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The effects of burial by sand on survival and growth of Pitcher's thistle (*Cirsium pitcheri*) along Lake Huron

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Abstract. Greenhouse experiments were conducted to determine the effects of sand burial on survival and growth of seedlings of *Cirsium pitcheri*. In 1992-1993, seedlings were buried to depths of 0, 25, 50, 75, and 100% of their height while in 1993-1994, the seedlings were buried to depths of 0, 4 cm (single burial), 4 cm (repeated burial of 1 cm every 8 days), 8 cm (single burial) and 8 cm (repeated burial of 2 cm every 8 days). Several physiological traits, net photosynthetic rate, chlorophyll a:b ratio, leaf area, number and length of leaves, number of internodes, amount of tillering, and biomass, were measured. The results showed that all seedlings died in the complete (100%) burial, 20 % died in the 75% burial and none died in the 0, 25 and 50 % burial treatments. Burial of seedlings to a depth of 25% stimulated their growth but 75% burial significantly decreased the total dry weight. Repeated burial treatments exhibited significantly greater stimulation of growth than single burial. Surviving seedlings grew through the sand deposit by elongating the stem and leaf petioles, increasing the number of nodes and the length of internodes. This elongation occurred at the expense of development of the root system indicating that available energy was re-allocated to above-ground parts.

Keywords: Burial tolerance; Morphological response; Physiological response; Seedling burial; Seed mass.

Introduction

Cirsium pitcheri (Pitcher's thistle, Asteraceae) is endemic to the western Great Lakes region of North America, where it is restricted to the sand dunes along the shorelines (Loveless 1984). McEachern et al. (1993) showed that the species is primarily found in foredune habitats containing 70% or more open sand. In Canada, it is considered a threatened (at high risk of extirpation) species (Burnett et al. 1989) which occurs on scattered locations in the sand dunes along Lake Huron at the Pinery and Inverhuron Provincial Parks, on the foredunes of Providence Bay and Carter Bay in Manitoulin Island, and at two locations along Lake Superior (Keddy & Keddy 1984; Keddy 1987). The species grows in a plant community dominated by three grasses, *Ammophila breviligulata*, *Calamovilfa longifolia* and *Andropogon scoparius*. Sand dune habitats are fragile and if proper management practices are not followed, recreational activities may decimate dune plant communities within a short period of time. Anthropogenic factors may influence populations of *C. pitcheri* in three ways, (1) construction of cottages leads to the loss of habitat, (2) construction of groins in the lake changes the normal deposition and erosion patterns of the lake and (3) trampling of vegetation by people kills plants and accentuates erosion. All these changes create disequilibrium in the population dynamics of plant species (Bowles & Apfelbaum 1989).

An important factor influencing populations of *C. pitcheri* and other plant species in sand dunes is recurrent movement of sand owing to wind and wave action and human trampling which subsequently leads to burial of plants. Sand movement may bury seeds, seedlings, and adult plants, to various depths thus increasing the vulnerability of the species (Maun & Riach 1981). However, several studies have shown that many sand dune species are well adapted to withstand dynamic and stochastic disturbance events (Pavlovic 1993) and some species may actually require burial in sand to maintain high vigour (van der Putten 1988, 1993; Olson 1958). Partial burial may increase shoot biomass (Eldred & Maun 1982), net photosynthetic rate (Yuan et al. 1993), number of buds per tiller, internode length of vertical rhizomes, and number of horizontal rhizomes (Disraeli 1984). Nevertheless, each species has an upper threshold limit beyond which it is unable to survive the burial episode. For example, Sykes & Wilson (1990) reported that only a few species survived complete burial in sand; however, all species survived partial burial to 66 % of their height. Along the Great Lakes, burial of plants may occur in single large episodes especially during winter or more often by gradual and repeated burial events during the summer (Davidson-Arnott & Law 1990). The response of a plant to each type of burial may vary because the plant will have to expend considerably greater amounts of energy to emerge from single large deposits. In contrast, plants adjust quickly to repeated and smaller burial deposits. Lee & Ignaciuk (1985) reported that under repeated burial conditions all foredune annuals showed an increase in total dry matter production as compared to controls.

As a consequence of the recent increase in white-tailed deer populations (Gedge & Maun 1994) and recreational overuse of the dune systems, *C. pitcheri* is in danger of extirpation from the southeastern shore of Lake Huron (Maun 1996a). As a monocarpic perennial, it must produce seeds and establish seedlings regularly so that at any one time all stage classes (seeds, seedlings, juveniles, adults) will be represented in the population. Any environmental stress that interrupts one of these stages will have a deleterious effect on the future of the population. A management strategy is needed not only to recover and rehabilitate the species but also to maintain the natural environment of its occurrence. In this study, we tested the effects of burial in sand, as an environmental stress, on the physiological and morphological responses of Pitcher's thistle seedlings to different depths of burial in sand. The objective was to determine the burial tolerance or stimulation response to single one time burial events and to gradual repeated burial episodes.

Material and Methods

Source of seed

For the 1992-1993 experiment, 219 seeds were collected in August 1992 from *C. pitcheri* plants growing along the shoreline at Pinery Provincial Park (43°15'N, 81°50'W) in southwestern Ontario, Canada. For the 1993-94 experiment, seeds were collected in August 1993 from a population at Providence Bay Provincial Park (45° 40' N; 82°17' W) on the southern shore of Manitoulin Island, Ontario, Canada. Sand used in both of these experiments was obtained from the same foredune at Pinery Provincial Park. Prior to its use the sand was air dried to kill nematodes if any and then sifted through a sieve to remove pebbles and detritus.

Seed mass and germination

In 1992-1993, each seed was numbered and then weighed to nearest 0.01 mg using an electronic balance. Four full seeds were then placed in each Petri dish containing two layers of filter paper and moistened with 8 ml of distilled water. The Petri dishes were sealed in metal canisters and placed for stratification in a cold room (4 °C) for 3 weeks. At the end of this period the seeds were dissected and the embryo removed from each seed. The embryos were incubated in a growth chamber maintained at temperatures of 25 °C day (14 h) and 13 °C night until they grew into seedlings. The seedlings were then planted in plastic pots (13 cm diameter) filled with sand. During 1993-1994, germination experiments revealed that the seeds did not require cold stratification. Instead, they were soaked in Petri dishes containing distilled water and then placed in the growth chamber as above. After 48 hr the seeds were dissected and the embryos incubated in the same growth chamber. The seedlings were planted in 20 cm diameter plastic pots filled with sifted sand. The potted plants in both experiments were then placed on benches in a greenhouse maintained at 24-25 °C day (15 h) and 15-18 °C at night. However, these temperatures were difficult to maintain in the greenhouse on warm sunny days. For both experiments, a weak nutrient solution (N, P, K) was added three times during the experimental period. Plants were watered every 2 days or as the surface layer dried out.

Experiment 1. Burial of seedlings, 1992-1993

When the seedlings were 7 weeks old, 50 plants of similar size were selected for the experiment. For burial, 10 cm diameter plastic drainage pipes of different lengths were placed on top of each pot and then filled with sand to the desired depth. Since ability to survive burial is most likely related to plant height, the seedlings were buried to 0 (control), 25, 50, 75, and 100% of their height based on the length of longest leaf. The absolute burial depths corresponded to 0, 5, 10, 15, and 20 cm of sand deposition, respectively. Ten replicates were used in this experiment.

The net CO_2 exchange rate was measured four times on sunny days at approximately one week intervals using infrared gas analyser (LI-6200 Portable Photosynthesis System). At each date of measurement three readings were taken from one leaf from each replication. Chlorophyll content per gram dry weight was determined by grinding leaf blade segments (approximately 0.6 g) with glass beads in 100% acetone in a chilled mortar and pestle (Elfman et al. 1986). Chlorophyll a:b ratio was then calculated from the absorbance readings at 645 and 663 nm.

Measurements of maximum leaf length and number of leaves were made regularly on all seedlings. After 8 weeks of burial the seedlings were harvested. The following morphological measurements were taken: total leaf area, leaf thickness, length of tap root, presence or absence of adventitious roots, length of stem, length and number of internodes and number of tillers. Leaf thickness was measured by cutting cross sections of leaves, mounting them on glass slides, and then measuring them under a compound microscope. The leaves were separated from the stem at the new soil surface and the stem was separated from the root at the original soil surface. The roots were washed with running tap water. The three fractions, leaves, roots and stems, of the harvested plants were then dried at 90 °C for 48 h and weighed.

Experiment 2. Burial of seedlings, 1993-1994

After 59 days of growth in the greenhouse, plants with an average maximum leaf length of 16.1 ± 0.3 cm were chosen for this experiment. Based on the results of Experiment 1, we used 8 cm as the maximum depth of burial. The burial treatments consisted of (1) no burial (control), (2) one time burial of 4 cm (25% of maximum leaf length), (3) one time burial of 8 cm (50% of maximum leaf length), (4) four repeated burials of 1 cm every eight days, and (5) four repeated burials of 2 cm every eight days. Nine replicates were used in this experiment. The physiological and morphological measurements taken in this experiment were similar to those of Experiment 1 with a few exceptions. Total chlorophyll content was estimated by using a Minolta SPAD-502 (Anon. 1989) chlorophyll meter on all but the scenescing leaves of plants nine days after the final repeated burial treatment. Length of leaf petioles and stem diameter were measured. Growth rates of newly emergent leaves were measured commencing the day after the final repeated burial treatment and continuing until the leaf length had reached 15 cm. The plants were harvested 78 days after the initial burial treatment. Root and stem data were recorded at harvest 78 days after the initial burial treatment. Plant fractions (leaves, roots, stems) in both burial experiments were dried at 85-90 °C for 48 h and then weighed.

Data analysis

The data for both experiments were analysed using the analysis of variance (ANOVA) for balanced data and the general linear model procedure (GLM) for unbalanced data (Anon. 1982). Root to shoot ratios were arcsine transformed before analysis. If ANOVA showed significant effects, Tukey's studentized range test (HSD) was used to determine significant differences between means at $P < 0.05$.

Results

Seed mass

Approximately 70% of the seeds collected in 1992 were empty (weighed < 2 mg). The remaining 30% of the seeds were filled and their mean seed mass was 12.0 ± 4.3 mg (Fig. 1). Approximately 50% of these seeds germinated. Only seedlings originating from seeds weighing > 7 mg survived.

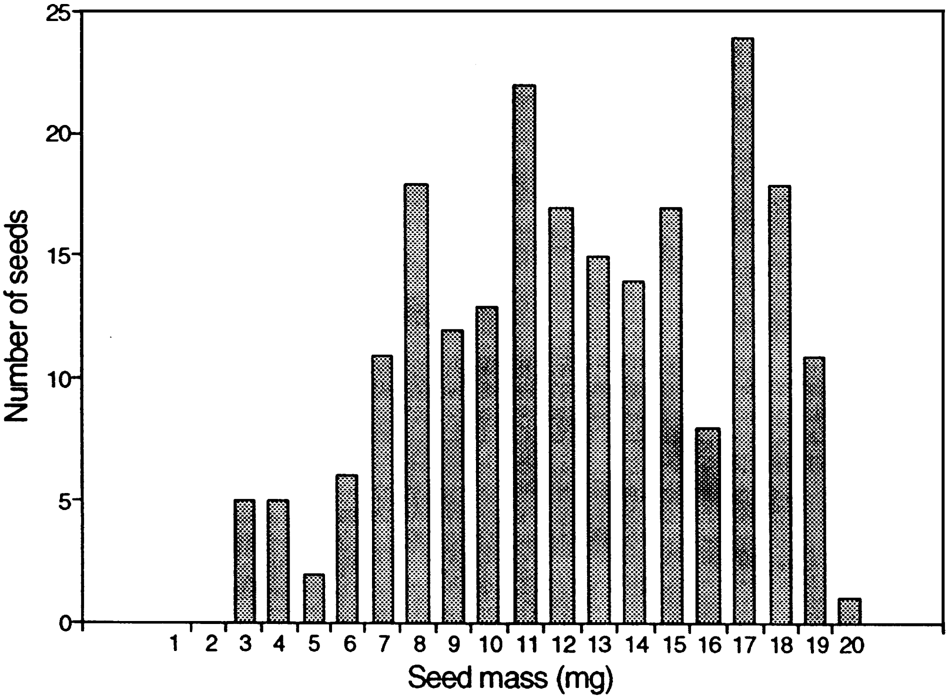

Fig. 1. Seed mass distribution of *Cirsium pitcheri* ($n = 219$; skewness = – 0.24).

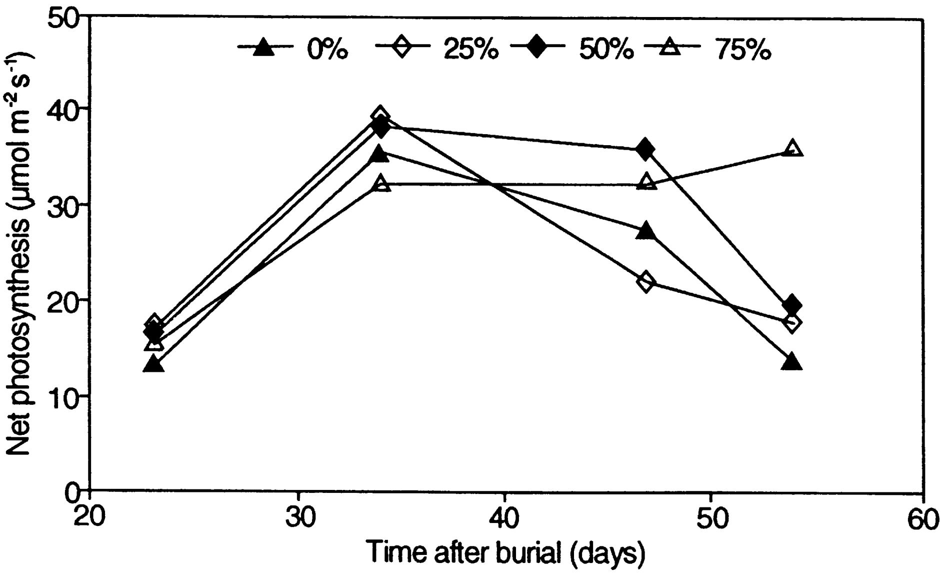

Fig. 2. Mean net photosynthetic rates over time by leaves of *Cirsium pitcheri* after emergence from burial depths of 0, 25, 50, and 75%. None of the plants in the 100 % burial treatment survived.

Experiment 1. Burial of seedlings, 1992-1993

All seedlings survived the 0, 25, and 50% sand burial treatments, 80 % survived the 75% burial but none survived the 100% sand burial. The mean rate of net photosynthesis initially increased in all surviving plants, but decreased later in all but the 75 % burial treatment in which the net photosynthetic rate was still increasing at the end of the experiment (Fig. 2). Buried plants (25%, 50%) exhibited higher mean net photosynthetic rates than controls on 3 out of 4 days of measurements but the differences were not significant.

The total chlorophyll content (mg g^{-1} dry weight) at the end of the experiment was significantly higher in the 75 % burial treatment as compared to control and other treatments. Similarly, the chlorophyll a:b ratio was sig-

Table 1. Mean (± S.D.) total chlorophyll content (mg/g dry weight), chlorophyll a/b ratio of leaves, and morphological measurements of *Cirsium pitcheri* after emergence from burial depths of 0, 25, 50, and 75% (*n* = 10, 10, 10, and 8, respectively) in Experiment 1.

	Burial (%)			
Variable	0	25	50	75
Chlorophyll content	2.70 ± 0.25 a	2.53 ± 0.34 a	2.98 ± 0.20 a	3.32 ± 0.42 b
Chlorophyll a:b ratio	2.63 ± 0.08 a	2.67 ± 0.07 a	3.07 ± 0.15 b	2.69 ± 0.08 a
Total leaf area (cm^2)	132 ± 13 a	138 ± 29 a	146 ± 32 a	69 ± 41 b
Leaf thickness (mm)	0.12 ± 0 a	0.17 ± 0.05 a	0.16 ± 0.03 a	0.16 ± 0.03 a
Number of internodes	1.00 ± 0 a	1.45 ± 0.87 ab	3.10 ± 1.1 bc	5.60 ± 1.5 c
Internode length (cm)	0.86 ± 0.25 a	4.23 ± 1.57 b	2.81 ± 1.08 b	2.03 ± 0.24 b
Tap root length (cm)	7.95 ± 0.98 a	7.50 ± 2.44 a	7.00 ± 1.33 a	3.94 ± 0.68 b
Leaf dry weight (g)	1.16 ± 0.15 a	1.20 ± 0.31 a	1.35 ± 0.33 a	0.56 ± 0.36 b
Stem dry weight (g)	0.05 ± 0.02 a	0.31 ± 0.09 b	0.45 ± 0.10 b	0.37 ± 0.19 b
Root dry weight (g)	1.91 ± 0.39 a	2.43 ± 0.74 a	2.01 ± 0.70 a	0.41 ± 0.32 b
Total dry weight (g)	3.08 ± 0.47 b	4.18 ± 0.66 a	3.79 ± 0.77 ab	1.48 ± 0.63 c

* Means in each row of a variable for the four burial depths followed by different letters are significantly different at $P < 0.05$ according to Tukey's Test (ANOVA). No plants survived the 100 % burial treatment.

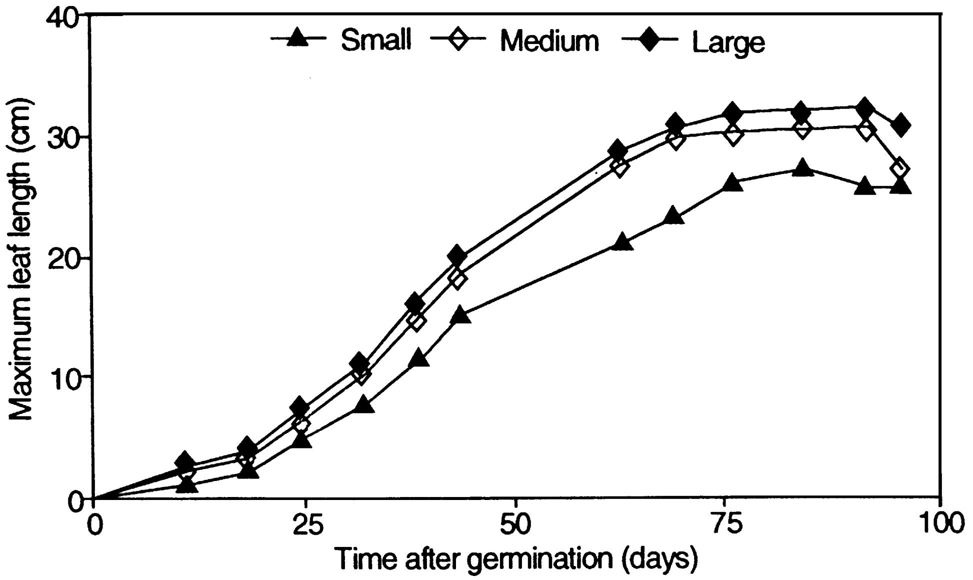

Fig. 3. Mean maximum leaf length (cm) over time for large, mid-sized, and small seed mass groups of *Cirsium pitcheri*.

nificantly higher in the 50 % burial treatment than control (Table 1). The number of leaves per plant were exchanged on a continual basis and stabilized at approximately 6 (control), 7 (25%, 50%), and 8 (75%) leaves per plant at the end of the experiment. The maximum leaf length of a seedling was related to seed mass (Fig. 3). The mean leaf length of seedlings from small seeds was significantly lower than those from the other two seed classes for most of the growing period (Fig. 3).

The total leaf area per plant did not differ significantly between the 0, 25, and 50% burial treatments (Table 1), but there was a significant decrease in the 75% burial treatment. Leaf dry weight followed the same pattern as leaf area, but leaf thickness did not vary significantly between any of the treatments (Table 1). The number of stem internodes increased with burial depth (Table 1). For example, plants buried to 50 and 75 % of their height had significantly more visible internodes per plant than control. The average internode length of buried treatments was also significantly higher as compared to control (Table 1).

The dry weight of stems in the burial treatment was significantly ($P < 0.05$) higher than the control; however, the burial treatments did not differ significantly among themselves (Table 1). Most of the stems in buried treatments had formed adventitious roots. Some buried plants also produced new tillers (1 to 5 per plant) from the crown of the stems. This was especially evident in the 75% burial group where 5 out of 8 plants had produced tillers. The length of the tap root and the root dry weight were not affected by the burial treatments except in the 75% burial depth in which there was a significant decrease (Table 1). The total dry weight per plant was significantly higher in the 25% burial treatment than control (Table 1). The 50 % burial depth did not differ from control but a significant decrease in dry weight was recorded in the 75 % burial treatment.

Experiment 2. Burial of seedlings, in 1993-1994

Burial of plants had a stimulatory effect on the maximum leaf length and number of leaves per plant of *C. pitcheri* (Fig. 4). Repeated burial of plants resulted in stimulation of plant growth within about 14-21 days. However, one time burial of 4 and 8 cm showed a delay of 15 and 40 days, respectively, in their stimulatory response (Fig. 4). At harvest (after 78 days), burial treatments had significantly ($P < 0.05$) greater leaf lengths than the control with no significant differences between the burial treatments. The apparent increase in leaf length on the last day of measurement is due to measurement of leaves from their point of attachment to the stem below sand which was only possible at harvest. The number of leaves at harvest was significantly greater than control for only the 8 cm repeated burial treatment (Fig. 4). The apparent rise in the number of leaves at harvest occurred because some of the leaves became visible only when the plants were harvested.

All burial treatments had significantly higher leaf

Table 2. Mean ± S.D. of growth measurements of *Cirsium pitcheri* plants subjected to different burial treatments of 0.4 cm (single burial), 4 cm (repeated burial), 8 cm (single burial) and 8 cm (repeated burial).

Variable*	Burial depth (cm)				
	0	4		8	
		Single	Repeated	Single	Repeated
Leaf growth rate (cm/day)	0.70 ± 0.31 a	1.15 ± 0.69 bc	1.38 ± 0.43 c	0.94 ± 0.83 ab	1.28± 0.84 c
Total leaf area (cm^2)	115.90 ± 51.41 a	175.6 ± 83.13 ab	201.10 ± 70.11 ab	206.90 ± 119.21 ab	290.60± 177.63 b
Chlorophyll reading (spad)	39.00 ± 6.38 a	41.60 ± 6.97 ab	44.00 ± 6.41 ab	46.50 ± 6.18 b	44.70± 6.19 ab
Petiole length (cm)	4.76 ± 1.51 a	7.79 ± 1.43 bc	7.85 ± 1.22 bc	7.32 ± 1.02 b	8.35± 1.70c
Number of internodes	0 ± 0 a	4.33 ± 0.71 b	5.11 ± 0.93 b	7.00 ± 1.32 c	7.44± 1.24 c
Stem length (cm)	0 ± 0 a	2.09 ± 0.51 b	2.33 ± 0.65 b	6.44 ± 1.15 c	6.11± 0.72 c
Stem diameter (mm)	5.89 ± 1.16 a	6.04 ± 0.89 a	6.44 ± 1.07 a	6.71 ± 0.96 a	7.16± 2.02 a
Belowground dry weight (g)	2.36 ± 0.86 a	4.16 ± 2.03 a	3.48 ± 1.57 a	2.90 ± 2.13 a	4.63± 2.37 a
Leaf dry weight (g)	1.17 ± 0.62 a	2.55 ± 1.09 ab	2.25 ± 0.99 ab	2.19 ± 1.34 ab	3.12± 2.13 b
Total dry weight (g)	3.53 ± 1.46 a	6.41 ± 3.00 ab	5.73 ± 2.55 ab	5.10 ± 3.33 ab	7.75± 4.47 b
Root/shoot ratio	2.15 ± 0.04 a	1.94 ± 0.07 a	1.54 ± 0.03 ab	1.27 ± 0.11 b	1.60± 0.05 ab

* Means in each row of a variable for the five burial treatments followed by different letters are significantly different at $P < 0.05$ according to Tukey's test (ANOVA).

growth rates (before reaching a length of 15 cm) than controls except the 8 cm single burial treatment (Table 2). The total leaf area at harvest was significantly greater for the 8 cm repeated burial treatment as compared to control (Table 2). Leaf area of all other treatments did not differ significantly. Except for the 8 cm single burial treatment, none of the other treatments had significantly greater total chlorophyll SPAD values than the control (Table 2).

At harvest in all replicates of the 8 cm single burial treatment, the leaves had decayed in situ, the stem had increased in length and the plant had produced new leaves at the apex. In contrast, in all other burial treatments the petioles of leaves were significantly longer than control (Table 2). Within the burial treatments, the 8 cm repeated burial treatment had significantly shorter petiole length than 8 cm single burial treatment (Table 2) and the leaves had survived on the nodes of the stem. More than one rosette was produced in one replicate of the 8 cm repeated burial treatment and one replicate of the 4 cm single burial treatment. Adventitious roots were found in the buried portion of the stems near the sand surface.

The stem lengths and the number of internodes in all burial treatments were significantly longer than control (Table 2). Similarly, 8 cm burial depths had significantly longer stems and greater number of nodes than the 4 cm burial treatments. Although stem diameter increased with burial depth there were no significant differences between control and any of the treatments (Table 2).

The belowground dry weight did not show any differences between treatments (Table 2). Leaf and total dry weight per plant were significantly greater than control only in the 8 cm repeated burial treatment (Table 2). The root to shoot ratio was significantly smaller in the 8 cm single burial treatment as compared to the 4 cm single burial and control treatments (Table 2). The 4 and 8 cm repeated burial treatments did not differ significantly from any of the burial treatments (Table 2).

Discussion

The populations of Pitcher's thistle (*Cirsium pitcheri*) are declining probably due to the recreational overuse of shoreline sand dune systems (Loveless 1984; McEachern 1992). Three major causes, erosion of sand, burial by sand, and herbivory by white-tailed deer, may lead to the demise of its populations. We will examine each factor separately. The erosion of sand from the base of plants is a consequence of recreational use of the dunes. Paths devoid of vegetation are created due to trampling by people (Liddle 1975). Wind erosion then enlarges the path thus creating a blowout. The erosion of sand exposes the roots of plants to wind and high temperatures and the plants die of desiccation. Burial by sand is a natural recurrent event in sand dune systems but trampling by humans accentuates it. Sand eroded from the windward side of a blowout is deposited on top of plants on the leeward side of it. Herbivory by white tailed deer is a recent threat to the populations of *C. pitcheri* (Maun

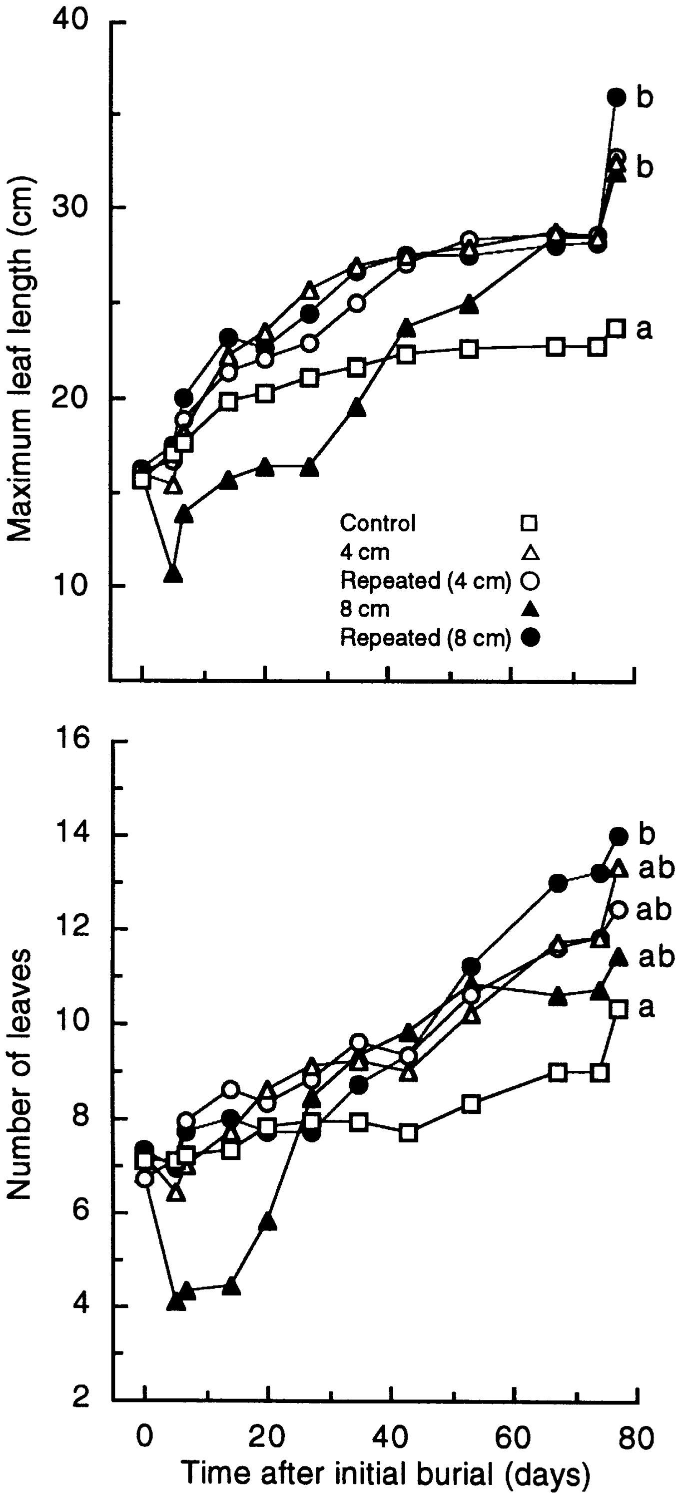

Fig. 4. Mean maximum leaf length (cm) and number of leaves per plant of *Cirsium pitcheri* under control and burial treatments on different days after initial burial. Means with different letters on the last date of harvest are significantly different at $P < 0.05$ according to Tukey's test.

& Crabe 1995) which results in consumption of leaves of juvenile plants and capitula of flowering plants (Phillips 1995).

In this study we examined the effects of burial of *C. pitcheri* plants under controlled conditions. The data showed that the plants did not survive when they were completely buried in sand. Following burial to 100% of a plant, the normal functioning of a leaf is impaired and it undergoes an etiolation response (Sykes & Wilson 1990). The photosynthetic area of a plant shifts from an energy manufacturing state to an energy consuming state. A plant may survive if the leaves are re-exposed within a few days after a burial episode (Harris & Davy 1988) or if they grow through the sand deposit. For emergence through a sand deposit, the plant requires energy reserves which are dependent on the season and stage at which a plant is buried. For example, in temperate latitudes where burial occurs in late fall, winter, or early spring (Davidson-Arnott & Law 1990), the chances of survival are good because the plant is dormant and has plenty of stored reserves (Maun & Lapierre 1984). In contrast, if complete burial occurs in the middle of summer, the chances of survival are low because the plant primarily depends on its photosynthetic area which has been overwhelmed by sand (Perumal 1994). Nevertheless, our data showed that *C. pitcheri* was not only capable of withstanding partial burial but also showed growth stimulation. Several studies have shown a similar stimulatory response of plants following partial burial in sand (Disraeli 1984; Eldred & Maun 1982; Maun & Lapierre 1984). The reasons for this increase are not well understood. The primary factor may be improved soil conditions for plant growth (Disraeli 1984), mycorrhizal fungi association (Little & Maun 1996), lowered water stress (Olson 1958) and temporary escape from harmful soil pathogens (van der Putten 1988, 1993). Apparently, several groups of fungi and nematodes affect the growth of *Ammophila arenaria* plants (De Rooij-van der Goes 1996).

Burial of plants also improved total chlorophyll content, chlorophyll a:b ratio and leaf thickness. Similar results were obtained on two dune colonizing grasses, *Ammophila breviligulata* and *Calamovilfa longifolia*, by Yuan et al (1993) who showed that burial in sand increased all three traits mentioned above. However, not all plant species show a positive burial response (Sykes & Wilson 1990) possibly due to different life history strategies.

Another important consideration in such studies is the mode of burial of plants. For example, how does gradual burial of plants compare with one time burial of the same magnitude. Data showed that gradual burial of plants to 4 or 8 cm depths produced higher values of most traits than the single burial treatment. The repeated burial treatment is more akin to the natural episodes of burial during summer and would allow plants to adapt more quickly than single one time burial (Lee & Ignaciuk 1985). One major difference was the length of time required to recover from burial. Single burial of plants precipitated a set-back and it took a long time for plants to recover. There was clear evidence of mortality of buried leaves in the 8 cm single burial treatment because the leaves below the burial level had decayed in situ. In contrast, the plants in the repeated burial treatments recovered quickly and exhibited enhanced growth mainly because a gradually buried plant has all or most of its leaf area intact and continues to grow unabated. When a plant is completely inundated by sand, it must divert all of its stored energy to the growing organs to emerge above the sand surface (Harris & Davy 1988). However, as soon as it emerges above the sand surface, it regains and even surpasses its previous physiological performance (Perumal 1994). Thus, in the long term no significant differences between the two burial treatments could be seen.

The *C. pitcheri* plants grew through the sand by the elongation of stem internodes, increase in the number of nodes, elongation of petioles of leaves and the formation of new tillers. A number of grasses also use some of these morphological responses to emerge above the sand deposits (Maun & Lapierre 1984; Disraeli 1984; Maun 1996b). The elongation of the stem in *C. pitcheri* occurred at the cost of development of the root system. Thus, after burial all energy was at first allocated to growth which allowed the plant to regain the photosynthetic material. Plastic responses to burial similar to the ones in *C. pitcheri* have also been found in other studies (Sykes & Wilson 1990). These mechanisms are all essential for survival in dune systems. However, as pointed out by Harris & Davy (1988) even a passive maintenance response may facilitate survival in frequently disturbed habitats. The gradual repeated burial was more conducive to petiole elongation than the one time burial of 4 or 8 cm. According to Sykes & Wilson (1990) several other plant species, such as *Hydrocotyle bonariensis*, responded to sand accretion by an increase in the length of leaf petioles.

We would now attempt to answer the question posed earlier. Is excessive burial in sand a cause of decline of *C. pitcheri* populations? The data show that juvenile vegetative plants of this species are well adapted to withstand small amounts of sand burial but excessive burial is detrimental to the plants. In natural populations, the amount of sand accretion ranged between 0.1 and 9 cm per year along Lake Huron (Perumal 1994) and 1 to 24 cm along Lake Michigan (McEachern et al. 1993). However, during the growing season (May-September), it may not exceed 3 cm. The plant can tolerate one time burial of about 15 cm or 75% of its height. However, since the experiment was done in a greenhouse and the plants in natural habitats are most often exposed to gradual sand burial, the chances of survival may be much higher. McEachern (1992) showed that large plants growing in the dunes may survive about 20 cm of sand deposition. Nevertheless, in natural areas used heavily for recreation the amount of sand accretion may be above the threshold for survival of the species. That may be why the species has disappeared from heavily used dunes. However, since *C. pitcheri* requires an open habitat with some sand movement, dune stabilization may also pose a threat to its continued existence.

Remarks on management

Successful management of existing populations and restoration of rare and threatened species requires an understanding of their life history parameters, a knowledge of the severity of natural and man-made environmental stresses and ability of the species to withstand such stresses (McEachern et al. 1993). On the foredunes of Lakes Huron and Michigan *C. pitcheri* is the only threatened plant species whose populations occur in a shifting disequilibrium with unpredictable consequences (Bowles & Apfelbaum 1989). Although the species thrives only in sand dune habitats with large scale dynamic and often stochastic disturbance regimes, it is susceptible to anthropogenic impacts which rarely if ever replicate natural disturbance regimes (Pavlovic 1993). That may be why *C. pitcheri* has been extirpated from all but the wilderness area of Pinery Provincial Park which is not easily accessible to park visitors. Thus for the preservation of remnant populations, restoration of extirpated populations and eventual delisting of *C. pitcheri*, we will propose several steps. 1. The wilderness area at the Pinery be given the status of a nature preserve. 2. More nature preserves of this type be created at other foredune sites containing *C. pitcheri* populations. 3. Select suitable areas on foredunes and artificially re-establish new populations of *C. pitcheri*. 4.Steps be taken to reduce the population size of white-tailed deer and to maintain it at an optimal density. Finally, a conservation strategy and recovery plan needs to be formulated for the long term management of *C. pitcheri* in Canada.

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