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Survival and Growth of *Chrysanthemum pacificum* Nakai Seedlings at an Inland Site

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Abstract Seeds of the maritime species *Chrysanthemum pacificum* were sown on bare ground some distance from shore to determine what factors prevent it from becoming established in inland areas. The sown area was divided into two plots. All emerging plants except *C. pacificum* were frequently removed from one of the plots (weeded plot), whereas the second plot was not manipulated (control plot). Although seed germination began simultaneously in the two plots, *C. pacificum* seedlings in the control plot were gradually covered by inland annuals and perennials that emerged naturally from buried seeds. Subsequent observations of the growth and survival of *C. pacificum* seedlings over three years revealed a marked difference between the two plots. Seedlings in the weeded plot grew well, sprouted new shoots, and flowered, and the number of surviving shoots increased over time. In contrast, seedling growth in the control plot was substantially lower than in the weeded plot. The number of surviving shoots decreased gradually, and only 10% of those observed in the first year survived to the end of the third year. These results indicate that although *C. pacificum* has the potential to grow and reproduce away from the seashore, it is unable to become established in the presence of naturally emerging inland plants. This inferior competitive ability could be one factor that makes it difficult for *C. pacificum* to become established in inland areas.

Key words: *Chrysanthemum pacificum*, competition, growth, habitat segregation, inland, maritime plants, seedling, survival.

Chrysanthemum pacificum Nakai is a typical maritime perennial that is distributed along the Japanese coast from the Boso peninsula, Chiba, to the Omae promontory, Shizuoka. On the Boso peninsula, this species forms dense tussocks < 1 m high that spread over cliffs and slopes facing the sea. Its high tolerance to salt spray is one of the main factors that enable *C. pacificum* to become established in these exposed habitats (Yura, 1997). Vegetation on coastal cliffs is sparse and composed mainly of short perennials such as *Farfugium japonicum* (L.) Kitam., *Peucedanum japonicum* Thunb., and *Boehmeria biloba* Wedd.; *C. pacificum* is one of the most frequently occurring species.

Similar to other maritime plants, the distribution of *C. pacificum* is strictly limited to the seashore, and, with few exceptions, this species is not found in inland areas even in the vicinity of the sea. Although *C. pacificum* seeds have no special means for broad dispersal, they may occasionally be dispersed to inland areas, where they could potentially germinate. *C. pacificum* also has rhizomes that contribute to the growth of the tussocks over time. The complete absence of *C. pacificum* from inland areas suggests that some factor(s) regularly prevent this species from becoming established at sites even a short distance from shore.

Seashore environments have been intensively investigated, and many characteristic factors that are harmful to inland plants have been described, including salt spray (Oosting, 1942; Boyce, 1954; Wagner, 1964; Parsons and Gill, 1968; Barbour, 1978; Cartica and Quinn, 1980; Sykes and Wilson, 1988; Yura, 1997), high soil salinity (Crawford, 1989; Ishikawa *et al.*, 1995; Packham and Willis, 1997), soil nutrient deficiencies (Kachi and Hirose, 1979; Pakeman and Lee, 1991a; Pakeman and Lee, 1991b), and frequent erosion or deposition of substrate

(Marshall, 1965; van der Valk, 1974; Avis and Lubke, 1985; Moreno-Casasola, 1986). In contrast, only a few studies have investigated the growth or survival of maritime species under inland conditions. Goldsmith (1973) conducted a competition experiment with the maritime species *Armeria maritima* and the inland species *Festuca rubura* and found that although the yield of *A. maritima* under non-saline conditions was higher than under saline conditions, *F. rubra* had a stronger competitive advantage over *A. maritima* under non-saline conditions. Okusanya (1979) compared the relative growth rates of some maritime cliff species to those of inland species, and showed that although maritime species did not require saline conditions to grow, the growth rates of inland species were higher than those of most maritime species under non-saline conditions.

Like most other maritime species, *C. pacificum* can easily be cultivated outdoors in pots of inland soil far away from the shore. Therefore, it may be assumed that the absence of naturally growing *C. pacificum* in inland areas is caused by its inferior competitive ability compared to inland plants. To verify the competitive disadvantage of *C. pacificum* seedlings, I conducted an outdoor experiment at an inland site where the abiological environment was considered suitable for the survival and growth of *C. pacificum*. The survival and growth rate of seedlings grown in a pure stand were compared to seedlings competing with naturally emerging inland plants. After *C. pacificum* seeds were sown on bare ground, the site was divided into two plots; in one plot, all emerging plants except *C. pacificum* were removed frequently, whereas the second plot was left unweeded. I then compared the growth and the number of shoots on *C. pacificum* seedlings in the weeded vs. the unweeded plots.

Materials and Methods

On 24 February 1996, *C. pacificum* seeds were sown on bare ground (40 m^2) in 32 quadrats (25×25 cm) in the experimental field of Ecology Park (35°35′N, 140°8′E), a study area belonging to the Natural History Museum and Institute, Chiba, Chiba-shi, Japan. Quadrats were arranged in a grid at intervals of at least 0.5 m. Seeds were collected in January 1996 from a maritime cliff in Misaki-machi, Chiba Prefecture, Japan, and enough seeds were sown to yield ~150 seedlings per quadrat.

The study site was originally covered by perennials such as *Solidago altissima* L., *Artemisia princeps* Pamp., and *Miscanthus sinensis* Anderss, and was weeded and tilled at the end of November 1995. Rhizomes and roots of these existing plants were removed from the soil as thoroughly as possible. The substrate of the area, including the experimental field, was andosolic, i.e., the soil was dark and contained material rich in volcanic ash and organic matter. The altitude of Ecology Park was 18 m a.s.l., and the nearest ocean was ~4 km to the west. No maritime plants, including *C. pacificum*, were found among the weeds and grasses growing naturally in or around the park.

After sowing, the study site was divided into two equal plots adjacent to each other with 16 quadrats per plot. In March, when the *C. pacificum* seeds began to germinate, many seedlings of other species also emerged from buried seeds. In late March, all seedlings of these other species, whether they had emerged inside or outside of the quadrats, were removed from one of the plots (weeded plot), whereas nothing was removed from the other (control) plot. Seedlings were removed frequently from the weeded plot through to the end of the study.

Surviving *C. pacificum* seedlings were counted regularly in the same six quadrats in each plot. The number of shoots on *C. pacificum* seedlings in each quadrat was counted every other week. When new aboveground shoots sprouted from the base of the seedlings, these shoots were counted as separate shoots, whether they emerged inside or outside the quadrats. The remaining ten quadrats in each plot were left for harvesting *C. pacificum* seedlings.

On 13 April, 14 June, 7 August, and 31 October, ten seedlings were harvested randomly from one quadrat in each plot to monitor the growth of *C. pacificum*. The quadrats from which seedlings were taken were excluded from the next harvest. Each harvested seedling was divided into stems, leaves,

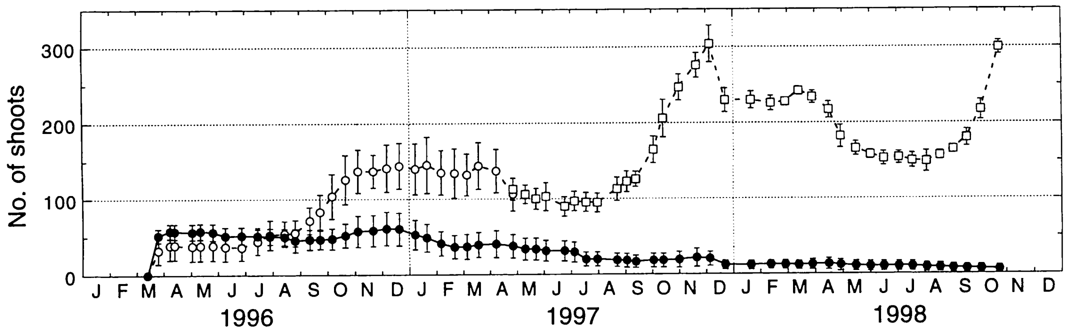

Fig. 1. Seasonal changes in the number of surviving *Chrysanthemum pacificum* shoots in a plot from which all other species were removed (weeded plot; open circles and squares) and in a plot that was left unweeded (control plot; closed circles). Values are mean±s.d. of six quadrats established in the control plot and six quadrats (February 1996–May 1997) and three quadrats (May 1997–November 1998) in the weeded plot. All quadrats had an area of 25×25 cm. *C. pacificum* seeds were sown on 24 February 1996.

and other parts (e.g., flowers). Because it was not possible to excavate whole roots, they were excluded from the measurements. After the lengths of all stems had been measured, they were dried at 70℃ for >48 h, and dry weights were determined. Stem lengths of the seedlings were calculated by adding the length of every stem obtained from each seedling.

I continued counting *C. pacificum* shoots over the next two years. In the weeded plots, the average number of shoots in the six quadrats increased and remained at >100 during the winter of 1996; therefore, three quadrats were selected from the original six quadrats and used for counting seedlings after May 1997.

On 23 October 1998, the day of the last count, the height of the tallest shoot in each quadrat was measured. Because *C. pacificum* plants in the control plot had abnormally elongated stems, the aboveground parts of all plants in the control plot were harvested on 4 November 1998. Harvested plants were divided into stems and leaves. After the stem lengths had been measured, the leaves and stems were dried at 70℃ to determine their dry weight. *C. pacificum* in the weeded plots were not harvested, because the numerous entangled shoots and rhizomes made it impossible to harvest the plants intact.

Results

Differences in the number of shoots in the two plots

In both plots, *C. pacificum* seeds began to germinate in March. Although the number of seedlings increased abruptly, it soon stabilized at about 50 seedlings per quadrat in both plots (Fig.1). The number of surviving seedlings did not show marked increases or decreases until the end of June.

Differences between the two plots became evident beginning in autumn of the first year. In the weeded plot, new shoots started to grow from the base of the seedlings. The number of new shoots increased rapidly until the total number of shoots reached almost 150 per quadrat, indicating that on average nearly two new shoots sprouted from each seedling. Simultaneous with the extension of new shoots, inflorescences began to appear at the terminus of main shoots. Flowering was observed in all quadrats in the weeded plot, and many seeds were subsequently fertilized and dispersed naturally.

With the development of new shoots in the weeded plot, the main shoots became senescent and died during the following spring (1997). The number of surviving shoots decreased to about 100 per quadrat, which was twice as many as in the previous summer. As mentioned above, the number of quadrats in which seedlings were counted was reduced to three in April 1997. The number of shoots in these three quadrats did not show considerable changes throughout the summer. New shoots sprouted from the base of extending shoots early in autumn, and increased as rapidly as in the first year (1996). Flowering was also observed in all quadrats. Extended shoots, whether they bore inflorescences or not, began to die in winter. Although some new, short shoots also died, probably due to intraspecific competition, 150 shoots remained in the summer of the third year (1998). Sprouting of new shoots and flowering were observed in the autumn of 1998. The maximum height of shoots in the three quadrats on 23 October 1998 was 38.5, 29.5, and 41.8 cm.

In contrast to the weeded plot, only a few new shoots grew from the base of *C. pacificum* seedlings in the autumn of the first year (1996) in the control plot. Therefore, the mean number of *C. pacificum* shoots increased only slightly by the end of the first year. All quadrats in the control plot gradually became dominated by other species, such as *Ambrosia artemisiifolia* L. var. *elatior* Desc., *Artemisia princeps* Pamp., *Oenothera biennis* L., and *Setaria faberi* Herrm., which were common weeds around the study area. Numerous seedlings of other species emerged from buried seeds, and most of them grew taller than *C. pacificum* seedlings; thus, *C. pacificum* became more shaded with increased growth of other species. The maximum height of *C. pacificum* seedlings in July of the first year (1996) was ~5 cm, while *A. artemisiifolia* var. *elatior* and *A. princes* measured 41 and 85 cm, respectively. In September, the maximum height of *C. pacificum* seedlings was 8 cm, whereas *A. princeps*, *S. faberi*, and *Trifolium pretense* L. were 136, 50, and 27 cm tall.

The number of surviving *C. pacificum* shoots in the control plots decreased in the second year (1997). In contrast to the previous year, *C. pacificum* plants were already densely covered by other species such as A. princeps, *Lolium multiflorum* Lam., *Erigeron annuus* L. and *T. pretense* in the spring. Although a number of *C. pacificum* plants survived the first half of the second year, the growth form of these individuals differed from that of seedlings in the weeded plot. All *C. pacificum* plants had slender and unusually elongated stems with leaves attached only around the terminus. Some plants were unable to remain upright and collapsed; all of their leaves withered and dropped, and these plants were considered dead. Although a few new shoots sprouted from the base of old shoots in the autumn, the total number of shoots in the control plot decreased by 77% during the second year (1997).

The reduction of *C. pacificum* plants in the control plot continued during the third year (1998). The dominant species covering *C. pacificum* plants were *A. princeps*, *Miscanthus sinensis* Anderss., *Solidago altissima* L., *E. annuus* and *Amphicarpaea edgeworthii* Benth. var. *japonica* Oliver, which were similar to those from the previous year (1997). As most stems of surviving *C. pacificum* shoots were not strong enough to support themselves, they tended to fall or lean on other plants. The maximum height of *C. pacificum* shoots in each of the six quadrats on 23 October 1998 was 29.3, 19.5, 14.6, 25.5, 19.6, and 15.9 cm, whereas the maximum stem length was 53.0, 37.5, 48.1, 48.2, 50.7, and 17.6 cm, respectively, indicating that most shoots had leaning or twisted stems. The number of surviving *C. pacificum* shoots at the end of the study (November 1998) was 10.2% of the maximum number recorded in the winter of the first year (1996–1997).

Comparison of the growth of *C. pacificum* between the two plots

The growth rate of *C. pacificum* seedlings in the weeded plot was much higher than in the control plot (Fig. 2). Differences in dry weights of the aboveground parts of the seedlings were already significant ($P < 0.01$, Mann-Whitney *U*-test) at the second harvest in June. At the fourth harvest in October, the average dry weight in the weeded plot was 73 times larger than in the control plot. Differences in the average dry weight of leaves and stems and in stem length were also large between the two plots in October 1996 (Table 1). At the last harvest on 4 November 1998, a total of 35 *C. pacificum* plants survived in six quadrats of the control plot. The average dry weight of the aboveground parts of these plants was 178.9 g (standard error = 27.2),

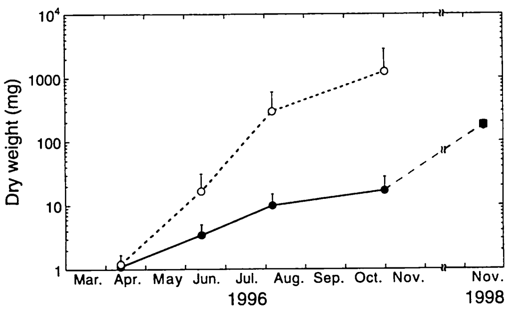

Fig. 2. Seasonal changes in the dry weight of the aboveground parts (whole plant minus roots) of *Chrysanthemum pacificum* seedlings in a plot from which all other species were removed (weeded plot; open circles) and in a plot that was left unweeded (control plot; closed circles). Aboveground parts of all *C. pacificum* plants surviving in the control plot in November 1998 were also harvested (closed square). Values are mean±s.d. of ten plants in 1996 and 35 in 1998.

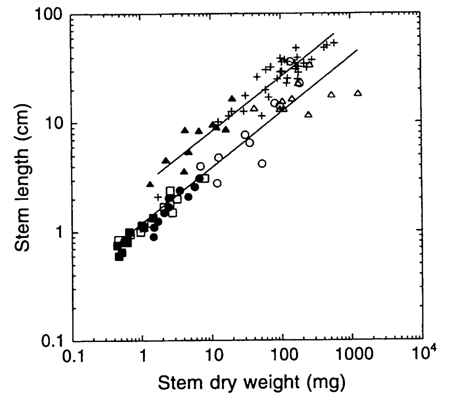

Fig. 3. Log-log (base 10) plot of stem dry weight against stem length of *Chrysanthemum pacificum* seedlings and plants harvested on 14 June (squares), 7 August (circles), and 31 October (triangles) 1996 from a plot in which all other species were removed (weeded plot; open squares, circles, and triangles) and a plot that was left unweeded (control plot; closed squares, circles, and triangles). Crosses represent plants that were harvested from the control plot on 4 November 1998. Solid diagonal lines are the regression lines obtained from all seedlings and plants harvested from the weeded plot (all open figures) and from the control plot on 4 November 1998 (crosses).

which was less than that of the seedlings harvested from the weeded plot in October 1996.

A weak correlation ($r=0.69$) was observed between stem dry weight and stem length obtained from the seedlings harvested from the weeded plots in June, August, and October 1996, when they were plotted on a double logarithmic plot (Fig. 3). A stronger correlation ($r=0.86$) between the two measurements was observed for plants harvested from the control plot in 1998. Although the slopes of the two regression lines were almost equivalent, the line for the control plants was higher than that of the seedlings from the weeded plot, indicating that plants in the control plot had longer stems than seedlings of the same stem dry weight in the weeded plot. The relationship between these two measurements obtained from seedlings harvested from the control plot in June and August 1996 was similar to the weeded plot. However, seedlings harvested in October 1996 had the relationship closer to plants harvested from the control plot in 1998.

Leaf dry weight was higher than stem dry weight for all but one seedling harvested from the weeded plot in 1996, while leaf dry weight was lower for all but one plant harvested from the control plot in 1998 (Fig. 4). The average ratio of leaf dry weight to stem dry weight of seedlings in the weeded plot (average±s.d.=3.6±2.0) was significantly higher ($P<0.001$, Mann-Whitney *U*-test) than that of the control plot (average±s.d.=0.23±0.23). Significant correlations between stem dry weight and leaf dry weight were also observed for plants harvested from both the weeded plot ($r=0.95$) and the control plot in 1998 ($r=0.76$). The points obtained from seedlings harvested from the control plots in 1996 had a tendency to shift over time from the regression line of the weeded plot to that of the control plot.

Discussion

The environment and natural vegetation of the study area were typical of an inland site. The intensity of salt spray and the sodium content of soil water in the study area were far lower than those of the seashore where *C. pacificum* grows naturally (Yura, 1997). In this inland site, *C. pacificum*

Table 1. Leaf dry weights, stem dry weights, and stem lengths of *Chrysanthemum pacificum* seedlings in weeded (W) and control (C) plots (means±s.d.).

Harvesting date	No.[a]	Leaf dry weight (mg)		Stem dry weight (mg)		Stem length (cm)[b]	
		W	C	W	C	W	C
13 Apr 1996	10	1.01±0.42	0.90±0.28	0.20±0.07	0.21±0.10	0.56±0.13	0.57±0.17
14 Jun 1996	10	14.2±12.4	2.69±1.31	2.51±2.19	0.75±0.34	1.65±0.71	0.91±0.24
7 Aug 1996	10	230±245	6.59±3.48	64.9±59.9	3.30±1.92	11.8±10.6	1.87±0.71
31 Oct 1996	10	683±753	8.46±6.46	428±576	8.45±4.75	41.9±28.8	5.94±2.33
4 Nov 1998	35		32.5±36.4		146±130		29.7±12.0

[a] Number of seedlings harvested from each plot.
[b] Total length of all stems obtained from one seedling.

was able to germinate, grow, reproduce vegetatively, and even set seed when other species were removed from the surrounding area (Fig.1, 2). Similar to studies by Goldsmith (1973) and Okusanya (1979), the results of this study demonstrated the inherent ability of the maritime plant *C. pacificum* to grow and reproduce in an area away from the seashore. Physical characteristics of the seashore, such as salt spray, are not obligatory environmental factors for *C. pacificum* to become established.

The main factor that prevented *C. pacificum* from becoming established in the inland site was competition by other species. Because seeds were initially sown on bare ground the competitive effect was minimal at the beginning of the study, even in the control plot. However, many seedlings of pioneer species that were common in the disturbed inland organic soil emerged and outgrew the *C. pacificum* seedlings that had germinated at the same time. When other species surrounding *C. pacificum* seedlings were not removed, the growth of *C. pacificum* was suppressed as early as June of the first year (1996), and only a few new sprouts were observed in autumn (Fig. 1, 2). The number of surviving shoots decreased after the second year (1997). The disadvantages of *C. pacificum* in competition with inland species may considerably reduce the probability of *C. pacificum* expanding its distribution from the shore to inland areas.

In addition to differences in seedling survival and growth rates, differences in plant growth form were also observed between the two plots (Fig. 3, 4). *C. pacificum* plants that had survived competition for three years in

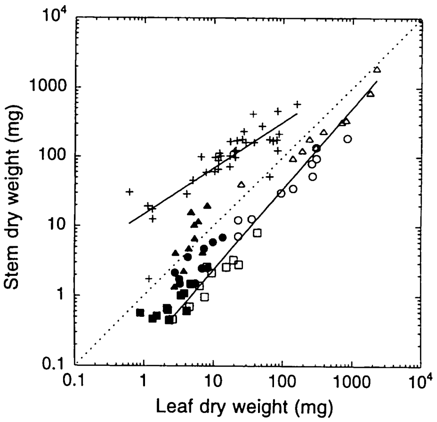

Fig. 4. Log-log (base 10) plot of leaf dry weight against stem dry weight of *Chrysanthemum pacificum* seedlings and plants harvested on 14 June (squares), 7 August (circles), and 31 October (triangles) 1996 from a plot in which all other species were removed (weeded plot; open squares, circles, and triangles) and a plot that was left unweeded (control plot; closed squares, circles, and triangles). Crosses represent plants that were harvested from the control plot on 4 November 1998. Solid diagonal lines are the regression lines obtained from all seedlings and plants harvested from the weeded plot (all open figures) and from the control plot on 4 November 1998 (crosses). A dotted diagonal line depicts the isometric relation between the two variables.

the control plot had an average dry weight comparable to that of the first year plants in the weeded plot, but they showed unusual growth forms (Table 1). Plants that had been competing with other species had a lower leaf dry weight and longer stem length than those in the weeded plot. Stem elongation is one of the typical responses that sun plants show under shaded conditions. Hiroi and Monsi (1963) found that shading caused a decrease in the allocation of dry matter to the leaves of *Helianthus annuus*. In response to shade cast by other plants, *C. pacificum* seemed to elongate its stems both by allocating more dry matter to them and by decreasing their linear density, i.e., the ratio of stem dry weight to stem length. However, because the competing species grew too tall, excessive stem elongation by *C. pacificum* resulted in shoots that leaned or collapsed without outgrowing the other plants. Considering the responses that competing *C. pacificum* showed in this experiment, it may be assumed that the main factors causing retarded growth and death of seedlings in the control plot were insufficient light intensity and the excessive growth responses of *C. pacificum*.

Although physical characteristics of the seashore are not obligatory environmental factors for *C. pacificum* to grow and reproduce, these factors, particularly salt spray, play an indispensable role in its habitat. Since most inland plants are susceptible to salt spray (Moss, 1940; Oosting, 1945; Numata *et al*., 1948), they cannot invade and become established around the seashore. Even when seeds of the vigorous inland weed *Solidago altissima* were artificially sown and germinated on a slope directly facing the sea, they were completely eliminated within a year due to frequent exposure to salt spray (Yura, 1997). Sea water functions as a kind of herbicide that selectively eliminates inland plants along the shore. Consequently, maritime species such as *C. pacificum*, which tolerate salt spray, can establish themselves without competing against inland plants. Although salt spray is physiologically unnecessary for *C. pacificum* to grow and reproduce, it is indirectly, or ecologically, necessary for survival and establishment in its original habitat, the seashore.

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内陸の地に播かれて発芽したイソギク実生の生存と成長

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千葉県内の岩石海岸ではごく普通に見られるイソギクが，内陸の地に生育していない理由を明らかにするために，内陸に裸地を造って種子を播き，発芽してきた実生の生存と成長を追跡した．種子が発芽した後に，裸地を除草区と対照区に分け，除草区からは，埋土種子等から出現するイソギク以外のすべての種を繰り返し除去した．一方の対照区では出現する種はすべてそのまま放置した．イソギクは両方の区でほぼ同時に発芽したが，対照区のイソギク実生は他の内陸の種に徐々に覆われて成長が遅くなり，生存しているシュート数も年々減少し，3年後には最初の年のシュート数のほぼ10%にまで減少した．一方の除草区では，イソギク実生は成長し，毎年新しいシュートを伸ばし，開花及び結実も見られた．生存シュート数も3年にわたり毎年増加した．これらの結果から，イソギクは，海岸から離れた内陸においても発芽し成長する十分な能力はあるものの，自然に発生してくる内陸植物との競争に勝てないことが内陸での定着を困難にしている一因であることが示唆された．