OBSERVATIONS ON THE REPRODUCTIVE ECOLOGY OF *THALASSIA TESTUDINUM* (HYDROCHARITACEAE). III. SPATIAL AND TEMPORAL VARIATIONS IN REPRODUCTIVE PATTERNS WITHIN A SEAGRASS BED

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ABSTRACT

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Spatial and temporal variations in the reproductive patterns of a population of *Thalassia testudinum* Banks ex König in Tampa Bay, Florida were observed from 1981 to 1983. Reproductive densities of 11.4, 20.7 and 10.0% were observed in 1981, 1982 and 1983, respectively. The significantly higher reproductive density in 1982 was due to a 3-fold increase in the temporally labile male phenotype. Sex ratios were male-biased only in 1982. In contrast, female short-shoot densities did not vary significantly during the study. Total and reproductive short-shoot densities generally decreased from the shoreward (shallower) fringe to the seaward (deeper) fringe of the bed. Spatial variations in female short-shoot densities were significant. Female short-shoots were prevalent near fringing areas of the bed, while males were predominant in the interior. This distribution pattern resulted in a negative correlation between male and female densities. The distribution and spatial separation of the sexes suggest an interaction of age with sex expression in this *Thalassia testudinum* population.

INTRODUCTION

Seagrasses are an important and often dominant component of shallow coastal environments (Phillips, 1960, 1978; Wood et al., 1969; den Hartog, 1970). Turtle grass, *Thalassia testudinum* Banks ex König, is the predominant seagrass species of the tropical west Atlantic, Caribbean and Gulf of Mexico (Stephens, 1968; Thayer and Ustach, 1981). The ecology, morphology and anatomy of *T. testudinum* have been relatively well documented (Phillips, 1960; Orput and Boral, 1964; Tomlinson and Vargo, 1966; Tomlinson, 1969a, b, 1972; Zieman, 1975), however, much of the previous work concentrated on clinal variations and systems level phenomena (McMillan, 1978; McMillan and Phillips, 1979; Durako and Moffler, 1981; Phillips and

Lewis, 1983). Consequently, as first stated by Tomlinson and Vargo (1966), fundamental biological information about this plant is needed.

Two modes of natural propagation, vegetative and sexual, are exhibited by *T. testudinum* and other seagrasses. Vegetative growth has been suggested as the dominant method of seagrass-bed maintenance and expansion (Phillips, 1972; Zieman, 1975). This suggestion was based on reproductive density (percentage of total short-shoots with male or female inflorescences) estimates of between 1 and 15% (Phillips, 1960; Orput and Boral, 1964; Zieman, 1975). More recent observations indicate that reproductive densities may be much higher (Moffler et al., 1981; Durako and Moffler, 1985). However, seed production appears to be quite variable in both space and time and natural seedling occurrence ranges from rare (Phillips, 1960; Zieman, 1975; Grey and Moffler, 1978) to abundant (Lewis and Phillips, 1980; Williams and Adey, 1983). The reasons for this variability are poorly understood. In fact, Zieman (1982) noted that information on sexual reproduction of south Florida seagrasses is "sketchy" at best. Since sexual reproduction is considered a basic requirement for genetic plasticity and successful growth in fluctuating coastal environments, an understanding of the reproductive ecology of *T. testudinum* is of paramount importance.

The present paper represents a continuation of investigations on various aspects of the reproductive ecology of *T. testudinum* (Grey and Moffler, 1978; Moffler et al., 1981; Moffler and Durako, 1982; Durako and Moffler, 1981, 1985). In this study we report on the spatial and temporal (year-to-year) variations in flowering patterns of a seagrass bed which produces viable fruits and seeds. Temporal variability and spatial gradients in flower production have not been reported previously.

MATERIALS AND METHODS

The study site (Fig. 1) was chosen based on our previous observations of *T. testudinum* fruit and seed production within Tampa Bay (Lewis et al., 1985). The seagrass bed at Egmont Key is approximately 18.5 ha and is dominated by *T. testudinum*. *Syringodium filiforme* Kützing (manatee grass) occurs sporadically, mixed with *T. testudinum*, in the mid-bed regions and as pure stands along the seaward (deeper) fringe of the bed. *Halodule wrightii* Aschers. (shoal grass) occurs mixed with *T. testudinum* along the shoreward fringe. Salinities at this site, which is at the mouth of the bay, are high and relatively stable (32—36‰).

Observations were made during the time of peak anthesis (May—June; Phillips, 1960; Orput and Boral, 1964; Marmelstein et al., 1968; Tomlinson, 1969b; Grey and Moffler, 1978) for 3 years (1981—83). Transects were established across the bed from the shoreward fringe to the seaward fringe (ca. 40 m). A total of eight separate transects were sampled. Two transects were sampled in 1981; three transects were sampled in both 1982 and 1983. Observations were made within a 625-cm^2 quadrat at alternate meters along
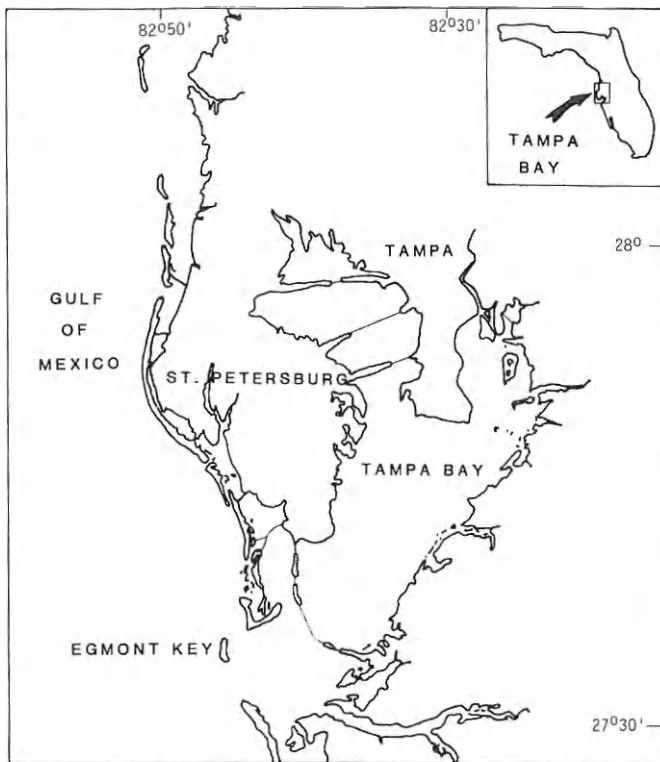
Fig. 1. Map of Tampa Bay, Florida showing location of Egmont Key.

the transect line. At each sample point, total density of *T. testudinum* short-shoots and number of short-shoots bearing male or female reproductive structures were recorded. Reproductive densities were estimated based on the presence of visible reproductive structures: buds, anthesis or post-anthesis flowers.

Normality of data was assessed utilizing the Kolmogorov-Smirnov D statistics (Stephens, 1974). Multiple regression analysis and analysis of variance were performed to determine the significance of spatial and temporal changes in the total and reproductive short-shoot densities. Significant effects were further evaluated using Duncan's multiple range tests. All calculations were performed utilizing Statistical Analysis System computer programs (Helwig and Council, 1979).

RESULTS

Reproductive short-shoots were observed during all three years (Table I). Short-shoot and reproductive densities were significantly higher in 1982 compared to the other two years. Since the reproductive density is expressed as a percent of the short-shoot density, the year-to-year variation in actual

TABLE I

Vegetative and reproductive short-shoot densities and sex ratios of *Thalassia testudinum* at Egmont Key, Florida

Variable	Year					
	1981		1982		1983	
Number of observations	34		59		62	
Short-shoots/m² *	505	(122)	788	(309)**	560	(363)
Reproductive short-shoot density (%)*	11.4 (9.9)		20.7	(17.7)**	10.0	(9.7)
Male short-shoot density (%)*	3.1 (4.8)		14.3	(18.8)**	4.8	(7.0)
Female short-shoot density (%)*	8.4 (10.7)		6.5	(7.9)	5.1	(8.5)
Male/female	0.35		1.87		0.74	

*Mean value and (standard deviation).
**Significantly greater than other two years at $P = 0.05$ level.

number of reproductive short-shoots is greater than the percentage figures indicate (mean number of reproductive short-shoots/transect: 1981, 58; 1982, 163; 1983, 56). Temporal differences in reproductive densities were

TABLE II

Summary of analyses of variance assessing the temporal and spatial variations in vegetative and reproductive short-shoot densities

Dependent variable	Independent variable	Degrees of freedom	F	Significance
Short-shoot	Year	2	18.27	**
density	Distance	21	4.21	**
	Year* distance	37	0.37	NS
Reproductive	Year	2	12.76	**
density	Distance	21	1.14	NS
	Year* distance	37	1.24	NS
	Short-shoot density	62	1.52	*
Male short-shoot	Year	2	12.42	**
density	Distance	21	1.33	NS
	Year* distance	37	1.00	NS
Female short-shoot	Year	2	1.71	NS
density	Distance	21	1.86	*
	Year* distance	37	0.51	NS

NS = not significant.
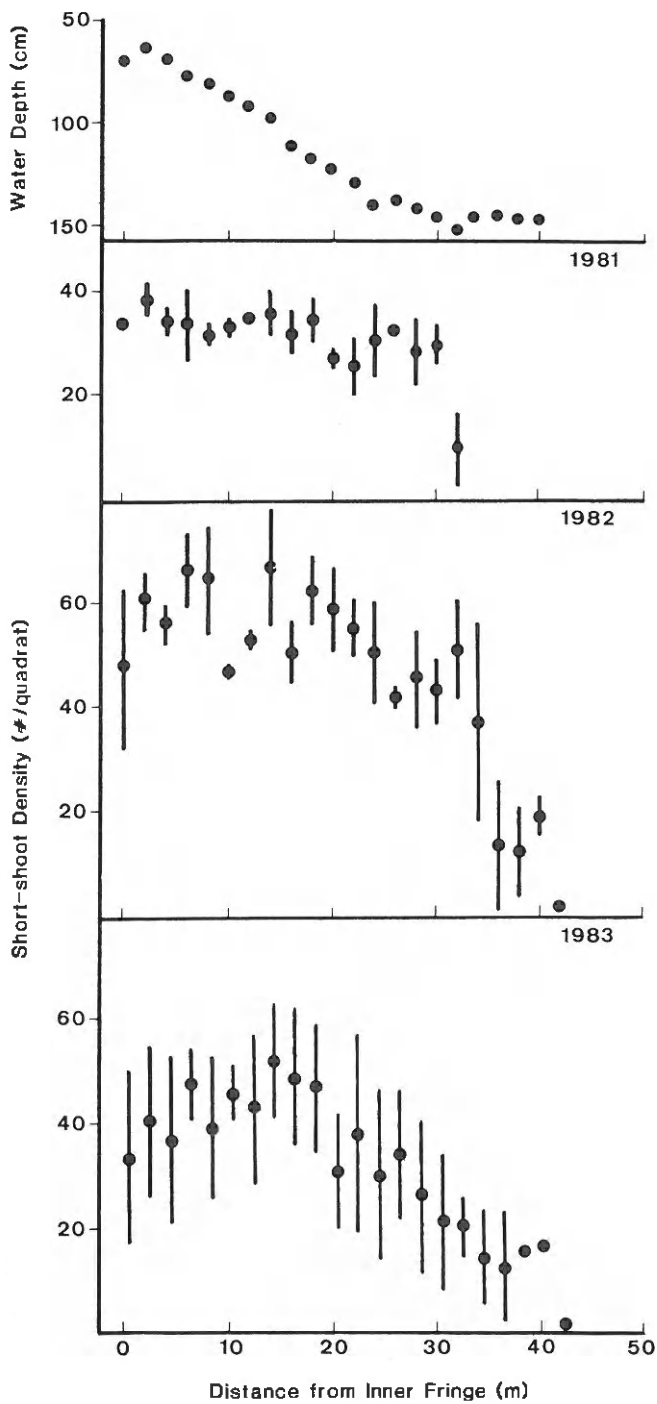* = significant at 0.05 level.
** = significant at 0.01 level.

Fig. 2. Water depths and *Thalassia testudinum* short-shoot densities (mean ± standard error) across the seagrass bed at Egmont Key.

due to variation in male short-shoot densities, which were also significantly higher in 1982. This high percentage of male short-shoots, which was three times that of the other years, resulted in a male-biased sex ratio in 1982. Sex ratios in 1981 and 1983, in contrast, were female biased (Table I). Mean female reproductive densities decreased from 1981 to 1983 (Table I), but this decrease was not significant (Table II).

Spatially, short-shoot densities generally decreased with increased distance (and depth) from the shoreward fringe (Fig. 2). Although short shoot densities changed significantly across the bed, and from year to year, the pattern of spatial variation was temporally consistent (i.e., not significantly different) (Table II). Relatively low short-shoot densities at the shoreward fringe stations were due, in part, to the presence of *Halodule wrightii*. Correspondingly, the lower densities at the deeper stations reflected the presence of *Syringodium filiforme*. Overall reproductive densities varied significantly between years and with short-shoot densities (Tables I and II), but did not vary significantly across the bed. When reproductive short-shoots were classified according to sex, however, spatial patterns were evident (Fig. 3). Male and female short-shoot densities exhibited a low, but significant negative correlation ($r^2 = -0.245$, $n = 155$, $P > 0.002$). Female short-shoots were predominant at the shoreward, and to a lesser extent at the seaward, regions of the bed, while male short-shoots were more common in the mid-bed region. More specifically, highest female densities occurred between 4 and 8 m from the shoreward fringe and male densities were highest over a broad area between 20 and 30 m from the shoreward fringe. Spatial variations for females were significant (Table II). Although male short-shoot densities were significantly different year to year, but not across the bed, and female short-shoot densities were similar over time, but different spatially, both sexes were consistent in their respective temporal and spatial patterns (Table II).

DISCUSSION

Temporal variation

Reproductive short-shoot densities of the Egmont Key *T. testudinum* population exhibited significant temporal variation, but at least 10% of the short-shoots flowered each year. Previous phenological data suggested that flowering in *T. testudinum* is erratic in this part of its geographical range (Phillips, 1960; Phillips et al., 1981). Phillips (1960) reported that 10% of the plants in Boca Ciega Bay (which connects with Tampa Bay) flowered in 1958, but he did not observe flowering north of Tarpon Springs. Flowering was subsequently observed as far north as the panhandle region of Florida (Marmelstein et al., 1968; Phillips et al., 1981). Grey and Moffler (1978) found reproductive short-shoots in 1976 at all nine of their sites in the Tampa Bay area. However, in a phenological study of *T. testudinum* con-
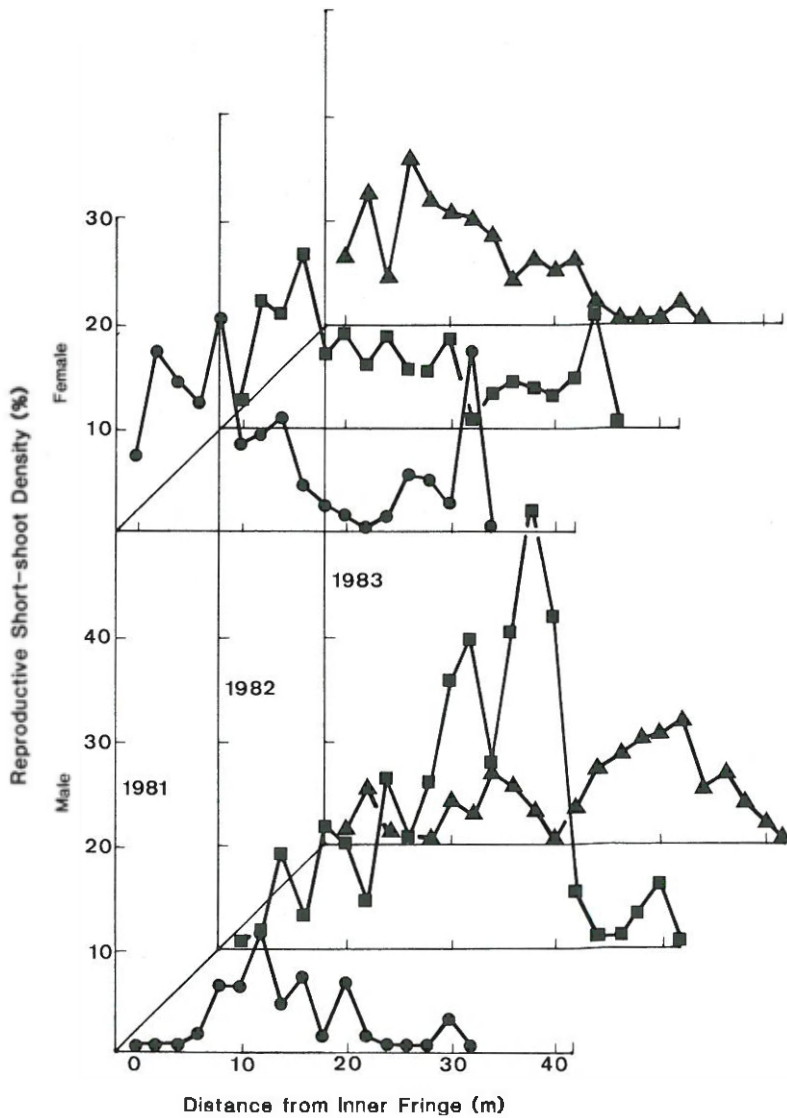
Fig. 3. *Thalassia testudinum* male and female short-shoot densities (as percent of total short-shoots) across the seagrass bed of Egmont Key.

ducted from 1976 to 1979 (Phillips et al., 1981), flowering was not observed at the Tampa Bay station during 1976 or 1977. The absence of reproductive material in the samples may have been due to the relatively small number of short-shoots that were examined (50/month) or reflected spatial (site or population) variability in flower production, rather than temporal variation as the authors suggest.

Species that inhabit a range of conditions or experience fluctuating levels

of environmental stress, such as *T. testudinum*, characteristically exhibit sexual ecoplasticity or labile sexual phenotypes (Charnov and Bull, 1977; Soule and Werner, 1981). Significantly higher total reproductive densities at Egmont Key in 1982 were due exclusively to the variation in male short-shoot densities, indicating that the male phenotype is more variable temporally than the female phenotype. In addition, the significant reduction in total short-shoot densities from 1982 to 1983 may suggest that high reproductive effort reduces short-shoot density the following year. A negative relationship between adult survivorship and annual reproductive effort reflecting the physiological costs of heavy reproductive effort exists in a number of plants and animals (Silvertown, 1980). Similarly, we might speculate that the high resource costs associated with sexual reproduction may reduce the proportion of reserves available for the production of new short-shoots.

Our qualitative observations suggested that subsequent seed production was also highest in 1982. These observations imply that the density of male short-shoots may be a controlling factor in the level of fruit and seed production in *T. testudinum*. Hydrophilous pollination, like wind pollination, may be energetically costly due to dilution effects and its dependency on tidal currents. At the same time, dioecism is not a very efficient reproductive strategy since only half or less of the plants in a population produce seeds (Cruden and Hermann-Parker, 1977; Pettitt et al., 1981). Segregation of the sexes ensures genetically variant progeny, but it may also result in diminished pollination because of spatial separation. Consequently, male-biased sex ratios, which may represent an adaptive strategy for ensuring successful pollination, are characteristic of dioecious species (Lloyd and Webb, 1977).

Environmental variables exert a significant influence on sex ratios through a diversity of mechanisms, such as differential growth, resource allocation, flowering propensity and mortality (Freeman et al., 1976; Lloyd and Webb, 1977). In some dioecious species, males exhibit a greater propensity to flower than females, resulting in inflated counts of males in certain years (Lloyd and Webb, 1977). We do not feel that this type of mechanism applies to *T. testudinum* since there are no reports that short-shoots of this species flower more than once. Little information exists on any life-history characteristics of male or female plants of *T. testudinum*, except for the recent observation that male short-shoots have significantly wider leaf blades than females (Durako and Moffler, 1985).

Flowering in *T. testudinum* is thought to be related primarily to temperature, i.e., increasing temperatures following winter minima (Phillips et al., 1981). This conclusion may be correct, but for reasons other than those previously suggested. Phillips et al. (1981) indicated that floral induction in *T. testudinum* occurred only between January and April. This is not the case. Early stage inflorescences have recently been detected as early as mid-October in Tampa Bay and are present throughout the reproductive season

(Moffler and Durako, 1982). Water temperature appears to be instrumental in influencing the development of inflorescences; mean inflorescence lengths remain very small until water temperatures begin to rise in April (Moffler and Durako, 1982). Size plays an important role in the physiological fate of an individual, thus the influence of water temperature may be important in determining reproductive densities in May and June. In support of this, average water temperatures in lower Tampa Bay from October to October were slightly higher in 1981/82 (24.3°C) compared to 1980/81 (24.0°C) and 1982/83 (23.5°C) (P. Steele, personal communication, 1984). What may be more significant is that the temperatures just before the winter minima (October, November, and December) averaged 4—5°C warmer in 1981 compared to the other two years. Moffler et al. (1981) observed short-shoots with immature fruits in January and suggested that warm fall temperatures may have induced this "phenological inversion" in Tampa Bay. Higher fall temperatures may result in a greater percentage of inflorescences reaching a size critical for surviving the lowest temperatures in January.

Spatial variation

Spatial patchiness in total sexual reproduction of *T. testudinum* has been observed by several researchers (Phillips, 1960; Marmelstein et al., 1968; Grey and Moffler, 1978). Patchiness, which may be important in between-site variability as suggested above, was not observed within the Egmont Key population between 1981 and 1983. Reproductive short-shoots were observed along entire transects, with the exception of the outermost samples. Spatial uniformity of total reproductive effort may reflect the relative stability (at least in terms of salinity) of this site. The presence of reproductive short-shoots in a *T. testudinum* population represents a favorable adaptation to a set of environmental factors (Phillips, 1960). However, patchiness in sexual reproduction may also be due to clonal variation (Cook, 1983). Thus, while year-to-year variations in reproductive effort may be explained by environmental (temperature) influences, the spatial reproductive patterns of the Egmont Key population may be indicative of a uniform clonal structure.

Variations in total reproductive densities were related to total short-shoot densities, contrasting earlier data where the two were independent (Grey and Moffler, 1978). Total and reproductive short-shoot densities decreased with depth, although the change in reproductive density was not statistically significant. Buesa (1974) reported a 50% reduction in *T. testudinum* leaf density from 0.5 to 1.5 m depths on the northwestern Cuban shelf. This reduction was attributed to lower total light energy, specifically a reduction in the red wavelengths, resulting in reduced photosynthetic and tissue growth rates. Light is also important in the energetics of sexual reproduction, affecting sex expression and selection (Heslop-Harrison, 1957, 1972; Barrett and Helenurm, 1981; Barrett and Thompson, 1982). Flowering

(anthesis) in *T. testudinum* occurs earliest in shallower beds progressing to deeper beds as the season progresses (Orput and Boral, 1964). Deeper short-shoots may lack sufficient food reserves to provide the energy needed for flower production early in the season. In addition, reproductive densities are higher early in the year and decrease through the summer possibly due to factors such as microbial infection or natural abortion (Moffler et al., 1981; Durako and Moffler, 1985). The decrease in total reproductive density with depth observed at Egmont Key may be due to the concomitant effects of these phenomena, and again reflects the increased "costs" of flowering.

Phillips (1960) reported that when *T. testudinum* was in flower, only one sex was observed and no mixing occurred. Grey and Moffler (1978) found that both sexes occurred together in their samples. Our data, for different years, suggest an intermediate pattern. A definite negative relationship existed between male and female short-shoot distribution at Egmont Key, but a degree of mixing was evident across the bed. Spatial separation of sexes has been supposed to be one reason for low fruit and seed production of *T. testudinum* in Tampa Bay (Lewis et al., 1985). However, we have observed relatively substantial seed production by the Egmont Key population. If pollen production is the factor limiting successful sexual reproduction, then a comparison of sex ratios and the distribution of males and females in populations known to produce viable seeds, versus those which do not, might provide valuable information regarding the pollination biology of *T. testudinum*.

The spatial distribution patterns of male and female short-shoots at Egmont Key may reflect the age structure of the bed. Fringe areas of sea-grass beds usually represent initial colonization of a substrate while the mid-bed regions are characterized as being older (Kenworthy et al., 1982). Predominance of female short-shoots near the fringes and males in the mid-bed regions, year after year, provides evidence for an interaction of age with sex expression in *T. testudinum*. Further evidence is provided by the observation that male short-shoots generally have greater leaf widths than females (Durako and Moffler, 1985). This implies that males are older than females, although factors such as environmental and/or clonal variation could be responsible for this sex related leaf width variation. Future investigations on the reproductive ecology of *T. testudinum* should attempt to resolve such questions as the interaction of sex with short-shoot or plant age and whether or not reproductive short-shoots flower in subsequent years.

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