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Longleaf Pine Ground-layer Vegetation in Francis Marion National Forest: Reintroduction, Restoration, and Vegetation Assembly

FINAL REPORT

SAVANNA RIVER SITE

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INTRODUCTION

Longleaf pine-dominated woodlands and savannas, characterized by an open pine-dominated canopy, a sparse mid-canopy, and a diverse ground-layer vegetation including grasses, forbs and low shrubs, once encompassed vast areas of upland habitats in the southeastern USA Coastal Plain from southern Virginia to eastern Texas. Most of this once vast ecosystem is gone forever, a victim of altered land use patterns and fire exclusion. Conservation and restoration of remnant longleaf pine stands are high priorities for southeastern plant ecologists and land managers (Frost 1993, Peet and Allard 1993).

Herein we report results of a series of inter-related studies concerned with restoration of longleaf pine savannas and woodlands of the outer Coastal Plain region of central South Carolina, in and around the Francis Marion National Forest north of Charleston, SC. The FMNF is the largest remaining area of longleaf pine woods in SC and is one of the largest in the Atlantic Coastal Plain. Restoration and management of longleaf habitats in FMNF are important to USDA Forest Service and local conservation groups. We report herein on research specifically funded by DOE. Results of other related studies are presented in Glitzenstein et al. (2001, 2002).

Candidates for Reintroduction

Much of our research has focused on three permanent study plots (PSPs) representative of different types of longleaf pine habitats in the FMNF. These plots were established to study effects of different burn regimes on longleaf pine groundcover vegetation. In addition, the plots are used for experiments on species introductions, the goal of which is to enhance plant community diversity of longleaf pine ground-layer vegetation. The rationale for these experiments is that species richness at plot and stand-level scales may have been reduced by a history of infrequent fire early in the 20th century as well as other anthropogenic impacts (e.g. logging, pine straw raking, etc.). An important question, therefore, concerns which, if any species, should be the targets of reintroduction efforts.

One approach to defining restoration targets is to sample "reference stands" (e.g. Provencher et al. 2001). Species encountered in high quality sites but not present in our PSPs might be considered for reintroduction studies. The preferred candidates would include species growing in similar environments to our PSPs. The easiest method for evaluating similarity in environment is through vegetation similarity. That is, candidate species for successful re-introductions are most likely to be found in stands that are similar in terms of vegetation composition to our three study sites.

The first study presented herein attempts to identify possible restoration candidates for the three PSPs utilizing a large study of "reference quality" longleaf pine stands in the Atlantic and eastern Gulf Coastal Plain.

Germination Tests

Germination data may often be critical for a successful introduction project. There is little point in collecting seed from species that produce few or no viable seeds. For species that do produce viable seed it is important to determine when to collect the seed so as to maximize viability and germination percentages. Another important question is whether seed is easy to germinate or requires sophisticated testing to identify germination cues. Little information is available on these questions for most longleaf pine ground-cover species. We report here on the results of numerous germination tests of FMNF longleaf pine ground-layer species, including some rare and threatened plants.

Garden-Scale Restoration Experiment

Whereas the ultimate goal of most projects is large-scale restoration, small-scale experiments can help to answer important questions and refine techniques. In this sub-study we examined establishment processes of longleaf pine groundcover plants in three specially constructed garden-type beds. The beds differed in surface soil texture and drainage, two factors known to influence composition of longleaf pine ground-layer communities. Species were experimentally introduced onto the gradients as seeds. Hydrology and soil moisture were monitored weekly. Questions addressed by the study were of both basic and applied interest. To begin with, we wanted to document rates and patterns of seedling germination and establishment for a variety of longleaf pine plants under competition-free or reduced-competition conditions. Previous experiments under field conditions indicated that establishment from seed is rare in undisturbed communities (Glitzenstein et al. 2001). Second, we were interested in effects of the experimental factors, soil texture and drainage. Previous hypotheses concerning effects of environmental gradients on longleaf pine groundcover composition (and indeed most other plant communities) have been derived entirely from correlative type studies (Walker and Peet 1982, Peet and Allard 1993, Goebel et al. 2001). Such studies leave may fail to detect the true causes and mechanisms of vegetation changes. While this is an important issue in basic research, there is also a clear relevance to restoration. If one has a clear understanding of the factors that influence community development it is then possible to reconstruct these communities even when all traces of original vegetation have been eliminated.

Light and Water-table Effects on Groundcover Composition

Previous studies correlating longleaf pine vegetation and environmental factors have investigated stand-level differences. In this study, we hoped to elucidate effects of two factors (light and hydrology) that might influence vegetation within the three PSPs. The main motivation was to determine whether these factors should be treated as co-variables in the prescribe-burn study. However, the results are also important in their own right. Relationships among light, hydrology and species composition might enable managers to manipulate canopy densities to enhance species richness, and restoration practitioners to target re-introductions to the appropriate microhabitat.

Light, Water and Fire Effects on Out-planted Grasses

Lastly, we report results of an introduction/enhancement study involving grasses *Aristida beyrichiana* (wiregrass) and *Ctenium aromaticum* (toothache grass). These two grasses are dominant ground-layer species over much of the range of longleaf pine, though *Ctenium* is limited to wetter sites. In FMNF *A. beyrichiana* is at the very northern limit of its range and is, and probably always was, a rare plant. This study was initiated before the present funding period. During this funding period, however, we quantified light and hydrology in the vicinity of out-planted grasses. The goal was to study interactive effects of canopy conditions, hydrology and fire on performance of the grasses.

METHODS

Permanent Study (Fire Research) Plots

The "dry" site is subxeric longleaf woodland with intermixed *Quercus laevis, Q. incana, Q. falcata, Q. margarettiae,* and *Carya alba*. The groundcover vegetation is dominated by *Schizachyrium scoparium, Andropogon* spp., *Quercus* sprouts, *Gaylussacia spp,* and *Vaccinium tenellum.* The soil is Chipley loamy fine sand (thermic coated Aquic Quartzipsamments). The "mesic" site is mesic longleaf woodland with occasional *Quercus marilandica* and *Q. stellata.* The ground-layer is dominated by *Schizachyrium* and *Aristida virgata* along with numerous forbs and low shrubs. Moist savanna patches are present as well but these are now mostly closed woods dominated by *Pinus taeda, Liquidamber styraciflua, Nyssa sylvatica* and *Q. phellos.* The soil is mapped as Craven fine sandy loam (clayey mixed thermic Aquic Hapludult). The "wet" site is moist flatwoods and intermixed wet savanna. Flatwoods patches are dominated by *Ilex glabra*, *Clethra alnifolia*, and *Arundinaria tecta;* savanna sections are dominated by mixed grasses including *Schizachyrium scoparium*, *Andropogon glomeratus, Muhlenbergia expansa,* and *Ctenium aromaticum.* Soils are mapped as Quitman loamy sand (fine loamy siliceous thermic Aeric Paleaquult)(soils information is from Long 1980 and SCS personal communication).

Reintroduction Candidates

Potential introduction/reintroduction candidates for the three PSPs were identified using a data-set consisting of 138 longleaf pine stands from South Carolina and Georgia. Eric Kjellmark and Pat McMillan collected most of the data. We contributed 13 stands and the remaining seven stands were contributed by Richard Duncan. In general, stands were selected which appeared to be in exemplary condition, i.e. with a history of frequent fire and limited soil disturbance. Our PSPs were included in the data-set, though the condition of these three stands was perhaps less pristine than the others.

The 138 stands were sampled using methods devised by University of North Carolina professors Bob Peet and Tom Wentworth. Data were collected from 20 m x 50 m (0.1 ha) plots subdivided into 10 10 m x 10 m "modules". Four contiguous modules were intensively sampled. In each of these four modules a series of nested plots was set up in two of the four corners. Nested plots included the following: 10 cm x 10 cm (level 5), 32 cm x 32 cm (level 4), 1.0 m x 1.0 m (level 3), and 3.16 m x 3.16 m (level 2). Starting with the smallest size plot, all species were recorded at each "level". After the two sets of nested plots were surveyed the entire module (level 1) was searched for any remaining species. Lastly, the entire 0.1 ha plot was searched for any additional ("residual") species not encountered in the four intensive modules. In addition to the level at which the species was encountered, the cover of each species was estimated using a modified Daubenmire scale.

To generate a single stand-level importance value for each species we summed level data across corners. Cover values were not used in the following analysis and will not be discussed here. Results of other studies (Glitzenstein et al.; in press) indicate that cover and importance values (IVs) generated as described above are generally strongly correlated (r coefficients > 0.8) and ordination results are similar regardless of which measure is used

We ordinated the IV data using DECORANA. We then selected potential donor sites using the following procedure. First, we examined the plot of ordination scores for the first two axes. For each PSP, i.e. potential restoration site, we identified the nearest ten stands in ordination space as defined by the first two axes. We then checked the proximity of these stands on the third ordination axis as well. Of the original ten stands, the three closest stands on the third axis were selected as the "best" potential donor sites. Any species occurring in the donor stands not already in the PSPs were identified as potential candidates for introduction.

Germination Tests

We collected and tested seed of 42 ground-layer species from 15 longleaf pine sites in or near the FMNF. Except for two roadside sites that were maintained by mowing, all sites had a recent history of fire and an open canopy dominated by longleaf pine. Two germination tests were conducted for each collection. For the first test, seeds (n=50 to 100) were placed in plastic germination trays on moist blotting paper. Trays were placed on a bench near a window at room temperature. No attempt was made to control for light or temperature regime. Seed germination was tracked for ≥ 3 months. For the second test, seedling trays (hereafter growing trays) with 38 cells/tray were filled with fine sand and placed in an outdoor nursery at the Santee Experiment Station, FMNF, under a light shade-cloth covering. Seeds were pressed flat on the sand with n=5 to 10 seeds/cell depending on seed availability. Germination was followed for two months. Fresh seed, i.e. seed collected not more than 3 weeks prior to the start of the test, was used in both tests. Germination conditions for the outdoor test took advantage of germination cues typically experienced by seeds of the test species.

To address the issue of optimal collection dates we collected seed from four species at two sites over a series of different collection dates. To avoid bias, we laid out transects and selected different random locations at each collection date.

Seeds were then collected from target plants (i.e., plants that had seeds) closest to the randomly chosen locations. To avoid skewing the results towards a few prolific plants, we also randomly selected a standard number of seed heads or inflorescence branches from each plant. Obviously immature or aborted seeds were not sampled. Sampling locations were added until at least 100 seeds had been collected for each target species, or all plants had been sampled.

Garden Experiment

Three 1 m x 3 m beds were established at the FMNF seed orchard in an area free of canopy trees. Soils in the area are of the Lenoir series, a sandy loam with a drainage-resistant clay subsoil at approximately 18 cm. To construct the beds we first removed vegetation and surface soils, exposing the subsoil. Beds were then leveled to a uniform depth approximately 17 cm below the soil surface, varying by 1-2 cm among the beds. The absolute elevation of each bed was exactly 14 cm above the water table as it stood on 14 April 1998, the day the beds were constructed. The surface soil was replaced in each bed, but with soil textures randomly assigned as follows. Bed #1 was back-filled with the sandy loam surface soil that had been removed during the process of excavating the beds. Bed #2 was filled with Lakeland sand surface soil (Long 1980). Finally, Bed #3 received a surface soil taken from a site mapped as Bonneau loamy sand (Long 1980). Each bed was reconstructed so that the filled soil formed a micro-elevation/drainage gradient with the highest end at 55 cm above the clay subsoil and the lowest end at 5 cm, with a constant slope in between. Obvious roots, rhizomes and other plant parts were removed before refilling the beds. Finally, a PVC pipe well (2" inner diameter, 5' long, 4' deep) was installed in each bed to monitor water level fluctuations.

To reduce edge effects, a small buffer of 5 cm was left on both sides of each bed. The beds were then subdivided into sections of 90 cm x 50 cm. Each section was then further subdivided into 2-cm rows, with each row consisting of a 1 cm wide planting strip and a 1 cm-wide buffer. Within the planting strip, potential planting locations were limited to increments of 2 cm beginning at 0 cm. As seeds of different species became available, they were planted into the bed by randomly selecting one planting location for each of the 25 rows. The same planting arrangement was used for each of the 18 sections (i.e., 3 beds x 6 sections/bed) to avoid confounding bed or gradient position with seed arrangement. The planting technique was to press seeds flat and then cover with a thin layer of soil. Seeds were covered with soil in part to keep them from moving away from their assigned gradient positions.

The experiment was initiated in early May 1998 and terminated in late November 1999. Sixteen species were planted onto the beds as the seeds became available. We selected species characteristic of a range of different longleaf pine type habitats, from xeric to hydric. Germination was monitored approximately weekly throughout the study, except during peak periods in late winter-early spring when periods of up to three weeks between censuses were required to tally all the emerging seedlings. Weed seedlings (i.e., seedlings of species not planted on the gradient), regardless of origin (i.e., true seedling or sprout), were identified to the extent possible, mapped, and pulled, usually within a few weeks after emergence. "Volunteers" of planted species were sometimes encountered, but these could generally be distinguished from planted seedlings because the latter tended to emerge at or near the planting locations.

In addition to monitoring seedling emergence, we monitored seedling growth and mortality for planted species, and seedling mortality for weeds that died before they could be pulled. These variables were monitored weekly during 1998. During 1999 growth and mortality were checked in May and September. In the September census we also recorded flowering and various measures of plant and inflorescence size.

Water levels in the wells were monitored on a weekly basis. We also measured soil moisture (i.e., matric potential) using a QuikDraw tensiometer obtained from Soil Moisture Equipment Corp. (Goleta, CA, USA). As it turned out, these two variables were strongly related (Glitzenstein et al. 2001), which suggests that hydrological variations strongly determine drought in Coastal Plain environments.

Effects of Light and Hydroperiod on Ground-layer Vegetation

Each PSP was subdivided into 21 fire treatment plots. Pretreatment vegetation data were collected prior to beginning the experimental treatments. We randomly located six 1.5 m x 2.0 m subplots within each fire treatment plot. Subplots were subdivided into 48 25 cm x 25 cm cells. All vascular plant species were tallied in each cell of every subplot. Subplot frequencies (i.e. numbers of cells/subplot) are the data used in this analysis.

Effects of light and hydrology were investigated using the pretreatment dataset. Pretreatment data were used so that fire treatment effects would not confound results. Hydrology was measured at the mesic and wet PSPs in temporary wells excavated 1-2 days following heavy rains in winter-spring 1997-1998. Sufficient time was allowed for water tables to equilibrate before collecting the data. Not all subplots could be sampled after each rain event. However, well data overlapped sufficiently among sample dates to allow calculation of linear regressions relating results among subplots. Using these regressions we were able to estimate the missing data. This approach was justified because well data were strongly correlated (r's > 0.8) across sample dates. In the analyses reported herein the hydrological data at each site consist of well measurements/estimates for single dates (i.e. March 22, 1998 for the mesic site, May 4 1999 for the wet site). These dates were selected because they had the highest ratios of measured to estimated data for the two sites. It should be noted that well measurements below the soil surface were recorded as negative numbers (e.g. −22.5 cm indicates the depth of the water table below the soil surface), whereas positive numbers indicated standing water. This convention should be kept in mind when interpreting correlation coefficients discussed in following sections.

Light was measured above samples of subplots using hemispherical canopy photos. Photos were scanned and the resulting digital data were interpreted using the WinPhoto software of Van der Steege (1994). This software calculates a percent sky measurement as well as direct beam, diffuse light, and total light penetration through canopy openings. Due to some uncertainties in photo orientation that still remain to be resolved results reported herein are for percent sky data only.

Vegetation data were analyzed using the common indirect ordination technique DCA (Ter Braak 1995). DCA axes were interpreted through correlation with light and well data.

Grass Plantings

Two sets of grass seedlings were planted out, the first in 1993-1994, the second in 1997. Results presented here pertain to the 1993 plantings. Forty-eight plants each of wiregrass and toothache grass were planted into each of seven plots at each of the three PSPs. Within each main plot the planted grasses were distributed equally among three randomly located subplots. Grass plugs were re-censused for survival and growth on each of several occasions, the last being in 1998. Following the last census a synthetic "importance value" was calculated for each species at every subplot. For wiregrass, IV was defined on an individual plant basis as the product of the number of tillers and the length of the longest tiller. The IV for the subplot as a whole was then the sum of the IVs for individual survivors. IVs for toothache grass were calculated similarly, except that individual plant IV was defined as the product of tiller numbers, tiller length and blade width (wiregrass, having needle-like leaves, did not have a "width" dimension).

Well data and canopy photo data were collected in the vicinity of sub-samples of grass subplots as described above for vegetation sampling subplots.

RESULTS AND DISCUSSION

Introduction Candidates

Most of the species identified as potential restoration/introduction candidates for the three PSPs are common species in Atlantic Coastal Plain longleaf pine woodlands and savannas (Table 1). With two exceptions, all the species are already found elsewhere in FMNF and could easily have been found in the PSPs. Perhaps the most interesting candidate species was wiregrass (*Aristida beyrichiana)*, which appeared on the list for the dry PSP. The appearance of wiregrass on this list tends to reinforce the conclusion that the absence of this widespread and dominant species from the FMNF (the exception is one small population found recently along Halfway Creek Road) is an historic or biogeographic artifact rather than an effect of environment *per se*. Another dry site introduction candidate, *Carphephorus odoratissimus* and the mesic site candidate *Iris verna*, are also widespread species strangely absent from FMNF though present in nearby areas. Several of the candidate species, (e.g. *Manfreda virginica, Buchnera floridana*) occur commonly in FMNF along roadsides but are found only rarely in the interior of longleaf stands. We hypothesize that these roadside plants, including globally rare species *Plantago* *sparsiflora* and *Schwalbea americana*, were formerly more common away from roads but became restricted to peripheral habitats by infrequent fire and overly dense canopies. The wet site candidate *Pinguicula lutea* (butterwort) is a common component of frequently burned high quality wet savannas throughout the SE Coastal Plain. In the FMNF it is strangely rare except in a few ditches and sites with a history of frequent fire, e.g. the long-term annual burn study plot along Tiger Corner Road. The loss of *Pinguicula* from most sites is again most likely a burn frequency effect; according to Elliott (1816-1824) the species was "very common" in moist savannas in the vicinity of FMNF during the first part of the 19th century.

Among the list of introduction candidates were a few uncommon to rare species (Table 1). Notable among these were wet site candidates *Calapogon barbatus* and *Asclepias longifolia*. *Calapogon barbatus* is considered rare in SC and is common in FMNF only in the Tiger Corner annual burn plots. *Asclepias longifolia* is also considered rare (Weakley 1999), but is found occasionally in FMNF wet savannas and along moist roadsides. One mesic site candidate species, *Solidago pinetorum* is interesting because FMNF appears to be just slightly beyond the southern edge of its range. However, we have recently discovered the species at SRS (JSG personal observation; specimen needs checking) so it is quite plausible that the plant could, or did, occur naturally in FMNF as well.

The above results notwithstanding, our main conclusion from this analysis is that our three PSPs are in fact relatively intact examples of mid-Atlantic Coastal Plain longleaf pine savannas and woodlands and are not in need of large scale restoration. This conclusion accords well with the results from our historical analyses, which indicate that common species of modern longleaf pine groundcover in FMNF have been observed in those same habitats by botanists for centuries (Glitzenstein et al. in prep). A secondary conclusion from the present work, however, is that the ordination approach does produce reasonable candidates for enhancing diversity of particular stands.

Germination Studies

The results of the germination study were reasonably encouraging (Table 2). Out of 42 species included in the study, 32 had a germination percentage greater than 20% in at least one test (Figure 1, top). This translates into a success ratio of 78% if a successful seed collection is defined as one with at least 20% germination. If species response is based on mean germination a success ratio of 74% is obtained, still quite good (Figure 1, middle). Finally, even in a "worst case scenario" (Figure 1, bottom), i.e., results for a species summarized according to its poorest test result, the success ratio is a respectable 57% (24 of 42 species). This includes tests from collections known to be sub-optimal due to excessively early or late collecting.

In practical terms our results mean that one should ordinarily be able to fill a seedling tray by placing 5 seeds into each partition, an operation that is not inordinately difficult. In addition to practical issues, several other observations of interest can be culled from the germination test results (Table 2, Figure 1). To begin with, it is apparent that there was no clear difference in germination percentages among the different plant families included in the study. That is, results within families were quite variable; some species in each family germinated well and other species germinated poorly. When the results for the different families are plotted by species, results for the two germination techniques are for the most part highly correlated (Figure 2). This is, of course, to be expected if the quality of seed is the major limitation to germination. When the plots are arranged so that growing tray germination is the y-axis and germination tray germination is the x-axis, the slope of the regression line relating the two variables is generally somewhat less than one. This indicates that germination in the germination trays was generally greater than in the growing trays. Again, this result is not too surprising given the more favorable substrate and higher humidity in the germination trays. A bit more interesting is the observation that substantial deviations from the various regression lines tended to be positive (i.e., above the line) rather than negative (i.e., below the line) (Figure 2). This suggests that certain species received stimulatory germination cues in the outdoor environment that were missed indoors. This appeared to be particularly true for some fall-seeding composites that, like the grasses mentioned earlier, most likely benefited from cold stratification prior to germination. Another striking example was the much higher germination of *Rhexia nashii* seeds collected in late October 1996 in the outdoor tray (60%) vs. 2.5% in the indoor tray (Table 2). This difference was particularly striking because the results of the two techniques were quite similar for another collection made at the same site earlier in the same month. It appears that *R. nashii* had developed some form of innate dormancy (*sensu* Fenner 1985) over less than a month, which was overcome by some unknown aspect of the outdoor environment.

The germination results for rare plants were perhaps of particular interest. In total, we tested seed germination of four species appearing on Walker's (1993) list of rare longleaf pine plants: *Parnassia caroliniana, Plantago sparsiflora, Rhexia aristosa,* and *Sporobolus pinetorum.* Walker (1993) lists this last species, recently described by Weakley and Peterson (1998), as Sporobolus spp. A fifth species, *Tridens ambiguus*, does not appear on the Walker (1993) list but is listed as rare by Weakley (1999). *Parnassia* and *Plantago* are forbs of wet pine savannas, *Rhexia aristosa*, another forb, inhabits cypress savannas and other wet depressions, and *Tridens ambiguus* is a grass that lives in wet pine savannas as well as depressions. *S. pinetorum* is a locally dominant grass in pristine wet savanna habitats over a very small area of southeastern North Carolina. It was not known from South Carolina until very recently. We discovered it in the FMNF while collecting seed at PL in 1996 and have since found it at a few other locations as well. The FMNF populations represent the currently known southern range limit for the species.

Except for *Rhexia aristosa*, which essentially failed to germinate in both indoor and outdoor tests, the germination test results for these five rare species were reasonably encouraging (Table 2). The two grasses, in particular, had high germination rates in the indoor test (51% for *Tridens,* 80% for *Sporobolus*), which indicates that they lack a cold stratification requirement. The *Parnassia* tests were carried out as part of an experiment to investigate seed density effects on germination. According to Fenner (1985) such effects, either positive or negative, are not uncommon in herbaceous plants. Additional factors in the experiment involved seed spacing (aggregated vs. dispersed) and whether or not seeds were covered with a thin layer of soil. Details of the experimental design are presented in Glitzenstein et al. (1998). The results indicated little effect of seed density or spacing (Figure 3). However, covering seeds with soil did produce a significant enhancement of germination (i.e., around 14 %; see Figure 3). This may indicate a negative effect of light (see Fenner 1985) or simply improved moisture uptake by the covered seeds.

Experimental Gradient (Garden) Study

In contrast to the results of introduction trials in intact longleaf groundcover (Glitzenstein et al. 2001), numerous seedlings of a variety of species successfully germinated (Table 3) and became established on the experimental gradients (Table 4). Germination was strongly related to hydrology/drought, with peak periods of germination strongly correlating with prolonged periods of high water tables and moist soils (Figure 4). Within this general limitation, there were interesting differences among species. Fall-fruiting grasses and composites tended to appear in late winter or early spring. In contrast, spring and summer fruiting species had two germination peaks, a minor peak in late spring shortly after seeds were deposited (or, in the case of our study, placed on the gradient) and a major peak in autumn (Figure 4). Legumes, which in our study included summer fruiting species *Rhynchosia reniformis* and *Tephrosia virginica*, were distinctive in that they tended to appear throughout the year and were apparently able to take advantage of relatively brief periods of favorable soil moisture. These differences in seedling germination patterns within longleaf pine groundcover species are reminiscent of similar differences within floodplain trees that are also related to seed size and time of seed deposition (Streng et al. 1989).

Experimental effects on species composition were apparent even during early phases of seedling appearance (Figures 5-7) and survival (Figures 8-11). For the most part, these effects were consistent with known habitat preferences and gradient relationships of the various study species (see next section) and helped to explain their natural distributions. For example, *Eupatorium leucolepis* and *Chaptalia tomentosa*, species known to occur in moist or wet longleaf pine habitats, had germination and survival curves skewed towards the lower or wetter end of the experimental gradients. In contrast *Liatris squarrosa, Vernonia angustifolia,* and *Chrysopsis gossypina,* species more typical of drier longleaf pine habitats, had germination and survival peaks closer to the higher and drier end of the gradients. *Schizachyrium scoparium*, the dominant grass in FMNF longleaf pine woodlands, germinated and survived best towards the middle of the gradient.

In a few cases, appearance and/or survival patterns on the gradients were not consistent with known distributions of species. However, in these few cases the inconsistency was reversed at a subsequent life stage. For example, the legume *Tephrosia virginiana,* a species characteristic of mesic-dry habitats, germinated best at the wet end of the gradient (Figures 5-7). However, *Tephrosia* seedlings survived and grew poorly at both ends of the gradients (Figures 8-11), so that by the end of the study the species was most important towards the mesic, central portion of the gradients (Figure 17). *Rhyncosia reniformis*, another legume, also germinated best towards the lowest, wettest end of the gradients (Figures 5-7). These seedlings tended to germinate in mid-summer during dry periods when the wettest parts of the gradients were moist rather than saturated. A fairly large number of these *Rhyncosia* seedlings germinated during the second year of the study and were still alive at the official termination date of the study in fall 1999. Though no data were collected, subsequent observations indicated that all or most of these seedlings were eliminated during the winter "wet" season. This suggests that the critical filter for *Rhyncosia* is its inability to tolerate long periods of saturated soils.

In addition to hydrological effects there were also some obvious effects of the soil texture differences among the three beds (Figures 12-18). The clearest example was *Chrysopsis gossypina* (Figure 13). This species germinated, survived and grew well on the sandiest of the beds and by the end of the study was a dominant species on the dry end of this bed. In striking contrast, *Chrysopsis* germinated, survived and grew poorly on the other two beds and at the conclusion of the study was represented on those beds by only a few small individuals. These results demonstrate clearly that for some species even minor soil texture differences can be critical for establishment and, ultimately, representation in the ground-layer community.

By the end of the study in fall 1999 mature individuals of several species were well established on the gradients and had assumed dominance-distribution patterns very similar to observed field distributions of those same species (Figures 12-18; see also next section). The most obvious explanation for failure to become established was poor seed viability. That is, species with low seed viability (i.e. low germination rates in indoor and outdoor tests) produced few seedlings and most of these were eliminated by chance factors. Other than seed viability, the main explanation for establishment failure was climate variability. For example, seeds of *Arnica acaulis,* a spring-fruiting composite, were introduced onto the experimental gradients in spring 1998 and again in spring 1999. Due to prolonged drought during 1998 that lasted into autumn (Figure 4), virtually no seeds of this species germinated in the first year of the study (Table 3). However, as a consequence of more favorable climate, numerous *Arnica* seedlings were observed in fall 1999 (Table 3). These seedlings appeared to be reasonably well established by the end of the study later that fall. However, field observations later in the winter indicated that these seedlings were literally washed off the gradients in a severe rainstorm. Thus the establishment failure of *Arnica* was due to two separate environmental "catastrophes" rather than a lack of suitability for the particular soils.

A second example of the importance of climate relates to *Chaptalia tomentosa*, another spring-fruiting species common in wet sandy pine savannas. *Chaptalia* was also introduced onto the experimental gradients in both 1998 and 1999. Like Arnica, germination of Chaptalia was inhibited by prolonged drought in 1998 and the few seedlings that did germinate died soon thereafter. In 1999, larger numbers of *Chaptalia* seedlings germinated on the wetter sections of the sand and loamy sand gradients (Figures 5-7). However, these seedlings were mostly eliminated by summer drought and *Chaptalia* was once again gone from the experimental beds by mid-summer. It appears that prolonged rains lasting late into the spring would be necessary for successful establishment of this species.

A practical conclusion from these results is that a successful introduction from seed requires a certain degree of good fortune in the form of favorable climatic conditions. Thus multiple trials may be necessary if one is going to use direct seeding to establish new populations of longleaf pine ground layer plants.

The results are also pertinent to a fundamental issue in plant community organization, i.e. the importance of stochastic effects on early establishment for composition of mature communities. Another conclusion relevant to basic ecological theory is the apparent irrelevance of competition as an explanation for gradient patterns or community composition. Most of the variation in species composition, whether across the experimental gradients or within particular gradient-sections, was evident very early on in the process of seedling germination and establishment. Competition may fine tune these patterns by accelerating the loss of poorly performing individuals and species, but this would appear to be secondary to the direct effects of environment in selecting for species capable of establishment and growth in particular habitats. In nature, frequent fires that limit woody plant development maintain compositional patterns determined by seedling-level processes.

Light and Drainage Effects on Intra-stand Ground-Layer Composition

DCA ordinations of subplot pretreatment data revealed low levels of interpretable variation. In each of the three PSPs less than 9% of the species composition variation was explained by the 1st ordination axis and less than 20% of the total variation was explained by the first 4 ordination axes. Since the fire treatment plots were selected so as to minimize within and between plot compositional variance these results are not particularly surprising. What is perhaps surprising is that the existing compositional variance, minor though it was, was to some extent explained by the two environmental factors we chose to measure.

At the wet site PSP both the first and second axes were significantly related to well depth (r's = -0.61, 0.22 respectively, n = 98, p's = 0.00, 0.03). Species scores along the first axis in particular were clearly consistent with the demonstrated hydrological gradient. For example the three species with the lowest first axis scores, *Eleocharis tuberculosa, Eriocaulon decangulare,* and *Dichanthelium scabriusculum* are commonly found in the wettest savannas whereas the three highest scoring species, *Hieracium gronovii, Solidago odora,* and *Polygala mariana* are plants of mesic-dry woodlands.

Wet site canopy cover (i.e. % sky in the hemispherical photographs) was moderately correlated with each of the first three DCA axes (r's = 0.36, 0.33, -0.30, respectively, n = 26) at probability levels that fell just short of conventional significance (p's = 0.07, 0.10, 0.13). Most likely slightly these results would be significant with a slightly larger sample size. In addition to possible effects on species composition, percent sky at the wet site was positively and highly significantly (r=0.52, p= 0.006) correlated with species richness (i.e. numbers of species per subplot). In contrast well depth was not significantly correlated (r=0.16, p=0.12) with species richness. Thus hydrology best explained species composition changes while variation in species richness was better explained by canopy cover. The relatively strong canopy effect on ground-layer richness suggests that high light levels allow for maintenance of higher levels of herbaceous diversity in shrub-dominated moist flatwoods with a history of at least moderately frequent fire.

Results for the mesic site PSP were somewhat similar. Well depth was again significantly correlated to two DCA ordination axes, the second and fourth (r's = 0.71, -0.21, p's = 0.00, 0.04, n= 101). The three highest-ranking species on the second ordination axis were *Tragia urens, Rhycosia difformis*, and *Ilex ambigua*, species of moderately dry, sandy, somewhat elevated microhabitats. In contrast, the three lowest ranking species on this axis were the beak sedges *Rhychospora elliottii, R. debilis*, and *R. fascicularis*, species characteristic of moister micro-depressional habitats.

Canopy-cover (i.e. percent sky) at the mesic site PSP was significantly correlated to the same two ordination axes as well depth (r's = -0.29, -0.22, p's = 0.02, 0.09, n=59). Interestingly, percent sky and well depth were themselves not at all correlated (r = 0.00, p = 0.99), so their mutual correlation with the same ordination axes reflected independent though related effects on this compositional gradient. Unlike at the wet site, canopy effects at the mesic site were not strongly correlated with species richness (r= 0.21, p= 0.11, n=59), though there was a weak positive relationship that would most likely turn out to be significant at the conventional level with a larger data set. We hypothesize that the reduced importance of canopy cover effects on species richness at this site was due to the generally more herbaceous dominated condition of the ground-layer. Lesser competition from shrubs may allow herbaceous plants to persist at somewhat reduced light levels.

Percent sky was the only environmental variable measured at the dry site and comparatively few photos were taken compared to the other two sites. Canopy effects at this site were not significantly related to either composition (r's < 0.27, p's > 0.2 for all axes, n = 24) or species richness (r = 0.19, p= 0.36). It is worth noting, however, that canopy openness levels were relatively low in all of the photos (< 30%). Thus this analysis probably did not constitute a meaningful test of canopy light effects at this site.

Planted Grasses

Wiregrass

Five years after out-planting, wiregrass importance at the wet site was significantly negatively correlated with well depth (r= -0.55, n=18, Figure 19) but not with any other factor (r's < 0.2, p's > 0.2). Since well depth increased (i.e. became less negative) with higher water tables, this result indicates that wiregrass importance in flatwoods and moist savannas is limited by high water tables. This result is consistent with observed field distributions of *Aristida beyrichiana* in the Carolinas (Taggart 1990, Peet and Allard 1993).

Fire history at the wet site was not significantly correlated with wiregrass importance in 1998. However, wiregrass plots with the least history of fire fell consistently beneath the regression line relating wiregrass importance values to well depths (Figure 19). Thus, controlling for hydrology, fire frequency did appear to influence outplanting success of wiregrass at the wet PSP.

In contrast to the wet site results, wiregrass IV at the mesic site was unrelated to hydrology ($r=0.05$, $p=0.85$). Apparently even subplots with highest water tables were not so consistently inundated as to limit survival and growth of wiregrass. Canopy and fire frequency effects (i.e. numbers of fires during the study period) also did not explain significant levels of observed variation in wiregrass importance at this site (r's < 0.3, p's > 0.2). The one significant correlation was with time since burn. Curiously this correlation was positive ($r=0.43$, $p=0.05$, $n=21$) indicating highest levels of wiregrass importance in plots that had gone the longest without fire. This result is consistent with the hypothesis that wiregrass is a strong competitor, at least in comparison to the other grasses, forbs and short shrubs prevalent at the mesic PSP. Barring strong competition from tall shrubs and tree sprouts (e.g. as at the wet PSP), longer intervals between fires might actually favor wiregrass dominance.

Lastly, wiregrass importance in the dry PSP was not significantly correlated with fire history. Well data were not collected at this site and only a few canopy photos were taken around out-planted grass plots. A plot of wiregrass importance versus fire frequency did yield a somewhat interesting pattern, however. Subplots fell into two rather distinct groups on this graph: a group of four subplots with higher levels of wiregrass importance and a large group with a much lower wiregrass importance. None of the subplots with the lowest fire frequency were in the subgroup with the higher levels of wiregrass importance. Furthermore, maximum importance of wiregrass did tend to increase with fire frequency, though mean importance was highest at the intermediate burn frequency (Figure 20). Finally, it is perhaps of interest that the limited photo data were at least consistent with a possible light effect on wiregrass importance at this site. Three photos were taken. Two of these were in relatively more open subplots, and these were subplots with high importance values for wiregrass. The third photo was of a closed canopy plot (12% percent sky) with a low importance value for wiregrass. More data will be required to confirm these preliminary results.

Toothache Grass

Toothache grass importance at the wet site was significantly positively correlated with fire frequency ($r=0.40$, $p=0.06$, $n=21$) but not with any other factor (r's < 0.15, p's > 0.5). This suggests that toothache grass importance in flatwoods is primarily limited by shrub competition, which is reduced in frequently burned plots. In contrast to wiregrass, toothache grass importance was not lower in the subplots with higher water tables. This explains why toothache grass can dominate wetter savanna sites with a history of frequent fire.

At the mesic site toothache grass importance was most highly correlated with percent sky, our measure of light penetrating the canopy. The correlation coefficient was positive, but fell just short of statistical significance ($r=0.36$, $p=0.10$, $n=21$). A hypothesis for future testing is that toothache grass importance is more limited by canopy cover in sites where shrub competition is less important.

CONCLUSIONS

Overall, this study represents significant progress in our understanding of compositional gradients in longleaf pine plant communities. We conclusively demonstrated the importance of water table depth as a controlling variable in wet and mesic habitats. We accomplished this not only by correlating this variable with vegetation patterns in the field but also by experimentally reproducing similar effects in a garden experiment. Light effects were less consistently demonstrated but probably were important nonetheless. Increasing the sample size of canopy photos and additional garden experiments appear to be warranted. The grass planting studies suggested that observed field distributions of dominant pine savanna grasses derive from complex interactive effects of fire history, hydrology and light environments. Lastly, our use of a regional longleaf data set to identify candidate species for introductions also appears to be a pioneering effort.

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Table 1. Introduction/reintroduction candidate species identified by DCA ordination analyses of the regional longleaf dataset (see text). For each PSP candidate species are those not present in the PSP but found in one or more of the three closest sites in ordination space. Species found in FMNF are starred.

Dry Site

Aristida beyrichiana *
Carphephorus odoratissima
Manfreda virginica *
Stylisma humistrata *

Mesic Site

Buchnera floridana *
Iris verna
Kuhnia eupatoroides *
Pycnanthemum flexuosum *
Rhynchospora perplexa *
Sabatia difformis *
Schrankia microphyllum *
Silphium compositum *
Solidago pinetorum
Solidago tortifolius *
Verbena carnea *
Vernonia angustifolia *

Wet Site

Asclepias longifolia *
Calapogon barbatus *
Pinguicula lutea *
Rhynchospora perplexa *
Sericocarpus linifolia *

Table 2. Results of germination tests 1996-1999. Letter code below species name is a collection site label. Collection dates are next to the site labels. Burn codes are as follows: D= dormant season burn, G = growing season burn, G -1 = growing season burn in the previous year; except for G - 1 all burns occurred less than 1 year prior to the date of seed collection. Column label "germ tray" indicates germination tests carried out in closed plastic germination boxes with seeds on moist blotting paper. Tests were performed on a bench placed next to a window at room temperature with no attempt to precisely control light or temperature. Column label "grow tray" is for outside germination tests carried out in standard horticultural trays filled with moist sand. For these latter tests seed was placed on top of cells within 1 month after it was collected from the field sites. Thus these seeds were exposed to a regime of natural light and temperature fluctuations. Numbers under column headings are germination percentages. If different from n=100, sample sizes are listed in parentheses after the germination results. For *Carphephorus tomentosus* stage of seed maturity is indicated after each line as follows: NE = pappus not expanded, E = pappus expanded, but heads not entirely opened, G = pappus expanded, heads opened, seeds arranged in a 360 degree pattern around the heads, thus appearing globose. This species is preceded by a large dot to indicate that it is locally rare. Globally rare species (Walker 1993), *Parnassia caroliniana, Plantago sparsiflora, Rhexia aristosa, Tridens ambiguus* and *Sporobolus pinetorum* are preceded by double stars. Results for *Parnassia* are given for covered (cov.) and uncovered (unc.) seeds (see also Figure 5).

		BURN SEASON	GERM TRAY	GROW TRAY
A. APIACEAE				
1. *Oxypolis filiformis*				
(AS)	10/05/99	G	75.3(150)	
B. ASTERACEAE				
1. *Arnica acaulis*				
(PL)	05/28/96	G	90.0	64.3(115)
(SO)	05/12/98	G	48.7(150)	
(SCTS)	05/24/99	D	57.3(150)	
2. *Aster concolor*				
(MS)	01/24/97	G	10.3(107)	1.4(73)
3. *Aster dumosus*				
(HC)	01/21/97	D	14.0	12.5(96)
(MS)	01/24/97	G	50.0(128)	47.4(97)
4. *Aster linariifolius*				
(HC)	01/21/97	D	5.0(80)	0.0(26)
(MS)	01/24/97	G	46.8(79)	48.0(25)

5. *Aster tortifolius*					
(HC)	01/21/97	D	20.7(29)	33.3(10)	
6. *Aster walteri*					
(HC)	01/21/97	D	78.7(61)	66.7(15)	
(MS)	01/24/97	G	63.7(104)	74.7	
7. *Bigelowia nudata*					
(HC)	11/27/96	D	52.0	51.0	
(HC)	01/21/97	D	29.8(57)		
(HC)	01/21/97	D	0.0(60) (ABORTED SEED?)		
8. *Carphephorus paniculatus*					
(HC)	10/26/96	D	1.8(57)	5.0(20)	
(HC)	11/27/96	D	35.0	30.4(92)	
(HC)	01/21/97	D	42.2(90)	42.0(88)	
(MS)	01/24/97	G	21.8(101)	19.0	
• 9. *Carphephorus tomentosus*					
(PL)	10/28/96	G	29.6(142)	45.0(80)	NE
(PL)	10/28/96	G		44.4(36)	E
(PL)	11/27/96	G	17.0(53)	41.6(36)	NE
(PL)	11/27/96	G	21.0	30.9(81)	E
(PL)	11/27/96	G	35.3(68)	72.2(54)	G
10. *Chaptalia tomentosa*					
(WH)	04/14/98	-	88.7(150)		
(SIM)	04/16/99	-	64.0(150)		
11. *Chrysopsis gossypina*					
(C169)	01/19/99	G	32.7(150)		
12. *Chrysopsis mariana*					
(MS)	01/24/97	G	28.3(99)	40.0(90)	
13. *Coreopsis oniscicarpa*					
(MS)	01/24/97	G	30.1(83)	28.9(45)	
14. *Erigeron vernus*					
(C195)	06/07/98	G	10.0(150)		
(SCTS)	05/24/99	D	1.2(80)		
15. *Eupatorium leucolepis*					
(MS)	01/24/97	G	43.0	27.1(96)	
(SO)	01/14/99	G-1	32.0(150)		
16. *Eupatorium rotundifolium*					

(HC)	01/21/97	D	24.0(121)	26.3(99)
(MS)	01/24/97	G	15.0	7.4(94)
(SO)	10/14/99	G-1	46.7(150)	
17. *Liatris squarrosa*				
(C195)	12/01/98	G	62.0(150)	
18. *Pityopsis graminifolia*				
(HC)	01/21/97	D	2.6(115)	2.0(99)
19. *Pterocaulon pycnostachyum*				
(HAC)	06/23/96	D	31.0	21.7(115)
(HAC)	06/29/96	D	42.0(115)	20.0
(HC)	07/02/99	D	44.7(150)	
20. *Solidago fistulosa*				
(MS)	01/23/97	G	49.1(57)	
21. *Solidago odora*				
(HC)	01/21/97	D	0.0(29)	0.0(20)
22. *Vernonia angustifolia*				
(C195)	10/24/98	G	35.3(150)	

B. FABACEAE

1. *Desmodium tenue*				
(HC)	01/21/97	D	59.6(57)	53.8(26)
2. *Lespedeza capitatus*				
(HC)	10/06/96	D	11.4(35)	
(MS)	01/23/97	G	7.3(41)	
3. *Rhynchosia reniformis*				
(HAC)	06/15/96	D	94.9(59)	42.4(59)
(HAC)	06/23/96	D	32.8(61)	13.3(60)
(HAC)	06/29/96	D	0.0(59)	0.0(60)
(C184)	06/22/98	D	48.7(150)	
4. *Tephrosia virginiana*				
(C195)		G	70.0(150)	

C. HYPERICACEAE

1. *Hypericum setosum*				
(HC)	01/21/97	D	13.4(120)	8.3(108)
(HC)	01/21/97	D	46.7(120)	

NOTE: top line is after 4 mo., bottom line is germination after 1.5 years.

D. MELASTOMATACEAE

**	1. *Rhexia aristosa*					
		(HC)	10/06/96	D	3.6(55)	0.0(55)
		(HC)	10/28/96	D	1.1(90)	6.2(81)
	2. *Rhexia nashii*					
		(HC)	10/06/96	D	56.7(60)	63.3(60)
		(HC)	10/28/96	D	2.5(80)	60.0(80)
	3. *Rhexia alifanus*					
		(HC)	10/06/96	D	12.0	2.0
		(HC)	10/26/96	D	9.0(95)	6.3(95)
		(HC)	11/27/96	D	22.1(68)	20.0(115)
		(HC)	01/21/97	D	13.4(98)	2.4(85)
		(C195)	09/13/98	G	4.7(150)	

E. ONAGRACEAE

	1. *Ludwigia virgata*					
		(HC)	01/21/97	D	6.1(115)	11.0

F. PARNASSIACEAE

**	1. *Parnassia caroliniana*					
		(BH)	12/19/94	D		34.0 (Cov)
		(BH)	12/19/94	D		20.0 (Unc)

G. PLANTAGINACEAE

**	1. *Plantago sparsiflora*					
		(WH)	6/15/98	Mowed		17.6(228)

H. POACEAE

	1. *Aristida virgata*					
		(HC)	01/21/97	D	48.4(93)	43.1(65)
		(MS)	01/23/97	G	58.3(103)	66.2(74)
	2. *Ctenium aromaticum*					
		(HC)	10/06/96	D	27.0	25.8(89)
		(HC)	10/28/96	D	30.0	23.1(91)
		(HC)	11/27/98	D	21.0	21.0
		(HC)	01/23/97	D	19.4(98)	29.8(94)
		(MS)	01/24/97	G	36.4(110)	20.9(110)
		(C195)	12/02/98	G	3.0(150)	
	3. *Muhlenbergia expansa*					
		(PL)	10/29/96	G	12.0	13.0

	4. *Panicum virgatum*				
	(MS)	01/23/97	G	9.9(91)	1.3(80)
	5. *Schizachyrium scoparium*				
	(PL)	10/24/96	G	5.0	11.0
	(C196)	11/23/98	G	55.3(150)	
**	6. *Sporobolus pinetorum*				
	(PL)	10/29/96	G	51.0	23.3(30)
**	7. *Tridens ambiguus*				
	(PL)	10/28/96	G	88.0	68.0

I. POLYGALACEAE

1. *Polygala lutea*				
(SO)	07/07/98	G	28.7(150)	

Table 3. Seedlings germinating on the three experimental gradients from May 1998 through November 1999. Seed number refers to number of seeds added during the experiment. Seedlings are individuals observed to originate from cotyledons or otherwise determined to be new germinants. Note that the few observed seedlings of *Oxypolis* and *Eupatorium rotundifolium* may be explained mainly by the inadequate observation period for these species (i.e., about 1 month between planting and the end of the experiment).

Species	# Seeds	Date Added	# Seedlings	Appearance (%)
Arnica acaulis (1998)	900	5/12-29/98	7	0.8
Arnica acaulis (1999)	450	6/16-21/99	65	14.4
Chaptalia tomentosa (1998)	450	5/12-15/98	7	1.6
Chaptalia tomentosa (1999)	450	4/18-29/99	44	9.8
Chrysopsis gossypina	450	1/29-2/8/99	94	20.9
Ctenium aromaticum	450	1/9-11/99	30	6.7
Erigeron vernus (1998)	450	6/15-16/98	12	2.7
Erigeron vernus (1999)	450	6/16-21/99	5	1.1
Eupatorium leucolepis	450	1/29-2/8/99	171	38.0
Eupatorium rotundifolium	450	10/14-29/99	7	1.6
Liatris squarrosa	450	1/9-11/99	111	24.7
Oxypolis filiformis	450	10/14-29/99	4	0.9
Polygala lutea	450	7/13-14/98	15	3.3
Pterocaulon pycnostachyum	450	7/14-15/99	31	6.9
Rhexia alifanus	450	9/22-23/98	27	6.0
Rhynchosia reniformis	450	6/23-25/98	44	9.8
Schizachyrium scoparium	450	11/30-12/14/98	118	26.2
Tephrosia virginiana	450	8/4/98	112	24.9
Vernonia angustifolia	450	10/24-28/98	74	16.4

Table 4. Additional results from the experimental gradients: survival, size, and reproduction in September 1999 of plants originating from seeds germinated prior to that date. Sample size (n) indicates the number of germinated seeds. Note that for some species (e.g., spring-summer fruiting species *Arnica* and *Pterocaulon*), most of the germination occurred after the September 1999 census and sample sizes shown below are consequently not as large for these species as they are in Table 3. Flowering is given as a percentage of living plants. Numbers under Ht/Len are mean values for plant height in cm unless followed by an L which indicates that leaf length measurements are given instead (this was for species with basal rosettes only). For species with a mixture of bolting and non-bolting stems, mean heights were calculated by assigning a height of 1 cm to individuals present only as rosettes.

	Bed 1 (sandy loam)				Bed #2 (sand)				Bed #3 (loamy sand)			
Species	n	% alive	% flower	Ht/Len	n	% alive	% flower	Ht/Len	n	% alive	% flower	Ht/Len
Arnica acaulis	4	0.0	--	--	2	0.0	--	--	3	0.0	--	--
Chaptalia tomentosa	7	0.0	--	--	22	0.0	--	--	19	2.1	0.0	0.8L
Chrysopsis gossypina	28	10.7	--	1.0	33	78.8	50.0	17.2	29	58.6	0.0	1.0
Ctenium aromaticum	12	0.0	--	--	7	0.0	--	--	11	33.3	0.0	6.7L
Erigeron vernus	4	0.0	--	--	3	0.0	--	--	12	0.0	--	--
Eupatorium leucolepis	53	17.0	44.4	20.9	42	67.3	81.5	34.2	68	61.8	52.4	25.5
Liatris squarrosa	34	52.9	5.6	2.2	43	51.2	50.0	15.0	34	82.4	14.3	4.1
Polygala lutea	4	0.0	--	--	3	33.3	100.0	15.0	4	25.0	0.0	1.9
Pterocaulon pycnostach.	1	0.0	--	--	--	--	--	--	--	--	--	--
Rhexia alifanus	9	0.0	--	--	1	0.0	--	--	3	0.0	--	--
Rhynchosia reniformis	11	27.3	0.0	0.7	10	10.0	0.0	0.9	22	63.6	0.0	0.9
Schizachyrium scoparium	59	49.2	31.0	25.8	25	72.0	72.2	49.0	34	55.9	31.6	23.5
Tephrosia virginiana	36	19.4	0.0	20.1	34	32.4	0.0	24.0	42	21.4	0.0	18.6
Vernonia angustifolia	25	16.0	0.0	10.2	22	50.0	18.2	12.2	26	38.5	0.0	8.3

FIGURE LEGENDS

1. Germination results summarized according to plant family. Top graph ("best case") includes the best germination results for each species; middle graph ("mean") includes means of all tests; bottom graph ("worst case") includes the single poorest result for each species.
2. Relationship between indoor (germination tray) and outdoor (growing tray) germination.
3. Relationship of Parnassia caroliniana germination to seed density. Also shown are effects of seed spacing and germination differences between covered (i.e. with a thin soil layer) and uncovered seeds.
4. Seedling appearance patterns on the experimental gradients as a function of hydrology and matric potential, a measure of soil moisture availability.
5. Germination patterns across the sandy loam gradient.
6. Germination patterns across the sand gradient.
7. Germination patterns across the loamy sand gradient.
8. Survival patterns across the sandy loam gradient.
9. Survival patterns across the sand gradient.
10. Survival patterns across the loamy sand gradient.
11. Survival patterns averaged across the three gradients.
12. Measures of *Schizachyrium scoparium* size across the three gradients at the end of the study.
13. Measures of *Chrysopsis gossypina* size across the three gradients at the end of the study.
14. Measures of *Rhynchosia reniformis* size across the three gradients at the end of the study.
15. Measures of *Eupatorium leucolepis* size across the three gradients at the end of the study.
16. Measures of *Vernonia angustifolia* size across the three gradients at the end of the study.
17. Measures of *Tephrosia virginica* size across the three gradients at the end of the study.
18. Measures of *Liatris squarrosa* size across the three gradients at the end of the study.
19. Wiregrass importance values at the wet site plotted as a function of well depth and fire frequency.
20. Wiregrass importance values at the dry site plotted as a function of fire history and percent sky (point lablels).

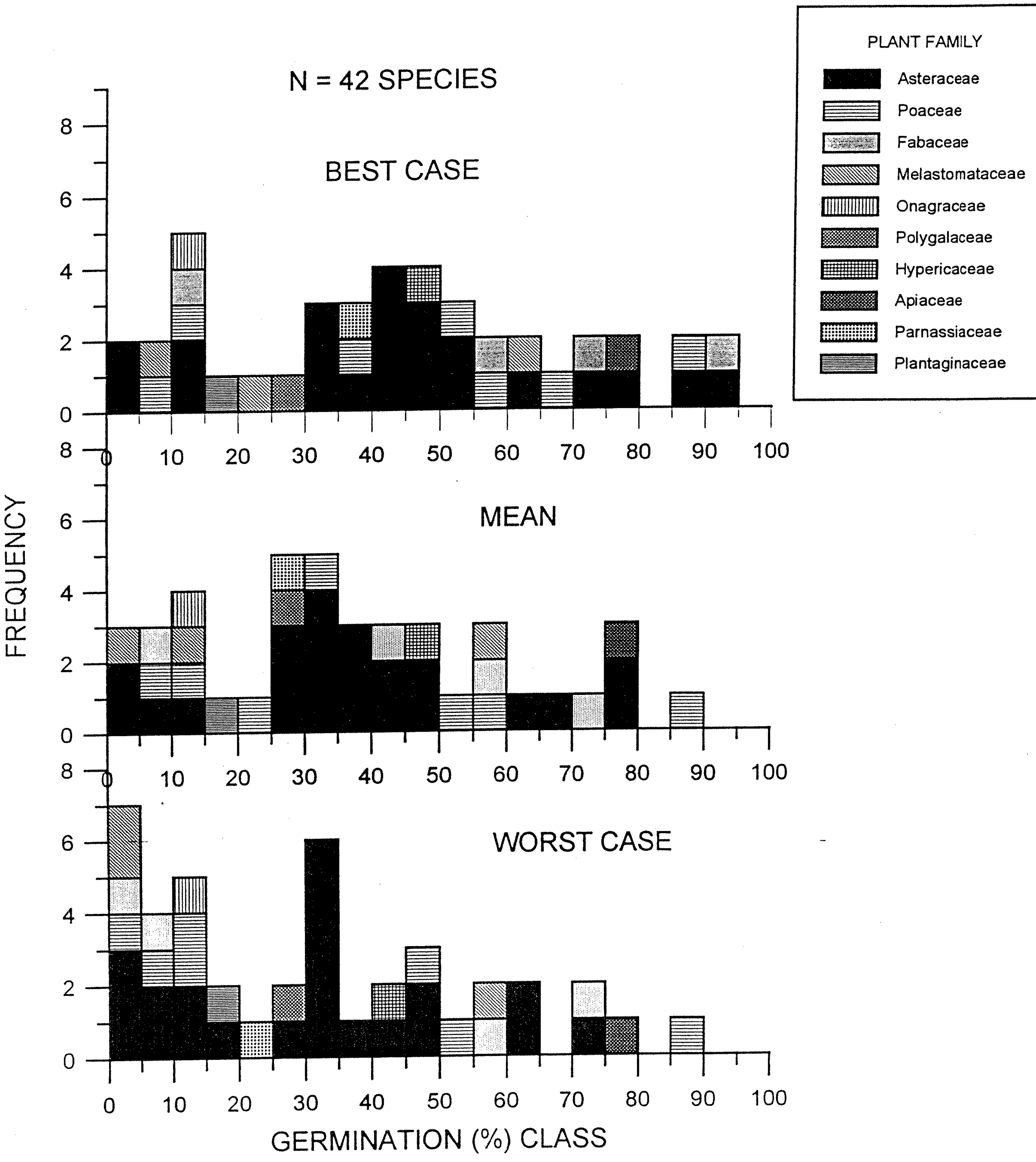

N = 42 SPECIES
BEST CASE
MEAN
WORST CASE
FREQUENCY
0
2
4
6
8
0
10
20
30
40
50
60
70
80
90
100
GERMINATION (%) CLASS
PLANT FAMILY
Asteraceae
Poaceae
Fabaceae
Melastomataceae
Onagraceae
Polygalaceae
Hypericaceae
Apiaceae
Parnassiaceae
Plantaginaceae

FIG. 4

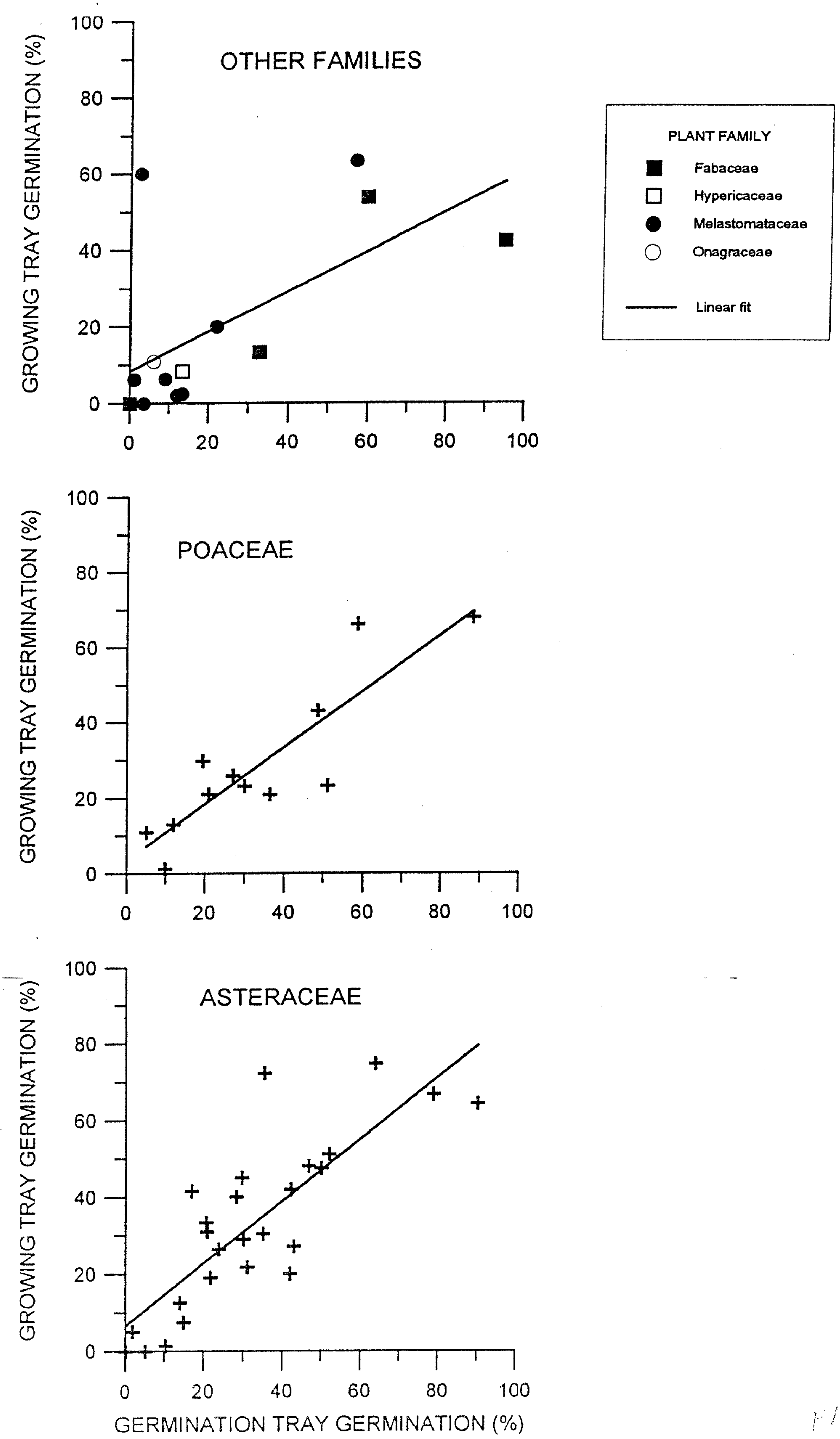

OTHER FAMILIES
POACEAE
ASTERACEAE
GROWING TRAY GERMINATION (%)
GERMINATION TRAY GERMINATION (%)
0
20
40
60
80
100
PLANT FAMILY
■ Fabaceae
□ Hypericaceae
● Melastomataceae
○ Onagraceae
Linear fit

FIG 2

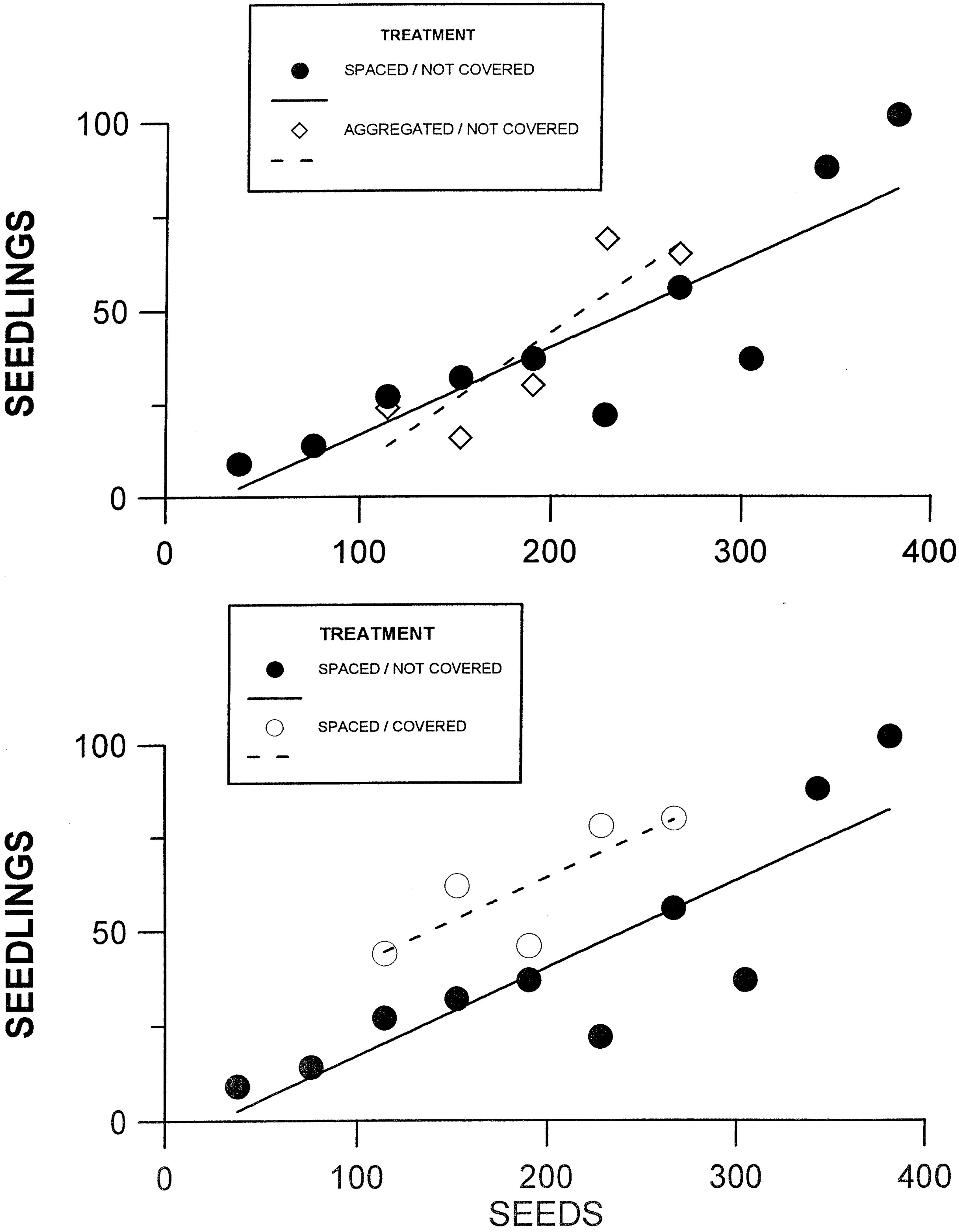

TREATMENT
● SPACED / NOT COVERED
◇ AGGREGATED / NOT COVERED
SEEDLINGS
100
50
0
0
100
200
300
400
TREATMENT
● SPACED / NOT COVERED
○ SPACED / COVERED
SEEDLINGS
100
50
0
0
100
200
300
400
SEEDS

Fig. 3

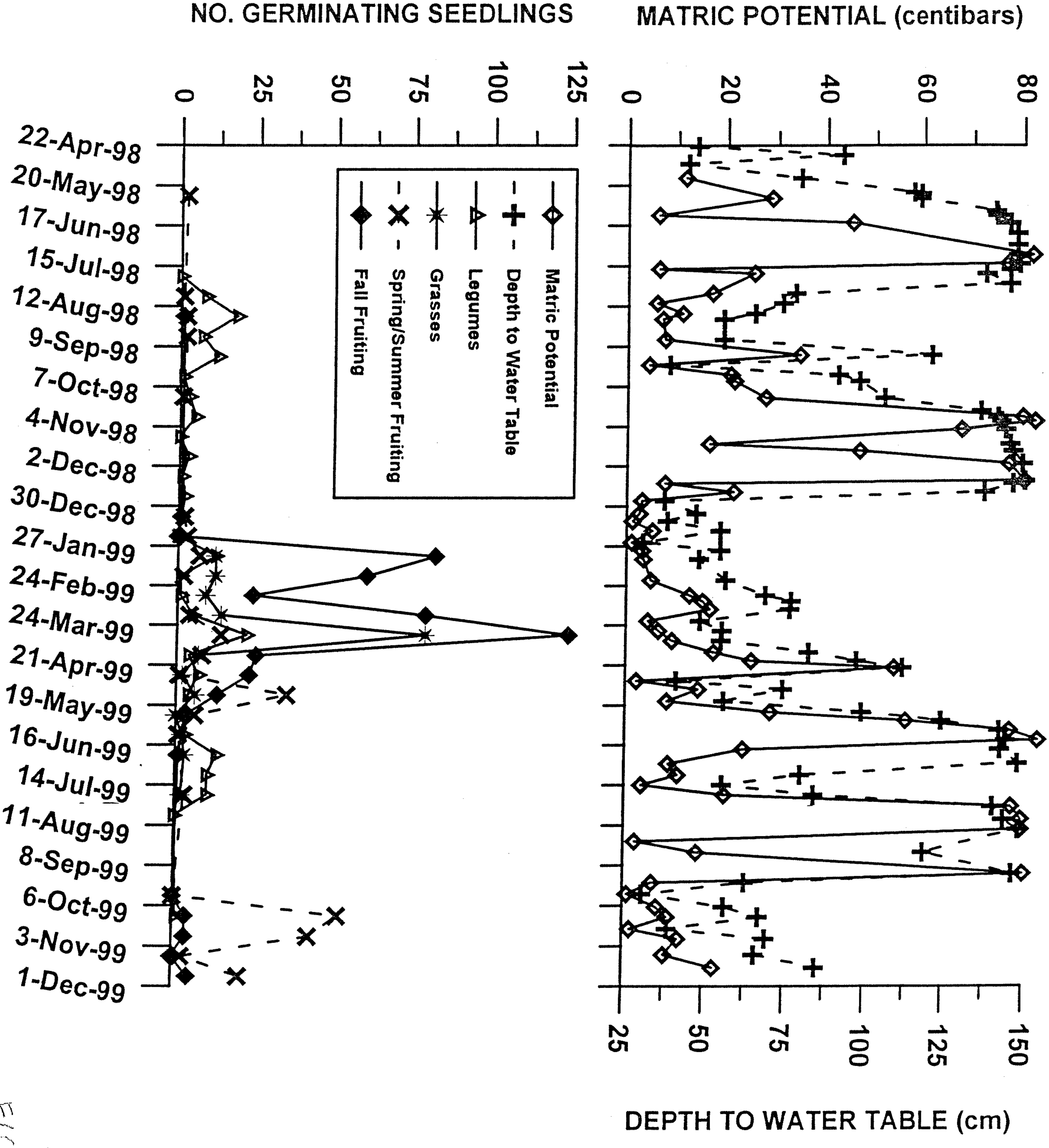

NO. GERMINATING SEEDLINGS
MATRIC POTENTIAL (centibars)
DEPTH TO WATER TABLE (cm)
0
20
40
60
80
0
25
50
75
100
125
25
50
75
100
125
150
22-Apr-98
20-May-98
17-Jun-98
15-Jul-98
12-Aug-98
9-Sep-98
7-Oct-98
4-Nov-98
2-Dec-98
30-Dec-98
27-Jan-99
24-Feb-99
24-Mar-99
21-Apr-99
19-May-99
16-Jun-99
14-Jul-99
11-Aug-99
8-Sep-99
6-Oct-99
3-Nov-99
1-Dec-99
Matric Potential
Depth to Water Table
Legumes
Grasses
Spring/Summer Fruiting
Fall Fruiting

FIG X 4

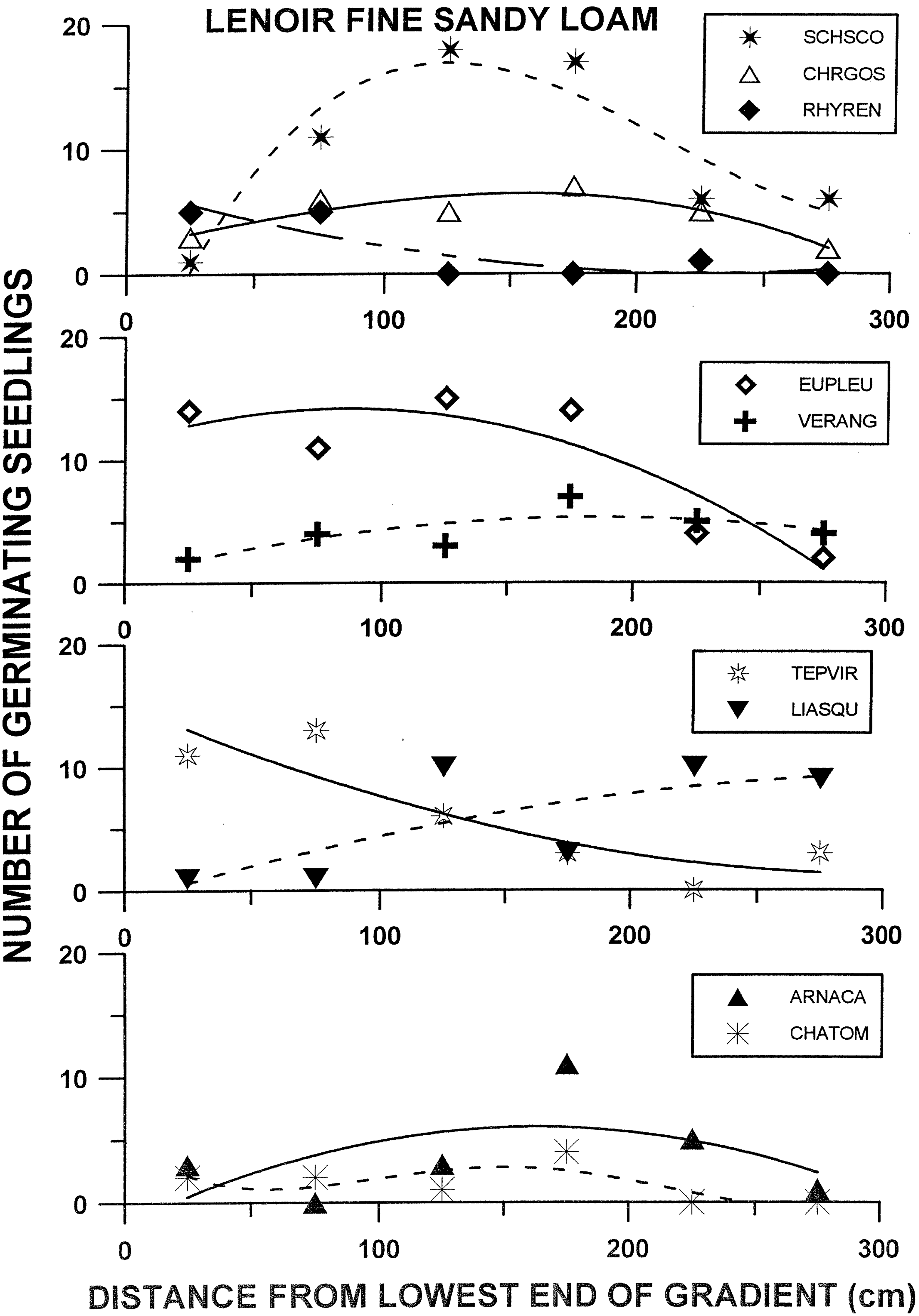

LENOIR FINE SANDY LOAM
SCHSCO
CHRGOS
RHYREN
EUPLEU
VERANG
TEPVIR
LIASQU
ARNACA
CHATOM
NUMBER OF GERMINATING SEEDLINGS
DISTANCE FROM LOWEST END OF GRADIENT (cm)
0
10
20
0
100
200
300

FIG 5

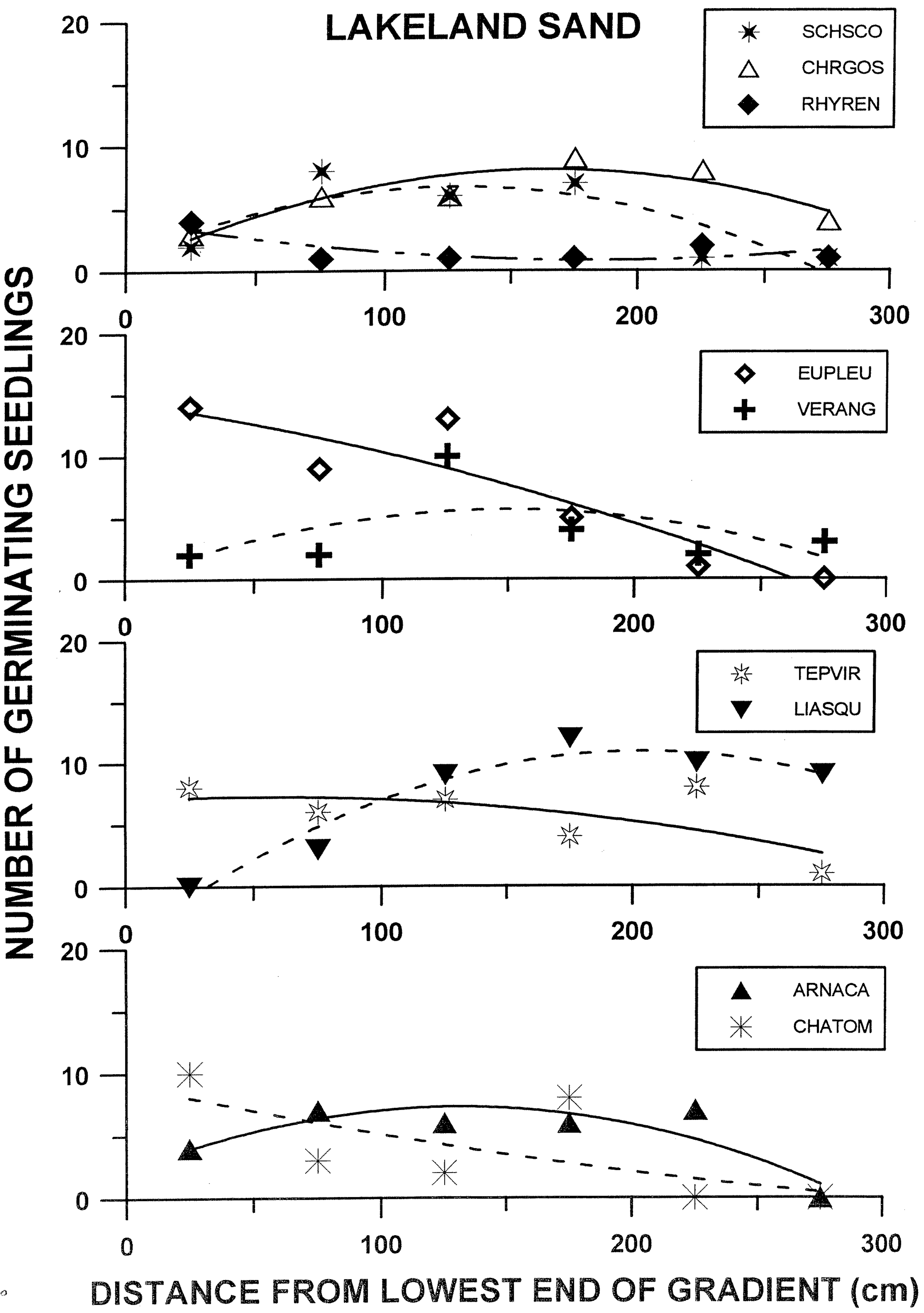

LAKELAND SAND
SCHSCO
CHRGOS
RHYREN
EUPLEU
VERANG
TEPVIR
LIASQU
ARNACA
CHATOM
NUMBER OF GERMINATING SEEDLINGS
DISTANCE FROM LOWEST END OF GRADIENT (cm)
0
10
20
0
100
200
300

FIG 6

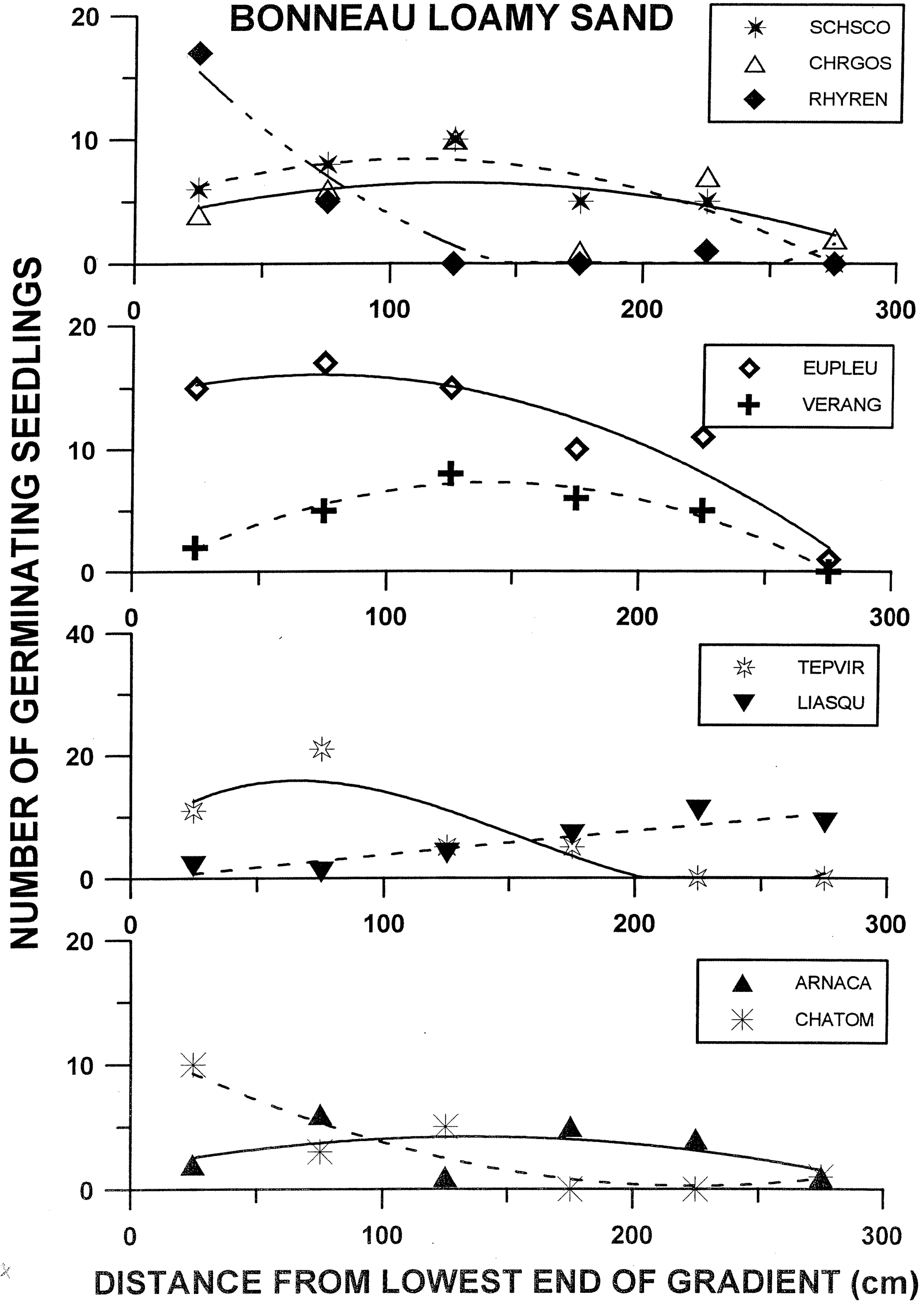

BONNEAU LOAMY SAND
SCHSCO
CHRGOS
RHYREN
EUPLEU
VERANG
TEPVIR
LIASQU
ARNACA
CHATOM
NUMBER OF GERMINATING SEEDLINGS
0
10
20
40
0
100
200
300
DISTANCE FROM LOWEST END OF GRADIENT (cm)

FIG 7

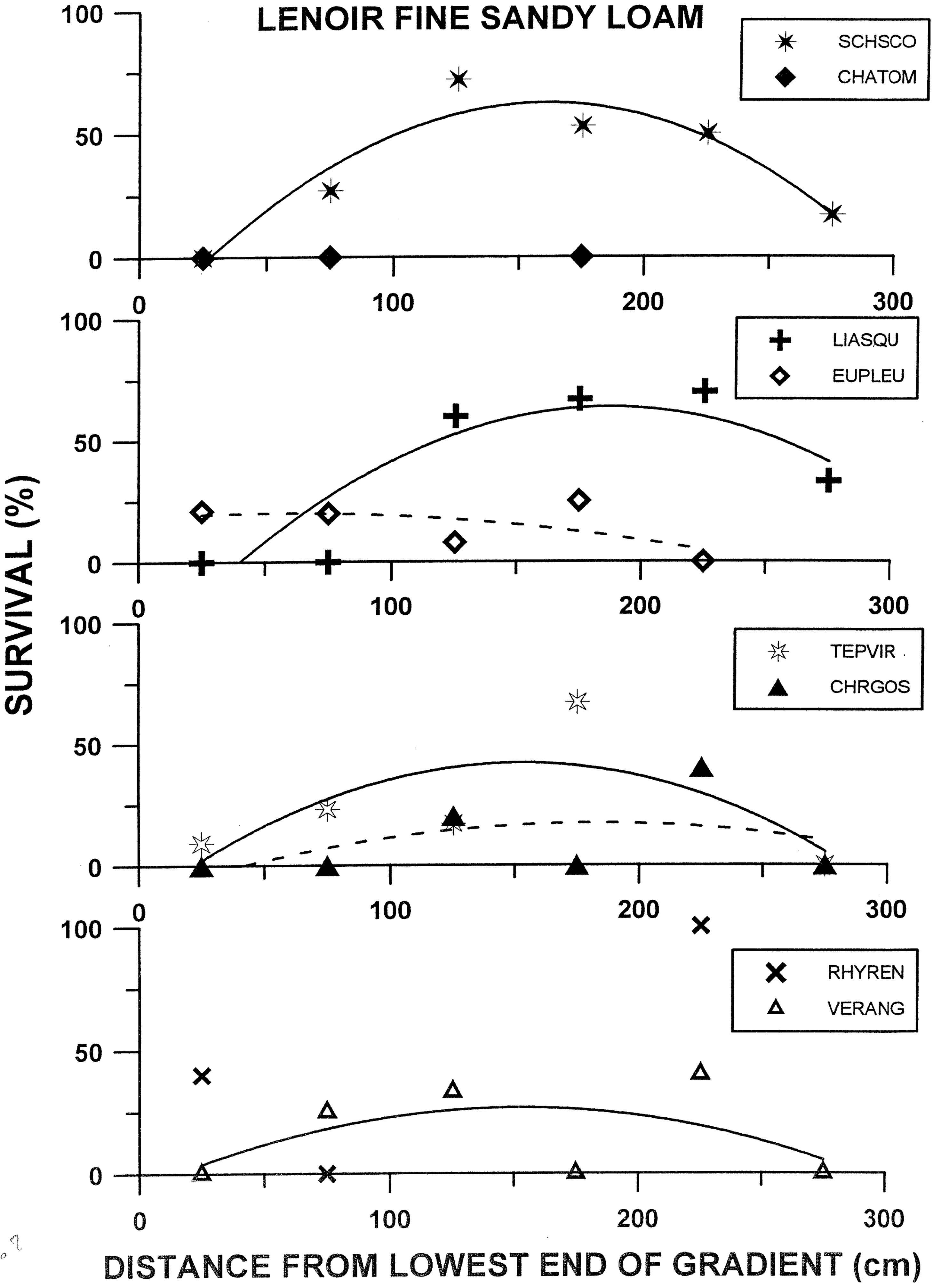

LENOIR FINE SANDY LOAM
SCHSCO
CHATOM
LIASQU
EUPLEU
TEPVIR
CHRGOS
RHYREN
VERANG
100
50
0
0
100
200
300
SURVIVAL (%)
DISTANCE FROM LOWEST END OF GRADIENT (cm)

FIG 8

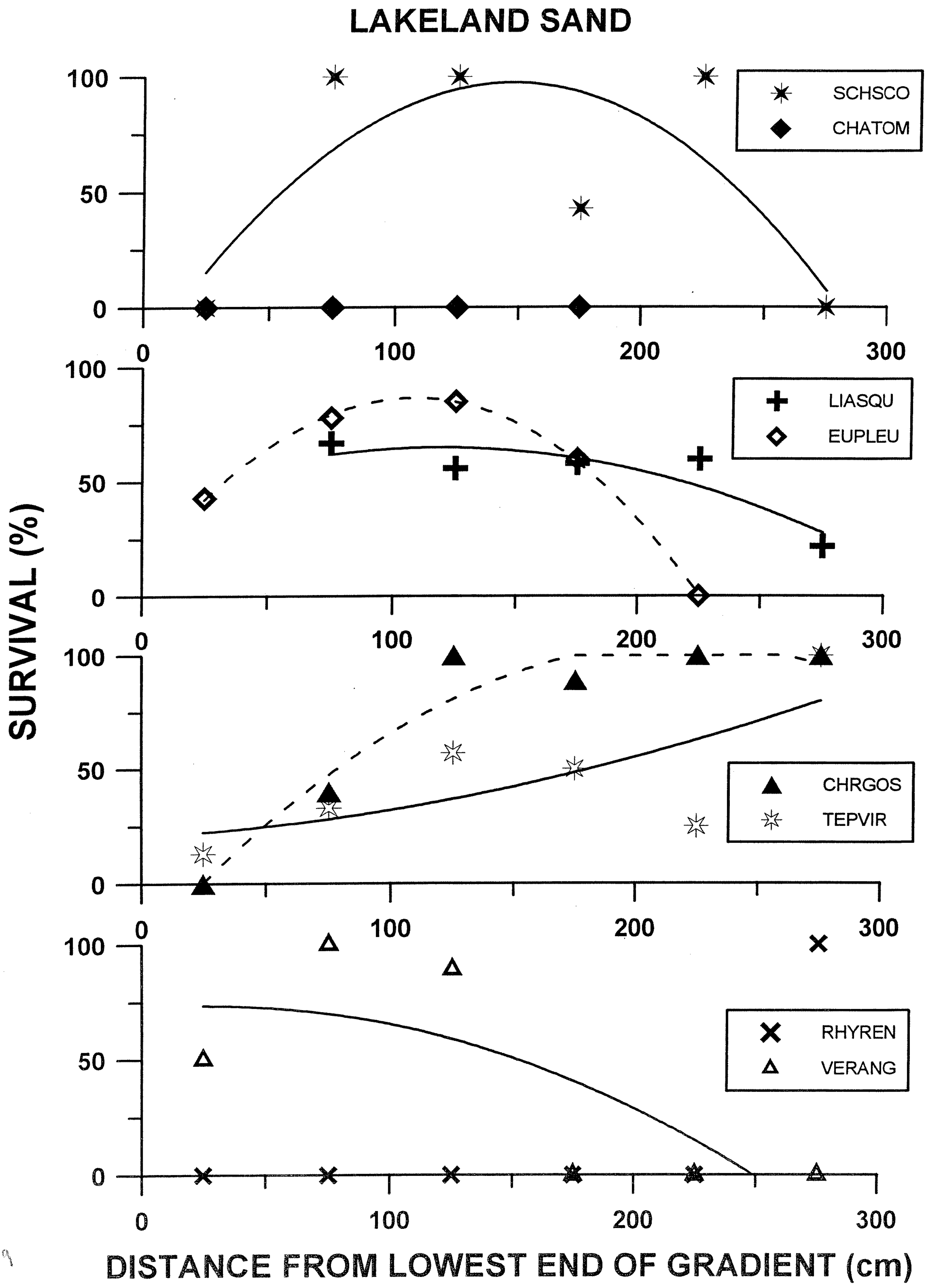

LAKELAND SAND
SCHSCO
CHATOM
LIASQU
EUPLEU
CHRGOS
TEPVIR
RHYREN
VERANG
SURVIVAL (%)
DISTANCE FROM LOWEST END OF GRADIENT (cm)
0
50
100
0
100
200
300

FIG 9

BONNEAU LOAMY SAND

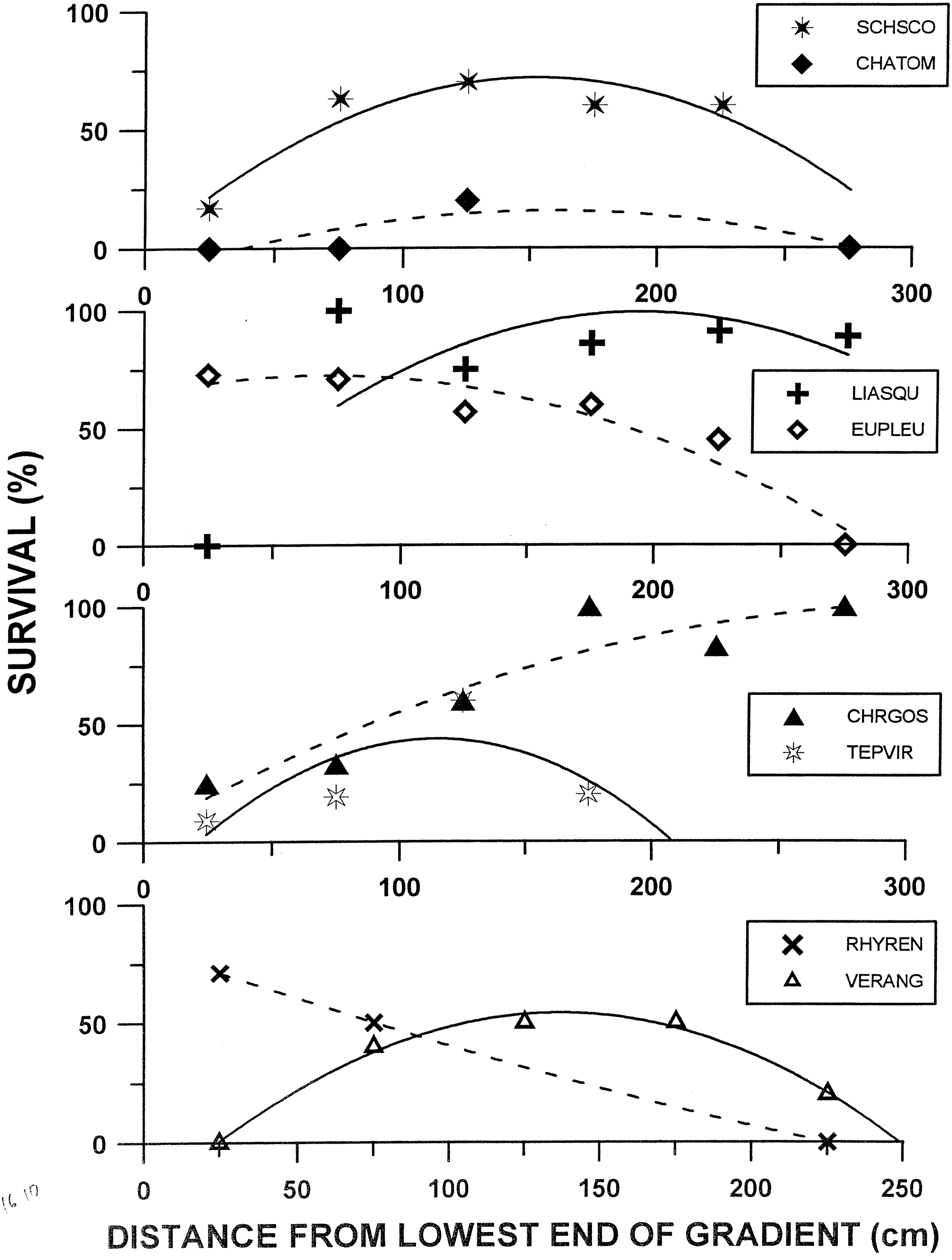


FIG 10

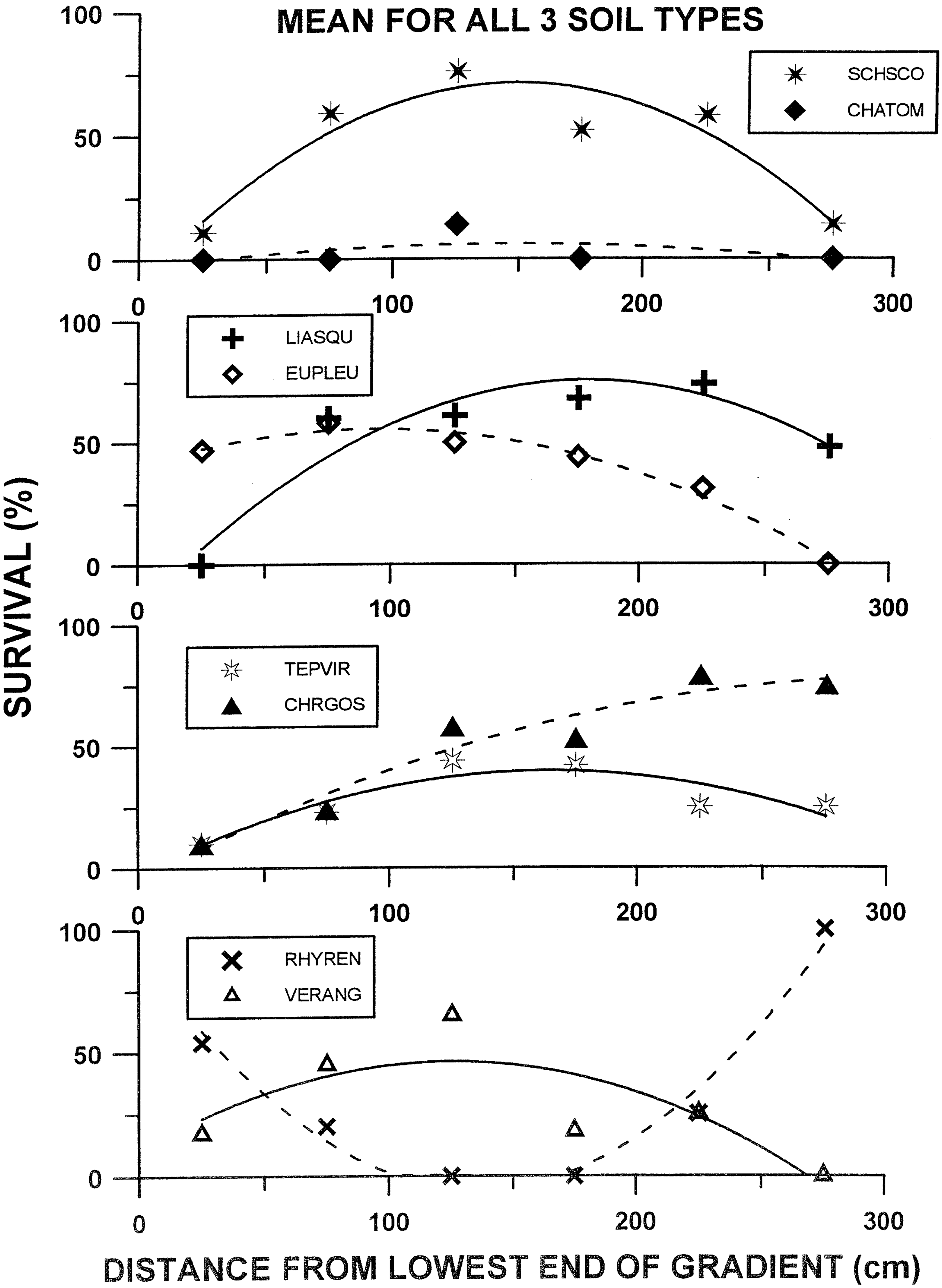

MEAN FOR ALL 3 SOIL TYPES
SCHSCO
CHATOM
LIASQU
EUPLEU
TEPVIR
CHRGOS
RHYREN
VERANG
SURVIVAL (%)
100
50
0
0
100
200
300
DISTANCE FROM LOWEST END OF GRADIENT (cm)

FIG
11

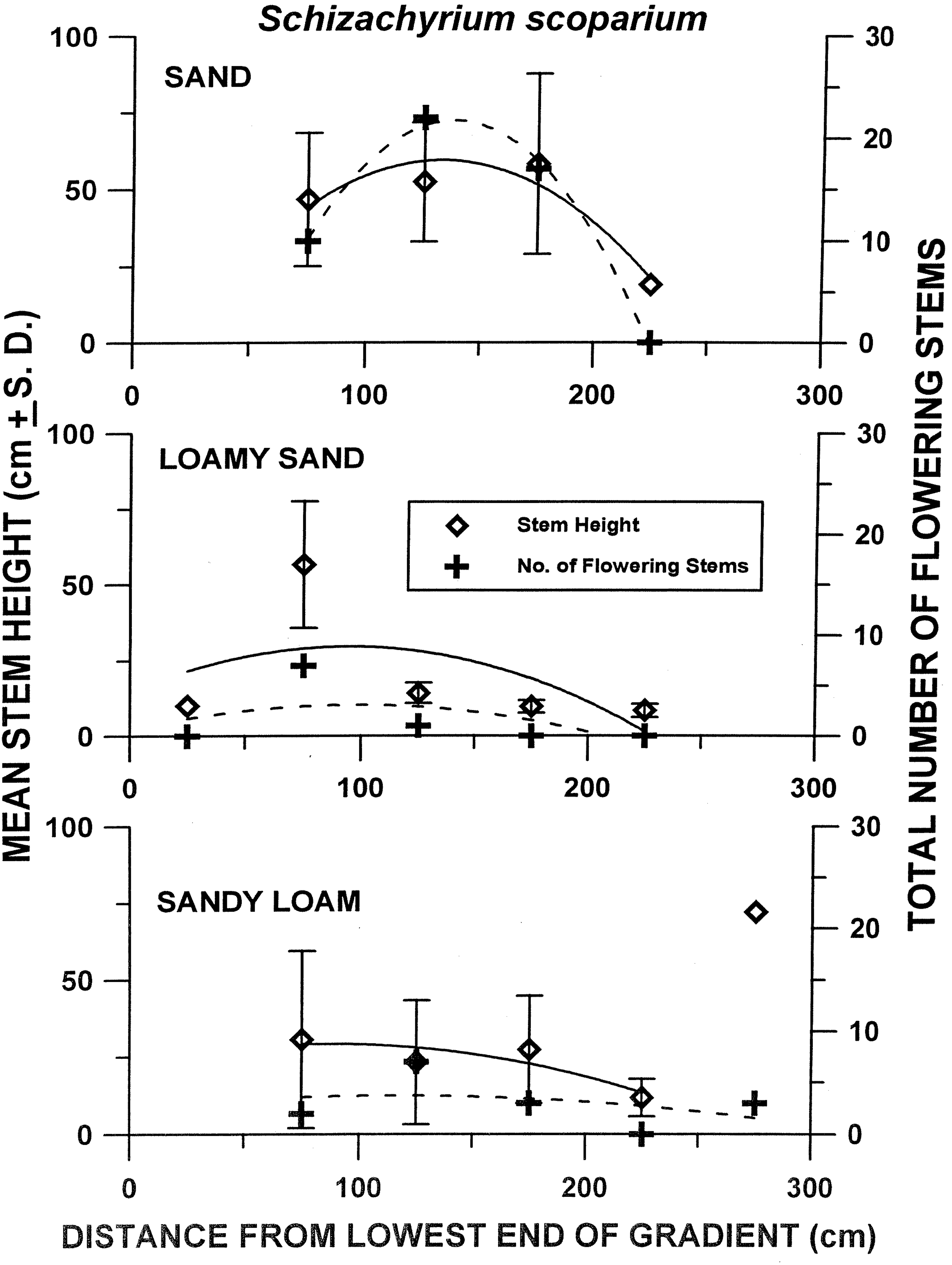
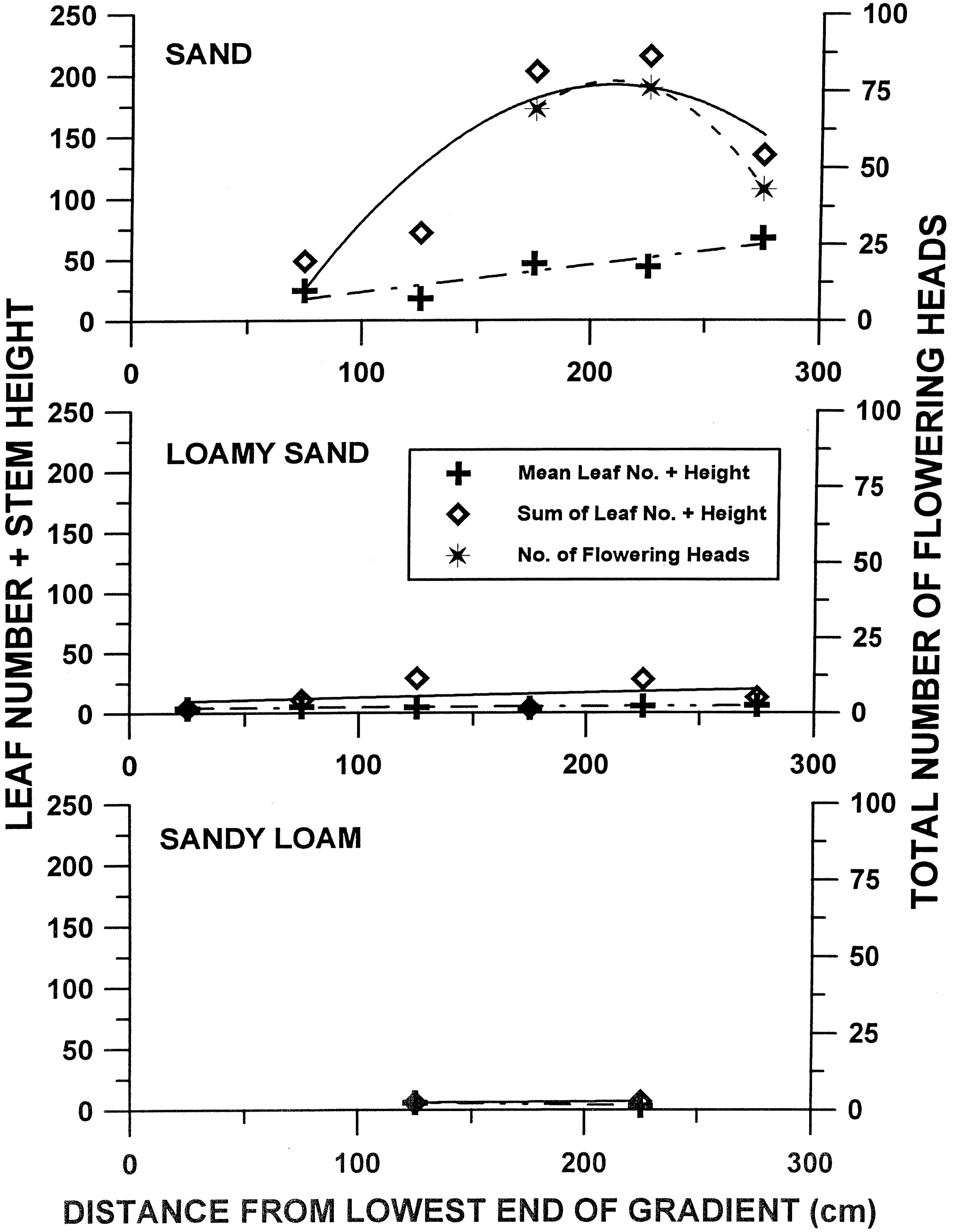

Schizachyrium scoparium
SAND
LOAMY SAND
SANDY LOAM
Stem Height
No. of Flowering Stems
MEAN STEM HEIGHT (cm ± S. D.)
TOTAL NUMBER OF FLOWERING STEMS
DISTANCE FROM LOWEST END OF GRADIENT (cm)
0
50
100
10
20
30
200
300

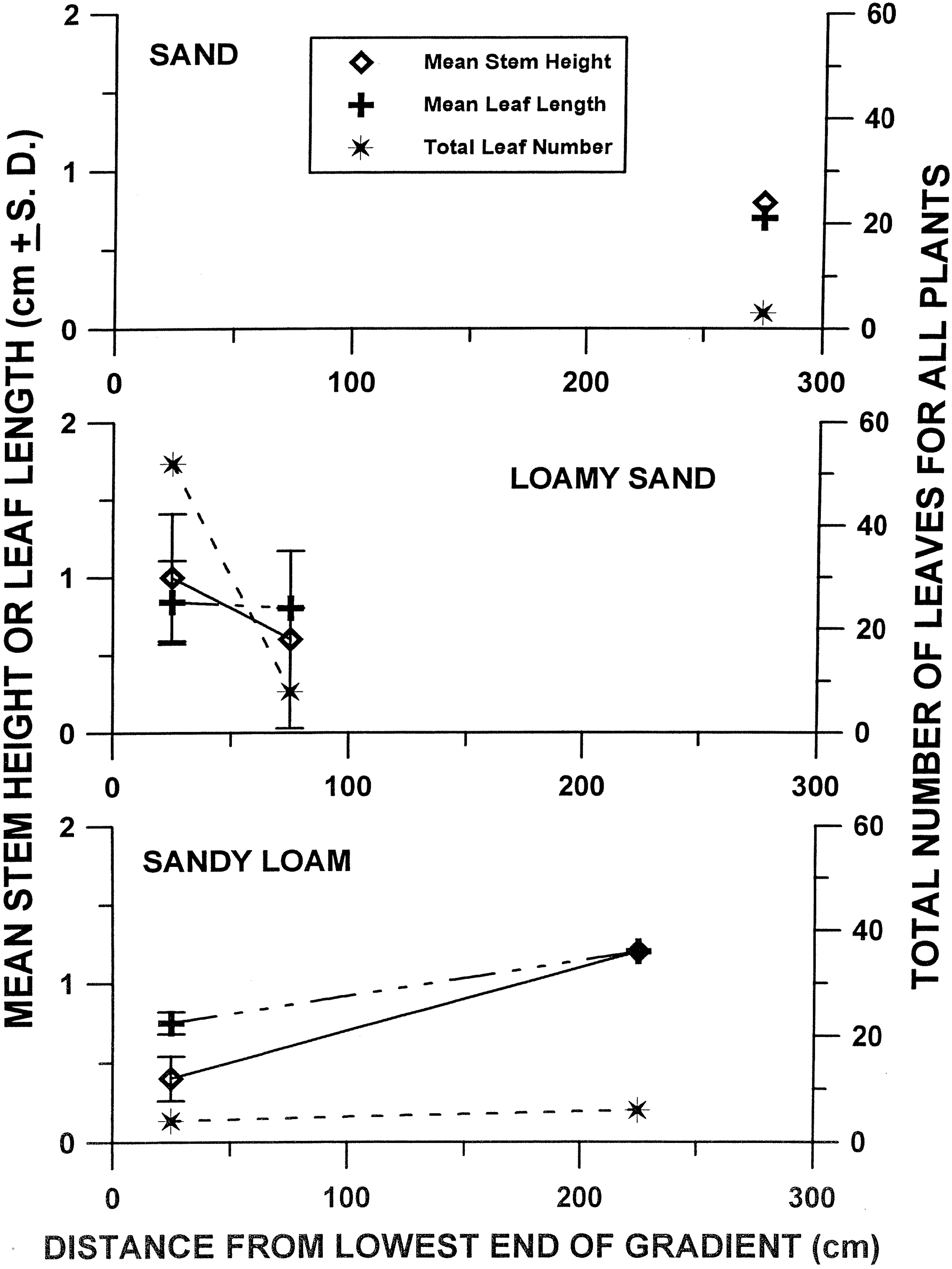
FIG 12



Chrysopsis gossypina

FIG

Rhynchosia reniformis



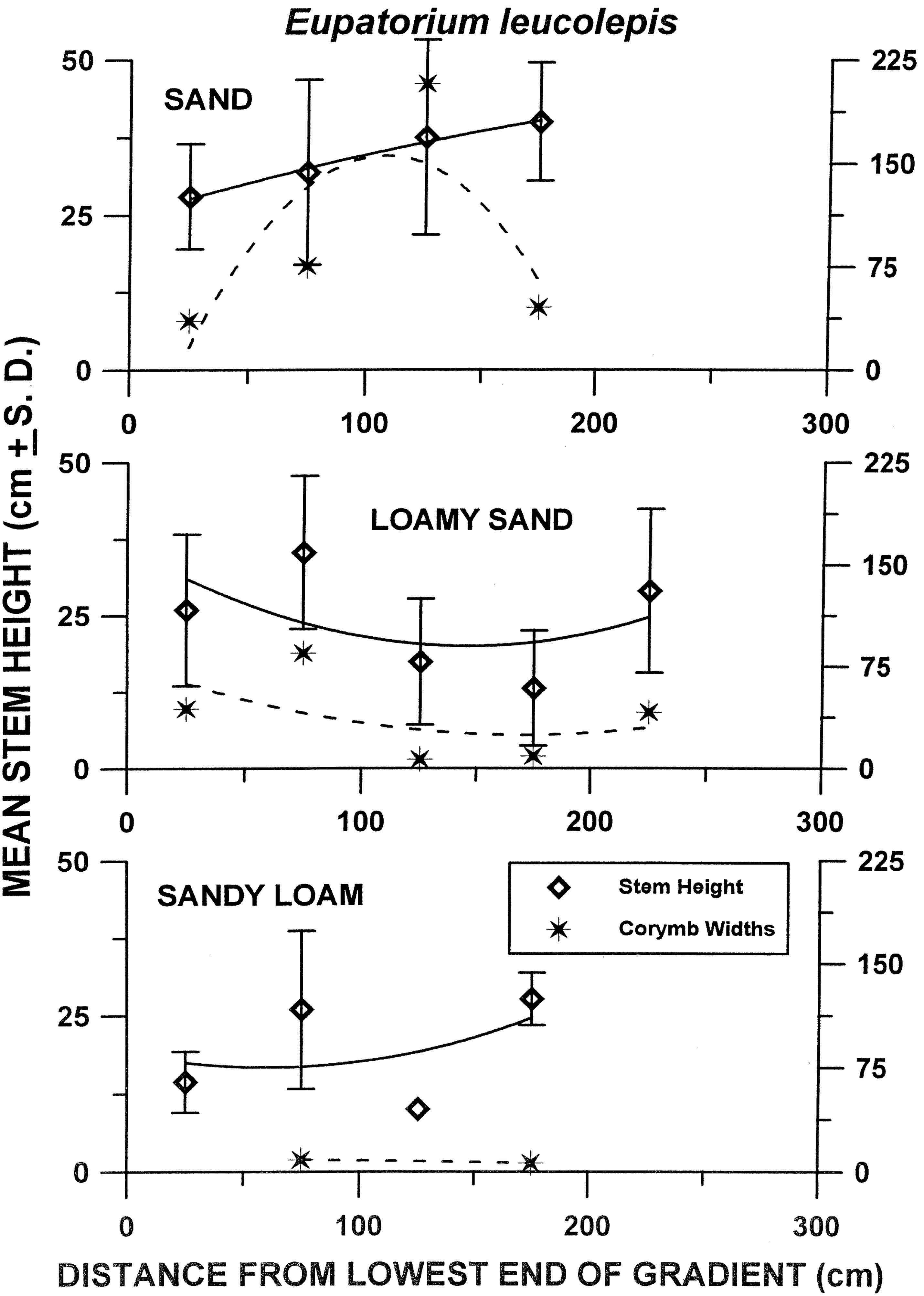
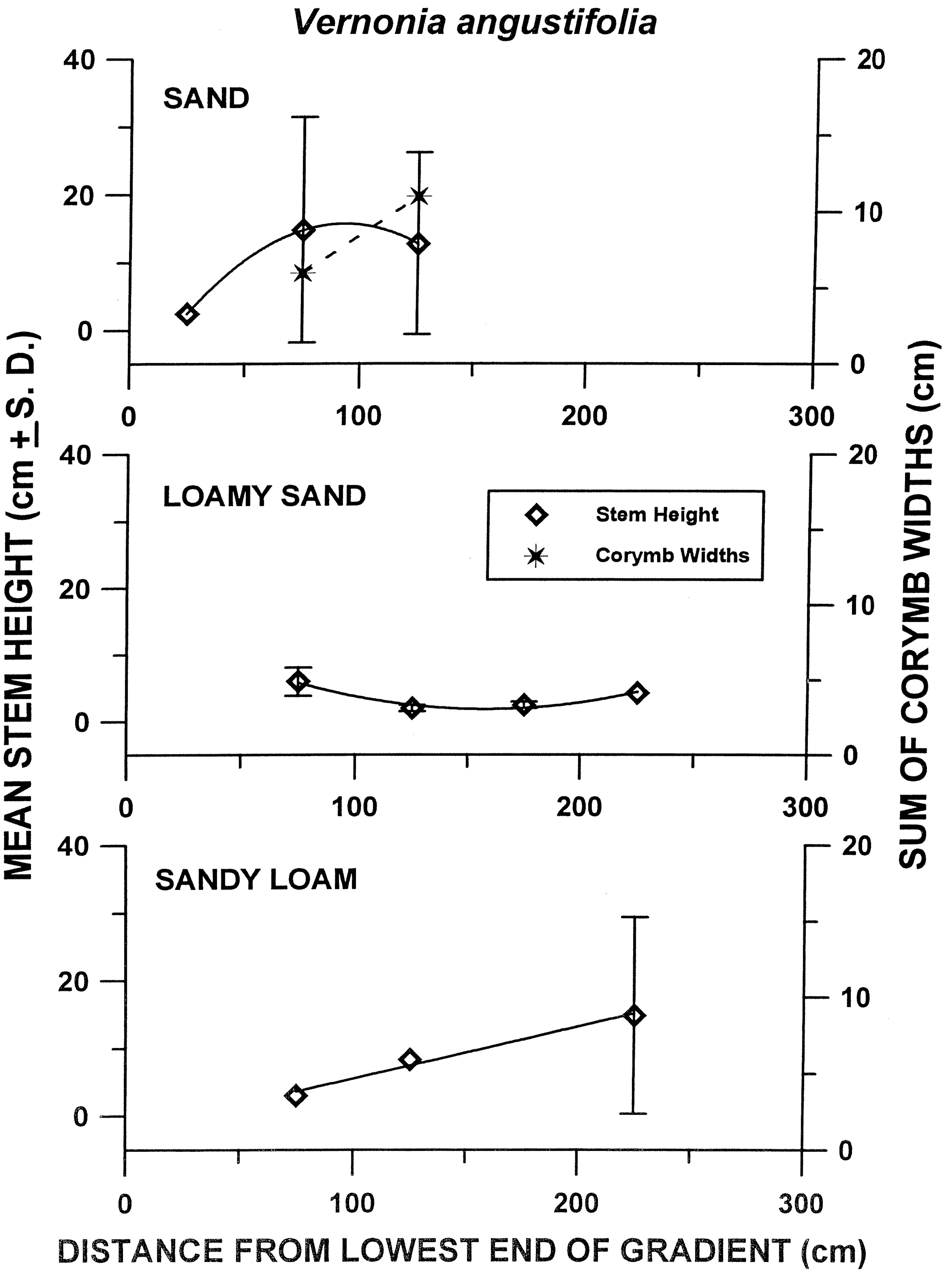

Eupatorium leucolepis
SAND
LOAMY SAND
SANDY LOAM
Stem Height
Corymb Widths
MEAN STEM HEIGHT (cm ± S. D.)
SUM OF CORYMB WIDTHS (cm)
DISTANCE FROM LOWEST END OF GRADIENT (cm)
0
25
50
0
75
150
225
0
100
200
300

FIG
15



Vernonia angustifolia
SAND
LOAMY SAND
SANDY LOAM
Stem Height
Corymb Widths
MEAN STEM HEIGHT (cm ± S. D.)
SUM OF CORYMB WIDTHS (cm)
DISTANCE FROM LOWEST END OF GRADIENT (cm)
0
20
40
10
100
200
300

F16
16

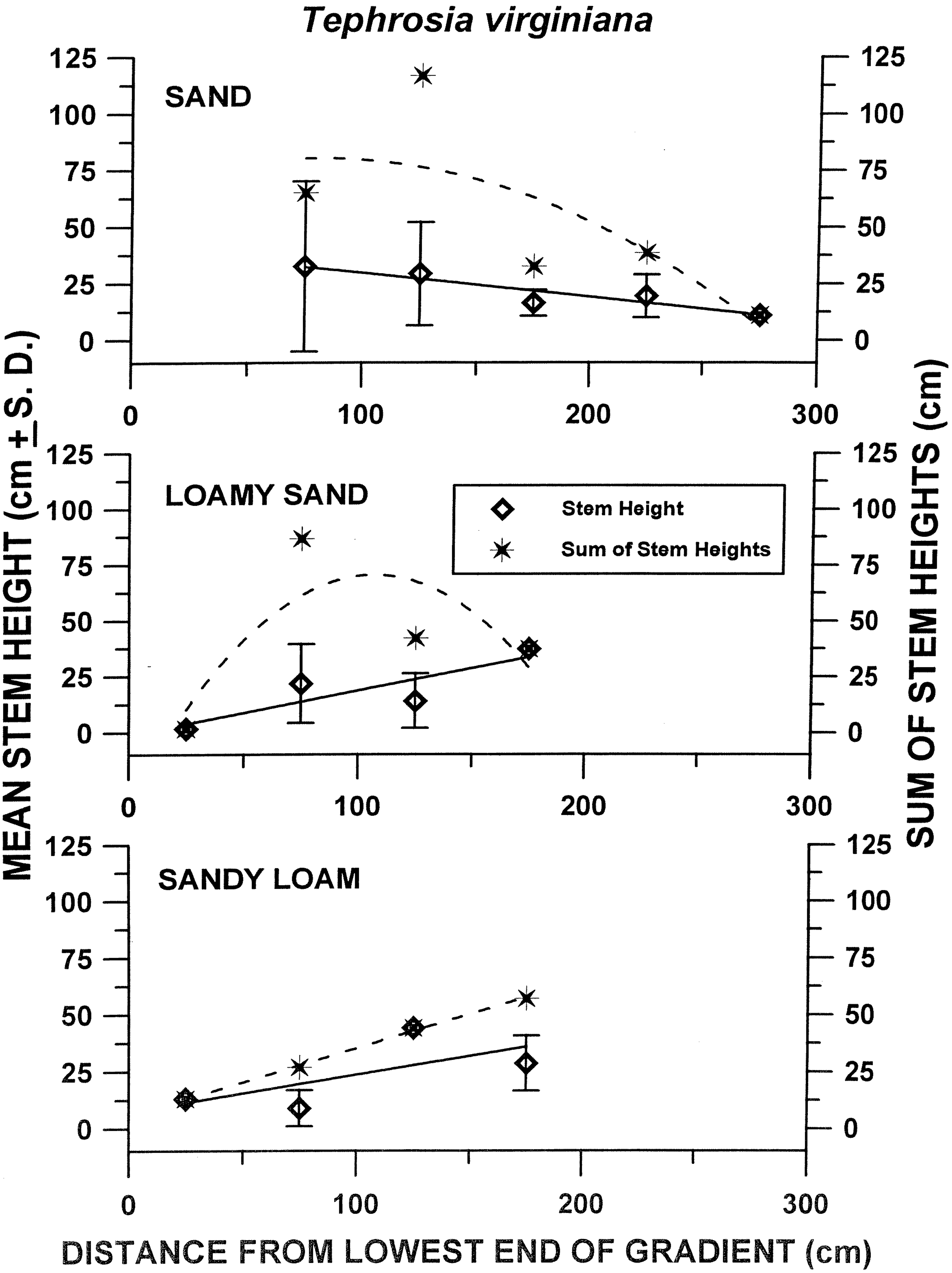

Tephrosia virginiana
SAND
LOAMY SAND
SANDY LOAM
Stem Height
Sum of Stem Heights
MEAN STEM HEIGHT (cm ± S. D.)
SUM OF STEM HEIGHTS (cm)
DISTANCE FROM LOWEST END OF GRADIENT (cm)
125
100
75
50
25
0
0
100
200
300

FIG
17

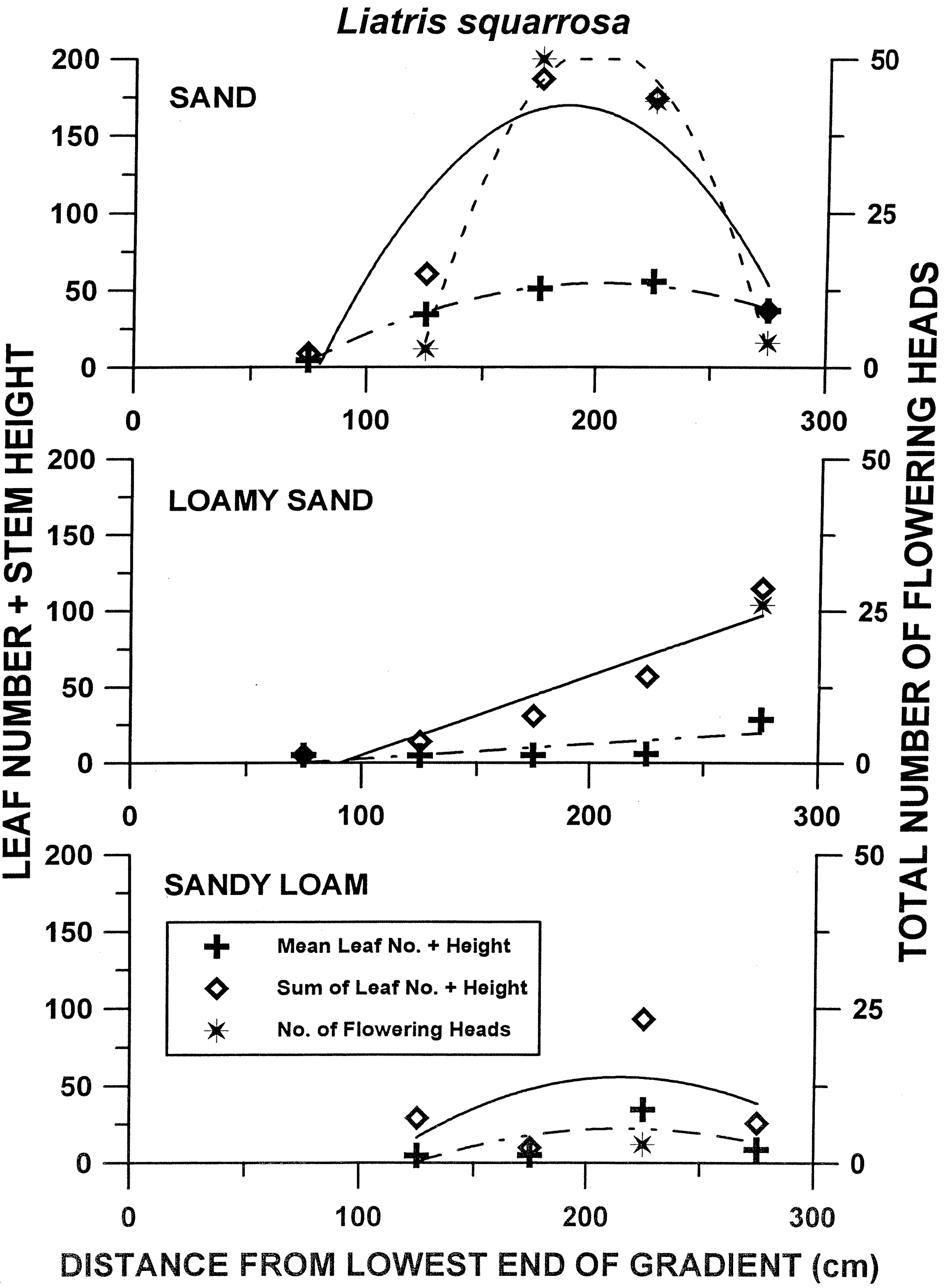

Liatris squarrosa
SAND
LOAMY SAND
SANDY LOAM
LEAF NUMBER + STEM HEIGHT
TOTAL NUMBER OF FLOWERING HEADS
0
50
100
150
200
0
25
50
0
100
200
300
Mean Leaf No. + Height
Sum of Leaf No. + Height
No. of Flowering Heads
DISTANCE FROM LOWEST END OF GRADIENT (cm)

FIG
18

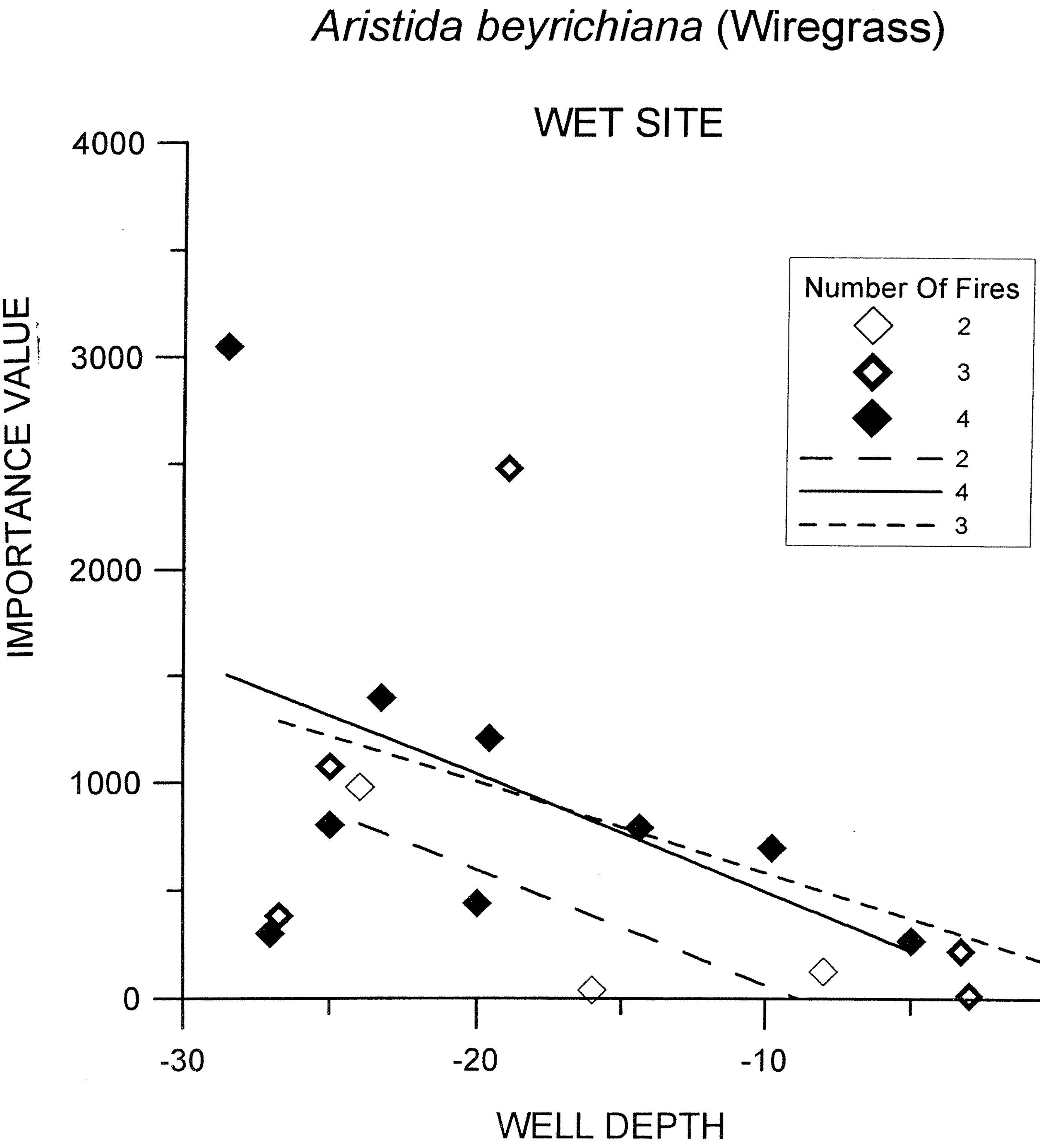
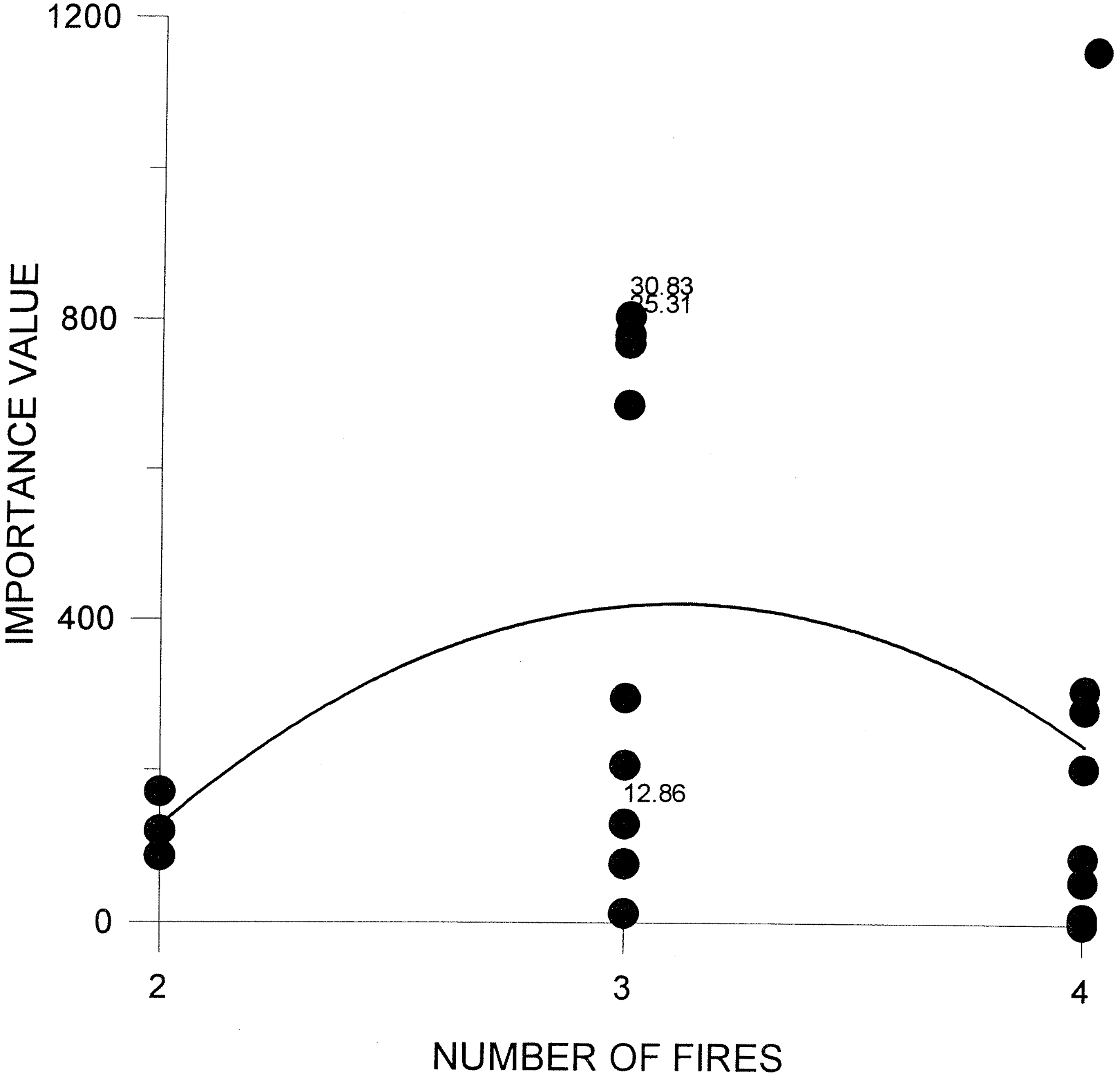

Aristida beyrichiana (Wiregrass)
WET SITE
IMPORTANCE VALUE
4000
3000
2000
1000
0
-30
-20
-10
0
WELL DEPTH
Number Of Fires
◇ 2
◈ 3
◆ 4
— — — 2
——— 4
- - - - 3

FIG 17



Dry PSP

Aristida beyrichiana

FIG 20