

SCIRPUS OLNEYI (CYPERACEAE) SHOWS PHENOTYPICAL DIFFERENTIATION IN A SALT MARSH ON THE EAST COAST OF THE U.S.A.

MAKIHICO IKEGAMI, DENNIS F. WHIGHAM & MARINUS J. A. WERGER

Abstract. The clonal plant *Scirpus olneyi* A. Gray, which grows in salt marshes, shows different growth forms. This species has two types of ramets; a ramet with a long rhizome and a ramet without or with a very short rhizome. In different communities this species shows different ramet architectures in combinations of the two types of ramets. To describe ramet architecture, growth forms, life history strategies and the features of different environmental communities, we conducted a field survey in a salt marsh at the Smithsonian Environmental Research Center (SERC) on the western shore of the Chesapeake Bay in the United States. We recognized six different types of communities present in different environments and found that *S. olneyi* showed various growth forms and propagation patterns among these communities. Plants produced short spacer ramets in patches where plants achieved high biomass and seed production, and long spacer ramets in patches where plants achieved low biomass and seed production. This result suggests that this plant can retain favorable patches with shorter spacer ramets, and can escape from unfavorable patches with longer spacer ramets.

Key words: clonal plant, ramet architecture, *Scirpus olneyi*, morphological variability

Makihiko Ikegami*, Department of Plant Ecology, Utrecht University, P.O. Box 80084 3508 TB Utrecht, The Netherlands, and SERC P.O. Box 28 647 Contees Wharf Road, Edgewater, Maryland, U.S.A. 21037

Dennis F. Whigham, SERC P.O. Box 28 647 Contees Wharf Road Edgewater, Maryland, USA 21037 and Department of Landscape Ecology, Utrecht University, P.O. Box 80084 3508 TB Utrecht, Netherlands

Marinus J. A. Werger, Department of Plant Ecology, Utrecht University, P.O. Box 80084 3508 TB Utrecht, Netherlands

INTRODUCTION

Environmental conditions around a plant can vary spatially and temporally, and individual plants must adjust to their environments to survive. As a result, plants tend to show different morphologies in different environments, reflecting phenotypic responses. For example, plants will allocate proportionally more biomass to belowground organs in patches with abundant light and low water availability, and allocate proportionally more biomass to aboveground organs in patches with low light levels and high water availability (Brouwer 1983; Werger 1983; Iwasa & Roughgarden 1984). This is because plants allocate proportionally more biomass to the organ whose function is most lim-

iting to the photosynthetic production of the plant (Aung 1974; Chapin 1980; Hutchings & De Kroon 1994).

Since clonal plants can spread horizontally by vegetative growth, each ramet has the potential to grow across a heterogeneous environment; thus, phenotypic differentiation of ramets can be important for the survival of clonal plants. This applies especially to architectural elements of the plant. For example, the plant may shorten or lengthen rooted nodes, as that may affect resource acquisition. The placement of ramets at the end of short rhizomes allows plants to form patches with high shoot densities, which are monospecific and apparently occupy areas for long periods of time. On the other hand, the placement of ramets at the end of long rhizomes allows plants to form patches with low shoot densities. In the foraging behavior of

* Present address: Forest Research, Alice Holt Lodge, Wrecclesham, Farnham, Surrey, GU10 4LH, UK; e-mail: makihiko@mbox.kyoto-inet.or.jp

clonal plants, short rhizomes are produced in order to occupy resource patches, while long rhizomes are produced to explore and subsequently colonize new resource patches (Lovett Doust 1981; Hartnett & Bazzaz 1983; Salzman & Parker 1985; Slade & Hutchings 1987a, b, c).

Scirpus olneyi A. Gray is a clonal species of brackish wetlands in North America which dominates plant communities over a wide range of environmental conditions, varying from brackish to freshwater sites and from shady to open habitats (McCormick & Somes 1982; Drake 1984). *S. olneyi* expresses phenotypic variability of architecture by producing two types of ramets, often within one clone. Some ramets have long rhizomes and others very short rhizomes (Fig. 1). Our garden experiment showed that *S. olneyi* pro-

duced short-rhizome ramets at a higher ratio under better quality conditions, and long-rhizome ramets at a higher ratio under poor quality conditions (Ikegami 2004). This phenotypic variability may enable *S. olneyi* to exploit resources in favorable patches while exploring the environment for other favorable patches in spatially heterogeneous ecosystems. To determine whether *S. olneyi* dominates in the field because of its phenotypic variability, it is important to compare the ramet architectures of this plant in different types of environments.

McCormick and Somes (1982) listed ten different plant communities associated with brackish marshes in Maryland. In the field, we studied *S. olneyi* in four of the communities they described: (1) *Typha* marsh (Cattail), (2) *Hibiscus* marsh (Rose-mallow), (3) *Spartina* marsh (Meadow Cordgrass/Spikegrass) and (4) *Scirpus* marsh (Threesquare) community. McCormick and Somes described the communities on the basis of associated plant species, but did not describe the environmental factors or the features of the plants in each community. Although *S. olneyi* is a dominant species in *Scirpus* marsh community, there are differences in the physical environments, shoot densities and shoot characteristics of *S. olneyi*. In this study we further subdivided the *Scirpus* marsh community into three types: *Scirpus* high marsh, *Scirpus* patchy marsh and *Scirpus* shaded marsh community. We hypothesized that *S. olneyi* changes rhizome length in response to different environmental conditions within the six habitats in this study, producing short-rhizome ramets in patches with better environmental conditions where plants achieve high shoot density, while producing long-rhizome ramets in patches with poor environmental conditions where plants achieve low shoot density. To characterize the variability of phenotypic morphology and reproductive output of this species in six different communities, we conducted field observations in a brackish wetland on the east coast of the U.S.A.

MATERIAL AND METHODS

The study was conducted in brackish tidal marshes at the Smithsonian Environmental Research Center

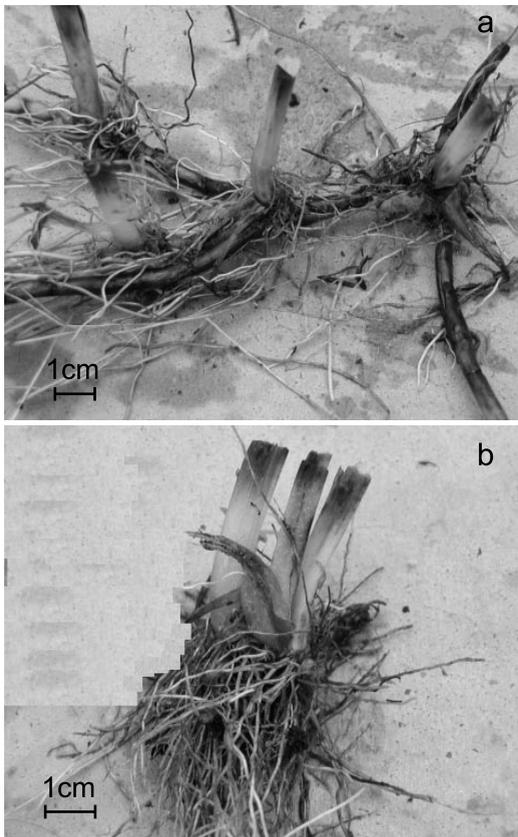


Fig. 1. Clonal architecture of *Scirpus olneyi* A. Gray. a – long-rhizome ramets, b – short-rhizome ramets.

(SERC) on the western shore of the Chesapeake Bay in the United States. The SERC property includes *ca* 3000 ha of the Rhode River (38°53'N/76°33'W). We investigated the brackish tidal marsh known locally as Hog Island Marsh, within the sub-estuarine portion of the Rhode River system.

Scirpus olneyi A. Gray (Three Square Grass), a member of the sedge family Cyperaceae, occurs in a broad range of salt marsh communities in both North and South America. It forms dense monospecific stands but also occurs in mixed stands with other plant species (McCormick & Somes 1982; Tiner & Burke 1995). This species is an emergent, rhizomatous, perennial macrophyte. An individual ramet consists of a shoot, roots and a tuber with or without a rhizome (Fig. 1). An individual ramet produces from one to three new ramets in a single growth season, and ramet production occurs throughout the growth season (Ikegami 2004). Tubers and rhizomes are located within 15 cm of the soil surface and persist for several years.

Aboveground shoots are erect, sharply triangular, and needle-like. They have short leaves up to 10 cm long, which are closely adpressed to the shoot and emerge from the lower part of the culm. Total culm height ranges from *ca* 50 to 200 cm. At our study sites, green shoots appear aboveground in April and persist into winter (December). Most shoots senesce during the autumn months following the onset of freezing temperatures. New ramets produced near the end of the growth season do not bear aboveground shoots.

Scirpus olneyi occurs in mesohaline, brackish tidal marshes at SERC. Brackish tidal marshes are transitional between tidal salt marshes and non-tidal freshwater marshes (McCormick & Somes 1982; Tiner & Burke 1995). Interstitial salinity varies seasonally within individual marshes, but typically mesohaline brackish marshes are defined as having interstitial salinities ranging from 5 to 18 parts per thousand (Whigham *et al.* 1989; Tiner & Burke 1995).

Brackish marshes at SERC are found in two habitats: high marsh and low marsh. High marsh habitats are only infrequently inundated by tides, occurring during storms or unusually high tides (Jordan *et al.* 1984). Low marsh habitats occur in areas that flood more frequently because the marsh surface is lower down in the intertidal zone, normally twice daily (Jordan *et al.* 1984). The tidal range in the Rhode River sub-estuary is approximately 50 cm. High marsh habitats typically have higher interstitial salinity than low marsh habitats because they are inundated less frequently. Variations in the flooding regime and salinity create a variety of environmental conditions resulting in a vegetation mo-

saic that is also spatially variable. *Scirpus olneyi* occurs in both low and high marsh habitats, but is most abundant in high marsh. Other dominant species in brackish marshes associated with high marsh habitats are *Distichlis spicata*, *Hibiscus palustris*, *Iva frutescens*, *Phragmites communis*, *Spartina patens*, *Spartina cynosuroides* and *Typha angustifolia* (Kartesz 1994).

In 1999, five observation plots measuring 50 × 50 cm each were established randomly in each of the six mentioned communities (Fig. 2). We recorded ramet status (sexual or vegetative) and the number of shoots in each plot. To describe and assess the environmental factors in each community, salinity, light availability and soil compactness were measured in each plot. Salinity usually affects plant growth negatively (Salzman & Parker 1985). Since salinity tolerance varies between plant species, plant distributions may be regulated by salinity in salt marshes. The salinity of the interstitial water was measured in the field with a hand-held refractometer (American Optical, TS METER), in samples collected from 10 cm depth with piezometers made of PVC pipe sealed at the base and having holes drilled into them near the base. Light is essential for plant growth and survival. Due to differences in site characteristics and shading by coexisting species, light availability varied between plant communities in our plots. Light levels were measured under clear sky in late July between 11:00 and 15:00 h (EST). We measured light levels three times and took the intermediate ?? mean ?? value. The light levels ($\mu\text{mol s}^{-1} \text{m}^{-2}$) were

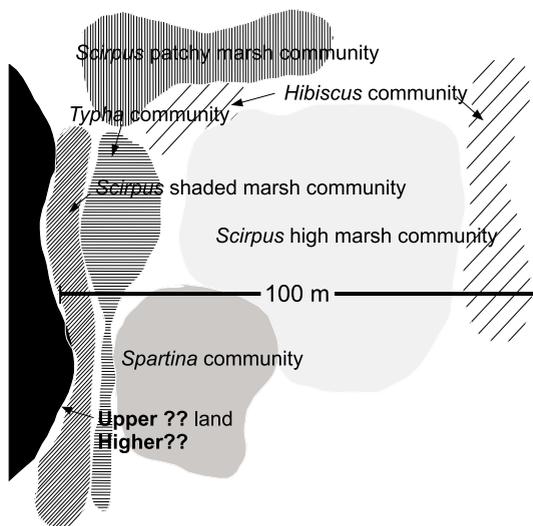


Fig. 2. Distribution of plant communities in the study site, Hog Island Marsh.

measured in the center of each plot inside the *Scirpus* canopy (50 cm from the ground) and above the *Scirpus* canopy (150 cm) using a LiCor Quantum Radiometer, Photometer Model LI-185A. In the salt marsh, soil compactness varied between plant communities. Since this species develop its rhizomes in the soil, soil compactness can affect rhizome architecture. Soil compactness was measured at nine points in each observation plot with a hand-held penetrometer (Eijkelkamp, Hand Penetrometer, Type 1B).

To characterize the morphological features of *Scirpus olneyi*, sods measuring 25 × 25 × 20 cm were excavated from Hog Island Marsh in 1999: one sample from each community in September and two samples from each community in December. The sample sods were randomly chosen from each community. Data on shoot morphology and biomass allocation, shoot heights, shoot diameter, weight of underground ramets (roots, rhizomes and tubers) and shoot weight were determined from the samples collected in September. The September and December samples were used for analyses of ramet architecture, ramet type (long or short rhizome) and rhizome length. Sods excavated in the field were brought back to the laboratory, and the entire ramet system, including tubers, rhizomes, roots and shoots, was extracted from the sediment. Each ramet was classified into one of two categories: short-rhizome ramet (tuber without a rhizome) or long-rhizome ramet (tuber with rhizome) (Fig. 1). After measurements of rhizome length and degree of branching, the ramets were separated into three further categories: current year's ramets, ramets older than one year, and dead ramets. The ramets were then dried for 72 h at 68°C for determination of dry weight.

In mid-September, inflorescences were collected from each plot to evaluate sexual reproductive effort. *S. olneyi* did not produce flowers in the *Scirpus* shaded marsh community, nor in the *Spartina* community. Inflorescences were collected from flowering shoots in each observation plot before they matured and fell to the ground, dried at room temperature for one week and weighed.

One-way ANOVA was used to compare the mean salinity, light level at 150 cm and 50 cm between the six communities, compactness between five communities, and sexual reproductive effort between four communities. We also used one-way ANOVA for length and number of branches of short and long rhizomes between the six communities after log-transformation to normalize the data. Every one-way ANOVA test was followed by the Bonferroni-Dunn test for multiple comparisons.

RESULTS

TYPHA COMMUNITY

Typha angustifolia (Cattail) was the dominant species in this community. Generally this community was located close to land, next to *Scirpus* shaded marsh community (Fig. 2). Salinity was low (Table 1), probably because of freshwater runoff from adjacent uplands. The substrate consisted of organic matter, mainly dead rhizomes and leaves of *T. angustifolia*, and soil compactness was low (Table 1). Because shoots and leaves of *T. angustifolia* were taller than those of *Scirpus*

Table 1. Salinity, soil compactness and light availability in the 6 communities described in the text. Data were measured from 5 observation plots in Sept. 1999. Interstitial salinity was measured at 2 points in each habitat, compactness at 9 points, and light at the center of each plot at 2 different heights: inside the vegetation canopy (50 cm) and above the vegetation canopy (150 cm). Light was measured as $\mu\text{mol s}^{-1} \text{m}^{-2}$. Data are means \pm SD. Different letters indicate significant differences between values ($P < 0.005$ for compactness, $P < 0.0033$ for salinity and light level) by one-way ANOVA followed by the Bonferroni-Dunn test for multiple comparisons. N/M means that compactness was not measured because sediment was too soft to be measured.

Community	Salinity (ppt)	Compactness (kg cm ⁻²)	Light level at 150 cm ($\mu\text{mol s}^{-1} \text{m}^{-2}$)	Light level at 50 cm ($\mu\text{mol s}^{-1} \text{m}^{-2}$)
Typha	9.6 \pm 0.8a	59.8 \pm 19.6a	1620 \pm 98.0a	620 \pm 116.6a
Spartina	8.3 \pm 2.5ac	122.9 \pm 39.5b	1606 \pm 90.2a	1606 \pm 90.2b
Hibiscus	8.5 \pm 1.2ac	66.8 \pm 49.8ac	1500 \pm 0.0a	274 \pm 81.9c
High Marsh	13.7 \pm 1.3b	146.7 \pm 38.9d	1560 \pm 49.0a	480 \pm 98.0ac
Patchy Marsh	11.5 \pm 1.1ad	26.4 \pm 21.5e	1630 \pm 107.7a	540 \pm 177.2a
Shaded Marsh	9.3 \pm 1.2ac	N/M	151 \pm 35.8b	92 \pm 30.6c
df and F values	df=5, F=20.8	df=4, F=65.9	df=5, F=20.8	df=5, F=20.8

Table 2. Characteristics of *Scirpus olneyi* A. Gray shoot and rhizome biomass in the 6 communities described in the text. Samples were collected from each of 6 communities in Sept. 1999. Data for shoot height and shoot diameter are means ± SD. Different letters indicate significant differences at P<0.0033 by one-way ANOVA followed by the Bonferroni-Dunn test for multiple comparisons.

Community	Shoot number	Shoot weight (g)	Shoot height (cm)	Shoot diameter (mm)	No. of current-year rhizomes	Weight per current-year rhizome (g)	Ratio of current/old year rhizomes	S/R ratio in current year
<i>Typha</i>	10	1.67	109.8±17.8a	5.68±0.63a	71	0.14	0.39	2.25
<i>Spartina</i>	10	0.73	58.8±22.9b	5.07±0.57a	24	0.20	1.77	1.23
<i>Hibiscus</i>	15	2.39	126.3±22.7ac	5.20±0.56a	152	0.22	0.13	2.87
High Marsh	35	0.72	65.2±13.7bd	3.75±0.74b	220	0.08	0.19	1.90
Patchy Marsh	73	0.93	75.9±20.1e	3.98±0.87b	232	0.15	0.46	1.55
Shaded Marsh	13	0.95	99.5±11.4a	4.99±0.42a	70	0.15	1.19	2.46
df and F values			d.f.=5, F=27.2	d.f.=5, F=19.9			weight or number ??	

Table 3. Belowground ramet architecture for *Scirpus olneyi* A. Gray in 6 different communities. Three samples were collected from each habitat in Sept. and Dec. 1999. The number of short and long rhizomes and the ratio of short rhizomes to all rhizomes are means of 3 samples; length and branching figures are means ± SD. Different letters indicate significant differences between values at P<0.05 by one-way ANOVA followed by the Bonferroni-Dunn test for multiple comparisons.

Community	Mean no. of short rhizomes	Mean no. of long rhizomes	Ratio of short rhizomes (%)	Mean length of short rhizomes (cm)	Mean length of long rhizomes (cm)	Short-rhizome ramets ??	Long-rhizome ramets ??
<i>Typha</i>	42.7	44.3	49.0	0.80±0.33a	5.91±3.50a	1.12±0.36a	1.70±0.70a
<i>Spartina</i>	7.7	24.0	24.2	0.89±0.33ac	5.28±2.57ab	1.00±0.00ab	1.35±0.51ab
<i>Hibiscus</i>	185.7	155.3	54.4	0.93±0.26bc	3.76±2.40c	1.12±0.33abc	1.37±0.53b
High Marsh	229.0	196.0	53.9	0.81±0.30a	3.51±1.66c	1.17±0.38abc	1.40±0.52b
Patchy Marsh	148.7	111.3	57.2	0.82±0.30a	4.53±2.89b	1.32±0.53bd	1.75±0.68a
Shaded Marsh	18.0	19.3	48.2	0.65±0.24ad	8.60±5.23d	1.47±0.78d	1.88±0.92c
df and F values				df=5, F=21.7	df=5, F=37.4	df=5, F=10.6	df=5, F=21.0

olneyi, light levels were low within the canopy at 50 cm above the ground (Table 1).

The number of *S. olneyi* shoots was lowest but not significantly so, and shoots in this community were higher than in other communities (Table 2). The shoot/root ratio was high (Table 2), resulting in low light availability. In this community, *S. olneyi* produced long and short-rhizome ramets in equal numbers, and the number of branches per ramet was intermediate (Table 3). Flowering shoots were few (Fig. 3).

SPARTINA COMMUNITY

Spartina patens was a major component of the vegetation of this community. *Scirpus olneyi* appeared to be invading from the margins. This community was located in high marsh, typically near the center of the marsh (Fig. 2). Salinity was low but varied between plots (Table 1). The compacted sediment was highly organic and consisted of thick rhizomes and roots of *S. patens* (Table 1). Light availability for *S. olneyi* was high, because *S. patens* shoots were horizontal during much of the growth season (Turitzin & Drake 1981) (Table 1).

Shoot density was low (Table 2), and shoot height and average shoot weight were lowest in

appearing on the top of hummocks. Salinity was relatively high (Table 1). Soil compactness varied, since the sediment between the hummocks was highly organic and very soft, whereas the sediment in a hummock was hard and consisted of thick rhizomes and roots of *S. patens* and *S. olneyi* (Table 1). Light availability was low on the hummocks (Table 1), but higher in open areas between hummocks.

Shoot density was high and shoots formed dense patches (Table 2). Shoot height and weight were intermediate compared with the values for other communities (Table 2). *Scirpus olneyi* produced many short-rhizome ramets which branched frequently (Table 3), forming dense clumps. *S. olneyi* produced an intermediate number of reproductive shoots and seeds relative to the values for other communities (Fig. 3).

SCIRPUS SHADED MARSH COMMUNITY

Only a few species, mainly *S. olneyi* and *Phragmites communis*, occurred in this community. This community was located on the boundary between dry land and marsh (Fig. 2). A feature of this community was low light availability due to overhanging tree branches (Table 1). Freshwater input from the adjacent upland mixed with tidal waters, resulting in intermediate salinity (Table 1). The sediment consisted of decomposed leaves from trees, and was too soft to be measured with the penetrometer (Table 1).

In this community, shoot density was lowest of all values (Table 2). Due to low light availability, *S. olneyi* produced tall shoots (Table 2) and had high shoot/root ratios (Table 2). Ramets had long rhizomes that frequently branched (Table 3). *S. olneyi* did not reproduce sexually in this community (Fig. 3).

DISCUSSION

Scirpus olneyi dominated the plant communities under a wide range of environmental conditions that occurred in close proximity (Fig. 2). The species showed high variability in density, shoot morphology, seed production and ramet ar-

chitecture. In patches with low light availability, *S. olneyi* invested strongly in aboveground parts. This pattern is in accordance with the findings of many other studies (Brouwer 1983; Werger 1983; Iwasa & Roughgarden 1984). *S. olneyi* showed variable clonal architectures, producing two types of ramets in different ratios within the six communities. *Scirpus olneyi* tended to have long-rhizome ramets within lower density communities such as shaded marsh, *Typha* and *Spartina* communities. In contrast, it produced short-rhizome ramets in dense communities such as *Scirpus* high marsh and *Hibiscus* communities.

It has been demonstrated that some clonal plants change the spacer length and branching frequency in response to varying environmental conditions (de Kroon & Knops 1990, de Kroon & Hutchings 1995). The length of spacers is closely related to the foraging behavior of plant species. Dong and de Kroon (1994) found that *Cynodon dactylon* produced shorter rhizomes under higher light conditions. Slade and Hutchings (1987a, b, c) showed similar results with *Glechoma hederacea*, and other reports are in line with these (Lovett Doust 1981; Harper 1985; de Kroon & Knops 1990; Hutchings & de Kroon 1994; Dong 1996). These studies suggest that the production of shorter spacer ramets allows plants to occupy better quality patches, while producing longer spacers allows plants to escape lower quality patches (de Kroon & Knops 1990; Dong & de Kroon 1994; de Kroon & Hutchings 1995). Our garden experiment also suggested that *S. olneyi* produced short-rhizome ramets at a higher ratio in better quality treatments (higher nutrients and better light conditions) than in poor quality treatments (Ikegami 2004).

Scirpus high marsh, patchy marsh and *Hibiscus* communities probably are better quality environments; the plants in these communities had the largest number of rhizomes and highest shoot weight and total biomass.

Seed production varied between communities. *Scirpus* high marsh community plants produced the largest number of flowering shoots and many seeds. Some model studies have suggested that clonal plants shift sexual reproduction under the

most stressful conditions (Sackville-Hamilton *et al.* 1987; Gardner & Mangel 1999). Other studies, however, indicate that plants that primarily propagate vegetatively are often associated with resource-poor environments, as vegetative propagules can survive harsher environments better than seedlings do (Raven *et al.* 1981; Callaghan 1988).

According to Abrahamson (1980), the balance between seed and vegetative propagation is affected by inter- and intraspecific competition. Abrahamson theorized that vegetative propagation would be advantageous at low plant density as it facilitates local spread and occupation, while seed propagation would be advantageous at high plant density as it enables dispersal to new and perhaps more favorable sites (Abrahamson 1980). This can explain the absence of seed production in the *Spartina* community and the high seed production in the *Scirpus* high marsh community. As ramet density increases, *S. olneyi* shifts its propagation strategy from exploring with ramets to spreading by seeds.

Growth experiments with different sources of *S. olneyi* material indicated that the high morphological variability results from phenotypic plasticity *sensu* Bradshaw (1965) (Ikegami 2004). It is likely that such a wide range of phenotypic response helps the species to exploit favorable patches and enables this sedge to dominate the vegetation in a variety of habitats.

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