Population Response of Bean Insect Herbivores to Inter– and Intraspecific Plant Community Diversity: Experiments in a Tomato and Bean Agroecosystem in Costa Rica[1]

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ABSTRACT

The population response of bean insect herbivores was examined with respect to inter-and intraspecific diversity using bean (*Phaseolus vulgaris*) and tomatoes (*Lycopersicon esculentum*) in Costa Rica. Auchenorryncha were the most common herbivores, constituting between 45.4% and 78.3% of the collected individuals over the course of the season. Increased interspecific diversity positively affected overall auchenorrynchous insect numbers. *Empoasca kraemeri* Ross and Moore (Homoptera: Cicadellidae) was primarily responsible for this trend. However, *Hortensia similis* Walker (Homoptera: Cicadellidae), the second most common species, had the opposite response to interspecific diversity. Increased intraspecific diversity (varietal mixture *vs* single varieties) did not affect numbers of Auchenorrhyncha at the level of entire plots. Still, there was a significant differential distribution within the varietal mixture plots, demonstrating the importance of local rather than long-range orientation. Various mechanisms responsible for, and the implications of, these results are discussed.

COMPENDIO

La dinámica poblacional de los insectos herbívoros del frijol, fue examinada en un sistema de cultivo asociado de frijol (*Phaseolus vulgaris*) y tomate (*Lycopersicon esculentum*) en Costa Rica. Se tuvo en cuenta la diversidad entre las diferentes especies de plantas y la variedad encontrada dentro de una misma especie. Los insectos del suborden Auchenorryncha fueron los herbívoros más comúnmente encontrados, representando entre el 45.4% y 78.3% de los individuos recogidos durante el ciclo vegetativo. El aumento de la diversidad entre las especies de plantas tuvo un efecto positivo en las poblaciones de Auchenorryncha. La saltahoja *Empoasca kraemeri* Ross y Moore (Homoptera: Cicadellidae) fue la principal causa de esta tendencia. En cambio, *Hortensia similis* Walker (Homoptera: Cicadellidae), la segunda especie más abundante después de *E. kraemeri*, mostró un decremento en su nivel poblacional cuando la diversidad entre las plantas fue aumentada.

En general, el aumento de la diversidad de variedades del frijol no afectó el nivel poblacional de Auchenorrhyncha, sin embargo, hubo una distribución diferencial de modo significativo dentro de las parcelas con mezclas de variedades, dando indicio de la importancia que tiene la orientación local para estos insectos. Las implicaciones de estos resultados y una discusión de los mecanismos responsables por este comportamiento son incluidos en el presente trabajo.

INTRODUCTION

The effect of plant community diversity on insect populations has been a central issue in ecology for a decade (e.g. 3, 8, 14, 15, 19).

It also has long been of concern to entomologists studying the effects of cropping systems on pest populations (e.g. 4, 7, 12). While it is clear from this work that plant diversity can play a key role in the determination of insect abundance, its effects are not always predictable. The majority of these studies have indicated that increased plant diversity lowers key pest populations; however, a significant number have shown the reverse (6, 20, 21).

Increased plant diversity may affect insect populations by means of spatial, structural, microclimatic or chemical changes in the plant community. The overall response of the insect population is a combination of within-patch behavior, such as tenure time, and between-patch behavior, such as orientation and colonization. Hassell and Southwood (9) note that herbivorous insects are attracted to patches by combinations of olfactory and visual cues, whereas within the patch food items are often selected through gustatory cues. Spatial array can affect colonization of patches through the percentage of bare ground (e.g. 18) and affect within-patch movement (22). Structural factors such as plant and leaf size and shape, along with color, may be important components of the search image of an insect and may

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affect both interpatch and within-patch movement. When examining the effects of plant diversity on insect populations, it is important to distinguish between inter-patch and within-patch effects and among the various mechanisms which may be involved. As Hassell and Southwood (9) point out, however, the forager itself defines the patch, and boundaries can be detected only through studying its behavior.

Agroecosystems provide ideal conditions under which to study plant diversity and insect populations because they allow the relatively precise manipulative experiments necessary to test ecological theory. Furthermore, using agricultural systems allows a quicker translation of theory into practice for the alleviation of pest problems.

In this study we examine the effects of plant community diversity on populations of Auchenorrhyncha (Homoptera) attacking common bean (*Phaseolus vulgaris* L.) in Costa Rica. We monitored insect populations in bean monoculture, mixtures or dicultures of two varieties of beans, and polycultures of beans and tomato (*Lycopersicon esculentum* M.). We manipulated both interspecific and intraspecific diversity, since species will tend to differ in size, shape and odor, while varieties may have more subtle differences such as nutrient content (e.g. 2, 11). We also manipulated spatial array in the interspecific polycultures in order to help narrow down the components involved in insect response. In general, we attempted to determine the composition of the Auchenorryncha community on beans in Costa Rica, to examine the population response of this community to plant diversity, and to identify important components of this interaction for further research.

MATERIALS AND METHODS

Tomatoes (var. Tropic; *L. esculentum*), black beans (var. Talamanca), and red beans (var. Mexico 80) (*P. vulgaris* L.) were grown in monocultures and dicultures at the Fabio Baudrit M. Agricultural Experiment Station of the University of Costa Rica, 5 km west of Alajuela, Costa Rica. The station is in the Meseta Central of Costa Rica, at an elevation of 840 m, with a mean annual temperature of 22°C with maximums of 34°C in March and minimums of 10.5°C in December. The average annual precipitation is 1900 mm, distributed from May to November. The soils are of the Saenz series.

Crops were grown from February through May 1982, running from the end of the dry season into the beginning of the rainy season. Five treatments were arranged in a randomized block design with four replications. Each treatment plot was 4.8 m x 4.8 m with a 1.2 m border separating plots. The relatively small plot size means that tests for significant differences between plots should be conservative.

We planted one bean monoculture of each variety, an alternate row mixture of both varieties, and two red bean/tomato polycultures. The inter-row polyculture had each crop in alternate rows, while the intra-row had both crops within each row. These two polycultures had the same overall density of each crop.

The crops were grown according to recommendations provided by agronomists at the Experimental Station. All treatments were planted at 0.6 m between rows, 10 cm between bean plants within a row and 60 cm between tomato plants within a row, except in the intra-row polyculture where tomatoes were spaced at 1.2 m with 0.6 m of beans planted between tomato plants. Pesticides were applied to the soil (Cytrolame, 25 kg/ha) and to the seed (Captan, 50% and Bemlate, 50%, at 302 g/4 kg of seed) at planting. Insecticides Orthene and Lorsban (15 g/16 L.) were applied during the first three weeks of germination. The plots were hand-weeded throughout the season, and irrigated for the first three months, before the start of the rainy season.

Tomatoes were tied to wire suspended from poles in the tomato rows when necessary. Bean germination was very high (< 90%), but tomato germination was lower because of dry conditions. Small tomato plants from outside the plots were transplanted in to fill holes left by ungerminated plants during the first month.

All treatments containing beans were sweep-sampled at approximately weekly intervals from the sixth through tenth week after planting. Based on a series of sweeps throughout the day to determine activity peaks, it was decided to complete all sweeps between 1400 and 1630. The same areas were swept on each date, and were different from the areas used for yield data (16). Three rows of beans of each interline tomato/bean diculture were swept, starting .6 m from the border, sweeping for 1.8 m per row, with five sweeps across a single row with a standard (38 cm diameter) sweep net. Thus a total of fifteen sweeps per plot and 5.4 m of row were sampled. In bean monocultures and bean/bean diculture, the samples were doubled, sweeping each row of beans, for a total of 30 sweeps and 10.8 m per plot. In certain comparisons, only 15 of these sweeps were used (see Figs.). In the intra-row diculture, three groups of beans (.6 m long) in each of three rows were swept at the same rate and total distance (15 sweeps, 5.4 m of beans). Collected insects from each plot were placed in killing jars, then sorted and identified. All sweep sample data were analyzed using the Wilcoxon matched-pairs signed ranks test, in comparisons that were planned prior to the initiation of the experiment.

RESULTS AND DISCUSSION

Composition of insect community

The most abundant herbivores found in the sweep samples were leafhoppers and planthoppers (Homoptera: Auchenorrhyncha), leaf beetles (Coleoptera: Chrysomelidae) and seed bugs (Hemiptera: Lygaeidae) (Table 1). Of the 29 species of Auchenorryncha, two cicadellid species (*Empoasca kraemeri* Ross and Moore and *Hortensia similis* Walker) together constituted between 45.4% and 78.3% of the number of individuals over the growing season (Table 2). *Diabrotica viridula* was the most abundant chrysomelid (Table 3).

Insect Response to Interspecific Plant Diversity

We found significantly more auchenorrynchous individuals in the intra-row tomato/red bean polycultures than in the red bean monoculture ($P < 0.01$). There was a similar, but not significant trend for the inter-row polyculture when compared to the monoculture (Fig. 1). This results appears to be largely due to the response of *E. kraemeri* (Cicadellidae: Typhlocybinae) which accounted for up to 63% of the Auchenorryncha (Table 2). When *E. kraemeri* was analyzed separately, there tended to be more individuals in both intra-row and inter-row polycultures than in the red bean monoculture ($P < 0.064$ and $P = 0.130$ respectively, Fig. 2).

Empoasca kraemeri is the most serious pest on beans in many parts of Central and South America (23), retarding plant growth and lowering seed production up to 97% (5). In the location of this study, *E. kraemeri* population levels were not high enough to affect yields. However, the results of this experiment suggest that tomato/bean polycultures might be problematic in areas where *E. kraemeri* has an important effect on bean yield, unless there are overriding yield advantages due to other factors (16).

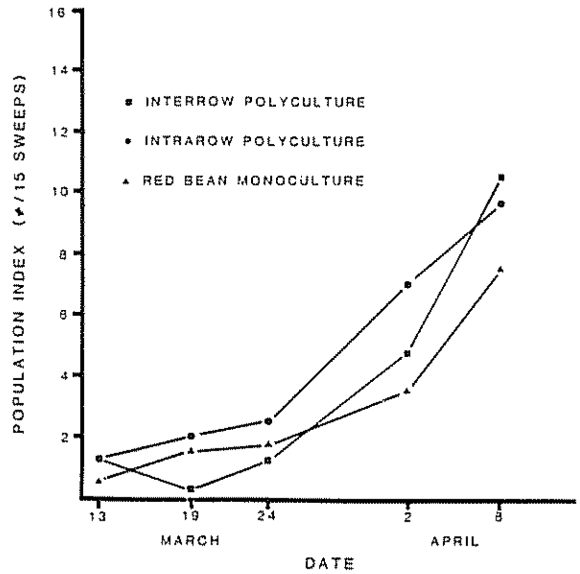

Fig. 1. Total Auchenorrhyncha in red bean monoculture and the two tomato/bean polycultures. Over the season there were significantly higher numbers in the intra-row polyculture than in the monoculture (P H 0.01, Wilcoxon).

In this study we were unable to confirm the mechanism by which the polycultures attracted more *E. kraemeri*. There are no records of this species attacking tomatoes, and we found no indication that it might do so. One factor which might have been important in attracting greater numbers of this insect to the polycultures is the relative amount of bare

Table 1. Total herbivore abundance (All treatments).

Date	Total Herbivore Insects	%	Total Auchenorrhyncha /	%	Total Beetles	%	Total Lygaeids	%	Other	%
13 March	65	100	55	84 6	6	9.2	0	0	4	6 2
19 March	91	100	58	63 7	22	24 2	6	6 6	5	5 5
24 March	139	100	60	43 2	30	21.6	32	23.0	17	12 2
2 April	248	100	152	61.3	38	15.3	52	21.0	6	2 4
8 April	322	100	241	74.8	16	5.0	56	17.4	9	2 8

Table 2. Auchenorrhyncha abundance (All treatments).

Date	Total Auchenorrhyncha	%	No. *Hortensia*	%	No. *Empoasca*	%	% *Hortensia* + *Empoasca*
13 March	55	100	24	43 6	1	1 8	45.4
19 March	58	100	32	55 2	6	10.3	65.5
24 March	60	100	10	16 7	21	35.0	51 7
2 April	152	100	30	19 7	89	58 6	78.3
8 April	241	100	30	12 4	152	63.1	75.5

ground in the various treatments Several studies have shown that plants surrounded by bare ground are more attractive to aphids than denser plantings or plants surrounded by weeds (10, 13, 17, 18). Altieri *et al.* (1) demonstrated that population levels of *E. kraemeri* nymphs and adults were significantly higher in weed-free monocultures than in unweeded plots. These authors suggest that this result is due to a repellent effect of the weeds, but the effect of bare ground may also have been important. In this study the inter-row polyculture clearly had a higher percentage of bare ground than the intra-row polyculture, while both had more bare ground than the bean monoculture. However, we found no significant difference between the numbers of *E. kraemeri* in the two polycultures. Further research on this factor could improve the design of cropping systems where *E. kraemeri* is an important pest.

Hortensia similis, the second most common species, is usually a minor pest of rice, corn, and beans, but occasionally reaches high densities and major pest status. It exhibited a distinctly different response to the cropping systems. Population levels were significantly higher in both red bean monocultures and intra-row tomato/bean polycultures than in the inter-row polycultures ($P < 0.05$ for both, Fig. 3).

The disruptive influence of rows of non-host plants may be the major factor responsible for this result. With chrysomelid beetles, Bach (3) showed that individuals have a greater tenure time in monocultures and Risch (14) demonstrated a higher emigration rate from polycultures than monocultures. He showed that longer flights occur after encountering the wrong host plant. Although the inter-row and intra-row polycultures had equal densities of beans and tomatoes, the continuous rows of tomatoes may have served as a greater barrier to insect movement than a single plant surrounded by bean plants. A leafhopper moving from a bean plant in the inter-row polyculture may have been more likely to encounter a non-host tomato plant than a leafhopper in the intra-row polyculture and thus might be more likely to leave the plot. Our results follow those of Cromartie (6). He found species-specific responses to diversity, with three species preferring low diversity and one preferring high diversity.

Insect response to intra-specific plant diversity

Overall numbers of Auchenorryncha did not differ among the red bean monoculture, the black bean monoculture and the red bean/black bean polyculture (Fig. 4). An interesting pattern emerged, however, when we compared numbers found on each bean variety within monoculture to the numbers found on the same variety within the bean polyculture. There were more hoppers on black beans within monocul-

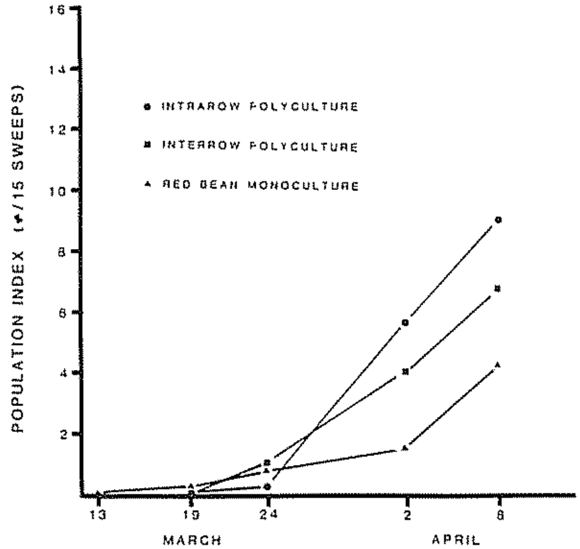

Fig 2 *Empoasca kraemeri* numbers in red bean monoculture and the two tomato/bean polycultures. The trend is for higher numbers over the season in the intra– and inter-row polycultures than in the monoculture ($P = 0.064$ and $P = 0.130$, respectively, Wilcoxon).

ture than on black beans within polyculture (p = 0.08), while red beans showed the opposite trend with more hoppers on the red beans within polyculture than within monoculture (p = 0.09). Within the polyculture alone, hoppers were more abundant on the red beans than on the black beans (p = 0.004) (Fig. 5).

Thus, the hoppers showed no preference between bean varieties at the plot level, but demonstrated a clear preference for red beans once inside the plot. This suggests that the cues used by hoppers for discrimination between patches are shared by the bean varieties and might include leaf size and shape, percent bare ground present in the patch, and other visual cues. Within the bean patch, preference appears to be based on chemical or nutritional differences between varieties. Thus, within the bean polyculture red beans attracted the hoppers from the black beans, leaving the overall plot density unchanged, but resulting in a significant difference between the two varieties.

This result has implications for the design of variety trials for pest-resistance evaluations of crops, since the scale of the trial and the availability of the other varieties may have an important effect on the outcome (24). When varietal mixtures or multiline cultivars are in use or under consideration, both within-patch and between-patch behavior of major pests should be studied.

CONCLUSIONS

It is clear from the results of this study that the effects of plant diversity on insect abundance depend on the particular behavioral response of an insect to the range of chemical, spatial, and structural changes that accompany increased diversity. It is also apparent that insects have species-specific responses to these variables, as found by Cromartie (6). Thus, in the design of cropping systems, each pest behavior must be studied. Beyond this, the behavioral response must be examined on at least two levels, inter-patch and within-patch. The percentage of bare ground in the patch appears to be an important determinant of the colonization behavior of *E. kraemeri*, whereas for *H. similis* the disruptive effect of nonhost plants on within-plot movement may determine abundance. Insect preference at the intra-specific level appears to occur as relatively fine discrimination between food items within a patch.

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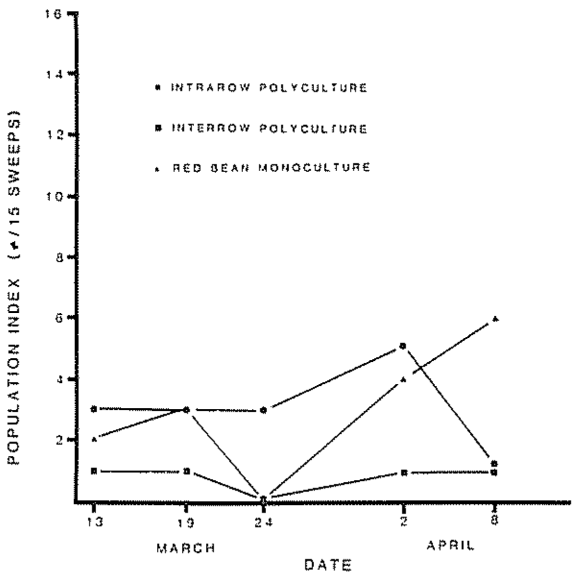

Fig. 3. *Hortensia similis* numbers in red bean monoculture and the two tomato/bean polycultures. Over the season numbers were significantly higher in the bean monoculture and the intra-row polyculture than in the inter-row polycultures ($P < 0.05$ for both, Wilcoxon).

Table 3. Chrysomelid abundance (All treatments).

Date	Total Chrysomelids	%	*Diabrotica viridula*	%	*D. balteata*	%	Flea Beetles	%
13 March	6	100	2	33.3	1	16.7	3	50
19 March	22	100	9	40.9	2	9.1	11	50
24 March	30	100	24	80.0	2	6.7	4	13.3
2 April	38	100	33	86.8	4	10.5	1	2.6
8 April	16	100	13	81.3	1	6.3	2	12.3

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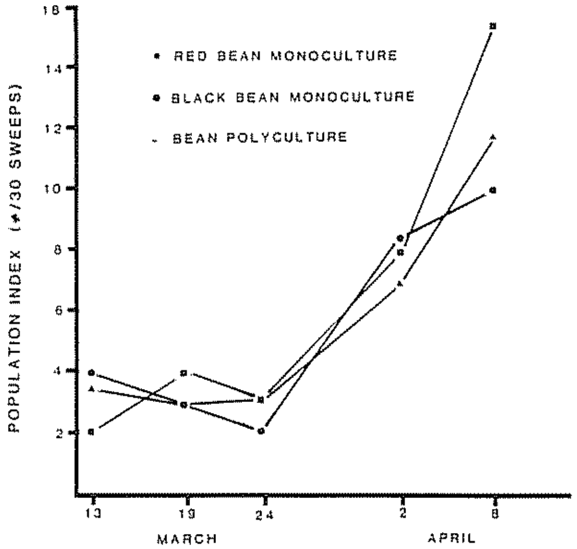

Fig. 4. Total Auchenorrhyncha in red and black bean monocultures and the polyculture of both. There are no significant differences.

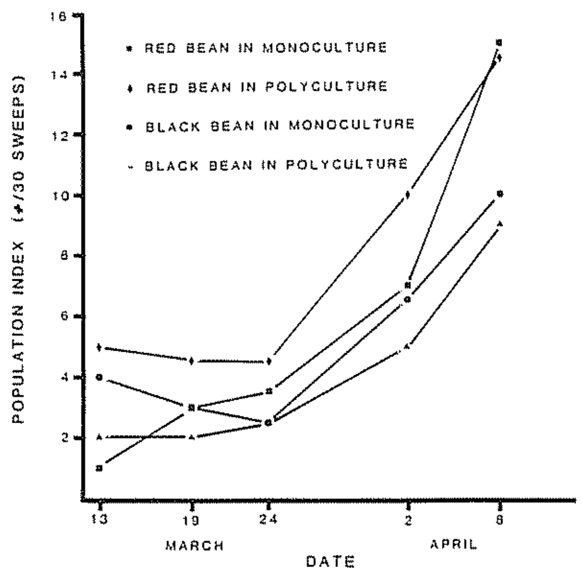

Fig 5. Total Auchenorrhyncha in red and black bean monocultures, and on the red and black bean components within the polyculture of both. Over the season there were higher numbers on black beans in monoculture than on black beans in polyculture (P = 0.08, Wilcoxon), while for red beans there were higher numbers in polyculture than in monoculture (P = 0.09, Wilcoxon). Within polyculture, there were higher numbers on red beans than on black beans (P = 0.004, Wilcoxon).

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Notas y Comentarios

La revolución verde en Africa

Si alguien está capacitado para ayudar a Africa negra a encontrar un camino para recuperarse de la declinación durante un cuarto de siglo de su agricultura, es Norman Borlaug. El Dr. Borlaug, que ha cumplido ya 73 años, es el ganador del Premio Nobel de la Paz, hace 17 años, por crear los trigos enanos que pusieron en marcha la revolución verde en Asia. Por mucho tiempo ha querido probar en Africa lo que funcionó en India y China.

Su fórmula es simple. Se comienza por reunir todos los datos disponibles en los centros internacionales de investigación agrícola, situados en lugares como México e India (los más antiguos de este tipo) sobre los tres principales cultivos de Africa: maíz, sorgo y mijo. Entonces se escogen uno o dos países para quienes los datos son mejores. ... Sudán y Ghana como resulta ser. Se reúnen una media docena de científicos realmente buenos, preparados para internarse en las estepas africanas por unos pocos años, hacerlos que armen un paquete de producción, y comenzar a probarlo en lotes de media hectárea en villorios de casas de paja

El paquete, dice Borlaug al corresponsal de **The Economist** (14-III-87, p. 56), trata de qué variedades plantar, cuándo y cómo plantarlas, cómo fertilizar, cómo controlar insectos y enfermedades. Basándose en los resultados de las pruebas del primer año, se ajustan las partes del paquete (demasiado fertilizante o muy poco, o la variedad A es mejor que la B) para mejorarlo

Para el siguiente año, el paquete modificado se prueba en cientos de parcelas de agricultores. Los rendimientos deben ser de más del doble para promover suficiente entusiasmo entre los agricultores como para que cambien sus viejos hábitos. Si esto sucede, se acude a los directores de la política del país y se les persuade a poner el fertilizante a disposición de los agricultores seis semanas antes de la siembra, prestarles dinero para que los compren (pagable después de la cosecha) y fijar un precio de sustentación garantizado de manera que puedan cancelar el préstamo.

Si los gobiernos pueden ser persuadidos, los agricultores deben hacer el resto. La prueba completa debe durar cuatro o cinco años a un costo de unos 5 millones de dólares. Borlaug mantiene que no debe ser probada en más de uno o dos países al comienzo, porque no hay suficientes científicos, por ahora, que saben cómo manejar con éxito la prueba.

Borlaug consiguió los 10 millones de dólares que necesitaba para el experimento de un octogenario filántropo japonés, Ryoichi Sasakawa, quien hizo su fortuna transformando las carreras de botes a motor en un gran deporte de apuestas en el Japón. La administración del proyecto no está trabajando sin tropiezos, debido a la tensión entre los puntos de vista de Borlaug y el de los dirigentes del Global 2000, la fundación formada por el ex presidente Jimmy Carter, que tiene el control total de los 10 millones de dólares.

Con todo, Borlaug tuvo éxito en mayo pasado en enviar a Sudán y Ghana varios científicos, la mayoría de los cuales trabajaron con él en India y Pakistán en los novecientos sesenta. No son más que cinco de ellos: los mismos cuatro mejicanos que obtuvieron los éxitos en el Punjab, la región que comparten India y Pakistán, hace ya 20 años, más un surcoreano más joven. Pero, en el primer año de sus contratos de dos años el grupo ha tenido notables éxitos, tanto en Sudán como en Ghana.

"Los profesionales mexicanos llamados por Borlaug son: Ignacio Narváez Morales, (Genetista), Marco A. Quiñones, (Genetista), Eugenio Martínez Salazar, (Patólogo), José A. Valencia Villareal.

En 420 demostraciones en las zonas secas de Sudán, los rendimientos por hectárea del sorgo aumentaron en seis veces. Casi 1500 de estas parcelas se están plantando con sorgo y mijo en el presente año. Nuevos paquetes han doblado los rendimientos en Ghana, donde Borlaug espera ver plantadas 800 parcelas en 1987. Si estos experimentos son capaces de producir tales impresionantes resultados otra vez este año, este será el momento propicio de tratar de persuadir a los gobiernos de Sudán y Ghana para probar más ampliamente los paquetes.

¿Tiene un enfoque como este la oportunidad de transformar la agricultura africana? Las enormes y poco pobladas tierras áridas africanas, con sus suelos agotados y deficiente transporte y comunicaciones, ofrecen un contraste doloroso al ambiente en que Borlaug y sus mexicanos trabajaron en el Punjab. La llanura del Punjab, con sus grandes uniformes, sol e irrigación, es casi un invernadero; y el Punjab de la India tenía un sistema de tenencia, educación e inversiones públicas que hicieron mucho más fácil para los agricultores tomar ventaja de las oportunidades de la revolución verde.

Aún así, Borlaug, que obutvo su Premio Nobel, tanto por la tenacidad de la idea que tenía metida en su mente, como por su ciencia, está seguro que el principio puede ser aplicado también en Africa. Recuérdese que las labores en el Punjab, también fueron llamadas un fracaso poco antes que produjeran el milagro de la producción alimenticia en la India (Cf. **Turrialba** 28:13).

Pero este es otro punto que no trataremos hoy. El ataque a la labor de los organismos en los que laboraban Borlaug y colegas, empezó cuando periodistas franceses bautizaron sus esfuerzos como "revolución verde", para inmediatamente comenzar, los mismos periodistas, sus ataques porque esta "revolución" no alteraba las estructuras políticas de las regiones afectadas, trampa en la que hasta el IICA cayó, al escoger a un periodista que escribi. a un comentario al respecto. Pero esto es ya otra historia que ya contaremos alguna vez. Por lo pronto, recordemos que en Africa ha habido revoluciones al gusto de esos periodistas, con cambios sociales, y en esos lugares se padece de hambre. En cambio, India ha duplicado en ese período su enorme población, pero su producción de alimentos ha crecido 30 por ciento más rápido que la población y ahora exporta trigo.

La humanidad ha descubierto nuevas maneras de diseminar el conocimiento, nuevos tipos de semillas, nuevas medicinas, nuevas fuentes de energía. Los africanos, con sus enormes espacios vacíos, tienen espacio para apoderarse de las oportunidades que están delante de la mente individual y abierta. En los próximos 25 años ellos podrían seguir el ejemplo de la India hacia la prosperidad, asombrando al mundo, y a ellos mismos. **A.G.**