughly equivalent to an 8 week reduction in growing season. This may be due in part to a depletion of carbohydrate reserves of week 0 plants due to anaerobic respiration during the flooded period (Barclay and Crawford 1983), or to tissue damage resulting from the build up of toxic compounds during and after the anoxic period, both within the plant (e.g., Oshino et al. 1973; Barclay and Crawford 1982; Hunter et al. 1983; Crawford and Zochowski 1984) and in the soil around the roots (e.g., Howeler 1973; Osawa and Ikeda 1976; Lynch 1977).

Plants that evolve with frequent flooding often have metabolic and morphological adaptations that allow them to avoid or tolerate the low oxygen levels associated with prolonged flooding (Vartapetian and Jackson 1997), including the enlargement of intercellular spaces to form aerenchyma tissue, which allows gas diffusion to and from the roots (Williams and Barber 1961; Armstrong 1979), the redirection of root elongation upward resulting in some roots reaching a higher oxygen content environment at or near the water surface (e.g., Ellmore 1981; Good et al. 1992), and the formation of large carbohydrate reserves, which allow plants to survive the anaerobic period (Brändle 1991). Plants that are able to survive and grow in both terrestrial and aquatic habitats often exhibit marked changes in morphology and physiology between the two environments. In our study, *H. umbellata* quickly altered its morphology following a rise in water level by extending the length of its petioles, so that the leaf blades were at the water surface. Such elongation is seen in many aquatic or amphibious species (Ridge 1987), which is thought to be initiated by elevated ethylene (Ku et al. 1970; Musgrave et al. 1972; Osborne 1984; Voesenek et al. 1993) and provides a diffusion pathway for gas transport between the atmosphere and those parts of the plant below the water surface. This may

Fig. 5. Effect of planting depth on total aboveground and belowground *H. umbellata* biomass (mean ± 1 SE) by week.



explain why the week 0 *H. umbellata* transplants at Wilson's Lake did not exhibit the same reduced growth and final biomass in response to the early summer flood as the week 0 *C. rosea* transplants (Fig. 4). *Coreopsis rosea* was able to produce stems with longer internode lengths under long-term flooding, as seen at Raynard's and Kempt-Back Lakes, where reduced leaf to stem ratios there seem to be related to longer spring flooding. In plants over 20 cm in height, these stems are often hollow, which would facilitate gas exchange. However, unlike *H. umbellata*, *C. rosea* does not appear to have mechanisms to quickly adapt to rapid water-level fluctuations and complete submersion.

Suitability of reservoirs as Atlantic Coastal Plain flora habitat

The results of our study suggest that reservoirs can provide an appropriate habitat for the establishment, and potentially the persistence, of certain Coastal Plain species, and may be able to support others, if the water fluctuation regime was altered somewhat. Over the time period covered in the present study, Raynard's Lake reservoir provided an appropriate habitat for *C. rosea*, but not for *H. umbellata*. Kempt-Back Lake, on the other hand, did not provide an appropriate habitat for either species, as the shoreline was not exposed for a sufficient number of days to allow the plants adequate growth and establishment to survive the fall storms. *Coreopsis rosea* was in fact largest above ground and had a greater number of flowers at Raynard's Lake than at Wilson's Lake (Fig. 4), which is unregulated. Although populations of *C. rosea* have not been previously reported on Raynard's Lake, over the course of our study, we observed that a population of *C. rosea* has become established. We suspect the plants dispersed to Raynard's Lake reservoir from Sloan's Lake, which is upstream from the reservoir and has a natural population of *C. rosea*. This is a further indication that Raynard's Lake reservoir provides an appropriate habitat for the establishment of this species, though longer-term observation will be necessary to see if *C. rosea* is able survive the between-year variation experienced at reservoir lakes, such as the periodic near complete draining necessary for dam repairs and maintenance.

Being lower on the shoreline, *H. umbellata* had a slightly different response to treatments than *C. rosea*. The earliest (week 0) plantings of *H. umbellata* did not flourish at Raynard's Lake reservoir as they did at Wilson's Lake (Fig. 4). *Hydrocotyle umbellata* did well in the first year, at least as far as could be measured with aboveground growth measurements (Fig. 2), but started growing later in the second year than at Wilson's Lake. The final biomass of the week 4 and 8 plants was similar to those at Wilson's Lake, but the week 0 plants at Raynard's Lake were much like those of later plantings and did not show the large advantage conferred by earlier planting at Wilson's Lake (Fig. 4). The lack of advantage of earlier planting of *H. umbellata* at Raynard's Lake in the second year after a successful first year suggests that conditions in the fall or winter at that reservoir might negate the positive influence of a longer growing season for low shoreline species such as *H. umbellata*. The water levels at Raynard's Lake began to drop in early September and continued to drop through the fall until they were over 3 m vertically below the high water mark, and did not begin to rise again until November, though the transplants were not covered until early January (Fig. 1). It is possible that *H. umbellata* experienced cold damage during the fall and winter of 2004–2005 while water levels were low. Water levels rose much sooner at Wilson's Lake (Fig. 1), and as a result, *H. umbellata* was not exposed to such cold temperatures in the fall and winter, as water temperatures would not decrease below 0 °C. In a garden experiment, Hazel (2004) noted that *H. umbellata* did not survive the winter when grown under terrestrial conditions, while *C. rosea* did, suggesting that upper shoreline Coastal Plain species may be more cold tolerant than low shoreline species. Frost tolerance varies widely among species, depending upon location of origin and the microhabitat they occupy (Larcher and Bauder 1981; Guy 1990; Bertrand and Castonguay 2003). Given that Nova Scotia is at the northern distribution limit of the ACPF, it is important to examine the temperature tolerance of *H. umbellata* and other species in the ACPF to determine if cold exposure in the fall is a factor limiting successful colonization of these species on reservoir lakes.

Alterations to the management of reservoir lakes could improve the quality of Coastal Plain flora habitat available there and enhance the success of establishment of Coastal Plain species. Opening the reservoir dams earlier in the

Fig. 6. Effect of planting depth on total, aboveground, and belowground biomass on *Coreopsis rosea* (mean ± 1 SE).

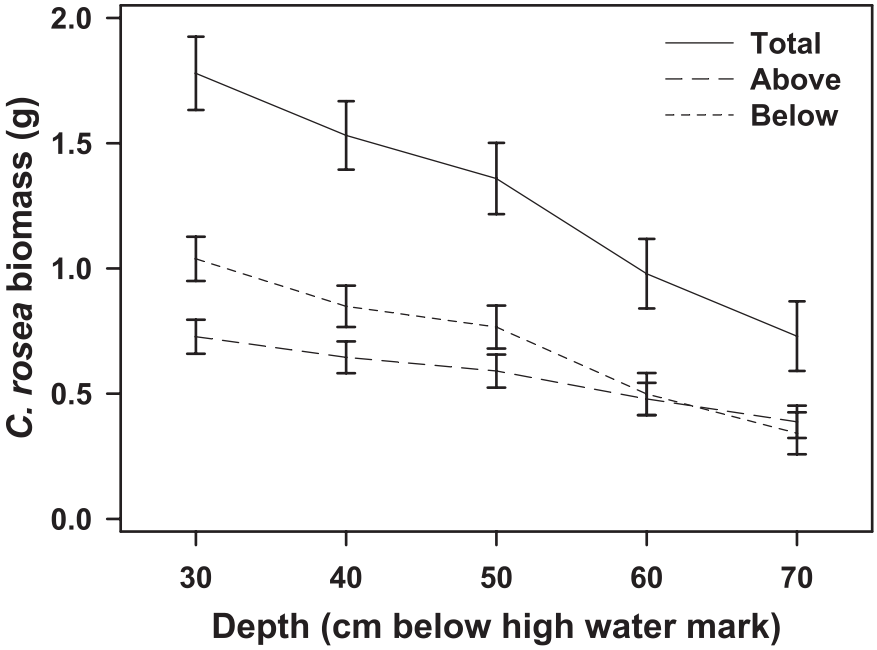


Table 3. Regression models for the relationships between final biomass and number of days above versus below water in *Hydrocotyle umbellata* and *Coreopsis rosea*.

Species	Source	Partial r^2	Parameter estimate (±SE)	Pr > |t|
Hydrocotyle umbellata	Intercept		–0.0357±0.0290	0.2192
	No. of days above water 1 May – 30 September	0.189	0.0012±0.0002	<0.0001
	No. of days below water 1 May – 30 September	0.022	0.0004±0.0002	0.0251
	Model r^2	0.211	n = 186	
Coreopsis rosea[a]	Intercept		–1.3931±0.4532	0.0024
	No. of days above water 15 April – 15 October	0.229	0.0063±0.0009	<0.0001
	No. of days below water 15 April – 15 October	0.061	0.0033±0.0008	<0.0001
	Model r^2	0.289	n = 191	

[a]For *C. rosea*, the number of days above and the number of days below water were corrected for differences in daily mean temperature assuming a Q_{10} of 2.0.

spring would reduce the length of spring flooding, enhancing plant growth through an increase in the number of days above water experienced by the plants in the growing season, and reducing the flooding damage experienced by the plants due to extended spring submersion. Opening the dam during periods of high precipitation would also reduce the impact of growing-season floods, and would improve the vigour, size, and flowering rates of plants there. If cold tolerance is an important limiting factor for the ACPF, an earlier rise in water levels in the fall may also be important to minimize freezing and cold damage. As discussed, reservoir management that ensured exposure of the lower shoreline for 49 to 71 d, or greater, would benefit *H. umbellata*, and exposure of the upper shoreline for 100 to 112 d, or greater, would benefit *C. rosea.*

There are likely other differences among and within these lakes that are critical for growth and survival of both of these species; our models relating exposure to biomass were only able to explain 21% of the variation seen in *H. umbellata* biomass and 29% of the variation seen in *C. rosea*. There remains a great deal of unexplained variation; differences in other environmental or physical conditions within and among the lakes should be examined to determine their importance to the growth and survival of these species. It is also critical that long-term studies be conducted, as it is quite possible that these species are limited by periodic events that occur only rarely.

Despite these limitations, the information gained from this study begins to address information gaps listed in the Atlantic Coastal Plain flora recovery plan (Boates et al. 2005), and has contributed tools for management and stewardship of the ACPF. This study has expanded our understanding of the environmental factors that limit *C. rosea* and *H. umbellata*, both high priority rare elements of the Coastal Plain flora, in particular, the effect of growing-season length, time spent above and below water, and flooding on growth and survival (Recovery plan strategy A, action 1 and 2.1.1). We have also established that vegetative propagation of these two species is possible, that they will readily grow in a greenhouse or growth chamber if given appropriate substrate and watering regime, and that transplants can have very high success rates in the first 2 years if placed in

an appropriate habitat (Recovery plan strategy A, action 2.5.1). This information will improve our capacity to manage these species and their habitat (Recovery plan strategy B, action 5.1 and 5.2), and will provide tools to industry (Nova Scotia Power) to better steward the watershed and Coastal Plain flora lakes (Recovery plan strategy C, action 6.2).

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