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Leaf Life Tables: A Viable Method for Assessing Sublethal Effects of Herbivory on Waterhyacinth Shoots

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Abstract

Natural enemies of waterhyacinth often do not kill the shoots but cause degrees of leaf mortality, although sporadic outbreaks of any of these agents may temporarily cause severe shoot injury. These mortality agents produce distinct spatial patterns of damage within shoots. Only *Sameodes albiguttalis* moth larvae, *Neochetina* spp. weevil adults and larvae, and occasionally environmental factors affect young leaves and destroy meristematic tissue, thereby effectively killing shoots. Most other factors cause superficial injury and usually only to older leaves. Leaf life tables show that damage caused by *S. albiguttalis* and the two species of waterhyacinth weevils results in an overall 34% reduction of leaf longevity. This is usually brought about by the early destruction of young leaves. Thus, even without direct shoot mortality a degree of control is achieved. Damage caused by *S. albiguttalis* larvae is sporadic and therefore of limited effect. That caused by *N. eichhorniae* is constant and effective. Leaf life tables provide an effective method of comparing impact of biological control agents on waterhyacinth when direct mortality of shoots does not occur.

Les Tableaux de Vie de Feuilles Comme Moyen Valable d'Évaluation des Effets Sous-Mortels des Attaques d'Herbivores sur les Pousses de la Jacinthe Aquatique

Il est fréquent que les ennemis naturels de la jacinthe aquatique soient la cause d'une mortalité plus ou moins importante parmi les feuilles sans tuer les pousses, quoique des éruptions sporadiques de ces agents puissent nuire gravement, mais temporairement, aux pousses. Les dommages causés par ces agents sont répartis à l'intérieur des pousses de manière distincte. Ce ne sont que les larves du *Sameodes albiguttalis* (lepidoptère), les adultes et les larves des charançons du genre *Neochetina*, et parfois, des facteurs de l'environnement, qui affectent les jeunes feuilles ou qui détruisent le tissu méristématique, et de ce fait tuent effectivement les pousses. La plupart des autres agents ne causent que du dommage superficiel, et ce en général seulement aux feuilles plus agées. Les tableaux de vie des feuilles de la jacinthe aquatique montrent que le dommage du au *S. albiguttalis* et aux deux charançons, amène une réduction globale de 34% dans la vie des feuilles, ce qui resulte, le plus souvent, de la déstruction précoce des jeunes feuilles. Ainsi, même sans mortalité directe des pousses, on arrive à un contrôle partiel. Le dommage du aux larves du *S. albiguttalis* est sporadique et donc d'un effet limité, mais celui au *N. eichhorniae* est constant et efficace. Les tableaux de vie de feuilles offrent un moyen efficace de comparison entre l'impact des divers agents de la lutte biologique contre la jacinthe aquatique, là où il n'y a pas de mortalité direct des pousses.

Introduction

Life tables (or survivorship tables) have a long history of use in the insurance business for actuarial purposes as a means of computing annuities. Deevey (1947) perhaps first recognized the utility of life tables for analyzing growth of animal populations in nature, although others (e.g. Pearl *et al.* 1941) had earlier applied these techniques to analysis of laboratory populations. Since that time, life table analyses have been used most extensively in animal population biology, especially in the analysis of insect populations.

Harcourt (1969) and Varley and Gradwell (1970) have reviewed the subject in great depth.

Few attempts have been made to study the demographics of plants by way of life table analyses. Notable among these are the studies by Hett and Loucks (1971), Hawksworth (1965), Namkoong and Roberds (1974), and Harcourt (1970). The interested reader should consult the reviews by Harper and White (1974) and Harper (1977). A particularly interesting example from the paper by Harcourt (1970) is his use of crop life tables to assess economic losses resulting from mortality factors by converting population parameters to monetary values. This yields cost-benefit data for pest management practices in agricultural crops. Life tables could be used in weed management to determine the value of mortality factors which affect the target plant. The resultant monetary figures could then be used to compare the cost-benefit of various control approaches.

Two types of life tables are often constructed. The first type is based upon data obtained by observing the successive mortality of individuals in a population as they increase in age. This is the age-specific, horizontal, or dynamic life table. The second type assumes a stable age distribution and is based upon the age structure of the population at a point in time and infers death rates from the decline in numbers of successive age-classes. This is the time-specific, vertical, or static life table. Krebs (1972), Southwood (1975), Dempster (1975), Deevey (1947), and others discuss types of life tables and their limitations and applications.

Life tables generally deal with whole organisms but in the case of waterhyacinth, the whole plant is difficult to study. The individual leaf is a more convenient unit to use in waterhyacinth population studies (Center 1981). There are many advantages of studying leaves. They are identifiable structural units. Leaves are produced singly at the stem apex and at regular intervals, so leaf age structure is determinable. Leaf production occurs at predictable and easily measured rates. Leaves are conspicuous organs and the most obvious feature of the plant. Leaves often comprise the majority of the biomass. Organisms which damage or kill leaves are easily identified. Biological control agents all feed upon or infest the leaves and affect leaf production and turnover. Leaves have a distinct life cycle. Leaves are easily tagged for repeated observation. Leaf age distributions are relatively stable.

The main disadvantage of studying leaves is that the point of death of a leaf is not always clear. A leaf should be considered dead when it is no longer functional. Because the leaf gradually senesces, death must be subjectively determined. Also, the loss of a leaf does not translate directly into reduced productivity or fitness. This is due to many reasons which have recently been reviewed by Crawley (1984). Also, organs other than the leaves may be more vitally important to the plant.

Population studies of waterhyacinth leaves have provided us with a great deal of useful information. The information is limited, however, and more is needed for a proper evaluation. Richards (1934) warned against inference drawn from a static system and applied to a dynamic one in terms of physiological change related to leaf age. A combined approach is necessary. Harvesting studies document changes, but studies of leaf dynamics provide insight into the process of change.

This paper provides examples of data from field studies in which I examine the within-shoot dispersion of various natural enemies on waterhyacinth. It concludes by using some of these data to construct an example of a time-specific life table to show how this technique might be used to compare the impact or importance of mortality factors. The interested reader should refer also to Abul-Fatih and Bazzaz (1980), Carpenter (1980), Nobel *et al.* (1979), Sagar and Mortimer (1976), and Harper (1977, 1981) for other examples and approaches.

Methods and Materials

Studies were conducted at 15 sites in Florida (Fig. 1) during a four-year period. Data are too extensive to be dealt with in detail so only examples will be presented.

Sampling consisted of examining waterhyacinth shoots, classifying the leaves by nodal position to age cohorts, and identifying factors which had damaged leaves. During 1978–80 we simply determined if each leaf on 100 shoots was or was not damaged by each particular agent and expressed the data as relative frequencies. A 100 × 100 cm frame was placed over the waterhyacinth to delimit a sample area. All plants were removed from within the frame and placed in a large plastic bag. Without apparent bias, 10 shoots were randomly withdrawn and examined. This was done 10 times on a transect across the site with samples taken at approximately equal intervals. Later, during 1980–82, the degree of damage done by each agent was estimated based upon percent of leaf area affected. The same general procedure was followed but only four were selected from each sample (40 total). Lamina and petiole were each assumed to represent 50% of the total leaf in this case. Factors which caused separation of the leaf from the shoot were considered to have caused leaf death.

Series of shoots were tagged at some sites to enable re-identification and re-examination. Tags were placed on youngest leaves and live leaves were counted. This enabled estimation of rates of leaf production and leaf death and development of a leaf budget for each shoot. These and untagged shoots were evaluated as described above at approximately monthly intervals. Leaf condition was evaluated based upon percent green and undamaged. Ten to fifteen plants were tagged at each site. Relocating these plants was difficult and time-consuming, but this enabled comparison of spatial and temporal effects.

Results

The spatial arrangement of waterhyacinth leaves is a function of time, so dispersion of leaf injury is also temporal. Patterns of damage varied spatially and depended upon whether leaf damage was random or selective (Figs. 2, 3, 4). If leaf injury was random then degree of damage increased from younger to older leaves and was directly proportional to duration of availability. In this case, both probability of and frequency of attack increased the longer the leaf was available.

If young leaves were selectively attacked then injury carried through, but didn't increase, as leaves aged. No apparent relationship existed between leaf position (or age) and injury intensity. Leaves were susceptible for a short time and then not harmed further.

If mature leaves were selectively attacked, damage sharply increased at one location within the shoot and leveled off thereafter. Rate of increase was dependent upon the degree of preference of the agent and the duration of persistent attack.

These three patterns of leaf injury (random, young leaf preferred, or mature leaf preferred) assume constant herbivore pressure and are basic and over-simplified. Many more complex patterns were observed. For example, some agents preferred certain leaves but not fastidiously so. Agents such as the waterhyacinth moth, *Sameodes albiguttalis* (Warren) (Lepidoptera: Pyralidae), destroyed meristematic tissue which stopped leaf production. Thus, the resultant injury did not carry over to other positions. Other

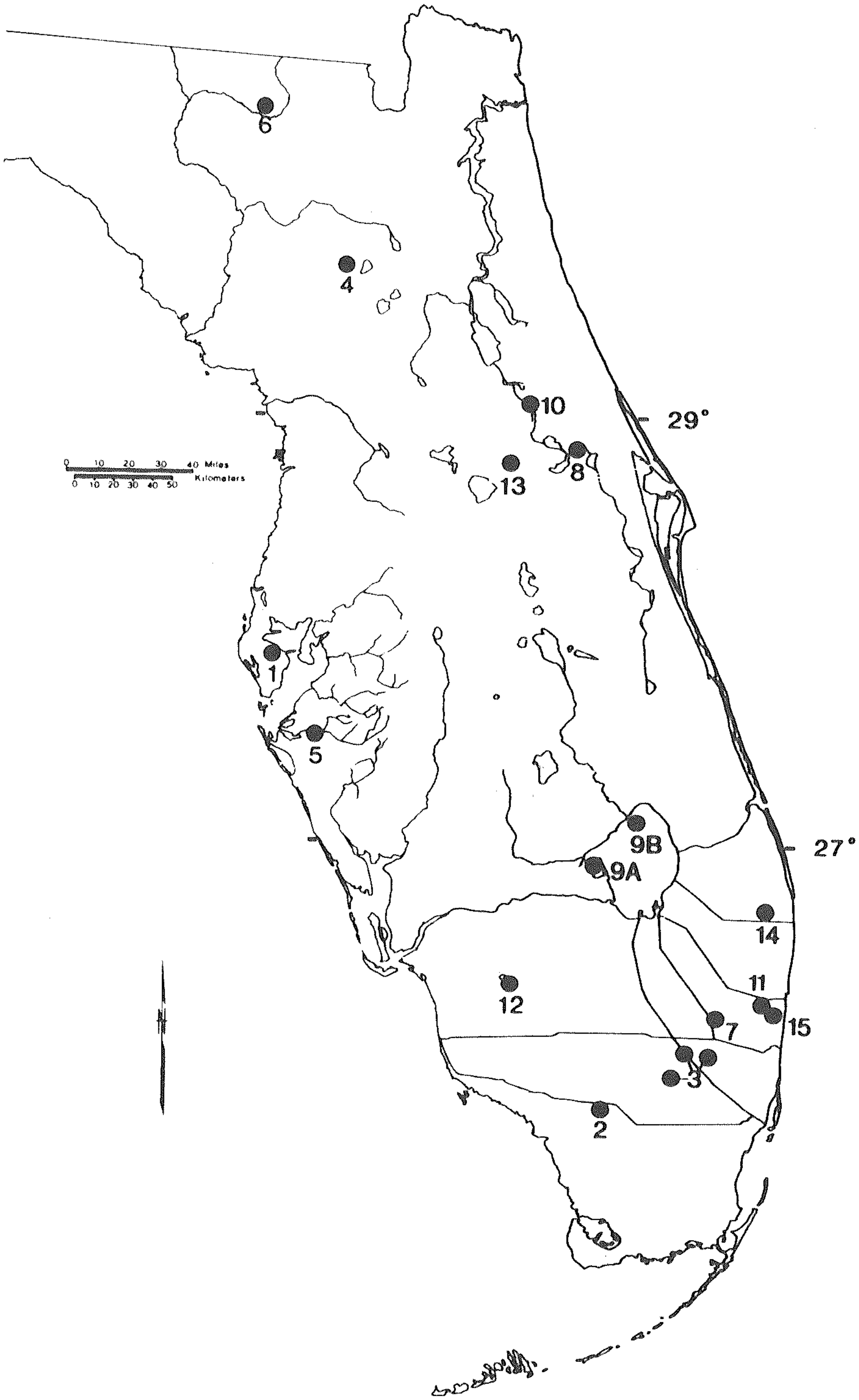

Fig. 1. The location of the 15 sites in Florida at which data on mortality of waterhyacinth (*Eichhornia crassipes* (Mart.) Solms.) leaves were obtained between 1978 and 1982.

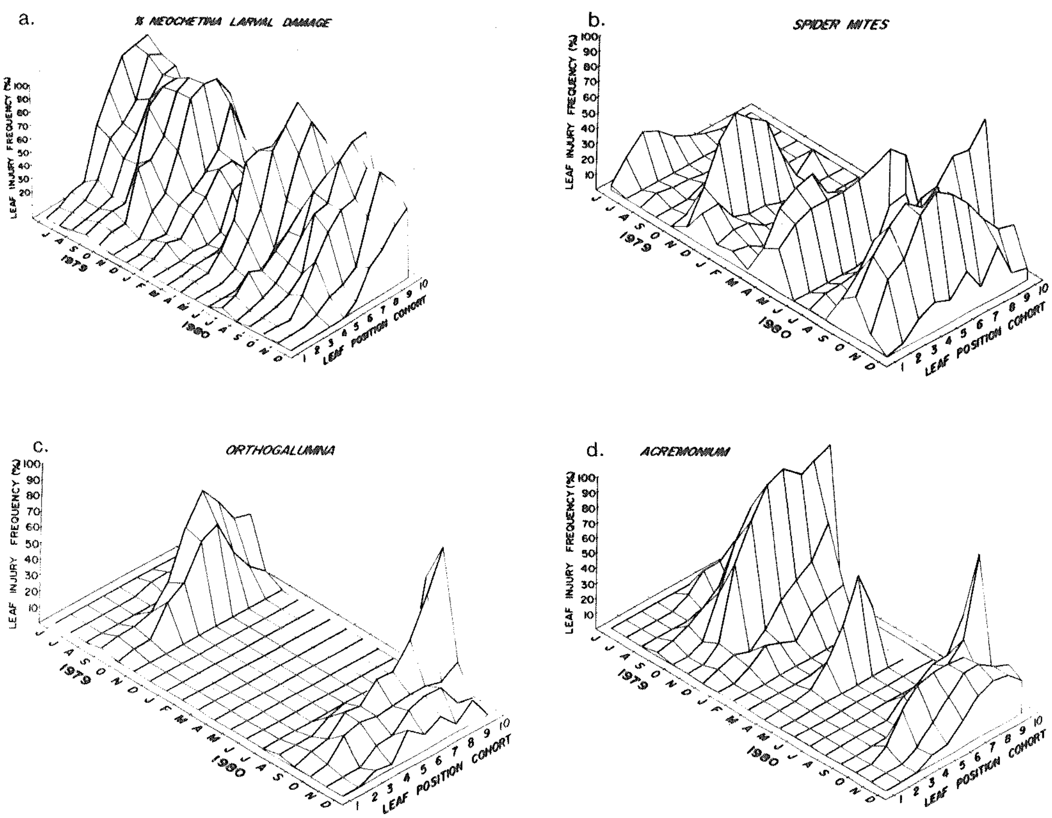

Fig. 2. Data from Lake Alice (site 4), Gainesville, FL, showing the relative frequencies at which leaves of various age classes were damaged or infested by: (a) weevil larvae; (b) spider mites; (c) waterhyacinth mites; and (d) zonate leaf spot disease. Note that spatial patterns of within shoot injury also varied seasonally.

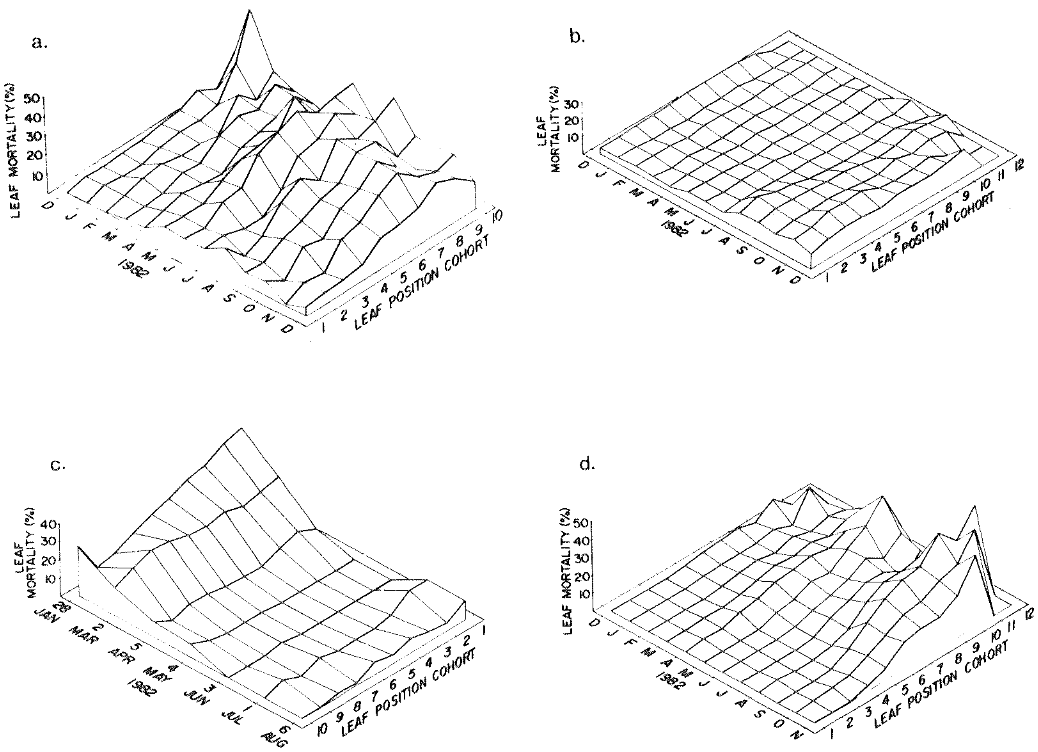

Fig. 3. Data showing the within-shoot spatial dispersion of leaf damage rated according to severity for: (a) weevil larvae; (b) weevil adults; (c) waterhyacinth moth larvae; and (d) zonate leaf spot disease. The leaf cohort axis in Fig. 3c is reversed when compared to the other three graphs. Data for Figs. 3a, b, and d are from Canal-M (site 14), near West Palm Beach, FL. Data for Fig. 3c are from Palm Aire, FL (site 15).

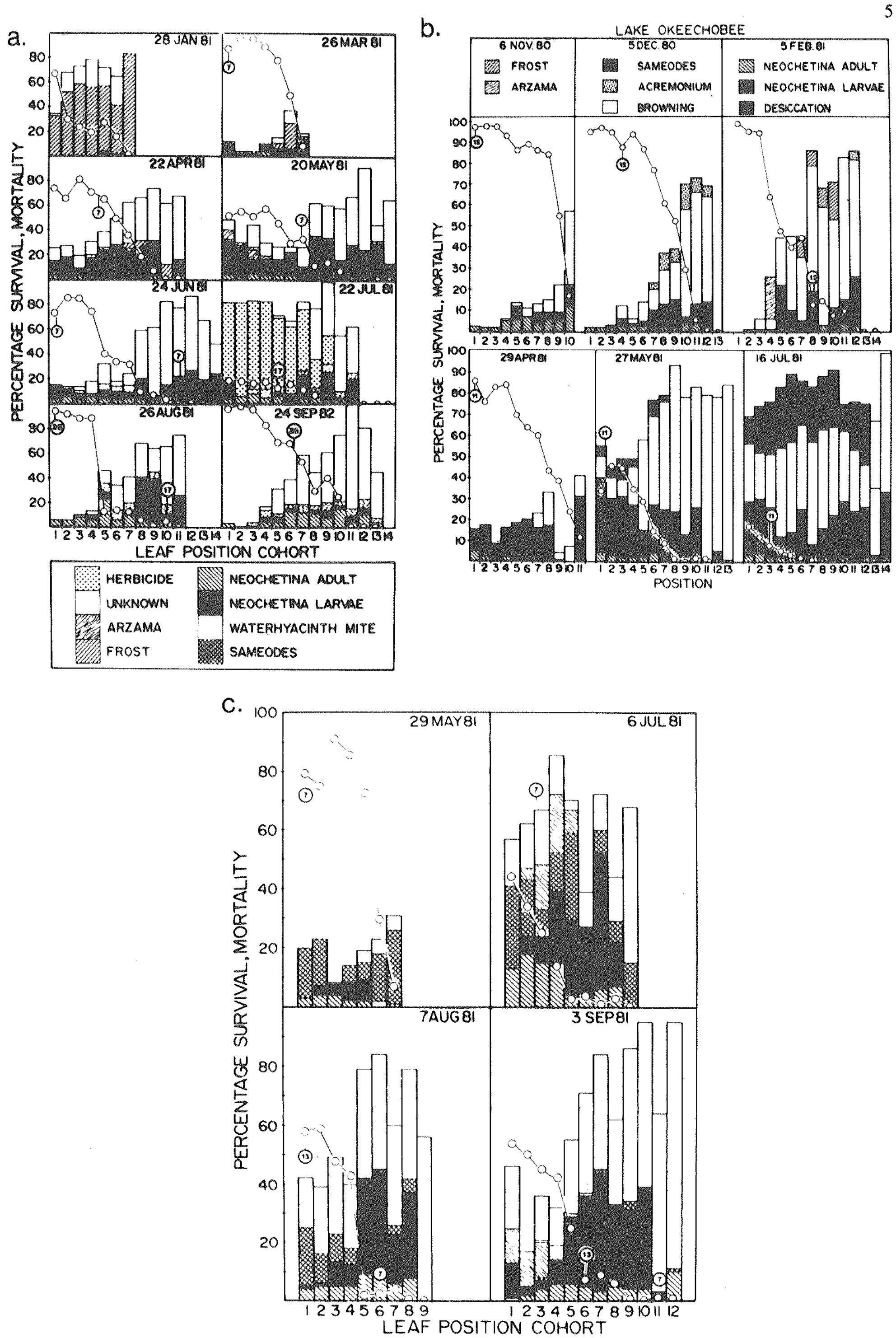

Fig. 4. Data from (a) the Saint John's River (site 10) near DeLand, FL; (b) Lake Okeechobee (site 9); and (c) Coral Springs, FL (site 11), showing relative amounts of damage (bars) caused by various organisms to waterhyacinth (*Eichhornia crassipes* (Mart.) Solms) leaves of varying ages. Dots represent average condition of leaves within each cohort. Small circled numbers show change in leaf position and condition as leaves increase in age. The same number represents the same leaf from one sampling date to the next. The legends in Figs. 4a and 4b also apply to Fig. 4c.

organisms preferred different leaves at different points in their life cycle. Early instar *S. albiguttalis* larvae preferred old leaves, but switched to young leaves as they matured. All exceptions to the basic patterns produced distinct, identifiable patterns, however.

Besides spatial–temporal influence on intra-shoot dispersion of leaf injury, seasonal factors played an important role as did the ability of the plant to outgrow or displace the injury. Seasonal abundance of each organism varied somewhat differently. Leaf production rates varied and were most rapid during the spring. Injured leaves were then replaced more quickly than during fall or winter. Damage appeared lower on the shoot in spring and seemed to 'move up' in fall. Leaves of equal age may have actually been attacked in both cases.

Waterhyacinth weevil (*Neochetina* spp.; Coleoptera: Curculionidae) larvae and adults produced distinctly different injury patterns within waterhyacinth shoots. Eggs are deposited in petioles of a mature leaf (third to fourth position) and hatch in about two wks. The leaf may be displaced two positions (to fifth or sixth) before first instar larvae are present. The larval period requires 30–45 days during which larvae do not readily move out of the original petiole. By then the shoot may have produced five or six leaves. The larva may then be in an old (tenth or eleventh position) leaf before it is large enough to do significant damage. Hence, weevil larval injury usually increased on older leaves. Mature larvae are capable of moving to young leaves. When leaf production slowed, weevil larvae seemed to injure younger leaves (e.g. see Figs. 2a, 3a, and 4c).

Neochetina spp. adults preferred young leaves. The lamina of the youngest leaf was often fed upon while only partially opened. Adults also fed on older leaves but not to the same extent. The resultant pattern of adult weevil injury was indistinct increasing slightly on older leaves (e.g. Fig. 3b) but otherwise with a very low or flat slope over leaf positions.

As mentioned above, *S. albiguttalis* larvae fed on both old leaves or young leaves. When plants were tall, with erect petioles, older leaves were apparently too tough for the larvae. Feeding was then restricted to softer, young, leaves. When the plants were small, early instar larvae fed on older leaves, usually those with soft, spongy, inflated leaf petioles. In this case, as the larvae matured they fed upon young petioles as well. The injury pattern induced by *S. albiguttalis* larval activity was thus variable depending upon plant form and extent of injury. In the former case, especially when the apical bud was destroyed, injury was very high on the first one or two leaf positions and zero thereafter. In the latter case the distribution may have been flat, high on young leaves and increasing on older leaves, or high on old leaves and decreasing on younger leaves (see, for example, Figs. 3c and 4).

The two species of mites produced quite different injury patterns. Spider mites (*Tetranychus tumidus* Banks; Acari: Tetranychidae) occurred in 'boom or bust' population cycles (Fig. 2b). Normally, this species of mite was present in waterhyacinth populations at very low levels. Leaf injury was sporadic and patchy. Occasionally outbreaks occurred and all leaves were affected. Shoots were almost never killed, however, and the outbreaks were generally short-lived. As the plants recovered, the leaf injury was progressively displaced to older leaves.

Waterhyacinth mites (*Orthogalumna terebrantis* Wallwork; Acari: Galumnidae) were never sufficiently common to discern a recurring pattern. They seemed restricted to older leaves (Fig. 2c). These organisms are leaf miners and remain on one leaf through their entire immature period. For this reason they are vulnerable to displacement. Their life cycle requires *c.* 3 wks, during which a waterhyacinth shoot could produce three or four leaves. Galleries were not conspicuous until after the adult emerged. Thus, even if eggs were deposited on young leaves, the injury may not have been apparent until leaves were older.

Zonate leaf spot, *Acremonium zonatum* (Sawada) Gams. (Hyphomycetes), was present at most sites but was usually restricted to old leaves. Figs. 2d, 3d, and 4b show that it was uncommon on younger leaves. When evaluated as to severity, values were usually low and extensive lesions were usually restricted to very old leaves (e.g. Figs. 3 and 4). This is partially related to an association with waterhyacinth mite injury but it also may result from antifungal properties of the leaves (Martyn 1977; Martyn and Freeman 1978). Some data suggest a link between *Acremonium* infection and increased rates of leaf production (Martyn and Freeman 1978) which would accelerate displacement of diseased leaves. In addition, the time involved in lesion development following inoculation may be considerable and the leaves may age considerably before symptoms appear.

Environmental factors such as frosts or droughts impacted waterhyacinth leaves much like spider mites (Fig. 4). They seldom occurred but they affected all leaves. Plants that survived produced new leaves and displaced the injury.

Other factors such as the pickerelweed borer (*Arzama densa* Walker; Lepidoptera: Noctuidae) and the pathogen *Cercospora* spp. (Hypomycetes) were too rare to assess in terms of their spatial distribution on shoots.

Rates of waterhyacinth leaf production varied greatly as shown in Table 1. High rates occurred in flowing systems or in systems with a high nutrient subsidy such as sewage lagoons. The lowest rates occurred when plants were under stress. Seasonally, leaf production rates were highest in spring (Center 1981). Generally speaking, the faster the shoots were able to regenerate damaged leaves, the less the impact of natural enemies.

Discussion

Several parameters are associated with life tables. The parameter x represents the age class or cohort for the interval considered. The number surviving at the beginning of the interval is denoted l_x and the number dying during the interval is denoted d_x. The rate of mortality expressed as the number dying as a proportion of the number entering the age interval is denoted q_x. The parameter T_x is the average number alive per cohort (L_x) summed over all cohorts ($T_x = \Sigma L_x$). The mean expectation for further life for those alive at the beginning of the interval is e_x and is the ratio of T_x/l_x. A specific mortality factor is usually referred to as a function, abbreviated d_xF. In studies of leaves a further parameter must be considered which we will refer to as leaf 'condition' (c_x). An animal cannot be partially dead but a leaf can be. The parameter c_x, therefore, merely represents the average proportion of the individual leaf which remains alive. Therefore l_x represents a value for the number present at the beginning of the interval (n_x) weighted for the average leaf condition (c_x) by deriving the product of the two ($l_x = n_x c_x$). The life table is actually a leaf budget for successive cohorts where losses are ascribed proportionally to various agents of mortality such as insects, disease, frost, etc. Leaf death refers to whole leaf 'equivalents' and may represent a composite of several leaves.

Table 2 presents a time-specific life table for all leaves which were quantitatively examined from the samples of 40 shoots from all sites. This is intended only as an example. Age-specific tables could be constructed in the same manner. Table 3 lists the d_x values for each d_xF on each cohort. Note the number of leaves present (n_x) changed from 870 to 699 from cohorts 6 to 7 indicating a loss of 171 leaves. The leaf

Table 1. Rates of leaf production and leaf death on waterhyacinth (*Eichhornia crassipes* (Mart.) Solms.) shoots at several sites. Plants were generally in poor condition at sites with shoots showing large leaf deficits (death rates exceeding leaf production rates).

Site No.	Site	Dates	Time (days)	Leaves/Day			Primary Mortality Factor/s
				Production	Death	Difference	
4	Gainesville	10.iii.1981– 7.x.1981	211	0.126	0.098	+0.028	*Neochetina*
6A	White Springs	13.viii.1980– 14.i.1981	154	0.048	0.085	−0.037	*Neochetina*, Frost
6B	White Springs	27.viii.1980– 14.i.1981	141	0.069	0.119	−0.050	*Neochetina*, Frost
6C	White Springs	6.v.1981– 4.xi.1981	173	0.087	0.106	−0.019	*Neochetina*
8	Snake Creek	30.x.1980– 10.xii.1980	40	0.125	0.152	−0.027	Cattle browsing
9A	L. Okeechobee	6.xi.1980– 5.ii.1981	92	0.085	0.135	−0.050	Senescense
9B	L. Okeechobee	29.iv.1981– 16.vii.1981	78	0.021	0.103	−0.082	Drought, *Sameodes*
10	Deland	26.iii.1981– 24.ix.1981	182	0.128	0.127	+0.001	Senescense
11A	Coral Springs	29.v.1981– 3.ix.1981	97	0.075	0.094	−0.019	*Sameodes*
11B	Coral Springs	13.x.1981– 12.xi.1981	30	0.108	0.114	−0.006	*Sameodes*
13	Wekiwa Springs	22.x.1981– 18.xi.1981	27	0.158	0.103	+0.055	None
14	West Palm	23.xii.1981– 30.xii.1982	372	0.114	0.124	−0.010	*Neochetina*
15	Palm Aire	28.i.1982– 6.viii.1982	190	0.150	0.138	+0.012	*Sameodes*

condition (c_x) changed from 49.9% to 38.4% for a loss of 11.5%. Thus $l_x(= n_x c_x)$ changed from 434 to 268. Effects of mortality factors, however, were based only upon c_x and represented cumulative effects. For example, adult weevil feeding accounted for *c.* 8% of the total 71.6% $(1 - c_x)$ deterioration in average leaf condition from cohort 1 to cohort 7. This must be converted in such a manner as to determine effects of weevil feeding upon cohort 6 leaves only. It can be determined that weevil feeding comprised *c.* 10% of the total leaf damage. The change in l_x was a loss of *c.* 77% so weevil damage contributed *c.* 8% to d_x for cohort 6 (i.e. 10% of 77%). Summing these values for all d_xF the total d_x for cohort 6 is 166. Subtracting d_x from l_x yields 268, the l_x for cohort 7. Dividing the l_x for cohort 7 by that for cohort 6 yields the proportion of cohort 6 surviving (S_x) which is 62%. Carrying through the calculations as described earlier, the expected life (e_x) for cohort 6 leaves is an additional 2 leaf positions. In other words, leaves which survive to position 6 can be expected to live to position 8, on average.

Table 2. Time-specific life table analysis for waterhyacinth (*Eichhornia crassipes* (Mart.) Solms.) leaf mortality. The data represent averages based on plants collected throughout Florida and during all seasons and, as such, represent a hypothetical 'average' population of leaves.

Leaf Position Cohort (X)	N_x	C_x	l_x	d_x	1000 q_x	e_x	L_x	T_x	S_x
0	1160	1.000	1160	235	202	5.37	1042	5600	1000
1	1160	.797	925	31	34	5.01	910	4558	801
2	1160	.771	894	17	19	4.12	886	3648	783
3	1160	.756	877	134	153	3.41	810	2762	768
4	1118	.665	743	136	183	2.89	675	1952	651
5	1028	.590	607	173	285	2.46	520	1277	532
6	870	.499	434	166	382	2.16	351	757	381
7	699	.384	268	119	444	1.95	208	406	236
8	518	.288	149	70	470	1.74	114	198	131
9	334	.238	79	50	633	1.56	54	84	71
10	187	.154	29	17	586	1.50	20	30	26
11	82	.150	12	9	750	1.25	8	10	7
12	38	.075	3	2	667	1.00	2	2	2
13	10	.090	1	1	1000	0	0	0	1

It should be obvious that leaves are not all equally important to the plant. A leaf must remain healthy to produce photosynthate and thereby contribute to energy demands. Older leaves are less likely to further contribute to the plant and have less remaining life to do so. The importance of a leaf cohort should be proportional to the area under the survivorship curve (Fig. 5) beyond that cohort and this value is equivalent to T_x. If the data represented observations over time this value would be leaf-days but in the time-specific case we will refer to this as leaf-cohort duration.

In theory, the more important biological control agents are those that reduce leaf-cohort duration the most; i.e. those that affect survival of the youngest leaves. In reality, this is not strictly true. The loss of a leaf must also be weighed against the cost of producing it. Loss of an immature leaf may therefore be less important than loss of a mature leaf. Generally, however, damaged immature waterhyacinth leaves continue to develop and are usually not lost. Thus, although considerable function may be lost, the structural cost would be considerable. The loss of leaf area persists for the life of

Table 3. Mortality factors (d_xF) for leaves from Table 2 with contributions of each d_xF to mortality rates of each cohort. Numbers are number dying of the 1160 base populations.

d_xF	Leaf Position Cohort Interval													
	0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–11	11–12	12–13	Total
S. albiguttalis	136	15	4	25	20	18	11	8	3	3	1	1	0	241
Arzama densa	2	0	0	0	0	0	0	0	0	0	0	0	0	2
Neochetina adult	38	5	3	15	11	11	9	5	3	2	0	0	0	102
Neochetina larva	33	7	5	42	39	45	45	30	15	9	2	1	0	273
Spider mite	4	1	1	4	3	3	2	1	1	0	0	0	0	20
Waterhyacinth mite	0	0	0	5	4	6	5	3	2	1	0	0	0	26
Zonal leaf spot	0	0	0	2	4	9	11	9	6	3	1	0	0	45
Frost	4	1	1	4	6	8	6	2	0	0	0	0	0	32
Partial leaf	0	0	1	11	10	13	10	5	3	3	0	1	0	56
Other	18	2	2	26	38	60	68	56	37	28	10	7	1	353
Total (d_x)[1]	235	31	17	134	135	173	167	119	70	49	14	10	1	1155

[1] Values of d_x may not agree with Table 2 due to rounding error.

the leaf. Further, we have not found compensatory increases in leaf production rates as a plant response to loss of leaf area. Since damage persists through the life of the leaf, agents which attack young leaves reduce leaf-cohort duration, and probably productivity, the most. In the example (Fig. 5) most mortality factors, such as pathogens and mites, affected only old leaves which were near the end of their life expectancy. Introduced biological control insects were essentially the only factors affecting young leaves (i.e. cohort 1). If it is assumed that neither *S. albiguttalis* nor *Neochetina* spp. were present and the life table data recalculated accordingly, the survivorship curve represented by the dotted line in Fig. 5 results. In this case, a new leaf has a life expectancy (e_x) of 7.3 cohort positions whereas otherwise the e_x was 5.4. Leaf cohort duration increased from 5600 to 8467 indicating that the insects account for a 34% reduction even without substantial shoot mortality.

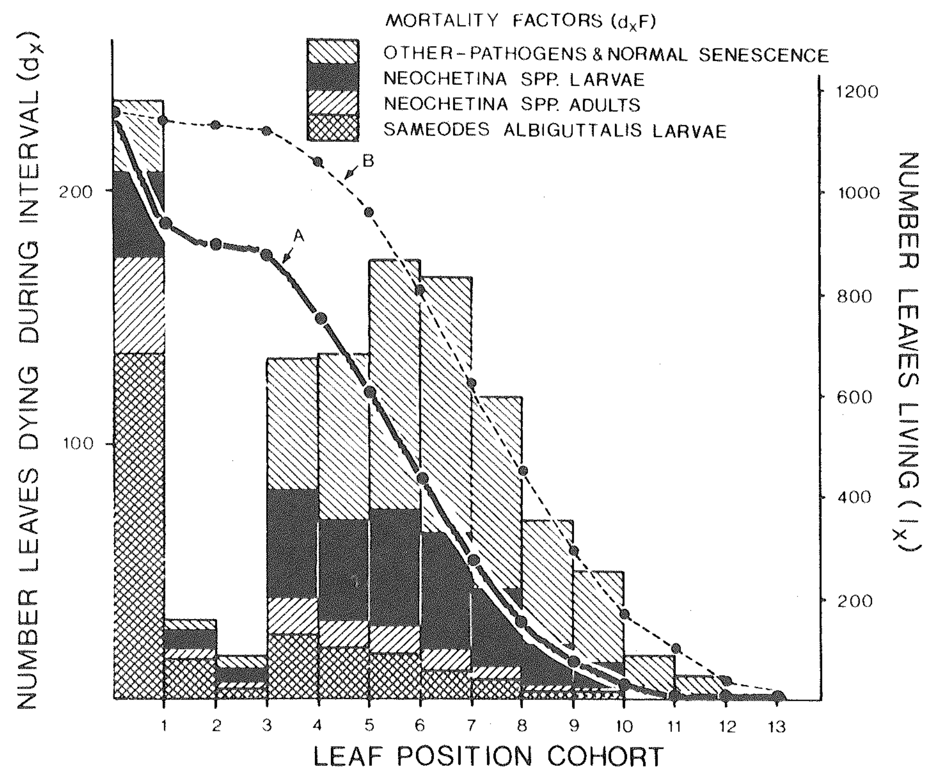

Fig. 5. Life table data from all plants examined from the samples consisting of 40 shoots averaged by leaf position cohorts over all dates and all sites. Line A shows the trend in survivorship (l_x) as leaves age and the bars represent the mortality factors (d_x) responsible for decreasing survivorship. Line B represents calculated survivorship after mathematically removing and re-distributing leaf mortality caused by *Sameodes albiguttalis* (Warren) larvae and *Neochetina* spp. larvae and adults. The result is a 50% increase in survival which indicates that these factors reduce leaf longevity by *c.* 34% primarily through the destruction of young leaves.

Waterhyacinth seems adapted to withstand leaf injury by rapid leaf production thereby soon replacing those injured. The impact of stress on a waterhyacinth shoot depends upon the replacement rate of a damaged leaf relative to the developmental time of the stress factor. Organisms which feed upon or infect leaves, then, are faced with the problem of being able to persist on the shoot. Either their life cycle must be in phase with the leaf's life cycle or they must be able to move to new leaves or other parts of the plants when the leaf dies. The various agents have apparently solved this problem in different ways. For biological control to be effective defensive strategies of the plant must be overcome. Only *S. albiguttalis* and the two weevil species seem to consistently do this.

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