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UPLAND RICE INSECT PESTS: THEIR ECOLOGY, IMPORTANCE, AND CONTROL

J.A. LITSINGER, A.T. BARRION, and
DANDI SOEKARNA

The International Rice Research Institute
P.O. Box 933, Manila, Philippines

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J.A. Litsinger[1], A.T. Barrion[2], and Dandi Soekarna[3]

ABSTRACT

The diversity of upland rice environments gives rise to a more heterogeneous insect fauna compared with the more homogeneous lowlands. A wide array of soil-inhabiting pests — ants, termites, white grubs, crickets, root aphids, root mealybugs, root bugs, and wireworms — common in upland rice cannot tolerate flooding. Seedling maggots replace the aquatic whorl maggots as vegetative foliar pests. Insect-vectored virus diseases are rare in upland rice. Small upland ricefields cause concentrations of the more vagile seed pests during ripening. The less stable upland environment — more restricted growing season, smaller area planted, greater drought stress — poses greater problems of survival to insects, which have overcome them by polyphagy, greater longevity, off-season dormancy, and/or dispersal. There is no one insect that specializes in upland rice. Yield losses to insects, however, are comparable to those of lowland rice. Cultural control methods include increased tillage, higher seeding rates, and crop rotation for soil pests. Foliar pests can be minimized by synchronous planting of early-maturing varieties. Plant resistance as a method of insect control has not been greatly exploited because the other breeding objectives of high yield, drought tolerance, and blast resistance take priority. Resistance to stem borers should be a high priority. A rich fauna of natural enemies exists, but they face even greater problems of survival than the pests. The normal low yields of upland rice preclude high levels of insecticide use. Seed treatment and baiting are low-cost methods, as is low-volume spraying.

[1]Entomologist, Entomology Department, International Rice Research Institute (IRRI), P.O. Box 933, Manila, Philippines. [2]Senior research assistant, Entomology Department, IRRI. [3]Senior researcher, Pest and Disease Section, Bogor Institute for Food Crops (BORIF), Jalan Cimanggu, Kecil 2, Bogor, Indonesia.

UPLAND RICE INSECT PESTS: THEIR ECOLOGY, IMPORTANCE, AND CONTROL

Upland ricefields are nonpuddled and unbunded, without the expectation of impounding water. They may be located in many settings — in isolated pockets surrounded by irrigated wetland fields, or along steep slopes of recently cleared forest. Each environment produces a unique composition of insect species.

Information on upland rice insect pests is limited and scattered among reports dealing with other rice cultures. We found eight reports specifically treating insect problems of upland rice culture (11, 59, 66, 79, 116, 120, 163, 176) but none worldwide in scope. Most literature focuses on one species or a group of related species. Table 1 lists upland rice insect pests that others have identified and those we have observed. Many citations refer to lists of pests with rice as a recorded host, or are based on insect habits.

Papers concerning upland rice often fail to distinguish between the two ecologically significant aspects — culture and environment — embodied in the term upland rice. It is dangerous to extrapolate results of studies of insect pests in well-drained fields where seeds of upland rice varieties are sown into dry soil (upland rice culture) but in an otherwise lowland environment (fields surrounded by flooded rice). Insects readily fly from the lowland ricefields to the fields planted in upland rice culture. These insects, therefore, are not necessarily upland rice insects. They breed on lowland rice and colonize upland rice. We gain greater ecological significance from faunistic records and ecological studies from an upland rice environment, where lowland ricefields are out of the effective dispersal range of most insect species (tens of kilometers away). In border areas where lowlands and uplands meet, studies cannot accurately represent either upland or lowland rice (181).

PEST GROUPS

Upland rice insects are more influenced by physical than by biological or socioeconomic parameters: 1) well-drained soils (lack of prolonged flooding or soil puddling), 2) high probability of drought during crop growth, 3) restricted growing season (lengthy nonrice fallow), 4) ricefields interspersed with other crops (diversified flora), and 5) low use of agrochemicals (because of low and unstable yield).

Although a dryland habitat represents an extreme hydrological condition, upland rice is host to all but the most aquatic insects (11, 176). Whorl maggots, caseworms, water weevils, and bloodworms require ponding. Many soil and seedling pests are not common in lowland ricefields. Deep water rice is established in dry soil and, therefore, has more in common with upland and rainfed lowland rice than with irrigated rice, even though water depths may later reach 1-3 m. Second to deep water rice, upland rice represents the most unstable rice environment for foliar insects. But upland rice is highly stable for soil insects.

The significance of abiotic factors in upland rice insect ecology will be apparent in a discussion of the most prevalent groups of insects attacking upland rice worldwide.

Soil-inhabiting pests

Well-drained, nonpuddled upland rice soils favor pests that pass at least one growth stage underground. Soil pests feed on underground plant parts (sown seed or roots), develop entirely in a subterranean habitat, and leave only for adult mating and dispersal flights. Soil pests include ants (Formicidae), termites (Isoptera), mole crickets (Gryllotalpidae), field crickets (Gryllidae), white grubs and black beetles (Scarabaeidae), root aphids (Aphididae), root-feeding mealybugs (Pseudococcidae), root-feeding bugs (Lygaeidae, Cydnidae), false wireworms (Tenebrionidae), wireworms (Elateridae), root weevils (Curculionidae), and soil-inhabiting cutworms (Noctuidae).

A subterranean environment limits mobility, particularly in locating food, and soil insects have adapted by 1) being long-lived either as individuals (beetles or orthopterans), as colonies of social insects (ants or termites), or as dependents on social insects (mealybugs and aphids), and 2) having a wide host range (all species).

Ants. Species of terrestrial ants, notably the ubiquitous fire ant *Solenopsis geminata* and harvester ants *Pheidole* spp., specialize in feeding on ungerminated grass seed. *Solenopsis* readily colonizes disturbed habitats, which in turn initially encourage the growth of grasses (39). Colonies of these granivorous ants have a specialized caste that processes seed for food. Foraging workers bring seed to

Table 1. Insect pests of upland rice worldwide.

Order	Family	Species	Distribution	Reference
Isoptera	Rhinotermitidae	*Coptotermes formosanus* Shiraki	Asia	85
		Heterotermes indicola (Wasmann)	Asia	82
	Termitidae	*Anacanthotermes viarum* (Koenig)	Asia	190
		Anacanthotermes rugifrons Mathur et Sen-Sarma	Asia	190
		Capritermes nitobei (Shiraki)	Asia	82, 85
		Cornitermes striatus (Hagen)	Latin America	151
		Procapritermes mushae Oshima	Asia	82, 85
		Pericapritermes nigerianus Silvestri (= *socialis*)	Africa	7
		Macrotermes natalensis (Haviland)	Africa	85
		Macrotermes bellicosus Smeathman	Africa	85
		Macrotermes gilvus (Hagen)	Asia	178
		Macrotermes spp.	Africa	12
		Odontotermes formosanus (Shiraki)	Asia	82, 85
		Procornitermes araujoi Emerson	Latin America	85, 195
		Procornitermes triacifer (Silvestri)	Latin America	195
		Trinervitermes geminatus Wasmann [= *ebenerianus* Sjostedt]	Africa	85
		Microcerotermes spp.	Asia	193
		Microtermes spp.	Asia, Africa	11, 12, 157
		Syntermes molestus (Burmeister)	Latin America	60, 85, 195
		Termites unspecified	Asia	72
Dermaptera	Forficulidae	*Diaperasticus erythrocephalus* Olivier	Africa	36
		Doru lineare (Eschscholtz)	Latin America	186
Orthoptera	Gryllotalpidae	*Gryllotalpa africana* Palisot de Baeuvois	Africa	12, 32
		Gryllotalpa orientalis (= *africana*) Burmeister[a]	Asia	59, 72, 76, 84
		Neocurtilla (= *Gryllotalpa*) *hexadactyla* (Perty)	Latin America	81, 150, 195, 203, 211
		Scapteriscus didactylus (Latreille)	Latin America	81
	Gryllidae	*Gryllus assimilis* (= *bimaculatus*) (Fabricius)	Asia	76
		Gryllus (= *Liogryllus*) *bimaculatus* de Geer	Asia	178
		Brachytrupes portentosus (Lichtenstein)	Asia	*b*
		Brachytrupes membranaceus Drury	Africa	48
		Plebeiogryllus plebejus (Saussure)	Asia	*b*
		Teleogryllus testaceus (Walker)	Asia	76, 178
		Teleogryllus occipitalis (Serville)	Asia	*b*
		Loxoblemmus haani Saussure	Asia	*b*
		Velarifictorus aspersus (Walker)	Asia	*b*
		Velarifictorus sp.	Asia	*b*
		Euscyrtus concinnus (de Haan)	Asia	*b*
	Pyrgomorphidae	*Atractomorpha burri* I. Bolivar	Asia	55
		Atractomorpha psittacina psittacina (de Haan)	Asia	178
	Tettigoniidae	*Conocephalus longipennis* (de Haan)	Asia	178
		Conocephalus maculatus (Lethierry)	Asia	178
		Conocephalus saltator Saussure	Latin America	65
		Euconocephalus varius (Walker)	Asia	178
		Caulopsis cuspidatus (Scudder)	Latin America	68, 81
		Caulopsis oberthuri Scudder	Latin America	68
		Phaneroptera furcifera (Stal)	Asia	178
	Tetrigidae	*Amphinofus* spp.	Asia	178
	Acrididae	*Aiolopus thalassinus tamulus* (Fabricius)	Asia	178
		Acrida willemsei Dirsch	Asia	178
		Gesonula mundata zonocera Navas	Asia	178
		Gonista bicolor (de Haan)	Asia	55
		Oxya japonica japonica (Thunberg)	Asia	72, 178
		Oxya hyla intricata (Stal)	Asia	178
		Oxya fuscovittata (Marschall)	Asia	78
		Oxya velox (Fabricius)	Asia	178
		Gastrimargus marmoratus grandis (Saussure)	Asia	178
		Xenocatantops humilis humilis Serville	Asia	55
		Hieroglyphus banian (Fabricius)	Asia	55, 72
		Hieroglyphus daganensis Krauss	Africa	6
		Hieroglyphus nigrorepletus (I. Bolivar)	Asia	82
		Hieroglyphus oryzivoros Carl	Asia	82
		Heteropternis respondens (Walker)	Asia	55
		Patanga succincta (Linnaeus)	Asia	54, 55, 59, 130
		Stenocatantops splendens (Thunberg)	Asia	55, 178
		Chondracris rosea brunneri Uvarov	Asia	55
		Trigonidium cicindeloides Rambur	Asia	78
		Locusta migratoria manilensis (Meyen)	Asia	55
		Locusta migratoria capito Saussure	Africa	82

Table 1 continued.

Order	Family	Species	Distribution	Reference
		Locusta migratoria migratorioides Reische et Fairmaire	Africa	33
		Schistocerca gregaria (Forskal)	Africa	33
		Schistocerca americana (Drury)	Latin America	82, 195
		Valanga nigricornis (Burmeister)	Asia	82
		Orphulella intricata Scudder	Latin America	68
Homoptera	Coccidae	*Pulvinaria sorghicola* De Lotto	Africa	246
		Pulvinaria iceryi (Guerin)	Latin America	186, 246
	Pseudococcidae	*Ctaennococcus* spp.	Asia	120
		Chorizococcus ilu Williams	Asia	245
		Dysmicoccus boninsis (Kuwana)[c]	Asia, Africa, Latin America	245
		Dysmicoccus brevipes (Cockerell)[c]	Asia, Africa, Latin America	117, 203, 245
		Dysmicoccus oryzae (Wirjati)[c]	Asia	245
		Geococcus (= *Ripersia*) *oryzae* (Kuwana)[c]	Asia	245
		Brevennia (= *Heterococcus*) *rehi* (Lindinger)	Asia	72, 245
		Nipaecoccus graminis (Maskell)	Africa	245
		Planococcoides lingnani (Ferris)	Asia	245
		Pseudococcus saccharicola Takahashi	Asia	245
		Pseudococcus spp.	Latin America	60
		Saccharicoccus sacchari (Cockerell)	Africa, Asia, Latin America	245
		Trionymus ceres Williams[c]	Asia	119, 245
		Trionymus sp.	Asia	*b*
		Mealybug unspecified	Asia	83, 84
	Aphididae	*Capitophorus* [= *Rhopalosiphum*] *prunifoliae* (Shinji)	Asia	221
		Rhopalosiphum maidis (Fitch)	Asia	249
		Rhopalosiphum padi (Linnaeus)	Asia, Africa	12, 97, 249
		Rhopalosiphum rufiabdominalis (Sasaki)	Asia, Africa, Latin America	66, 76, 120, 195, 203, 221, 229, 240, 249
		Tetraneura akinire Sasaki	Asia	221, 249
		Tetraneura basui HilleRisLambers	Asia	249
		Tetraneura nigriabdominalis (Sasaki) (= *Dryopeia hirsuta*)	Asia, Africa	7, 12, 30, 76, 227, 229
		Tetraneura radicicola Strand	Asia	249
		Paracletus cimiciformis von Heyden [= *Forda harukawai* Tanaka]	Asia	249
		Pineus harukawai (Inouye)	Asia	228
		Geoica lucifuga (Zehntner)	Latin America, Asia	76, 195, 229, 249
		Geoica setulosa (Passerini)	Asia	249
		Anoecia fulviabdominalis (Sasaki)	Asia	249
		Anoecia corni (Fabricius)	Asia	221, 229, 249
		Hysteroneura setariae (Thomas)	Africa, Asia Latin America	7
		Sipha glyceriae (Kaltenbach)	Asia	249
		Root aphid unspecified	Asia	72, 120
	Cercopidae	*Deois schach* (Fabricius)	Latin America	61, 68, 194
		Sepullia (= *Denoplux*) *nigropunctata* Stal	Africa	29
		Tomaspis (= *Deois*) *fluxuosa* (Walker)	Latin America	61, 68, 194
		Tomaspis (= *Deois*) *flavopicta* (Stal)	Latin America	61, 68, 194
		Tomaspis (= *Deois*) *completa* (Schmidt)	Latin America	68
		Tomaspis (= *Zulia*) *entreriana* (Berg)	Latin America	68
		Tomaspis (= *Mahanarva*) *fimbriolata* (Stal)	Latin America	68, 194
		Tomaspis (= *Aeneolamia*) *spectabilis* (Distant)	Latin America	219, 233
		Aeneolamia varia Fennah	Latin America	81, 111
		Aeneolamia postica (Walker)	Latin America	203
		Abidama producta Walker	Asia	54
	Delphacidae	*Sogatella furcifera* (Horvath)	Asia	59, 241
		Nilaparvata lugens (Stal)	Asia	30, 59, 72, 84, 241
		Sogatodes oryzicola (Muir)	Latin America	61, 67, 150
		Sogatodes cubanus (Crawford)	Latin America	150
		Sogatodes pusanus (Distant)	Asia	*b*
		Peregrinus maidis (Ashmead)	Latin America	186
		Laodelphax striatellus (Fallen)	Asia	18
	Cicadellidae	*Recilia dorsalis* (Motschulsky)	Asia	59, 241
		Nephotettix nigropictus (Stal)	Asia	59, 241

Table 1 continued.

Order	Family	Species	Distribution	Reference
		Nephotettix virescens (Distant)	Asia	59, 241
		Nephotettix modulatus Melichar	Africa	217
		Cofana spectra (Distant)	Asia	59, 241
		Graphocephala spp.	Latin America	61, 66
		Hortensia similis (Walker)	Latin America	61, 66, 81, 150
		Exitianus obscurinervis (Stal)	Latin America	61, 66
		Balclutha spp.	Latin America	66
		Draeculacephala clypeata Osborn	Latin America	81, 150
		Cicadulina bipunctella (Matsumura)	Asia	*b*
Hemiptera	Lygaeidae	*Cymoninus turaensis* (Paiva)	Asia	178
		Ninus insignis Stal	Asia	178
		Pachybrachius nervosus Horvath	Asia	30
		Caenoblissus pilosus Barber	Asia	83
		Blissus leucopterus (Say)	Latin America	42, 81, 150, 203
		Blissus spp.	Asia	30
		Dimorphopterus cornutus novaeguineae Ghauri	Asia	80
		Dimorphopterus similis Slater	Africa	62
		Paromius piratoides (Costa)	Asia	178
	Cydnidae	*Pangaeus* spp.	Latin America	195
		Aethus indicus (Westwood)	Asia	178
		Geotomus pygmaeus (Dallas)	Asia	178
		Stibaropus molginus Schiodte	Asia	178
		Cyrtomenus bergi Froeschner	Latin America	203
		Cyrtomenus ciliatus (Palisot de Beauvois)	Latin America	203
		Cyrtomenus crassus Walker	Latin America	203
		Tominetus spp.	Latin America	203
	Alydidae	*Riptortus linearis* (Fabricius)	Asia	55, 178
		Riptortus spp.	Africa	12
		Leptocorisa acuta (Thunberg)	Asia	72, 78, 120, 214
		Leptocorisa biguttata (Walker)	Asia	214
		Leptocorisa palawanensis Ahmad	Asia	*b*
		Leptocorisa oratorius (Fabricius)	Asia	59, 120, 178
		Leptocorisa chinensis Dallas	Asia	114
		Leptocorisa solomonensis Ahmad	Asia	178
		Leptocorisa spp.	Asia	54
		Stenocoris southwoodi Ahmad	Africa	6, 36, 82
		Stenocoris claviformis Ahmad	Africa	12
		Mirperus torridus Westwood	Africa	6, 12, 82
	Coreidae	*Cletus trigonus* (Thunberg)	Asia	178
	Corimelaenidae	*Alkindus atratus* Distant	Latin America	81, 150
		Scaptocoris divergens Froescher	Latin America	60
		Scaptocoris castaneus Perty	Latin America	15, 195
	Pentatomidae	*Scotinophara tarsalis* (Vollenhoven)	Asia	59
		Scotinophara scotti Horvath	Asia	120
		Eysarcoris (= *Stollia*) *ventralis* (Westwood)	Asia	178
		Dolycoris indicus Stal	Asia	78
		Macrina juvenca Burmeister	Africa	36
		Tantia antiguensis (Westwood)	Latin America	186
		Tantia gelii Schout	Africa	36
		Tantia perditor (Fabricius)	Latin America	186
		Pygomenida varipennis (Westwood)	Asia	*b*
		Menida spp.	Asia	55
		Nezara viridula (Linnaeus)	Asia, Africa	12, 30, 54, 55, 78, 82, 120
		Oebalus poecilus (Dallas)	Latin America	61, 66, 81, 195
		Oebalus ypsilon-griseus (de Geer)	Latin America	61, 65, 66, 195, 211
		Oebalus grisescens (Sailer)	Latin America	150, 195
		Tibraca limbativentris (Stal)	Latin America	61, 66, 81, 150, 219, 233
		Aspavia armigera (Fabricius)	Africa	6, 12, 82
		Diploxys fissa Erichson	Africa	6, 82
		Acrosternum marginatum (Palisot de Beauvois)	Latin America	186
		Acrosternum spp.	Latin America	186
Thysanoptera	Thripidae	*Frankliniella rodeos?* Pergande	Latin America	61, 66
		Bregmatothrips venustos Watson	Latin America	68
		Stenchaetothrips (= *Baliothrips*) *biformis* (Bagnall) (= *Chloethrips oryzae* (Williams)	Asia	213, 235
		Haplothrips priesnerianus Bagnall	Asia	178

Table 1 continued.

Order	Family	Species	Distribution	Reference
Coleoptera	Scarabaeidae Dynastinae	*Heteroligus* (= *Aphonoproctus*) *meles* Billberg (= *Heteroligus meles robustus* Prell)	Africa	36
		Alissonotum pauper Burmeister	Asia	82
		Alissonotum simile Arrow	Asia	209
		Dyscinetus dubius (Olivier)	Latin America	28, 195, 233
		Dyscinetus gagates Burmeister	Latin America	20, 195
		Dyscinetus spp.	Latin America	60
		Eutheola humilis Burmeister	Latin America	20, 28, 81, 195, 203, 233
		Eutheola bidentata (Burmeister)	Latin America	121, 203
		Heteronychus andersoni Jack	Africa	82
		Heteronychus bituberculatus Kolbe	Africa	82
		Heteronychus licas (Klug)	Africa	82
		Heteronychus mosambicus Peringuey (= *Heteronychus oryzae* Britton)	Africa	4, 6, 48, 82
		Heteronychus lioderes Redtenbacher	Asia	77, 82, 207
		Heteronychus arator (Fabricius)	Africa	82
		Heteronychus plebejus (Klug)	Africa	57, 82
		Heteronychus pseudocongoensis Ferreire	Africa	32
		Heteronychus rugifrons Fairmaire	Africa	82
		Heteronychus rusticus niger (Klug)	Africa	82
		Heteronychus spp.	Africa	17
		Lachnosterna longipennis (Blanchard)	Asia	82
		Lachnosterna spp.	Asia	120
		Ligyrus fossator Burmeister	Latin America	82
		Ligyrus nasutus Burmeister	Latin America	203
		Ligyrus (= *Scarabaeus*) *ebenus* (de Geer)	Latin America	20, 195
	Dynastinae	*Ligyrus humilis* Burmeister	Latin America	60, 82
		Maladera castanea (Arrow)	Asia	82
		Maladera orientalis (Motschulsky)	Asia	82
		Maladera japonica Motschulsky	Asia	82
		Phyllognathus dicynsius (Fabricius)	Asia	82
	Melolonthinae	*Exopholis hypoleuca* (Wiedemann)	Asia	117
		Lachnosterna [= *Holotrichia*] *consanguinea* (Blanchard)	Asia	122
		Leucopholis rorida (Fabricius)	Asia	82, 117
		Lepidiota blanchardi Dalla Torre	Asia	76, 82
		Leucopholis irrorata (Chevrolat)	Asia	76, 134
		Serica interrupta Walker	Asia	76
		Holotrichia longipennis (Blanchard)	Asia	122
		Holotrichia serrata Fabricius	Asia	122
		Holotrichia leucophthalma (Wiedemann)	Asia	82
		Holotrichia seticollis Moser	Asia	77, 78
		Holotrichia mindanaoana Brenske	Asia	*b*
		Stenocrates spp.	Latin America	71, 195
		Ataenius spp.	Latin America, Asia	203
		Phyllophaga aequata (Bates)	Latin America	203
		Phyllophaga caraga Saylor	Latin America	203
		Phyllophaga chiriquina (Bates)	Latin America	203
		Phyllophaga dasypoda (Bates)	Latin America	203
		Phyllophaga elegans Saylor	Latin America	203
		Phyllophaga hondura Saylor	Latin America	203
		Phyllophaga latipes (Bates)	Latin America	203
		Phyllophaga montriesi (Blanchard)	Latin America	203
		Phyllophaga parvisetis (Bates)	Latin America	203
		Phyllophaga sanjosicola Saylor	Latin America	203
		Phyllophaga setifera (Burmeister)	Latin America	203
		Phyllophaga (= Holotrichia) helleri Breuske	Asia	82, 117, 159
		Phyllophaga spp.	Latin America	81, 150
		White grub unspecified	Asia	84
	Rutellinae	*Lagochile trigona* (Host)	Latin America	82
		Anomala dimidiata var. *barbata* Burmeister	Asia	77, 78, 82
		Anomala humeralis (Burmeister)	Asia	76
		Anomala lurida (Blanchard)	Asia	76
		Anomala sulcatula (Burmeister)	Asia	76
		Anomala varians (Olivier)	Asia	82
		Anomala antigua (Gyllenhal)	Asia	82
		Anomala pallida (Fabricius)	Asia	82

Table 1 continued.

Order	Family	Species	Distribution	Reference
		Anomala polita (Blanchard)	Asia	82
		Adoretus caliginosus Burmeister	Asia	82
		Adoretus compressus (Weber)	Asia	82
		Papuana hubneri (Fairmaire)	Asia	82
		Papuana inermis Prell	Asia	82
		Popillia cupricollis Hope	Asia	78
	Tenebrionidae	*Gonocephalum depressum* (Fabricius)	Asia	82, 117, 178
		Gonocephalum acutangulum (Fairmaire)	Asia	82, 117
		Gonocephalum simplex (Fabricius)	Africa	82
		Epitragus sallei Champion	Latin America	203
		Anaedus punctatissimus Champion	Latin America	203
	Elateridae	*Aeolus* spp.	Latin America	195
		Agriotes spp.	Latin America	195
		Agriotes mancus (Say)	Latin America	203
		Conoderus spp.	Latin America	195
		Aeoloderma brachmana (Candeze)	Asia	*b*
		Wireworm unspecified	Asia, Latin America	60, 73, 117
	Languriidae	*Anadastus filiformis* (Fabricius)	Asia	200
	Chrysomelidae	*Dicladispa viridicyanea* (Kraatz)	Africa	36
		Trichispa sericea (Guerin)	Africa	11
		Oediopalpa sternalis (Weise)	Latin America	61, 66, 68
		Oediopalpa guerini (Baly)	Latin America	61, 66, 68
		Chaetocnema cylindrica (Baly)	Asia	225
		Chaetocnema denticulata Stephens	Latin America	61, 66, 68, 81
		Chaetocnema basalis (Baly)	Asia	178
		Aulacophora sp. nr. *similis* Olivier	Asia	55
		Monolepta cavipenne Baly	Asia	55
		Monolepta bifasciata (Hornstedt)	Asia	*b*
	Chrysomelidae	*Monolepta signata* Olivier	Asia	55
		Cerotoma atrofasciata Jacoby	Latin America	203
		Diabrotica adelpha Harold	Latin America	203
		Diabrotica balteata Leconte	Latin America	203
		Diabrotica graminea Baly	Latin America	203
		Diabrotica speciosa (Germar)	Latin America	61, 66, 68
		Diabrotica limitafa quindecimpunctata (Germar)	Latin America	195
		Diabrotica melanocephala (Fabricius)	Latin America	195
		Diabrotica spp.	Latin America	61, 81
		Altica (= *Fondia*) *madagascariensis* (Allard)	Africa	57
		Altica spp.	Asia	178
		Epitrix cucumeris (Harris)	Latin America	203
		Epitrix spp.	Latin America	81
		Oulema oryzae (Kuwayama)	Asia	82
		Disonycha (= *Donacia*) spp.	Latin America	195
		Flea beetle unspecified	Asia	120
	Coccinellidae	*Chnootriba* (= *Epilachna*) *similis assimilis* Mulsant	Africa	6, 11
	Curculionidae	*Atactogaster inducens* Walker	Asia	185
		Hypomeces squamosus (Fabricius)	Asia	120
		Tanymecus discoidalis Gyllenhal	Africa	82
		Phaulosomus musculinus (= *mus*) Csiki	Africa	82
		Neobaridia amplitarsis Casey	Latin America	66, 68, 195, 233
Lepidoptera	Lymantriidae	*Psalis pennatula* (Fabricius)	Asia	117
		Laelia suffusa (Walker)	Asia	117
		Euproctis virguncula (Walker)	Asia	117
		Euproctis minor (Snellen)	Asia	117
		Euproctis xanthorrhoea (Kollar)	Asia	117
	Amatidae	*Amata* sp.	Asia	A. S. Pradhan, unpubl. data
	Arctiidae	*Diacrisia obliqua* (Walker)	Asia	82
		Creatonotus gangis Linnaeus	Asia	82
	Limacodidae	*Latoia* (= *Parasa*) *bicolor* (Walker)	Asia	82
	Eupterotidae	*Nisaga simplex* Walker	Asia	182
	Noctuidae	*Sesamia botanephaga* Tams & Bowden	Africa	12
		Sesamia nonagroides botanephaga Tams et Bowden	Africa	6, 36
		Sesamia calamistis Hampson	Africa	6, 8, 11, 12, 36
		Sesamia inferens (Walker)	Asia	59, 82, 84, 240
		Spodoptera eridania (Cramer)	Latin America	150
		Spodoptera mauritia acronyctoides Guenee	Asia	30, 59, 196
		Spodoptera frugiperda (J. E. Smith)	Latin America	28, 61, 66, 68, 81, 150, 152, 195, 203, 219, 233

Table 1 continued.

Order	Family	Species	Distribution	Reference
		Spodoptera exigua (Hubner)	Africa	32, 217
		Spodoptera exempta (Walker)	Africa	32, 33, 36, 217
		Spodoptera ornithogalli (Guenee)	Latin America	150
		Mythimna loreyi (Duponchel)	Asia	30
		Mythimna separata (Walker)	Asia	178
		Mythimna (= *Pseudaletia*) *latifascia* [= *adultera* (Schaus)] (Walker)	Latin America	195
		Mythimna (= *Pseudaletia*) *sequax* (Fabricius)	Latin America	68
		Mythimna roseilinea (Walker)	Asia	*b*
		Mythimna yu (Guenee)	Asia	*b*
		Mocis frugalis (Fabricius)	Asia	30, 117
		Mocis latipes (Guenee)	Latin America	66, 68, 149, 150, 203, 219, 233
		Platysenta (= *Spodoptera*) *compta* (Walker)	Asia	A. Barrion, unpubl. data
		Agrotis ipsilon (Hufnagel)	Latin America, Africa	33, 68, 81, 150, 195, 203
		Agrotis spp.	Latin America	60
		Achaea janata (Linnaeus)	Asia	117
		Eldana saccharina Walker	Africa	36
		Armyworm unspecified	Asia	72, 84
	Pyralidae	*Cnaphalocrocis medinalis* (Guenee)	Asia	30, 45, 59, 72, 84, 233
		Marasmia bilinealis Hampson	Africa	36
		Marasmia trapezalis (Guenee)	Africa	32, 217
		Marasmia (= *Susumia*) *exigua* (Butler)	Asia	220
		Marasmia ruralis (Walker)	Asia	*b*
		Marasmia patnalis Bradley	Asia	*b*
		Marasmia spp.	Asia	*b*
		Leaf roller unspecified	Asia	72
		Maliarpha separatella Ragonot	Africa	12, 57
		Maliarpha sp.	Asia	*b*
		Chilo auricilius Dudgeon	Asia	*b*
		Chilo partellus (Swinhoe)	Africa	12, 92
		Chilo polychrysus (Meyrick)	Asia	59, 72
		Chilo diffusilineus J. de Joannis	Africa	6, 12, 29
		Chilo suppressalis (Walker)	Asia	59, 72
		Chilo zacconius Blezzinski	Africa	6, 11, 12
		Crambus spp.	Latin America	203
		Acigona loftini (Dyar)	Latin America	203
		Acigona chrysographella (Kollar)	Asia	82
		Scirpophaga incertulas (Walker)	Asia	59, 72
		Scirpophaga innotata (Walker)	Asia	59, 200
		Scirpophaga nivella (Fabricius)	Asia	*b*
		Elasmopalpus lignosellus (Zeller)	Latin America	28, 60, 61, 66, 81, 150, 162, 195, 203, 219, 233
		Diatraea saccharalis (Fabricius)	Latin America	28, 66, 81, 111, 150, 195
		Rupela albinella Cramer	Latin America	111
		Stem borer unspecified	Asia	72
		Undetermined stem borer nr. *Maliarpha*	Asia	*b*
	Gelechiidae	*Brachmia arotraea* Mayr	Asia	55
		Brachmia spp.	Africa	32
	Hesperiidae	*Parnara guttata* Bremer et Grey	Asia	*b*
		Parnara naso Fabricius	Asia	55
		Pelopidas agna agna (Moore)	Asia	164
		Pelopidas mathias (Fabricius)	Asia, Africa	36, 155, 217
		Pelopidas conjuncta conjuncta (Herrich-Schaffer)	Asia	*b*
		Borbo fanta Evans	Africa	6
	Satyridae	*Melanitis leda ismene* Cramer	Asia	84, 213
		Mycalesis anophis Hew	Asia	30
		Mycalesis spp.	Asia	*b*
Diptera	Cecidomyiidae	*Orseolia oryzae* (Wood-Mason)	Asia	72, 88, 131, 181
		Orseolia oryzivora Harris et Gagne	Africa	6, 11, 32, 218
	Chloropidae	*Steleocerellus* (= *Mepachymerus*) *ensifer* (Thomson)	Asia	205
		Oscinella spp.	Asia	205
		Gaurax spp.	Asia	205
		Chlorops oryzae Matsumura (= *kuwanae* Aldrich)	Asia	82
	Muscidae	*Atherigona oryzae* Malloch	Asia	30, 82, 117, 130
		Atherigona exigua Stein	Asia	82, 117, 178

Table 1 continued.

Order	Family	Species	Distribution	Reference
		Atherigona orientalis Schiner	Asia	82
		Atherigona indica Malloch	Asia, Africa	82, 205
	Diopsidae	*Diopsis longicornis* (= *thoracica*) Macquart	Africa	11, 12, 48
		Diopsis spp.	Africa	217
	Agromyzidae	*Pseudonapomyza asiatica* Spencer	Asia	213
		Pseudonapomyza spicata (Malloch)	Asia	*b*
		Agromyza oryzae Munakata	Asia	*b*
Hymenoptera	Formicidae	*Acromyrmex landolti balzani* (Emery)	Latin America	61, 68, 195
		Acromyrmex landolti fracticornis (Forel)	Latin America	61, 195
		Acromyrmex heyeri (Forel)	Latin America	61, 68, 195
		Atta bisphaerica Forel	Latin America	61, 68, 195
		Atta capiguara Goncalves	Latin America	14, 61, 68, 195
		Atta laevigata (F. Smith)	Latin America	61, 68, 195
		Atta opaciceps Borgmeier	Latin America	61, 195
		Solenopsis geminata (Fabricius)	Asia	*b*
		Pheidole sp.	Asia	*b*
		Pheidologeton diversus Jerdon	Asia	*b*
		Monomorium pharaonis (Linnaeus)	Asia	*b*
		Ants unspecified	Asia	120

[a]*G. orientalis* formerly recorded in Asia as *G. africana*. [b]Philippines, reported in this study. [c]Subterranean root feeders.

subterranean nests. Foraging ants will feed on germinated seeds only when the supply of ungerminated seed is low. However, these ant specialists feed on a wide variety of plants and thus help control grassy weeds (39). This dual pest/benefit role extends from tending ants, which protect honeydew-excreting pest species including root aphids and mealybugs (workers repel potential predators and even selectively kill parasitized aphids), to predators of leaf- and stem-feeding rice pests such as leaffolders, armyworms, white grubs, and stem borers (117).

The upland rice environment is particularly well suited to ants because of the lack of flooding. Frequent tillage perpetuates grasses and granivorous species that are highly adapted to constructing new nests in recently tilled fields. Ant nests, however, are relatively shallow, and tilling with a moldboard plow can destroy them. Also, upland ricefields are usually small and isolated, and a given area in a small field has more field borders than it has in a larger field, allowing high rates of infiltration from more sedentary species such as *Pheidole* that do not colonize tilled fields but nest in soil under shrubs and trees along field borders. *Pheidole* workers forage into fields from borders and store seed in their nests. In slash-and-burn or other no-tillage rice cultures, nests would be preserved in the field and possibly lead to high rates of seed predation. However, granivorous species do not prefer forest habitats.

Damage is characterized by reduced, usually patchy plant stand (120). Seed-thieving ants greatly prefer rice, but they can be selective regarding plants they collect and store. They harvest more seed than they can consume, so patches of germinating surplus seed (such as *Rottboellia*) will sprout from their nests during the rainy season.

In Latin America, leaf-cutting ants (*Atta* spp. and *Acromyrmex* spp.) occur only in upland fields and defoliate young rice plants (47, 68). They take leaves to fungal gardens in underground nests where fungi predigest the plant material.

Termites. Subterranean termites of the family Termitidae, which lack symbiotic protozoa to help digest plants, are the most frequently mentioned termite pests of upland rice (11, 85, 120). This family cultures fungi in special underground cells — fungal combs made of half-digested plant material (117). The fungi, inoculated onto the combs, break down plant material into food that termites can digest. The termites then consume the fungal combs. These grassland termites build nests below the plow layer in upland ricefields. The colonies attack living plants only when dead plant material is not available. They will attack a drought-stressed crop but prefer older plants having greater cellulose content. They will damage newly planted crops where clean culture has removed vegetation.

Infestations are worse in deep, light-textured soils with low moisture content. The first sign of damage is yellowing of older leaves (195). Termites feed on roots (the plant yellows, then wilts, and finally collapses) and germinating seed (loss of stand), or move above ground at night to cut seedlings at ground level, which they cover with soil for later consumption. Soft-bodied termites are highly sensitive to desiccation. They live within a self-contained system of airtight chambers and build surface tunnels lined with mud and body secretions (carton) to maintain more than 90% relative humidity. Termites can be located by their tunnels.

Termites apparently can withstand limited submergence (157) and can be a pest of dry lowland seedbeds (117), perhaps by having nests below perched water tables.

Termites appear to do more damage in Latin America where large ricefields are plowed with tractors depriving termites of preferred vegetation and forcing them to live on rice plants. In Asia, upland ricefields are typically small with large field border areas (ecotones) where termites can forage for preferred food other than growing rice plants. All grassland termites do not feed on rice. In an upland area in Batangas Province, Philippines, ricefields are commonly infested by *Hospitalitermes luzonensis* (Oshima); however, this termite does not damage rice. In the same province, though, *Macrotermes gilvus* (Hagen) feeds on rice seedlings (178).

In Africa, termites may damage rice even though fields are small and surrounded by perennial vegetation. These termite species perhaps prefer rice over other hosts.

Mole crickets. Nymphs and adults are nocturnal and burrow through soil, feeding on roots of a wide variety of plants, or forage above ground as predators of insects. Adults live 3-5 mo and are even cannibalistic. Mole crickets prefer low-lying, moist upland soils with high organic matter (11, 81). In the lowlands they inhabit rice bunds or nonflooded fields. Adults are highly mobile and can leave a flooded field to locate a more suitable habitat. Losses show as wilted plants (from root feeding) or reduced stands (120). Damage is more common near field borders, where mole crickets relocate after tillage (126).

Field crickets. Nymphs and adults of field crickets have similar nocturnal habits and damage rice as much as mole crickets do. Piles of weeds removed from fields attract them. They make subterranean nests and tunnel through the soil to feed on roots. Some species prefer seed to roots. Others feed at the base of stems, causing deadhearts.

Tunnel entrances surrounded by excavated soil are easily seen. Young plants are cut at ground level and stored in underground cells. Field crickets are highly polyphagous, as are all soil pests (117). Sachan et al (198) reported that field crickets prefer maize to upland rice. Like mole crickets, field crickets cannot survive in standing water and are, therefore, more prevalent in upland fields.

White grubs and black beetles. Scarab beetles that feed on living roots as larvae but not as adults are called white grubs or chafers (Melolonthinae, Rutellinae), and those that feed as adults but not as larvae on plant crowns are called black beetles (Dynastinae). In the tropics, chafers or white grubs have a 1-yr life cycle starting with adults emerging from the soil about 1 mo after the first downpour of the rainy season (134, 159). They lay eggs at the same time farmers sow upland rice. The rice passes its most susceptible stage, and damage is mostly avoided when the white grubs are small. After several months, the long-lived larvae are large enough for two or three to denude the root system of mature rice (223). This intensity of damage is rare, but wilting occurs when root loss is combined with drought stress.

The larvae need damp (not saturated or dry) soil to survive and pass the unfavorable dry season 0.5-2 m underground in aestivation in the moist soil. The first heavy rains of the season (20-30 mm/d) stimulate the grubs to resume activity, and after several weeks they develop into pupae and adults and eventually dig their way to the soil surface and fly to nearby trees to seek food and mates. The adults of most white grub species feed only on trees, but in some species, notably *Eutheola humilis*, the adults defoliate and cut off stems at ground level (28). *Eutheola bidentata* damages sugarcane fields in Venezuela (121). Floods kill white grubs (208). Grasslands can support large populations and, therefore, white grubs can be more abundant in newly planted upland ricefields that were previously fallow (81).

Black beetles live up to a year; adults can attack a crop at any stage by burrowing into the soil (127) and feeding at the base of stems to cause whiteheads (207). Adults emerge with the early rains and are normally more abundant and do more damage on a young rice crop with small root systems (38, 81).

The larvae feed only on dead organic matter in dryland fields and do not attack rice. Adults are highly mobile and, although sensitive to flooding, can invade a field soon after it drains (115).

Root aphids. Several genera of migratory aphids feed on the roots of upland rice (249). Populations build up more in light-textured soils with high percolation rates. Damage has also been reported from dry seedbeds of lowland rice (52). Tending ants — *Pheidole, Crematogaster, Tetramorium, Lasius, Tapinoma* — are necessary for root aphids to multiply. Ants harbor aphids in their nests over winter or during unfavorable periods and relocate them on rice plants, digging tunnels along the root systems to allow these soft-bodied insects to penetrate the soil. Most intensive studies on aphid life histories have been done in temperate environments (158, 222, 229). Root aphids fly to rice plants at the beginning of the rice season and pass through several generations, continually developing winged forms to relocate on alternate grassy hosts until winter, when they move to perennial hosts, usually trees. Yield loss occurs mainly through reduced tillering, but infested plants become yellow and stunted, and, in extreme cases, wilt (227). Aphid populations build up gradually, so damage usually begins in the late vegetative and reproductive growth stages.

Root-feeding mealybugs. More than half of the mealybug species on rice feed on roots (245). Being soft bodied, mealybugs are not adapted to living underground, but they survive because tending ants (the same species that tend root aphids) dig burrows for them and move them from plant to plant. Well-drained soils help mealybugs survive. Although six species are recorded as subterranean root pests of rice, we found no report citing damage. Root-feeding mealybugs are probably more prevalent on perennial grasses than on short-lived annual rice.

The most common rice mealybug, *Brevennia rehi*, is a foliar feeder favored by lack of rain; apparently it is responsible for high yield loss in Northeast India and Bangladesh (N. Panda, pers. comm., as stated by IRRI [106]). This report needs confirmation. Mealybug damage was only briefly mentioned in another report (156).

Root weevils. A few species of upland weevils (*Hypomeces, Donacia, Atactogaster*) attack rice roots as larvae and feed on stems and leaves as adults. Damage is patchy. The larvae are not adapted to submergence and are true upland soil weevils as opposed to the so-called water weevils. They rarely become sufficiently abundant to cause damage. Adults on rice foliage or the soil surface show that the roots are being attacked by the grubs. Root weevils are highly polyphagous (185).

Root beetles. Soil-inhabiting false wireworms *Gonocephalum* spp. are reported in upland ricefields. The adults and larvae normally feed on decaying organic matter, but land preparation for upland rice removes these sources. The larvae feed on seedling roots, and nocturnal adults roam on the soil surface to cut off seedlings at ground level (82). This group of ground beetles is highly omnivorous; adults even prey on stem borer larvae (183). True wireworms (Elateridae) feed on living roots, but rice as a host has been reported infrequently (117). In Latin America, the highly polyphagous larvae of *Diabrotica* rootworms are also recorded on rice.

Root bugs. Upland rice seedlings can be attacked by the adults and nymphs of chinch bugs *Blissus and Caenoblissus* and brown bug *Scaptocoris*, which feed on the roots with their sucking mouthparts (80, 83). Three genera of burrower bugs — *Aethus, Geotomus*, and *Stibaropus* — are common in grasslands in the Philippines and may attack the first crop (rice or maize) planted after the dry season. Chinch bugs are most abundant after a dry spell. These insects are large and can kill seedlings or stunt and reduce tillering on older plants. They prefer other hosts and rarely damage rice. Adults can also feed on developing rice grains (81).

Cutworms. Soil-dwelling noctuid larvae hide underground during the day to avoid predation by birds and become active at night above ground, cutting off young plants at ground level (hence the name cutworm). Larvae drag severed plants into burrows. The larvae have wide host ranges and pupate in the soil. *Agrotis ipsilon* occurs worldwide and appears to be the most common cutworm pest of upland environments but is more prevalent in lowland rice, particularly in dry seedbeds.

Foliar pests

Other groups of insects are adapted to upland environments because they pass one growth stage underground, either as egg (in hemimetabolous species) or pupa (in holometabolous groups).

Rice seedling maggots. Atherigona flies occur in nonflooded environments in Asia and Africa (180). Feeding of larvae, one per tiller, causes deadhearts. Flies, as opposed to moths, only secondarily evolved as phytophagous pests from a saprophagous origin. *Atherigona* larvae secondarily feed on decaying tillers, whereas larvae of stem borer moths actively feed on living tillers to cause deadhearts. Seedling maggots will die if they cannot sever a tiller on which to feed as it decays. Plants die under heavy attack, whereas lighter infestations cause stunting, delayed maturity, and ragged leaves (236).

Eggs are laid only on actively growing plants (49), and damage occurs within the first week after crop emergence (170). Larvae pupate more in stems than in soil. Seedling maggot attack is highly seasonal (206), normally peaking 2-3 mo after the onset of the rainy season. These pests possibly aestivate over the dry season. Rice is only one of their many graminaceous crop and weed hosts.

The rice stem maggot *Chlorops oryzae* is adapted to temperate upland and lowland rice growing regions of Asia. In Japan and China upland rice grows in mountainous regions, a habitat of this chloropid fly. The larvae tunnel into the stems. The stem maggot is more damaging during the seedling stage. Larvae hibernate in grasses.

The several dipterans reported as stem maggots in dry-seeded lowland seedlings in India (205) could presumably attack upland rice.

Leaf miners. Leaf miners are common on wheat and maize but are rarely reported on upland rice (213). Three leaf miners are more prevalent on upland than lowland rice in the Philippines. *Pseudonapomyza asiatica, P. spicata*, and *Agromyza oryzae* attack at the seedling stage. The larvae develop inside the tunnels they construct in the parenchyma tissue. *P. spicata* and *A. oryzae* prefer maize, *Eleusine*, and other grasses to rice. *P. spicata* can become abundant on wheat.

Leaf beetles. Chrysomelid and coccinellid leaf beetles scrape or otherwise remove leaf tissue as larvae or adults or both. This damage accelerates desiccation of plants. The larvae of some species are root feeders. Flea beetles *Epitrix* and *Chaetocnema* and rootworms *Diabrotica* spp. feed on rice foliage only as adults. Their root-feeding larvae have hosts other than rice. The adults and larvae of the hispa-like *Oediopalpa* spp. beetles of Brazil and *Chnootriba* (=*Epilachna*) beetle of Africa feed on upland rice leaves. *Oediopalpa* spp. larvae are leaf miners. *Chnootriba* is also prevalent in lowland environments (11). Leaf beetles prefer vegetative rice (81).

The rice hispa *Dicladispa armigera* is not reported on upland rice and prefers more aquatic habitats. In Central Africa, however, *Dicladispa viridicyanea* attacks upland rice in the vegetative stage as well as lowland seedbeds. *Trichispa sericea* is reported on upland rice in West Africa and Madagascar (57).

The rice leaf beetle *Oulema oryzae*, much like *Chlorops oryzae*, is adapted to temperate regions of Asia and is usually a pest on lowland rice but seldom on upland rice in the mountains (82). The adult hibernates on grasses.

Armyworms. Species of grassland-adapted *Spodoptera, Platysenta*, and *Mythimna* larvae create widespread epidemics. They can defoliate ricefields, generally in patches, from early vegetative growth to harvest (41). Armyworms pupate in the soil and highly favor upland rice (34). Adults can disperse long distances to colonize even remote upland areas. They become more abundant than their natural enemies, particularly after favorable rains following a prolonged drought (196). The drought kills the armyworm and natural enemies (mainly parasites), but the armyworm can recolonize rapidly.

The natural increase in soil fertility from mineralization of soil N over the drought period promotes luxuriant plant growth to foster a rapid buildup of these highly fecund species. Weeding rice increases the likelihood of damage. The parasites normally return to control the armyworms, but not until after serious damage.

Outbreaks on upland rice have been reported in Ghana (3), Zanzibar (38), Central Africa (36), Panama (165), Brazil (28), Malaysia (196), and India (167). Defoliation may be severe, often leaving only the base of stems. Armyworm larvae hide during the day under litter or in soil cracks. At night they ascend plants to feed. Larvae pupate in the soil.

Thrips. Thrips frequent upland rice, but damage is less than in the lowlands. Thrips larvae and adults feed on leaf blades by rasping, causing leaf rolling and stippling. Thrips prefer vegetative stage rice, and their survival increases during drought (heavy rain washes them from foliage), although drought stress usually outweighs thrips damage. Drought and thrips cause leaf rolling in upland rice (235), but thrips have been overlooked perhaps because of their small size. Thrips are most numerous in dry season irrigated rice. The combination of favorable plant growth and lack of rainfall is ideal for thrips. In contrast, the lack of rainfall in upland rice hurts the crop and eventually the thrips, whose numbers must decline.

In Latin America, *Frankliniella rodeos* attacks panicles before they emerge from the boot, causing sterile grains.

Stem bugs. Black bugs are the most common group of rice stem-feeding Hemiptera in Asia. The most frequently mentioned species — *Scotinophara coarctata* and *S. lurida* — prefer aquatic habitats and therefore could not occur in upland rice as sometimes reported. Upland species in the same genus — notably *S. tarsalis* and *S. scotti* — are morphologically similar and remove sap from stems of grasses and upland rice. The upland species are notably more abundant in upland rice planted near forests.

In Latin America, the large pentatomid *Tibraca limbativentris* causes deadhearts and whiteheads on upland rice. Both adults and nymphs remove sap from internodes of plants more than 3 wk old. Tillers are killed by mechanical damage and by the entry of secondary microbial infection. This damage is often confused with that of lepidopterous stem borers (233). Eggs are laid on the leaves and stems. Nymphs are gregarious. This species can also be found on irrigated rice. Drought reduces population buildup.

Stem borers. Lepidopterous and dipterous stem borers are widely recorded on upland rice, but cultural practices and alternate hosts determine abundance. Except for *Elasmopalpus lignosellus*, numbers usually build up toward the end of the crop growth cycle. Therefore, late-maturing varieties, staggered planting, and lack of flooding favor stem borer buildup. Many stem borer species can lie dormant in the stubble after harvest, and their survival is encouraged by panicle harvesting (leaving tall stems) and lack of tillage after harvest.

Stem borers disperse and lay many eggs. Many species are polyphagous; however, the monophagous *Maliarpha separatella, Diopsis longicornis, Scirpophaga incertulas*, and *S. innotata* can also be abundant on upland rice. *Chilo suppressalis* develops faster and becomes larger when reared on upland than on lowland rice (226).

The lesser corn stalk borer *Elasmopalpus lignosellus* is semisubterranean and is perhaps the stem borer most adapted to upland rice (129). Highly polyphagous, it infests maize, peanut, and cowpea. It attacks seedling rice (one larva can kill up to four plants before maximum tillering) (195). *Chilo* and *Maliarpha* stem borers prefer older plants. But *Scirpophaga* spp. will attack young plants even in the nursery. *Elasmopalpus* larvae tunnel into the stems at or below the soil level, causing deadhearts. Larvae are not found in their tunnels inside stems because, when disturbed, they retreat into cases made from soil particles bound by silk. The cases are attached to the tunnel entrance (143). This behavior probably evolved as protection from natural enemies. Larvae pupate in the soil. The lesser corn stalk borer is more abundant during drought; damage is often confused with that of drought (233). This species prefers sandy soils, and its distribution within a field may relate to soil texture (143).

Diatraea saccharalis, aside from the lesser corn stalk borer, is frequently a stem borer pest in Latin America. According to Teran (233) rice and maize are more preferred hosts than sugarcane, its namesake.

Acigona chrysograpella is a less known upland rice stem borer in Asia with habits similar to *Elasmopalpus* (82) because it is not found in lowlands. *Acigona* has grassy weed alternate hosts. As a moth it is often confused with the dark-headed stem borer *Chilo polychrysus* and striped stem borer *Chilo suppressalis*.

Other common upland rice stem borers are also reported in the lowlands. The dominant species in upland rice vary greatly with location. In Uttar Pradesh, India (78), and in Japan (123), the pink stem borer *Sesamia inferens* is more prevalent.

In Kenya, the principal rice stem borer is *Chilo partellus* (92). The lowland African stem borers *Maliarpha separatella, Diopsis longicornis*, and *Sesamia calamistis* are less abundant on upland than on lowland rice (217) but perhaps cause greater yield loss because plant injury is greater if combined with drought stress (92). The stalk-eyed stem borer *Diopsis* is more prevalent in wet habitats (6, 11, 217).

In Central and West Africa, *Maliarpha* and *Sesamia calamistis* are the dominant stem borers of upland rice (8, 9, 10, 11). *Chilo diffusilineus* and *Chilo partellus* inhabit the upland savannas, whereas *Chilo zacconiu* prefers the lowlands (11). *Maliarpha* is most abundant in the mangrove swamp habitats (91), coastal regions (16), or rain forest zones (11) of Africa and appears to be the homologue of *Scirpophaga incertulas*. The yellow stem borer can also be prevalent in upland rice (120, 167). The sugarcane borer *Eldana saccharina* is so far only a potential pest of upland rice (91) despite Grist and Lever's (82) warning.

Grasshoppers and locusts. Short-horned grasshoppers and locusts — *Locusta, Patanga, Schistocerca* — lay eggs in the soil, inhabit grasslands, and develop into swarms to seriously damage upland rice from time to time (173). Large numbers can destroy a field, leaving only the stubble. In low numbers, grasshoppers can cut panicles (173). Farmers may not plant if locust swarms are imminent. Prolonged dry weather followed by favorable rain favors development of large swarms (173). Usually breeding in dry grasslands, they disperse to attack crops including upland rice (191). Eggs are susceptible to desiccation during drought and to inundation during seasonal rains. With favorable soil moisture over consecutive seasons, natural enemies cannot prevent a large population increase, leading to migratory swarms (64).

Most grasshoppers on rice are adapted to uplands (107), but lowland rice grasshoppers *Hieroglyphus* spp. and *Oxya* spp. occur occasionally on upland rice (2, 82). They lay eggs on rice foliage. Nymphs are semiaquatic.

The gryllid *Euscyrtus concinnus* is a pest of lowland and deep water rice in Bangladesh and Thailand. In the Philippines, it damages upland rice grown in isolated pockets near lakes. The gryllid nymphs and adults feed on the central portions of foliage, leaving only the midrib and leaf margins.

Leaffolder. Pyralid moths whose larvae fold leaves to make a feeding shelter occur worldwide (217) but are apparently most common in Asia. Leaffolders attacking rice in Asia are a complex of species (26). *Cnaphalocrocis medinalis*, the best-known rice leaffolder in Asia, may prefer grassy weeds over rice (86). It is a late colonizer of upland rice. *Marasmia exigua*, a lowland species (220), prefers rice to grass species (86) and colonizes upland rice during the early growth stages. *Marasmia patnalis* is the most commonly encountered species in upland rice in the Philippines. Perennial grasses are their alternate hosts, and they can survive year-round in upland rice environments. The leaffolders *Marasmia ruralis* and *Marasmia* spp. are least abundant. Dormancy is unknown in leaffolders. *Cnaphalocrocis medinalis*, however, is known as a migrant (90). Leaffolders remove photosynthetic tissue; attack during the flag leaf stage is particularly injurious. Populations are normally held in check by natural enemies, but leaffolders become particularly abundant in conditions of high plant fertility and shade.

Butterflies. Skippers *Pelopidas mathias* and *Borbo fanta* are more prevalent in African lowland than in upland habitats (6), but extensive studies in Japan and China showed that *Pelopidas mathias* prefers an upland habitat (155). *Parnara guttata* seasonally migrates between lowland and upland areas and is equally abundant in both environments (164).

The green horned caterpillar *Melanitis leda ismene* is more abundant in lowlands (212), but our experience in the Philippines suggests that *Pelopidas mathias* and *Melanitis leda ismene* are often more abundant in uplands than in lowlands. Bamboo *Bambusa* spp. annually sustains *P. mathias* populations in the Philippine uplands. Adults feed on nectar from flowers and migrate to upland rice during the late vegetative stage.

Butterflies hide in the shade during the day. They seldom become numerous, probably because of high egg predation. Egg and larval parasitization are often low. Butterflies can readily disperse long distances to seek remote upland ricefields. However, they have low biotic potential, and even if predation rates are low they rarely become abundant. Upland environments, with their diverse microhabitats, can provide more favorable sites than lowland rice plains.

Butterfly pests of rice have broad host ranges and become dormant during unfavorable times of the year.

Polyphagous Lepidoptera. The larvae of many polyphagous moths are reported to defoliate upland rice: tussock moths *Psalis pennatula, Laelia suffusa, Euproctis virguncula, E. minor*, and *E. xanthorrhoea*; slug caterpillar *Laotia bicolor*; hairy caterpillars *Nisaga simplex* and *Amata* spp.; and wooly bears *Diacrisia obliqua* and *Creatonotus gangis*. Many of these polyphagous larvae migrate and are transients in rice, including *Heliothis armigera* and *H. zea*, highly polyphagous species (82).

Gall midges. The Asian rice gall midge *Orseolia oryzae* (88, 131) and its African counterpart *O. oryzivora* (6, 11, 12, 32, 217) prefer lowland to upland rice. Gall midges in rainfed areas are prevalent only during the rainy season and disperse poorly. Their alternate hosts (wild rices, *Leersia, Ischaemum*, and *Paspalum*) are mostly aquatic grasses and are less likely to be near upland rice areas. In an area of mixed upland, floating, and rainfed lowland rice cultures in northern Thailand, upland rice, which is planted a month earlier, was attacked first, but subsequent populations were much lower than in rainfed lowland or floating rice. Low numbers of gall midges passed the dry season on perennial weeds such as *Paspalum* (88).

Shoot aphids. Reports of aphids attacking upland rice plants are few (249). Without maize, the maize leaf aphid *Rhopalosiphum maidis* attacks upland rice in the Philippines. The plum peach aphid *Hysteroneura setariae* was reported in Sierra Leone to infest leaves and unripened grain (7). *Sipha glyceriae* caused transverse linear necrotic striae in rice leaves in Italy (172). Heavy rains held populations in check. Rice is not a preferred host for shoot aphids.

Leafhoppers and planthoppers. Cicadellids and delphacids disperse easily and readily colonize upland rice from nearby lowland areas. A study in Sarawak (241) showed similar species in upland and lowland rice. *Nephotettix* species dominated. The most prevalent species, accounting for 90-95% of the sweep net samples, were *N. virescens, N. nigropictus, Nilaparvata lugens, Sogatella furcifera, Cofana spectra,* and *Recilia dorsalis.* Lowlands had higher populations. Katanyukul and Chandaratat (120) monitored hopper numbers in upland and lowland fields of northern Thailand and found similar results. A comparative study of planthoppers in Fiji showed more brown planthopper (BPH) and whitebacked planthopper (WBPH) in wetland rice than in lowland rice, and hopperburn was prevalent in lowland areas with standing water (89).

Hopperburn in upland ricefields in Asia is rare (84). In Batangas, Philippines, isolated fields of upland rice become hopperburned infrequently from WBPH. A report from Fiji cites hopperburn from BPH and WBPH (250). In these two situations, upland rice was grown on highly fertile soil, and N fertilizer was applied. Hoppers respond to better nutrition. Normally upland rice is grown on poor soil and receives no fertilizer.

In Asia, upland rice areas are normally not far from lowland ricefields — a source of hoppers. Otherwise hopper species with greater polyphagy than BPH or *Nephotettix virescens* would be dominant.

In Africa, leafhoppers and planthoppers do not become abundant on upland rice (6, 11) probably because lowland rice is not widely planted nearby. The only reported hopperburn was from *Nilaparvata maeander* in breeder plots receiving high N rates in Nigeria (98). Hoppers, however, are a greater problem in Latin America, where large grassland areas breed polyphagous species (*Graphocephala* spp., *Hortensia* spp., *Exitianus obscurinervis, Balclutha* spp., and *Draeculacephala* spp.), which then disperse to cause hopperburn on seedling rice (68). Rosetto et al (195) reported *Graphocephala* spp. and *Hortensia* spp. to be equally abundant on upland and lowland rice.

The leafhopper and planthopper epidemics in Asia that caused severe losses from hopperburn and virus diseases over the past several decades occurred principally on lowland rice. Except in a few isolated cases (160), upland rice has been spared from tungro, grassy stunt, and ragged stunt virus diseases vectored by green leafhopper (GLH) and BPH (123). Virus diseases have occurred in upland rice where lowland rice was nearby. Rice dwarf disease, however, was first recorded on upland rice in the Philippines (187). Virus diseases can be perpetuated only on living plants or insect vectors, and no living rice — planted, ratooned, or volunteer — grows year-round in upland areas except in a few with 12 mo of rainfall.

The smaller brown planthopper *Laodelphax striatellus* occurs in upland rice in Japan (18). It spreads black-streaked dwarf and stripe viruses between winter wheat and barley to lowland rice. Early planting of lowland rice nurseries spreads these viruses, but upland rice has remained uninfected.

The principal vectors of rice virus diseases generally have narrow host ranges, and alternate hosts in the grass family are mostly annuals, dying in the dry season. Some virus vectors such as BPH can disperse long distances, but few do. The restriction of upland rice and weed hosts to the rainy season, the small area planted to upland rice, and the hopper vectors having narrow host ranges all work against virus diseases in upland rice.

In Latin America, *Sogatodes oryzicola* and *S. cubanus* transmit hoja blanca virus disease, but reports on upland rice are rare except in the favored upland areas of Colombia, Peru, and Venezuela (35, 42). *S. oryzicola* occurs in Brazil on upland rice, but hoja blanca has not been reported (67). *S. oryzicola* has a wide host range (10) similar to WBPH in Asia. WBPH, however, is not known to transmit any virus disease.

In Africa, pale yellow mosaic virus is endemic to swampy lowland areas where rice ratoons year-round (19) and is mechanically vectored mainly by hispid beetles. A minor vector, a flea beetle *Chaetocnema* spp., is an upland rice pest, and upland ricefields near endemic areas occasionally contract the virus.

Spittle bugs. Cercopid nymphs produce a protective frothy covering that looks like saliva. In Latin America, spittle bugs damage upland rice. In parts of Brazil where upland ricefields are surrounded by pastures, adults migrating from grasses can damage rice severely and cause complete hopperburn in a young rice crop within a week of colonization (194, 195). Dispersal to rice occurs even if pastures are verdant, and spittle bugs prefer pasture grasses to rice (168). Nymphs are rarely abundant enough to damage rice. Regular rainfall favors their development (233).

Seed pests

Alydid and pentatomid bugs are seed pests of upland rice worldwide. In Asia, *Leptocorisa* spp. prevail. Their habits make them particularly suitable for upland rice: 1) they feed on many grasses (and therefore can survive the early wet season before rice sets its grain); 2) adults are long-lived and mobile, allowing them to find isolated plantings of rice (besides seed bugs, only birds and rats appear to have this capability); and 3) adults aestivate in forested areas or sugarcane fields during the dry season when neither rice nor grassy weeds are present (199). Rice seed bugs concentrate on small-scale upland ricefields because they can actively search them out. The prevalence of groves of trees characteristic of upland environments ensures nearby aestivation sites, keeping the seed bugs close by.

Leptocorisae are uncommon in lowland rice plains because: 1) their populations are diluted in a sea of rice planted more or less at the same time (they can only feed on rice during the milk to hard dough stages), 2) they lack aestivation sites, and 3) weedy fallow areas are limited.

The lowlands of Asia are dominated by *L. oratorius*, which lays its eggs high on the foliage (199). *L. acuta* and *L. solomonesis* oviposit at ground level, the former on litter and the latter loose on the ground. These egg laying habits explain their environmental preferences (214). In Japan, the postdiapause adults of *L. chinensis* migrate from mountainous areas to upland ricefields during flowering (114).

Pentatomid bugs prevail in Latin America (81, 82, 195), and in Africa, pentatomid and coreid bugs are equally cited (6, 82). Damage is often characteristic of the species (5). *Eysarcoris ventralis* and *Menida* spp. are the common pentatomid seed bugs of Philippine upland rice, but they prefer *Echinochloa* spp. grass seed to rice. *Nezara viridula* occurs worldwide and is often more abundant in the uplands (54). We saw few reports of seed bugs on upland rice, but seed bugs apparently operate equally between lowland and upland rice. Good dispersal is necessary for species that can feed for only 2-3 wk on a crop and must first find those crops at ripening stages.

Other pest species feed on flowers. In Mato Grosso, Brazil (194), and Santa Cruz, Bolivia, the panicle weevil *Neobaridia amplitarsis* attacks rice during flowering (68, 233). The larvae are rice stem borers; adults feed at the bases of spikelets, causing empty grains. Also in Latin America, the cydnid *Alkintus atratus* is a seed bug as an adult and nymph (194).

A number of beetles feed on pollen — coccinellids, *Diabrotica*, *Aulacophora*, and *Monolepta* (55) — but because rice is self-pollinating and fertilization occurs before spikelets open, they pose no threat to yield.

PEST ECOLOGY

We now look at characteristics of the life cycles of upland rice insect pests to learn how each plays an adaptive role in upland rice ecology.

Life history strategies

Oryza sativa does not tolerate drought well, so upland rice is highly seasonal, normally grown in the wettest months of the year. Usually, rice is present for less than half of the year. The rice-free fallow poses serious problems of survival to upland rice insects, which have evolved at least four mechanisms to overcome the cyclical lack of a host: 1) polyphagy, 2) longevity, 3) dormancy, and 4) vagility (dispersal).

Polyphagy. Polyphagy is defined as having hosts of at least two botanical families; oligophagy, of more than one genus; and monophagy, of only one genus (40) — in our case, *Oryza*. Most wild rices, however, are aquatic and therefore are normally far removed from upland rice habitats; otherwise more would be alternate hosts for upland rice insects. The highly monophagous rice pests — *Scirpophaga incertulas*, *Nilaparvata lugens*, and *Nephotettix virescens* in Asia and *Maliarpha separatella* and *Diopsis longicornis* in Africa — occur on upland rice but are more abundant in lowland culture. They can specialize in rice because they are highly vagile and can attack all growth stages. By specializing in rice, monophagous rice pests can outcompete related but polyphagous species. Intensive and extensive lowland rice culture has favored monophagous species. *Rupela albinella* (Cramer), the only monophagous species in Latin America, is rarely reported on upland rice (111).

Because of its limited temporal and spatial existence, upland rice has not favored the evolution of specialized species. Chang (44) shows evidence that upland rice has only recently been cultured by man from the lowlands; thus, pests have had little time to fully adapt to the crop. All but the lowland-adapted insect pest species have alternate plant hosts to rice. Root pests with limited mobility are highly polyphagous. Pests that specialize in one growth stage — e.g., seedling maggots, seed bugs — are oligophagous or polyphagous.

Most alternate hosts of rice pests are annual grasses, which also are seasonal. Upland rice is also a host, but not the preferred one, of the most highly polyphagous species: soil pests, grasshoppers, armyworms, and *Nezara viridula*.

The dry season poses a great obstacle to an upland rice insect's survival, and only some perennial plant hosts are suitable food during the off-season. Polyphagy allows upland rice insects to survive during the rainy season when plants — both annual and perennial — are actively growing and therefore more nutritious.

Longevity. The ability of an insect to live 2-3 mo without undergoing dormancy helps species such as root-feeding white grubs (as larvae) and seed-feeding bugs (as adults) to survive unfavorable periods. White grubs are not highly fecund and their life strategy is to improve survivorship of limited progeny. Their subterranean habitat hides them from many natural enemies. But root tissue is not highly nutritious, so they must eat great quantities and need a large insect biomass to digest it. Other soil-inhabiting, root-feeding insects have short life cycles but are more fecund.

Seed pests need greater longevity as adults to locate a host at early grain development and give sedentary offspring time to develop. Few groups of upland rice insects live long in active development. Polyphagy and longevity only increase their ability to survive during the rainy season. Other mechanisms are needed to survive the dry season.

Dormancy. In the tropics, the nonrice season is the dry season, while in temperate areas, the off-season is winter. Many upland rice insects undergo dormancy in summer (aestivation) or winter (hibernation). Dormancy is simply inactivity; during winters with prolonged temperatures below 10 °C, insects find shelter and cease movement. Activity is resumed with warmer temperatures. A deep state of inactivity, termed diapause, occurs in some species that prepare physiologically (having low metabolism and converting gonads to fatty fuel reserves) for the unfavorable season (148). They enter diapause in anticipation of unfavorable weather and resume activity after favorable weather begins, usually in response to photoperiod or through a delayed response to a stimulus such as heavy rainfall (237). Not all individuals of a population have the same threshold for environmental responses for entering or terminating diapause — this is seen as a mechanism to prevent total mortality if a false cue appears, such as a sudden warm spell in winter or rain in the middle of the dry season (154).

Probably, more upland rice insects undergo dormancy than we realize. Candidates are *Atherigona* spp., root aphids, root weevils, crickets, leaf beetles, thrips, and seed bugs. Insects known to enter various states of aestivation are *Leptocorisa* spp. adults (199), *Maliarpha separatella* larvae (9), *Scirpophaga innotata* larvae (117), *Chilo partellus* larvae (21), *Scirpophaga incertulas* (179), white grub larvae (134), *Patanga succincta* adults (6, 82), and *Schistocerca gregaria* eggs (82).

Insects known to enter hibernation are *Laodelphax striatellus* nymphs (124), *Chilo suppressalis* larvae (125), *Sesamia inferens* larvae (146) — but not *S. calamistis* (8); *Diatraea saccharalis* larvae (75); *Scirpophaga incertulas* larvae (125); *Hieroglyphus*, *Locusta*, and *Oxya* grasshopper eggs (82); and *Pelopidas mathias* pupae (232).

Leptocorisa oratorius and *L. acuta* adults aggregate on trees, sugarcane, or other shady, moist sites. *L. palawanensis*, confined to Sulu and Palawan, Philippines, lives on the grass *Brachiaria mutica* (Forsk.) Stapf in the absence of rice. The adults can live for 5 mo. When aestivating, their rate of metabolism drops and they do not feed. They will, however, puncture plant tissues of their aestivation host in search of water. This behavior has led to errors of the host range of rice bugs (1). Aestivation quickly terminates with rain, probably meaning aestivation is not deep.

Some stem borers aestivate as mature larvae in rice stubble or in straw stacked as livestock feed. However, mortality increases proportionally with the duration of the dry season even if the stubble remains undisturbed. If the stubble is plowed for a crop following rice, few stem borers survive. Rainfall terminates dormancy, but it normally takes several weeks for moths to develop and emerge.

Last-instar white grub larvae tunnel 1-2 m deep in the soil to construct pupal chambers in which they aestivate. The larvae are very sensitive to dryness, so pupal chambers are sealed to conserve body moisture. Aestivation terminates with the first heavy rains, but as in stem borers, 3-4 wk pass before adults develop.

Insects may respond differently in each region to cold temperature or drought. Biotypes or local populations may evolve (56). Local populations of *Scirpophaga incertulas* or *Patanga succincta* may have become adapted to prevailing conditions.

Vagility. The ability to disperse combined with high fecundity or short life cycles enable some upland rice pests to better exploit the temporarily favorable upland habitat. Armyworms, skippers, and locusts actively travel hundreds of kilometers in air fronts such as intertropical convergence zones to descend onto upland rice fields far from their breeding grounds (31). Several generations can build up on alternate hosts in the grass family before rice is planted. These large insects are active fliers. Smaller insects such as thrips, aphids, and planthoppers passively migrate long distances by the wind.

Other species can readily travel tens of kilometers — stem borers, leaffolders, leafhoppers, cutworms, spittle bugs, leaf beetles, seed bugs, ants, and termites.

The least dispersive species are white grubs, mealybugs, seedling maggots, crickets, weevils, and gall midges.

Each species has evolved a unique set of attributes to enable it to survive and adapt to the changing upland environments. Several evolutionary avenues lead to fitness (Table 2), but there is no reason to believe one set of attributes is better than another (224).

Drought

Well-drained rainfed upland soils are subject to drought if rains do not fall within 2-3 wk. Prolonged drought followed by favorable rains stimulates armyworm and locust outbreaks, but mealybugs, root aphids, and thrips become numerous only after dry spells, for two reasons. First, heavy rain normally kills soft-bodied foliage-feeding thrips and mealybugs, and soil-inhabiting root aphids and root mealybugs. Drought eliminates this source of mortality. Second, the rice plant responds to drought by breaking down proteins into soluble N compounds, which enter the phloem and are taken up by these sap-feeding insects (245). Greater nutrition, therefore, leads to greater survivorship and fecundity.

Small rice area

Except in the highly mechanized, large landholdings of Latin America, upland ricefields typically are patchy within a highly diverse flora. The small fields result in higher ratios of perimeter to area than with the typically larger lowland ricefields. Upland ricefields themselves may be intercropped with cereals, legumes, or root crops. Mixed intercropping with a wide variety of species also occurs in tribal slash-and-burn agriculture (50, 74).

Upland ricefields tend to be small because of the labor needed to clear land in slash-and-burn areas and to till land to minimize weeds. Rice requires more tillage than does maize because rice competes less well with weeds. Upland rice is more a subsistence than a cash crop, and small areas (1 ha) can feed a family.

Small fields favor some insect pests such as some ant species that can forage from more permanent field borders. Trees provide food and mating sites for white grubs (134) as well as aestivation sites for *Leptocorisa* spp. (199). Field border grasses plus those within a ricefield provide alternate food for all but the highly monophagous upland rice colonizers and a habitat for natural enemies.

Table 2. Life history patterns of upland rice insects or insect groups.

Pest	Host range			Longevity			Dormancy		Vagility			Fertility		
	Monophagy (*Oryza* spp.)	Oligophagy (grasses, sedges)	Polyphagy (angiosperms)	Low (<3 wk)	Medium	High (>2 mo)	Yes	No	Low (<1 km)	Dispersive	Migratory	Low (<50 eggs)	Medium	High (>500 eggs)
Ants			x			x		x		x				x
Termites			x			x		x		x				x
Mole crickets			x			x		x		x		x		
Field crickets			x			x		x		x		x		
White grubs			x			x	x		x			x		
Root aphids			x			x	x				x			x
Mealybugs		x		x				x	x					x
Seedling maggots		x		x			x		x				x	
Leaf beetles			x		x			x		x			x	
Armyworms			x		x		x				x			x
Thrips		x		x				x			x		x	
Chilo spp.		x			x		x			x			x	
Maliarpha	x				x		x			x			x	
Locusts			x		x		x				x		x	
Gall midges		x		x			x		x				x	
Nephotettix virescens	x			x				x		x			x	
Leptocorisa spp.			x		x		x			x			x	
Leaffolders		x		x				x	x				x	
Sogatella furcifera		x		x			x			x			x	

All this appears to favor insect pest buildup, but the contrary is true. Loevinsohn (138) showed that insect pest populations respond exponentially with the proportion of land devoted to rice up to about 75% of the area; then the rate of response declines. In most upland rice areas, the rice crop occupies less than 50% of the area; therefore, the potential for population buildup is low. This relationship may not hold for seed pests that can locate small ricefields.

Another outcome of the highly diverse flora and physical environment of upland rice is that each upland rice area has a unique composition of insect pests.

For example, in Tanauan, Batangas, Philippines, the main upland rice pests are rice leaffolder (RLF), armyworm *Mythimna separata*, WBPH, ants *Solenopsis geminata*, and white grub *Leucopholis irrorata*. Sixty kilometers away in Real, Quezon, the main pests are seedling maggot *Atherigona oryzae*, flea beetle *Chaetocnema basalis*, thrips *Stenchaetothrips biformis*, and rice bug *Leptocorisa oratorius*. In a third Philippine upland rice site in Claveria, Misamis Oriental, Mindanao, the main pests are ants *Solenopsis geminata;* seedling maggot *Atherigona oryzae*; white grubs *Holotrichia mindanaoana* and *Leucopholis irrorata;* stem borers *Sesamia inferens*, *Chilo auricilius*, *C. suppressalis*, *Scirpophaga incertulas*, *S. innotata*, and *Acigona chrysographella*; root aphids *Tetraneura nigriabdominalis* and *Rhopalosiphum rufiabdominalis*; leaffolders *Marasmia patnalis* and *Cnaphalocrocis medinalis*; armyworm *Mythimna separata*; and rice bug *Leptocorisa oratorius*. The great diversity of insect problems is typical for upland rice and makes control efforts more difficult, particularly regarding breeding for insect resistance.

Low yield potential

Most upland rice is grown on low-nutrient and mineral-toxic soils, which, when combined with erratic rainfall, make upland rice a highly risky crop for the farmer to invest in costly soil amendments and land management. Often upland rice is grown far from markets, making inputs even more expensive. Farmers growing a subsistence crop hesitate to invest in costly inputs to raise yields.

Even having varieties that could double existing yield potential under present management levels would probably not prompt many farmers to use purchased insecticide unless the risk of crop failure were reduced such as it was with irrigation systems in lowland rice.

The Tanauan, Batangas, site is atypical for upland rice. The soils and rainfall pattern are favorable, and because of its nearness to Manila, farmers have cash resources from sales of vegetables to purchase fertilizer. They applied an average of 60 kg N/ha after panicle initiation and obtained 2.5-3.5 t/ha yields. The high fertility is one reason why RLF, armyworms, and WBPH developed into large numbers. Farmers, however, used no insecticide on upland rice although they did on vegetables.

The poor growing conditions for rice generally mean poor growth and low fecundity for insect pests feeding on it, notwithstanding the release of stored nutrients in response to drought that temporarily benefits phloem feeders.

IMPORTANCE OF UPLAND RICE PESTS

Visits to upland ricefields normally reveal few insect pests. Loevinsohn (138) and Loevinsohn et al (139) compared insect abundance using annual light trap catches in upland, rainfed lowland, and irrigated lowland sites in the Philippines. Although only one upland site was studied, data showed equal or fewer insects at the upland site than at the rainfed lowland sites, and fewer than at the irrigated sites (Table 3). Multiple regression analysis showed that the key factors explaining insect abundance among a set of cropping intensity variables were the number of rice crops grown per year, followed by area devoted to rice. Table 3 shows that the upland rice site had only 1 rice crop per year and that rice was planted in only 20% of the area. Fertilizer and insecticide use had little bearing on the trend. The farmers at the upland site applied 60 kg N/ha, higher than at most irrigated sites.

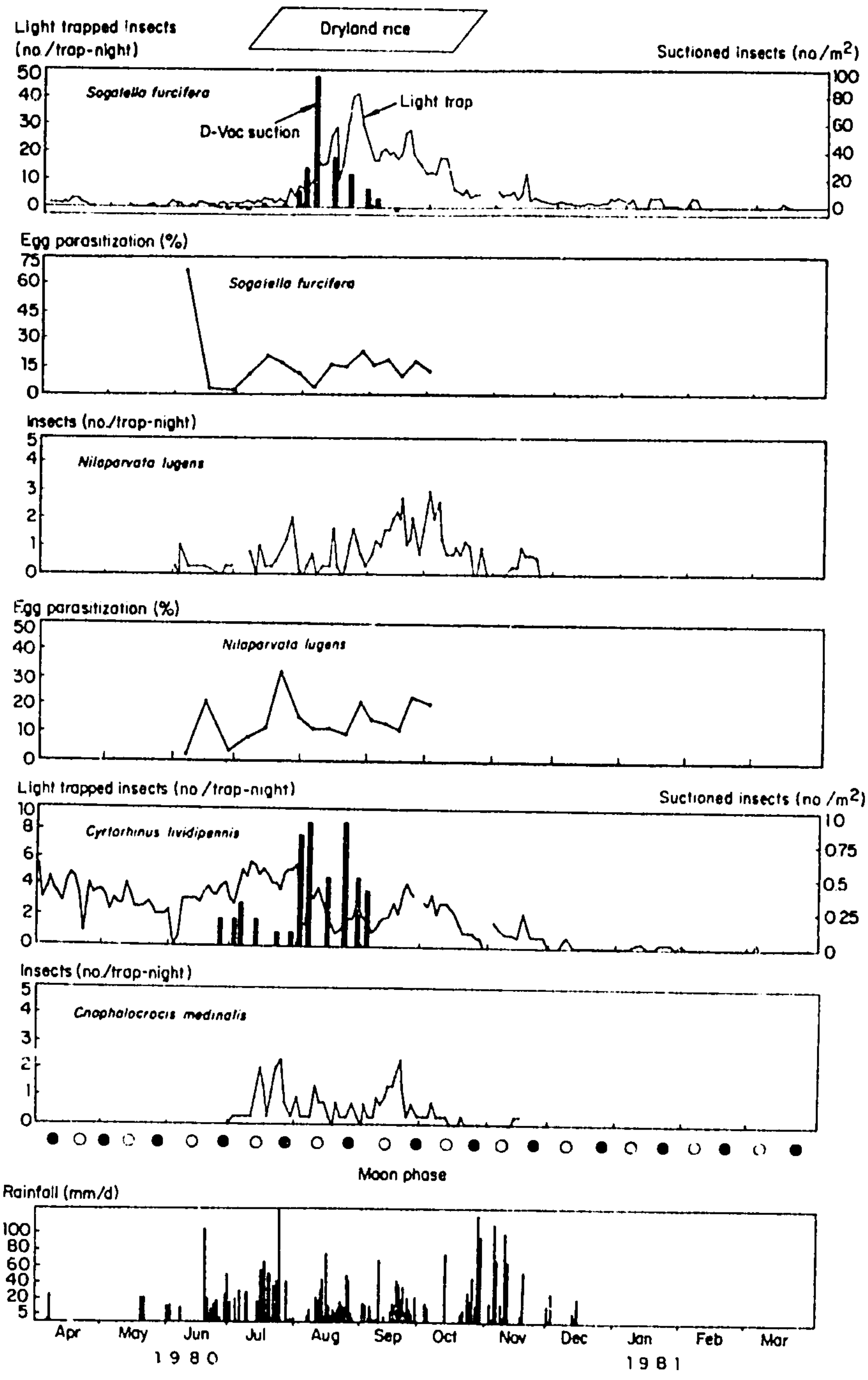
Insect occurrence at the upland site was comparable to that at the Cagayan rainfed lowland site, particularly in 1982 when drought prevented many farmers from planting (only 40% of the rice area eventually was planted that year). More favorable weather occurred in 1980 and 1981, which supported greater rice areas and consequently more insects. The most intensive site for insect pests was South Cotabato, Mindanao, where farmers plant 2.3-2.5 rice crops per year with irrigation. The Zaragoza, Nueva Ecija, site also had high pest abundance, and at this site the fields were highly asynchronous. Asynchrony was the third most important factor in explaining rice insect abundance.

Rice cropping intensity in upland areas is bound to remain low. Only one rainfed upland crop is possible per year. (Farmers in Claveria, Misamis Oriental, Mindanao, Philippines, tried a second upland rice crop in 1984, a year of favorable rains, but no harvest was possible because of drought, blast, and birds.) Rice area is also bound to remain low because of the high labor and power requirements to prepare the land (because of weeds) and because upland rice will not compete with lowland rice as a cash crop. Some upland rice sites with prolonged rainy seasons, however, are planted asynchronously, such as the Claveria site.

The seasonal abundance of upland rice insect pests attracted to a light trap was graphed for crop year 1980-81 in Tanauan, Batangas (Fig. 1, 2). WBPH was the most common rice hopper, and its population peaked at the midgrowth stage as it does in lowland rice. D-Vac suction samples showed an earlier peak than that from a light trap, indicating emigration. WBPH usually emigrate after the vegetative stage. Populations in 1980 reached levels that caused patches of slight yellowing in some fields. WBPH probably cause hopperburn in Batangas. They immigrate year-round, as shown by low levels in the light trap. BPH, however, were scarce in the light trap and not collected with

Table 3. Abundance of rice insect pests and factors in rice cropping intensity of Philippine upland, rainfed lowland, and irrigated lowland locations where light traps were operated daily for at least 1 yr.

	Rainfed upland	Rainfed lowland							Irrigated lowland				
		Pangasinan		Cagayan			Iloilo		Santa Maria, Laguna 1982-83	Nueva Ecija		South Cotabato	
	Cale, Tanauan, Batangas 1980-81	Caaringayan, Manaoag 1979-80	Caaringayan 1980-81	Bangag, Solana 1980-81	Bangag 1981-82	Bangag 1982-83	Buray, Oton 1979-80	Santa Monica, Oton 1979-80		Cabanatuan 1981-82	Zaragoza 1981-82	Avancena, Koronadal 1983	Namnaman, Koronadal 1983
Insect (kerosene light trap catch no./yr)													
Nephotettix virescens	650	1,240	500	1,800	330	210	3,400	1,600	160	360	18,400	5,500	2,900
N. nigropictus	210	–	–	140	90	20	–	–	1,700	–	–	3,200	1,700
Recilia dorsalis	710	180	890	630	140	170	2,400	800	690	–	–	4,200	4,600
Nilaparvata lugens	130	300	520	750	180	60	3,300	1,600	740	310	31,000	13,000	8,200
Sogatella furcifera	1,700	310	210	3,300	610	270	980	1,600	6,300	–	–	12,000	6,700
Cyrtorhinus	600	540	3,200	290	160	330	120	410	620	–	–	21,000	12,000
Scirpophaga spp.	50	410	150	180	220	270	30	1,000	540	610	270	11,000	6,100
Cnaphalocrocis medinalis	70	70	200	140	100	6	60	250	60	60	1,900	300	200
Chilo suppressalis	0	–	–	30	20	0	6	3	160	–	–	0	0
C. auricilius	0	–	–	20	3	60	20	3	0	–	–	–	–
Sesamia inferens	0	–	–	80	60	3	80	10	51	–	–	–	–
Cropping intensity													
Rice crops (no./yr)	1.0	1.0	1.2	1.0	1.0	1.0	1.3	1.7	1.9	2.0	2.0	2.5	2.3
Rice area (%)	20	85	85	60	70	40	85	85	90	85	80	70	70
Fertilizer (kg N/ha)	60	20	20	0	0	0	30	30	40	60	40	30	30
Insecticide (no. of applications/crop)	0	0.4	0.4	0	0.3	0	1.3	1.3	3.0	5.0	4.0	3.3	3.3

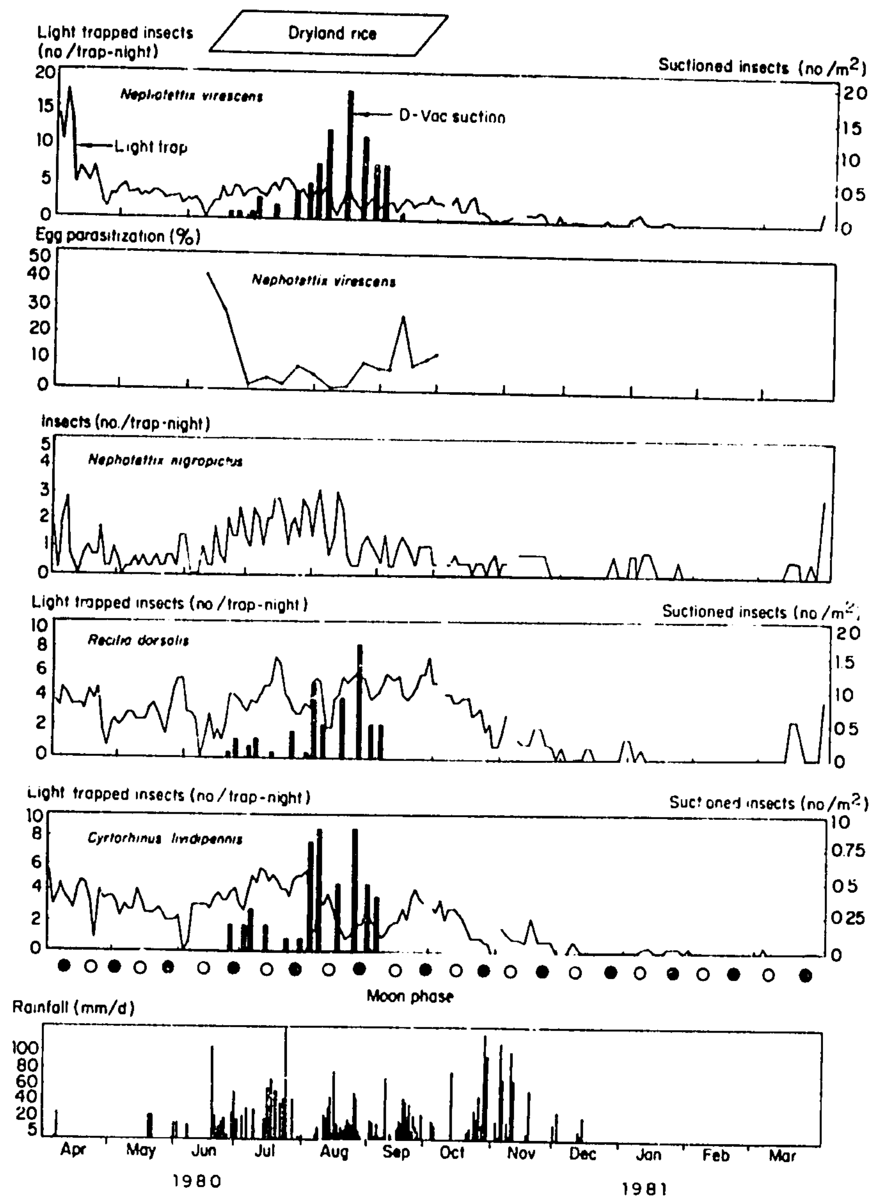


1. Seasonal abundance measured by light trap and D-Vac suction sampler of whitebacked planthopper *Sogatella furcifera*, brown planthopper *Nilaparvata lugens*, and leaffolder *Cnaphalocrocis medinalis* and planthopper egg parasites and mirid predator *Cyrtorhinus lividipennis* set against cropping pattern, daily rainfall, and moon phase. Tanauan, Batangas, 1980-81.

the D-Vac. *Cyrtorhinus* build up on the crop coterminous with WBPH buildup. *Cyrtorhinus* disperses during the rainy season. RLF, not readily collected in light traps, was prevalent only during the rice crop.

Nephotettix virescens was more abundant than *N. nigropictus* in the light trap collections, and on the crop, GLH population peaked at the reproductive stage, as did zigzag leafhopper (ZLH). *Cyrtorhinus* tracked the populations of planthoppers and leafhoppers. Both GLH species were collected year-round in the light trap, indicating immigration from nearby irrigated rice areas. Possibly because of the low populations, insect numbers did not correlate with moon phase, although reports indicate that more hoppers are collected in light traps during full moon (109).

Because upland rice shares most of the lowland rice pests and those pest species are generally less important to upland rice than lowland rice, there is a general belief that insect pests are less important on upland than lowland rice. A review of limited data on upland rice shows an average of 10-21% yield loss from insect pests, on a par with that of lowland rice determined by the same methodology (132) (Table 4) . McGuire and Crandall (144) made a similar estimate for Central America. Cramer (51), however, estimated 3.5% yield loss in South America based on a similar pest complex — stem borers and seed bugs — attacking irrigated rice in North America. This estimate did



2. Seasonal abundance measured by light trap and D-Vac suction sampler of green leafhoppers *Nephotettix virescens* and *N. nigropictus* and zigzag leafhopper *Recilia dorsalis,* their egg parasites, and mirid predator *Cyrtorhinus lividipennis* set against cropping pattern, daily rainfall, and moon phase. Tanauan, Batangas, 1980-81.

not account for soil pests and was not based on field data. Akinsola (11) cited mainly data from irrigated rice areas in Africa but estimated yield losses of upland rice between 15 and 30% from insects. However, losses in Thailand over a 4-yr period ranged from 1 to 13%, averaging 5% (106).

Yield loss data, however, should be interpreted with caution (184). The Philippine data were all derived from trials on farmers' fields under farmers' normal agronomic management practices, except for Bukidnon and Capiz, where researchers used fertilizer. Batangas farmers are atypical because of high levels of fertilizer used. The trials in Brazil were carried out at an experiment station, but conditions were similar to those of local farmers.

Carbofuran granules were used in every trial as a broad-spectrum insecticide applied basally with the seed. An objection to using insecticides to measure yield losses is that insecticides can directly or indirectly stimulate plant growth in the absence of pests. Carbofuran granules are phytotonic to rice (239). The prevailing hypothesis is that carbofuran prevents soil bacteria from consuming fertilizer. The phytotonic effect is through greater availability of fertilizer to the plant. Denitrifying bacteria are known to be more active in aerobic than anaerobic soils; therefore it may not be mere coincidence that the highest recorded yield losses (22-69%) occurred in those trials with 12-30 kg basal N/ha. On the other hand, control with carbofuran granules may not be as good as a seed treatment against seed pests, and perhaps yields would have been higher if a systemic seed treatment insecticide had been used.

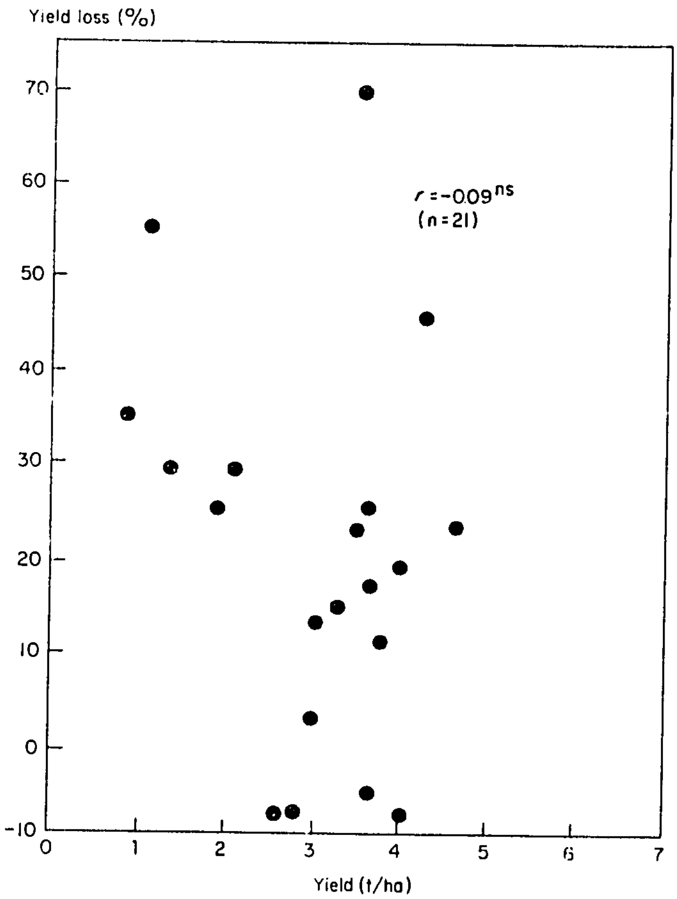
The 1979 and 1980 trials in Batangas had two full-protection treatments, one using carbofuran granules and the other using bendiocarb WP as a seed treatment. Plots protected with bendiocarb yielded higher than those protected with carbofuran granules. The other trials in the

Table 4. Yield losses to insect pests and yield responses to insecticide in upland rice in the Philippines, Brazil, and Upper Volta.

Location	Year	Cultivar	Yield (t/ha)			Yield loss (%)					Basal N (kg/ha)	Reference
			Protected with carbofuran	Protected without carbofuran	Check	Total		Vegetative	Reproductive	Ripening		
						Protected with carbofuran	No carbofuran					
Philippines												
Pili, Camarines Sur	1975	Bursiging puti	1.4	–	1.0	29	–	–	–	–	0	100
Tanauan, Batangas	1974	Kinanda	3.3	–	2.8	15	–	–	–	–	0	99
	1974	Dagge	1.1	–	0.5	55	–	–	–	–	0	99
	1975	Kinanda	3.6	3.4	2.7	25	21	6	0	–7	0	100
	1975	Dagge	3.5	2.4	2.7	23	–11	–	–	–	0	100
	1976	Dagge	3.1	2.4	3.0	3	–20	–	–	14	0	101
	1977	Dagge	3.0	2.7	2.6	13	4	–	–	–	0	101
	1978	Dagge	2.7	–	2.9	–7	–	–	–	–	0	102
		UPL Ri5	3.7	–	3.3	11	–	–	–	–	0	102
	1979	Dagge	2.6	2.9	2.8	–7	3	23	18	–1	0	102
		UPL Ri5	4.0	4.3	3.3	18	23	14	11	6	0	102
	1980	Dagge	3.0	3.1	2.9	3	7	5	3	10	0	103
		UPL Ri5	4.0	4.2	4.3	–7	–2	0	–10	–5	0	103
Pangantucan, Bukidnon	1979	UPL Ri5	4.2	–	2.3	45	–	8	4	8	30	104
	1980	UPL Ri5	4.6	4.7	3.6	22	23	2	10	9	30	104
Dumarao, Capiz	1979	UPL Ri5	3.5	2.5	1.1	69	56	22	7	7	30	104
Brazil												
Goias, Minas Gerais	1977	IAC47	1.9	–	1.5	24	–	–	–	–	12	66
	1978	IAC47	2.1	–	1.5	28	–	–	–	–	12	66
	1979	IAC47	0.9	–	0.6	35	–	–	–	–	12	66
Upper Volta												
Farako-Ba	1977	IRAT10	3.8	–	4.0	–5	–	–	–	–	–	242
	1978	IRAT10	6.6	–	4.3	35	–	–	–	–	–	243
Mean						21	10					

Philippines, which had two treatments offering protection with and without carbofuran granules, relied on further control with foliar sprays and not on seed dressings. The carbofuran-protected plots had an 18% yield loss compared with only 10% with foliar sprays. This yield difference is probably due to differences in protection against sown-seed pests (foliar sprays do not control sown-seed pests) rather than phytotonic effects because basal fertilizer was used in only 2 of the 10 comparisons.

The recorded yield losses were not related to yield potential (Fig. 3). One might expect higher yielding crops to have higher percentage of yield losses, but this was not the case. One reason is that insect damage exacerbates plant injury from drought stress. Low yielding fields from drought stress would show disproportionate differences between insect-protected and -unprotected treatments. Shoot and root pests would be more responsible for losses from drought stress than sown-seed pests. A second reason concerns seed pests, which would have a greater impact on low tillering, low yielding varieties such as Dagge. Low tillering varieties cannot fill in the space created by removal of seeds; however, UPL Ri5 is high yielding because it tillers actively, which can close the canopy to provide greater weed control.



3. Correlation between upland rice yield and yield loss caused by insects measured in 21 trials in the Philippines, Ivory Coast, and Brazil.

In the 9 Philippine trials where yield losses were measured by growth stage, 10% of the yield loss (21%) occurred at the vegetative stage, and 5% occurred at each of the reproductive and ripening stages. This result is similar to the pattern of yield loss in lowland rice measured by successive treatments where the crop is unprotected at each growth stage but protected during the other growth stages.

However, the insect complexes responsible for vegetative stage yield losses in upland rice are entirely different than in lowland rice. The key vegetative stage pests in lowland rice are aquatic, whereas those in upland rice are sown-seed (sown in soil), root, and seedling pests. This difference may explain why agriculturists have overlooked the importance of upland rice insect pests. Many reports of upland rice pests in Asia have focused on major lowland species (46, 108).

It is also surprising that the vegetative stage of upland rice would record the highest yield losses, because several studies have shown that upland rice can readily recover from foliage removal during that stage (147, 152, 165, 188). Upland rice possesses a high ability to compensate for early loss of foliage and will even be stimulated by foliage removal to produce a higher yield than plants without any foliage removed (63, 192, 231). The reason for this apparent discrepancy, however, is that yield loss at the vegetative stage does not occur from leaf area loss but from pests removing sown seed and feeding on developing tillers and roots — damage that cannot be readily compensated for.

Measuring yield losses in upland rice environments is further complicated by a report from Brazil that greater yield losses occurred in response to better insect control. Insecticide seed treatments resulted in denser plant stands, which in turn created a selectively more favorable environment for blast (69). This result was particularly exacerbated when carbofuran granules were used in seed furrows. Aside from a greater plant stand, carbofuran may have augmented the N level and stimulated blast. If so, carbofuran should be replaced with another insecticide, or the seeding or fertilizer rates decreased.

Other methods to determine the impact of upland rice pests were to interview farmers or to develop single species correlations of population levels and yield loss. Ferreira (66) did both in Brazil. Most (75%) Goias farmers reported insect losses in upland rice, and 25% said those losses averaged 37%. This result is consistent with the yield losses measured by field trials in the same state (Table 4). For every 10% of seedlings removed by leaf-cutting ants, a 1% yield loss is predicted. Similarly, Ferreira (66) found that an average of 5.3% thrips per panicle before panicle initiation meant 3 times more unfilled grains.

CONTROL METHODS

Upland rice insect pests may be controlled by cultural, genetic, biological, and chemical methods.

Cultural control

Crop husbandry to reduce upland insect pest populations can be classified into practices effective in a single field and those effective only at the community level. Cultural controls should come first in a pest management program. They have broad, stable effects, as pests have little possibility of overcoming them through selection of biotypes (138). On the other hand, some cultural controls work only with high labor or power inputs, and community-wide methods require coordination of many farmers.

Planting time. The luxury of being able to shift the time of planting upland rice is open only to farmers in areas with a prolonged rainfall pattern, low cropping intensity, or mechanized land preparation. Generally, planting as soon as the rainy season begins will lower populations of most insect pests. Insect populations are low after a dry season or winter fallow; delayed planting lets them build up on alternate hosts that grow vigorously with the first seasonal rains. This first flush of weeds grows luxuriantly with mineralized N released during the dry season and made available to the plants with the rains. It is also agronomically advantageous for the rice crop to tap this natural fertility and grow vigorously to compete with weeds and to tolerate pest infestation.

Early plantings tend to escape seedling maggots. Upland rice in Batangas is planted in May and June with the first rains. Farmers are highly motivated to plant early to escape drought and typhoons near harvest. An August planting would be severely attacked by *Atherigona oryzae*. At two other Philippine upland sites Real, Quezon, and Claveria, Misamis Oriental seedling maggots damage rice because farmers have a longer growing season and plant 2 mo or more after the onset of the rainy season. Batangas farmers plant early because of a shorter rainfall period and the desire to harvest before the typhoon season peaks.

Early plantings combined with early-maturing varieties provide higher crop tolerance for white grubs. Aestivation terminates with the first rains, but 5-6 mo are needed for the resting larvae to develop into beetles, emerge, and lay eggs, and for larvae to reach the damaging third-instar stage (134). In Batangas, this normally is enough time for harvest.

In Brazil, however, delayed planting is a suggested cultural control for the lesser cornstalk borer and insect pests favored by drought (66, 195). Cropping intensity in Brazil is low, and delayed planting places the rice crop in the most stable rainfall period, reducing likelihood of drought.

In many areas farmers are motivated to plant other crops before rice, and although it would be desirable to avoid infestations by planting rice early, farmers lack the labor and time to do so on a low priority crop.

Tillage. Upland rice soils are light textured and can be plowed during the dry season, not only to gain time for planting with the first monsoon rains but also to desiccate soil insects and weeds such as nutsedge that form rhizomes. However, because most soil insects lie below the plow layer, dry season plowing will have little effect on them. Plowing when the soil is wet from the first monsoon rains will expose soil insects that tunnel close to the soil surface to predatory birds, chickens, dogs, and even man (field crickets, mole crickets, and white grubs are delicacies in many traditional diets).

The greatest degree of insect control from tillage comes from plowing soon after rice harvest when most soil insects lie close to the soil surface and stem borers are in the rice stubble. White grubs are mature, and tillage exposes them to predators. Timely control will protect the crop following rice and lower the population for succeeding years. Plowing under the rice stubble helps it decompose, killing stem borer larvae inside.

Frequent tillage destroys ant nests but not termites. Tillage and clean culture, however, remove food for termites, which then may attack a young rice crop. Scarab beetles also prefer to oviposit in recently tilled fields. No-tillage rice culture such as dibbling favors the survival of soils insects and insects that pupate or lay eggs in the soil. Zero tillage, however, conserves predators of the GLH (37).

Planting method. To lessen the impact of soil insects, broadcasting seed or planting in furrows is preferred over dibbling in hills. Crickets are large enough to eat seedlings in a hill, and tillering normally cannot fill in the missing space. Often, dibbled seed is not well covered and is easily found by foraging insects, rodents, and birds.

Plant density. Increasing seed density protects the crop against seed and seedling pests, especially ants, particularly if the crop will germinate and emerge quickly.

Intercropping. In India, rice intercropped with cotton or pigeon pea had lower GLH and WBPH populations than rice alone (201). Maize and upland taro are common in the Philippines. The change in pest status from intercropping is highly location-specific (133) and the net effect can be either nil, beneficial, or detrimental (189). For example, Batangas farmers intercrop taro in their upland ricefields. A hornworm, *Agrius convolvuli* (Linnaeus), which normally feeds on taro, will feed on nearby rice plants. Intercropping probably would not affect seed pests. A companion crop planted with rice and having greater tolerance for root damage or being toxic may act as a trap crop to root-feeding pests. Aerial-feeding pests would be most affected by intercropping. Shoot aphids, leaf beetles, stem borers, and hoppers would be likely candidates to note effects. On the other hand, the companion crop such as maize may be more benefited than rice from intercropping (137).

Weeding. Weeding during the first month after crop establishment will force pests such as armyworms, which prefer grassy weeds, onto the young rice. Soil insects will move to the rice crop. Clean culture also may force termites to attack rice. Leaving certain weeds may be the optimal solution (13).

Fertilizer. Increasing N fertilizer on lowland rice has favored higher populations of planthoppers, leafhoppers, and leaffolders. However, because of the need to temper fertilizer use on upland rice to prevent blast, fertilizer rates will be lower than is common for lowland rice, causing relatively less hopper and leaffolder population buildup. However, in upland rice areas without a history of blast, such as Batangas, farmers apply high rates of N and consequently the crop has high infestation levels of WBPH and RLF. The farmers lessen insect buildup by splitting the fertilizer into two to three applications but do not apply fertilizer at the vegetative stage because this produces a tall crop which will easily lodge during typhoons. Greater crop fertility leads to greater insect survival (better nutrition), larger insects (to eat more foliage), and greater fecundity (to lay more eggs) (128, 145, 171). Not all insect species respond equally, however. Increasing rates of N, P, and K increased *Diatraea saccharalis* and *Chaetocnema* flea beetle but reduced thrips (66). Zn reduced deadheart density from the lesser cornstalk borer.

Flooding. Although most upland rice areas do not have access to water, flooding the fields is recommended in areas of Brazil for root bug and white grub control (195).

Crop rotation. Tillage before planting a crop after rice harvest will control stem borers and other pests remaining on the stubble and will unearth soil pests. Planting a non-graminaceous crop after rice is recommended for termite control (66). Crop rotation is less needed in upland rice culture than in lowlands because a crop-free period is assured even after harvest of crops following rice.

Mulching. Vinyl plastic mulching designed for weed control in upland rice in Japan resulted in an unusually high infestation of *Chilo suppressalis* (93, 94, 95). Mulched upland rice grew more luxuriantly and attracted more ovipositing moths than unmulched rice. Also, the rice plant and stem borers matured more quickly and a partial generation of young instars overwintered in the stubble.

Early-maturing varieties. Quickly maturing crops reduce the number of pest generations that can build up. Rapid crop establishment of an early-maturing variety in particular will lessen white grub and stem borer damage. White grub larvae in the last instar are highly destructive, so an early-maturing variety will escape serious root loss. Stem borers build up slowly in rice to become abundant in a late-maturing crop and cause whiteheads. Numbers of some species increase exponentially with each succeeding generation, so a variety that matures 1 mo earlier than another will have less insect damage. Early-maturing varieties, however, will not lessen seed pest damage, either in the soil or on a standing crop.

Synchronous planting. Insects feeding on the aerial portions of rice plants disperse from early to late planted fields. As insect numbers increase exponentially with each generation, pests build up where neighboring farmers stagger their plantings. In Batangas, farmers plant upland rice within 1 mo, use 120-d varieties, and plant at the start of the rainy season. In Misamis Oriental, farmers stagger their plantings up to 3 mo apart and use a set of varieties that mature in 4-7 mo. Insect pest damage, particularly from stem borers, is greater in Misamis Oriental. Also, seedling maggots damage rice there because rainfall favors frequent planting of maize. In Batangas, rice escapes seedling maggots because of a distinct dry season and synchronous early planting with the onset of rains.

Therefore, combinations of cultural practices — early planting, synchronous planting, crop rotation, and early-maturing varieties — protect the rice crop against most insect pests.

Plant resistance

Because upland rice has few specialized insect pests and many insect types attack the crop worldwide, regional breeding and strong international cooperation are required.

Sown-seed pests are economically controlled by insecticide seed treatment and should therefore receive low priority in breeding objectives.

Root pests are normally costly to control with insecticides, but finding resistant sources may be difficult. Tanaka (229), for example, failed to find varieties resistant to root aphids. Selecting for large root biomass perhaps should be the strategy for pests such as white grubs that remove roots. Painter (174), however, cites varieties of crops tolerant of or resistant to root pests. Some sorghum varieties are high in cyanide, so rice/sorghum might incorporate broad-spectrum chemical resistance.

Seedling vigor and drought tolerance are high priority breeding objectives, so new upland rices should have larger root systems and be able to tolerate higher levels of root loss. Some root loss in older plants is beneficial if it stimulates new root development and therefore enhances intake of soil nutrients (53).

The rice seedling maggot *Atherigona* spp. may be controlled through resistant varieties. A large breeding effort on sorghum has had fair success in developing varieties resistant to *A. soccata* Rodani (251). A field trial comparing 10 upland rice varieties showed differences among varieties varying from 11 to 40% damaged tillers (215). However, resistance to one *Atherigona* species may not cross over to others.

Shiraki (210) reported that upland rice stems were harder than lowland rice stems, perhaps because of a higher silicon content, and thus were more resistant to yellow stem borer. The normal low tillering of upland rice varieties produces a higher percentage of infested tillers than would occur in higher tillering lowland rice under a similar egg density. The corollary, therefore, is to select for high tillering upland rices.

Stem borers are the main targets of breeders in Africa (57, 161, 204) but much of the screening is done under lowland conditions (11, 96, 218). As with *Atherigona*, species may have to be dealt with independently; however, initial results show cross resistance between African and Asian species (92).

In Brazil, screening for insect resistance focuses on local pest problems. Varieties tolerant of *Elasmopalpus lignosellus* and resistant to *Diatraea saccharalis* have been identified (70, 153). Current work also emphasizes *Tibraca limbativentris* and *Tomaspis* (= *Deosis*) *flavopicta* (66). These insect pests not only cause high yield losses, they also are difficult to control chemically or by other means.

Many upland rice varieties are early maturing and are resistant to pests such as gall midge (181). Early maturity is often a highly desirable trait to escape pest buildup, but it is not true resistance, because if those varieties are planted late, they will be as damaged as an early planted susceptible variety.

Perhaps the most cosmopolitan of all upland rice pests are the seed pests (ripening stage), which pose a particular problem because seeds are used as food for humans. Any toxic substance introduced genetically may also be toxic to man unless it can be placed only in the hull. Selecting for hairiness or long awns will meet with problems during threshing, particularly manual threshing. Threshers will complain of itching and increased dust levels.

Attempts at IRRI to find resistance to the rice bug *Leptocorisa* have not been promising. Pentatomids bore through the lemma or palea, but hairy seeds or seeds with awns that deter bugs promote complaints from threshers. Seed bugs *Leptocorisa* and *Stenocoris* enter the seed through the opening between the lemma and palea, but varieties with narrow openings are difficult to mill.

Breeding priorities should concentrate on insect groups that are most difficult to control by other means. Stem borers appear to be the most widespread group that significantly damages rice and is hard to manage by other means.

Biological control

Very few studies of natural enemies of rice pests in upland environments were found in the literature. Therefore, we have not compiled a list of species. We present a list of natural enemies found in upland ricefields near Tanauan, Batangas, for some common foliar pest species (Table 5).

Much of the following information comes from studies in the lowlands or from crops other than rice.

Quality of natural enemies. Natural enemies might be used against the social insects — ant and termites. Some predator species live in their nests and mimic their appearance and behavior. Introducing a more aggressive ant species to displace pest ant colonies is a possibility (169). Pathogens, as potential natural enemies, have received little attention (113). Natural enemies as a group, however, have not been shown to be important in regulating ant and termite numbers.

The nocturnal behavior and subterranean habitat of mole crickets and field crickets protect them from many natural enemies. There are only limited records of natural enemies for these groups of pests: some pathogens (87) but mainly parasites — scelionids on eggs and sphecids on nymphs and adults. Sphecid wasps *Larra carbonaria* (Smith), *L. luzonensis* Rohwer, and *L. sanguinea* Williams specialize in mole crickets, paralyzing them and dragging them into their nests as food for their young. Other sphecid species — *Liris aurulenta* (Fabricius), *Motes manilae* (Ashmead), *M. subtessellatus* (Smith), and *M. laboriosus* (Smith) — specialize in field crickets.

White grubs, on the other hand, have been serious enough to have been extensively studied for control by natural enemies (112, 140, 141). Scoliid parasites *Campsomeris* spp. have been introduced into the Philippines for control of *Leucopholis irrorata*. The researchers who introduced them during an outbreak era claimed that the white grub was controlled (142), however, it is normal for pest epidemics to subside, and there was no direct evidence to indicate that the parasite was responsible. A more promising method might be to identify, isolate, mass produce, and apply bacterial and fungal pathogens to the soil. The Japanese beetle in North America has been controlled by the commercially available bacterial preparation *Bacillus popillae* or milky disease (71). Spores sprayed on the soil and plowed under remain active for years.

Root aphids and mealybugs readily succumb to predators and parasites once their tending ants are controlled. The larvae and adults of a coccinellid beetle ? *Scymnus* sp. prey on *I. nigriabdominalis* in slash and burn upland rice. Baits treated with insecticide may be used to control tending ants by killing their young (244).

Root-feeding bugs, false wireworms, wireworms, and root weevils are normally of such little importance that the role of natural enemies has not been assessed. A possibility, however, might be to augment parasitic nematodes. But, these soil-inhabiting nematodes would have to be mass produced.

A large number of natural enemies are known for cutworms. The problem is that cutworms colonize the crop soon after land preparation at the beginning of the rainy season, when natural enemy populations are low. Control would involve mass producing and releasing key species.

The egg stage is the part of the seedling maggot life cycle on which to focus for natural enemy control by parasites or predators because eggs are highly exposed. Egg parasites or predators would probably have be mass produced and released. Little information is available on what species to try or how to mass produce them.

A eulophid wasp, *Hemiptarsenus* sp., effectively regulates the leaf miner *Pseudonapomyza spicata* on wheat and rice and should be conserved.

Leaf beetles whose larvae and eggs are laid in the ground would be more difficult to control by natural enemy manipulations. But species such as hispid beetles with eggs and larvae on leaves are vulnerable to parasites and predators.

Natural enemies of thrips on rice are little known.

Table 5. Parasites recorded from upland rice insect pests in Tanauan, Batangas, Philippines, 1977-84.

Order	Family	Species	Host stage
		Leaffolders Cnaphalocrocis, Marasmia *spp.*	
Hymenoptera	Braconidae	*Cardiochiles philippinensis* Ashmead[a]	Larva
		Cotesia angustibasis (Gahan)	Larva
		Cotesia nr. *cypris* (Nixon)	Larva
		Cotesia nr. *taeniaticornis* (Nixon)	Larva
		Chelonus munakatae Munakata	Egg to larva
		Chelonus spp.	Egg to larva
		Macrocentrus philippinensis (Ashmead)	Larva
		Orgilus spp.	Larva
	Ichneumonidae	*Ischnojoppa luteator* (Fabricius)	Larva
		Itoplectis narangae (Ashmead)	Larva
		Temelucha philippinensis (Ashmead)	Larva
		Temelucha stangli (Ashmead)[a]	Larva
		Trichomma cnaphalocrosis Uchida	Larva
	Bethylidae	*Goniozus* nr. *triangulifer* Kieffer	Larva
	Elasmidae	*Elasmus albopictus* Crawford	Larva
		Elasmus spp.	Larva
	Encyrtidae	*Copidosomopsis nacoleiae* (Eady)	Egg to larva
	Chalcididae	*Brachymeria excarinata* Gahan	Pupa
		Brachymeria lasus (Walker)	Pupa
Diptera	Tachinidae	*Zygobothria ciliata* (Wulp)	Larva
		Argyrophylax nigrotibialis (Baranov)	Larva
		Yellow stem borer Scirpophaga incertulas	
Hymenoptera	Braconidae	*Bracon chinensis* Szepligeti	Larva
		Chelonus spp.	Larva
		Chelonus munakatae Munakata	Egg to larva
		Cotesia flavipes Cameron	Larva
		Stenobracon nicevillei (Bingham)[a]	Larva
		Tropobracon schoenobii (Viereck)	Larva
	Ichneumonidae	*Amauromorpha accepta metathoracica* (Ashmead)	Larva
		Eriborus sinicus (Holmgren)	Larva
		Ischnojoppa luteator (Fabricius)	Larva
		Isotima nr. *dammermani* Rohwer	Larva
		Temelucha philippinensis (Ashmead)[a]	Larva
		Temelucha stangli (Ashmead)	Larva
		Trichomma cnaphalocrosis Uchida	Larva
		Xanthopimpla stemmator (Thunberg)	Larva to pupa
		Charops brachypterum Gupta and Maheswary	Larva
	Chalcididae	*Brachymeria* spp.	Pupa
	Eulophidae	*Tetrastichus schoenobii* Ferriere	Egg
	Trichogrammatidae	*Trichogramma chilonis* Ishi	Egg
		Trichogramma japonicum (Ashmead)	Egg
	Scelionidae	*Telenomus rowani* (Gahan)[a]	Egg
	Pteromalidae	*Trichomalopsis apanteloctena* (Crawford)	Egg, pupa
Diptera	Tachinidae	*Peirbaea* spp.	Larva
		Zygobothria ciliata (Wulp)	Larva
		Gold fringed borer Chilo auricilius	
Hymenoptera	Ichneumonidae	*Trichomma cnaphalocrosis* Uchida	Larva
		Xanthopimpla stemmator (Thunberg)[a]	Larva to pupa
		Pink stem borer Sesamia inferens	
Hymenoptera	Braconidae	*Stenobracon nicevillei* (Bingham)	Larva
		Armyworms Mythimna separata, Spodoptera mauritia acronyctoides	
Diptera	Tachinidae	*Zygobothria atropivora* (Robineau-Desvoidy)[a]	Larva
Hymenoptera	Eulophidae	*Euplectrus chapadae* (Ashmead)	Larva
	Chalcididae	*Brachymeria* spp.	Larva
	Braconidae	*Cotesia* spp.	Larva
		Rice skipper Pelopidas mathias *and green horned caterpillar* Melanitis leda ismene	
Hymenoptera	Chalcididae	*Brachymeria* sp. nr. *marginata* Cameron	Larva
Diptera	Tachinidae	*Argyrophylax nigrotibialis* (Baranov)[a]	Larva
		Brown semilooper Mocis frugalis	
Diptera	Tachnidae	*Argyrophylax nigrotibialis* (Baranov)	Larva
Hymenoptera	Ichneumonidae	*Xanthopimpla punctata* (Fabricius)	Larva to pupa

[a]Most dominant.

Normally, predatory thrips prey on herbivorous thrips. Natural enemies of stem bugs — *Scotinophara* and *Tibraca* — are, in order of importance, egg parasites and predators, fungal pathogens, and nymphal/adult parasites. Egg parasites could either be introduced from other areas or mass produced and released.

Armyworms are normally held in check by the activities of egg and larval parasites. When these natural enemies fail, usually because of drought, armyworms become epidemic. It may be worthwhile, therefore, to release parasites during the rainy months following a drought. Virus diseases of larvae would be another avenue to explore for armyworms.

Parasites have been traditionally considered for biological control attempts against stem borers, usually by releasing exotic species (166). This approach has not met with success, and new avenues should be explored. The role of predators and pathogens is little understood and deserves greater attention. Egg parasitism rates are normally reasonably high but should be supplemented with effective egg predators. Orthopterans are potential egg predators. *Metioche vittaticollis* (Stål), *Anaxipha longipennis* (Saussure), and *Conocephalus longipennis* (de Haan) feed on stem borer eggs. *Metioche* and *Anaxipha* specialize in eggs with no hair such as *Chilo* spp. The omnivorous *Conocephalus* specializes in eggs covered with hairs; it is a proven egg predator of *Scirpophaga* spp. but has the discouraging habit of eating rice grain (65).

Grasshoppers have egg (scelionid) and nymphal/adult (nemestrinid, tachinid, and sarcophagid) parasites. Among pathogens, protozoans have been recorded most frequently. Control of locust species by natural enemies could concentrate on their habitual breeding areas.

Leaffolders have rich complexes of natural enemies, some adapted to upland rice (22, 27), ranging from egg predators (gryllids, coccinellids) to larval parasites (braconids, ichneumonids) to larval predators (ants and carabids) to larval pathogens (viral and fungal diseases). Efforts to augment these natural enemies should focus on the egg predators (rearing, releasing) and viral or fungal pathogens (culturing, spraying).

Parasitization of the large, conspicuous larvae of skippers, green horned caterpillars, and other polyphagous Lepidoptera by tachinids and chalcids is normally low. Egg parasites and predators are perhaps the key to their control.

Gall midges are parasitized by pteromalids and platygasterids that aestivate within their larval host between seasons. Shoot aphids are preyed upon by coccinellids, syrphids, and chrysopids.

Planthoppers and leafhoppers have egg parasites and predators as well as nymphal/adult parasites and predators; their rich complex of natural enemies includes fungal pathogens. The principal egg parasites are mymarids and trichogrammatids. Egg predators are normally mirid plant bugs that suck out the yolk. Nymphal/adult parasites are dryinids on planthoppers, pipunculids on leafhoppers, and strepsiptera on both. Spiders dominate the nymphal/adult predators. Spittle bugs move to rice from pasture grasses and biocontrol would be successful only if carried out before they immigrate into ricefields.

Biological control tactics for hemipterous seed bugs would follow those outlined for stem bugs.

Comparison of environments. Natural enemies are perhaps faced with even greater constraints than insect pests to survive and reproduce in upland environments. They have adapted and survived by having wide host ranges, the ability to aestivate or hibernate over unfavorable seasons, and the ability to disperse, or by other mechanisms. Comparing the most dominant and therefore the most adapted species of natural enemies collected in various environments in the Philippines, we can understand how different rice environments are.

Anagrus optabilis, a mymarid planthopper egg parasite, is equally adapted to all Philippine rice environments (Table 6). It is selective for planthoppers and even parasitizes eggs of the maize planthopper *Peregrinus maidis* in upland areas. *A. flaveolus* also parasitizes maize planthopper eggs but is most prevalent on BPH in the irrigated wetlands. *Gonatocerus* spp., like *A. optabilis* on BPH and WBPH, attacks the eggs of GLH in all rice environments. It is also found parasitizing the eggs of the white rice leafhopper *Cofana spectra*. *Oligosita naias*, a trichogrammatid egg parasite, attacks BPH and WBPH in the wetlands and has no other host. A related species, *O. aesopi*, specializes in GLH in wetland environments. Dryinid, strepsipteran, and pipunculid nymphal and adult parasites of planthoppers and leafhoppers also specialize either in hopper species or environments. Among the dryinids, *Pseudogonatopus flavifemur* prefers the lowlands and BPH, while *P. nudus* has no environmental preferences but is adapted only to WBPH. The main dryinid species on GLH, *Haptogonatopus* spp., is most dominant in rainfed lowlands and also attacks other leafhoppers within *Amrasca*, *Cicadulina*, and *Balclutha*.

Strepsiptera are more dominant on planthoppers than leafhoppers. The *Elenchus* species in the Philippines attack all species of planthoppers within the genera *Sogatella*, *Sogatodes*, *Nilaparvata*, *Harmalia*, and *Opiconsiva*. *Elenchus yasumatsui* is adapted to the major rice environments but prefers BPH in rainfed and WBPH in wetland environments. *Halictophagus munroei* and *H. spectrus* attack GLH and *Cofana spectra*, respectively.

Pipunculids are mainly parasitic on leafhoppers. Each species has a unique environmental preference. *Tomosvaryella oryzaetora* prefers *Nephotettix nigropictus*, and *Pipunculus javanensis* attacks *Deltocephalus* spp., which are more abundant in upland than irrigated lowland environments. *T. subvirescens* attacks *Nephotettix virescens* and prefers the lowlands. *Pipunculus mutillatus* is an upland rice parasite and attacks only *Nephotettix* species.

More than 17 recorded species of leaffolder parasites in the Philippines attack species of *Cnaphalocrocis* and

Table 6. Dominant natural enemies of rice pests in upland, rainfed lowland, and irrigated lowland rice environments of the Philippines.

Natural enemy		Environment		
Host stage	Species	Upland	Rainfed lowland	Irrigated lowland
	Brown planthopper *Nilaparvata lugens*			
Parasite				
Egg				
Mymaridae				
	Anagrus optabilis (Perkins)	x	x	x
	Anagrus flaveolus Waterhouse			x
Trichogrammatidae				
	Oligosita naias Girault		x	
Nymph/Adult				
Dryinidae				
	Pseudogonatopus flavifemur Esaki et Hashimoto		x	x
Elenchidae				
	Elenchus yasumatsui Kifune and Hirashima	x	x	x
	Whitebacked planthoppers *Sogatella furcifera* and *Sogatodes pusanus*			
Egg				
Mymaridae				
	Anagrus optabilis (Perkins)	x	x	x
Trichogrammatidae				
	Oligosita naias Girault		x	x
Nymph/Adult				
Dryinidae				
	Pseudogonatopus nudus Perkins	x	x	x
Elenchidae				
	Elenchus yasumatsui Kifune et Hirashima		x	x
	Green leafhopper *Nephotettix virescens*			
Parasite				
Egg				
Mymaridae				
	Gonatocerus spp.	x	x	x
Trichogrammatidae				
	Oligosita aesopi Girault		x	x
Nymph/Adult				
Pipunculidae				
	Tomosvaryella subvirescens Loew	x		x
	Tomosvaryella oryzaetora (Koizumi)		x	x
	Pipunculus mutillatus (de Meijere)	x		
Dryinidae				
	Haplogonatopus spp.		x	
	Rice leaffolders *Cnaphalocrocis, Marasmia*			
Egg				
	Copidosomopsis nacoleiae (Eady)	x	x	x
Larva				
Braconidae				
	Cardiochiles philippinensis Ashmead	x		
Ichneumonidae				
	Trichomma cnaphalocrosis Uchida		x	
	Temelucha stangli (Ashmead)			x
Pupa				
Chalcididae				
	Brachymeria excarinata Gahan	x	x	x
	Brachymeria lasus (Walker)	x	x	x
	Brachymeria nr. *tachardiae* group	x	x	x
	Yellow stem borer *Scirpophaga incertulas*			
Parasite				
Egg				
Scelionidae				
	Telenomus rowani (Gahan)	x	x	x
Eulophidae				
	Tetrasticus schoenobii Ferriere			x
Larva				
Braconidae				
	Stenobracon nicevillei (Bingham)	x		
Ichneumonidae				
	Temelucha philippinensis (Ashmead)	x		
	Temelucha stangli (Ashmead)		x	x
	Amauromorpha accepta metathoracica (Ashmead)			x

continued on next page

Table 6 continued.

Natural enemy		Environment		
Host stage	Species	Upland	Rainfed lowland	Irrigated lowland
	Gold fringed borer *Chilo auricilius*			
Larva-pupa				
Ichneumonidae				
	Xanthopimpla stemmator (Thunberg)	x	*a*	x
Pupa				
Pteromalidae				
	Trichomalopsis apanteloctena (Crawford)	*a*		x
	Pink stem borer[b] *Sesamia inferens*			
Parasite				
Larva				
Braconidae				
	Stenobracon nicevillei (Bingham)	x	*b*	*b*
	Armyworms *Mythimna, Spodoptera*			
Larva				
Tachinidae				
	Zygobothria atropivora (Robineau-Desvoidy)	x	x	
Braconidae				
	Cotesia spp.			x
	Skipper *Pelopidas mathias* and green horned caterpillar *Melanitis leda ismene*			
Egg				
Trichogrammatidae				
	Trichogramma spp.			x
Scelionidae				
	Undetermined Scelionid			x
Larva				
Tachinidae				
	Argyrophylax nitrotibialis (Baranov)	x	x	
Pteromalidae				
	Trichomalopsis apanteloctena (Crawford)			x
Predator				
Coenagrionidae				
	Agriocnemis femina femina Brauer		x	x
	Ischnura senegalensis Rambur			[illegible]
Miridae				
	Cyrtorhinus lividipennis Reuter		x	x
Nabidae				
	Stenonabis tagalicus (Stal)	x		
Veliidae				
	Microvelia douglasi atrolineata (Bergroth)			x
Coccinellidae				
	Micraspis crocea (Mulsant)	x	x	x
Vespidae				
	Eumenes campaniformis (Fabricius)	x		
Formicidae				
	Diacamma spp.	x		
	Odontoponera transversa (F. Smith)	x		
Carabidae				
	Chlaenius spp.	x		
	Ophionea nigrofasciata Schmidt-Goebel		x	
	Ophionea ishii ishii Habu		x	x
Gryllidae				
	Anaxipha longipennis (Saussure)	x	x	
	Metioche vittaticollis (Stal)	x	x	x
Tettigoniidae				
	Conocephalus longipennis (de Haan)	x	x	x

[a]No rearing made on rainfed lowland. [b]No rearing made on rainfed lowland or irrigated lowland.

Menasmia. Among the larval parasites, the braconid *Cardiochiles philippinensis* is most adapted to an upland environment. It also parasitizes *Hydelepta indicata*, a common leaffolder of legumes. The ichneumonids *Trichomma cnaphalocrosis* and *Temelucha stangli* occur more in the lowlands. *T. stangli* is most adapted to irrigated lowlands and also parasitizes *Chilo* and *Scirpophaga* stem borer larvae. *T. cnaphalocrosis* is most prevalent in rainfed lowlands and parasitizes oriental maize borer *Ostrinia furnacalis* (Guenee) larvae. The leaffolder pupal parasites not only occur equally in all environments but also have wide host ranges — parasitizing species of *Ostrinia, Maruca, Hydelepta*, and *Homona* — in maize and legumes.

The principal egg parasite of yellow stem borer (YSB) *Telenomus rowani* is widely adapted to all environments and has an unusual alternate host —*Tabanus* eggs (25).

Tetrasticus schoenobii specializes only in YSB and occurs mainly in irrigated lowlands — further proof that YSB is most adapted to the wetter environments.

Larval parasites of YSB are highly environment-specific. The braconid *Stenobracon nicevillei* occurs only in upland rice but also attacks the pink stem borer (PSB). *Temelucha philippinensis*, an ichneumonid, occurs in upland rice and also parasitizes the larvae of *Chilo suppressalis*. *Amauromorpha accepta metathoracica*, like *T. stangli*, is most adapted to the irrigated lowlands.

The dark-headed stem borer (DHSB) *Chilo polychrysus* was not collected in all rice environments, and the gold fringed borer *Chilo auricilius* and PSB were collected only in upland rice. *Xanthopimpla stemmator*, an ichneumonid larval parasite, appears to be widely adapted, whereas *Trichomalopsis apanteloctena*, a pteromalid pupal parasite, occurs mostly in wetlands and also parasitizes larvae of *Chilo suppressalis* and *Pelopidas mathias*.

Armyworms *Mythimna* and *Spodoptera* have two main larval parasites — a tachinid *Zygobothria atropivora* in rainfed environments and a braconid *Cotesia* spp. in irrigated lowlands.

The butterfly pests *Pelopidas* and *Melanitis* have trichogrammatid egg parasites found only in irrigated lowland environments.

Two larval parasites show environmental preferences — *Argyrophylax nigrotibialis*, a tachinid in rainfed habitats, and *Trichomalopsis apanteloctena* in irrigated ricefields. *A. nigrotibialis* also attacks the sweet potato hornworm *Agrius convolvuli*, and *T. apanteloctena* parasitizes DHSB.

Predators as a group show more distinct environmental preferences. The aquatic damselflies Coenagrionidae are most abundant in the lowlands. *Cyrtorhinus* is also most adapted to the lowlands. The nabid *Stenonabis tagalicus* occurs only in the uplands and is also prevalent on legumes. The coccinellid lady beetles, wasps, and ants are more prevalent in upland areas. *Micraspis crocea* larvae prey on a variety of aphids attacking legumes and maize. *Eumenes campaniformis*, a vespid mud wasp, makes nests in trees and is therefore most adapted to the more botanically diverse uplands. Soil-dwelling ants cannot tolerate flooding.

Upland environments are habitats to arboreal carabid beetles. Three species of *Chlaenius* beetles prey on leaffolder larvae and are perhaps more important than parasites (27).

The gryllids and tettigoniids are widely adapted egg predators, not only on rice but also on maize and legumes. They feed on eggs of most insects that are laid on leaves.

The spider community of upland rice environments is rich in species. At one site (Batangas, Philippines) 31 species have been recorded (23). Of the 176 spider species recorded in Philippine ricefields, about one-half (82) occur in upland rice. The spider species of upland rice environments overlap more with those of rainfed lowland than with those of irrigated lowland rice (24). The same study showed that of the three environments, irrigated rice has the greatest spider species diversity, followed by rainfed lowland and upland. However, of the 10 most prevalent ricefield spiders, 9 were abundant in upland rice, showing wide adaptation. All three spider guilds — orb-web, space-web, and hunting spiders — were prevalent in upland ricefields. There were, however, differences in environmental preferences for some spider species.

Of the orb-weavers, *Tetragnatha mandibulata* was particularly abundant, *T. japonica* was low, and *Leucauge decorata* was absent in upland rice.

As in other environments, *Atypena formosana* was the most dominant space-web spider, however, its relative numbers were lower than for lowland sites. Among hunting spiders, *Oxyopes javanus* and *Lycosa leucostigma* were more abundant and *Lycosa pseudoannulata* was less abundant in upland compared with lowland rice environments.

Extensive rearing of rice insect pests in upland, rainfed lowland, and irrigated sites over an 8-yr period in the Philippines provided insight into the effectiveness of parasites as natural enemies (Table 7, 8). Most of the data are from large sample sizes taken over at least one crop, which overcomes the pitfalls expressed by Van Driesche (238).

YSB egg parasitization was surprisingly similar across all environments. Larval parasitization was highly dynamic among sites and even years within the same site but showed somewhat lower levels in uplands than in irrigated wetlands. This would have been predicted for egg parasites as well, since YSB is adapted to the lowlands and so must be its parasites. This is evidence that *Telenomus rowani* is as good at dispersing as its main hosts. *T. rowani* clings onto the anal tufts of female YSB and parasitizes eggs as they are laid. This phoresy may explain its wide adaptation. The more specialized lowland YSB larval parasites, therefore, appear more effective than their upland counterparts with more alternate hosts.

Low collection levels of PSB larvae, especially in the wetlands, make comparisons between environments difficult. Low levels of larval parasitization were recorded in both rainfed environments. Except in the Cagayan rainfed wetland site in 1980, low levels of larval parasitization were evident at irrigated and rainfed sites alike. No differences by environment were evident. Higher levels of parasitization occurred in Sarawak during a 1967 outbreak, also from tachinids. Rothschild (197) indicated that higher parasitization occurred in upland rice areas.

Skipper and green horned caterpillar larval parasitization rates were generally low and showed no environmental effect. Highest activity occurred in Cagayan in 1980 (48% parasitization). Although larval parasitization levels of RLF were variable year to year, activity appeared greater in the irrigated lowlands than in the uplands. Again, the highest levels were recorded in Cagayan in 1980. Cagayan has extensive grasslands and fallow around the rice areas and a relatively long rainfall period. Rainfall in 1980 was good for crop growth and apparently for increase of larval parasites.

Table 7. Parasitization rates of rice planthoppers and green leafhopper in upland, rainfed lowland, and irrigated lowland environments. Philippines, 1976-84.[a]

Environment and site	Year	Egg parasitization (%)			Nymphal/adult parasitization (%)		
		BPH	WBPH	GLH	BPH	WBPH	GLH
Upland							
Batangas	1976				2 (47)	9 (1800)	8 (101)
	1979				8 (39)	14 (212)	6 (127)
	1980	15	17	12			
	1982				4 (51)	12 (304)	9 (116)
Rainfed lowland							
Iloilo	1976	0 (69)	–	0 (471)	0 (200)	–	4 (600)
	1977				9 (214)	7 (462)	10 (725)
	1978	11	–	11	10 (1259)	11 (270)	10 (362)
	1981				8 (235)	3 (313)	12 (870)
Cagayan	1980	44	46	52	6 (900)	5 (900)	5 (900)
	1981	48	55	56	3 (800)	1 (800)	3 (800)
	1982	40	44	49			
	1984				6 (14)	3 (81)	28 (211)
Pangasinan	1976				7 (197)	10 (274)	9 (764)
	1978	13 (436)	13 (379)	14 (457)	17 (198)	3 (116)	5 (647)
	1979				11 (486)	16 (871)	7 (1204)
	1982				18 (275)	19 (88)	8 (305)
Irrigated lowland							
Laguna	1977				11	7	21
	1978				31		
	1979	14	4	4	28		
	1980	7	8	20			
	1981			56		26	16
	1983				7 (278)	16 (1650)	27 (1921)

[a]Sources of data: *All sites:* A. T. Barrion, unpublished, 1977-82; *Batangas:* R. F. Apostol, unpublished; *Iloilo and Pangasinan:* 136; *Cagayan:* B. Canapi, unpublished; *Laguna:* 175; P. C. Pantua, unpublished; 118; 234; 43; Carino and Shepard, unpublished. BPH = brown planthopper *Nilaparvata lugens*, WBPH = whitebacked planthopper *Sogatella furcifera*, GLH = green leafhopper *Nephotettix virescens*. Figures in parentheses are sample sizes.

Tauber et al (230) reported that internal, external, and genetic factors influence the seasonal activity of parasitoids.

Hopper egg parasites, but not nymphal/adult parasites, were also particularly abundant at the Cagayan site; possibly the egg parasites have more alternative hopper prey in the weedy areas than nymphal/adult parasites.

The seasonal dynamics of hopper egg parasites can be seen for upland rice in Batangas (Fig. 1, 2), and for rainfed lowland rice in Pangasinan (135) and Cagayan (105). Levels of BPH, WBPH, and GLH egg parasitization were comparable in upland and irrigated lowland environments. Except for some high rates of parasitization early in the season, the parasitization rate tended to be steady in all environments. However, hopper nymphal/adult parasitization levels were more similar in the rainfed environments and lower than in irrigated rice.

Overall, parasites do not appear highly effective by themselves against upland or even lowland pests. Among natural enemies, parasites have attracted the most attention because they can be more readily assessed.

Predators and pathogens lend themselves better to management practices. Predators, the most important group of natural enemies in ricefields, are difficult to quantify. On the other hand, pathogens appear less important but can be readily cultured and disseminated.

The natural enemy community of upland rice is rich in species and differs significantly from that of lowland rice. These beneficial organisms must be conserved by applying insecticides judiciously, particularly sprays. Seed or soil placement of chemicals minimizes exposure to natural enemies. The strategy to derive the greatest benefit from natural enemies is to allow the greatest number of beneficial species to thrive. Then, perhaps at least one species will be effective against each pest at any time, overcoming the variable abundance of each species within and between years.

Programs to introduce exotic species or mass produce indigenous ones are ambitious and expensive because they require trained people on a sustained, not ad hoc, basis.

Chemical control

Insecticides offer rapid and efficient control of upland insect pests (190) but should be used only after other control measures have been considered. Insecticides are rarely used on upland rice because of cost (32). Upland rice yields are normally too low to justify the expenditure. Also, most upland rice is grown as a cash crop. Spraying upland rice is more difficult than lowland rice because water is less accessible. Government subsidy programs to provide pesticides to tribal peoples for upland rice production have created problems of toxicity to humans because isolated people have had no experience to be able to handle pesticides safely.

However, insecticide use has been justified when a crop is

Table 8. Parasitization rates of lepidopterous pests in upland, rainfed lowland, and irrigated lowland environments. Philippines, 1976-84.[a]

Environment and site	Year	Parasitization (%)									
		YSB		GFB larva	PSB larva	Earcutting caterpillar larva	Swarming caterpillar larva	Skipper caterpillar larva	Greenhorned caterpillar larva	RLF larva	Brown semilooper larva
		Egg	Larva								
Upland											
Batangas	1977	–	0 (57)	–	0 (63)	–	0 (71)	–	0 (106)	11 (142)	2 (101)
	1978	43 (4697)	8 (451)	5 (38)	3 (40)	6 (61)	2 (58)	15 (57)	13 (129)	13 (1286)	4 (30)
	1979	59 (4135)	12 (320)	13 (11)	5 (28)	9 (45)	6 (46)	7 (23)	8 (160)	9 (1152)	8 (26)
Rainfed lowland											
Iloilo	1976	–	0 (10)	0 (10)	0 (7)		0 (19)	22 (13)	15 (180)	5 (76)	
	1978		0 (54)	0 (3)	0 (17)	9 (64)	4 (78)	3 (73)	0 (121)	0 (191)	
	1979	64 (2350)	16 (84)			6 (17)		0 (6)	18 (68)	25 (104)	
	1981	56 (1322)	18 (304)					0 (5)	12 (51)	18 (138)	
Pangasinan	1976	60 (77)[b]	62 (82)					0 (111)		5 (39)	
	1978	58 (53)[b]	5 (51)								
Cagayan	1979	59 (713)	8 (101)			6 (34)	0 (7)	0 (11)	4 (28)	15 (286)	
	1980					62 ([illegible])		48 (177)		61 (140)	
	1981		0 (5)			12 (20)		13 (45)		14 (92)	
Irrigated lowland											
Laguna	1974	62	8								
	1974-75	50	41								
	1975	43	72								
	1978	96 (623)	21 (24)							33 (60)	
	1979	83 (2017)	18 (110)					8 (62)	11 (89)	22 (400)	
	1980	78 (1625)	20 (75)			0 (16)		4 (72)	9 (80)	7 (270)	
	1983	60								30	

[a]Sources of data: *All sites:* A. T. Barrion, unpublished, 1977-82; *Batangas:* R. F. Apostol, unpublished; *Iloilo and Pangasinan:* 136; *Cagayan:* B. Canapi, unpublished; *Laguna;* 175; P. C. Pantua, unpublished; 118; 234; 143; Carino and Shepard, unpublished. YSB = yellow stem borer *Scirpophaga incertulas*, GFB = gold fringed borer *Chilo auricilius*, PSB = pink stem borer *Sesamia inferens*, earcutting caterpillar *Mythimna separata*, swarming caterpillar *Spodoptera mauritia acronyctoides*, skipper *Pelopidas mathias*, green horned caterpillar *Melanitis leda ismene*, RLF = rice leaffolders *Cnaphalocrocis medinalis* and *Marasmia* spp., brown semilooper *Mocis frugalis*. Figures in parentheses are sample sizes. [b]Egg masses.

Table 9. Effect of seeding rate and insecticide on plant density and yield of Dagge upland rice. Batangas, Philippines, 1976.[a]

Seeding rate (kg ai/ha)	Insecticide seed treatment	Dosage (kg ai/ha)	Plant density (no./m-row) at 14 DE	Yield (t/ha)
50	None	–	35 a	2.0 a
50	Carbofuran F	1.0	38 ab	2.3 a
100	None	–	45 bc	2.5 a
100	Carbofuran F	1.0	51 cd	2.3 a
100	Dieldrin WP	1.0	52 cd	2.2 a
150	None	–	59 d	2.2 a

[a]Av of 8 fields. DE = days after crop emergence. In a column, means followed by a common letter are not significantly different at the 5% level by DMRT. F = flowable, WP = wettable powder.

threatened by epidemics of locusts or armyworms. New technology stressing efficiency has minimized insecticide cost.

Seed treatment is normally inexpensive and can be economically justified in many cases (66). Treating seed with systemic insecticide (216) but not chlorinated hydrocarbons (247) is most effective in controlling seedling maggots. Foliar sprays have to be repeated to obtain control and often are washed off by frequent early season rains. Granular insecticides are effective, but required dosages are too expensive to justify except under heavy infestation (247). When directed against first-instar larvae, banding granules in seed furrows (177) can be effective against white grubs at low dosages (0.25 kg ai/ ha) (134). Seed treatments are not promising for white grub control (248).

Seed treatment is also effective against ants and may be cheaper than increasing the seeding rate. In Batangas, treating 50 kg seed/ ha was as effective as increasing the seeding rate to 100 kg/ ha and using untreated seeds (Table 9). In Brazil, seed treatments control termites and other soil insects including the lesser corn stalk borer (66). Domiciano (58), however, found seed treatments inconsistent in their effect against high populations of lesser corn stalk borer.

Baiting can be an inexpensive way of controlling ants, seedling maggot flies, mole crickets, and field crickets. Baits made of locally available material and impregnated with insecticide can be sparingly distributed, taking advantage of the pests' ability to disperse and encounter bait sites.

The new low-volume, hand-held, controlled-droplet sprayers may offer an advantage over high-volume knapsack sprayers for controlling foliar pests. Upland rice canopies are more open than those in lowland rice, and better droplet penetration should result. Controlled droplet applicators would be ideal for seedbugs and defoliators.

CONCLUSION

Upland rice is attacked by a wider array of insect pests than is lowland rice, mainly because of the addition of soil pests. Generally, population levels of lowland rice pests are lower in upland than lowland rice, leading many people to conclude that insect pests are not important on upland rice.

Yield losses from insect pests in upland rice often are comparable to those of lowland rainfed or irrigated rice (0-30%), but usually from different pests. The principal groups are soil pests feeding on sown seed and roots, followed by seedling pests. These groups have largely gone unnoticed, leading researchers to conclude that stem borers and seed bugs are the most important pests (17). Yield loss trials that pinpoint major pests need to include seed treatments. Granules applied in the furrow may not give adequate protection from many seed pests.

The floristic and pedological diversity of upland rice environments is matched by the diversity of arthropods, both pests and their natural enemies. Irrigation has homogenized lowland rice environments. Flooded soils tend to have the same properties and to eliminate soil pests. The spatial and temporal dominance of cultivated rice has benefited specialist pests.

Upland rice has no specialist arthropod species. The monophagous pests on upland rice prefer the lowlands where rice evolved. Rice in the uplands exists only because of man, and even though lowland rice predates upland rice, specialist species evolved. Wheat, maize, and sorghum do not have monophagous pests, leading us to conclude that there is no evolutionary advantage for insects to have narrow host ranges in upland graminaceae.

Pests have adapted to the uplands not only by having wider plant host ranges but also by having long life cycles, undergoing dormancy, or being dispersive. Each pest has a unique life history strategy suited to highly unpredictable environments. In a given year, some insect species can better exploit upland rice as a food source, but no pest is a serious one every year on upland rice.

The low yielding potential of upland rice means less quantity and lower quality of food for pests to exploit, but also less incentive for farmers to undertake control.

The most effective control would be early and synchronous planting of early-maturing upland rice varieties to prevent insect pest buildup. Breeding for insect resistance should initially focus on stem borers because they are very difficult to control by other means. Biocontrol efforts should first stress conservation of natural enemies, predators, and pathogens rather than parasites. Efficient chemical control includes seed treatment or baiting for seed, seedling, and some root pests, and using controlled droplet sprayers for spot treatments against foliar pests and seed bugs when economic thresholds are reached.

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