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NUTRITIONAL ECOLOGY OF SEED-SUCKING INSECTS OF SOYBEAN AND THEIR MANAGEMENT

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Most aspects of an insect's life, such as behavior, physiology, and ecology are, in one way or another, inserted within the context of nutrition. The study of insect nutrition has evolved from the knowledge of basic nutritional requirements, amounts and rates of food eaten, digested, assimilated and converted to tissue growth (i.e., insect dietetics), to a more involving concept, including changes in behavior and physiology, as an answer to a variable environment, seeking to reach an ideal life history performance. This will have a cost to the relative contribution to the next generation (i.e., a cost of fitness), ending up with ecological and evolutionary consequences, such as the attainment of different lifestyles. This holistic view in the study of insect nutrition is called 'insect nutritional ecology' (Scriber & Slansky, 1981; Slansky 1982 a, b; Slansky & Scriber, 1985; Slansky & Rodriguez, 1987).

Within this broad scope of nutritional ecology, the seed-sucking guild of insects associated with soybean [*Glycine max* (L.) Merrill] will be analyzed. This guild includes mostly pentatomids, and more than 50 species associated with soybean fields have been recorded in the Americas (Panizzi & Slansky, 1985a). Of these, only few species are important pests, such as the cosmopolitan southern green stink bug, *Nezara viridula* (L.), the green stink bug, *Acrosternum hilare* (Say), the small green stink bug, *Piezodorus guildinii* (Westwood), and the brow stink bugs of the genus *Euschistus*. Other soybean seed-suckers include hemipterans of the families Alydidae and Coreidae (Kogan & Turnipseed, 1987; Panizzi, unpublished).

The characteristics of the soybean seed and their impact on insect performance will also be discussed. The seed-suckers life history strategies, including aspects of feeding, development, reproduction, natural enemies and defense, alternate host plants, and decision-making and responses to variable biotic and abiotic factors,. will be covered. In addition, taking in account their feeding habits, references will be made to tactics for management of seed-sucking insects, such as manipulation of planting time and varieties of different maturity dates, use of trap crops and use of resistant varieties. Finally, directions for future research within the scope of nutritional ecology will be suggested.

SOYBEAN SEED CHARACTERISTICS AND IMPACT ON INSECT PERFORMANCE

Several seed characteristics (e.g., nutrient and water content, presence of allelochemicals, seed size, pod wall thickness, pod pilosity, seed abundance, etc.) have positive or negative effects on nymph and adult performance of seed-suckers associated with soybean. This is particularly evident to seed-suckers feeding on seeds of different plant species (see references in Slansky & Panizzi, 1987, for several species of different families of Hemiptera), and to a lesser extent, to seed-suckers feeding on seeds or pods of soybean at different phenological stages. For example, *N. viridula* and *P. guildinii* show a different nymph and adult performance when fed glabrous or pubescent soyben pods, or mature or immature soybean seeds (Tables I and II).

Nutrients and allelochemicals

Compared to other plant parts, seeds tend to be packages of highly concentrated nutrients (Slansky & Scriber, 1985). In the case of soybean, seeds have a relatively high content of protein (32.2% dw) and oil (21.8% dw) when compared to seeds of other common legumes, such as green bean, *Phaseolus vulgaris* L. (24.2 and 1.2% dw, respectively – Earle & Jones, 1962). In addition, protein quality of soybean seeds, measured as weight gain/protein ingested (protein efficiency ratio-PER) is higher (2.4) than that observed to green bean seeds (0.5), as well as the percent protein digestibility of seeds as determined for rats (70.1 – 82.9 for soybean and 36.3 – 56.0 for green bean; Bressani & Elias, 1980).

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TABLE I

Comparison of nymph and adult *Nezara viridula* and *Piezodorus guildinii*, showing differences in performance when feeding on soybean pods or seeds at different phenological stages and with different structural characteristics (initial number of insects in parentheses)

Species/Food	Nymph*		Adult		References
	Total mortality (%)	Total developmental time** (X ± SE)	Total longevity** (X ± SE)	Eggs/female (X ± SE)	
Nezara viridula					Panizzi & Slansky (unpublished)
Soybean pods (glabrous) (20)	10.0	24.4 ± 0.58 b^{+}	–	.	
Soybean pods (pubescent) (40)	22.5	23.2 ± 0.70 b	38.4 ± 3.1^{++}	110.0 ± 11.8	
Soybean seeds (mature) (40)	32.5	35.1 ± 1.53 a	30.1 ± 6.3	23.0^{+++}	
Soybean seeds (immature) (40)	40.0	26.7 ± 0.93 b	–	–	
Piezodorus guildinii					Panizzi & Slansky (1985b) Panizzi (1987b)
Soybean pods (pubescent) (80)	52.5	20.2 ± 0.56 c	69.6 ± 12.8	28.0 ± 16.0	
Soybean seeds (mature) (80)	71.2	23.3 ± 1.30 ab	34.4 ± 6.4	9.3 ± 2.4	
Soybean seeds (immature) (80)	77.5	21.3 ± 0.84 bc	–	–	

*From 2nd stage to adult.

**Data for females.

+ Means followed by the same letter, are not significantly different at $P = 0.05$ using Duncan's multiple range test.

++ Mean value for females + males.

+++ Only one female oviposited out of 10.

As the soybean seeds mature, changes in their chemical composition varies, as well as the water content. For example, vitamins decrease markedly as the seeds mature and increase upon sprouting (Bates & Matthews, 1975). Protein and lipid contents of green mature seeds (seeds full size and plant leaves starting to yellow) change from 36.7 to 39.4% dw and from 20.5 to 21.5% dw, respectively, with maturation; water content decreases from 69.4 to 8.0% during this period (Bates et al., 1977). In addition to these variabilities, the chemical composition of soybean seeds changes with the feeding activity of seed-suckers, i.e., oil content will decrease and protein will increase; changes in the percentage of different fatty acids will occur as well (references in Panizzi & Slansky, 1985a).

In addition to the nutrients mentioned above, allelochemicals or secondary substances are present in soybean seeds, which have or may have toxic and/or repellent properties to insects. These include lectins (phytohemagglutinins), which are mostly localized in the cotyledons reaching maximum content at seeds maturity (Rüdiger, 1984). Lectins of green bean seeds have a severe toxic effect on vertebrates (Liener, 1980) and on insects as well (Janzen et al., 1976). Soybean lectins are known to inhibit the growth of *Manduca sexta* (Johannson) larvae (Shukle & Murdock, 1983). Other allelochemicals common on seeds of *Glycine* spp. and *Phaseolus* spp., include flavonoids, alkaloids, steroids and phenolic acids (Kogan, 1986). Also referred in the literature are antinutritional factors present in soybean seeds, such as trypsin inhibitors, anti-vitamins and phytic acid, among others (Liener, 1979).

Data on the impact of allelochemicals on the seed-sucker performance are very limited. No studies were found in the literature on this subject for seed-sucking insects associated with soybean. However, phytoalexins (isoflavonoids), a group of inducible antibiotic compounds, have been shown to be active against herbivores, including soybean leaf eaters (Hart et al., 1983). The fact that nymphs of *N. viridula* and *P. guildinii* showed greater mortality, and nymphs and adults of *N. viridula*, showed greater feeding preference for immature soybean pods, compared to immature soybean seeds (Table II), suggest that, by removing, the pod walls, phytoalexins were produced, having toxic and/or repellent effects on the insects; these compounds are known to be induced by mechanical injury (Kuc et al., 1976).

Physical/structural characteristics

Many physical/structural characteristics of seeds and/or pods, such as pilosity, seed hardness, space between pod wall and seed, may hinder nymphs of having a normal feeding

TABLE II

Total mortality of *Nezara viridula* and *Piezodorus guildinii* nymphs, and feeding preference of *N. viridula* nymphs and adults exposed to immature soybean pods and seeds. The greater nymph mortality on, and the smaller feeding preference for immature seeds, suggest a possible impact of phytoalexins (induced by injury during pod wall removing) repelling or being toxic to the insects (initial number of insects in parentheses; from Panizzi 1987a)

Species/Food	Total mortality (%)		Feeding preference frequency^{+}			
			Nymphs		Adults	
			A	B	A	B
Nezara viridula	Test 1	Test 2				
Soybean pods (immature) (40)	22.5	32.5	227*	182	64*	53*
Soybean seeds (immature) (40)	40.0	65.0	185	162	39	31
Piezodorus guildinii						
Soybean pods (immature) (80)	52.5	–	–	–	–	–
Soybean seeds (immature) (80)	77.5	–	–	–	–	–

$^{+}$ A = total number of times feeding or on the food, B = total number of times feeding.

*Asterisk indicates significant difference at P = 0.05, using chi-square test.

TABLE III

Comparison of nymph survivorship of different species of seed-sucking insects, feeding on seeds or pods of soybean at different phenological stages and with different strutuctural characteristics; note the deleterious effects of pubescence and hardness of seedcoat on most species; *Megalotomus parvus*, however, seems to be more adapted to feed on mature seeds than on immature pods (initial number of insects in parentheses)

Species/Food	Mortality during 2nd Instar (%)	References
Nezara viridula		Panizzi & Slansky (unpublished), Panizzi & Rossini (1987)
Soybean pods (glabrous) (20)	0.0	
Soybean pods (pubescent) (40)	10.0	
Soybean seeds (mature) (40)	15.0	
Soybean pods (pubescent and mature) (60)	81.7	
Piezodorus guildinii		Panizzi (1987b)
Soybean pods (pubescent) (60)	27.5	
Soybean seeds (mature) (60)	47.5	
*Thyanta accerra**		Jones (1979)
Soybean pods (pubescent) (50)	42.0	
Soybean pods (glabrous) (50)	10.0	
Megalotomus parvus		Panizzi (unpublished)
Soybean pods (pubescent)	71.6	
Soybean seeds (mature)	10.0	

*Mortality during total nymph developmental time.

activity. In soybean, for example, early instar nymph mortality is probably related to both, presence of pod hairs (trichomes) and hardness of the seedcoat; removal of these hairs decrease early instar nymph mortality of several species of hemipterans. When seed hardness and dried pubescence, as in the case of mature soybean pods, act together, a more drastic mortality of young nymphs occurs. However, the hemipteran *Megalotomus parvus* (Westwood) (Alydidae) seems to be more adapted to feed on mature seeds than on immature soybean pods, in contrast to what is observed for pentatomids (Table III). Interesting to note that young nymphs of *N. viridula* all die when feeding on pods of the wild legume *Sesbania vesicaria* (Jacq.) Ell., but most survive on exposed seeds; this is because young nymphs are unable to reach the seeds in the pods due to an air space that separates the seeds from the pod wall [lenght of second instar (first instar nymphs do not feed) mouthparts is ca. 1.82mm; distance of seeds from pod walls ranges from 2 to 4 mm; Panizzi & Slansky, unpublished].

Seed abundance and size

Seed abundance and availability to seed-suckers is a major factor regulating their dynamics on diverse ecosystems. In the case of soybean, hemipterans need to rapidly colonize the field as the seeds appear, because this is an ephemeral nutritional resource. These insects start colonization with the setting of pods (except *P. guildinii,* that usually appears during flowering) with the population peaking during the filling of pods. As early-maturing varieties senesce, and become unatractive for feeding and reproduction, adults move to later maturing varieties (Todd & Herzog 1980; Panizzi & Slansky, 1985a). As the soybean crop is harvested migration to alternate host plants occurs (Section Host plants). Usually, the hemipterans migrate to native leguminous plants and/or to other plants, such as those of the genus *Brassica,* as in the case of *N. viridula.* These plants provide nutrients during periods of low food sources availability. In the north area of Paraná state (23°S latitude), *P. guildinii* explores wild leguminous plant species of the genus *Indigofera,* which provide seeds during most of the year (Panizzi, unpublished).

Few studies have been done on the influence of seed size and abundance on seed-suckers nutritional ecology (Slansky & Panizzi, 1987). On soybean, it is known that small-seeded genotypes (< 10g per 100 seeds) show less damage than larger-seeded cultivars (> 13g per 100 seeds). This is because the former cultivars have two to three times greater number of pods-seeds/plant than the later; with the number of seeds damaged/day by hemipterans being relatively constant [e.g., 1.8 (Ishikura et al., 1955); 3.9 (Kishino, 1980); 3.4 - 3.7 (Panizzi et al., 1986)] it will result in a less percentage of damaged seeds for cultivars with a greater number of pods-seeds/plant, compared to ones with smaller number of pod-seeds/plant (Table IV).

SEED-SUCKER LIFE HISTORY STRATEGIES

Feeding, digestion, excretion, and quantitative food utilization

The Hemiptera obtain nutrients and water through the stylets, which are inserted into the food source. They are known to produce a saliva that will solidify on ejection forming the stylet-sheath, and to produce a watery saliva that contains digestive enzymes (Miles, 1972). Stylet-sheaths have been used as an indicative

TABLE IV

Comparison of damage inflicted by pentatomids on soybean genotypes with large seeds (> 13g per 100 seeds) and small seeds (< 10g per 100 seeds). Note that small seeded genotypes show a greater number of pods and seeds/plant, than large-seeded genotypes, resulting in less % damaged-seeds

Genotypes	Number/Plant				Punctures/ pod	References
	Pods	Seeds	Damaged seeds	Damaged seeds (%)		
Large-Seeded	42.3	67.5	10.1	15.0	–	Panizzi et al. (1986)*
Small-Seeded	78.5	115.1	9.6	8.3	–	
Large-Seeded	31.2	–	–	99.3	-	Link & Estefanel (1982)**
Small-Seeded	65.4	–	-	83.0	–	
Large-Seeded	–	–	–	–	28.9	Rossetto et al. (1981)***
Small-Seeded	–	–	–	-	11.9	

*Greenhouse plants submitted to one *N. viridula* attack during two days.

**Field plants submitted to heavy attack by several species of pentatomids, mostly *N. viridula.*

***Greenhouse plants submitted to *N. viridula* attack. Mean values of punctures/pod obtained by visual examination, examination under the stereoscope, and using a dye.

of feeding activity of *N. viridula* on immature soybean seeds (Bowling, 1980).

Feeding punctures on soybean seeds cause minute darkish spots, and chalky areas appear, which are air spaces produced when the cells contents are drawn out (Miner, 1966). Later, dark discoloration may surround the punctures and the inner membrane of the seedcoat may be abnormally fused to the cotyledons (references in Panizzi & Slansky, 1985a).

In general, seed-sucking insects are not adapted to feed in foods other than seeds. For example, nymphs of *N. viridula* starve and die when offered stems or leaves of soybean (Jones, 1979; Panizzi & Slansky, unpublished). Although polyphagous and specialized to feed on seeds, seed-sucking hemipterans show differences in performance depending on species offered even within one plant family. For instance, the pentatomids *P. guildinii* and *N. viridula* have their reproductive performance, longevity and survivorship, and adult fresh body weight, drastically affected by feeding on seeds of leguminous plants of different species (Panizzi & Slansky, 1985b, and unpublished). Also, food-switching is an important component of the nutritional ecology of hemipterans (Section Host plants).

Facultative predation and/or cannibalism has been reported for seed-sucking hemipterans. The pentatomid *N. viridula* may show cannibalism when reared in the laboratory, mostly 4-5th instar nymphs that attack molting and teneral late instars and adults (Harris & Todd 1981; Kester et al., 1984); eggs are also consumed by adults when they are not removed from rearing cages after certain period of time following oviposition (Panizzi, personal observations).

Quantitative food utilization studies on the seed-sucking guild are not common, and data are available four only few species (Slansky & Panizzi, 1987). In general, consumption rates of both nymphs and adults, are low, but growth rates are moderately high, and assimilation efficiency (= approximate digestibility), net growth efficiency (= efficiency of conversion of digested food) values, are high, as compared to other feeding guilds, such as foliage-chewing Lepidoptera (Table V).

Development

Hemipterans pass through five nymphal stadia before reaching the adult stage. The newly hatched nymphs usually stay on their egg shells during the first instar. Feeding during this period usually does not occur, as in the case of *N. viridula* (Bowling, 1980). The young nymphs have a strong tendency to aggregate, though this habit diminishes as development advances (Kiritani, 1964).

Soybean seeds are inaccessible to first instar nymphs. Not only the characteristics of the soybean pod (e.g., hairyness, thickness of pod wall) but the size and weak structure of the mouthparts prevent these young nymphs from feeding. Gregariousness apparently compensates for the inability of the nymphs to feed. A synchronization in hatching and molting is observed during this phase of development. The colony develops like a whole and a stimulatory group effect may be acting. During

TABLE V

Comparison between seed-suckers (nymphs) and foliage chewing (larvae) with relation to quantitative food utilization, measured by several parameters*. Note that, except for RCR, values for all parameters are higher for seed-suckers than for foliage-chewing insects (from Slansky & Scriber 1985)

Feeding Guilds and Limits	RCR		RGR		AD		NGE	
	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range	$\bar{X}$	Range
Seed-suckers	0.36	0.14-0.58	0.27	0.10-0.57	73	50-92	89	40-96
Foliage-chewing**	1.46	0.31-6.60	0.17	0.03-0.80	41	12-98	37	2-93
Characterization limits								
Low	<1		<0.1		<30		<40	
Moderate	1-2		0.1-0.6		30-50		40-60	
High	>2		>0.6		>50		>60	

*RCR = relative consumption rate; RGR = relative growth rate; AD = approximate digestibility; and NGE = net growth efficiency. RCR and RGR are expressed as mg dw/day/mg dry larval weight. AD and NGE are expressed as percentage values.

**Lepidoptera feeding on tree foliage.

this period muscle and cuticle hardening occurs, and the nymph metabolism is mainly based on the energy accumulated on the previous stage (egg) by the female. Feeding on this period is not critical, but any disturbance that may occur on the colony will threat survival.

During the second instar, nymphs move from the egg shells and aggregate on the fruiting structures of the soybean plant. This is an evidence that their required nutrients are present in the seeds, rather than in the leaves, flowers or stems. In general, nymph mortality of several species of pentatomids tends to be greatest during the second instar (e.g., Villas Bôas & Panizzi, 1980; Panizzi & Herzog, 1984; Panizzi 1987b). However, with the increase of group size, mortality of *N. viridula* will decrease (Kiritani, 1964). This is an evidence that gregariousness is an adaptation for feeding, and has a positive effect on survival of young nymphs.

As the nymphs advance in their development the gregarious behavior seems to diminish. During the third instar, as is observed to *N. viridula,* nymphs may split into smaller groups clustered on feeding sites and in nearby shelters. However, they may stay as a whole group up to the third instar or even later, depending on the availability of the food in that particular feeding site. Often, as the nymphs get bigger, the increasing demand for food will lead to the decision of stay as a whole group or split in smaller groups and look for alternative favorable feeding sites. In soybean fields both situations can be observed. When the nymph colony is perturbed gregariousness is temporarily broken, and depending on the intensity of the perturbation, nymphs may return to the previous situation or form small groups.

During the fourth instar, a greater competition for food is observed, and as a result nymphs start dispersing. Fourth and fifth instar nymphs of *N. viridula* and *P. guildinii* are the major nymphal ages involved in colonization of soybean fields by walking (Panizzi et al., 1980; Schumann & Todd, 1982).

The fifth instar nymph may be considered the most critical in the whole nymphal development of hemipterans. During this instar, the insect must feed on a highly nutritional food, in order to originate an adult with maximum reproductive potential. Yeargan (1977) found fifth instar nymphs of *A. hilare* damaging a greater percentage of seeds than any other stage, including adults. Mortality during fifth instar, particularly at the time of molting to an adult is high, similarly to what occurs during the second instar. Probably, the profound modifications that occur in shape and body constitution, with the insect reaching its maturity, have a great impact on survival.

Developmental period of nymphs is known to be affected by temperature, with decreasing temperatures causing a delay in nymphal development (e.g., Kehat & Wyndham, 1972); field data suggest that fifth instar nymphs of *N. viridula* show an arrested development (partial hibernation) with decrease in temperature (Ferreira & Panizzi, 1982). Usually longer time is required for hemipterans to complete the fifth stage compared to earlier stages (e.g., Villas Bôas & Panizzi, 1980; Biehler & McPherson, 1982; Sites & McPherson, 1982; Panizzi & Herzog, 1984; Panizzi & Slansky, 1985b).

After passing through five nymphal stages, hemipterans reach the adult stage. Male and female adults look very much alike, but differences in color, body shape, and principally body size are observed (Table VI). Feeding activity also differ between sexes. Females feed for a greater portion of time than males. This is probably because females require greater amounts of nutrients for reproduction than do males (Lockwood & Story, 1986a).

Host plants

As the hemipterans reach the adult stage, they look for plants were to feed and reproduce. Host plant choice by the adult depend upon several factors, including presence of attractants and/or deterrents, that will make the plant more or less preferred for feeding and/or oviposition. In general, a positive correlation exists between oviposition preference and suitability for nymph development [e.g., *N. viridula* usually does not oviposit on leaves of castor bean, *Ricinus communis* L.; nymphs do not develop well when feeding on fruits of this plant (Panizzi & Meneguin, unpublished)].

As the soybean plants reach pod-setting, field colonization takes place, initially by adults (Costa & Link, 1982), and later by nymphs (Panizzi et al., 1980). When plants senesce, movement to alternate food sources occurs, with several plants being used as overwintering hosts. The movement to these plants from soybean, and vice versa, has been studied for several hemipterans in different parts of the world (see references in Panizzi & Slansky, 1985a). This will implicate in switch of food from nymph to adult stages, and/or among sub-

TABLE VI

Comparison between female and male hemipterans associated with soybean, with regard to body size and color

Species Parameters	Female	Male	References
Nezara viridula			
Fresh body weight**	133.8	105.1	Kester et al. (1984)
Piezodorus guildinii			
Fresh body weight**	56.3*	46.6	Panizzi & Slansky (1985b)
Body color	Reddish band along the edge of the body (mature adults)	Yellowish band along the edge of the body (mature adults)	Galileo et al. (1977)
Megalotomus parvus			
Fresh body weight**	33.4*	24.6	Panizzi (unpublished)
Body color	Dark brown; no clear band on body sides	Pale brown; clear band on both body sides	
*Leptoglossus zonatus****			
Fresh body weight**	124.8*	102.5	Panizzi (unpublished)

*Asterisk indicates female value significantly greater than male, $P = 0.05$.
**Fresh body weight (mg) of newly emerged adults feeding on soybean pods.
***This coreid usually feeds on corn, but may feed on soybean.

sequent generations, having a variable impact to the hemipterans. This switch in food source and consequent impact on seed-sucker performance has been little investigated, and seems to be an important component of the nutritional ecology of this feeding guild (Table VII).

Reproduction and longevity

After the plant is chosen by adult hemipterans and feeding has taken place, reproduction will follow. The mating behavior and consequent oviposition of many species of hemipterans have been studied. The duration of copulation is greatly variable. For example, to *N. viridula* it may last from 1 to 165 hours (Harris & Todd, 1980). Males appear to regulate duration of copulation, but either the duration or frequency of copulation does not correlate with egg fertility (McLain, 1981).

Mating activity and oviposition are influenced by photoperiod and hemipterans seem to have a diel periodicity. For example, *N. viridula* will show a peak of oviposition around 7:00 PM and after 10:00 PM oviposition is almost none (Harris & Todd, 1980). Sound production by males and females of *N. viridula*, is an important component associated with mating behavior (Harris et al., 1982).

N. viridula females mate repeatedly and eggs are laid in masses with increasing size and decreasing intervals between the successive ovipositions; repeatedly mated females begin oviposition after two to four weeks of their emergence, and can deposit fertile eggs for a relatively long period, after the death of the paired males. Unmated females can produce a normal number of unfertilized eggs, and live longer than the mated ones (Kiritani, 1963).

Adult longevity of seed-sucking hemipterans has been studied in many species, and varies according to the insect sex, sexual activity, and nutritional quality of the food. In some cases [e.g., *Euschistus heros* (Villas Bôas & Panizzi, 1980)] males are reported to live longer than females. Reduced longevity of reproductive females may be due to the "strain" of egg-laying, which, by diverting energy and nutrients away from the maintenance of the females, shortens its life (for further discussion, see Slansky, 1980). On the other hand, Panizzi & Smith (1977) found similar longevities between sexes of *P. guildinii* feeding on soybean pods. Also, for the stink bugs *A. hilare* (Miner, 1966) and *Thyanta perditor* (F.) (Panizzi & Herzog, 1984), there is either little difference in longevity of males and females, or females live longer than males. Clearly, further evaluation of the reproductive strain hypothesis, using data from a variety of insects, is necessary to assess its validity. Differences in longevity between sexes is also influenced by the food nutritional

TABLE VII

Impact of food-switch from nymph to adult, on reproductive performance and longevity of hemipterans associated with soybean. In general, food-switch from nymph to adult improves adult performance, specially if adult food is inadequate, as in the case of *Nezara viridula* fed raw peanuts; if adult food is adequate, a change in food from nymph to adult will tend to be detrimental to adults, as in the case of *Piezodorus guildinii* adults fed *Sesbania aculeata* or *Indigofera hirsuta* (number of adults in parentheses)

Adult food source (Nymph)	% Females ovipositing	Number/Female		% Egg fertility ($\bar{X} \pm SE$)	Total longevity^{+} (days)	References
		Egg masses ($\bar{X} \pm SE$)	Eggs ($\bar{X} \pm SE$)			
		Nezara viridula				Panizzi & Slansky (unpublished)
Soybean pods						
(soybean pods)$^{++}$	76.5 (13)	1.9 ± 0.2	110.0 ± 11.8	61.5 ± 10.2	35.6 ± 3.1	
(green bean pods)$^{++}$	90.0 (9)	2.4 ± 0.4	149.1 ± 20.4	70.0 ± 9.6	39.4 ± 3.6	
Peanuts						
(peanuts)$^{++}$	60.0 (3)	3.0 ± 1.0	99.7 ± 50.4	26.1 ± 11.2	32.4 ± 12.3	
(green bean pods)$^{++}$	100.0 (10)	5.7 ± 1.0	*446.4 ± 93.7	*62.3 ± 10.3	52.7 ± 8.0	
		Piezodorus guildinii				Panizzi & Slansky (1985b), Panizzi 1987b
Indigofera hirsuta L.						
(*I. hirsuta* pods)$^{+++}$	90.0 (9)	*12.2 ± 2.2	*204.8 ± 35.9	73.2 ± 3.5	–	
Peanuts						
(*I. hirsuta* pods)$^{+++}$	30.0 (3)	1.3 ± 0.3	3.3 ± 1.2	30.0 ± 15.3	–	
Sesbania aculeata Pers.						
(*S. aculeata* pods)$^{++}$	91.7 (11)	8.4 ± 1.2	205.1 ± 41.4	89.8 ± 3.9	–	
(soybean pods)$^{++}$	83.3 (10)	5.5 ± 1.3	101.9 ± 28.4	94 7 ± 2.0	–	

$^{+}$ Data for females.
$^{++}$ Comparisons of adults fed same food, and nymphs fed different foods.
$^{+++}$ Comparison of adults fed different foods, and nymphs fed same food.
* Asterisk indicates significant difference at $P = 0.05$.

quality. For example, males of *P. guildinii* live longer than females when fed green beans or soybean pods. On peanuts (*Arachis hypogaea* L.) longevity for both sexes is similar, and on mature soybean seeds, females live ca. 2X longer than males (Panizzi & Slansky, 1985b). Thus, food quality may affect adult life both directly (poor food reducing longevity) and indirectly through its effect on reproductive output ("strain").

Natural enemies and defense

Seed-sucking insects are attacked by a variety of natural enemies, including arthropod parasitoids and predators, reptiles, amphibians, birds, mammals, and fungi (references in Slansky & Panizzi, 1987).

Among the arthropods that attack seed-suckers associated with soybean, the hymenopterous egg parasitoids are the most important group of natural enemies. At least 12 species of egg parasitoids of different species of phytophagous pentatomids are reported to occur in South America soybean fields (Panizzi & Slansky, 1985a; Corrêa-Ferreira, 1986). Of these, *Trissolcus basalis* (Woll.) and *Telenomus mormideae* Lima are the major species (Corrêa-Ferreira, 1986).

Tachinids are the most common parasitic flies of seed-suckers on soybean. In North America, at least 13 species of tachnids are reported, and *Trichopoda pennipes* (F.) is the most important species; in South America, *Eutrichopodopsis nitens* Blanchard is the principal tachinid attacking *N. viridula* (Panizzi & Slansky, 1985a; Corrêa-Ferreira, 1984).

Not many data are available concerning predators of seed-sucking insects in soybean agroecosystems. In southern USA, the red imported fire ant, *Solenopsis invicta* Buren, is the predominant predator of *N. viridula* eggs and nymphs (Stam, 1978; Krispyn & Todd, 1982).

Plant characteristics (e.g., plant architecture, odor, etc.) may influence host location by natural enemies. For example, *N. viridula* feeding on plants with an upright growth habit, with fruiting structures more or less exposed, show a higher rate of parasitism by *T. pennipes*, than *N. viridula* on plants with procumbent growth habit (Todd & Lewis, 1976); *N. viridula* is less abundant on lodged soybean plants, as compared to those on the upright position (Link & Storck, 1978). Also, *N. viridula* is apparently less susceptible to *E. nitens* attack when present on the overwintering host plant castor bean, *R.*

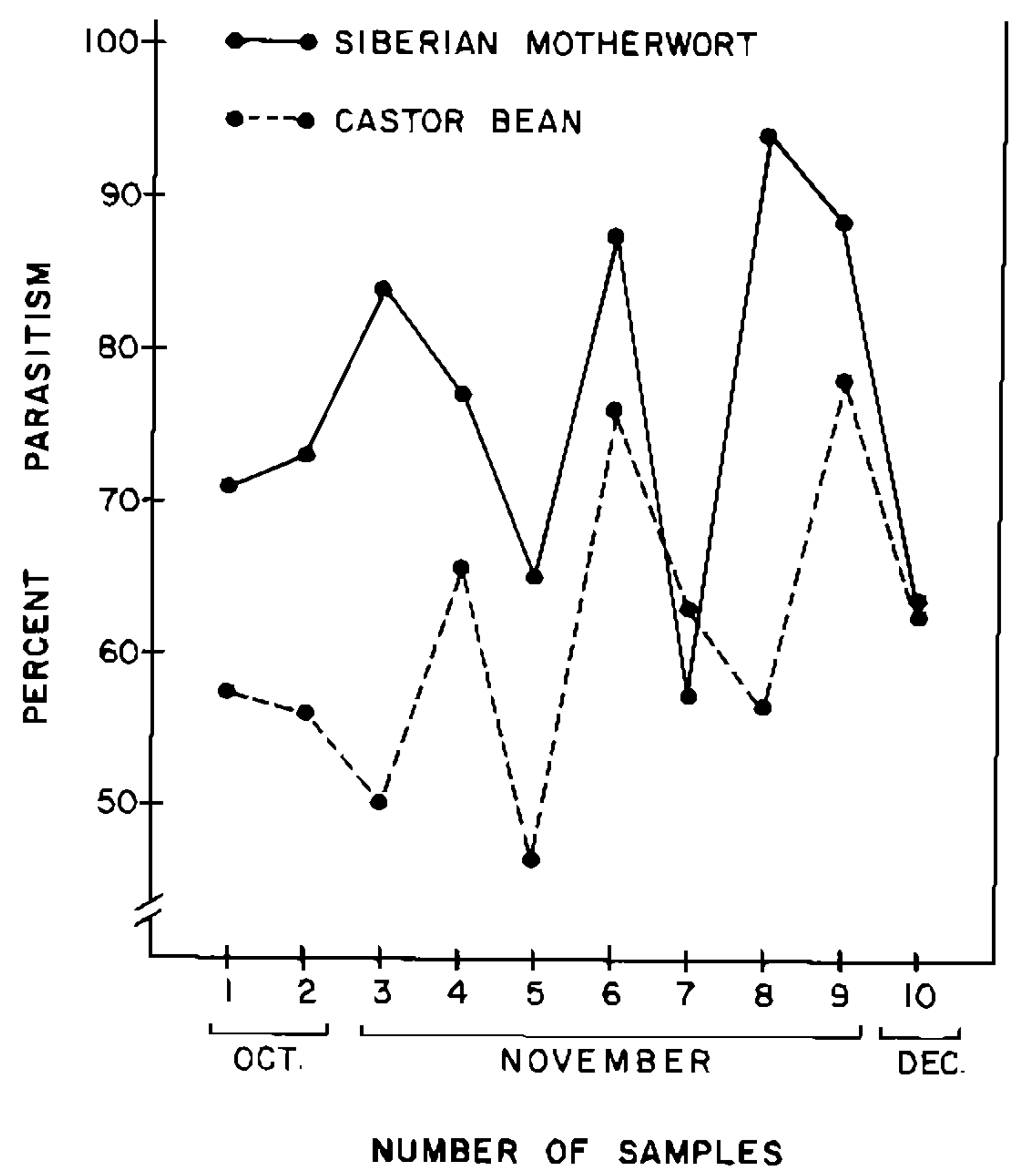

Fig. 1. Percent parasitism by *Eutrichopodopsis nitens* on *Nezara viridula* adults collected on two different overwintering host plants [siberian motherwort, *Leonurus sibiricus* (Labiatae), and castor bean, *Ricinus communits* (Euphorbiaceae)]. Note that stink bugs show a greater rate of parasitism when present on the first host as compared to the second.

communis, than when on siberian motherwort, *Leonurus sibiricus* L. (Fig. 1). Possible reasons to explain this result include the height of the plants (castor bean 1-3 m vs. siberian motherwort < 1m), blooming of siberian motherwort that may attract adult flies of *E. nitens* (flowers are abundant and highly attractive at least to bees), and the more protective habitat provided by siberian motherwort plant communities, as compared to a more open and exposed situation found on castor bean plant communities.

Defensive mechanisms of seed-suckers against natural enemies include cryptic coloration, drop to the ground, aposematic coloration, scent glands, females guard of eggs and young nymphs, and gregarious behavior (see references in Slansky & Panizzi, 1987). Of these mechanisms, gregarious behavior of nymphs, chemical defense produced by metathoracic scent glands by adults (the reason by which they are called "stink bugs"), and nymph (particularly late instars) and adult drop to the ground, are used as defense by the pentatomids *N. viridula* and *P. guildinii* (Panizzi, personal observation). Aggregated nymphs of *N. viridula* suffer less predation by the hemipteran *Podisus maculiventris* (Say) and by the fire ant, *S. invicta* (Lockwood & Story, 1986b).

Coping with variable abiotic and biotic factors

The variable nature of abiotic factors (e.g., temperature, relative humidity, photoperiod) and biotic factors (e.g., food availability and quality, intraspecific and interspecific competition is a constant challenge to seed-suckers. Therefore, they must adapt to this changing environment in order to attempt to achieve their optimal life history performance. For example, with decreasing temperatures *N. viridula* will turn dark in color (Harris et al., 1984). This may be an adaptation to better pull up body temperature when basking in the sun. This basking behavior of *N. viridula* is more pronnounced during early morning (from 7:00 - 9:00 AM) on clear days. On clouded days it is extended and stink bugs can be found on the soybean plant canopy surface around midday; this behavior may be used to improve the effectiveness of insecticide applications (Waite, 1980; see also Lockwood & Story, 1986a). At low temperatures, aggregations formed by *N. viridula* nymphs may accelerate development, increase intake of atmospheric water, and protect against desiccation (Lockwood & Story, 1986b). *N. viridula* hatching is a function of a photoperiodically entrained rhythm, and dependent of temperature (Lockwood & Story, 1985).

Constraints from low food availability can be overcome by obtaining some nutrients from other plant tissues other than seeds, but feeding on seeds is a condition to normal nymph development and reproduction of seed-suckers (Slansky & Panizzi, 1987). When starved, these insects may increase food consumption (e.g., *N. viridula* female gained ca. 27 mg in 24 hours, after being starved during 24 hours; non-starved females gained ca. 9 mg in the same period of time – Panizzi & Rossini, unpublished), and utilize the lipid reserves, which may vary with insect age and food source (Table VIII).

Intraspecific density often improves food consumption, developmental rates, weight gain, and survival, but there is a limit to the benefits of increased density. However, seed-suckers abundance in the field usually do not reach levels of density that will be detrimental to their performance (references in Slansky & Panizzi, 1987).

Interspecific competition is more likely to occur, because of many potential competitors for seeds. In soybean fields in addition to the seed-suckers, many types of organisms may compete for seeds including seed-chewing

TABLE VIII

Body weight and lipid content of adult female+ of *Nezara viridula* fed different foods, and starved continuously for two weeks. Differences in total body lipid content is due to nutritional quality of the food (> for soybean pods than for *Crotalaria lanceolata* pods), and to the use of lipid reserves as a result of starvation (number of insects in parentheses)

Food source	Body weight (dry mg)	Lipid		References
		(%)	(mg)	
Soybean pods	49.6* (7)	18.7*	9.5*	Panizzi & Slansky (unpublished)
Crotalaria lanceolata E. Mey. pods	28.8 (10)	4.6	1.3	
Starved++				
Day 1	47.3* (8)	31.7*	15.0*	Panizzi & Rossini (unpublished)
Day 15	30.1 (8)	10.5	3.0	

* Asterisk indicates significant difference at P = 0.05.
\+ Age 4-12 days.
++ Starved in the presence of water.

Lepidoptera, mites, seed-pathogens, and others. However, this has not been investigated, particularly with regard to the many species of hemipterans that occur simultaneously on fruiting soybean plants.

SEED-SUCKERS MANAGEMENT IN RELATION TO THEIR FEEDING HABITS

Many tactics can be used to manipulate population of seed-suckers in soybean fields, other than the classical use of chemical control (i.e., insecticide application) or management of biocontrol agents (i.e., mainly egg and adult parasitoids). These tactics (see below) take in account feeding habits of seed-suckers, such as preference for fruiting plants, with consequent movement from alternate host plants to soybean at the time of pod-setting. Also, the use of varieties with short reproductive period to avoid seed-suckers attack, and of varieties less preferred, tolerants or with antibiotic attributes will be discussed.

Time of planting

The cultural practice of manipulating time of planting in order to minimize the impact of seed-sucking insects to soybean has been investigated. Results of these studies are somewhat contradictable. For example, early plantings of soybean of the same maturity group are reported to be more damaged than late ones, and a higher number of seed-suckers are reported to occur on early than on late planted soybean (Miner, 1966; Jones & Sullivan, 1978; Panizzi et al., 1979). However, higher populations of stink bugs may be present on late than on early planted soybean, at least for some varieties tested (Schumann & Todd, 1982), and planting date may have a non-significant effect on stink bug populations (Buschman et al., 1984). These contrasting results may be in part explained by the presence of different wild host plants in the vicinity of soybean fields, influencing timing of movement and abundance of population of these insects invading the crop. Also, planting large areas at the same time will dilute the populations of seed-suckers, and by using early maturity varieties (Section Early maturity varieties), most of the damage will be avoided. Clearly, further investigations need to be carried out to test the validity of time of planting to manage this pest problem in soybean. Cultural practice such as this, however, may be limited by economic and agronomic parameters. For example, each variety has its optimum time for planting, and changes in planting time may result in yield loss independent of seed-suckers damage. Time of planting (i.e., early plantings on restricted areas) can also be used as a trap crop (Section *Trap crops*).

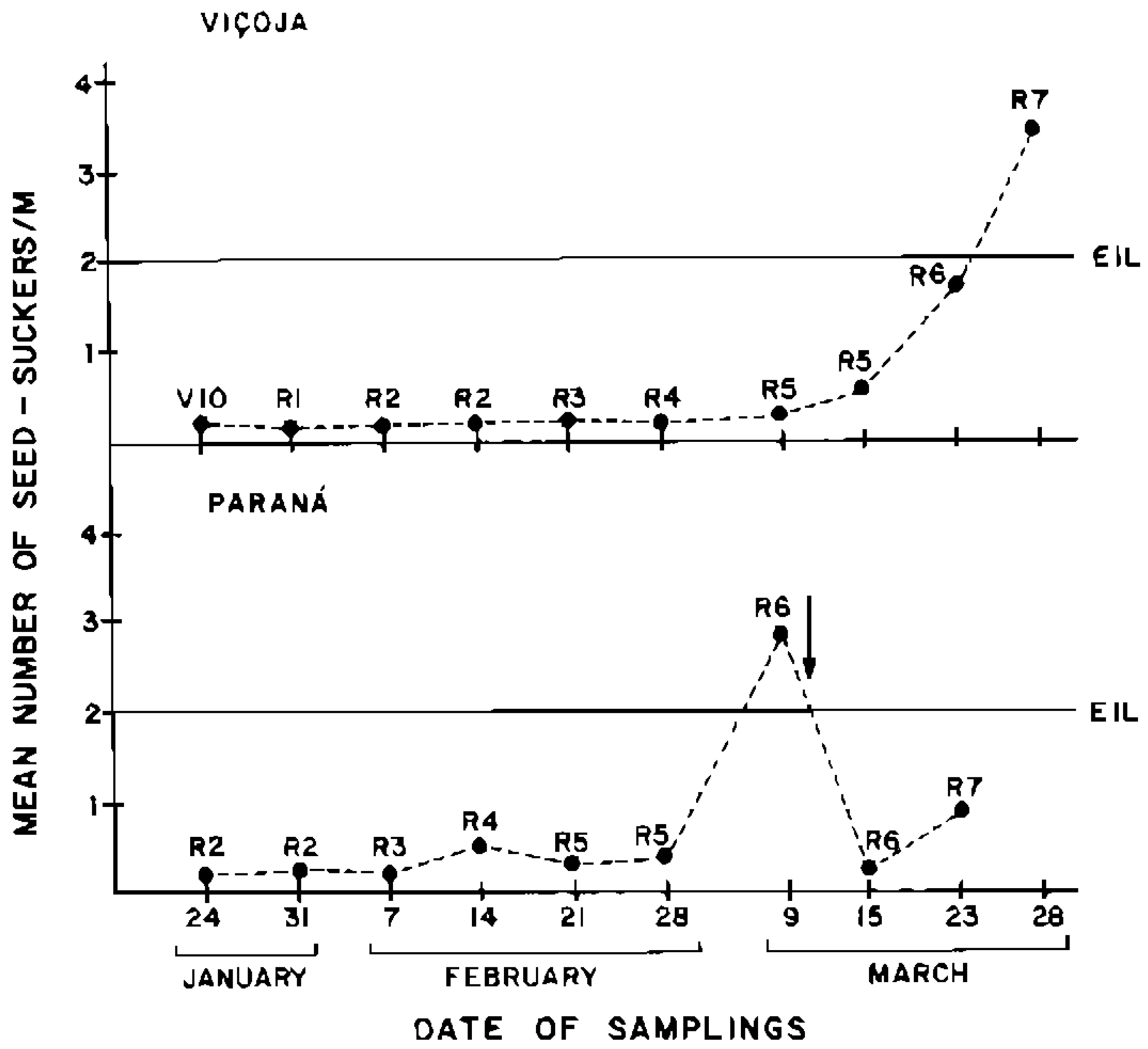

Fig. 2. Dynamics of stink bug populations on soybean of two different maturity groups. Populations will start increasing on the early maturity variety 'Paraná', and insecticide is applied (indicated by the arrow) before spreading of insects to the whole field. This properly timed insecticide application, restricted to the trap area is sufficient to maintain the pest population, on the surrounded later maturity variety 'Viçoja', below the economic injury level (EIL), at the time of pod-filling, when soybean is more susceptible to this pest attack (from Panizzi, 1980). Growth stages of soybean (from Fehr et al., 1971): V10 = ten nodes on the main stem with fully developed leaves beginning with the unifoliolate node. R1-R2 = beginning bloom - full bloom. R3-R4 = beginning pod-full pod. R5-R6 = beginning seed-full seed. R7 = beginning maturity.

Early maturity varieties

Generally, early maturity varieties of soybean escape seed-suckers damage by maturing before insect populations reach a level that may cause reduction in seed yield. Several studies indicate that as the period from blooming to maturation increase, the damage caused by seed-suckers also increases (references in Panizzi & Slansky, 1985a). In Brazil, where the problem with seed-suckers is severe early maturity varieties are widely grown. However, the massive use of varieties within a narrow range of maturity may be a risk to the total production, mainly in years with low water availability. In addition, other agronomic problems may arise, such as dealing with a large amount of soybean ready to be harvested at the same time. Despite these potential problems, growers will use early maturity varieties instead of later ones, because these will certainly experience increased damage by seed-suckers.

Trap crops

The trap crop concept consists of using a small space (usually ⩽ 10% of the total area) at the border of the soybean field, planted one to two weeks earlier and/or at the same time, with a variety that will mature before the one being used in the main area. In both cases, soybean at the edge of the field will start with pods earlier, and attract seed-suckers. These will be eliminated in this restricted area with insecticides (Fig. 2; Newsom & Herzog, 1977; Panizzi, 1980; McPherson & Newsom, 1984; see also Ragsdale et al., 1981 and Schumann & Todd, 1982). The use of a more attractive plant as a trap, such as cowpea, *Vigna unguiculata* L., will improve stink bug control, and final soybean yield (Jackai, 1984).

As in the case of the two tactics mentioned before, trap cropping may be of limited use. One condition to its success is a proper planning of planting time by all growers of a particular region, in order to have a synchronized effect of plant phenology in attracting the first generation of seed-suckers colonizing the field. This technique seems to have a better chance of success in isolated fields (Newsom & Herzog, 1977).

Resistant varieties

The use of resistant varieties is an important component of integrated pest management programs. Efforts have been made to find soybean resistant genotypes that will have detrimental effects to seed-suckers or may be less preferred and/or more tolerant to their feeding damage. The genotypes PI 229358, 227687, 171451, and ED 73-371 were found to have an adverse effect on *N. viridula* nymph development (Turnipseed & Sullivan, 1975). Of these genotypes PI 229358 was the most consistently resistant cultivar, causing significant higher mortality, slower development, and lower weight gain for nymphs, as compared to those on commercial varieties (Jones & Sullivan, 1978). Several other soybean PI's show moderate levels of resistance, including PI 171444 with a high level of resistance to *N. viridula*. Non-preference (antixenosis), antibiosis, and probably escape in time contribute to the high field resistance of this genotype to seed-suckers (Kester et al., 1984).

The search for the chemical factors involved in the expression of resistance of soybean genotypes to insects has been somewhat frustrating. Attempts to elucidate the chemical bases of resistance in the above mentioned PI's, revealed that compounds such as pinitol, phenolic acids,

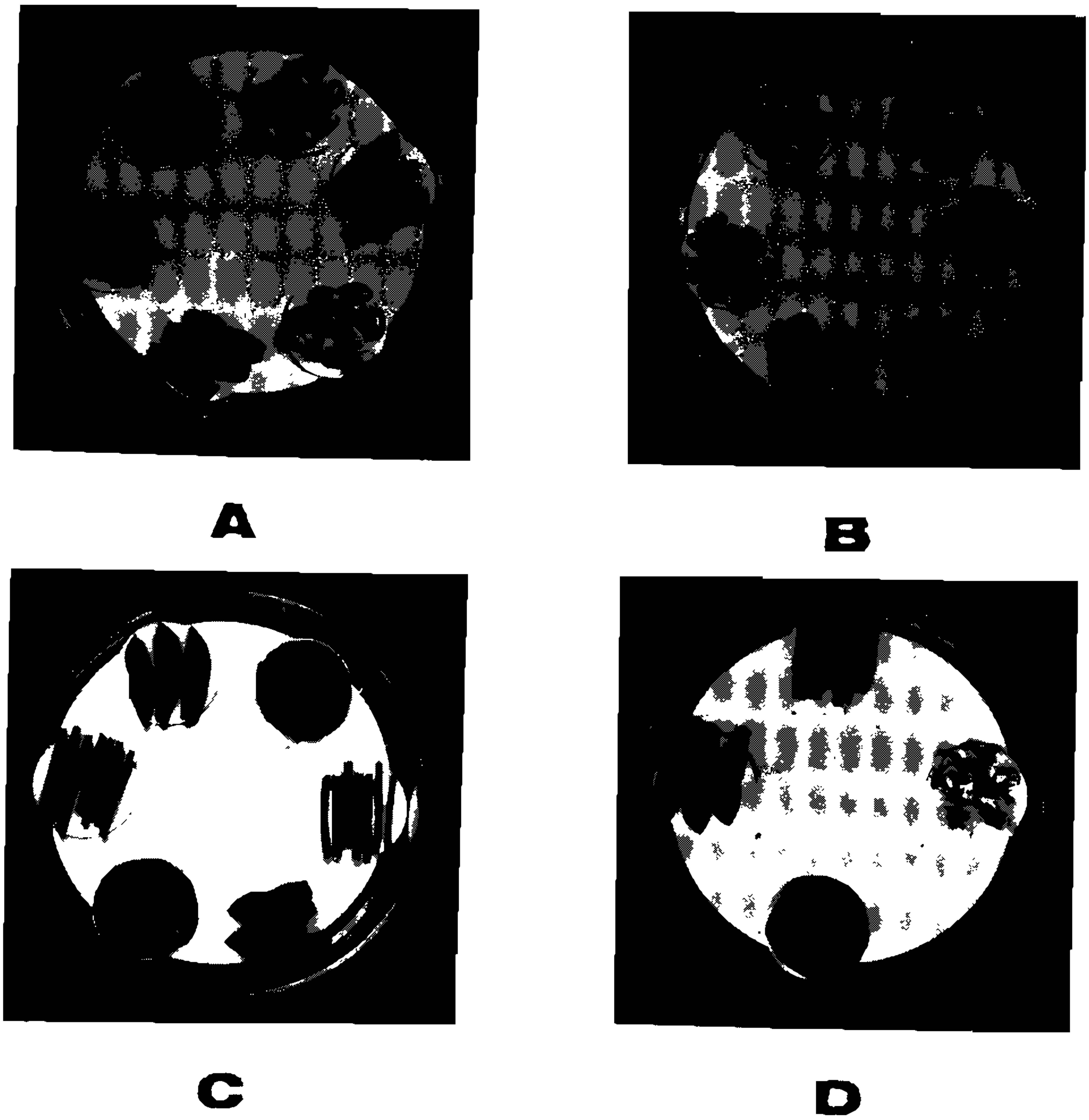

Fig. 3. Food choice preference tests. A = two choices (pubescent soybean pods vs. immature seeds); B = two choices (immature vs. mature seeds); C = three choices (leaves vs. pubescent pods vs. petioles + stems); and D = four choices (pubescent pods vs. leaves vs. flowers vs. petioles + stems) (based on Kogan, 1972).

and isoflavonoid phytoalexins may be involved (see Kogan, 1986, for details).

In general, soybean genotypes that may have one or more attributes of resistant are tested at the field level, but feeding preference may be tested in the laboratory. For example, a choice test method using an arena, with different foods put alternately near the perimeter of the arena, may be used (Fig. 3). Starved nymphs or adults of seed-suckers are released in the center of the arena with moistened filter paper. Food preference (i.e., presence of the insect on the food and whether feeding or not) is recorded. Clearly, results obtained with this methodology must be complemented with field trials to determine if the preferences detected in the laboratory also occur in the field. This methodology may be useful for testing antixenosis type of resistance. Finally, it seems that tolerance, such as that observed to small-seeded genotypes (Section Seed abundance and size) will prevail as the main type of resistance of soybean against seed-suckers.

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

Seed-suckers are a major pest of soybean, and despite the information available on their feeding impact on seed yield and quality, much more research is needed to better understand the interactions between this pest complex and the soybean crop.

Data on the effects food may have on nymph and adult biology are still lacking. For example, how the different amounts and proportions of nutrients and allelochemicals in seeds and pods of soybean and the food physical attributes, will influence prefeeding behavior and postfeeding performance is unknown; the chemical bases of resistance is still being speculated (Kogan, 1986), and the physical characteristics such as seed size and number vs. seed-sucker damage, require further investigations.

Many aspects of the seed-suckers life history on this particular agroecosystem should be investigated. For instance, data on interspecific, and in particular, intraspecific competition of the many species that occur simultaneously, and explore the same nutritional resource are literally unknown. The same can be said about the impact of natural enemies, such as predators and parasites, to seed-suckers. Studies on how much a parasitized hemipteran (e.g., *N. viridula* hosting a tachinid larva) will feed, disperse, reproduce, and so on, are higly desirable. Seed-suckers changes in behavior, as a response to variable biotic (e.g., decrease in food quality) and abiotic (e.g., decrease in temperature) factors, as the soybean crop advances toward maturity should be investigated. Will the insect increase the rate of food consumption, and speed up development as the crop mature? Will it increase the basking behavior to compensate decrease in temperature? What are the causes and timing of migration to alternate host plants? And, finally, what will be the consequences of those switches in food sources to the insect fitness? These and many other questions raised here and elsewhere (see Slansky & Panizzi, 1987) should be answered. The several tactics referred to earlier, with potential use to manage seed-suckers on soybean agroecocystems, will certainly be improved, as research data on both basic and applied aspects be generated and analyzed within the paradigm of insect nutritional ecology.

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