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Resource allocation to prey capture tissue in the aquatic carnivorous plant Utricularia vulgaris in northwestern Montana waters

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Resource Allocation to Prey Capture Tissue in the Aquatic Carnivorous Plant, *Utricularia vulgaris*, in Northwestern Montana Waters

By

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Utricularia vulgaris L. plants were collected in northwestern Montana, from sites assumed to differ in dissolved inorganic nutrient availability. Plants were found to vary in their extent of prey capture tissue (bladders). To test the hypothesis that waters of low nutrient availabilities induce greater development of prey capture tissue than do waters of higher nutrient availabilities, U. vulgaris plants were raised under controlled laboratory conditions.

A common garden experiment was conducted, and U. vulgaris plants were found to retain site-specific characteristics of bladder production and other morphological traits. It was concluded that these traits are under the control of genotype and/or the environment of the turion-forming plants rather than under the control of the environment under which turions develop into plants.

Several experiments were conducted in which turions from the same site were exposed to different concentrations of nutrients and prey. Feeding regime and nutrient solution strength did not significantly affect morphological measurements used as indicators of prey capture tissue development. Duration of dormancy (i.e. length of time before experiments were begun) did affect morphological measurements. Development of prey capture tissue observed in lab-grown plants was primarily explained by their sites of origin. Plants originating from sites thought to have lower nutrient levels exhibited more prey capture tissue than did plants originating from sites thought to be rich in nutrients.

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Chapter One

Introduction

Carnivorous plants have been studied for years, both as objects of popular curiosity and as subjects for physiological research, because of the paradox they represent as "heterotrophic autotrophs" (Lüttge, 1983). While the plants are now known to absorb nutrients from captured prey, the necessity of these supplements for plant survival and reproduction is still a matter of debate (Lüttge, 1983; Sorenson and Jackson, 1968). Some species are obligate carnivores while others seem to be facultatively carnivorous (Skutch, 1928), growing indefinitely without ancillary resources, although perhaps not as vigorously as with prey inputs, or not to reproductive stages (Arber, 1920; Dore Swamy and Mohan Ram, 1971; Sorenson and Jackson, 1968).

The costs and potential benefits of carnivory are also not clear, and seem to vary with the fertility of particular habitats (Benzing, 1987). Prey-trapping

structures are thought to be modified leaves (Juniper, 1986), so that ontogenetic costs of production are perhaps not high. However, traps are less suitable for photosynthesis than are leaves, especially the more advanced trapping mechanisms (Benzing, 1987), so that a high return in terms of nutrients is necessary to compensate for the resource outlay.

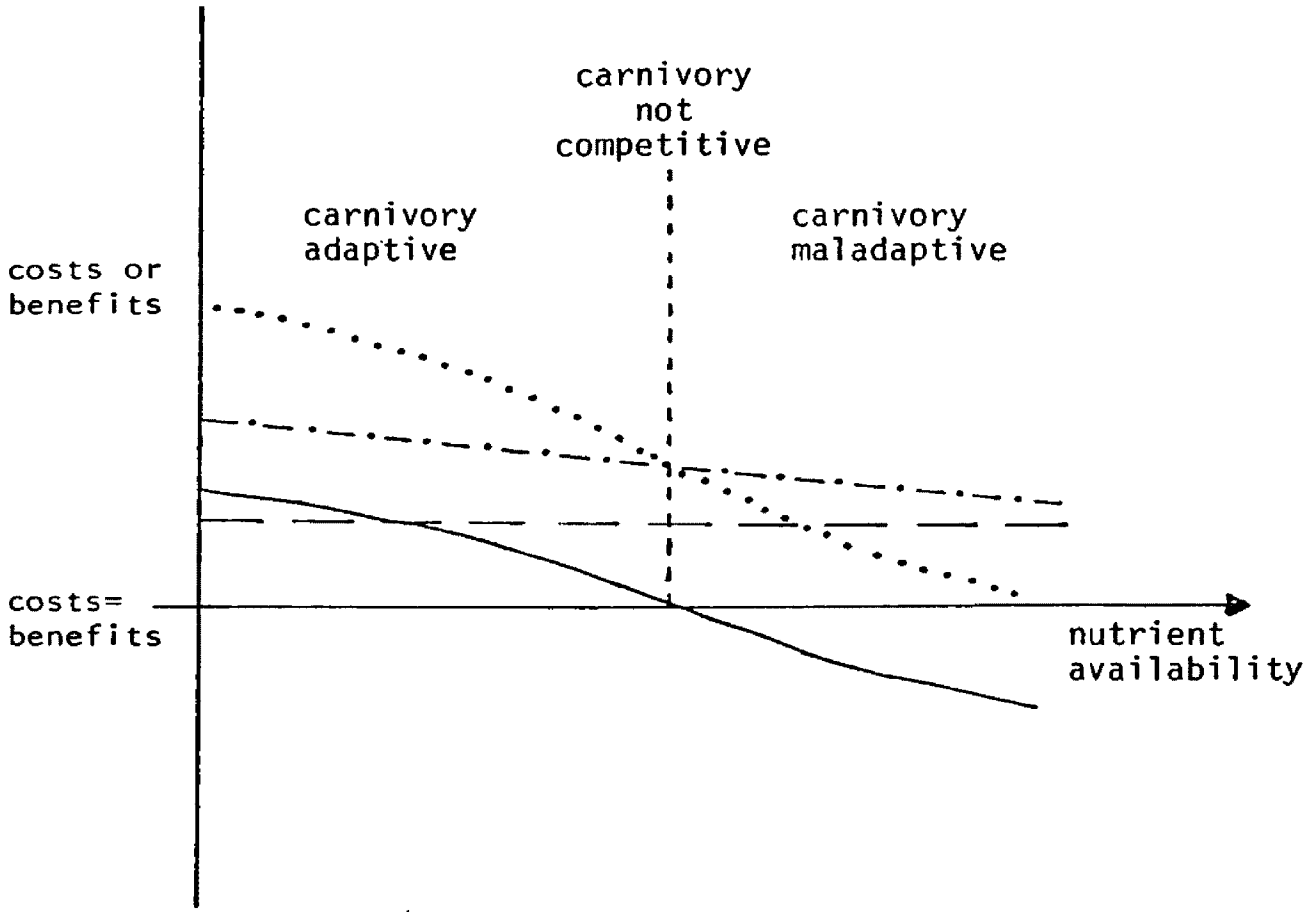
Resources shunted to trap production may diminish the pool available for flowering, fruiting, and general growth (Bloom, Chapin, and Mooney, 1985), but the ability to supplement inorganic nutrient sources may allow these plants to survive in areas where non-carnivorous plants are poor competitors. These areas are most likely to be those which are limited by nutrients and not by light, water or some other factor, since the carnivorous habit can only supplement nutrient supplies (Benzing, 1987). In short, the costs must be outweighed by the benefits in areas where carnivorous plant species are common and populations are large (Benzing, 1987; Heslop-Harrison,

1978).

The development of a strategy to mitigate substrate nutrient paucity raises questions of resource allocation in these plants: how does a plant divide its resources between formation of prey capture tissue (PCT) and other tissues under varying environmental conditions, and how flexible is this resource allocation?

In a nutrient-poor environment, PCT development requires no more materials than it does in a nutrient-rich environment. But, energy costs to obtain these materials might be greater due to their relative dilution. However, the benefits of ancillary resources should be greater in the extreme environment than in an environment where nutrients are readily available. That is, both the costs and benefits of trap possession probably decrease as nutrient availability increases. Figure 1 shows these cost-benefit relationships, and suggests that carnivory is only adaptive in habitats with low to moderate nutrient availabilities. A carnivorous

Figure 1. Hypothetical Changes in Costs and Benefits of Bladder Production in Utricularia vulgaris as Nutrient Availabilities Increase



Legend:

Material costs — — —

Material and energy costs —•—•—•—

Gross benefits (i.e. relative importance of nutrients gained from carnivory) •••••••

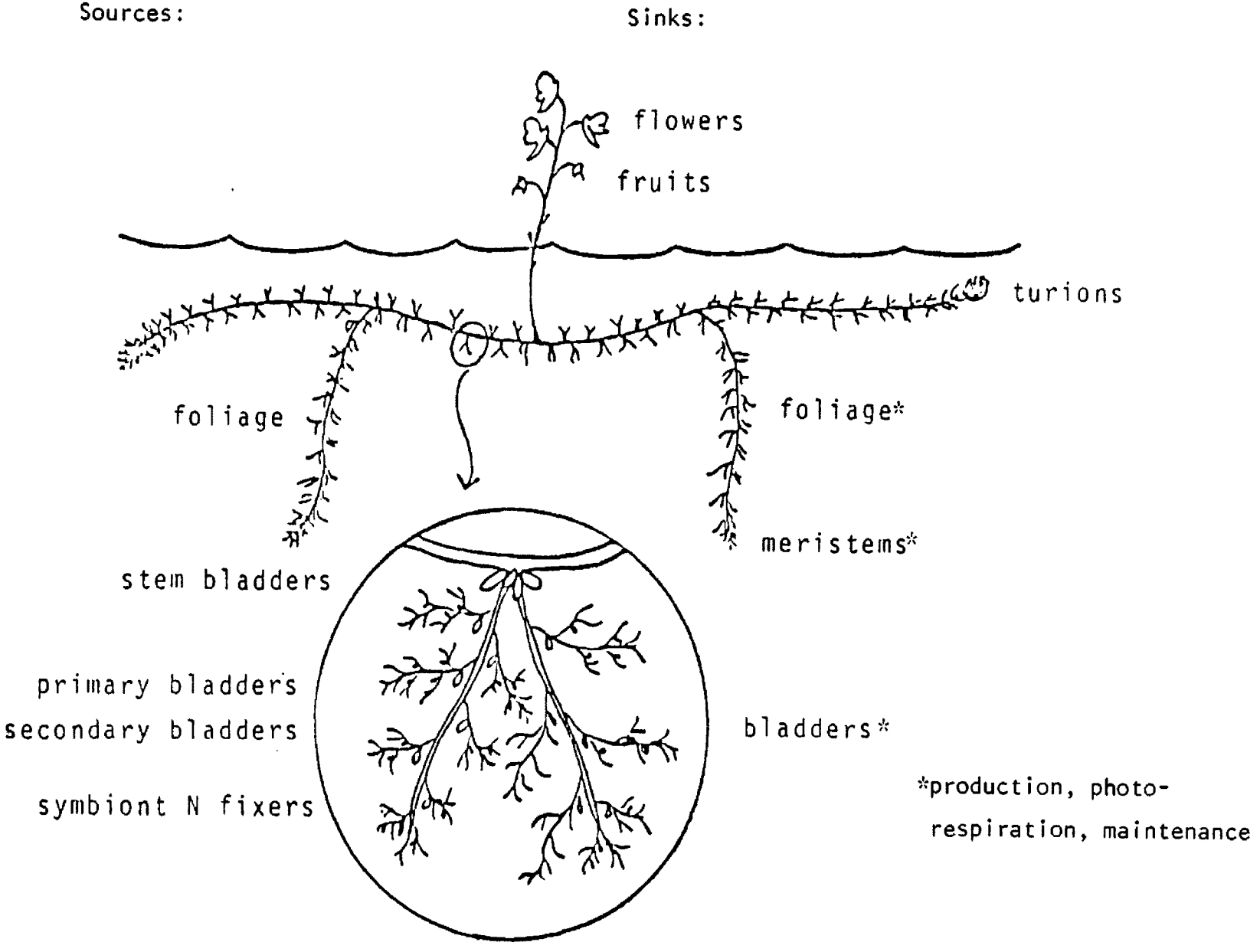
Net benefits (i.e. gross benefits - material and energy costs) ————

plant species would be expected to allocate more resources to PCT development in its nutrient-poor habitats, and more to non-PCT when growing in nutrient-rich sites. Indeed, Givnish et al. (1984) report that some carnivorous plants produce only non-PCT, or tissue with reduced carnivorous function, during seasons when nutrient availability is not the limiting factor to growth.

My research centered on this allocation question, with respect to the aquatic carnivorous plant, *Utricularia vulgaris* L.: do *U. vulgaris* plants growing in waters of low nutrient availability allocate more of their carbon resources to PCT production (bladders) than do *U. vulgaris* plants growing in waters of greater nutrient availability? Potential sources and sinks of energy and materials in *U. vulgaris* are diagrammed in Figure 2.

To investigate the above question, one needs to know the nutrient and prey levels to which a plant is exposed.

Figure 2. General Morphology of Utricularia vulgaris Showing Energy and Material Source and Sink Compartments



Since field sampling for nutrient levels is fairly ambiguous, and for prey levels even less conclusive, due to patchiness in space and time (Wetzel, 1983), I raised *U. vulgaris* under controlled laboratory conditions.

Bladderworts can be raised under controlled conditions from turions, embryonic plants that arise vegetatively on the "parent" plant in fall, are dormant in winter, and develop into mature plants in spring. Turions are protected by a layer of mucilage, thus bladders are axenic. The dormancy of turions can be broken experimentally by high temperatures (Winston and Gorham, 1979a.)

Because turions already possess bladders, a preliminary question must be addressed before the above prediction can be examined, namely, is bladder production controlled genetically, controlled by the conditions to which the turion-forming "generation" was exposed, or controlled by the conditions in which the plant develops from the turion? Part of my research focused on this

problem of control of bladder production.

While much work has been done on carnivorous plant taxonomy, morphology, and trapping physiology, only a few studies have examined the effects of prey nutrients on growth in carnivorous plants, and even fewer have addressed resource allocation (Bosserman, 1983; Luttge, 1983; Pringsheim and Pringsheim, 1962). In this study, I used laboratory and field experimentation to compare resource allocation to PCT by *Utricularia vulgaris* plants under differing prey and nutrient regimes.

My study consisted of three parts:

1. Summer field collections of mature *U. vulgaris* plants to compare morphological characters and extent of PCT tissue in plants from different sites.
2. A common garden experiment to compare development of PCT and other tissues in plants grown from turions collected from two different sites, when these turions were grown under the same dissolved nutrient conditions, without prey supplements.

3. A "diet" experiment to compare the effects of different dissolved nutrient levels and feeding regimes on development of PCT and other tissues in plants grown from turions collected from two different sites.

These three experiments were designed to examine the degree of development of PCT under nutrient-poor and nutrient-rich conditions, i.e. to test my resource allocation prediction that a greater proportion of resources are allocated to PCT under nutrient-poor conditions. The experiments also would show whether *U. vulgaris* plants respond to ambient conditions despite past history. The experiments would not distinguish whether any influence of past environment was due to "parental" genotype, to "parental" developmental environment, or both.

Chapter Two

Study Organism

Utricularia vulgaris, the greater or common bladderwort, is an aquatic, floating, rootless, carnivorous plant (Hitchcock and Cronquist, 1973). It is a member of the family Lentibulariaceae, which includes other carnivorous plant genera. The genus *Utricularia* holds about 250 species, including other floating aquatics like *U. vulgaris*, semi-terrestrial and terrestrial forms, and epiphytes. The genus is thought to have evolved by the Pliocene era (Muller, 1981), and fossil turions of *U. vulgaris* have been found from the German interglacial period (Jung, 1976). The chromosome number of *U. vulgaris* is n = 18 to 20 (Kondo, 1969).

U. vulgaris is circumboreally distributed in slow-moving streams, lakes, ponds, boggy areas, and wet meadows, and is fairly common (Ceska and Bell, 1973; Meyers and Strickler, 1979; Rossbach, 1939). Its

habitats range from acidic through neutral to alkaline, and vary in temperature, nutrient availability, light availability, and associated species (Ceska and Bell, 1973; Rossbach, 1939; this investigation).

The growth form of *U. vulgaris* is stoloniferous, with side branches at a distance from the apical meristem(s). Leaves arise alternately, are highly dissected and generally two-parted at the base, with a few teeth on some segments (Ceska and Bell, 1973; Crow and Hellquist, 1985; Fig. 2.) However, the terms "stem" and "leaf" are used mainly for convenience since organ morphology in *U. vulgaris* is not readily homologous with other vascular plants. The vegetative plant has been suggested to be entirely a root system, a stem system, or a single, much divided leaf, as well as a stem and leaf combination (Arber, 1920; Sculthorpe, 1967).

U. vulgaris grows at branch tips and decays behind, often fragmenting into several pieces, each of which can survive and propagate. Indeed, the vegetative

propagation capablities of *U. vulgaris* are incredible: almost any cell, whether of flower, leaf, stem, or turion leaf (see below), can become meristematic, dividing to form a new stem and eventually populating an entire pond (Arber, 1920; Goebel, 1904 and Glűck, 1906 in Sculthorpe, 1967).

U. vulgaris also reproduces sexually, through the formation of yellow, bilaterally symmetric flowers which are supported on a scape above the water surface (Hitchcock and Cronquist, 1973). Flowers may be self-fertilizing (Winston and Gorham, 1979a) or chasmogamous. Pollen is stephanocolporate (Kapp, 1969; Thanikaimoni, 1966) and fruits are capsules with many small, endospermless seeds (Ceska and Bell, 1973; Hitchcock, Cronquist, and Ownbey, 1959).

U. vulgaris is perennial, overwintering in cold climates through the formation of turions, or winter buds (Rossbach, 1939; Sculthorpe, 1967). Turions are clusters of leaves with condensed internodes that are formed in

late summer, or when the plant experiences cold, nutrient or water stress (Maier, 1979; Sculthorpe, 1967). Turions are covered by coarser leaves, turn brownish when mature, and possess a thick coating of mucilage. These structures usually remain attached to the senescing parental stem (which by autumn is only a tough vascular strand within a spongy cortical layer, most leaves having abscised), and are pulled downward by this stem, so that they overwinter below the ice (Arber, 1920; this investigation). With further decay of the old plant, the turions are released and float to the surface. As temperatures warm in the spring these turions reflex, green up and elongate into new plants (Winston and Gorham, 1979a). Turions may fragment and single coarse leaves may each give rise to several plantlets. Turions are high in starch and stored materials, and therefore can withstand drying and freezing well (Maier, 1973; Winston and Gorham, 1979a).

Utricularia vulgaris has a reduced vascular system,

consisting mainly of a few, poorly developed tracheids and small groups of phloem elements. There is an endodermis, and the cortex has lacunae and some fibrous ground tissue (Sculthorpe, 1967). It follows the C-3 photosynthetic pathway, and bladders are photosynthetic (Lüttge, 1983). Photosynthetic rates are probably low relative to terrestrial plants (Thai, Haller, and Bowes, 1976).

The common bladderwort captures crustaceans, insect larvae, fish fry, rotifers and other aquatic organisms, sometimes including algae and the vascular plant *Wolffia*, in small bladders, or utricles, by suction (Botta, 1976; Hegner, 1925; Roberts, 1972). The utricles are of three types: stem bladders, occurring in clusters of zero to five at petiole bases; primary bladders, usually larger, 0.5 to 5 mm long, occurring singly near the principal bifurcations of each leaflet; and secondary bladders, smaller, and occurring at distal leaf divisions (Hitchcock and Cronquist, 1982; Wallace, 1977, 1978;

this investigation; Fig. 2). These three types are all functional and capture prey of different sizes (Wallace, 1977).

Bladders vary in size and number per leaflet, and are formed while the leaflet is still part of the bunched, meristematic tip. They seem to arise from both leaf and stem tissue, but exact homology is under contention (Arber, 1920; Heywood, 1978). Utricles are light to bright green when young, sometimes with a reddish, anthocyanin shading, becoming violet to black with age and use (Botta, 1976; Lloyd, 1933; this investigation).

Utricles consist of a thin layer of cells, nearly transparent, with many two- and four-armed glands that secrete digestive enzymes (acid phosphatase, protease, esterase) and absorb digestive products (Slack, 1979). Utricles are attached to the stem and the leaflet arms by short stalks and easily abscise, with age as well as poor growing conditions, algal infections, and excessive

movement or handling (Lloyd, 1933; Sorenson and Jackson, 1968; this investigation). Bladders have a trap door that seals tightly, and two types of hair-like organs, called antennae and bristles (Darwin, 1897), project from this area. Antennae are long, branched processes which may help to guide prey to the traps, or to protect the tripping mechanism from too large aquatic visitors (Johnson, 1987; Meyers and Strickler, 1979). Bristles are non-branched, shorter organs which function as triggers to open the door, allowing an inrush of water and prey (Hegner, 1925; Lűttge, 1983; Sydenham and Findlay, 1973). The bladder cells actively transport chloride anions outward, and sodium and potassium cations inward, resetting the bladder, and forcing it to assume a concave shape when ready to fire. There may also be an electrical, excitatory step in trap firing (Sydenham and Findlay, 1973).

Prey live for varying periods of time within the bladders, and are digested gradually (Arber, 1920). Some

algal species and protozoans not only survive, but grow and multiply within the utricles. Some of these algae are cyanophytes, and fix nitrogen which is then released to the plant (Botta, 1976; Wagner and Mshigeni, 1986). Some large prey, such as mosquito larvae and fish fry, are caught by head or tail and ingested in segments (Hegner, 1925).

Utricularia does not have major economic value, although it is eaten by a few fish and provides shade and shelter for them, and is used as fodder for pigs and cattle (Sculthorpe, 1967). The plants also help control mosquito larvae populations (Jha, Jha, and Kumari, 1978; Schwartz, 1974; Skutch, 1928), help control the spread of schistosomiasis in the Caribbean by capturing flukes (Gibson and Warren, 1970), and may help control the spread of radioactive waste (Deksbakh, 1964). *U. vulgaris* may also have some value as a "green fertilizer" in rice fields because of the cyanophyte nitrogen fixers associated with it (Wagner and Mshigeni,

1986; Woelkering, 1976). *U. vulgaris* is occasionally a nuisance weed in waterways (Heywood, 1978).

Chapter Three

Literature Review

The phenomenom of carnivory in plants has prompted investigations into why it might be adaptive, and what selection pressures might have led to its evolution. The general consensus is that carnivory fills macro- and micronutrient needs for plants in low nutrient environments (Folkerts, 1982; Heslop-Harrison, 1978). Carnivorous plants seem to have adequate photosynthetic pigments for securing carbon (Pringsheim and Pringsheim, 1962), and many carnivorous plants have reduced root systems suggesting prey inputs are compensatory (Schmucker and Linnemann, 1959, in Aldenius, Carlsson and Karlsson, 1983).

Heslop-Harrison (1978) reported that nitrogen and phosphorous are important gains from carnivory, but which is more important depends on the habitat (Benzing, 1987). On the other hand, Folkerts (1982) suggested that the acid nature of many carnivorous plant habitats decreases

micronutrient availability, hence carnivory may give its greatest benefit in securing these elements. He also felt that carnivory may only be important when the habitats are under nutrient stress (e.g. when Gulf Coast pitcher plant bogs have not been fire-swept in a long time.)

I. Feeding Experiments

Feeding experiments have been performed on several species of carnivorous plants, and differing results have been found. Aldenius et al. (1983) grew *Pinguicula vulgaris* L. on local soil and enriched local soil, with and without insect supplements. They found that both watering with a complete nutrient solution and addition of insects caused increased dry weights, increased numbers and lengths of leaves, and increased nitrogen and phosphorous tissue concentrations. They concluded that *P. vulgaris* was using nitrogen and phosphorous from the captured insects, as well as some other

substance that helped the roots take up nitrogen, perhaps iron or molybdate ions. Their experimental plants came from two sites that differed in nutrient richness, and the benefits of the insect enhanced diet were greatest in the plants from the richer site. This result does not agree with the general hypothesis that the most benefits of carnivory are realized by plants from the poorest sites (Chandler and Anderson, 1976; Givnish et al., 1984; Sorenson and Jackson, 1968). Aldenius et al. suggested phenological variation between the two sites might be a confounding variable, but also noted that, if a prey input increased root uptake of minerals, then richer soils would lead to better growth.

Karlsson and Carlsson (1984) also worked with *P. vulgaris*, simulating insect capture by applying blocks of agar containing nitrogen, phosphorous, or microelements to the leaves. They found that phosporous blocks induced biomass increases, and concluded that phosphorous was the most important supplement gained by

carnivory in the common butterwort. They also reported that application of nitrogenous agar caused an increase in root to leaf weight ratios.

For another species of butterwort, *Pinguicula lusitanica* L., Harder and Zemlin (1967c) found increased leaf development, increased chlorophyll, and more flowers on plants grown on nitrogen- and phosphorous-deficient inorganic media that were given *Drosophila*, egg yolk, or ammonium phosphate. Untreated plants did not flower. Harder and Zemlin (1968) also found that *Pinus* pollen given to *P. lusitanica* leaves caused an increase in number of leaves and diameter of rosettes, as well as slowing aging, promoting flowering, and deepening the plants' green color. Nonetheless, these researchers (1967c) felt that unambiguous proof for enhancement of plant development by captured prey inputs had only been given for *Drosera* and *Utricularia*.

Chandler and Anderson (1976) similarly experimented with species of *Drosera*, growing plants in sand cultures

deficient in nitrogen, sulfur, phosphorous, or the micro-elements, and feeding with *Drosophila*. Using *D. binata* Labill., they found that optimal growth occurred with insect supplements and a nitrogen-deficient medium, while added nitrate inhibited growth. Chandler and Anderson found increased growth in *D. whittakeri* Planch. when flies were given to plants lacking root access to any nutrients or to inorganic sources of nitrogen and sulfur, but not in plants denied phosphorous or microelements. However, *Drosophila* supplementation did cause increased phosphorous tissue concentrations on phosphorous deficient and complete media.

For another tuberous species of sundew, *Drosera erythrorhiza* Lindl., Pate and Dixon (1978) found *Drosophila* to be an effective source of nitrogen and phosphorous.

Fabian-Galan and Salageanu (1969) observed translocation of carbohydrates and amino acids from prey to the plant in *Drosera capensis* L., and from prey in

mature traps to growing points in *Aldrovanda vesiculosa* L., but not from young traps.

Christensen (1976) found that *Sarracenia flava* L. plants deprived of soil nutrients and prey were fairly small and showed some chlorosis. Plants grown on poor soil and fed insects had increased tissue concentrations of nitrogen and phosphorous, but not of calcium, magnesium, or potassium. Plants grown with abundant fertilizer and given insects did not show increased tissue concentrations relative to plants grown with fertilizer but not given insects. Christensen hypothesized that insectivory may interfere with nutrient uptake when nutrients are abundant.

Hermann, Platt, and von Ende (1987, pers. comm.) found increases in growth and clone numbers in *S. flava* plants that were fed. They did not observe effects until a year or more had elapsed but suggested the impacts of withholding prey could be ameliorated by the underground storage organ this species possesses.

Plummer and Kethley (1964) observed absorption of amino acids, peptides, and other nutrients from prey by leaves of *S. flava*. They decided that the gains from carnivory may be greater for immature plants than for adults.

Roberts and Oosting (1958) reported that various previous experiments on *Dionaea muscipula* Ellis were inconclusive, and found that fed plants in their study showed more vigorous vegetative growth, but that unfed plants watered with distilled water did better than unfed plants watered with an inorganic nutrient solution (excessive concentrations or wrong proportions of nutrients were suggested as a possible cause.)

Observers of *Utricularia*, like those of terrestrial carnivorous plants, have noted more vigorous growth in plants which capture prey. Skutch (1928) reported that putting asparagin, albumen or flesh extract into bladders with pipettes resulted in increased chlorophyll in bladder antennae and larger bladders (including "giant"

bladders in *U. vulgaris* that measured 6.2 mm in length). Also, several adventitious shoots arose from the leaves bearing treated utricles. Another consequence of the artificial feeding was formation of two bladders per stalk and stimulation of leaf apices to form bladders. Skutch recorded the results of Bűsgen's (1888) feeding trials as well: treated *Utricularia vulgaris* plants were longer and developed more leaves than unfed plants, and in one series of experiments, untreated plants formed unseasonal turions while fed plants grew well.

One of the classic feeding studies of *Utricularia* was undertaken by Pringsheim and Pringsheim (1962). Their *U. exoleta* R. Braun plants showed good vegetative growth in inorganic nutrient solutions but only flowered if organic compounds were added (peptone and meat extract). Pringsheim and Pringsheim (1967, in Sorenson and Jackson, 1968) further found peptone and beef extract necessary for good vegetative growth in *U. minor* L. and *U. ochroleuca* R. Hartman, but could not induce flowering

with organic additives.

Sorenson and Jackson (1968) experimented with *U. gibba* L. in magnesium- and potassium-deficient and complete media, and fed paramecia to some plants. They discovered that feeding did not cause a growth increase in plants in complete media and only caused a small increase in plants in the magnesium-deficient media. However, fed plants in their potassium study, in both complete and incomplete media, did elongate significantly more than unfed plants. Paramecia treatments also increased the number of internodes, and allowed formation of more bladders, but the latter result was confounded by differing intensities of algal infection which caused bladder abscission. Sorenson and Jackson's experiments supplied live prey, so that utricles were activated in the study, which was not the case in other research reviewed here.

Dore Swamy and Mohan Ram (1969, 1971) grew *U. inflexa* Forsk. axenically and tried adding beef extract, casein

hydrolysate, peptone, tryptone, and yeast extract. All of these organic nitrogen sources enhanced vegetative growth, but depressed flowering, and yeast extract completely inhibited flowering. Dore Swamy and Mohan Ram observed flowering with and without glycine in the medium, and concluded that animal protein is not necessary for flowering in *U. inflexa*. They also found that beef extract, casein, and tryptone delayed bladder abscission, while high light (6000 lux) promoted bladder reddening and abscission. Mohan Ram, Harada, and Nitsch (1972) confirmed that *U. inflexa* could use nitrate as its nitrogen source.

Harder (1963), raising *U. exoleta* in a mineral nutrient solution and treating some plants with autoclaved *Daphnia* infusions, found that untreated plants became dormant, while supplemented plants flowered. Peptone extract also induced flowering. He inferred that natural carnivory is not a strategy for nutrient assistance, but rather a source for

reproductive cycle requirements. Harder and Zemlin (1967a), however, induced flowering in *U. stellaris* L. without animal supplements.

Harder (1970a) tried various proportions of nutrient solution and autoclaved *Daphnia* (ranging from 18 to 4500 *Daphnia* per 100 ml of solution) on five species of *Utricularia*, and found increases in dry weights of *U. minor*, *U. exoleta*, and *U. ochroleuca* when 300 or more *Daphnia* were administered. *Daphnia* decoctions induced flowering in *U. exoleta*, but no flowering was observed for *U. vulgaris*, *U. minor*, or *U. ochroleuca* whether or not these species were "fed".

Johnson (1987) noted that absorbed nutrients were rapidly moved to the growing points of *Utricularia*, and Coleman, Lollar, and Boyd (1971) found quick movement of phosphorous from bladders to stems and leaves when *U. inflata* Walt. plants were exposed to radioactively labelled ostracods. They also stated that the carnivorous absorption pathway is probably more

important than the foliar absorption route only in infertile waters.

Harder and Zemlin (1967c) addressed the possibility of carnivorous plants using carbon from captured prey. They found that growth in *U. stellaris*, *U. exoleta*, *U. minor*, *U. ochroleuca*, and *U. vulgaris* was enhanced by saccharose and glucose, and to a lesser extent by fructose, maltose and cellobiose. Flowers were more abundant on plants grown in solutions with added sugar. These effects were seen in plants grown under light and dark conditions, but were more apparent in the light-cultured plants. Harder (1970a) determined that sugar added to nutrient solutions had a greater effect on growth and flowering in these five species than did *Daphnia* decoctions. Harder and Zemlin (1967b) found growth promotion by sugar in a non-carnivorous submerged aquatic, *Apogoneton distachius*, as well. Harder (1970b) observed dry weight increases in *U. minor* plants grown in an inorganic solution and beef extract when sugar and

acetate were added. The extent of the increase depended on concentrations of the sugar and acetate: more acetate allowed lower sucrose concentration for maximum effect and vice versa. With sucrose supplementation, he also recorded growth in plants held in darkness, albeit less growth than in plants exposed to light.

Similarly, Dore Swamy and Mohan Ram (1969) found that increased sucrose levels in growth media for *U. inflexa* resulted in development of lateral branches by release of apical dominance, and that higher levels of sucrose induced morphological change: 6% caused bushy plants with short internodes, and 8% caused bushy, dark green plants with small pigmented bladders and reduced flowering. On the other hand, they (1971) recorded poor growth in plants grown in darkness on a medium including sucrose and glycine: small leaves, light green coloration, and elongated stems. Bladders, however, were no different from those of light-grown plants.

For *Drosera*, Chandler and Anderson (1976) determined

by low level light experimentation that insects were not an important carbon source.

In summary, the literature on plant feeding research suggests that carnivorous plants derive nitrogen, phosphorous, sulfur, and some micronutrients from their prey, but that the actual nutrient of greatest importance depends on the species and the environment. Further, the necessity of ancillary resources for completion of the life cycle also depends on species and habitat. Lastly, some carnivorous plants can use the carbon skeletons of prey, but none have been found to survive without photosynthesis.

II. Constraints and Confounding Factors

In the literature, there has also been some mention of constraints on the benefits of carnivory, and of factors confounding the demarcation of such gains. Moeller (1978) noted that carbon may be limiting for *Utricularia purpurea* Walt., which does not use

bicarbonate. Thus, experiments which do not provide sufficient inorganic carbon in a form the experimental species can use may not find the growth increases expected from insect dietary additions.

Botta (1976) listed species of cyanophytes that survive indefinitely in bladders of *Utricularia obtusa* Sw., *U. platensis* Speg., and *U. foliosa* L., and Bosserman (1983) mentioned nitrogen fixation by periphyton associated with *U. purpurea*, *U. juncea* Vahl, and *U. inflata*. Wagner and Mshigeni (1986) measured nitrogen fixation by epiphytes and bladder-dwelling algae of *U. inflexa* and suggested the process is intensive enough to give the association potential as a biofertilizer. They also raised the possibility of nitrogen contributions to *Utricularia* by heterotrophic bacteria. Consequently, *Utricularia* and other aquatic or phytotelm (water-holding) carnivorous plants may have a third nitrogen source.

Rossbach (1939) reported that *Utricularia* species of

northern regions which form turions usually develop fewer flowers than their more southerly conspecifics, and only infrequently produce fruit. Thus turions may be resource sinks not considered in feeding experiments. Similarly, Skutch (1928) explained that the turion food supply may compensate for prey inputs in recently sprouted plants, another factor to be considered in analysis of feeding experiment results. Tubers as nutrient sources and sinks in *Drosera erythrorhiza* were noted by Pate and Dixon (1978).

The photosynthetic contribution of trapping organs (Hegner, 1925; Lűttge, 1983) also confounds cost/benefit analyses.

Lastly, Moeller (1980) discussed the effects of temperature on growth in *U. purpurea*, and Maier (1979) showed effects of light intensity on production in *U. vulgaris*. These and other environmental factors interact with substrate fertility and prey nutrient inputs to produce observed growth and development of

plants.

III. Evolutionary Aspects

Some recent papers have explored models for the evolution of carnivory and attempted to conduct cost/benefit analyses. Thompson (1981) compared insectivory with myrmecophily (ant-fed plants), suggesting both nutrient supplementation strategies evolved in response to similar ecological conditions. He noted that insectivory is advantageous in moist, low nutrient habitats, since such species use water freely in glandular secretion and absorption processes, while epiphytic myrmecophily is the workable design for open canopy forest sites where dryness prohibits insectivory.

Benzing (1986) agreed that ecological factors limit carnivorous plants to moist, exposed habitats, where photosynthesis is not limited and costs for secretory lures and other trapping implementia are not excessive.

He further stated that myrmecophily is a less costly strategy and therefore found in more stressful habitats.

Juniper (1986) postulated that the origins of carnivory are polyphyletic, and present convergence represents a limited number of techniques to compensate for habitat sterility. He noted that elements of the suite of carnivory characters are found in many other plants, and only in situations where carnivory would be advantageous did the entire syndrome evolve.

Bloom et al. (1985) applied economic theory to calculate how plants should develop in order to maximize growth in their environments, and pointed out the necessity of considering nutrients and water as currency as well as carbon--the usual base for analysis. They deduced that carnivory occurs when stocks of water and nutrients are imbalanced. Growth in nutrient-poor environments must be slow, but plants of these habitats adjust for their supply levels and are less flexible in allocation patterns than are plants of more fertile

habitats. Nutrient-starved plants were also predicted to show less sequestering of resources for sexual reproduction.

Givnish et al. (1984) suggested the main advantage of carnivory is increased photosynthesis via mineral nutrient supplementation allowing increased photosynthetic rates and/or increased numbers of photosynthetic units. They hypothesized that photosynthetic benefits will level out when factors other than nutrients become limiting. This supports the rule of thumb mentioned earlier, that prey capture is most advantageous in the least rich sites. Givnish et al. concluded that the greatest benefits of carnivory will accrue to plants in moist, sunny, low nutrient habitats, while in dry or shaded low nutrient habitats, benefits will be less and level out sooner.

Benzing (1987) added that carnivory is rare because capture and absorption of prey is not an economical way to supplement nutrient uptake in most environments.

These "generally unfavorable energetics" also prevent carnivorous plants from being vast, dominant communities.

Chapter Four

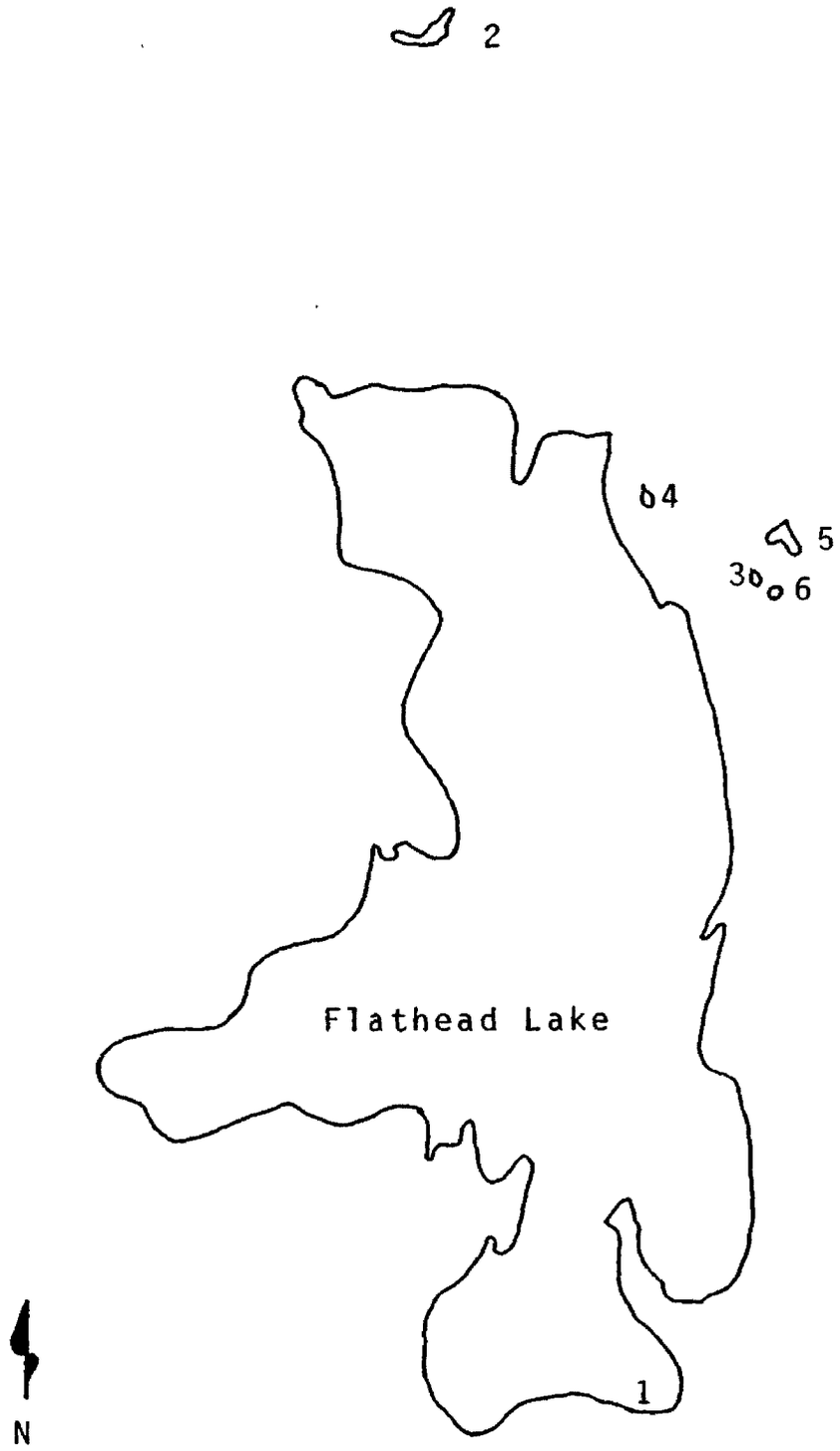
Study Sites

Plants and turions were collected in Flathead and Lake Counties of Montana. Sites varied in size, water chemistry, plant species composition, and size and vigor of *Utricularia vulgaris* populations. Turions for laboratory experimentation were collected from three sites: East Bay of Flathead Lake, McWenneger's Slough, and Tykeson Pond; plant materials from these as well as three other sites were examined: Daphnia Pond, Loon Lake, and "Tykeson's Kettle". Locations of these sites are shown in Figure 3.

East Bay, Flathead Lake, is a shallow, marshy area with numerous aquatic plant species including *Hippurus vulgaris* L., *Myriophyllum spicatum* L., *Potamogeton* spp., *Ranunculus* sp., *Typha latifolia* L., *Utricularia minor*, and *U. vulgaris* (nomenclature follows Dorn, 1984).

Water in East Bay is clear beyond the depths at which *Utricularia* is found. Flathead Lake is classed as

Figure 3: Study Site Locations



1. East Bay, Flathead Lake
   Lake County
   T22N R19W Sec. 5-6

2. McWenneger's Slough
   Flathead County
   T28N R20W Sec. 6

3. Tykeson Pond
   Lake County
   T26N R19W Sec. 16

4. Daphnia Pond
   Lake County
   T26N R19W Sec. 1

5. Loon Lake
   Lake County
   T26N R19W Sec. 10

6. "Tykeson's Kettle"
   Lake County
   T26N R19W Sec. 15

oligo-mesotrophic (Stanford, Stuart, and Ellis, 1983), but East Bay itself is probably mesotrophic. (This classification, and the trophic levels for the other sites, are based on one-time water chemistry measurements, including conductivity, pH, alkalinity,and dissolved oxygen, as well as on water color and hydrophyte species composition.) The substrate is sandy in open water, silty under *Typha* stands. *U. vulgaris* is found in several locations within East Bay: among the *Typha* stands, in open, shallow water near *Typha*, and in windrows with other floating macrophytes and detritus. *U. vulgaris* is not a dominant plant in this site (cover 5 to 25%), but is found in small patches.

McWenneger's Slough is a large shallow slough, wooded on the southeast, open to the north and west, which contains a luxuriant, diverse plant assemblage. Besides *U. minor* and *U. vulgaris*, species found in the slough include: *Carex* spp., *Ceratophyllum demersum* L., *Chara* sp., *Elodea nuttallii* (Planch.) St. John, *Lemna trisulca*

L., *L. turionifera* L., *Myriophyllum spicatum*, *Nuphar lutea* L., *Polygonum amphibium* L., *Potamogeton* spp., *Sagittaria* sp., *Scirpus* sp., *Spirodela polyrhiza* (L.) Schleiden, *Typha latifolia* and *Wolffia columbiana* Karsten.

The summer Secchi disk transparency is 0.5 m, and the water is meso- to eutrophic. The substrate is coarse and sandy in some places, a thick silt in others. *U. vulgaris* grows at various depths in the Slough, among the other macrophytes. Plants are large and healthy, growing in patches, varying from 25 to 50% cover. Of the sites described, and others in Lake County that were visited, McWenneger's Slough is the mother lode for *U. vulgaris*--plants are by far the largest, longest, and most vigorous there.

Tykeson Pond is a small, shallow, somewhat dystrophic pond surrounded by open forest to the south and east and by logging roads to the north and west. It is dominated by *Menyanthes trifoliata* L., and also hosts *Carex* spp.,

Lemna turionifera, *Nuphar lutea*, *Phalaris arundinacea* L., *Potamogeton natans* L. and other *Potamogeton* spp., *Potentilla palustris* (L.) Scop., and *U. vulgaris*. The water is soft and dark, with a summer Secchi depth of 0.25 m. Sediments are peaty, brown, and coarse. *U. vulgaris* grows densely with 50 to 75% cover.

Daphnia Pond is also small and shallow, a late successional pond dominated by the emergent plants *Phalaris arundinacea*, *Scirpus* sp., and *Typha latifolia*. Other macrophytes in Daphnia Pond include: *Ceratophyllum demersum*, *Lemna turionifera*, *Myriophyllum spicatum*, *Nuphar lutea*, *Polygonum amphibium*, *Potamogeton natans* L. and other *Potamogeton* spp., and *U. vulgaris*. The summer Secchi depth in the dark, dystrophic water is 0.18 m. At the steep bank edges, the substrate is gravelly, but in most areas there is an organic, mucky bottom.

U. vulgaris seems localized in distribution in Daphnia Pond, contrary to reports from earlier years (Sheldon, 1987, pers. commun.). During 1987, *U. vulgaris*

occurred in the south end of the pond, among the *Typha* stems and in openings in the emergent stands. Plants grew singly in the cattails and in small groups in the openings, with cover increasing from 5 to 25% to 25 to 50% respectively.

Loon Lake is a forested lake with an extensive mat developing on the northwest side. Aquatic vegetation is characterized by *Carex* spp., *Chara* sp., *Elodea canadensis* Michx., *Myriophyllum spicatum*, *Najas flexilis* (Willd.) Rost. and Schmidt, *Nuphar lutea*, *Polygonum amphibium*, *Potentilla palustris*, *Scirpus* sp., *Typha latifolia* and *U. vulgaris* (with *U. minor* as well, on the mat). The water is clear to the depths at which *U. vulgaris* is found, about 0.80 m, and the lake is mesotrophic. The substrate is silty and marl is present. *U. vulgaris* grows singly, and is scattered, with a cover ranking of 1 to 5%.

"Tykeson's Kettle" is an unnamed, more or less mesotrophic, sunken pond in the forest adjacent to

Tykeson Pond. Much of its surface is covered thickly by *Lemna turionifera*; other macrophytes present are *Chara* sp., *Myriophyllum spicatum*, *Nuphar lutea*, *Phalaris arundinacea*, *Potamogeton* spp., and *U. vulgaris*. Where there is no *Lemna*, the summer Secchi depth is 0.5 m. The sediments are brown, organic and silty. *U. vulgaris* grows in small patches, 5 to 25% cover.

All sites described, except McWenneger's Slough, have been created or affected by glacial activity; the Slough is an artifact of meanders of the Flathead River (Alt and Hyndman, 1986). All six areas are subject to ice formation in the winter, and East Bay is also subject to major water level fluctuations due to drawdown for hydroelectric purposes. East Bay further differs from the other sites in being the only one which is influenced by water inputs other than ground water and precipitation, i.e. the others have no inlets or outlets.

Climate is similar for all sites, a "modified North Pacific Coast type", with one-half the annual

precipitation falling between May and July (NOAA, 1985). The mean yearly maximum temperature is 55.8 °F, the yearly minimum is 33.0 °F. Precipitation averages 15.36 inches per year, excluding an average 50.8 inches of snow. Annually, about 71 days are clear, 80 partly cloudy, and 214 cloudy (Kalispell, Montana averages; NOAA, 1985).

Chapter Five

Methods and Materials

I. Summer Field Collection

I gathered intact plants of *Utricularia vulgaris* at six sites (Fig. 3) in late July and August of 1987, and transported these samples in local water. Within a few days of collection, I determined the following for the sample plants: stem diameter at one representative point, length of plant or shoot section (some plants were broken during handling), number of leaves (leaflet pairs) per plant, and number of primary bladders per leaflet for at least 13 leaflets on each plant. Although I counted bladders for the current year's growth of each plant, with handling, some bladders abscissed. Consequently, I estimated the potential number of bladders per leaflet based on a growth pattern discerned from previous observations. I did not count stem bladder or secondary bladder positions since their

presence and number are more variable than those of primary bladders, and since some of them had abscissed also.

I computed summary statistics for the variables measured and for indices computed from them: leaflet pairs per cm of stem, number of bladders (or positions) per plant (average bladders per leaflet x two leaflets per leaf x total leaves) and bladders (or positions) per cm of stem (total bladders/length). I drew boxplots for these variables for each site, and conducted a multivariate analysis of variance (MANOVA).

My data were quite variable and may have violated the MANOVA assumptions, depending how conservatively one follows the assumption guidelines (Ott, 1984; Patterson, 1988, pers. comm.). Specifically, the variance was not common to the different sites, and this inequality was made worse by the small and unequal sample sizes. Samples were neither random nor independent. The assumption of normal distribution for each variable in

the population was probably adequately met. Because the assumptions of parametric statistics may not have been met, I also conducted a nonparametric MANOVA.

Because of the small sample sizes, I could not test for differences among populations for all variables measured (Patterson, 1988, pers. comm.). I chose four variables that would roughly indicate development of PCT versus other tissues and allow testing of my allocation hypothesis: bladders per leaflet, per plant and per cm, and leaflet pairs per cm. In my laboratory experiments, I used slightly different, more appropriate, indicator variables for PCT development, but I did not have the necessary data to compute these indicators in the Summer Field Collection.

I assumed that dissolved inorganic nutrient levels regulate allocation of resources to PCT, while carnivorous nutrient inputs control the amount of growth within the allocation framework. Plants receiving many nutrients via the carnivorous pathway might be expected

to decrease allocation of resources to PCT if overall (i.e. foliar and carnivorous) nutrient uptake was the regulating mechanism. However, the limited lifespan of traps suggests this is not the case. Bladders, for example, darken and decay with use, and *Dionaea* leaves may only catch three insects before becoming inactive (Slack, 1979).

A plant stimulated by low substrate nutrient availability to produce many traps will continue to be stimulated to allocate resources to PCT. The quantity of nutrients reaped by these traps will affect the amount of growth the plant can complete, and whether or not it can flower. Thus, carnivorous plants growing in nutrient-poor sites which have large populations of potential prey should exhibit high levels of PCT, but also be large-sized.

For *Utricularia vulgaris*, and other aquatic carnivorous plants, sites with few dissolved nutrients usually also have low prey populations. Accordingly,

based on my allocation hypothesis, I expected the greatest numbers of bladders per cm to occur in plants collected from the poorest sites. I expected bladders per plant to be highest in the largest plants, i.e. those from the richest site. Numbers of leaflet pairs per cm and bladders per leaflet should be intermediate for plants from both nutrient-poor and nutrient-rich sites, since good growth increases numbers of leaflet pairs and bladders per leaflet, while allocation to PCT does so as well.

Anomalous sites with low dissolved nutrient levels but high potential prey populations should produce *U. vulgaris* plants with fairly high values for all four indices. I did not examine prey availability at any of the sites.

II. Common Garden Experiment

In October, 1987, I collected *Utricularia vulgaris* turions from East Bay and McWenneger's Slough, by

severing the persistent stem of the summer growth 2-3 cm from the turion base. I selected plants haphazardly and took one (occasionally two) turions per plant. I transported the turions in local water in an insulated container.

I later rinsed the turions in tap water to remove algae, detritus, and mucilage, and placed them into aquaria filled with distilled water (separated by site). I put the aquaria into a controlled temperature room (CTR) where turions were exposed to about 450 ft-c fluorescent and incandescent light (General Electric light meter type 214) on a 14 hour photoperiod, with the temperature set for 30 °C. The dormancy-breaking procedure closely followed Winston and Gorham (1979a).

I added distilled water as needed to keep turions submerged. Turions from McWenneger's Slough developed rampant algal coverings which I removed by rubbing and rinsing.

Due to temperature control difficulties, in one week

I moved the turions to a growth chamber (Percival model PT80) set for the same conditions, but with 850 ft-c of fluorescent and incandescent light.

When sufficient turions had begun to sprout (approximately 2 weeks after collection), I began the Common Garden Experiment. I placed nine sprouted turions from East Bay and nine from McWenneger's Slough into two trays (33.5 x 26 x 8.5 cm), one for each site, filled with nutrient solution.

I used Pringsheim and Pringsheim's (1962) nutrient solution throughout the growing period for this experiment, diluted to one-half strength to slow algal growth (Knight, 1987, pers. comm.). The nutrient solution formula by weight, in distilled water, is:

KNO_3	0.02%	
$(NH_4)_2HPO_4$	0.002%	
$MgSO_4.7H_2O$	0.001%	
$CaSO_4$ (saturated)	2 ml/100	
Minor element solution		1 ml/100

Minor element solution:

EDTA	0.02%

$FeSO_4.7H_2O$	0.07%
$ZnSO_4.7H_2O$	0.001%
$MnSO_4.1H_2O$	0.0002%
$CuSO_4.5H_2O$	0.0000005%
H_3BO_4	0.001%
$Co(NO_3)_2.6H_2O$	0.0001%
$Na_2MoO_4.2H_2O$	0.0001%.

Pringsheim and Pringsheim's solution uses $MnSO_4.4H_20$; I substituted $MnSO_4.1H_2O$ because it was more readily available. Approximate pH values for the nutrient solution were: 6.4 for one-half strength, (Orion Research Digital Ionalyzer/501), 6.3 for full strength, and 6.7 for one-tenth strength (the latter strengths were used in the Diet Experiment, described below).

The turion trays were kept in the CTR, set at 24 °C during the day, and 18 °C at night, under about 400 ft-c of fluorescent and incandescent light. I later transferred the plants to larger containers (53 x 23 x 14 cm).

I started a replicate of this experiment one week later, when more turions had sprouted, using 14 East Bay plants and 14 McWenneger's Slough plants in 46 x 24 x 15

cm aquaria. Complete experimental design is shown in Figure 4.

Nutrient solution was added whenever needed to maintain levels, and nutrient solution was changed completely once in the Replicate 1 aquaria to control algal growth. No prey were offered to plants in this experiment.

After four weeks of growth I took a series of measurements on each plant: stem diameter at one representative point on each branch longer than 3 cm, or at three points along the stem if single-stemmed; length for each segment; number of leaflet pairs per segment; length of ten healthy, mature leaflets; number of bladders on 15 representative leaflets. Bladders tended to fall off with algal infection and handling, so I estimated the potential number of primary bladders per leaflet as before, again not counting stem or secondary bladder positions. I recorded wet (blotted) weights for each plant (Ohaus model B300 electronic digital scale)

Figure 4. Experimental Design for the Common Garden Experiment

Site of Turion Collection	East Bay	McWenneger's Slough
Replicate	1	1
Experiment ran from 10/28-11/27	9 turions	9 turions
Replicate	2	2
Experiment ran from 11/4-12/5	14 turions	14 turions

Modified Pringsheim and Pringsheim (1962) nutrient solution at one-half strength and no prey for all treatments.

All treatments were exposed to summer conditions: 24 °C day, 18 °C night, 14 hour photoperiod, approximately 400 ft-c for four weeks.

and noted presence or absence of new turions.

I measured each plant in a large white enamel tray, with the plants in shallow water. Measurement precision was lowered by the water and by the flimsy nature of the plants. I dried all plants for about 24 hours at 35 °C and recorded dry weights.

I repeated the measurement process for plants in the second replicate experiment after they had grown for four weeks.

For both replicate experiments, I calculated summary statistics by site. I used the variables of the Summer Field Collection, plus leaflet length and bladders per gm (total bladders/dry weight). I also drew boxplots for the variables, for each site and each replicate. I analyzed the effects of independent variables (collection site, replicate experiment) on dependent variables (morphological measurements) using MANOVA, in order to consider overall variation simultaneously (Patterson, 1988, pers. comm.).

Since my data base was small, I again chose four key variables for the MANOVA: leaflet length, leaflet pairs per cm, and bladders per cm and per gm. If developing turions respond primarily to ambient conditions, there should be no significant differences between sites for these variables. However, if developing plants retain site-specific traits, it would be more difficult to test PCT predictions. Based on my allocation hypothesis, I expected plants grown from turions from sites thought to be low in nutrients to have higher numbers of bladders per cm and per gm (standardized measures of PCT development). I also expected these plants to have intermediate numbers of leaflet pairs per cm (leaflet pairs per cm can indicate good growth and/or PCT development) and shorter leaflets (leaflet length indicates general good growth). I expected turions from sites thought to be rich in nutrients to grow into plants with long leaflets, intermediate numbers of leaflet pairs per cm, and few bladders per cm and per gm.

Where the MANOVA showed an interaction between variables, I drew profile plots, using the means for each site and replicate experiment for the variables in question. Once again, my data and sample sizes were not in strict adherence to MANOVA assumptions, so I conducted nonparametric tests.

I used the categorical variable, presence or absence of new turions, to further verify the plants' capacity for response to ambient conditions. Presence or absence of new turions would also indicate the suitability of the growing conditions.

For this variable, I computed a chi-square test for replicate experiments separately and in combination. I also calculated Cramer's V (same as phi for the combined replicates), and the contingency coefficient. When the four treatments were considered separately, 25% of the cells had expected frequencies less than five, which makes chi-square accuracy, and that of the related statistics, borderline. Accordingly, I computed lambda,

a statistic based on proportional reduction of error (Norušis, 1986).

III. Diet Experiment

In late October, 1987, I collected *Utricularia vulgaris* turions from Tykeson Pond and McWenneger's Slough. Some turions were allowed to germinate in distilled water under high temperatures, following methods outlined in the Common Garden Experiment. I rinsed the rest and refrigerated them at 1-3 °C.

After two weeks, many McWenneger's turions had sprouted and I began the Diet Experiment. Germination of Tykeson turions was sporadic and unsuccessful, so these turions were not used. I placed nine McWenneger's sprouts in each of six treatment trays (33.5 x 26 x 8.5 cm), dividing turions so that each tray had plants of approximately equal size and developmental stage.

These trays were Treatments 1-6 in the experimental design shown in Figure 5. Trays contained about 5 l of

Figure 5. Experimental Design for the Diet Experiment, Showing Treatment Number

	Nutrient Solution Strength			
	full		one-tenth	
0	1	15	3	18
	7	21	10	24
10	5	14	6	17
	9	20	12	23
100	2	13	4	16
	8	19	11	22
	fall	winter	fall	winter

Experimental Season

All trays were exposed to summer conditions: 24°C day, 18°C night, 14 hour photoperiod, approximately 850 ft-c for four weeks, in a variety of growth chambers and controlled temperature rooms.

Treatments 5-12 started one week after Treatments 1-4.

Treatments 13-24 started eleven weeks after Treatments 1-4.

Treatments 13-18 were for turions collected from Tykeson Pond, all other treatments were for turions collected from McWenneger's Slough.

one-tenth or full strength concentrations of the nutrient solution used in the Common Garden Experiment (Pringsheim and Pringsheim, 1962). One week later, I started replicate treatments, again using nine McWenneger's Slough turions per tray. These trays were Treatments 7-12.

I added nutrient solution when needed to Trays 1-12 and fed them weekly, by adding the appropriate number of *Daphnia* to each tray and briefly stirring the tray contents. Plants slated to receive no prey were treated identically to plants offered prey.

Treatment Trays 1-6 had to be moved several times from one growth facility to another. In addition, my initial feeding method (modelled after Sorenson and Jackson, 1968) proved to be too stressful for the fragile plants. Hence, I did not use data from plants in these trays in statistical tests.

Algal growth in all 12 trays was problematic, and when necessary, I changed nutrient solutions entirely

and scrubbed trays. I also removed algae by floating paper towelling on the solution surface and discarding the towelling with adhered algae. The solution of some trays was filtered with a fish aquarium system.

After four weeks of growth, I terminated the experiment and took measurements as I did in the Common Garden Experiment. I did not weigh individual plants, but recorded wet and dry weights for each treatment tray. I divided the tray dry weights by the number of experimental plants per tray to estimate individual plant weight, and divided that weight into the tray mean for bladders per plant to calculate bladders per gm.

Nine weeks after Treatments 7-12 were begun, I removed McWenneger's Slough and Tykeson Pond turions from refrigeration and put them under high temperatures to break dormancy. After about one week, I used these sprouts for Treatments 13-24 in Figure 5. I used eight Tykeson sprouts per tray for Treatments 13-18, and nine McWenneger's sprouts per tray for Treatments 19-24.

After four weeks, I ended this portion of the experiment and recorded data as described in the Common Garden Experiment. I again computed summary statistics and drew boxplots for the variables.

I used Trays 7-12 and 19-24 to compare differences in season of turion germination as well as nutrient solution and feeding treatment differences. I used Trays 13-24 to compare the effects of collection site and treatments, in effect, a second, more complex common garden experiment. The four key variables I chose for MANOVA were the same as for the Common Garden Experiment, except that I did not use bladders per gm since I did not have weights for individual plants. Instead I used bladders per leaflet. I ran MANOVA on Treatment Trays 7-24 for the four variables, and on the ranks for these variables, and plotted profiles using tray means where interactions between factors were indicated.

For the trays acting as a common garden experiment, I expected variables to have high, medium, or low values

as described in the Common Garden Experiment section.

For trays used to examine effects of nutrient solution strength and feeding regime, I expected turions grown in one-tenth strength solution to develop as plants from nutrient-poor sites: short leaflets, intermediate numbers of bladders per leaflet and leaflet pairs per cm, and many bladders per cm. For turions grown in full strength nutrient solution, I expected long leaflets, intermediate numbers of bladders per leaflet and leaflet pairs per cm, and few bladders per cm. I expected increasing prey availability to increase growth, but not to change the relative extent of the indicator variables, as explained in the Summer Field Collection section.

I calculated the chi-square statistic for presence or absence of new turions in Trays 1-24, as well as Cramer's V and the contingency coefficient. Since a majority of the cells had expected frequencies less than five, I also calculated the lambda statistic.

In this study, I intended for light, temperature and

photoperiod conditions to be identical for all treatment trays. However, due to the necessity of using several controlled environment facilities, conditions were not identical, and the extent of fluctuation varied also. The variation between treatment conditions confounds interpretation of experimental results.

Chapter Six

Results

I. Summer Field Collection

Utricularia vulgaris plants from the six sites had definite differences in growth forms and size. The effect of site of origin was significant at $p = 0.000$ for each of the four key variables: bladders (or positions) per leaflet, leaflet pairs per cm, bladders per plant, and bladders per cm. Summarized results of the multivariate analysis of variance, and of the MANOVA on the ranked variables, are shown in Table 1.

Summary statistics for the variables measured are shown in Tables A1-A3, and boxplots for each variable, Figures A1-A7, show the extent of variation between and within sites (Appendix A). The complete MANOVA results are also given in Appendix A, in Tables A4 and A5.

II. Growth under Laboratory Conditions

The *Utricularia vulgaris* plants did not grow particularly well under laboratory conditions. Treatment trays and aquaria were susceptible to algal infections (mostly *Chlamydomonas* and *Euglena* types), which seemed to increase fragmentation in the plants. Some trays developed unidentified fungal and/or rotifer or small invertebrate scums. Growth periods longer than four weeks were desirable, but plant health was prohibitive.

Growth forms varied from long, delicate, hair-like leaves to stunted, flatter, thicker, coarser leaves along the same stem. Shoots grew from the tips of turion leaves as well as in one to several directions from the old stem axis. Plant color varied from light to dark green, with McWenneger's Slough plants darker than those from Tykeson Pond and East Bay. McWenneger's plants were also more massive and more mucilaginous than plants from the other sites.

Bladders originated on all plants but did not persist and did not develop to maturity in many cases. The

degree of algal infection seemed positively correlated to bladder abscission, as Sorenson and Jackson (1968) noted.

Leaves that had been part of the turions extended and were clearly distinguishable from newly developed leaves. These old turion leaves did possess some bladders. The old turion end of many plants darkened and decayed into fragile, slimy pieces.

Germination of collected turions was quicker in January than in November. Plants from all three collecting locations formed new turions during the experimental period.

III. Common Garden Experiment

When grown under common conditions, the *Utricularia vulgaris* plants from East Bay and McWenneger's Slough showed differences in morphology similar to those observed in mature plants collected from the field. For some of the variables measured, differences seemed to be increased or reduced relative to differences observed in

field-collected plants, but this was not tested statistically.

Summarized results from parametric and nonparametric MANOVA on the four key variables (leaflet length, bladders per cm, leaflet pairs per cm and bladders per gm) are shown in Table 2. There were no significant differences between the two replicate experiments for any of the variables, while the effect of collection site was significant for all variables in parametric and nonparametric tests except bladders per cm. In addition, a significant interaction occurred between the site and replicate factors, which confounds the magnitude of the site effect. The interaction was only important (i.e. intersecting rather than off-parallel profiles) for the bladders per cm variable. The profile plot for this interaction is shown in Figure B12 (Appendix B). According to the ranked MANOVA, the interaction was also fairly important for the variables leaves per cm and bladders per gm ($0.05 < p < 0.10$).

For the one categorical variable measured, presence or absence of new turions, there was no relationship between site of origin and development of turions when replicates for each site were analyzed together. When the four sets of plants were examined separately, the chi-square value was significant, and the other statistics of association supported this. Statistics for this variable are given in Table 3.

Summary statistics for variables for each site are given in Tables B1-B4 (Appendix B). Boxplots for these variables, Figures B1-B11 (Appendix B), display the extent of variation between sites and between replicates of the experiment. Tables B5-B10 in Appendix B show the complete MANOVA results.

The correlation between wet and dry final weights for each plant was 0.89.

IV. Diet Experiment

In the Diet Experiment, the greatest differences in

measurements were due to plants originating from different sites. Like the mature plants collected from the field, plants grown from turions from Tykeson Pond were smaller in leaflet length, and had fewer bladders per leaflet, but had more leaflet pairs and bladders per cm than the McWenneger's Slough turions (bladders per cm was not significantly different in field plants; Tables C1-C3, Figs. C2, C3, C6, C8, Appendix C). Again the degree of difference between sites seemed to change for lab-grown plants relative to field-collected plants.

The site effect was statistically significant, as summarized parametric and nonparametric MANOVA results show for Trays 13-18 (Tykeson Pond) and Trays 19-24 (McWenneger's Slough; Table 4). An interaction occurred between feeding regime and collection site for these 12 treatment trays, but was only important for the bladders per cm variable in the full strength solution treatment. The profile plot for this interaction is

shown in Figure C9 (Appendix C). For the other three key variables, all the interaction profiles showed only slight departures from parallel, as may be seen on the boxplots (Figs. C2, C3, and C6, Appendix C).

For plants grown from turions collected only from McWenneger's Slough, bladders per leaflet and per cm differed significantly between experimental seasons. Feeding regime and nutrient solution strength did not have statistically significant effects on any of the variables used as indicators of growth and PCT development. Summarized results of parametric and nonparametric MANOVA for Treatment Trays 7-12 and 19-24 are shown in Table 5.

The experimental season factor interacted with the feeding regime factor, and with the solution strength factor. These interactions were important, as the profile plots show (Figs. C10 and C11, Appendix C). Solution strength and feeding regime also interacted (Fig. C12), more so in the winter than in the fall

experimental period.

For the categorical variable, presence or absence of new turions, there was a significant correlation with season of turion germination. New turions were rarely formed in the fall, but were common in the winter treatments. Counts, chi-square and related statistics, and the lambda value are given in Tables 6 and 7.

Summary statistics for all 24 trays are given in Tables C1-C4, and boxplots for each variable are shown in Figures C1-C8 (Appendix C). Final weights per tray are shown in Table C5; wet and dry weights correlated well: $r = 0.98$.

Table 1. Significance of Collection Site on Morphological Characters in *U. vulgaris* Plants Collected in Summer*

Significance of Univariate F Statistic
Parametric
(Nonparametric)

	Variable			
Factor	Bladders per leaflet	Leaflet pairs per cm	Bladders per plant	Bladders per cm
Collection Site	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)

*Summary of Tables A4 and A5, Appendix A

Table 2. Significance of Collection Site, Replicate Experiment, and the Interaction between These, on Morphological Characters in *U. vulgaris* Plants Raised from Turions in a Common Garden Experiment*

Significance of Univariate F Statistic
Parametric
(Nonparametric)

	Variable			
	Leaflet length in cm	Leaflet pairs per cm	Bladders per cm	Bladders per gm
Factor				
Collection Site	0.033 (0.023)	0.001 (0.000)	0.637 (0.557)	0.011 (0.020)
Replicate Experiment	Not significant in multivariate analysis			
Interaction				
Site-Replicate	0.813 (0.761)	0.229 (0.085)	0.000 (0.000)	0.238 (0.066)

*Summary of Tables B5-B10, Appendix B

Table 3. Influence of Collection Site and Replicate Experiment on Formation of New Turions by U. vulgaris Plants Raised from Turions in a Common Garden Experiment

Count Expected Value Column %	New Turions	
Pond Replicate	Absent	Present
East Bay 1	11 6.5 100%	0 4.5 0%
East Bay 2	2 8.8 13.3%	13 6.2 86.7%
McWenneger's 1	11 6.5 100%	0 4.5 0%
McWenneger's 2	6 8.2 42.9%	8 5.8 57.1%

For replicate experiments separately/together:

Chi-square	26.69/1.70
Degrees of freedom	3/ 1
Significance level	0.00/0.19
Cramer's V (Phi)	0.76/0.18
Contingency coefficient	0.61/0.18
Lambda	0.62/0.00

Table 4. Significance of Collection Site, Nutrient Solution Strength, Feeding Regime, and Interactions between these Factors, on Morphological Characters in U. vulgaris Plants Raised from Turions in a Diet Experiment*

Significance of Univariate F Statistic
Parametric
(Nonparametric)

	Variable			
	Leaflet length in cm	Bladders per leaflet	Leaflet pairs per cm	Bladders per cm
Factor				
Collection Site	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
Feeding Regime	0.080 (0.177)	0.370 (0.124)	0.002 (0.049)	0.040 (0.096)
Solution Strength	Not significant in multivariate analysis			
Interaction				
Site-Feeding	0.375 (0.501)	0.067 (0.184)	0.031 (0.459)	0.011 (0.026)
Site-Solution	Not significant in multivariate analysis			
Feeding-Solution	Not significant in multivariate analysis			
Site-Solution-Feeding	Not significant in multivariate analysis			

*Based on Trays 13-24; Summary of Tables C6-C19, Appendix C

Table 5. Significance of Experimental Season, Nutrient Solution Strength, Feeding Regime, and Interactions between these Factors, on Morphological Characters in *U. vulgaris* Plants Raised from Turions in a Diet Experiment*

Significance of Univariate F Statistic
Parametric
(Nonparametric)

	Variable			
	Leaflet length in cm	Bladders per leaflet	Leaflet pairs per cm	Bladders per cm
Factor				
Experimental Season	0.163 (0.135)	0.000 (0.000)	0.847 (0.823)	0.022 (0.051)
Feeding Regime	Not significant in multivariate analysis			
Solution Strength	0.111 (Not significant in multivariate analysis)	0.055	0.198	0.994
Interaction				
Season-Feeding	0.842 (0.892)	0.001 (0.000)	0.625 (0.538)	0.626 (0.619)
Season-Solution	0.720 (0.707)	0.338 (0.275)	0.001 (0.000)	0.030 (0.003)
Feeding-Solution	0.553 (Not significant in multivariate analysis)	0.031	0.266	0.387
Season-Solution-Feeding	Not significant in multivariate analysis			

*Based on Trays 7-12 and 19-24; Summary of Tables C20-C33, Appendix C

Table 6. Influence of Nutrient Solution and Feeding Treatments on Formation of New Turions by U. vulgaris Plants Raised from Turions in a Diet Experiment

Count Expected Value* Column %	Tray** 1	2	3	4	5	6
New turions						
absent	13 7.8 100.0%	9 5.4 100.0%	5 4.8 62.5%	2 4.2 28.6%	9 5.4 100.0%	13 7.8 100.0%
present	0 5.2 0.0%	0 3.6 0.0%	3 3.2 37.5%	5 2.8 71.4%	0 3.6 0.0%	0 5.2 0.0%
	7	8	9	10	11	12
absent	10 6.0 100.0%	13 7.8 100.0%	12 7.2 100.0%	9 5.4 100.0%	9 5.4 100.0%	9 5.4 100.0%
present	0 4.0 0.0%	0 5.2 0.0%	0 4.8 0.0%	0 3.6 0.0%	0 3.6 0.0%	0 3.6 0.0%

*Based on no association between new turion formation and treatment tray
**These treatments were conducted during the fall experimental season; complete treatment details are given in Fig. 5.

Table 6. Influence of Nutrient Solution and Feeding Treatments on Formation of New Turions by U. vulgaris Plants Raised from Turions in a Diet Experiment (cont'd.)

Count Expected Value * Column %	Tray** 13	14	15	16	17	18
New turions						
absent	0 2.4 0.0%	0 4.2 0.0%	0 3.6 0.0%	0 6.0 0.0%	0 4.2 0.0%	1 4.8 12.5%
present	4 1.6 100.0%	7 2.8 100.0%	6 2.4 100.0%	10 4.0 100.0%	7 2.8 100.0%	7 3.2 87.5%
	19	20	21	22	23	24
absent	6 4.8 75.0%	2 6.6 18.2%	7 6.6 63.6%	7 7.2 58.3%	1 7.2 8.3%	1 7.2 8.3%
present	2 3.2 25.0%	9 4.4 81.8%	4 4.4 36.4%	5 4.8 41.7%	11 4.8 91.7%	11 4.8 91.7%

*Based on no association between new turion formation and treatment tray
**These treatments were conducted during the winter experimental season; complete treatment details are given in Fig. 5.

Table 7. Statistics Showing the Association between Formation of New Turions and Treatments for *U. vulgaris* Plants Raised from Turions in a Diet Experiment*

Chi-square	167.99
Degrees of freedom	23
Significance level	0.00
Cramer's V	0.86
Contingency coefficient	0.65
Lambda	0.77

*Based on all Trays

Chapter Seven

Discussion

I. Summer Field Collection

As Tables A1-A3 and Figures A1-A7 (Appendix A) show, individual variation in plant measurements within sites was often large; indeed, morphological variation along individual plants was extensive in all three experiments. The samples for these measurements were not random or large, accounting for much of the non-normal distribution patterns. However, the multiple analysis of variance and the MANOVA on ranks (Table 1) both show that the pond in which *Utricularia vulgaris* plants grew had a significant effect on their size and development, and on PCT allocation based on four indices.

However, PCT indices (leaflet length, bladders per leaflet, leaflet pairs per cm, bladders per cm) were not significantly different between all sites; sites whose plants exhibit similar morphologies probably possess

similar nutrient availabilities. For example, plants collected from East Bay did not differ significantly from McWenneger's Slough plants for bladders per leaflet, bladders per cm, or leaflet pairs per cm. Nutrients are probably almost as available in the Bay as they are in the Slough. Bladders per plant did differ between the two sites--no doubt a reflection of the greater length of the Slough plants.

The significant site effect revealed by the MANOVA is, of course, expected: better conditions induce more growth than do poor conditions. Not having extensive water quality data, I cannot definitively rank the six sites by trophic status. One-time water chemistry measurements and vascular hydrophyte species composition (Schuyler, 1987, pers. comm.) suggest that McWenneger's Slough is by far the richest site. As expected, McWenneger's plants were the largest and most vigorous, exhibiting the highest values for bladders per leaflet and bladders per plant. Having a high number of bladders

per leaflet can lead to a high number of bladders per plant, but plants which increase their number of leaflets per unit length, or dissection of leaflets, also increase total bladder number.

McWenneger's plants did not have the greatest values for the other two variables used as indicators of growth and PCT allocation--leaflet pairs per cm, and bladders per cm. The higher values for these variables were found in plants from sites thought to be more nutrient-poor, based on water chemistry and hydrophyte diversity (Schuyler, 1987, pers. comm.; Wetzel, 1983). The higher values indicate a shunt of resources towards PCT, since increased bladders per cm values are not as linked to good growth as bladders per plant values are, as explained in Materials and Methods. Increased leaflet pairs per cm could also indicate an allocation of resources towards PCT, but that shunt is confounded by the other roles of leaflets.

Leaflet pairs per cm and bladders per cm were highest

at sites thought to be least fertile--Tykeson Pond and "Tykeson's Kettle". Tykeson Pond is dystrophic, and nutrients may well be unavailable. "Tykeson's Kettle" seemed to be mesotrophic, but it may be that the abundant *Lemna* plants take up most of the available nutrients as well as much of the incident light.

PCT levels can probably be adjusted in different ways, by adding leaflet pairs, by adding bladders per leaflet, or both. Pond chemistry and light availability may influence which of these strategies plants will follow, in accordance with allowable strategies dictated by genotype.

Since high PCT levels can be achieved in several ways, I cannot differentiate nutrient-rich sites from nutrient-poor ones based on my limited data. The rich site plants may not be allocating any extra resources to PCT, but their growth pattern forms bladders as it forms leaves. The poor site plants meanwhile may allocate resources to PCT, sacrificing general growth, resulting

in small-sized plants with many leaflet pairs per cm and bladders per leaflet. Increasing the number of leaflets increases PCT as well as increasing foliar absorption and photosynthetic capabilities, so the plants may be relying on more than one strategy for survival. I would expect that rich site plants which automatically have much PCT do not depend on carnivorous inputs to the extent that plants do which specifically allocate resources to PCT development. To verify this expectation, it would be necessary to discern whether a given site's plants used the foliar or carnivorous pathway as the main nutrient input route, perhaps through the use of labelled nutrients.

Sources of error in the summer data are many, and interpretation of the meager results cannot be extensive. Measurements depended on which part of the plant was measured, whether in a young area with unextended internodes, a mature area, or a senescing portion which had already lost bladders and leaves.

Moreover, the ponds did not differ solely in nutrient availabilities, but were of different sizes and depths, so that temperatures, lengths of ice-free seasons, etc. varied greatly. For example, Tykeson Pond and East Bay turions were mature earlier in the fall than were those of McWenneger's Slough. Certainly plant developmental stage also varied during the summer. Developmental stage and length of growing season probably have an effect on bladder number: the "leaves" of *U. vulgaris* may actually be branching systems (Arber, 1920; Sculthorpe, 1967), and conditions which encourage continued growth may increase the number of bladders per leaflet.

Nonetheless, trapping capacity and PCT allocation vary significantly between sites. These could be genetic differences, with each pond's population an ecotype, where characteristic genes dominate because of natural selection, where gene combinations have been fixed by genetic drift/founder effect, or where each population is clonal. On the other hand, the differences between

sites could be entirely environmental. That would mean a high degree of plasticity, not unusual for aquatic plants (Sculthorpe, 1967), but unusual for plants adapted for life in resource-poor environments (Bloom et al., 1985). Thirdly, and most likely, the differences could be due to an interaction of genetic and environmental factors. The summer data show that there is a site effect on resource allocation in *U. vulgaris*, but do not reveal the underlying cause.

II. Common Garden Experiment

A common garden experiment allows one to distinguish between effects of current environment and effects of genotypes or past environments. Within a common garden, the *Utricularia vulgaris* plants grown from turions from two sites did not grow to similar size, but retained some of their apparently site-specific traits. For example, the McWenneger's plants were larger in the turion stage, and finished the experiment with

significantly longer leaflets than the East Bay plants. Bladders per gm and leaflet pairs per cm were also significantly different between sites in the Common Garden Experiment. I do not know if the variable bladders per gm was significantly different among mature plants collected from East Bay and McWenneger's Slough, because I have no weight data for the Summer Field Collection.

Surprisingly, leaflet pairs per cm was not significantly different between those two sites for plants collected in the field. Perhaps with more time, the differences seen in the lab would have disappeared, as the East Bay plants compensated for their initial smaller size as turions. On the other hand, differences between East Bay and McWenneger's Slough plants might increase with time. If development could be followed longer, an increasing or decreasing trend in differences might suggest the relative importance of "parental" environmental conditions versus current environmental

conditions in controlling morphological variables like PCT. The observation of a tendency toward change in the extent of morphological differences between plants grown from turions from the two sites suggests plants may indeed respond to current conditions.

The significant effect of site (MANOVA, Table 2) on morphology in these plants suggests that natural variation is not solely due to ambient environmental factors. Differences could be genetic, although the extent of variation within treatment cells and that between replicate experiments for plants grown from turions from the same site, seems excessive if each population is ecotypic. Or, differences could have been pre-set in the turions by the "generation" that formed the turions. Growing these plants through another "generation" would discriminate between these alternatives, since genetic differences would persist while any "parental" environment effect should disappear since the new turions would have been formed under the

common garden conditions. I did not examine the newly formed turions to any extent, so cannot say if any differences between Tykeson Pond and McWenneger's Slough turions seemed likely to persist into the next "generation".

Turion formation is, in itself, a resource sink. Variations in the tendency to produce turions, or the rapidity of formation, could affect other growth in *U. vulgaris*. Turion formation is induced by cold, drought, nutrient or light stresses (Maier, 1973; Winston and Gorham, 1979a); probably by light or crowding effects in this case.

As the chi-square and related statistics and the lambda value show (Table 3), turion formation was not correlated with collection site, therefore that response was probably largely controlled by current environmental conditions in the common garden. As the results of the separate replicate analysis show, however, turion formation was correlated with replicate experiment.

No plants formed new turions in the first replicate. The difference may be due to more crowded conditions in the second replicate (more plants, smaller aquaria), or to other differences in growing conditions.

The plants in the second replicate may have been more likely to produce turions and go dormant because they had recently been in the dormant stage. Moreover, these plants grew from turions which left the dormant stage less readily than the plants in Replicate 1 (the quick sprouters). Winston and Gorham (1979a) found that *Utricularia vulgaris* turions collected in Alberta, Canada, when the "parental" plants were senescing, were in a state of innate dormancy, from which turions induced to sprout soon reformed turions. The McWenneger's turions were in this stage when I collected them; the East Bay and Tykeson turions had probably passed into the imposed dormancy stage since their "parental" stems were dead. Turions induced to sprout from imposed dormancy did not reform turions in Winston

and Gorham's study. Their growing conditions were probably more favorable than mine. Winston and Gorham (1979b) found dormancy to be hormonally controlled.

U. vulgaris plants observed in the field at Nimrod Warm Spring (Montana, Granite County, T12N R15W Sec. 14) had not formed turions in November, 1987, while plants at Tykeson Pond, East Bay, and McWenneger's Slough had done so. The Nimrod plants also did not form turions under conditions of cold, low light, and low nutrients (tap water), although they eventually died, but under the same conditions East Bay, Tykeson, and McWenneger's plants did form turions. Thus, the species does not seem to have an endogenous rhythm that dictates turion formation, but rather responds to various environmental cues in a manner controlled by its physiological state. Of course, the Nimrod plants could be a warm spring ecotype, where the endogenous rhythm has a different setpoint.

In any event, if turions are formed by plants of differing size and vigor, as was the case for the

McWenneger's and East Bay plants, those turions will start the next "generation" with a built-in size difference. During my experimental period, and perhaps during the relatively short growing season of many northwestern Montana bodies of water, this initial handicap may never be overcome. For example, if a "parent" plant grows in poor conditions and produces a tiny turion, that turion, even if placed in optimal conditions, may never grow as vigorously as another turion formed under better conditions but placed into a suboptimal habitat. Several "generations" of turion formation under good conditions, by plants originating from different sites, are probably necessary before the effect of vigorous "parent" plants could definitely be ruled out.

A lag effect could also be due to preconditioning. The environment that influences the "parent" plant's health and indirectly affects the turion also directly affects the early development of the turion. Bud and

seed formation are thought to be developmental stages that are particularly sensitive to preconditioning (Rowe, 1964). During turion formation and maturation, environmental conditions may induce changes that affect later gene expression. Conditions during turion maturation may also cause changes in growth factor proportions in the turion, as Gutterman, Thomas, and Heydecker (1975) found for *Lactuca scariola* seeds. Accordingly, even if plants from different sites had identical genotypes, preconditioning of turions could cause observable differences in morphology. The turions I collected were in different stages of maturation at different sites, as mentioned earlier, so preconditioning effects would certainly be possible in my experiments.

Furthermore, *Utricularia vulgaris* turions are not sexually produced propagules, but rather a perennating extension of the "parent" plant. Consequently, any acclimation a *U. vulgaris* plant may have undergone could be retained in the overwintering plant to be

expressed when dormancy is broken.

Therefore, morphological differences that I observed between plants from different sites in the Common Garden Experiment have several, not mutually exclusive, explanations:

1. Genetic differences, i.e. ecotypes at each site;
2. Differences in "parental" plant vigor and ability to endow turions ("parental" environment indirectly affects turion);
3. Differences in the turions' early environments ("parental" environment directly affects turion);
4. Differences in environmental conditions of "parent" plants, causing acclimation that was not lost during dieback to the turion phases.

My data do not allow me to determine which explanation, or what combination of explanations, is correct. Nonetheless, these data can be examined for agreement with my hypothesis that plants from poorer waters will develop more PCT.

Plants grown from turions from East Bay had more leaflet pairs per cm and bladders per gm than did plants grown from turions from McWenneger's Slough. This suggests that the lab-grown McWenneger's plants do not need to invest as much of their carbon supply in PCT. In the lab experiment, they may have had more nutrients than the East Bay plants to begin with, because of their larger turions, and they may have received more nutrients by foliar absorption through their longer leaflets. In the field, McWenneger's plants probably get more nutrients by foliar absorption from the water than they get from prey. The McWenneger's plants might have benefitted from developing more PCT under the common garden conditions (assuming nutrients were less available in the nutrient solution than in the field), but may not have done so due to preconditioning and acclimation effects. Again, following development for several "generations" in the common garden environment would help to clarify what is occurring.

Analyses of representative turions for starch and nutrient levels, and tissue analyses of experimental plants would allow comparison of resource allocation efficiency and success.

The interaction effect between replicate experiment and collection site for bladders per cm has a number of possible explanations. The replicates were started one week apart, had different numbers of plants (9 or 14) in slightly different-sized aquaria, and had minimally different growth regimes. A crowding effect, differences in degree of algal infection, or other factors could have caused the opposite response levels of bladders per cm in the second replicate. That other variables measured were not also affected is perplexing, but the nonparametric MANOVA (Table 2) does indicate some interaction ($0.05 < p < 0.10$) between site and replicate for the variables leaflet pairs per cm and bladders per gm. Neither MANOVA shows an interaction for leaflet length; some morphological characters may be more

responsive than others to conditions during development from turion to plant.

The Common Garden Experiment ignored the effect of prey on *Utricularia vulgaris*, in order to remove as many confounding factors as possible. In the field, plants from one site may respond differently to prey than plants from another site, especially if such plants differ in their allocation to PCT, as discussed in Materials and Methods. Accordingly, my results need to be field checked, and further experimentation would also enhance the tentative conclusions that I have drawn. (Part of the Diet Experiment, however, acts as a common garden experiment with prey.)

Without information on nutrient saturation levels for *Utricularia vulgaris* growth, I cannot say whether the nutrient solution used is a good, mediocre, or sub-optimal medium. Hence it is not clear if the plants were under sufficient nutrient stress to maximize their production of PCT.

III. Diet Experiment

In the Diet Experiment, plants did not respond to their treatment conditions in a statistically significant manner. Observed tendencies suggest plants may respond minimally to ambient conditions; with longer experimental periods, this response might increase. That there were interactions between treatment factors was not surprising, most organisms respond to a suite of factors in their environments so that they optimize survival, growth, development and reproduction. The interactions make the results harder to interpret; nonetheless, several trends are apparent.

Plants grown from Tykeson turions had shorter leaflets than those grown from McWenneger's turions, when grown under common garden conditions. (I noted that field-collected Tykeson plants appeared to have shorter leaflets also, but I have no data to support this observation.) Leaflet length is related to turion size, since many leaflets are developed to primordial stages

when the turion is formed. Having fewer nutrient/energy reserves in their small turions could also have affected leaflet length in lab-grown Tykeson plants, since leaves seem to be indeterminate systems, as mentioned earlier.

The number of bladders (or positions) per leaflet was less for plants grown from Tykeson Pond turions than for those from McWenneger's turions grown under the same conditions, as it was for field-collected plants from the two sites. Few bladders per leaflet correlates with having shorter leaflets. However, the difference between plants from the two sites was not so dramatic for this variable as for some of the others. This suggests the lab-grown Tykeson plants may compensate for shorter leaflets by increasing the degree of dissection of leaflets, which increases bladder number because primary bladders generally occur near the points of bifurcation.

Further, field-collected and lab-grown Tykeson plants had more leaflet pairs per cm than field and lab McWenneger's plants. This can be another developmental

strategy to increase trap number, provided that leaflets are highly dissected, as I noted above. However, the increase in leaflet number also increases foliar absorption potential (and the need to do this concurs with the probable nutrient-deficient state of the organism), and enhances photosynthetic capabilities. The stimulus for increasing leaflet number is not discernible from my experiment.

The higher bladders per cm values for lab-grown Tykeson plants relative to lab-grown McWenneger's plants suggest that the increase in leaflet pairs per cm was indeed due to the necessity of increasing nutrient inputs from carnivory. Perhaps the plants from large turions made at a rich site (McWenneger's) do not need the nutrient inputs from carnivory, while the plants from small turions made at a poor site (Tykeson) do. In the Summer Field Collection, bladders per cm was not significantly different between the two sites; with time the lab difference might have disappeared.

These between site differences seen in the lab experiments agree with my hypothesis of increased allocation of resources to PCT in less fertile sites. Interestingly, Tykeson Pond plants increased the number of bladders per cm with increasing feeding levels, while McWenneger's Slough plants did not. This response agrees with my assumption (see Materials and Methods) that dissolved nutrient levels regulate PCT allocation, while prey inputs affect growth. This increase also shows a response by the plants to ambient conditions.

The data from the Diet Experiment also seem to agree with my conclusions from the Common Garden Experiment, that past history of the individual plant and/or the early environment of the turion play a role in "progeny" development. Treatments 13-24 acted as a common garden experiment between plants from more disparate sites. Again the common conditions did not induce similar growth or PCT development in turions from different sites, and significant differences for morphological measurements

seen in field-collected plants were also found under lab conditions. Differences in morphology were greater for this common garden experiment, comparing Tykeson Pond with McWenneger's Slough, than for the comparison of East Bay with McWenneger's. Since East Bay seems to be more similar to McWenneger's Slough in terms of nutrient availabilies, this result was expected. As I stated in the Common Garden Experiment section, continued experimentation, perhaps including genotype studies (e.g. electrophoresis), would be necessary to determine the cause of morphological differences between *U. vulgaris* plants from different sites.

Looking at plants grown from turions only from McWenneger's Slough, there was a significant effect of experimental season on the variables bladders per leaflet and bladders per cm. Generally there were more bladders per leaflet in plants grown during the winter. This may be related to depletion of starch and other reserves in the turions by the plants while they remained dormant

(Maier, 1973; Winston and Gorham, 1979a.) Thus the developing plants would have a greater need to supplement nitrogen, phosphorous and other minerals by carnivory than plants grown in the fall from less depleted buds. In nature, by spring, turion reserves would be very low, and developing plants in nutrient-poor environments would probably have to develop more PCT more quickly than would plants developing from turions held only until winter and raised under laboratory conditions. The bladders per cm response also may be related to turion reserve depletion, but the interaction for this variable between experimental season and nutrient solution strength makes explanation difficult.

Nutrient solution strength and feeding regime did not, by themselves, have significant effects on any of the morphological measurements analyzed by MANOVA. Bladders per leaflet, leaflet pairs per cm, and bladders per cm were affected by interactions of these factor levels with each other and with experimental season, so

that main effects cannot be determined. Obviously, the PCT stimulation process is complicated. An effect of nutrient solution strength or feeding regime might have shown if development had been followed for a longer time, as past "generation" influences decreased.

Unlike the other three key variables, leaflet length for lab-grown plants did not vary significantly with season, prey or nutrient level. This morphological trait seems to be tied to the turion, and all turions from the same site were approximately the same size.

The development of new turions occurred more often in the winter treatment trays than in the fall ones, and more often on Tykeson Pond plants than on McWenneger's Slough ones. This may be explained by the turion reserve drop over time, so that new plants in the winter experimental trays were more sensitive to growing conditions. Tykeson Pond turions were smaller than McWenneger's turions, so reserve depletion may have been more serious for them.

New turion formation was not greatly correlated with feeding level or nutrient solution strength, although turion formation did seem to be more common in trays providing few dissolved nutrients. It may be that none of the experimental conditions were suitable for good growth in the plants, but rather were stressful, inducing reversion to the dormant phase. New turion formation could also be tied to hormone levels in the old turion which increase the probability of turion formation (Winston and Gorham, 1979b) and act to prevent plant growth during fleeting warm periods in winter.

Using the tray weights to compute bladders per gm gives data which support my hypothesis: Tykeson plants had many more bladders per gm than did McWenneger's plants.

Overall, I think the variable bladders per gm is the best indicator for development of PCT stimulated by the need to increase nutrient uptake. High bladders per leaflet values can be due to good growth, without

reflecting an increasing reliance on carnivory. Any increase in trapping capacity due to increased leaflet pairs per cm is confounded with leaflet roles in photosynthesis and nutrient absorption. Bladders per cm values do standardize trapping potential, but do not show any shunting of resources from general growth to PCT development. But high bladders per gm values mark the plant that allocates resources to PCT.

Unfortunately, I have no weight data for the Summer Field Collection of *Utricularia vulgaris*, and the weight data for the Diet Experiment is not for individual plants. Thus I must mainly interpret resource allocation in these two experiments using the less appropriate indices of leaflet pairs per cm, bladders per leaflet, and bladders per cm.

I did not collect data on the occurrence of stem and secondary bladders. Yet plants from nutrient deficient habitats may boost PCT through these traps instead of, or in addition to, increasing numbers of primary

bladders. Of course, increasing the number of leaflet pairs and the degree of leaf dissection, which boosts primary bladder numbers, would also increase numbers of stem and secondary bladders.

With regard to the constraints mentioned in the Literature Review, my experimental conditions probably were not restrictive. Temperatures were equal to summer temperatures in *Utricularia vulgaris* habitats. Light availability in the lab was at least as great as in the darker-watered study sites. Carbon dioxide should have been sufficiently available, since the trays were open to diffusion, and the nutrient solution was buffered. Although *U. purpurea* was found to be unable to use bicarbonate (Moeller, 1978), *U. vulgaris* probably can. Moeller states that the aquatic vascular plants dependent on free carbon dioxide are usually rosette plants, which *U. vulgaris* is not. It is more similar to *Elodea* and *Ceratophyllum*, which do use bicarbonate (Moeller, 1978).

However, sources of error in this study were many. One such source is the problem of not being able to insure that *Daphnia* were trapped and digested rather than dying and adding to the nutrient solution. My initial feeding method would have taken care of this problem, but would also have killed the experimental plants. The loss of bladders and incomplete maturation of bladders, due to algal growth, handling, and other laboratory effects, decreases the likelihood that all or even most of the *Daphnia* were captured. Bladder abscission may also be related to nutrient availabilities: Bloom et al. (1985) noted that leaves senesce when the carbon budget becomes negative. Bladders are modified leaves, and the growing conditions may not have provided a positive budget.

Elimination of variation in temperature and light regimes would be advantageous, as would be better control of algal growth. Larger growing containers and a flow-through nutrient solution system would probably allow

the experimental period to continue for longer than four weeks (Knight, 1987, pers. comm). Larger sample sizes would improve statistical inference. Data defining nutrient and prey availabilities for each site would eliminate doubt from my assumptions regarding trophic status and the mechanism regulating resource allocation to PCT. Most importantly, related field work is necessary to validate the conclusions I have drawn.

Nevertheless, overall my data support my research hypothesis, that *Utricularia vulgaris* plants grown to maturity in waters of lower nutrient availabilities allocate more of their carbon resources to PCT development than do *U. vulgaris* plants in richer waters (based on water chemistry and hydrophyte diversity). My data also suggest that ambient conditions in which turions develop into plants exert little control over bladder production, at least during initial weeks of growth. Rather, the plants' genotypes and/or past environments (of past growing phases as well as turions'

early history) seem to exert more control over bladder production.

Carnivory, as an adaptation, allows plants to colonize areas they otherwise could not. It is reasonable that, along with the evolution of carnivory, came mechanisms to regulate the extent of its use. Carnivory apparently does not allow plants to adapt to new conditions very rapidly, which may contribute to the relative rarity of the carnivorous habit.

Summary and Conclusions

The following hypothesis was stated for the carnivorous plant Utricularia vulgaris: plants growing in sites relatively low in dissolved, inorganic nutrients will exhibit less vigorous growth but will allocate more resources to prey capture tissue (PCT) than plants growing in nutrient-rich sites.

Based on collections of mature plants from a series of sites thought to possess a range of nutrient levels, plants from poorer sites do exhibit less vigorous growth, while producing more bladders per cm of stem.

Based on allowing turions from these sites to develop for four weeks under common garden conditions, plants from poorer sites do exhibit less vigorous growth while producing more bladders per cm of stem and per gram of plant.

The common garden experiments also showed that allocation of resources to PCT appeared to be controlled largely by genotype and/or the environment under which the turion was formed (the field environment) rather than the environment in which the turion developed into a plant (the lab environment). Periods of development longer than four weeks might have reduced (or increased) differences in plants from different sites. Following plants over several vegetative "generations" in a common garden would be required to determine if genotype or a lagged environment effect has greatest control over PCT development.

As a consequence of the genetic/lagged environment effect, experiments exposing the developing turions to different prey levels

and inorganic nutrient levels for four weeks showed little effect of these treatments on PCT development/allocation. If PCT allocation is not solely genetically controlled, but requires several turion "generations" before plants respond to lab conditions, these treatments may eventually be found to affect PCT allocation.

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Appendix A. Data Summaries, Complete MANOVA Results, and Boxplots for *Utricularia vulgaris* Plants Collected in Summer

Table A1. Data Summaries for Utricularia vulgaris Plants Collected in Summer: Stem Diameter, Plant Length, and Leaflet Pairs per Plant by Collection Site

Collection Site	Stem Diameter in mm	Total Length in cm	Leaflet Pairs per Plant
Tykeson			
Mean	1.03	9.18	19.33
Std. Deviation	.05	2.31	5.28
Minimum	1.00	5.60	12
Maximum	1.10	11.60	27
Sample Size	6	6	6
Daphnia			
Mean	.98	18.98	31.75
Std. Deviation	.05	6.62	6.85
Minimum	.90	10.00	22
Maximum	1.00	25.20	37
Sample Size	4	4	4
Loon			
Mean	1.67	10.03	14.67
Std. Deviation	.32	2.72	8.33
Minimum	1.30	7.50	8
Maximum	1.90	12.90	24
Sample Size	3	3	3
East Bay			
Mean	1.17	19.23	20.75
Std. Deviation	.42	3.36	3.30
Minimum	.90	15.40	17
Maximum	1.80	23.60	25
Sample Size	4	4	4
Kettle			
Mean	.92	25.82	60.60
Std. Deviation	.13	5.60	8.08
Minimum	.70	18.30	50
Maximum	1.00	33.70	72
Sample Size	5	5	5

Table A1. Data Summaries for Utricularia vulgaris Plants Collected in Summer: Stem Diameter, Plant Length, and Leaflet Pairs per Plant by Collection Site (cont'd.)

Collection Site	Stem Diameter in mm	Total Length in cm	Leaflet Pairs per Plant
McWenneser's			
Mean	2.43	40.70	48.33
Std. Deviation	.52	4.87	7.31
Minimum	1.80	34.20	38
Maximum	3.00	47.50	60
Sample Size	6	6	6
TOTAL			
Mean	1.39	21.83	34.39
Std. Deviation	.66	12.33	18.14
Minimum	.70	5.60	8
Maximum	3.00	47.50	72
Sample Size	28	28	28

Table A2. Data Summaries for Utricularia vulgaris Plants Collected in Summer: Leaflet Pairs per cm, Bladders/Positions per Leaflet, and Bladders/Positions per Plant by Collection Site

Collection Site	Leaflet Pairs per cm	Bladders/ Positions per Leaflet	Total Bladders/ Positions per Plant
Tykeson			
Mean	2.11	8.86	330.78
Std. Deviation	.26	2.05	69.52
Minimum	1.72	6	216
Maximum	2.42	12	406
Sample Size	6	6	6
Daphnia			
Mean	1.76	7.79	501.61
Std. Deviation	.32	.67	141.32
Minimum	1.47	7	300
Maximum	2.20	8	600
Sample Size	4	4	4
Loon			
Mean	1.39	10.73	312.55
Std. Deviation	.42	1.23	166.38
Minimum	1.07	10	158
Maximum	1.86	12	489
Sample Size	3	3	3
East Bay			
Mean	1.08	13.20	549.05
Std. Deviation	.03	2.20	132.45
Minimum	1.05	11	426
Maximum	1.12	16	674
Sample Size	4	4	4
Kettle			
Mean	2.38	10.67	1301.54
Std. Deviation	.23	1.13	283.38
Minimum	2.14	10	992
Maximum	2.73	12	1763
Sample Size	5	5	5

Table A2. Data Summaries for Utricularia vulgaris Plants Collected in Summer: Leaflet Pairs per cm, Bladders/Positions per Leaflet, and Bladders/Positions per Plant by Collection Site (cont'd.)

Collection Site	Leaflet Pairs per cm	Bladders/ Positions per Leaflet	Total Bladders/ Positions per Plant
McWenneger's			
Mean	1.18	15.24	1480.83
Std. Deviation	.06	1.16	294.14
Minimum	1.11	13	1017
Maximum	1.26	16	1936
Sample Size	6	6	6
TOTAL			
Mean	1.69	11.22	804.20
Std. Deviation	.54	3.02	531.46
Minimum	1.05	6	158
Maximum	2.73	16	1936
Sample Size	28	28	28

Table A3. Data Summaries for Utricularia vulgaris Plants Collected in Summer: Bladders/Positions per cm by Collection Site

Collection Site	Bladders/ Positions per cm
Tykeson	
Mean	36.79
Std. Deviation	6.59
Minimum	29.63
Maximum	48.42
Sample Size	6
Daphnia	
Mean	27.07
Std. Deviation	2.56
Minimum	23.81
Maximum	30.00
Sample Size	4
Loon	
Mean	29.65
Std. Deviation	8.42
Minimum	21.05
Maximum	37.87
Sample Size	3
East Bay	
Mean	28.65
Std. Deviation	5.56
Minimum	22.31
Maximum	35.82
Sample Size	4
Kettle	
Mean	50.64
Std. Deviation	4.22
Minimum	43.38
Maximum	54.22
Sample Size	5

Table A3. Data Summaries for Utricularia vulgaris Plants Collected in Summer: Bladders/Positions per cm by Collection Site (cont'd.)

Collection Site	Bladders/ Positions per cm
McWenneger's	
Mean	36.16
Std. Deviation	3.98
Minimum	29.72
Maximum	40.76
Sample Size	6
TOTAL	
Mean	35.81
Std. Deviation	9.33
Minimum	21.05
Maximum	54.22
Sample Size	28

Table A4. Parametric MANOVA Showing the Effect of Collection Site on Four Variables (Bladders/Positions per Leaflet, Bladders/Positions per Plant, Bladders/Positions per cm, Leaflet Pairs per cm) Measured on *Utricularia vulgaris* Plants Collected in Summer

Multivariate Tests of Significance (S = 4, M = 0, N = 8 1/2)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	2.39620	6.57394	20.00	88.00	.000
Hotellings	21.11353	18.47434	20.00	70.00	.000
Wilks	.00421	13.44509	20.00	63.97	.000
Roys	.92798				

Univariate F-tests with (5,22) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Bladders per leaflet	194.99891	51.78811	38.99978	2.35401	16.56742	.000
Bladders per cm	730.99787	621.79472	346.19957	28.26340	12.24904	.000
Bladders per plant	6680333.38	945878.094	1336066.68	42994.4588	31.07532	.000
Leaflet pairs per cm	6.78723	1.22813	1.35745	.05582	24.31653	.000

Table A5. Nonparametric MANOVA Showing the Effect of Collection Site on Four Variables (Bladders/Positions per Leaflet, Bladders/Positions per Plant, Bladders/Positions per cm, Leaflet Pairs per cm) Measured on *Utricularia vulgaris* Plants Collected in Summer

Multivariate Tests of Significance (S = 4, M = 0, N = 8 1/2)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	2.27359	5.79454	20.00	88.00	.000
Hotellings	12.84090	11.23579	20.00	70.00	.000
Wilks	.00986	9.67699	20.00	63.97	.000
Roys	.87018				

Univariate F-tests with (5,22) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Bladders per leaflet	1444.30000	382.70000	288.86000	17.39545	16.60549	.000
Bladders per cm	1240.70000	586.30000	248.14000	26.65000	9.31107	.000
Bladders per plant	1531.71667	295.28333	306.34333	13.42197	22.82402	.000
Leaflet pairs per cm	1501.63333	325.36667	300.32667	14.78939	20.30689	.000

Figure A1. Boxplots for Utricularia vulgaris Plants Collected in Summer: Stem Diameter by Collection Site

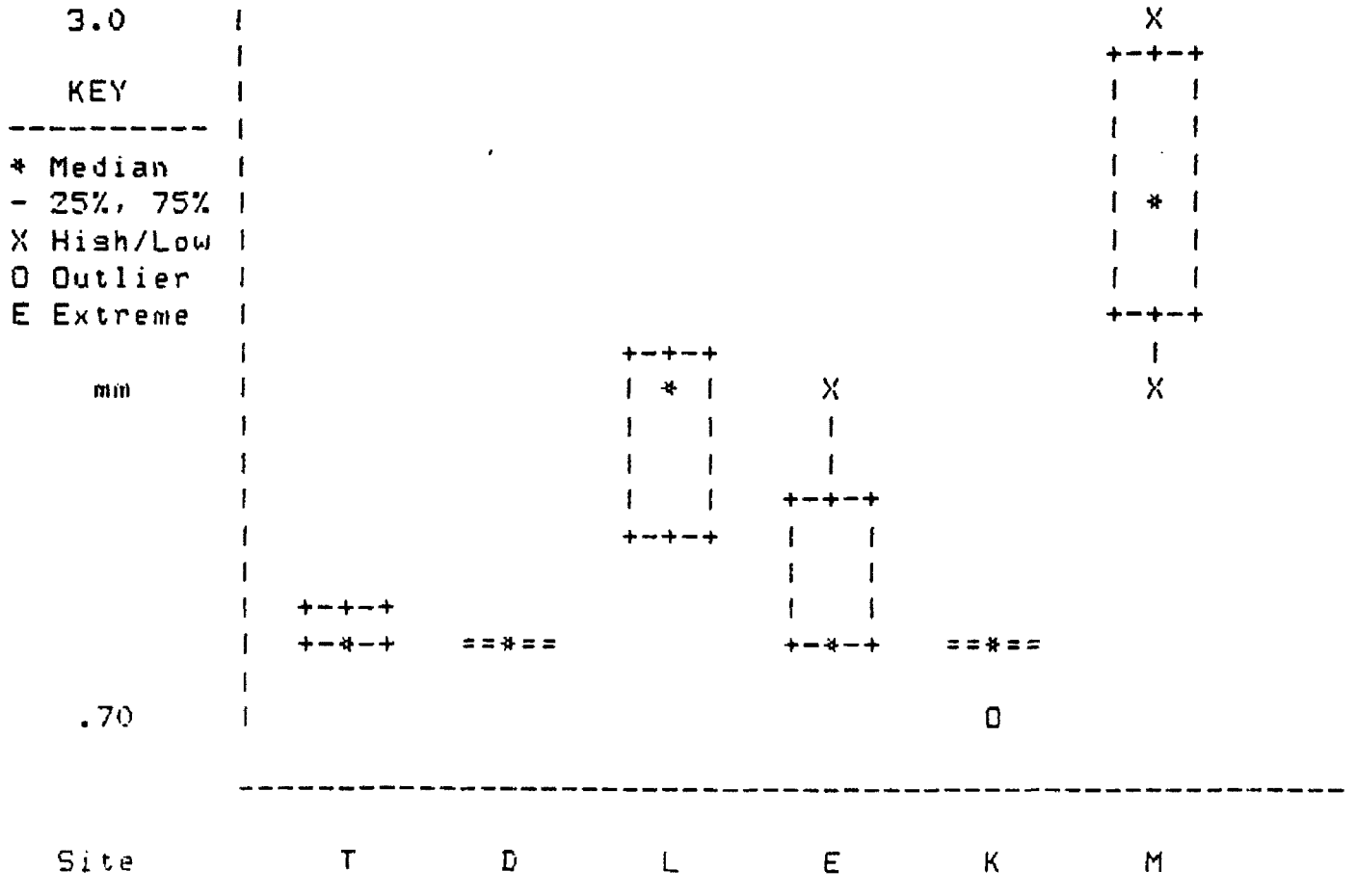


Figure A2. Boxplots for Utricularia vulgaris Plants Collected in Summer: Bladders/Positions per Leaflet by Collection Site

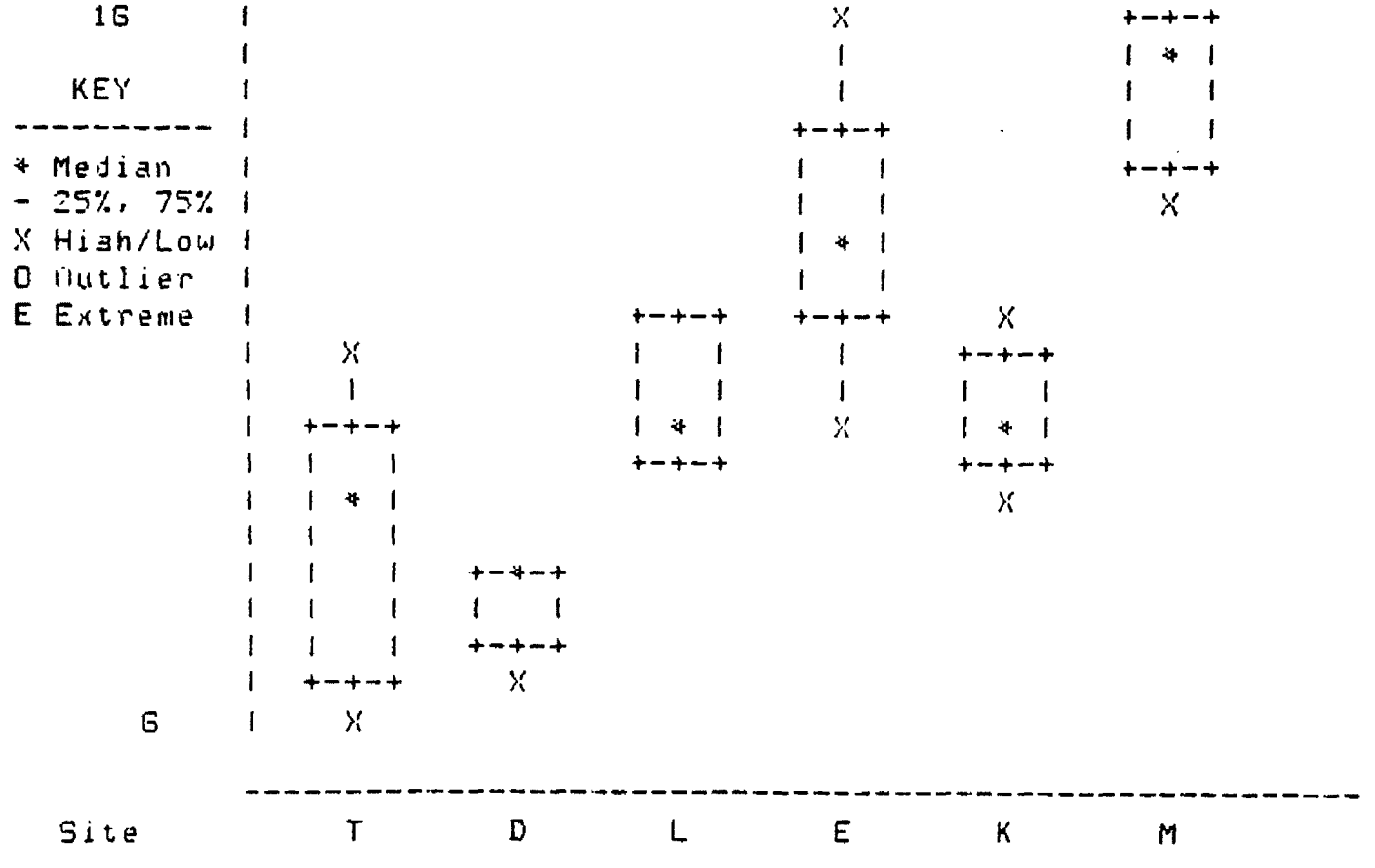


Figure A3. Boxplots for Utricularia vulgaris Plants Collected in Summer: Length of Plant or Piece by Collection Site

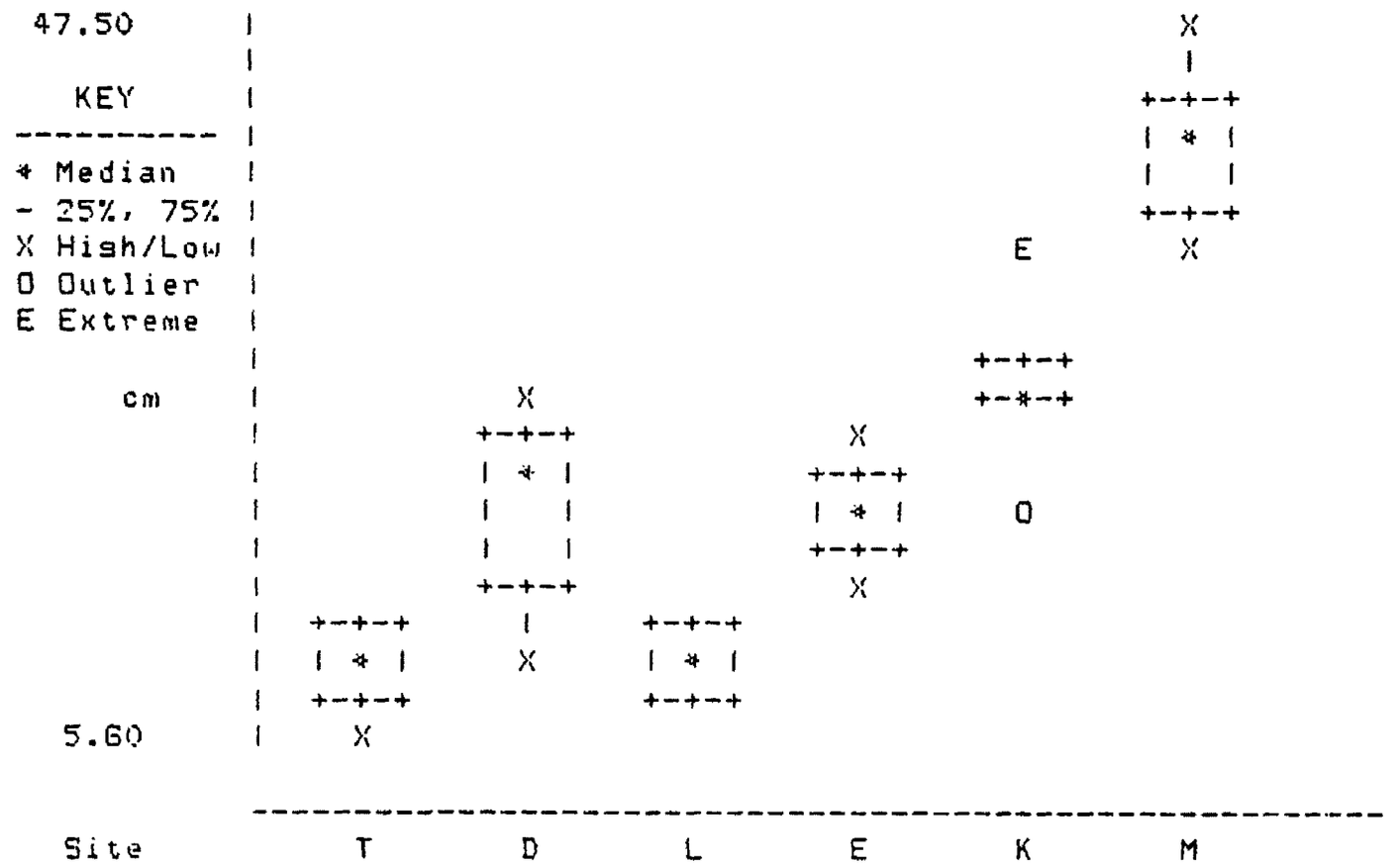


Figure A4. Boxplots for Utricularia vulgaris Plants Collected in Summer: Leaflet Pairs per Plant by Collection Site

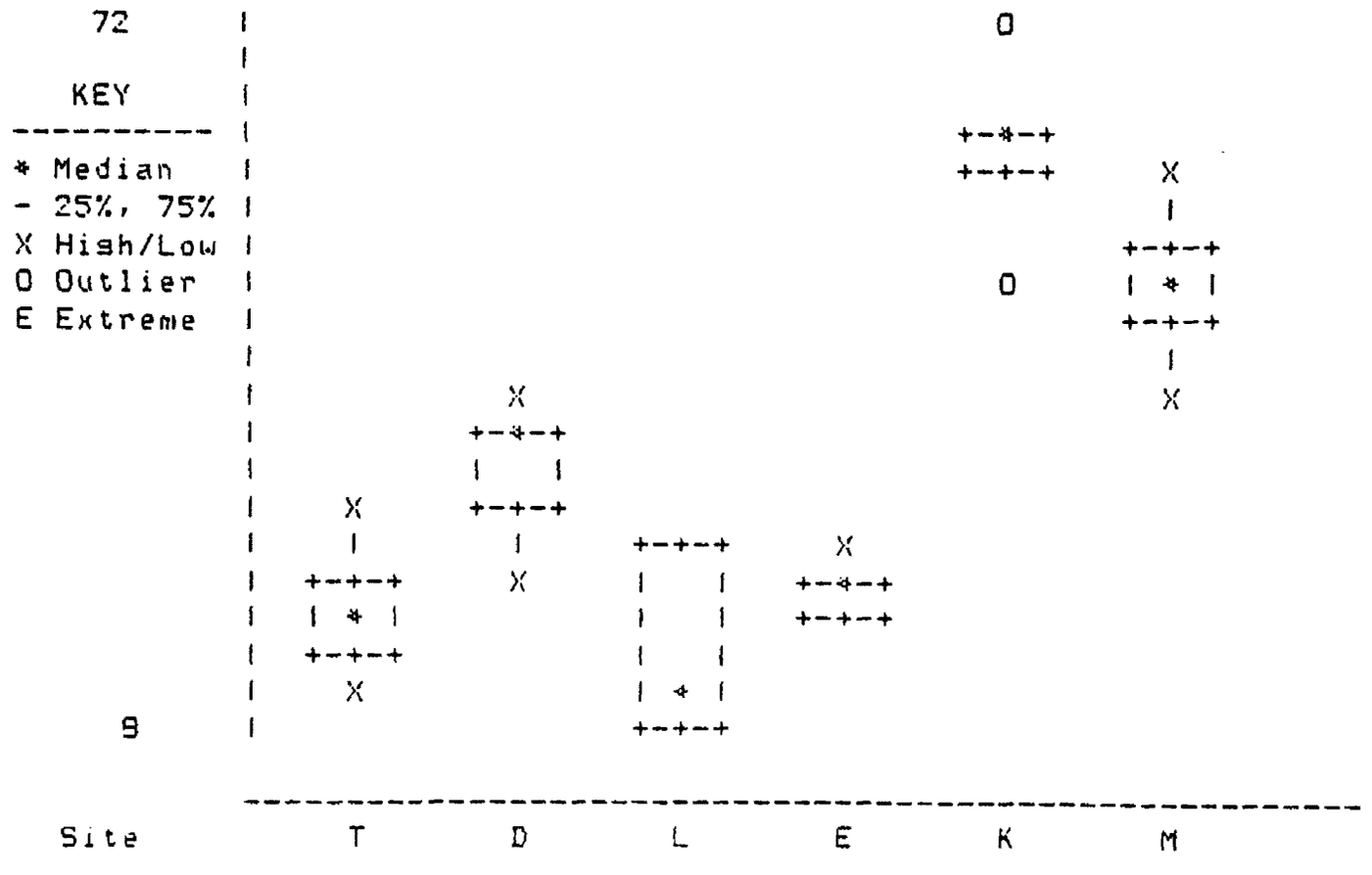


Figure A5. Boxplots for Utricularia vulgaris Plants Collected in Summer: Leaflet Pairs per cm by Collection Site

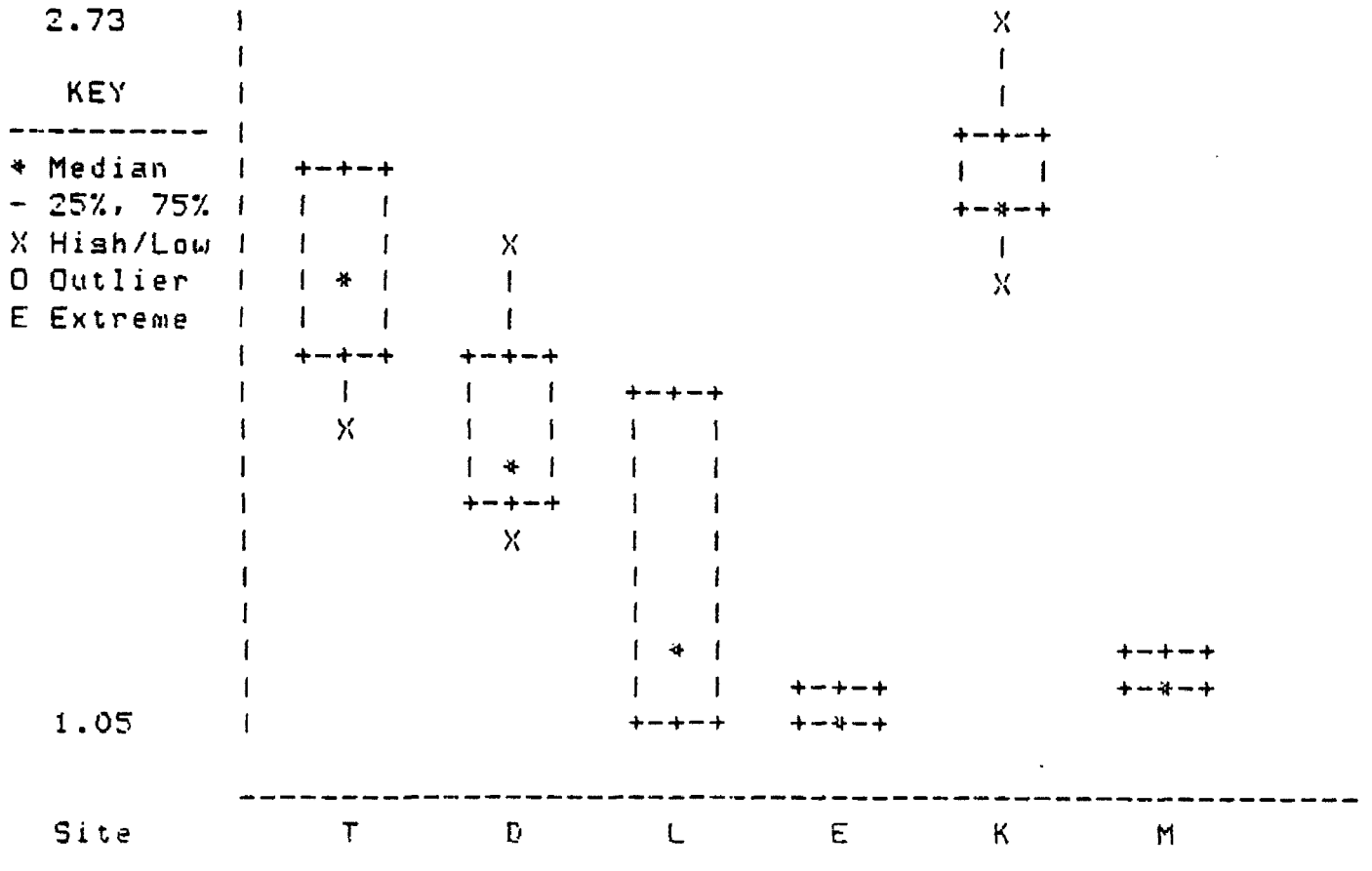


Figure A6. Boxplots for Utricularia vulgaris Plants Collectd in Summer: Bladders/Positions per Plant by Collection Site

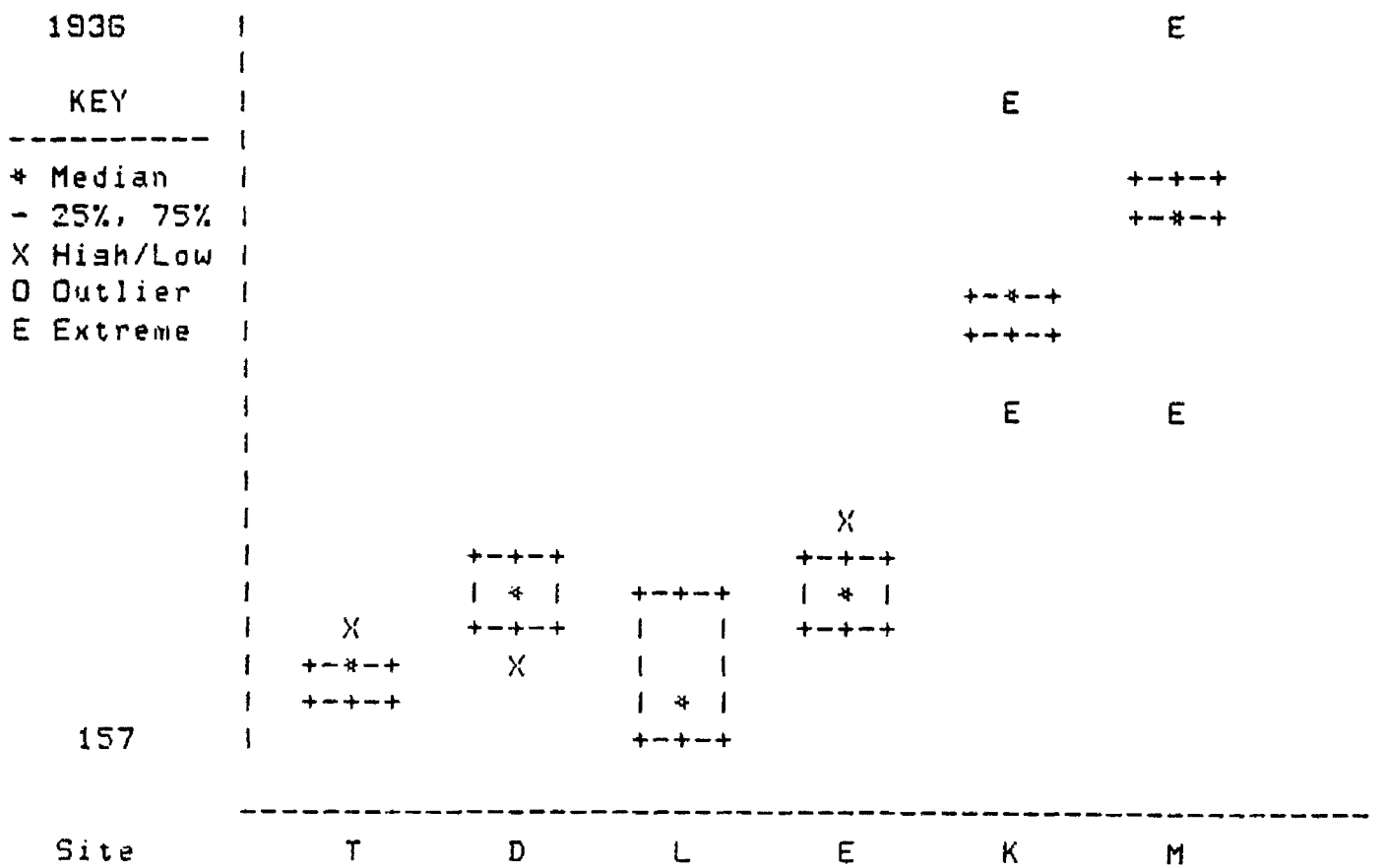
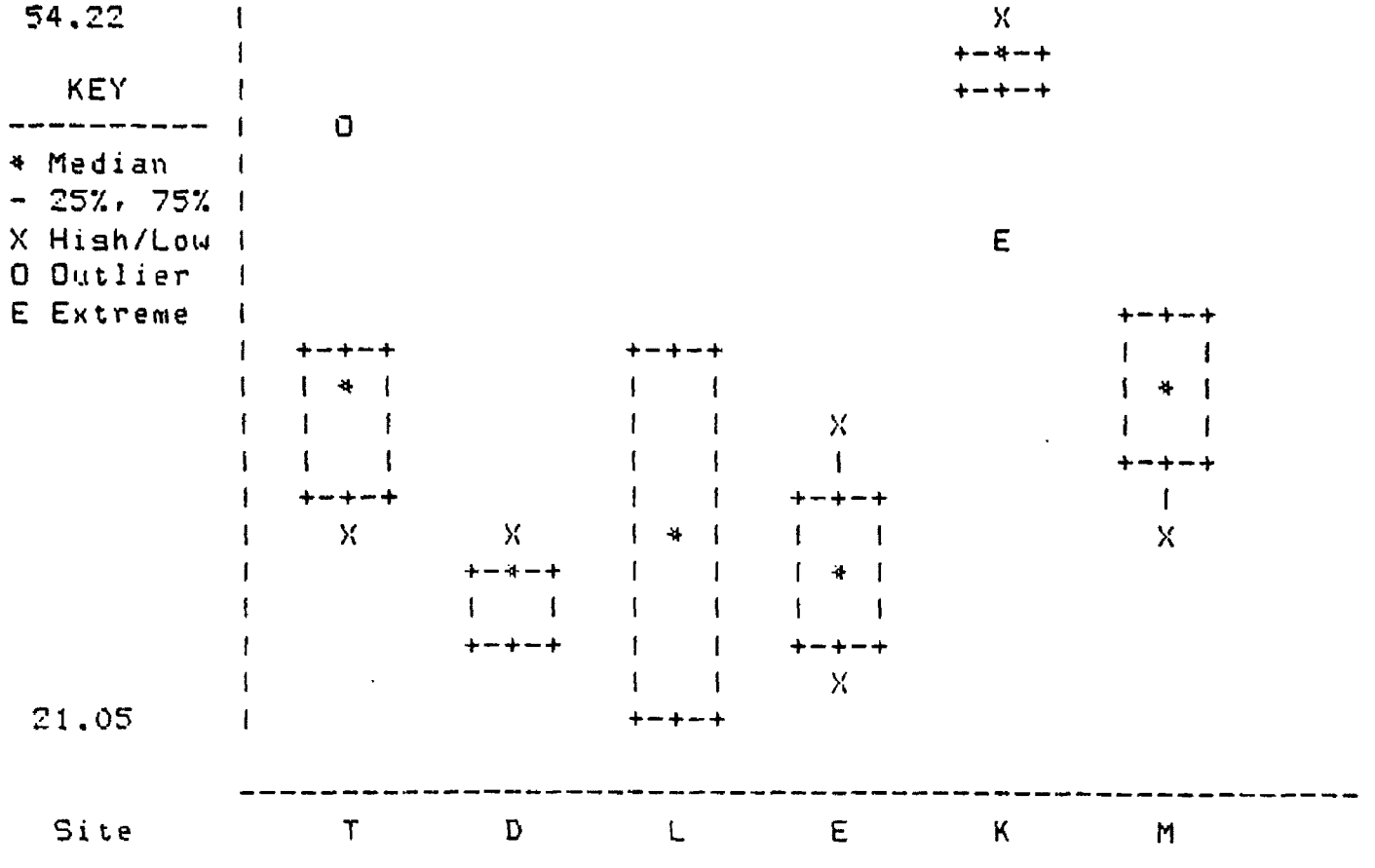


Figure A7. Boxplots for Utricularia vulgaris Plants Collected in Summer: Bladders/Positions per cm by Collection Site



Appendix B. Data Summaries, Complete MANOVA Results, Boxplots, and Profile Plots for *Utricularia vulgaris* Plants Raised from Turions in a Common Garden Experiment

Table B1. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Stem Diameter, Leaflet Length and Plant Length by Collection Site and Replicate

Site Replicate	Stem Diameter in mm	Leaflet Length in cm	Total Length in cm
East Bay 1			
Mean	.71	1.96	30.62
Std. Deviation	.13	.45	13.12
Minimum	.50	1.45	7.60
Maximum	.88	2.78	51.20
Sample Size	11	11	11
East Bay 2			
Mean	.56	1.71	27.36
Std. Deviation	.19	.43	15.13
Minimum	.13	1.11	7.20
Maximum	.83	2.46	60.80
Sample Size	14	12	14
McWenneser's 1			
Mean	.98	2.25	27.30
Std. Deviation	.17	.46	7.72
Minimum	.70	1.53	13.30
Maximum	1.27	3.10	39.90
Sample Size	10	10	10
McWenneser's 2			
Mean	.86	1.94	28.52
Std. Deviation	.09	.27	12.43
Minimum	.70	1.58	7.70
Maximum	1.00	2.64	51.10
Sample Size	13	13	13

Table B1. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Stem Diameter, Leaflet Length and Plant Length by Collection Site and Replicate (cont'd.)

Site Replicate	Stem Diameter in mm	Leaflet Length in cm	Total Length in cm
TOTAL			
Mean	.76	1.95	28.41
Std. Deviation	.22	.43	12.35
Minimum	.13	1.11	7.20
Maximum	1.27	3.10	60.80
Sample Size	48	46	48

Table B2. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Leaflet Pairs per Plant, Leaflet Pairs per cm, and Bladders/Positions per Leaflet by Collection Site and Replicate

Site Replicate	Leaflet Pairs per Plant	Leaflet Pairs per cm	Bladders/ Positions per Leaflet
East Bay 1			
Mean	110.73	3.56	10.16
Std. Deviation	53.84	.47	1.15
Minimum	24	2.99	8
Maximum	219	4.31	12
Sample Size	11	11	11
East Bay 2			
Mean	94.07	3.74	7.96
Std. Deviation	42.58	.66	1.31
Minimum	39	2.95	6
Maximum	181	5.42	10
Sample Size	14	14	14
McWenneser's 1			
Mean	71.90	2.65	11.05
Std. Deviation	18.85	.33	1.56
Minimum	31	2.25	8
Maximum	97	3.17	13
Sample Size	10	10	10
McWenneser's 2			
Mean	81.23	3.09	11.35
Std. Deviation	27.22	.79	1.62
Minimum	28	2.16	8
Maximum	134	4.83	14
Sample Size	13	13	13

Table B2. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Leaflet Pairs per Plant, Leaflet Pairs per cm, and Bladders/Positions per Leaflet by Collection Site and Replicate (cont'd.)

Site Replicate	Leaflet Pairs per Plant	Leaflet Pairs per cm	Bladders/ Positions per Leaflet
TOTAL			
Mean	89.79	3.30	10.03
Std. Deviation	39.65	.78	1.97
Minimum	24	2.16	6
Maximum	219	5.42	14
Sample Size	48	48	48

Table B3. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Bladders/Positions per Plant, Bladders/Positions per cm, and Bladders/Positions per gm by Collection Site and Replicate

Site Replicate	Total Bladders/ Positions per Plant	Bladders/ Positions per cm	Bladders/ Positions per gm Dry Weight
East Bay 1			
Mean	2220.30	71.79	10763.85
Std. Deviation	1036.47	7.59	7063.27
Minimum	570	57.73	5178.18
Maximum	4000	84.47	28790.67
Sample Size	11	11	11
East Bay 2			
Mean	1532.43	59.05	14032.73
Std. Deviation	773.35	14.84	15404.82
Minimum	437	36.92	4200.00
Maximum	2872	88.90	62400.00
Sample Size	14	14	14
McWenneger's 1			
Mean	1614.56	58.25	5234.67
Std. Deviation	550.17	8.61	1415.41
Minimum	587	44.13	3005.80
Maximum	2535	68.05	6852.41
Sample Size	10	10	10
McWenneger's 2			
Mean	1894.09	68.32	7239.24
Std. Deviation	826.77	9.28	1756.15
Minimum	605	52.40	4471.88
Maximum	3627	81.20	10999.42
Sample Size	13	13	13

Table B3. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Bladders/Positions per Plant, Bladders/Positions per cm, and Bladders/Positions per gm by Collection Site and Replicate (cont'd.)

Site Replicate	Total Bladders/ Positions per Plant	Bladders/ Positions per cm	Bladders/ Positions per gm Dry Weight
TOTAL			
Mean	1805.13	64.31	9610.78
Std. Deviation	835.99	11.96	9444.06
Minimum	437	36.92	3005.80
Maximum	4000	88.90	62400.00
Sample Size	48	48	48

Table B4. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Final Wet and Dry Weights by Collection Site and Replicate

Site Replicate	Blotted Weight in gm	Final Dry Weight in gm
East Bay 1		
Mean	2.644	.253
Std. Deviation	1.610	.138
Minimum	.39	.08
Maximum	6.13	.46
Sample Size	11	11
East Bay 2		
Mean	1.610	.193
Std. Deviation	1.199	.140
Minimum	.16	.01
Maximum	4.20	.41
Sample Size	15	15
McWenneser's 1		
Mean	3.837	.334
Std. Deviation	2.155	.165
Minimum	.80	.10
Maximum	7.37	.69
Sample Size	11	11
McWenneser's 2		
Mean	2.895	.303
Std. Deviation	2.100	.182
Minimum	1.11	.09
Maximum	8.66	.82
Sample Size	14	14

Table B4. Data Summaries for Utricularia vulgaris Plants Raised From Turions in a Common Garden Experiment: Final Wet and Dry Weights by Collection Site and Replicate (cont'd.)

Site Replicate	Blotted Weight in gm	Final Dry Weight in gm
TOTAL		
Mean	2.666	.266
Std. Deviation	1.910	.162
Minimum	.16	.01
Maximum	8.66	.82
Sample Size	51	51

Table B5. Parametric MANOVA Showing the Effect of Collection Site on Four Variables (Leaflet Length, Leaflet Pairs per cm, Bladders/Positions per cm, Bladders/Positions per sm) Measured on *U. vulgaris* Plants Raised from Turions in a Common Garden Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 18 1/2)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.38487	6.10042	4.00	39.00	.001
Hotelling	.62568	6.10042	4.00	39.00	.001
Wilks	.61513	6.10042	4.00	39.00	.001
Roys	.38487				

Note.. F statistics are exact.

Univariate F-tests with (1,42) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet Length	.78372	6.80126	.78372	.16193	4.83974	.033
Leaflet Pairs per cm	5.27800	16.72252	5.27800	.39816	13.25612	.001
Bladders per cm	22.83592	4242.31304	22.83592	101.00745	.22608	.637
Bladders per sm	166280190	975634277	166280190	23229387.6	7.15818	.011

Table 86. Parametric MANOVA Showing the Effect of Replicate on Four Variables (Leaflet Length, Leaflet Pairs per cm, Bladders/Positions per cm, Bladders/Positions per sm) Measured on U. vulgaris Plants Raised from Turions in a Common Garden Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 18 1/2)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.15486	1.78661	4.00	39.00	.151
Hotellings	.18324	1.78661	4.00	39.00	.151
Wilks	.84514	1.78661	4.00	39.00	.151
Roys	.15486				

Note.. F statistics are exact.

Univariate F-tests with (1,42) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.86997	6.80126	.86997	.16193	5.37233	.025
Leaflet pairs per cm	.52260	16.72252	.52260	.39816	1.31256	.258
Bladders per cm	47.68313	4242.31304	47.68313	101.00745	.47208	.496
Bladders per sm	998820.692	975634277	998820.692	23229387.6	.04300	.837

Table B7. Parametric MANOVA Showing the Effect of the Interaction Between Collection Site and Replicate on Four Variables (Leaflet Length, Leaflet Pairs per cm, Bladders/Positions per cm, Bladders/Positions per sm) Measured on U. vulgaris Plants Raised from Turions in a Common Garden Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 18 1/2)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.36898	5.70116	4.00	39.00	.001
Hotellings	.58473	5.70116	4.00	39.00	.001
Wilks	.63102	5.70116	4.00	39.00	.001
Roys	.36898				

Note.. F statistics are exact.

Univariate F-tests with (1,42) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.00914	6.80126	.00914	.16193	.05646	.813
Leaflet pairs per cm	.59246	16.72252	.59246	.39816	1.48802	.229
Bladders per cm	1672.76537	4242.31304	1672.76537	101.00745	16.56081	.000
Bladders per sm	33246863.9	975634277	33246863.9	23229387.6	1.43124	.238

Table B8. Nonparametric MANOVA Showing the Effect of Collection Site on Four Variables (Leaflet Length, Leaflet Pairs per cm, Bladders/Positions per cm, Bladders/Positions per mm) for *U. vulgaris* Plants Raised from Turions in a Common Garden Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 18 1/2)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.53841	11.37275	4.00	39.00	.000
Hotellings	1.16644	11.37275	4.00	39.00	.000
Wilks	.46159	11.37275	4.00	39.00	.000
Roys	.53841				

Note.. F statistics are exact.

Univariate F-tests with (1,42) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet Length	883.44107	6679.51827	883.44107	159.03615	5.55497	.023
Leaflet pairs per cm	2661.97843	5286.78721	2661.97843	125.87589	21.14764	.000
Bladders per cm	46.81903	5606.92541	46.81903	133.49822	.35071	.557
Bladders per mm	918.26210	6538.78520	918.26210	155.68536	5.89819	.020

Table B9. Nonparametric MANOVA Showing the Effect of Replicate on Four Variables (Leaflet Length, Leaflet Pairs per cm, Bladders/Positions per cm, Bladders/Positions per mm) for *U. vulgaris* Plants Raised from Turions in a Common Garden Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 18 1/2)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.15355	1.76874	4.00	39.00	.155
Hotellings	.18141	1.76874	4.00	39.00	.155
Wilks	.84645	1.76874	4.00	39.00	.155
Roys	.15355				

Note.. F statistics are exact.

Univariate F-tests with (1,42) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet Length	601.74177	6679.51827	601.74177	159.03615	3.78368	.058
Leaflet pairs per cm	93.89712	5286.78721	93.89712	125.87589	.74595	.393
Bladders per cm	93.21797	5606.92541	93.21797	133.49822	.69827	.408
Bladders per mm	349.35138	6538.78520	349.35138	155.68536	2.24396	.142

Table B10. Nonparametric MANOVA Showing the Effect of the Interaction Between Collection Site and Replicate on Four Variables (Leaflet Length, Leaflet Pairs per cm, Bladders/Positions per cm, Bladders/Positions per mm) for *U. vulgaris* Plants Raised from Turions in a Common Garden Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 18 1/2)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.37786	5.92173	4.00	39.00	.001
Hotellings	.60736	5.92173	4.00	39.00	.001
Wilks	.62214	5.92173	4.00	39.00	.001
Roys	.37786				

Note.. F statistics are exact.

Univariate F-tests with (1,42) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet Length	14.88830	6679.51827	14.88830	159.03615	.09362	.761
Leaflet pairs per cm	392.13011	5286.78721	392.13011	125.87589	3.11521	.085
Bladders per cm	2647.41644	5606.92541	2647.41644	133.49822	19.83110	.000
Bladders per mm	555.75562	6538.78520	555.75562	155.68536	3.56974	.066

Figure B1. Boxplots For Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Stem Diameter by Collection Site and Replicate

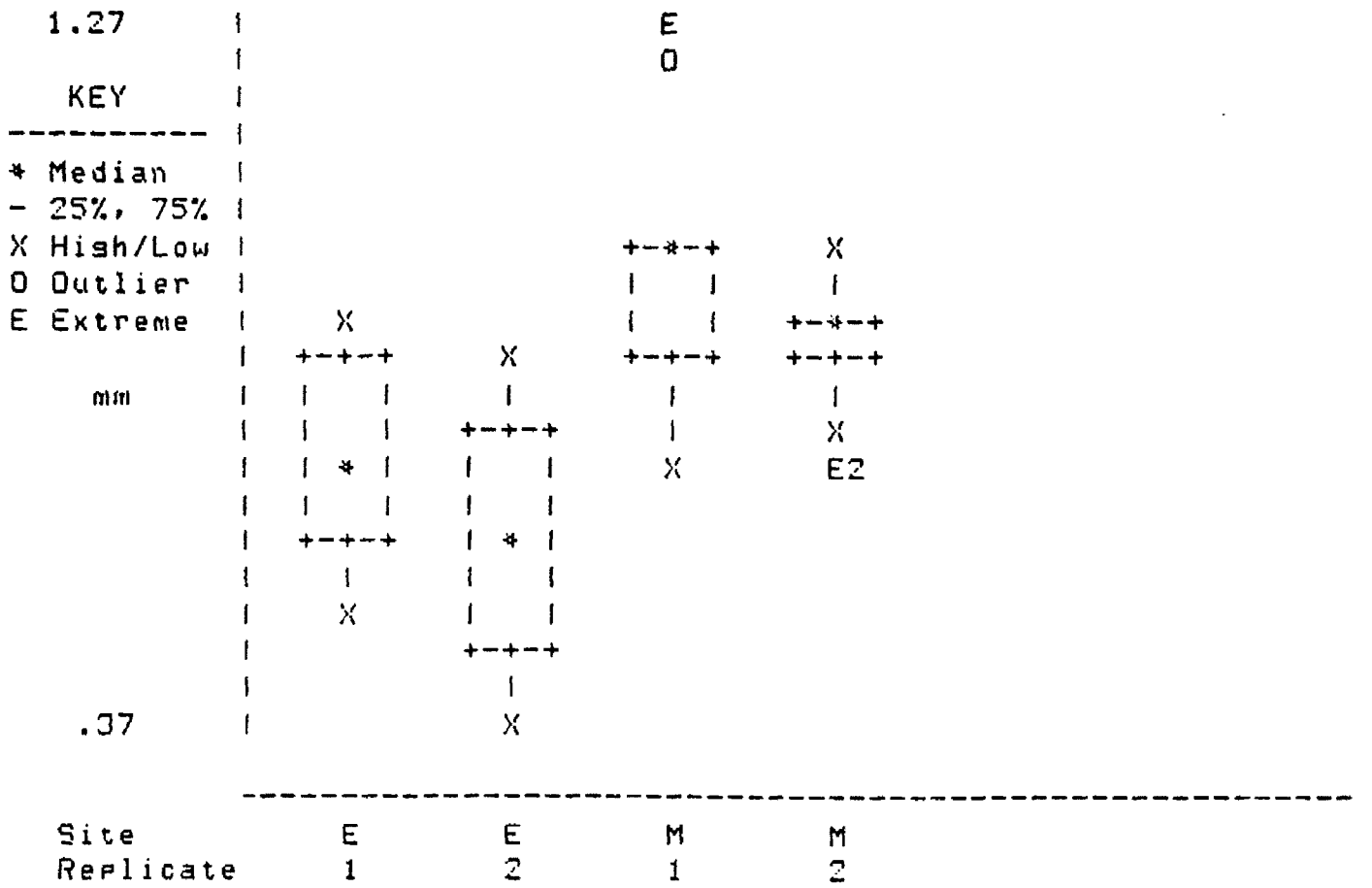


Figure 82. Boxplots for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Leaflet Length by Collection Site and Replicate

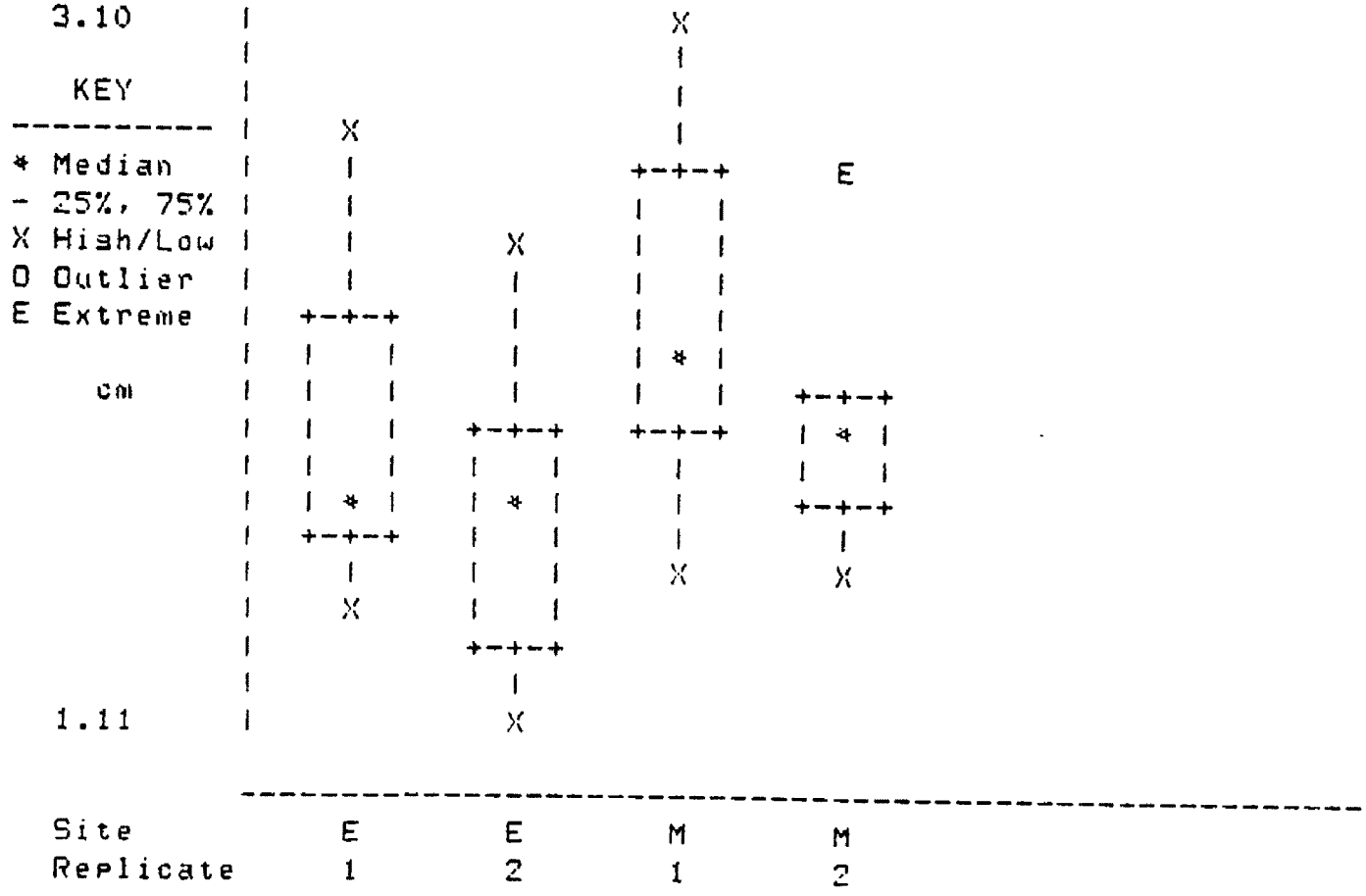


Figure B3. Boxplots for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Bladders/Positions per Leaflet by Collection Site and Replicate

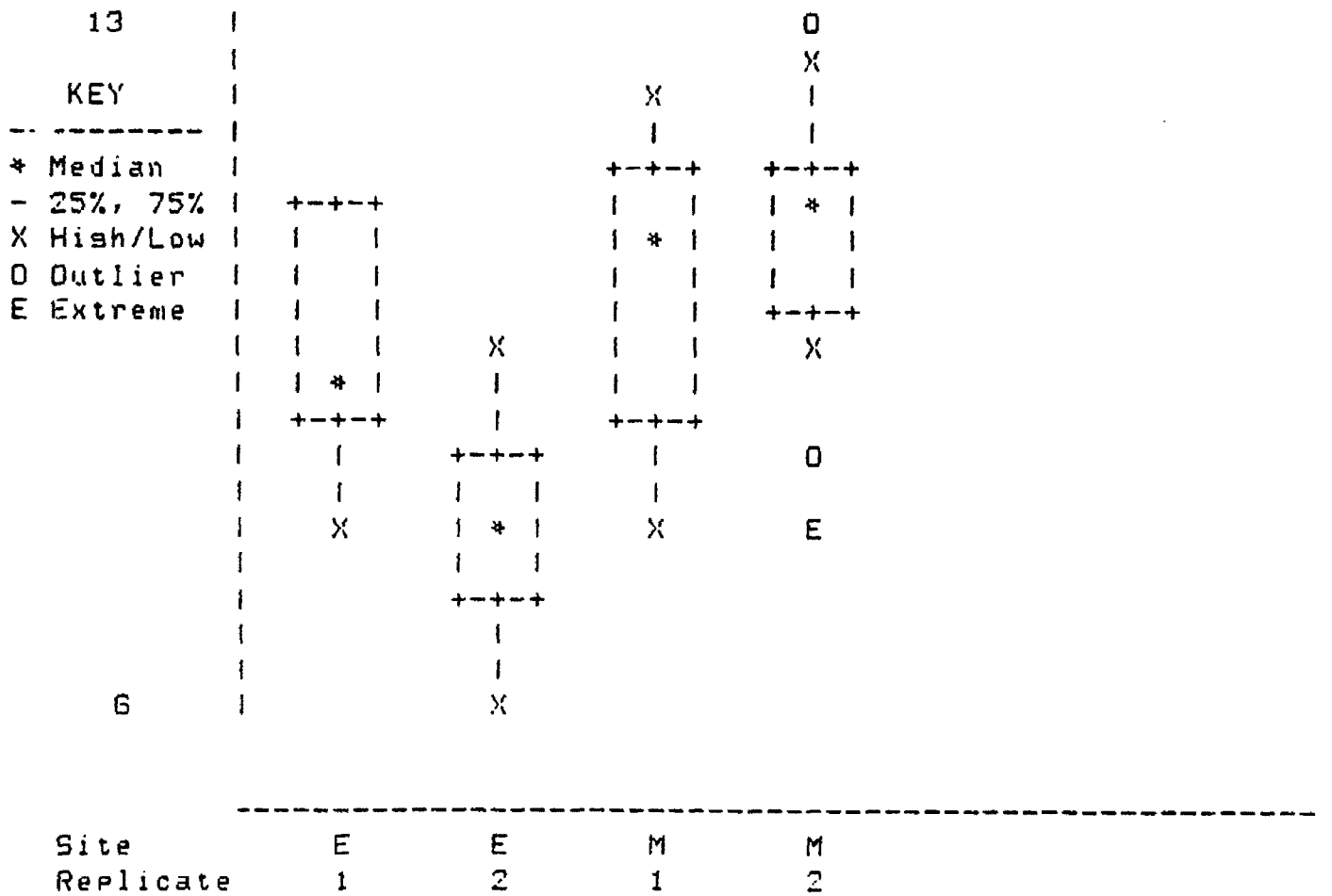


Figure B4. Boxplots for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Length of Plant by Collection Site and Replicate

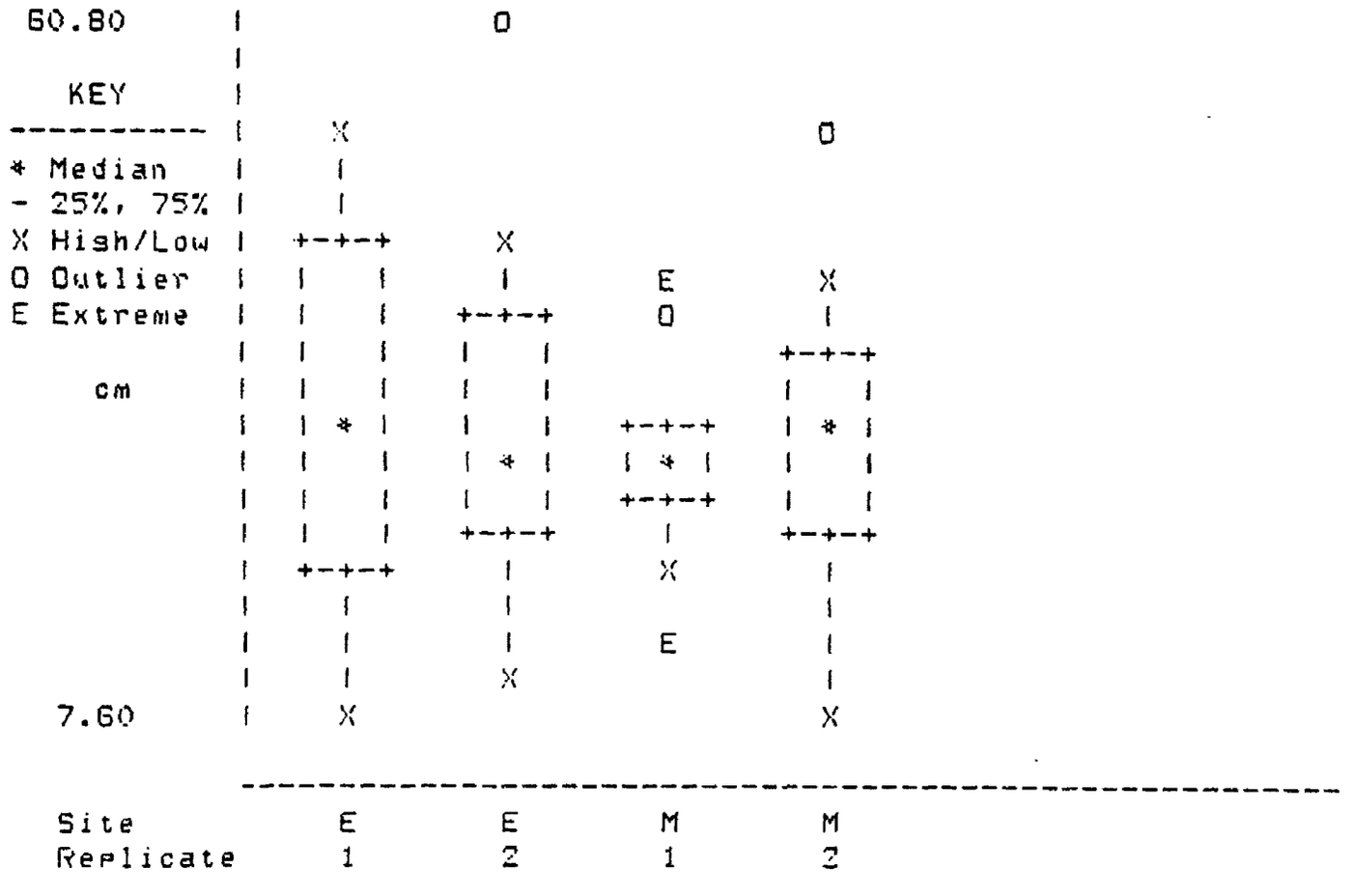


Figure B5. Boxplots for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Leaflet Pairs per Plant by Collection Site and Replicate

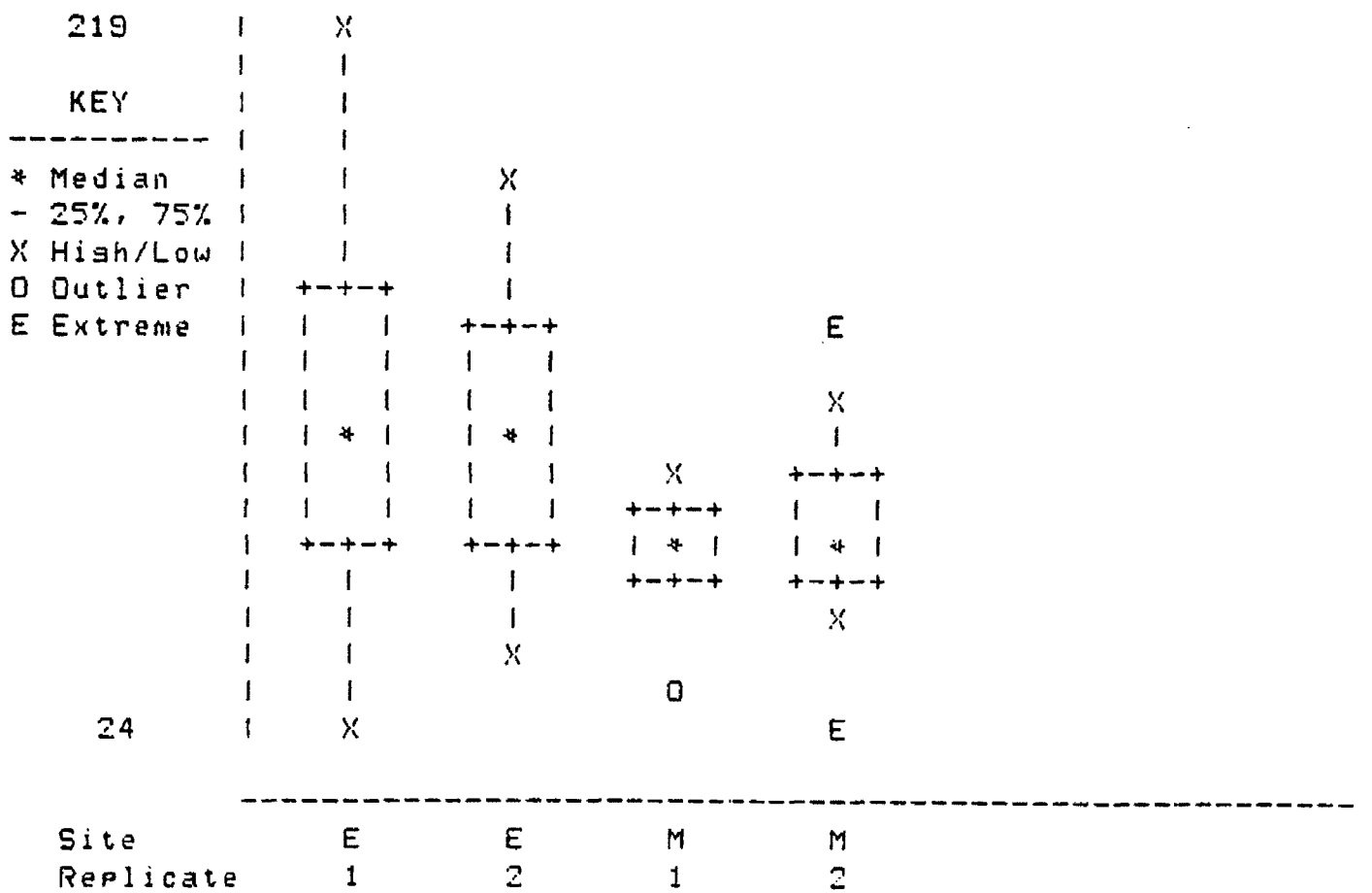


Figure 86. Boxplots for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Leaflet Pairs per cm by Collection Site and Replicate

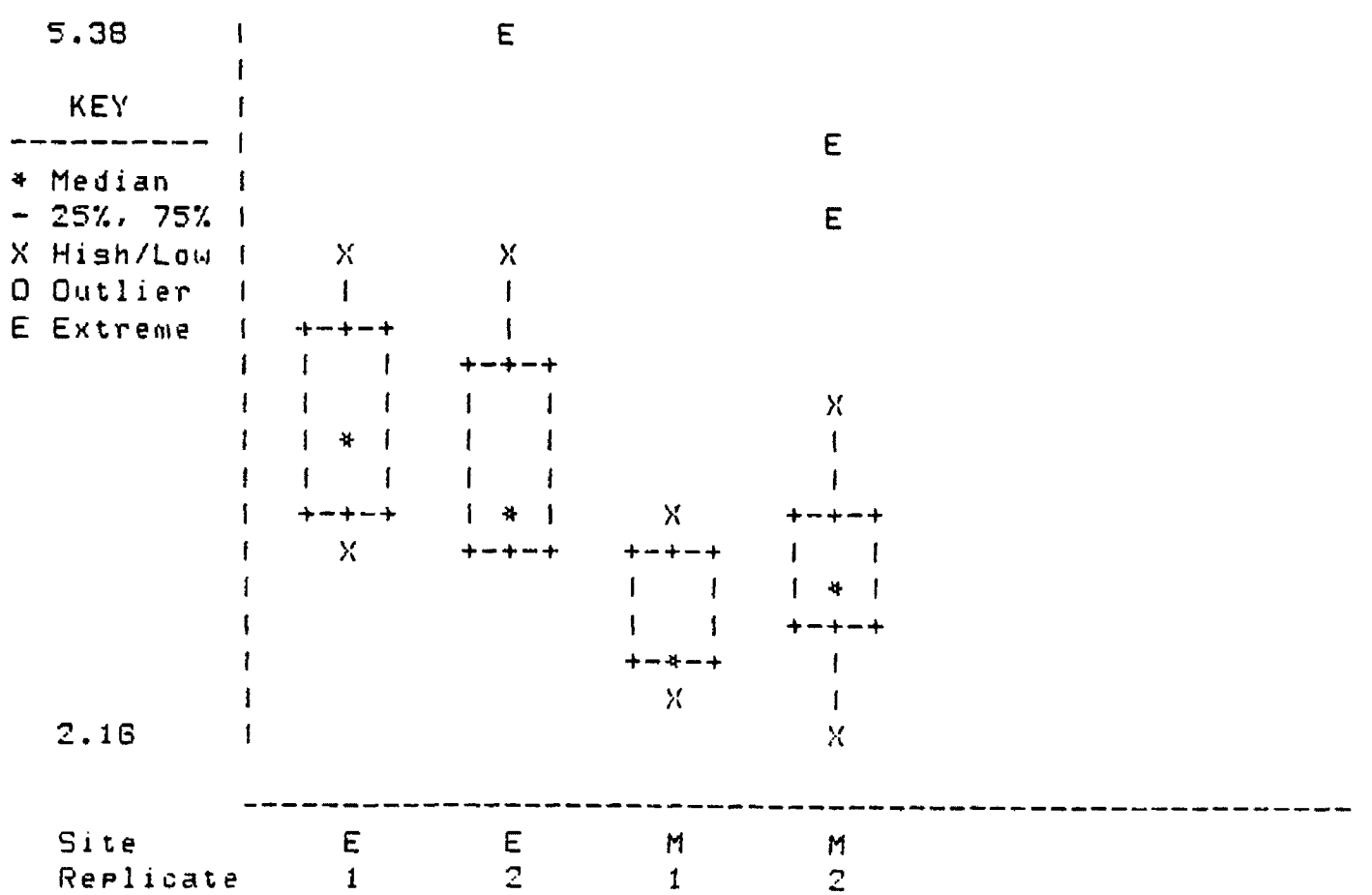


Figure B7. Boxplots for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Bladders/Positions per Plant by Collection Site and Replicate

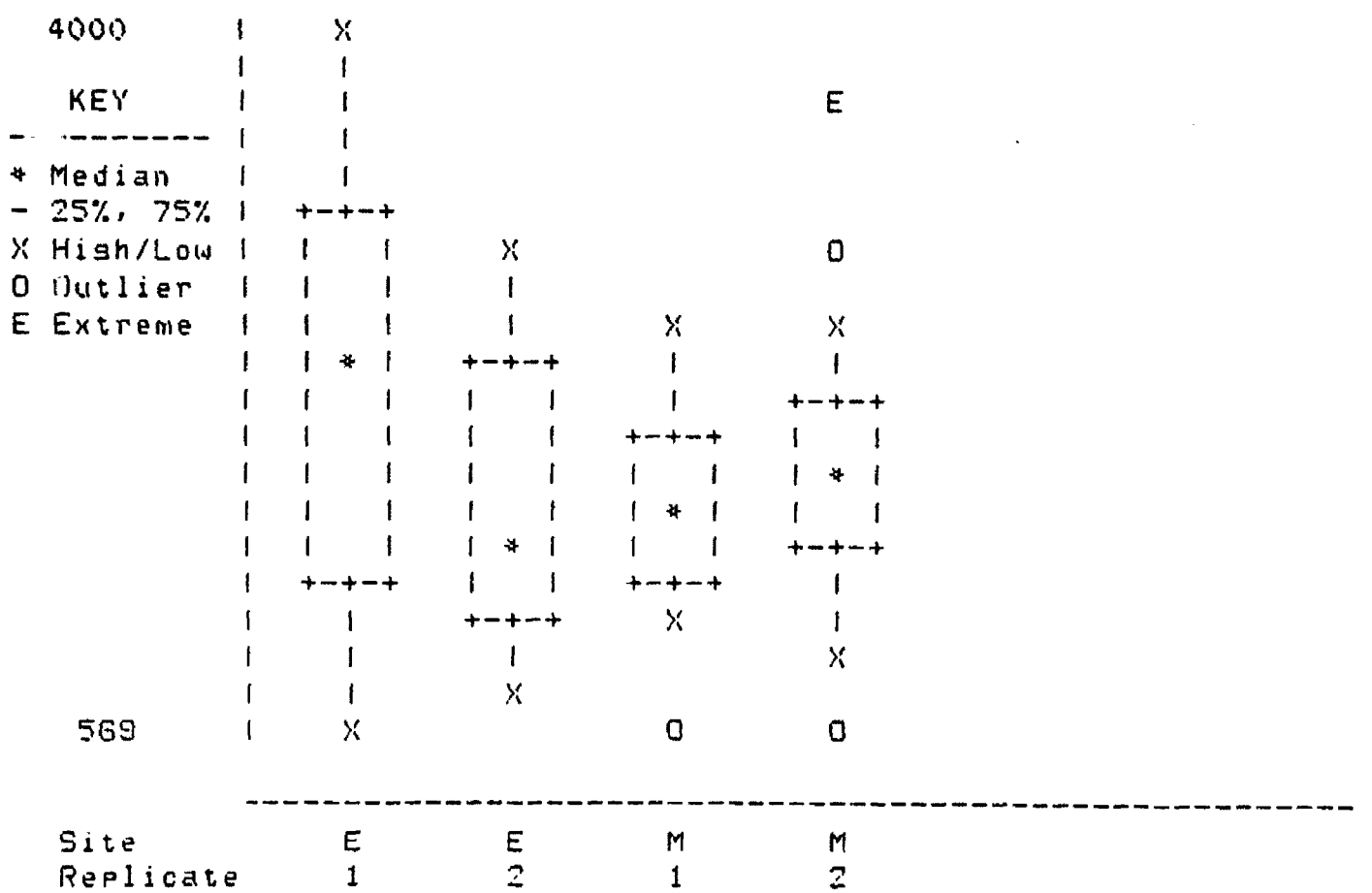


Figure 88. Boxplots for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Bladders/Positions per cm by Collection Site and Replicate

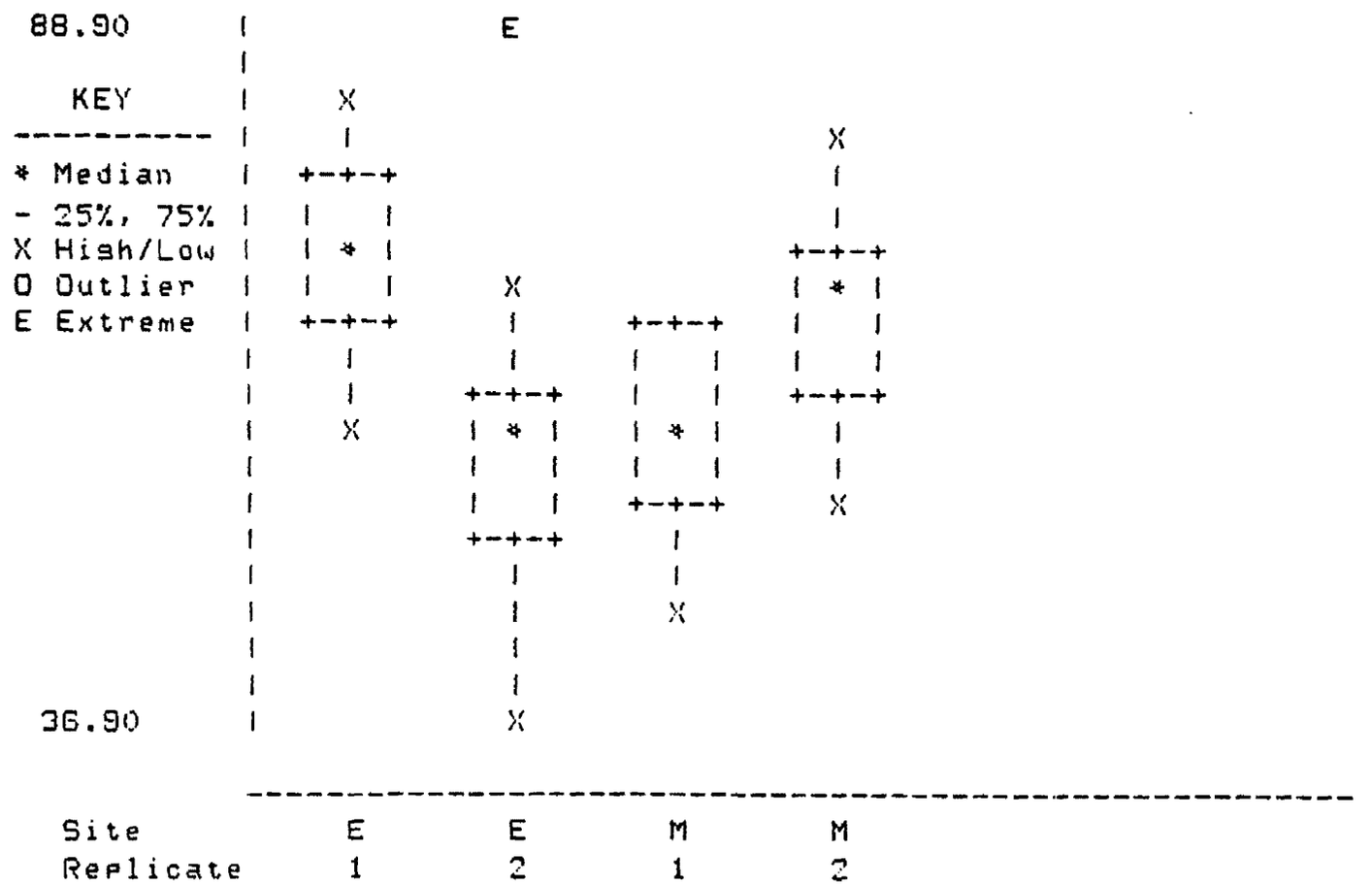


Figure B9. Boxplots for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Bladders/Positions per sm by Collection Site and Replicate

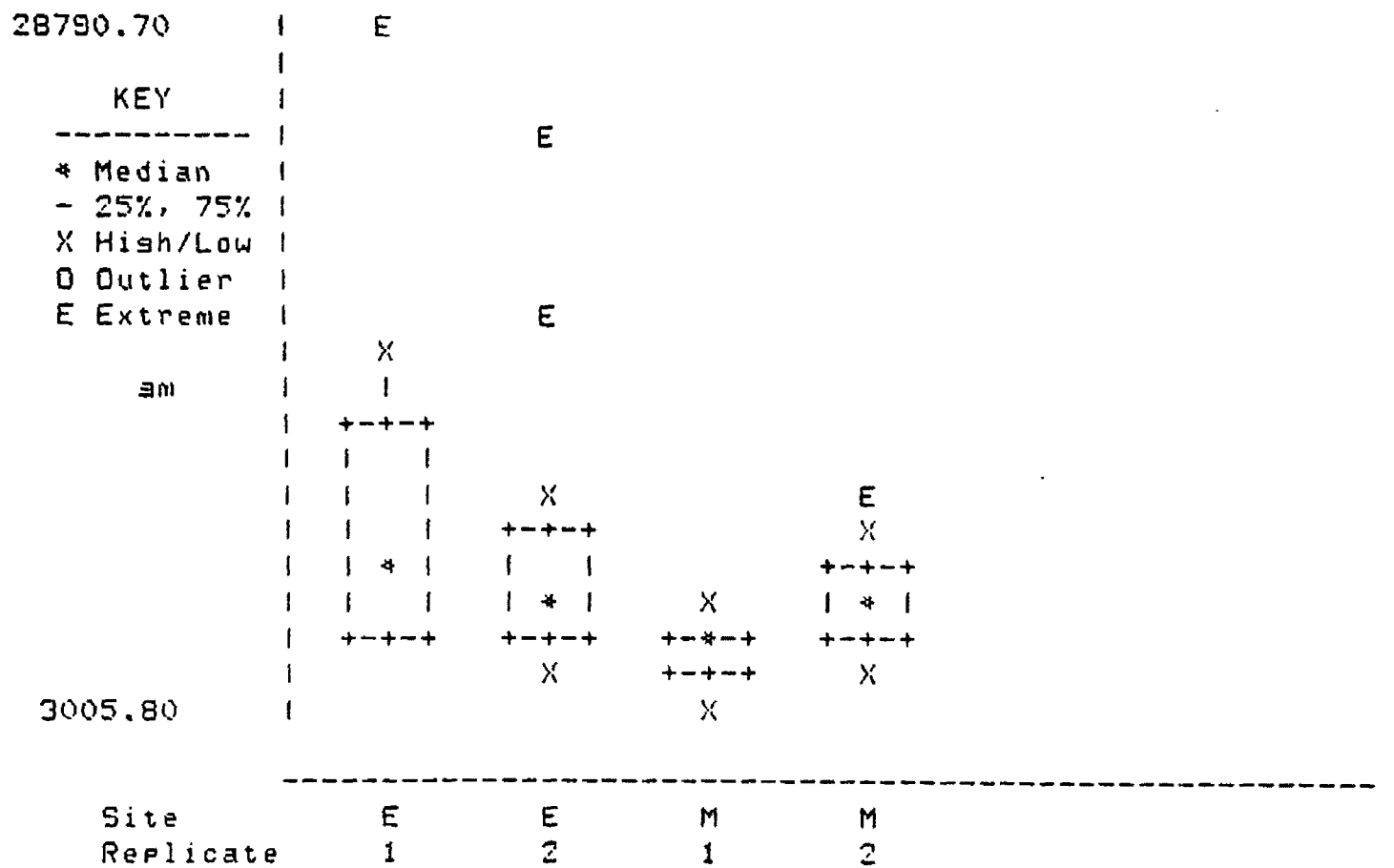
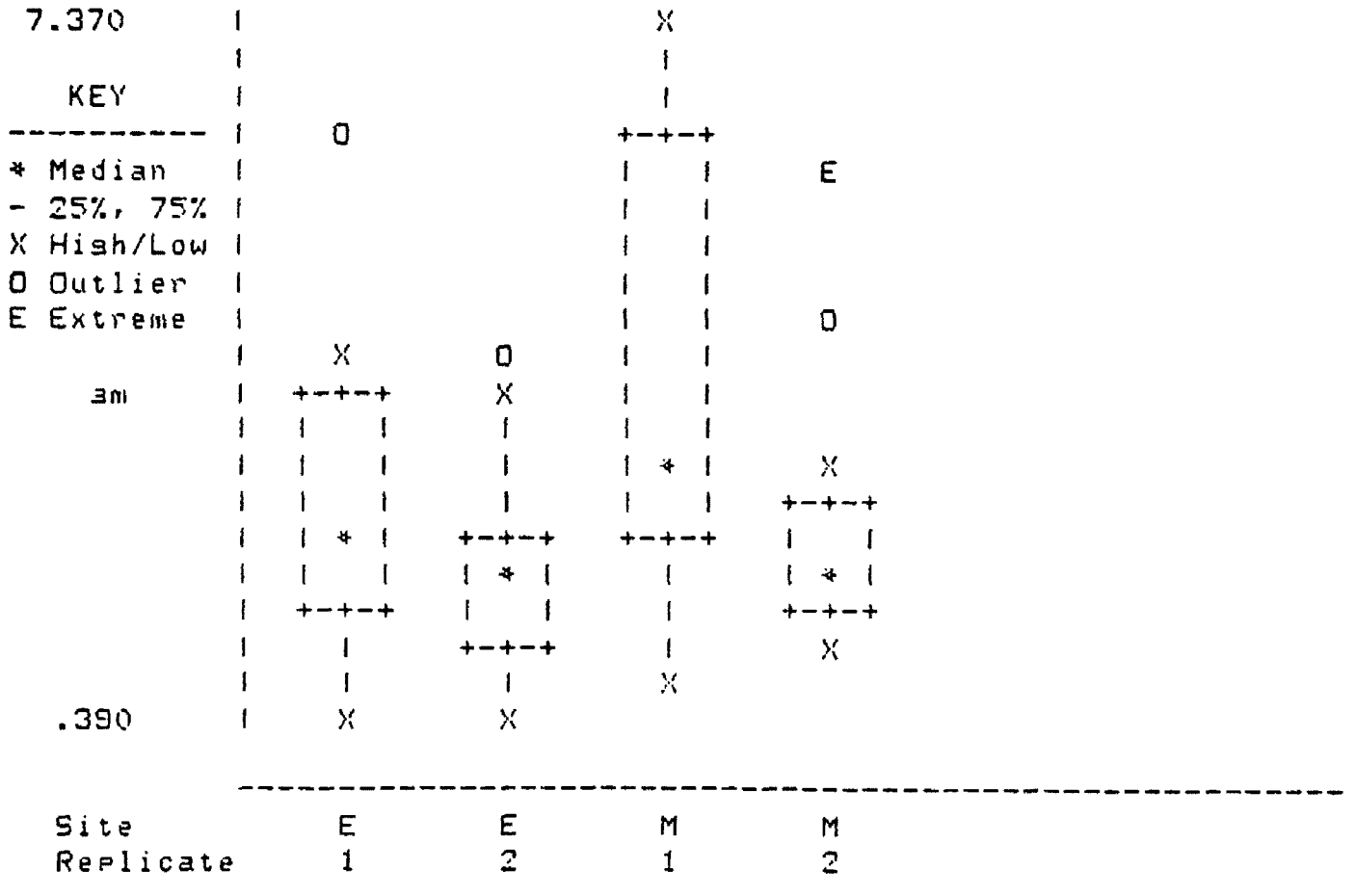


Figure B10. Boxplots for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Final Wet (Blotted) Weight by Collection Site and Replicate



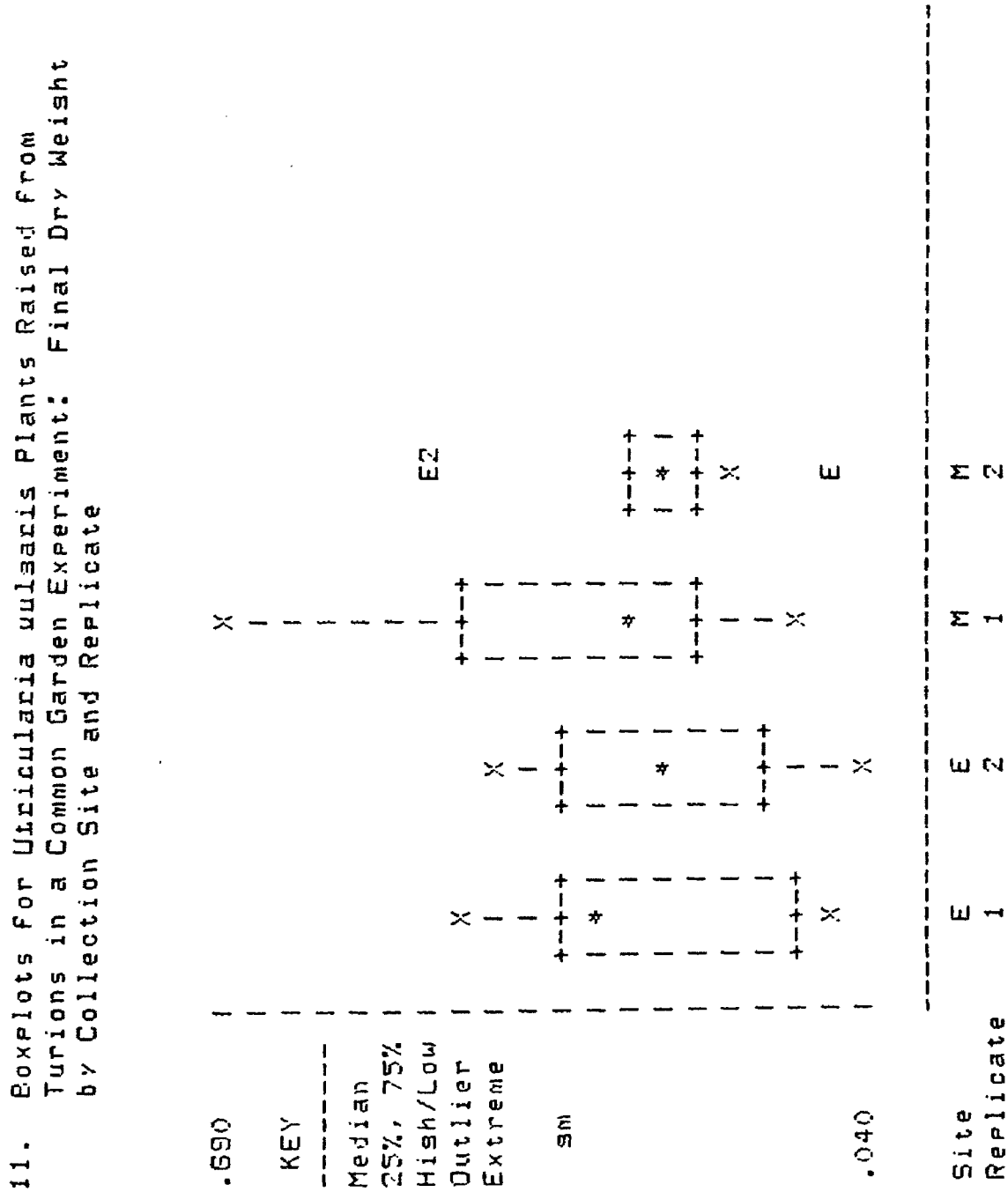
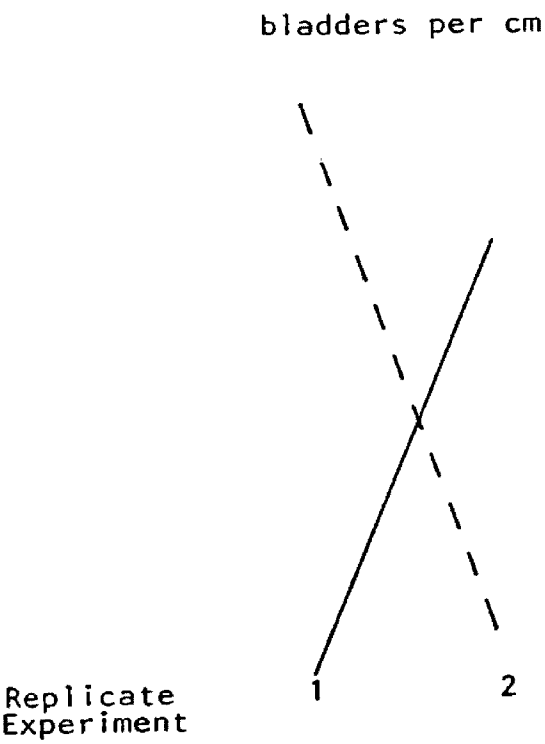


Figure B11. Boxplots for Utricularia vulgaris Plants Raised from Turions in a Common Garden Experiment: Final Dry Weight by Collection Site and Replicate

Figure B12. Profile Plot for the Interaction of Collection Site and Replicate Experiment on Bladders per cm for U. vulgaris Plants Raised from Turions in a Common Garden Experiment

Key:
East Bay — — —
McWenneger's Slough ———



Appendix C. Data Summaries, Complete MANOVA Results, Boxplots, and Profile Plots for *Utricularia vulgaris* Plants Raised from Turions in a Diet Experiment

Table C1. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Stem Diameter, Leaflet Length, and Plant Length by Treatment Tray

Treatment Tray	Stem Diameter in mm	Leaflet Length in cm	Total Length in cm
1			
Mean	.94	1.95	16.95
Std. Deviation	.11	.48	15.07
Minimum	.76	1.46	6.30
Maximum	1.13	2.99	64.90
Sample Size	13	11	13
2			
Mean	.85	2.13	16.33
Std. Deviation	.16	.42	4.35
Minimum	.53	1.56	9.30
Maximum	1.00	2.72	22.00
Sample Size	9	8	9
3			
Mean	.96	2.29	13.78
Std. Deviation	.06	.55	4.60
Minimum	.84	1.37	9.10
Maximum	1.05	2.96	20.60
Sample Size	8	6	8
4			
Mean	.92	2.42	16.13
Std. Deviation	.18	.35	9.95
Minimum	.60	1.91	5.20
Maximum	1.20	2.94	33.20
Sample Size	7	6	7
5			
Mean	.90	2.19	44.98
Std. Deviation	.12	.25	16.93
Minimum	.63	1.85	18.00
Maximum	1.00	2.51	68.70
Sample Size	9	9	9

Table C1. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Stem Diameter, Leaflet Length, and Plant Length by Treatment Tray (cont'd.)

Treatment Tray	Stem Diameter in mm	Leaflet Length in cm	Total Length in cm
6			
Mean	.84	1.93	21.60
Std. Deviation	.17	.44	9.65
Minimum	.53	1.10	10.20
Maximum	1.03	2.37	46.10
Sample Size	13	13	13
7			
Mean	.88	1.99	42.75
Std. Deviation	.19	.29	19.56
Minimum	.64	1.55	20.80
Maximum	1.24	2.40	71.40
Sample Size	10	10	10
8			
Mean	.81	2.00	32.22
Std. Deviation	.15	.22	12.00
Minimum	.60	1.71	16.10
Maximum	1.10	2.46	59.50
Sample Size	13	12	13
9			
Mean	.84	2.09	38.31
Std. Deviation	.13	.28	15.21
Minimum	.62	1.59	16.20
Maximum	1.02	2.40	63.60
Sample Size	12	12	12
10			
Mean	.71	1.87	37.43
Std. Deviation	.11	.36	19.70
Minimum	.53	1.44	16.00
Maximum	.84	2.41	68.60
Sample Size	9	9	9

Table C1. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Stem Diameter, Leaflet Length, and Plant Length by Treatment Tray (cont'd.)

Treatment Tray	Stem Diameter in mm	Leaflet Length in cm	Total Length in cm
11			
Mean	.82	1.87	35.92
Std. Deviation	.19	.26	24.03
Minimum	.54	1.26	15.00
Maximum	1.19	2.21	79.80
Sample Size	9	9	9
12			
Mean	.81	2.02	37.47
Std. Deviation	.09	.28	26.96
Minimum	.60	1.65	15.00
Maximum	.93	2.57	101.80
Sample Size	9	9	9
13			
Mean	.60	1.27	16.53
Std. Deviation	.14	.22	11.08
Minimum	.40	.98	5.90
Maximum	.70	1.48	31.90
Sample Size	4	4	4
14			
Mean	.33	1.08	9.97
Std. Deviation	.21	.19	5.03
Minimum	.10	.78	5.30
Maximum	.53	1.31	18.50
Sample Size	7	7	7
15			
Mean	.44	1.17	15.58
Std. Deviation	.08	.19	8.11
Minimum	.33	.86	5.00
Maximum	.56	1.35	25.70
Sample Size	6	6	6

Table C1. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Stem Diameter, Leaflet Length, and Plant Length by Treatment Tray (cont'd.)

Treatment Tray	Stem Diameter in mm	Leaflet Length in cm	Total Length in cm
16			
Mean	.41	1.51	22.70
Std. Deviation	.22	.37	11.15
Minimum	.13	1.05	12.30
Maximum	.70	2.17	48.90
Sample Size	10	10	10
17			
Mean	.42	1.42	18.10
Std. Deviation	.20	.19	11.16
Minimum	.10	1.19	7.90
Maximum	.67	1.64	38.50
Sample Size	7	7	7
18			
Mean	.48	1.13	9.44
Std. Deviation	.24	.21	4.19
Minimum	.10	.82	4.20
Maximum	.80	1.42	16.30
Sample Size	8	8	8
19			
Mean	.95	1.87	19.28
Std. Deviation	.22	.46	9.20
Minimum	.80	1.15	7.40
Maximum	1.40	2.60	33.80
Sample Size	8	8	8
20			
Mean	.89	1.98	20.43
Std. Deviation	.13	.31	6.75
Minimum	.70	1.45	11.50
Maximum	1.13	2.44	33.50
Sample Size	11	11	11

Table C1. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Stem Diameter, Leaflet Length, and Plant Length by Treatment Tray (cont'd.)

Treatment Tray	Stem Diameter in mm	Leaflet Length in cm	Total Length in cm
21			
Mean	.84	1.94	24.74
Std. Deviation	.18	.23	7.52
Minimum	.63	1.63	15.00
Maximum	1.17	2.26	36.00
Sample Size	11	11	11
22			
Mean	1.05	1.94	35.21
Std. Deviation	.21	.19	15.37
Minimum	.80	1.65	17.40
Maximum	1.33	2.35	68.30
Sample Size	12	12	12
23			
Mean	.93	1.94	33.33
Std. Deviation	.21	.38	19.69
Minimum	.68	1.30	14.80
Maximum	1.33	2.57	78.70
Sample Size	12	12	12
24			
Mean	.85	1.72	25.78
Std. Deviation	.20	.28	10.49
Minimum	.57	1.34	15.32
Maximum	1.30	2.40	53.40
Sample Size	12	12	12

Table C2. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Leaflet Pairs per Plant, Leaflet Pairs per cm, and Bladders/Positions per Leaflet by Treatment Tray

Treatment Tray	Leaflet Pairs per Plant	Leaflet Pairs per cm	Bladders/ Positions per Leaflet
1			
Mean	50.15	3.25	11.92
Std. Deviation	33.12	.81	.95
Minimum	21	2.22	11
Maximum	150	5.20	13
Sample Size	13	13	12
2			
Mean	47.78	2.97	11.28
Std. Deviation	12.44	.42	1.17
Minimum	30	2.31	10
Maximum	63	3.56	13
Sample Size	9	9	9
3			
Mean	63.25	4.52	10.08
Std. Deviation	24.64	.51	2.69
Minimum	36	3.96	8
Maximum	97	5.24	16
Sample Size	8	8	8
4			
Mean	67.43	4.68	11.10
Std. Deviation	30.67	1.41	1.65
Minimum	35	3.58	9
Maximum	119	7.50	14
Sample Size	7	7	7
5			
Mean	110.00	2.61	11.84
Std. Deviation	27.01	.59	1.09
Minimum	65	2.11	10
Maximum	148	3.61	14
Sample Size	9	9	9

Table C2. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Leaflet Pairs per Plant, Leaflet Pairs per cm, and Bladders/Positions per Leaflet by Treatment Tray (cont'd.)

Treatment Tray	Leaflet Pairs per Plant	Leaflet Pairs per cm	Bladders/ Positions per Leaflet
6			
Mean	79.31	3.74	9.41
Std. Deviation	33.86	.60	1.23
Minimum	46	2.93	8
Maximum	165	4.80	12
Sample Size	13	13	13
7			
Mean	121.70	2.87	11.24
Std. Deviation	54.33	.28	1.18
Minimum	55	2.49	10
Maximum	198	3.26	13
Sample Size	10	10	10
8			
Mean	94.46	2.91	10.44
Std. Deviation	37.97	.45	1.11
Minimum	43	2.26	8
Maximum	165	3.72	12
Sample Size	13	13	13
9			
Mean	105.92	2.83	11.41
Std. Deviation	38.50	.28	1.00
Minimum	52	2.32	9
Maximum	179	3.29	13
Sample Size	12	12	12
10			
Mean	121.78	3.44	9.94
Std. Deviation	53.01	.56	1.46
Minimum	69	2.65	7
Maximum	205	4.50	12
Sample Size	9	9	9

Table C2. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Leaflet Pairs per Plant, Leaflet Pairs per cm, and Bladders/Positions per Leaflet by Treatment Tray (cont'd.)

Treatment Tray	Leaflet Pairs per Plant	Leaflet Pairs per cm	Bladders/ Positions per Leaflet
11			
Mean	112.89	3.35	10.07
Std. Deviation	62.32	.48	1.04
Minimum	56	2.77	9
Maximum	229	4.13	11
Sample Size	9	9	9
12			
Mean	115.89	3.21	11.46
Std. Deviation	77.49	.51	.91
Minimum	43	2.51	10
Maximum	302	4.21	13
Sample Size	9	9	9
13			
Mean	58.00	4.21	8.90
Std. Deviation	18.17	1.44	1.39
Minimum	35	2.48	8
Maximum	79	5.93	10
Sample Size	4	4	4
14			
Mean	47.14	5.30	9.47
Std. Deviation	12.32	1.55	1.07
Minimum	27	2.81	7
Maximum	65	7.64	10
Sample Size	7	7	7
15			
Mean	86.67	5.98	9.40
Std. Deviation	37.45	1.09	.87
Minimum	36	4.76	8
Maximum	142	7.47	10
Sample Size	6	6	6

Table C2. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Leaflet Pairs per Plant, Leaflet Pairs per cm, and Bladders/Positions per Leaflet by Treatment Tray (cont'd.)

Treatment Tray	Leaflet Pairs per Plant	Leaflet Pairs per cm	Bladders/ Positions per Leaflet
16			
Mean	95.90	4.29	9.71
Std. Deviation	45.89	.59	1.33
Minimum	51	3.49	8
Maximum	206	5.46	11
Sample Size	10	10	10
17			
Mean	83.29	4.74	9.72
Std. Deviation	47.06	.63	.67
Minimum	40	3.96	9
Maximum	165	5.95	11
Sample Size	7	7	7
18			
Mean	47.50	5.20	9.66
Std. Deviation	18.59	1.07	.50
Minimum	18	3.99	9
Maximum	79	6.84	10
Sample Size	8	8	8
19			
Mean	60.63	3.33	12.37
Std. Deviation	24.57	.73	1.40
Minimum	33	2.23	10
Maximum	92	4.46	14
Sample Size	8	8	8
20			
Mean	63.91	3.19	11.31
Std. Deviation	18.64	.43	1.57
Minimum	42	2.56	9
Maximum	95	3.98	13
Sample Size	11	11	11

Table C2. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Leaflet Pairs per Plant, Leaflet Pairs per cm, and Bladders/Positions per Leaflet by Treatment Tray (cont'd.)

Treatment Tray	Leaflet Pairs per Plant	Leaflet Pairs per cm	Bladders/ Positions per Leaflet
21			
Mean	75.64	3.15	11.80
Std. Deviation	16.92	.42	1.20
Minimum	48	2.43	10
Maximum	105	3.67	14
Sample Size	11	11	11
22			
Mean	90.75	2.68	12.34
Std. Deviation	30.41	.38	.84
Minimum	50	2.08	11
Maximum	142	3.40	14
Sample Size	12	12	12
23			
Mean	96.17	3.12	11.68
Std. Deviation	44.38	.77	1.43
Minimum	62	2.45	10
Maximum	202	5.14	14
Sample Size	12	12	12
24			
Mean	78.75	3.24	10.84
Std. Deviation	24.02	1.07	.82
Minimum	50	2.11	9
Maximum	133	6.40	13
Sample Size	12	12	12

Table C3. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Bladders/Positions per Plant and Bladders/Positions per cm by Treatment Tray

Treatment Tray	Total Bladders/ Positions per Plant	Bladders/ Positions per cm
1		
Mean	1202.72	73.66
Std. Deviation	928.90	15.62
Minimum	490	50.37
Maximum	3900	99.46
Sample Size	12	12
2		
Mean	1084.12	67.28
Std. Deviation	333.16	13.59
Minimum	694	44.92
Maximum	1571	88.75
Sample Size	9	9
3		
Mean	1329.50	91.51
Std. Deviation	755.11	27.92
Minimum	603	62.40
Maximum	2703	148.51
Sample Size	8	8
4		
Mean	1543.34	103.24
Std. Deviation	875.29	30.39
Minimum	649	69.01
Maximum	3284	151.00
Sample Size	7	7
5		
Mean	2633.87	61.01
Std. Deviation	761.69	9.89
Minimum	1248	50.79
Maximum	3651	78.14
Sample Size	9	9

Table C3. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Bladders/Positions per Plant and Bladders/Positions per cm by Treatment Tray (cont'd.)

Treatment Tray	Total Bladders/ Positions per Plant	Bladders/ Positions per cm
6		
Mean	1456.91	70.86
Std. Deviation	518.19	17.14
Minimum	724	46.10
Maximum	2684	113.37
Sample Size	13	13
7		
Mean	2752.99	64.33
Std. Deviation	1309.98	6.73
Minimum	1357	49.79
Maximum	4794	75.49
Sample Size	10	10
8		
Mean	1984.12	60.59
Std. Deviation	847.03	10.20
Minimum	936	40.70
Maximum	3454	74.99
Sample Size	13	13
9		
Mean	2365.81	64.78
Std. Deviation	726.63	10.34
Minimum	1241	49.46
Maximum	3723	80.38
Sample Size	12	12
10		
Mean	2489.82	68.50
Std. Deviation	1279.76	14.80
Minimum	990	40.57
Maximum	4647	89.40
Sample Size	9	9

Table C3. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Bladders/Positions per Plant and Bladders/Positions per cm by Treatment Tray (cont'd.)

Treatment Tray	Total Bladders/ Positions per Plant	Bladders/ Positions per cm
11		
Mean	2241.75	67.63
Std. Deviation	1201.81	12.15
Minimum	1262	47.62
Maximum	4672	84.12
Sample Size	9	9
12		
Mean	2655.17	73.45
Std. Deviation	1815.74	11.48
Minimum	1124	55.27
Maximum	6926	91.44
Sample Size	9	9
13		
Mean	1030.63	74.92
Std. Deviation	393.74	30.88
Minimum	705	50.19
Maximum	1601	119.44
Sample Size	4	4
14		
Mean	903.39	98.14
Std. Deviation	300.99	20.71
Minimum	511	56.22
Maximum	1361	116.50
Sample Size	7	7
15		
Mean	1623.13	113.08
Std. Deviation	744.54	26.90
Minimum	710	83.06
Maximum	2878	147.34
Sample Size	6	6

Table C3. Data Summaries for Utricularia vulgaris Plants raised from Turions in a Diet Experiment: Bladders/Positions per Plant and Bladders/Positions per cm by Treatment Tray (cont'd.)

Treatment Tray	Total Bladders/ Positions per Plant	Bladders/ Positions per cm
16		
Mean	1900.21	82.34
Std. Deviation	1065.90	7.24
Minimum	1081	70.00
Maximum	4477	91.56
Sample Size	10	10
17		
Mean	1659.66	92.26
Std. Deviation	1015.78	14.33
Minimum	688	68.12
Maximum	3410	115.81
Sample Size	7	7
18		
Mean	919.03	100.24
Std. Deviation	379.38	20.41
Minimum	372	79.22
Maximum	1580	135.02
Sample Size	8	8
19		
Mean	1507.52	83.32
Std. Deviation	661.33	24.22
Minimum	733	46.67
Maximum	2333	118.92
Sample Size	8	8
20		
Mean	1428.45	72.47
Std. Deviation	418.22	16.36
Minimum	877	52.21
Maximum	2352	95.42
Sample Size	11	11

Table C3. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Bladders/Positions per Plant and Bladders/Positions per cm by Treatment Tray (cont'd.)

Treatment Tray	Total Bladders/ Positions per Plant	Bladders/ Positions per cm
21		
Mean	1788.75	74.00
Std. Deviation	457.69	10.07
Minimum	1107	49.96
Maximum	2559	86.22
Sample Size	11	11
22		
Mean	2214.69	66.55
Std. Deviation	679.81	12.62
Minimum	1336	48.79
Maximum	3332	90.76
Sample Size	12	12
23		
Mean	2210.07	73.04
Std. Deviation	982.60	20.29
Minimum	1471	50.34
Maximum	4848	124.61
Sample Size	12	12
24		
Mean	1713.86	71.09
Std. Deviation	575.32	29.25
Minimum	1100	46.41
Maximum	3050	160.35
Sample Size	12	12

Table C4. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Bladders/Positions per sm by Treatment Tray

Treatment Tray	Bladders/ Positions per sm
1	7478.05
2	6294.89
3	4748.21
4	3662.16
5	7140.01
6	7575.93
7	9493.07
8	9733.42
9	10103.10
10	9700.60
11	12933.17
12	11433.75
13	11778.63
14	31618.65
15	30433.69
16	33932.32
17	29788.77
18	33419.27
19	10963.78
20	10008.25
21	11642.75
22	8227.95
23	9404.55
24	9222.57

Table C5. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Final Wet (Blotted) and Dry Weights by Treatment Tray

Treatment Tray	Blotted Weight in gm	Final Dry Weight in gm
1	34.66	1.93
2	27.20	1.55
3	38.50	2.24
4	47.97	2.95
5	56.92	3.32
6	32.12	2.50
7	54.23	2.90
8	44.05	2.65
9	43.48	2.81
10	34.27	2.31
11	30.43	1.56
12	30.56	2.09
13	4.22	.35
14	3.99	.20
15	4.65	.32
16	10.61	.56
17	6.36	.39
18	3.58	.22
19	22.45	1.10
20	24.97	1.57
21	27.16	1.69

Table C5. Data Summaries for Utricularia vulgaris Plants Raised from Turions in a Diet Experiment: Final Wet (Blotted) and Dry Weights by Treatment Tray (cont'd.)

Treatment Tray	Blotted Weight in gm	Final Dry Weight in gm
22	49.09	3.23
23	40.69	2.82
24	32.38	2.23

Table C6. Parametric MANOVA Showing the Effect of Collection Site on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 45 1/2)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.69453	52.86262	4.00	93.00	.000
Hotellings	2.27366	52.86262	4.00	93.00	.000
Wilks	.30547	52.86262	4.00	93.00	.000
Roys	.69453				

Note.. F statistics are exact.

Univariate F-tests with (1,96) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	9.84522	8.11073	9.84522	.08449	116.52973	.000
Bladders per leaflet	122.43504	127.22390	122.43504	1.32525	92.38645	.000
Leaflet pairs per cm	81.74156	68.37827	81.74156	.71227	114.76145	.000
Bladders per cm	9783.93945	37163.1876	9783.93945	387.11654	25.27389	.000

Table C7. Parametric MANOVA Showing the Effect of Feeding Regime on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 45 1/2)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.15102	1.91941	8.00	188.00	.059
Hotellings	.17254	1.98422	8.00	184.00	.051
Wilks	.85107	1.95233	8.00	186.00	.055
Roys	.13563				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,96) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.43814	8.11073	.21907	.08449	2.59294	.080
Bladders per leaflet	2.66452	127.22390	1.33226	1.32525	1.00529	.370
Leaflet pairs per cm	9.11411	68.37827	4.55705	.71227	6.39790	.002
Bladders per cm	2569.02405	37163.1876	1284.51203	387.11654	3.31815	.040

Table C8. Parametric MANOVA Showing the Effect of Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 45 1/2)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.04032	.97682	4.00	93.00	.424
Hotellings	.04201	.97682	4.00	93.00	.424
Wilks	.95968	.97682	4.00	93.00	.424
Roys	.04032				

Note.. F statistics are exact.

Univariate F-tests with (1,96) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.07844	8.11073	.07844	.08449	.92846	.338
Bladders per leaflet	.34901	127.22390	.34901	1.32525	.26335	.609
Leaflet pairs per cm	2.35922	68.37827	2.35922	.71227	3.31224	.072
Bladders per cm	622.20186	37163.1876	622.20186	387.11654	1.60727	.208

Table C9. Parametric MANOVA Showing the Effect of the Interaction between Collection Site and Feeding Regime on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 45 1/2)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.22363	2.95844	8.00	188.00	.004
Hotellings	.27581	3.17181	8.00	184.00	.002
Wilks	.78054	3.06626	8.00	186.00	.003
Roys	.20308				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,96) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.16758	8.11073	.08379	.08449	.99174	.375
Bladdders per leaflet	7.37643	127.22390	3.68822	1.32525	2.78304	.067
Leaflet pairs per cm	5.13419	68.37827	2.56709	.71227	3.60408	.031
Bladders per cm	3641.31997	37163.1876	1820.65999	387.11654	4.70313	.011

Table C10. Parametric MANOVA Showing the Effect of the Interaction between Collection Site and Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on U. vulgaris Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 45 1/2)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.07830	1.97507	4.00	93.00	.105
Hotellings	.08495	1.97507	4.00	93.00	.105
Wilks	.92170	1.97507	4.00	93.00	.105
Roys	.07830				

Note.. F statistics are exact.

Univariate F-tests with (1,96) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.36948	8.11073	.36948	.08449	4.37323	.039
Bladders per leaflet	2.53029	127.22390	2.53029	1.32525	1.90930	.170
Leaflet pairs per cm	.27918	68.37827	.27918	.71227	.39195	.533
Bladders per cm	40.92115	37163.1876	40.92115	387.11654	.10571	.746

Table C11. Parametric MANOVA Showing the Effect of the Interaction between Feeding Regime and Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 45 1/2)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.10310	1.27722	8.00	188.00	.258
Hotellings	.10984	1.26313	8.00	184.00	.265
Wilks	.89908	1.27025	8.00	186.00	.261
Roys	.07358				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,96) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.43536	8.11073	.21768	.08449	2.57648	.081
Bladders per leaflet	2.74730	127.22390	1.37365	1.32525	1.03652	.359
Leaflet pairs per cm	.01300	68.37827	.00650	.71227	.00912	.991
Bladders per cm	119.60925	37163.1876	59.80462	387.11654	.15449	.857

Table C12. Parametric MANOVA Showing the Effect of the Interaction Between Collection Site, Feeding Regime and Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 45 1/2)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.14561	1.84523	8.00	188.00	.071
Hotellings	.16058	1.84666	8.00	184.00	.071
Wilks	.85828	1.84616	8.00	186.00	.071
Roys	.11032				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,96) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.05485	8.11073	.02742	.08449	.32460	.724
Bladders per leaflet	2.00293	127.22390	1.00146	1.32525	.75568	.472
Leaflet pairs per cm	2.68215	68.37827	1.34107	.71227	1.88281	.158
Bladders per cm	1339.87725	37163.1876	669.93863	387.11654	1.73059	.183

Table C13. Nonparametric MANOVA Showing the Effect of Collection Site on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on U. vulgaris Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 45 1/2)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.75198	70.49206	4.00	93.00	.000
Hotellings	3.03192	70.49206	4.00	93.00	.000
Wilks	.24802	70.49206	4.00	93.00	.000
Roys	.75198				

Note.. F statistics are exact.

Univariate F-tests with (1,96) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	179022.505	192209.602	179022.505	2002.18335	89.41364	.000
Bladders per leaflet	239102.834	225969.458	239102.834	2353.84852	101.57953	.000
Leaflet pairs per cm	244427.693	222530.110	244427.693	2318.02197	105.44667	.000
Bladders per cm	89042.8961	307909.663	89042.8961	3207.39232	27.76177	.000

Table C14. Nonparametric MANOVA Showing the Effect of Feeding Regime on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 45 1/2)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.31461	4.38665	8.00	188.00	.000
Hotellings	.43206	4.96874	8.00	184.00	.000
Wilks	.69299	4.67928	8.00	186.00	.000
Roys	.28826				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,96) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	7059.05797	192209.602	3529.52898	2002.18335	1.76284	.177
Bladders per leaflet	10031.0184	225969.458	5015.50918	2353.84852	2.13077	.124
Leaflet pairs per cm	14445.0650	222530.110	7222.53251	2318.02197	3.11582	.049
Bladders per cm	15386.6635	307909.663	7693.33174	3207.39232	2.39863	.096

Table C15. Nonparametric MANOVA Showing the Effect of Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on U. vulgaris Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 45 1/2)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.01556	.36748	4.00	93.00	.831
Hotellings	.01581	.36748	4.00	93.00	.831
Wilks	.98444	.36748	4.00	93.00	.831
Roys	.01556				

Note.. F statistics are exact.

Univariate F-tests with (1,96) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	388.42241	192209.602	388.42241	2002.18335	.19400	.661
Bladders per leaflet	279.52708	225969.458	279.52708	2353.84852	.11875	.731
Leaflet pairs per cm	2748.26919	222530.110	2748.26919	2318.02197	1.18561	.279
Bladders per cm	1285.48577	307909.663	1285.48577	3207.39232	.40079	.528

Table C16. Nonparametric MANOVA Showing the Effect of the Interaction between Collection Site and Feeding Regime on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 45 1/2)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.24095	3.21904	8.00	188.00	.002
Hotellings	.29838	3.43140	8.00	184.00	.001
Wilks	.76534	3.32637	8.00	186.00	.001
Roys	.21114				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,96) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	2784.97734	192209.602	1392.48867	2002.18335	.69549	.501
Bladders per leaflet	8110.11958	225969.458	4055.05979	2353.84852	1.72274	.184
Leaflet pairs per cm	3642.39374	222530.110	1821.19687	2318.02197	.78567	.459
Bladders per cm	24267.0100	307909.663	12133.5050	3207.39232	3.78298	.026

Table C17. Nonparametric MANOVA Showing the Effect of the Interaction between Collection Site and Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 45 1/2)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.07869	1.98589	4.00	93.00	.103
Hotellings	.08541	1.98589	4.00	93.00	.103
Wilks	.92131	1.98589	4.00	93.00	.103
Roys	.07869				

Note.. F statistics are exact.

Univariate F-tests with (1,96) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	5432.58571	192209.602	5432.58571	2002.18335	2.71333	.103
Bladders per leaflet	2489.44405	225969.458	2489.44405	2353.84852	1.05761	.306
Leaflet pairs per cm	7448.16851	222530.110	7448.16851	2318.02197	3.21316	.076
Bladders per cm	13277.7308	307909.663	13277.7308	3207.39232	4.13973	.045

Table C18. Nonparametric MANOVA Showing the Effect of the Interaction between Feeding Regime and Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 45 1/2)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.07532	.91969	8.00	188.00	.501
Hotellings	.08018	.92205	8.00	184.00	.499
Wilks	.92525	.92098	8.00	186.00	.500
Roys	.06680				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,96) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	7677.92023	192209.602	3838.96011	2002.18335	1.91739	.153
Bladders per leaflet	5883.91229	225969.458	2941.95615	2353.84852	1.24985	.291
Leaflet pairs per cm	360.13726	222530.110	180.06863	2318.02197	.07768	.925
Bladders per cm	3587.10261	307909.663	1793.55131	3207.39232	.55919	.574

Table C19. Nonparametric MANOVA Showing the Effect of the Interaction between Collection Site, Feeding Regime and Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 45 1/2)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.12818	1.60924	8.00	188.00	.125
Hotellings	.13731	1.57910	8.00	184.00	.134
Wilks	.87578	1.59419	8.00	186.00	.129
Roys	.07618				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,96) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	245.00191	192209.602	122.50095	2002.18335	.06118	.941
Bladders per leaflet	3527.65355	225969.458	1763.82678	2353.84852	.74934	.475
Leaflet pairs per cm	10085.5912	222530.110	5042.79560	2318.02197	2.17547	.119
Bladders per cm	13400.7155	307909.663	6700.35775	3207.39232	2.08904	.129

Table C20. Parametric MANOVA Showing the Effect of Experimental Season on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on U. vulgaris Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 55)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.35279	15.26282	4.00	112.00	.000
Hotellings	.54510	15.26282	4.00	112.00	.000
Wilks	.64721	15.26282	4.00	112.00	.000
Roys	.35279				

Note.. F statistics are exact.

Univariate F-tests with (1,115) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.17458	10.20612	.17458	.08875	1.96712	.163
Bladders per leaflet	26.95324	154.90420	26.95324	1.34699	20.00994	.000
Leaflet pairs per cm	.01255	38.54306	.01255	.33516	.03745	.847
Bladders per cm	1418.87705	30241.2424	1418.87705	262.96732	5.39564	.022

Table C21. Parametric MANOVA Showing the Effect of Feeding Regime on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 55)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.08989	1.32940	8.00	226.00	.230
Hotellings	.09516	1.32034	8.00	222.00	.234
Wilks	.91168	1.32493	8.00	224.00	.232
Roys	.06625				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,115) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.36554	10.20612	.18277	.08875	2.05940	.132
Bladders per leaflet	5.98287	154.90420	2.99143	1.34699	2.22082	.113
Leaflet pairs per cm	.29319	38.54306	.14659	.33516	.43739	.647
Bladders per cm	52.50844	30241.2424	26.25422	262.96732	.09984	.905

Table C22. Parametric MANOVA Showing the Effect of Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 55)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.10006	3.11331	4.00	112.00	.018
Hotellings	.11119	3.11331	4.00	112.00	.018
Wilks	.89994	3.11331	4.00	112.00	.018
Roys	.10006				

Note.. F statistics are exact.

Univariate F-tests with (1,115) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.22862	10.20612	.22862	.08875	2.57605	.111
Bladders per leaflet	5.06025	154.90420	5.06025	1.34699	3.75670	.055
Leaflet pairs per cm	.56287	38.54306	.56287	.33516	1.67941	.198
Bladders per cm	.01279	30241.2424	.01279	262.96732	.00005	.994

Table C23. Parametric MANOVA Showing the Effect of the Interaction between Experimental Season and Feeding Regime on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on U. vulgaris Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 55)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.20738	3.26819	8.00	226.00	.002
Hotellings	.25925	3.59703	8.00	222.00	.001
Wilks	.79346	3.43375	8.00	224.00	.001
Roys	.20324				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,115) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.03062	10.20612	.01531	.08875	.17252	.842
Bladders per leaflet	19.92624	154.90420	9.96312	1.34699	7.39656	.001
Leaflet pairs per cm	.31622	38.54306	.15811	.33516	.47174	.625
Bladders per cm	246.99472	30241.2424	123.49736	262.96732	.46963	.626

Table C24. Parametric MANOVA Showing the Effect of the Interaction between Experimental Season and Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on U. vulgaris Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 55)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.14350	4.69106	4.00	112.00	.002
Hotellings	.16754	4.69106	4.00	112.00	.002
Wilks	.85650	4.69106	4.00	112.00	.002
Roys	.14350				

Note.. F statistics are exact.

Univariate F-tests with (1,115) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.01142	10.20612	.01142	.08875	.12871	.720
Bladders per leaflet	1.24745	154.90420	1.24745	1.34699	.92610	.338
Leaflet pairs per cm	3.57797	38.54306	3.57797	.33516	10.67549	.001
Bladders per cm	1268.27533	30241.2424	1268.27533	262.96732	4.82294	.030

Table C25. Parametric MANOVA Showing the Effect of the Interaction between Feeding Regime and Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on U. vulgaris Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 55)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.13441	2.03525	8.00	226.00	.043
Hotellings	.14615	2.02787	8.00	222.00	.044
Wilks	.86927	2.03169	8.00	224.00	.044
Roys	.09613				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,115) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.10566	10.20612	.05283	.08875	.59525	.553
Bladders per leaflet	9.65718	154.90420	4.82859	1.34699	3.58472	.031
Leaflet pairs per cm	.89854	38.54306	.44927	.33516	1.34047	.266
Bladders per cm	503.60465	30241.2424	251.80233	262.96732	.95754	.387

Table C26. Parametric MANOVA Showing the Effect of the Interaction between Experimental Season, Feeding Regime and Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on U. vulgaris Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 55)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.05641	.81998	8.00	226.00	.586
Hotellings	.05878	.81553	8.00	222.00	.590
Wilks	.94405	.81780	8.00	224.00	.588
Roys	.04645				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,115) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	.11058	10.20612	.05529	.08875	.62298	.538
Bladders per leaflet	.07824	154.90420	.03912	1.34699	.02904	.971
Leaflet pairs per cm	.74206	38.54306	.37103	.33516	1.10704	.334
Bladders per cm	409.65818	30241.2424	204.82909	262.96732	.77891	.461

Table C27. Nonparametric MANOVA Showing the Effect of Experimental Season on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 55)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.31262	12.73419	4.00	112.00	.000
Hotellings	.45479	12.73419	4.00	112.00	.000
Wilks	.68738	12.73419	4.00	112.00	.000
Roys	.31262				

Note.. F statistics are exact.

Univariate F-tests with (1,115) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	5821.10819	294778.841	5821.10819	2563.29427	2.27095	.135
Bladders per leaflet	47735.3177	304693.706	47735.3177	2649.51049	18.01666	.000
Leaflet pairs per cm	115.90920	264484.102	115.90920	2299.86175	.05040	.823
Bladders per cm	12468.0631	367512.367	12468.0631	3195.75971	3.90144	.051

Table C28. Nonparametric MANOVA Showing the Effect of Feeding Regime on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 55)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.09404	1.39382	8.00	226.00	.200
Hotellings	.09932	1.37806	8.00	222.00	.207
Wilks	.90790	1.38598	8.00	224.00	.204
Roys	.06368				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,115) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	10961.8949	294778.841	5480.94747	2563.29427	2.13824	.123
Bladders per leaflet	10421.8334	304693.706	5210.91671	2649.51049	1.96675	.145
Leaflet pairs per cm	1623.41851	264484.102	811.70925	2299.86175	.35294	.703
Bladders per cm	1835.92632	367512.367	917.96316	3195.75971	.28724	.751

Table C29. Nonparametric MANOVA Showing the Effect of Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on U. vulgaris Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 55)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.04361	1.27678	4.00	112.00	.283
Hotellings	.04560	1.27678	4.00	112.00	.283
Wilks	.95639	1.27678	4.00	112.00	.283
Roys	.04361				

Note.. F statistics are exact.

Univariate F-tests with (1,115) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	6436.48054	294778.841	6436.48054	2563.29427	2.51102	.116
Bladders per leaflet	8834.16705	304693.706	8834.16705	2649.51049	3.33426	.070
Leaflet pairs per cm	2567.24625	264484.102	2567.24625	2299.86175	1.11626	.293
Bladders per cm	1.10440	367512.367	1.10440	3195.75971	.00035	.985

Table C30. Nonparametric MANOVA Showing the Effect of the Interaction between Experimental Season and Feeding Regime on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 55)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.23314	3.72764	8.00	226.00	.000
Hotellings	.29999	4.16234	8.00	222.00	.000
Wilks	.76820	3.94624	8.00	224.00	.000
Roys	.22723				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,115) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	584.69410	294778.841	292.34705	2563.29427	.11405	.892
Bladders per leaflet	43988.6505	304693.706	21994.3253	2649.51049	8.30128	.000
Leaflet pairs per cm	2866.71450	264484.102	1433.35725	2299.86175	.62324	.538
Bladders per cm	3082.24890	367512.367	1541.12445	3195.75971	.48224	.619

Table C31. Nonparametric MANOVA Showing the Effect of the Interaction between Experimental Season and Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on U. vulgaris Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 1, M = 1 , N = 55)

Test Name	Value	Exact F	Hypoth. DF	Error DF	Sig. of F
Pillais	.21243	7.55257	4.00	112.00	.000
Hotellings	.26973	7.55257	4.00	112.00	.000
Wilks	.78757	7.55257	4.00	112.00	.000
Roys	.21243				

Note.. F statistics are exact.

Univariate F-tests with (1,115) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	363.46444	294778.841	363.46444	2563.29427	.14180	.707
Bladders per leaflet	3182.39779	304693.706	3182.39779	2649.51049	1.20113	.275
Leaflet pairs per cm	43182.1906	264484.102	43182.1906	2299.86175	18.77599	.000
Bladders per cm	28927.1869	367512.367	28927.1869	3195.75971	9.05174	.003

Table C32. Nonparametric MANOVA Showing the Effect of the Interaction between Feeding Regime and Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 55)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.11367	1.70238	8.00	226.00	.099
Hotellings	.12465	1.72947	8.00	222.00	.093
Wilks	.88783	1.71617	8.00	224.00	.096
Roys	.09839				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,115) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	3424.44731	294778.841	1712.22365	2563.29427	.66798	.515
Bladders per leaflet	17083.2980	304693.706	8541.64901	2649.51049	3.22386	.043
Leaflet pairs per cm	5601.38492	264484.102	2800.69246	2299.86175	1.21777	.300
Bladders per cm	5897.76143	367512.367	2948.88071	3195.75971	.92275	.400

Table C33. Nonparametric MANOVA Showing the Effect of the Interaction between Experimental Season, Feeding Regime and Nutrient Solution Strength on Four Variables (Leaflet Length, Bladders/Positions per Leaflet, Leaflet Pairs per cm, Bladders/Positions per cm) Measured on *U. vulgaris* Plants Raised from Turions in a Diet Experiment

Multivariate Tests of Significance (S = 2, M = 1/2, N = 55)

Test Name	Value	Approx. F	Hypoth. DF	Error DF	Sig. of F
Pillais	.05602	.81406	8.00	226.00	.591
Hotellings	.05782	.80232	8.00	222.00	.601
Wilks	.94468	.80820	8.00	224.00	.596
Roys	.03739				

Note.. F statistic for WILK'S Lambda is exact.

Univariate F-tests with (2,115) D. F.

Variable	Hypoth. SS	Error SS	Hypoth. MS	Error MS	F	Sig. of F
Leaflet length	3142.54624	294778.841	1571.27312	2563.29427	.61299	.543
Bladders per leaflet	790.58724	304693.706	395.29362	2649.51049	.14919	.862
Leaflet pairs per cm	3994.40196	264484.102	1997.20098	2299.86175	.86840	.422
Bladders per cm	2079.30169	367512.367	1039.65084	3195.75971	.32532	.723

Figure C1. Boxplots for U. vulgaris Plants Raised from Turions in a Diet Experiment: Stem Diameter by Treatment Tray

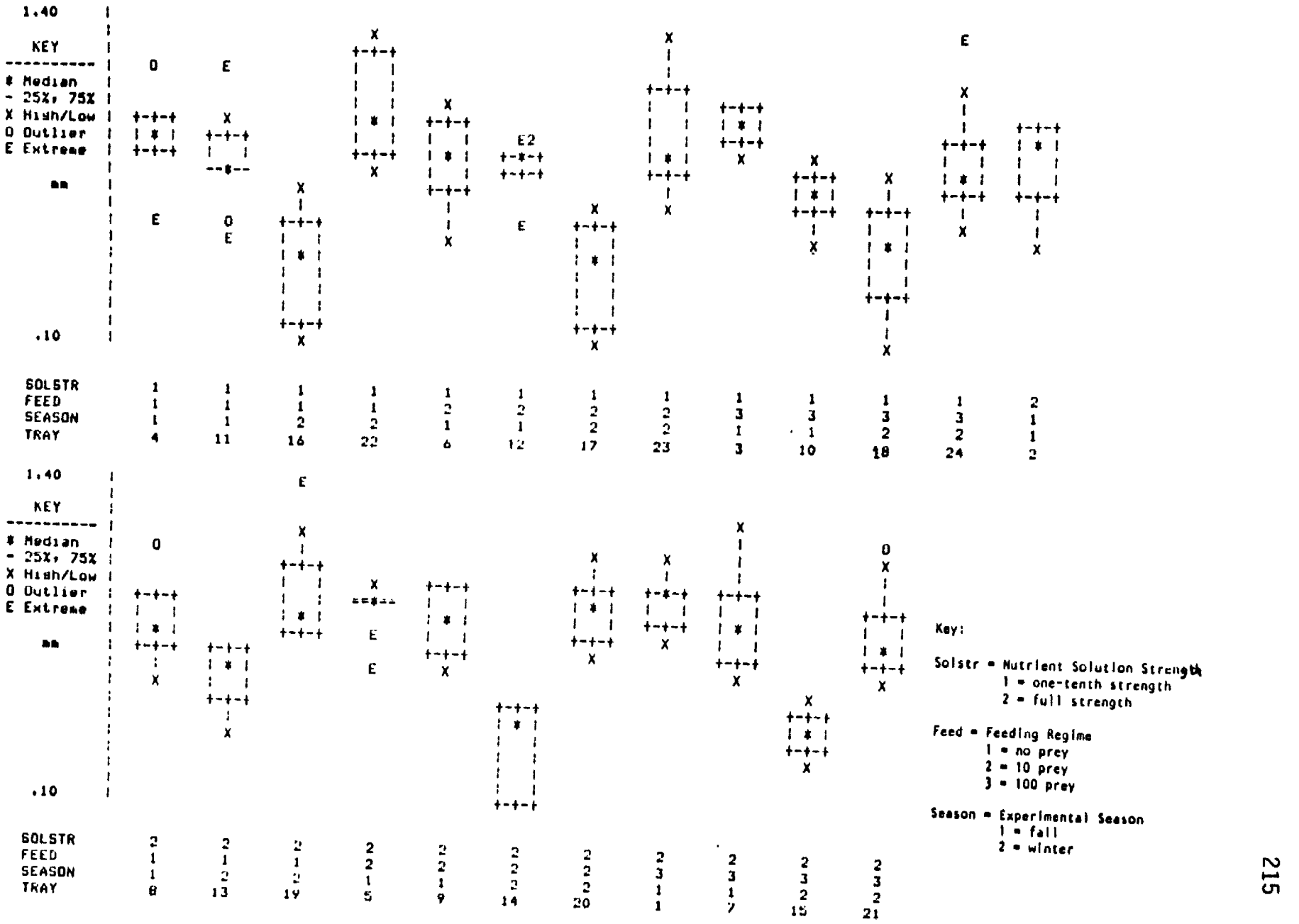


Figure C2. Boxplots for U. vulgaris Plants Raised from Turions in a Diet Experiment: Leaflet Length by Treatment Tray

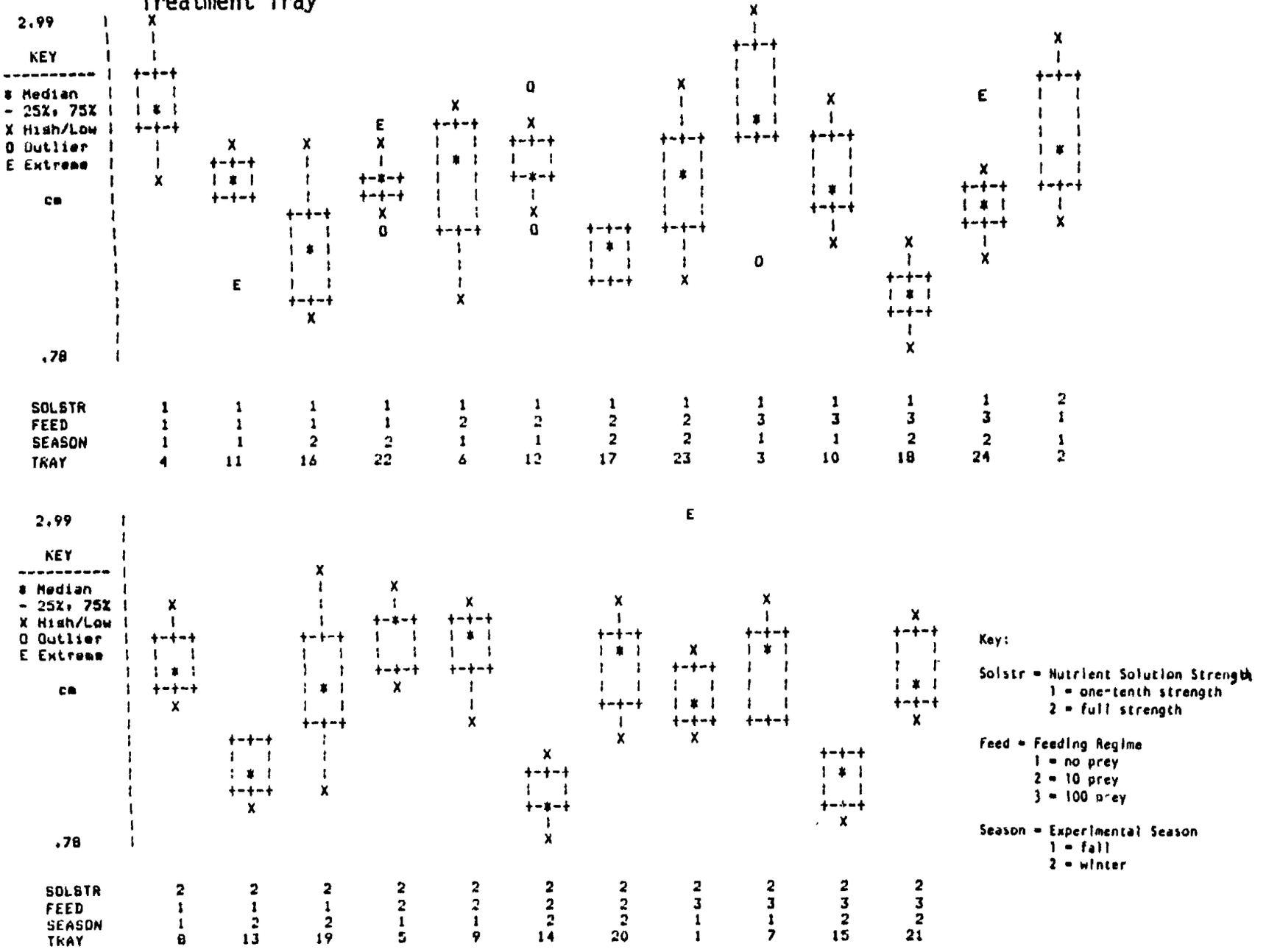


Figure C3. Boxplots for U. vulgaris Plants Raised from Turions in a Diet Experiment: Bladders/Positions per Leaflet by Treatment Tray

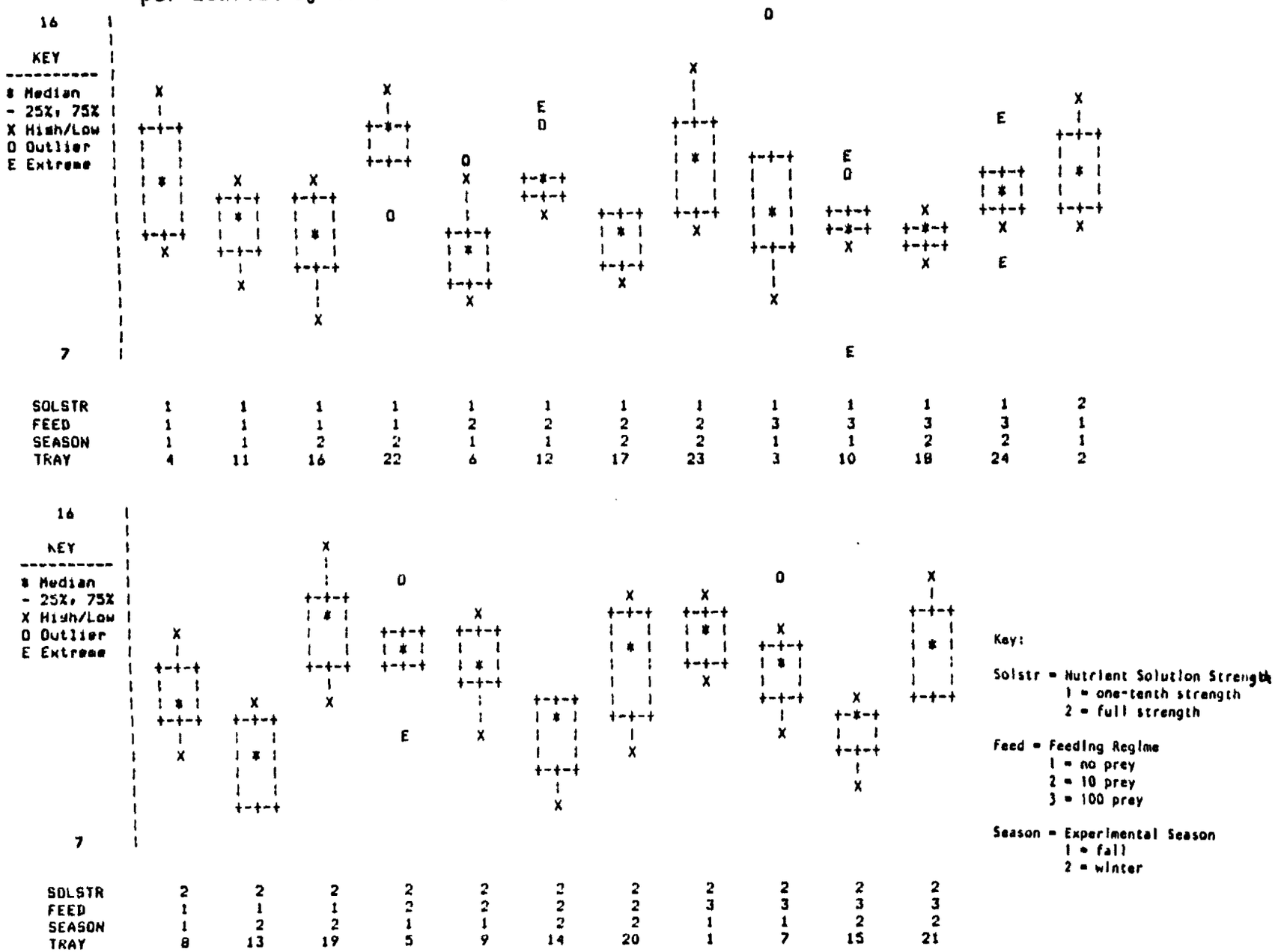


Figure C4. Boxplots for U. vulgaris Plants Raised from Turions in a Diet Experiment: Length of Plant by Treatment Tray

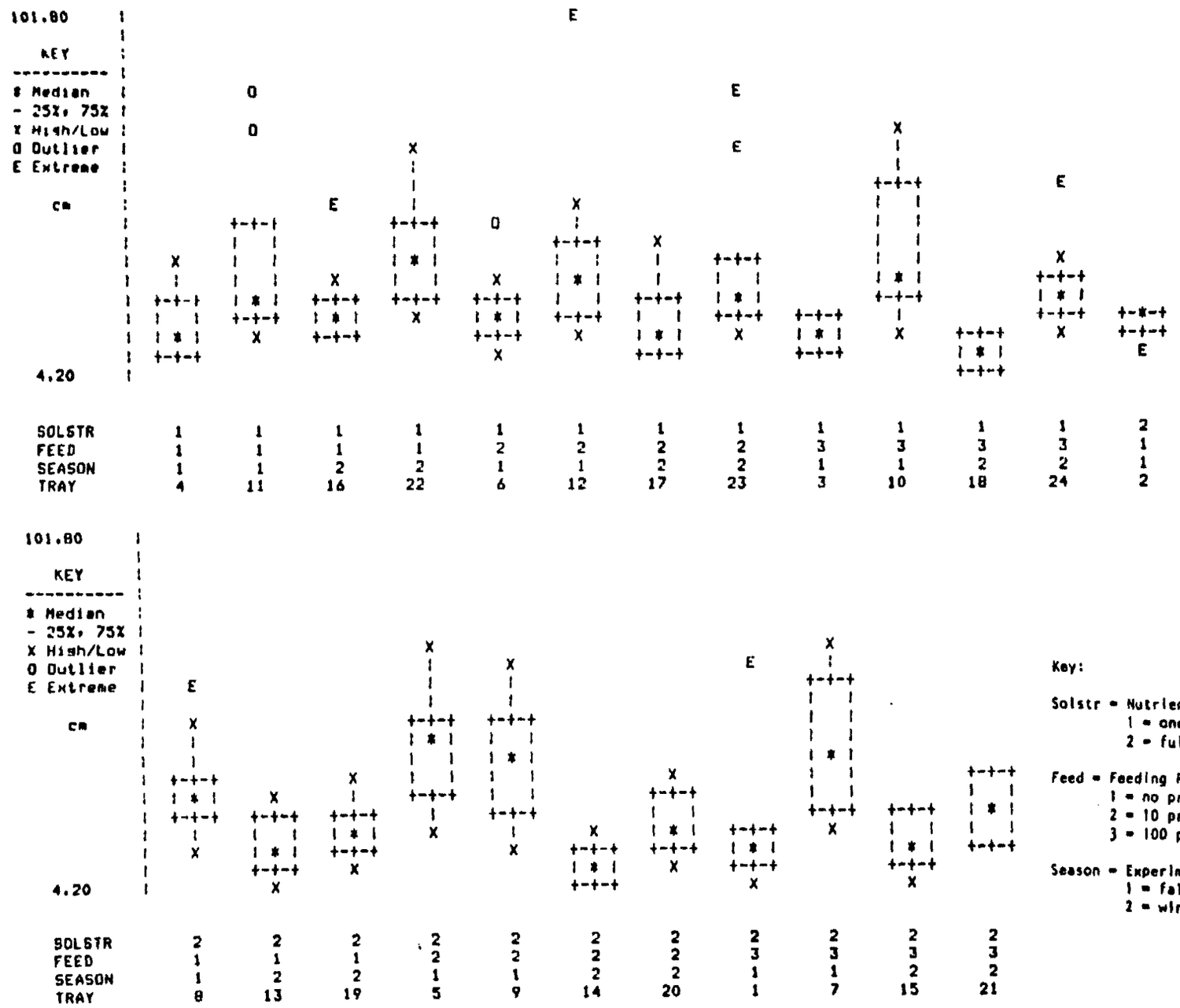


Figure C5. Boxplots for U. vulgaris Plants Raised from Turions in a Diet Experiment: Leaflet Pairs per Plant by Treatment Tray

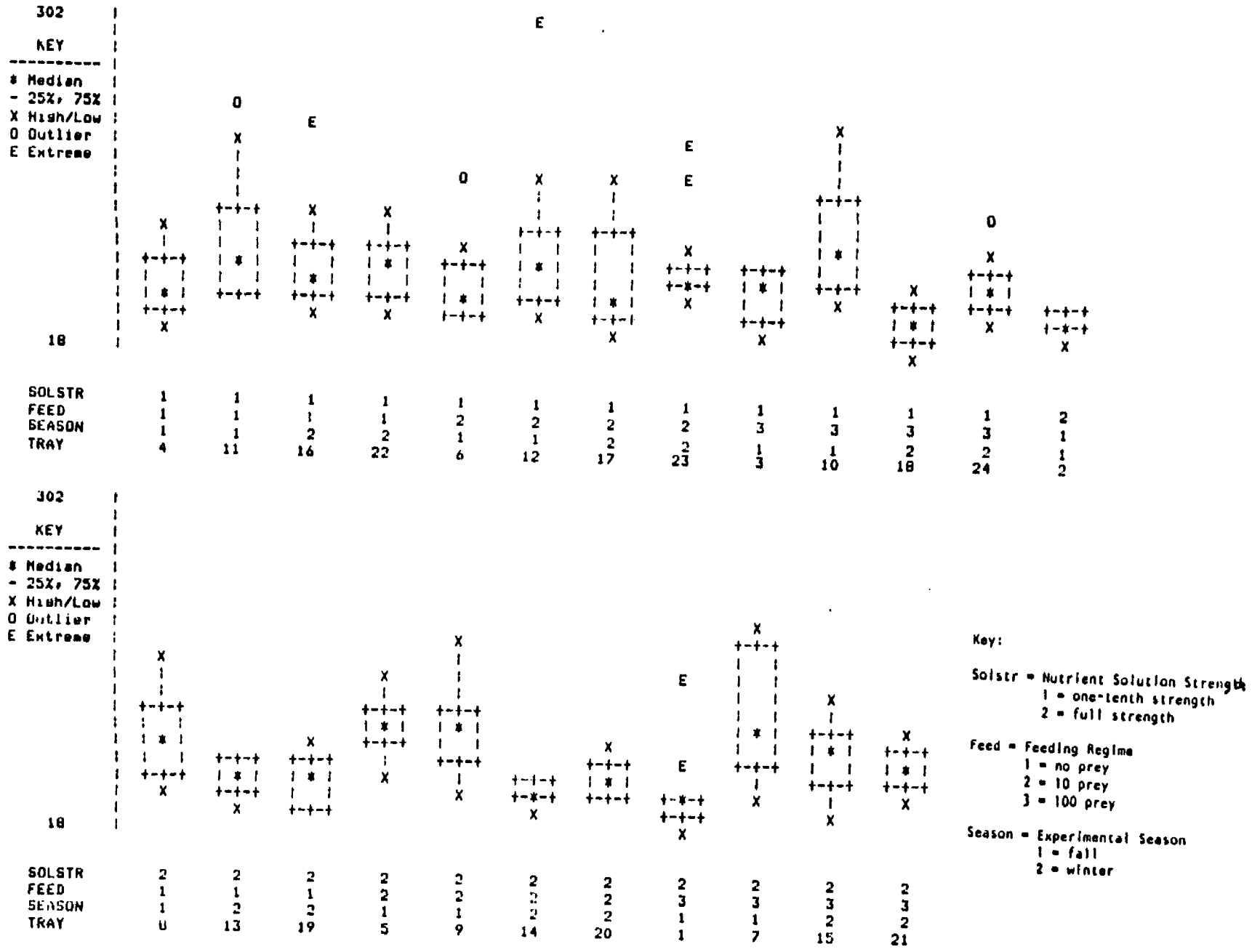


Figure C6. Boxplots for U. vulgaris Plants Raised from Turions in a Diet Experiment: Leaflet Pairs per cm by Treatment Tray

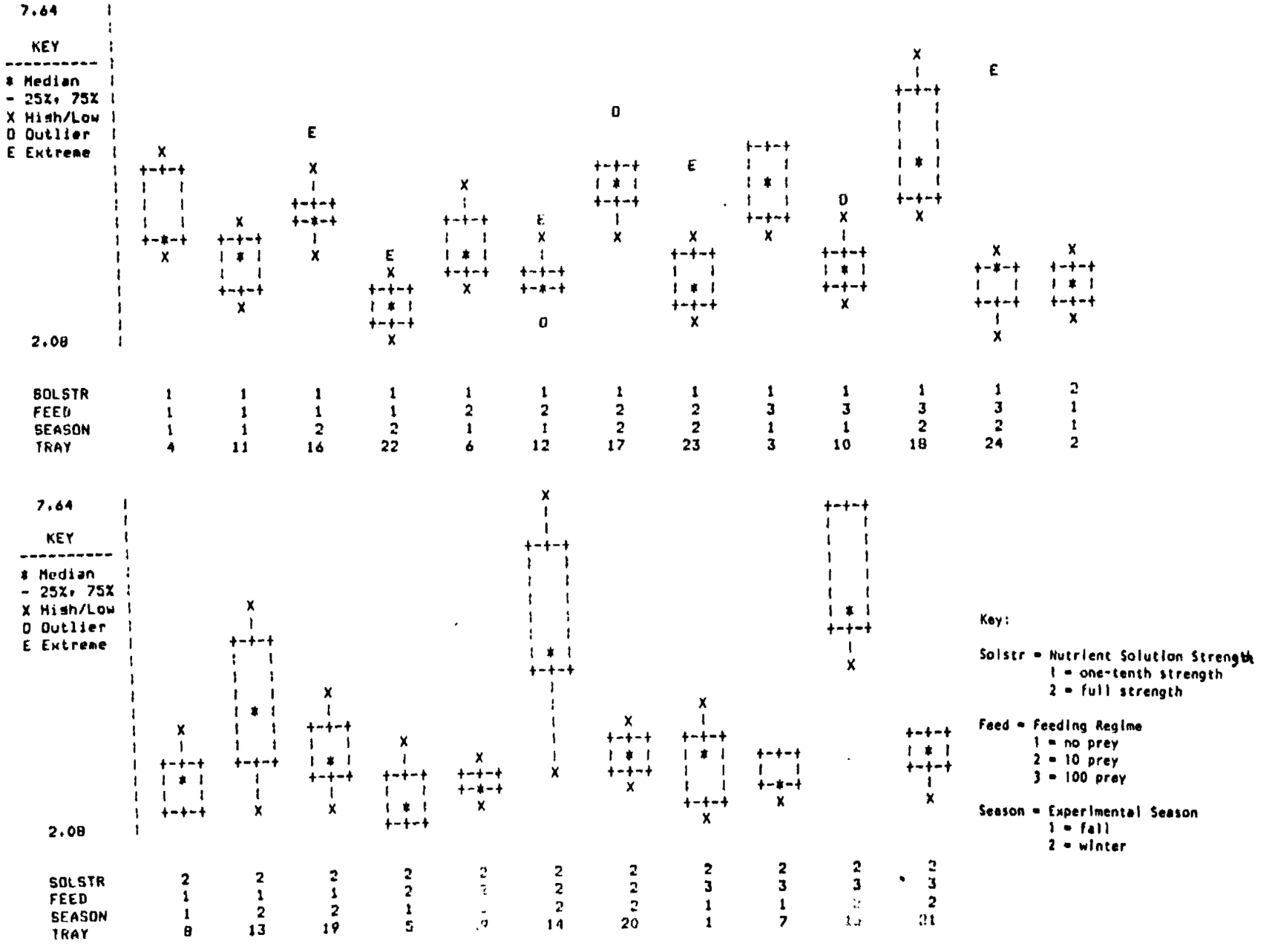


Figure C7. Boxplots for U. vulgaris Plants Raised from Turions in a Diet Experiment: Bladders/Positions per Plant by Treatment Tray

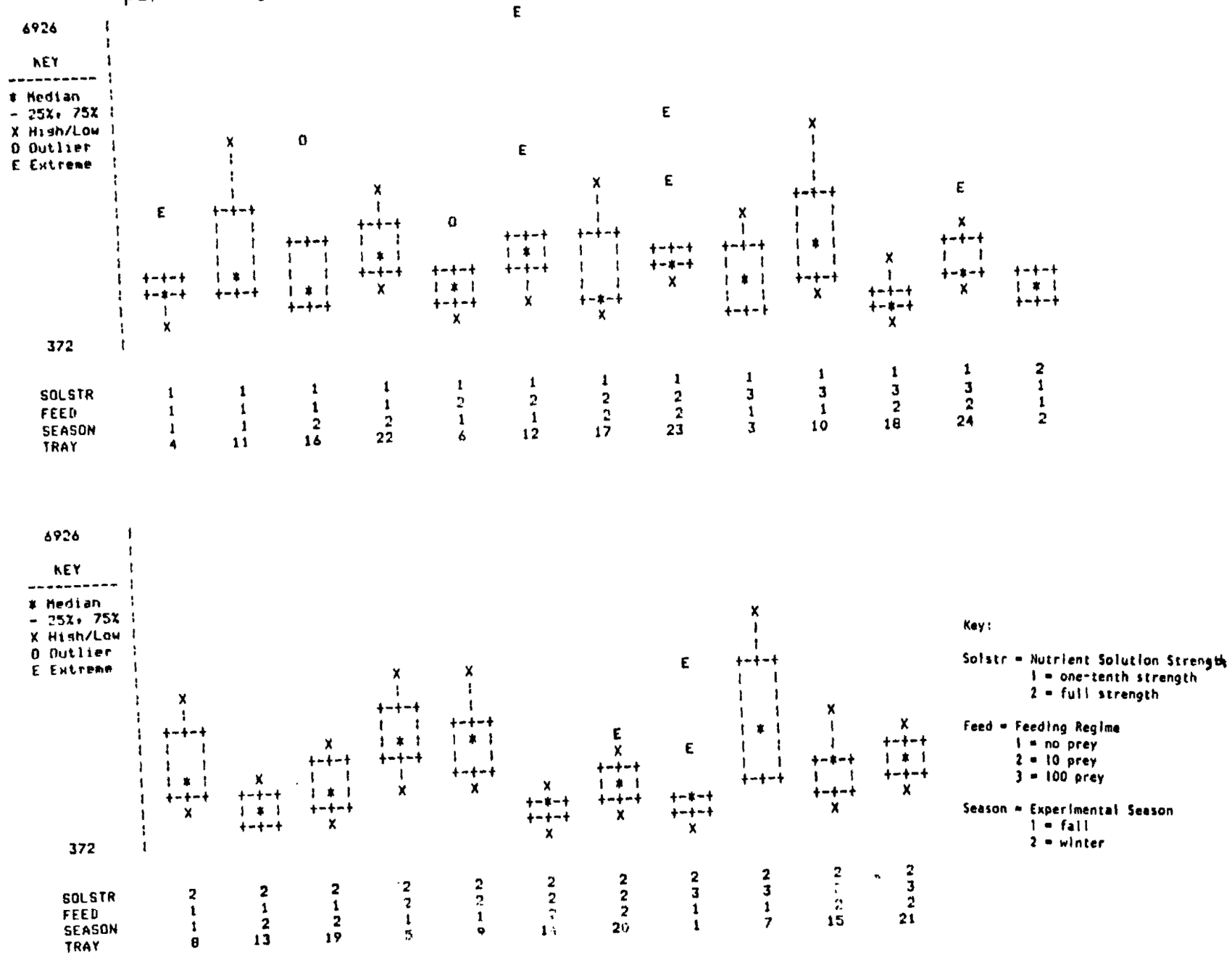


Figure C8. Boxplots for U. vulgaris Plants Raised from Turions in a Diet Experiment: Bladders/Positions per cm by Treatment Tray

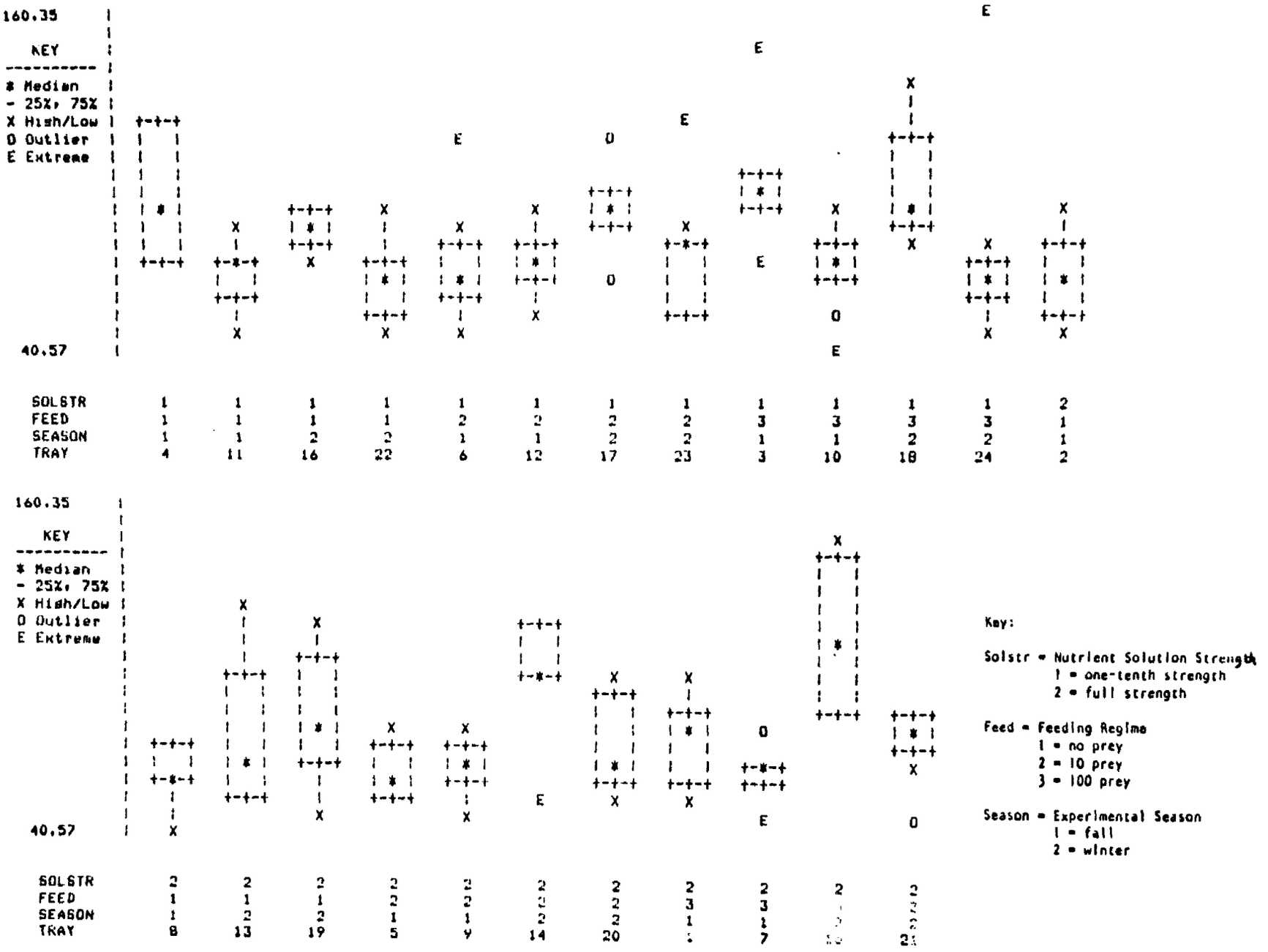
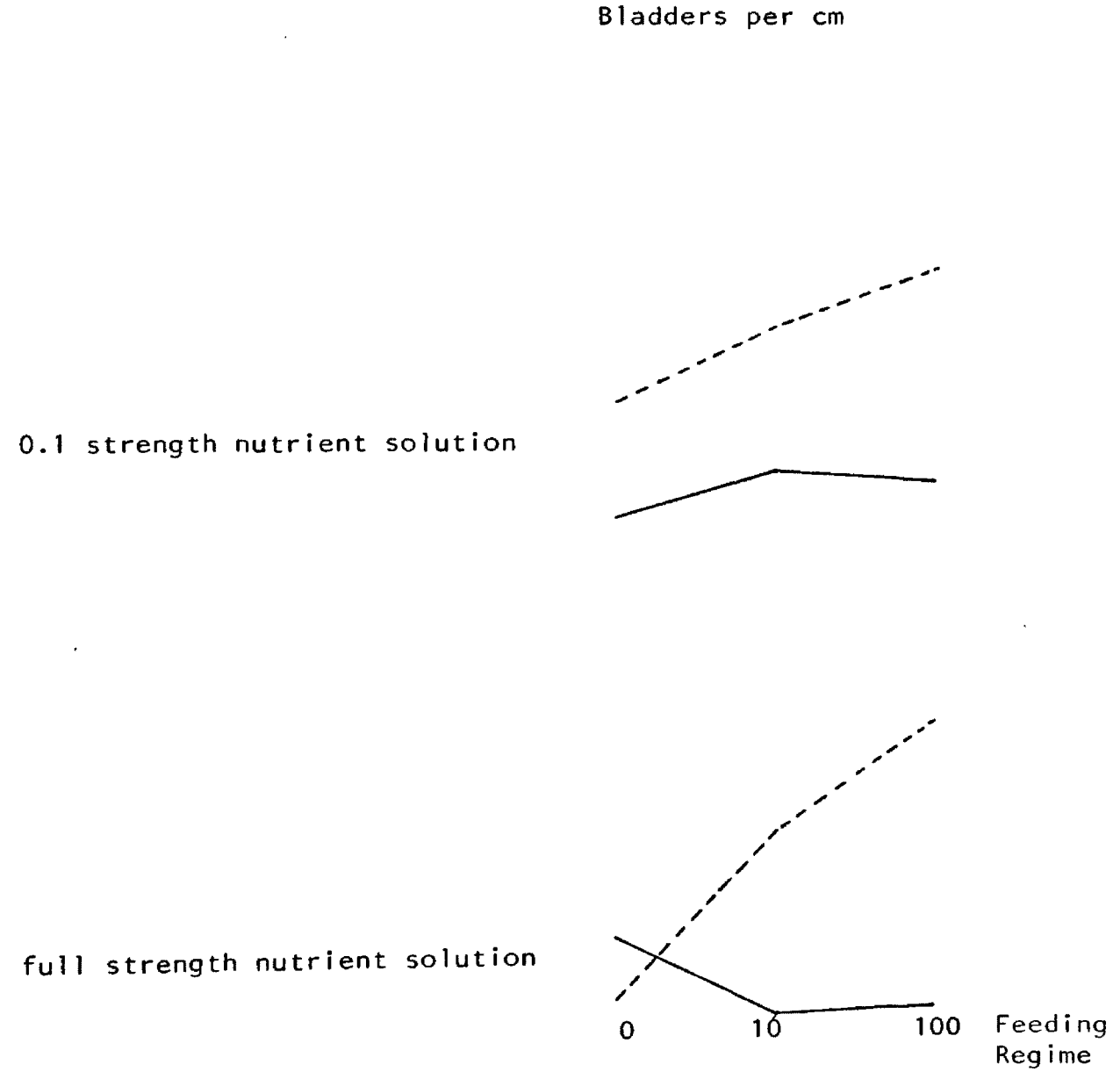


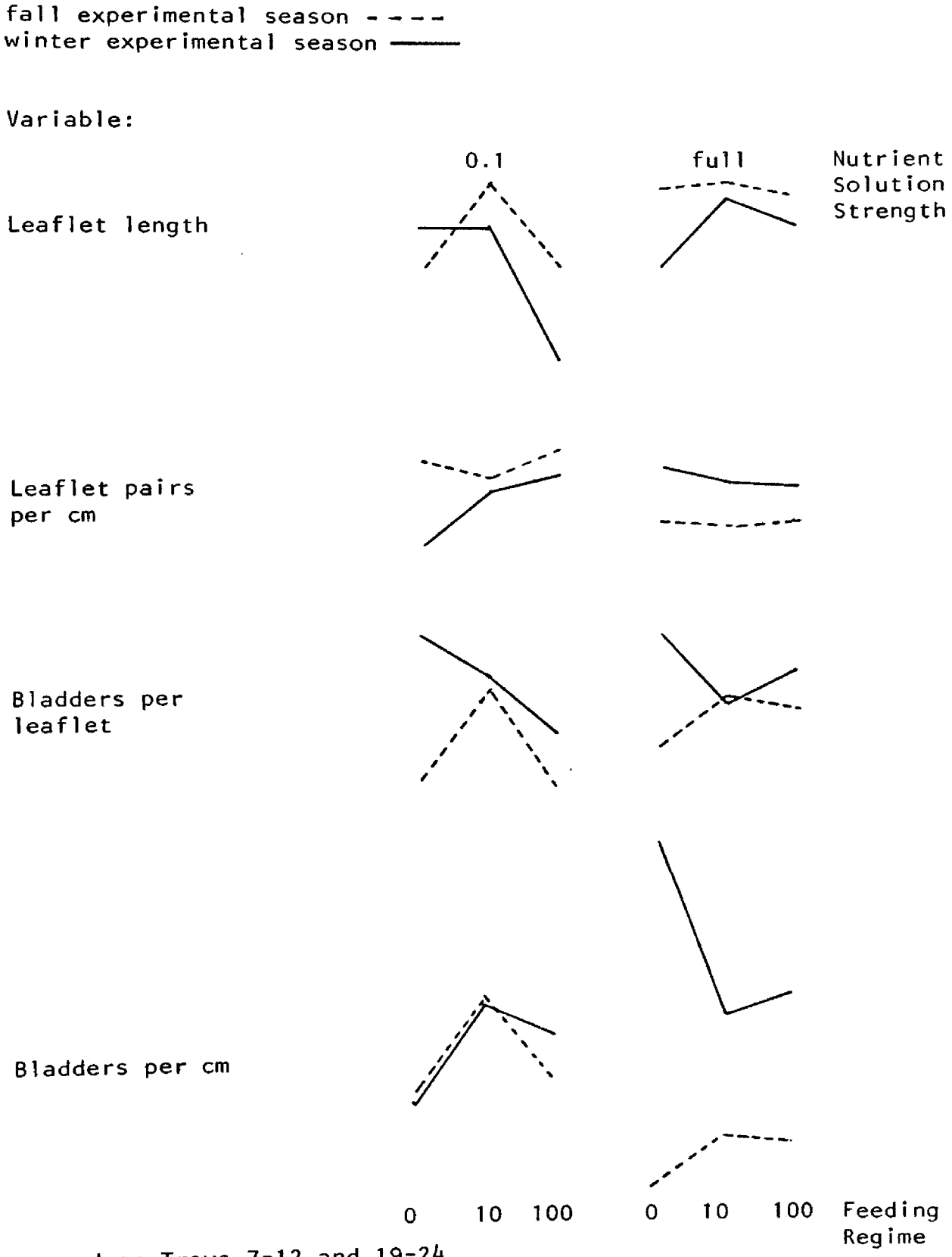
Figure C9. Profile Plot for the Interaction of Collection Site and Feeding Regime on Bladders per cm for U. vulgaris Plants Raised from Turions in a Diet Experiment*

Key:
Tykeson's Pond - - - -
McWenneger's Slough ———



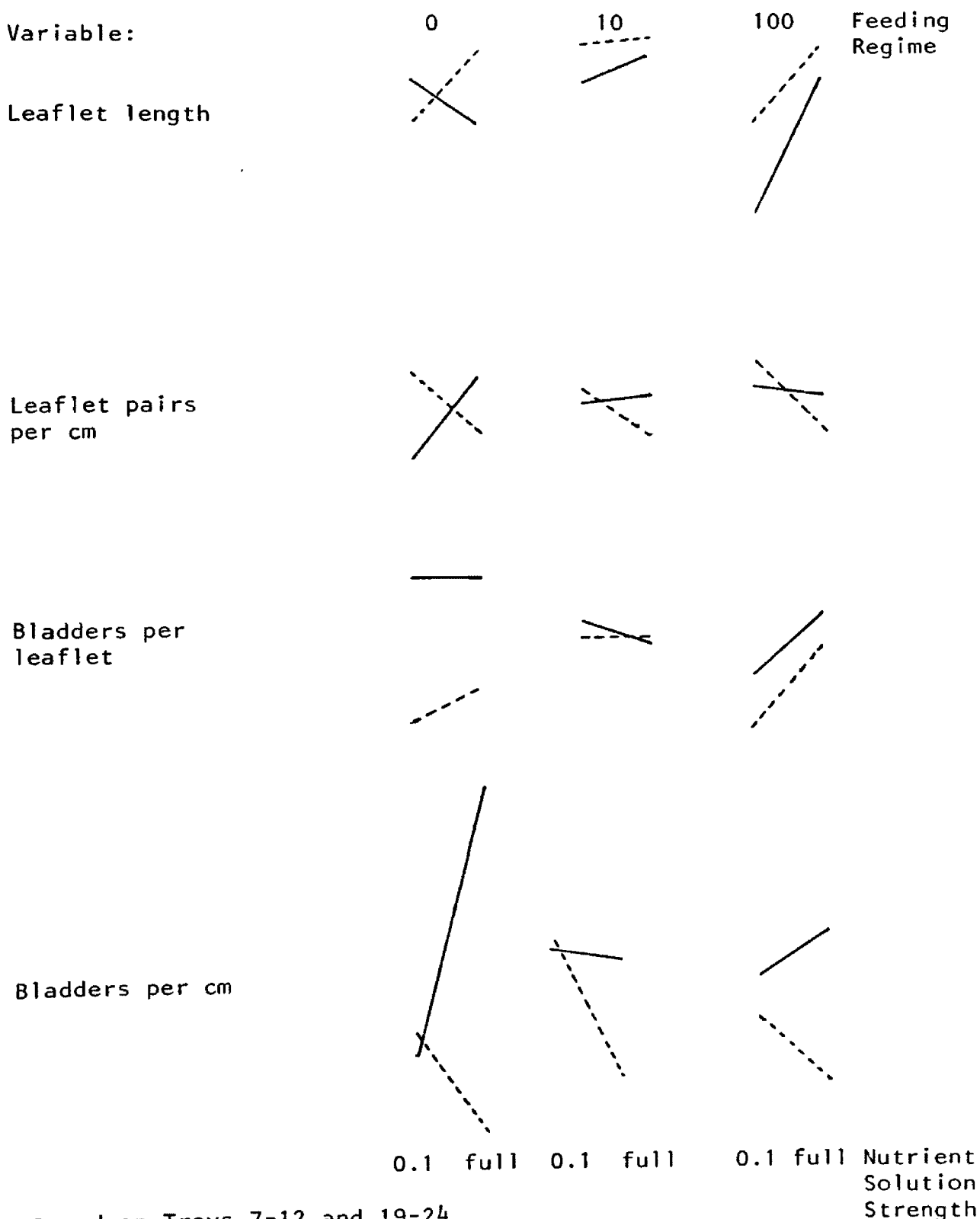
*Based on Trays 13-24

Figure C10. Profile Plot for the Interaction of Experimental Season and Feeding Regime on Key Variables for U. vulgaris Plants Raised from Turions in a Diet Experiment*



*Based on Trays 7-12 and 19-24

Figure C11. Profile Plot for the Interaction of Experimental Season and Nutrient Solution Strength on Key Variables for *U. vulgaris* Plants Raised from Turions in a Diet Experiment*

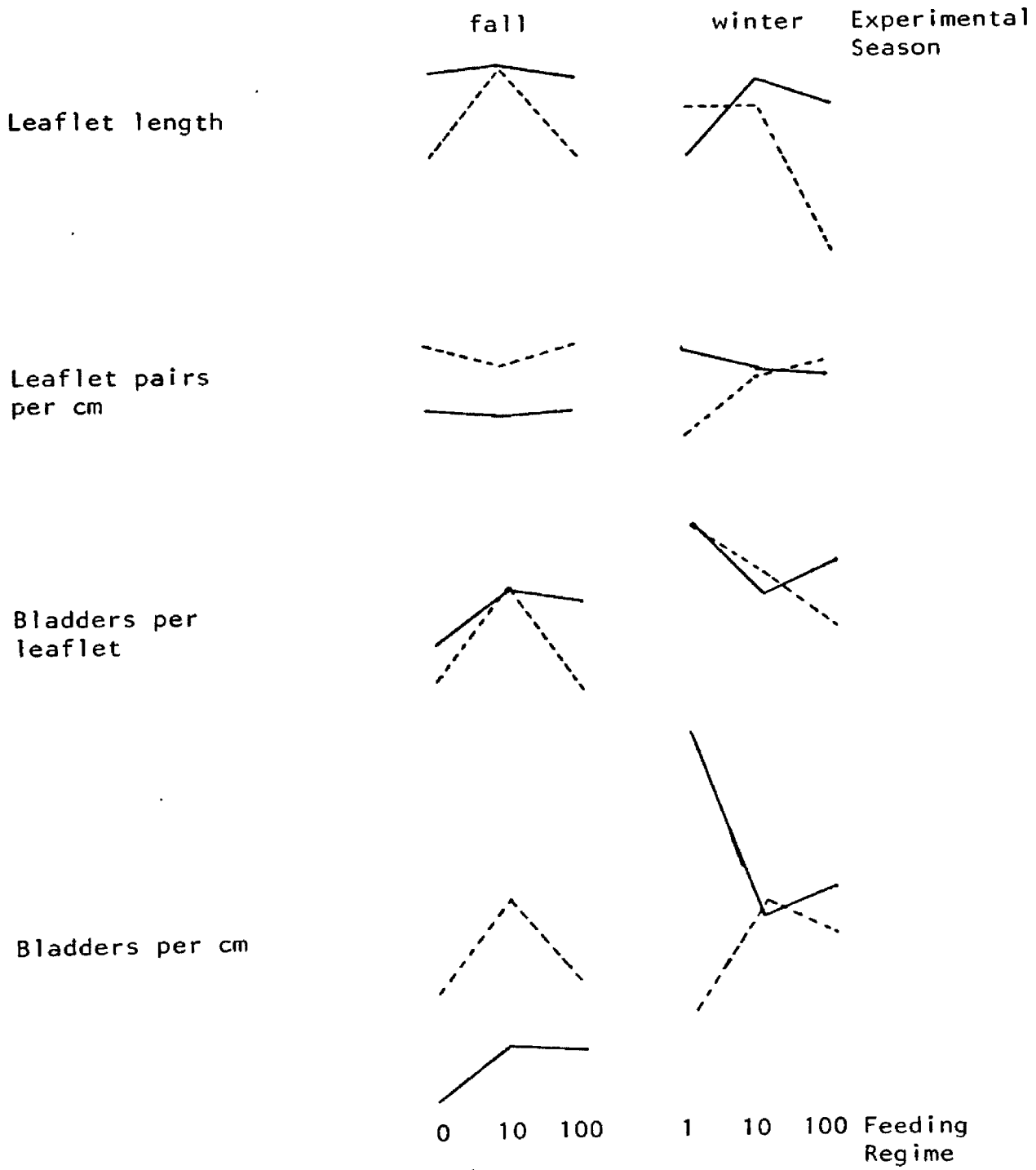


*Based on Trays 7-12 and 19-24

Figure C12. Profile Plot for the Interaction of Feeding Regime and Nutrient Solution Strength on Key Variables for *U. vulgaris* Plants Raised from Turions in a Diet Experiment*

Key:
0.1 strength nutrient solution - - - -
full strength nutrient solution ———

Variable:



*Based on Trays 7-12 and 19-24