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Population dynamics of herbivorous insects and potential arthropod natural enemies on *Alnus* species in Kabale district, Uganda

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Abstract

Monitoring populations of pests and their natural enemies under different management situations and seasonal weather parameters provides extremely useful information for taking preventive measures against pest outbreaks. The abundance, spatial and temporal distributions of herbivorous insects and arthropod natural enemies on *Alnus* species were monitored at four sites in Kabale district, Uganda between June 1999 and August 2000. Chewing insects, dominated by Coleoptera (75%), constituted the majority of insect herbivores sampled. Dominant and potentially serious pests of *Alnus* included *Apion globulipenne*, an unidentified Chrysomelidae (Coleopt. 27), *Phymateus viridipes*, *Coloborrtics corticina* and a *Cacopsylla* species (Homoptera: Psyllidae). Spiders were the predominant natural enemies accounting for 64% of the total natural enemies encountered, followed by parasitic Hymenoptera (30%). There were marked spatial and temporal variations in arthropod abundance. Among sites, mean abundance of total insect herbivores and total natural enemies on *A. acuminata* over 15 months ranged from 3.8–8.5 and 3.3–4.7 individuals per 1-m branch length respectively. Over the same period, mean number of total insect herbivores and total natural enemies on *A. nepalensis* that was studied at only one site were 11.9 herbivores and 4.2 natural enemies per 1-m branch length. Populations of most insect orders increased in the wet season although the greatest herbivore abundance was evident in the dry season. Further studies are necessary on the impact and management strategies of the potentially important insect pests and natural enemies on *Alnus*.

Introduction

Alnus species, including *A. acuminata* and *A. nepalensis* were first introduced in Uganda in 1988 through the agroforestry research networks for Africa (AFRENA), Uganda project (Okorio et al. 1994). Farmers in Kabale district have identified *A. acuminata* as the most preferred multipurpose tree species for on-farm production of fuelwood and poles which are crucial for their livelihood (van Houten 1997). The *Alnus* species are also important for several other products and services, including provision of timber, stakes and shade for crops such as coffee, and for soil improvement and watershed management (National Academy of Science 1980; Russo 1995; Neil 1997; Dhyani 1998; van Houten 1997). Major efforts are underway to support the expansion of *Alnus* species in Uganda especially in the Kigezi highlands (T. Raussen, pers. comm., 1999).

However, recent studies on pest problems on agroforestry tree species in Uganda have indicated a wide range of pest infestations on *Alnus* species (Maiteki and Owera 1996; Roux 1999; Nyeko 2001). Nyeko (2001) showed that *Septoria* brown leaf spots and defoliation by insects can significantly reduce the survival and growth rates of *A. acuminata* and *A. nepalensis* seedlings in nurseries and the field. Herbivorous insects have been reported as causing over 70% defoliation on some field *A. acuminata* trees in Kabale district, Uganda (Nyeko 2001). One

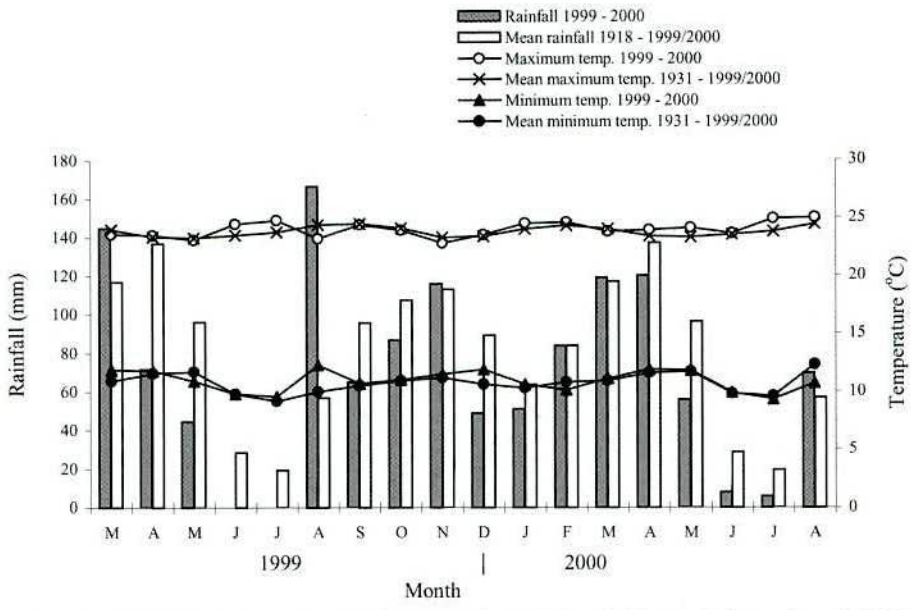

Figure 1. Rainfall and temperature profiles in Kabale district Uganda from 1918 to 2000 and during study period (March 1999–August 2000), Raw data from Kabale district meteorological department through AFRENA Project, Kabale.

major conclusion from these studies is that pests, particularly insects and pathogens may jeopardise the cultivation of the potentially important *Alnus* species in Uganda. Owing to the increasing demand for the *Alnus* species in the country, it is important that appropriate strategies to limit pest infestations on the species are developed and passed to farmers. Unfortunately, there has been no study on the ecological factors governing pest populations on the *Alnus* species not only in Uganda, but throughout Africa. Lack of such information may result in ignoring serious pests or over-reacting to minor ones (Boa and Bentley 1998), and may thus impede development of acceptable control measures (Walter and Parry 1994).

Regular and prolonged monitoring of populations of herbivorous insects and their natural enemies under different management situations and seasonal weather parameters provides necessary information for determining the conditions that favour the build up of pests. This information is extremely useful for taking preventive measures against pest outbreaks (Rao et al. 2000). Censuses of insects are also necessary to determine the influence of insects on plant growth and development, because the damage inflicted by sucking insects may not be readily apparent (Southwood 1987; Fensham 1994). Thus the abundance of sucking insects can be used as an indirect measure of the damage they cause. The objective of this study was to assess the composition, and spatial and temporal dynamics of herbivorous insects and potential natural enemies on *Alnus* species in Kabale district, Uganda.

Materials and methods

The study area

Kabale district lies at latitude 0°6′ S and longitude 29°57′ E in southwestern Uganda. The district is dominated by conical shaped interlocking hills (the Kigezi highlands) at approximately 2000 m above sea level with an area of 1,827 km^2. The annual rainfall pattern in the district is bimodal with peaks in March and April, and October and November ranging between 1,000 mm–1480 mm per annum (Figure 1). A brief dry spell occurs in January and a drier period from June to August. The monthly temperature averages 17.5 °C, which sometimes drops to about 10 °C at night. The vegetation in Kabale district includes bamboo forest and afro-alpine shrubs, but intense human activity in the district is steadily changing this type of vegetation (Rwabwoogo 1997).

Sampling size and technique

The incidence and abundance of herbivorous insects and potential arthropod natural enemies on *A. acumi-*

Table 1. . Characteristics of sites and sampling size used for monitoring arthropod abundance and damage on *Alnus* species in Kabale district, Uganda.

Site	Characteristics
Buhara	Young, sole *Alnus* acuminata AFRENA seed orchard established in 1997 at mid-slope. A total of 90 trees spaced 2 m × 2 m were present during the study. Two branches were sampled from each of 20 trees during each sampling occasion. Tree canopies were open at the onset of the study but later closed starting December 1999. Slashing and spot weeding were done to suppress weeds.
Kachwekano1	Old AFRENA multi-purpose tree species trial established in 1989 at low- to mid-slope. Both *Alnus acuminata* and *A. nepalensis* were available for study. Other multipurpose tree species, in line plots, included *Markhamia lutea, Grevillea robusta, Casuarina cunninghamania, C. equisetifolia, Leucaena* species, *Cupressus lusitanica, Erythrina abyssinica and Vernonia amygdalina.* A number of herbaceous and woody weeds were also present. There were 15 trees of each *Alnus* species in three rows of five trees. For each *Alnus* species, five branches were sampled from each of six trees during every sampling occasion. Within-row tree canopies were closed throughout the period of study. Because of accumulated litter in the dry season, four experimental trees were burnt by wildfire in early July 2000.
Kachwekano2	Old sole *A. acuminata* AFRENA seed orchard established in 1990 near hilltop. Tree canopies were closed throughout the study period with virtually no undergrowth. There were 40 trees at a spacing of 4 m × 4 m at the onset of the study. Five branches were sampled from each of seven trees during each sampling occasion.
Kachwekano3	AFRENA trial with *A. acuminata* and *Calliandra calothyrsus* coppices at mid-slope. *A. acuminata* coppices were two years old at the onset of the study. Maize, beans and wheat were planted in different seasons during the study. Because the woody species were closely spaced (0.5 m) within rows, they were periodically pruned and thinned to allow for crop growth. Two branches were sampled from each of 20 trees during each sampling occasion.

nata and *A. nepalensis* (at Kachwekano1 only) was monitored monthly between June 1999 and August 2000 at four sites (Table 1). Sampling took place in the last week of each month. *Alnus* coppices that were initially selected for this study at Kachwekano3 were cut down in January 2000 by AFRENA in order to continue earlier agronomic studies. Sampling at this site in subsequent months was, however, continued in adjacent plots starting with 8-month old *A. acuminata* coppices in February 2000.

The total number of branches sampled during each sampling occasion varied between sites because of differences in the number and age of the trees that were available for sampling at each site (Table 1). Only branches 0.5–3 m above ground were sampled. Branch beating and hand picking methods were used for sampling arthropods. Randomly selected branches were carefully approached and held over a 100 cm × 75 cm tray. The branches were then beaten, and any fallen arthropod collected using an aspirator. Thereafter the foliage was thoroughly searched for any remaining arthropods that were picked by hand. A standard branch length corresponding to the length of the sampling tray (100 cm) was used at all sites throughout the study. This sampling technique is not capital intensive, but the yields of arthropods in samples may be low (Majer et al. 1996). The low yield of material was remedied by sampling a large quantity of branches, although arthropods that are better equiped to fly away were liable to be undersampled. Where possible, the identity and number of such escapees were determined.

Arthropods were sorted into orders and species codes within 1–3 days after collection. Where possible, immature insect samples were raised to adult stages, for identification and possibilities of parasitoid emergence, by feeding them on the foliage of the *Alnus* species from which they were collected. All arthropod samples were stored in labelled vials under 99.7% alcohol and later taken for identification at Kawanda Agricultural Research Institute (KARI), Uganda. However, identification of samples to species level was incomplete because of limited reference collection at KARI. Unidentified insects were assigned species codes that were used in data analysis. The determination of phytophagous status of sap-sucking insects and most natural enemies was unequivocal. However, chewing species were provided with fresh *Alnus* leaves for five days in the laboratory to ensure that the insects feed on the *Alnus* species. Literature (Borror et al. 1989) was used to ascertain the feeding guilds of some arthropods species whose

feeding habits could not be established readily in the field or laboratory.

Data analysis

In order to determine the seasonal effects on arthropod abundance, the 15 months of study were split into five seasons following the rainfall pattern recorded over the study period (Figure 1). Thus dry season 1 (June–July 1999), wet season 1 (August–November 1999), dry season 2 (December 1999–January 2000), wet season 2 (February–May 2000), and dry season 3 (June–August 2000). The original data from each site were aggregated to arthropod families, orders and feeding guilds. Some of these categories occurred very rarely and, consequently, some were combined for statistical analysis. Overall, 17 categories were generated including: Apionidae, Chrysomelidae, other herbivorous Coleoptera, total herbivorous Coleoptera, Lepidoptera, Orthoptera, Psocoptera, total chewing insects, Hemiptera, Homoptera, other sucking insects, total sucking insects, total insect herbivores, parasitic Hymenoptera, spiders, other natural enemies, and total natural enemies. Spiders were not differentiated into smaller categories (orders or species) due to lack of reference collection and taxonomic expertise at KARI.

For every site, pivot table in Microsoft Excel 2000 computer package was used to calculate the total number of individuals and species in each arthropod group. Berger-Parker species dominance index (D), that is simple and free of sample bias (Southwood 1987), was calculated using the equation $D = N_{max}/N_T$; where N_{max} is the abundance of dominant species and N_T equals to total catch. By substituting N_{max} in the equation with the abundance of dominant insect orders, dominance indices were calculated for the dominant insect orders for two arthropod categories, other sucking insects and other natural enemies, which comprised insect orders with few individuals.

Analysis of variance (ANOVA) was used to compare the abundance of arthropods over sites, seasons and *Alnus* species. Prior to ANOVA, the monthly data for each branch were summarised into average number of individuals in each arthropod group using descriptive statistics. Data were $\log_{10}(x + 1)$ transformed after checking for distribution using the Anderson-Darling test, that has good power and is especially effective at detecting departure from normality in the high and low values of a distribution (Minitab Inc 2000). ANOVA was performed on the transformed data using 2 models. Firstly, a two-way ANOVA, with site and season as the main factors, was fitted to the data on arthropods sampled from *A. acuminata* in order to compare the arthropod abundance on the species at different sites and seasons. Secondly, a two-way ANOVA with *Alnus* species and season as main factors was performed in order to compare, over seasons, the arthropod abundance on *A. acuminata* and *A. nepalensis* that coexisted only at Kachwekano1.

Results

Total arthropods collected in this study, summed across the four sites and two *Alnus* species consisted of 29,776 individuals, of which 78% were insects and 22% spiders (Table 2). Mites were only very occasional and were not counted or recorded. Herbivorous insects and natural enemies comprised 66% and 34% of total arthropods respectively. Chewing insects, comprised of the orders Coleoptera (75%), Psocoptera (20%), Lepidoptera (3%) and Orthoptera (2%), constituted 76% of total insect herbivores sampled. *Apis mellifera* was observed causing conspicuous and prevalent leaf perforations on *Alnus*, but the abundance of the bees was not assessed in this study because they can sting aggressively. Sucking insects that constituted 24% of total insect herbivores consisted mainly of Homoptera (56%) and Hemiptera (20%). Spiders (64%) and Hymenoptera (30%) were the dominant natural enemies encountered. Other natural enemies, including predatory Coleoptera (mostly Coccinellids), Hemiptera (Reduviidae), Mantodea and Neuroptera were rare. With few exceptions, dominant arthropod species and functional groups were similar between sites and between *Alnus* species (Table 2).

Although herbivorous insects were more abundant than natural enemies at all the study sites (Table 2), significant spatial and temporal variability was evident in the abundance of arthropod groups over the 15 months of study (Figures 2 and 3, Table 3). The ratios of chewing insects to sucking insects encountered on *A. acuminata* at Buhara, Kachwekano1 (*A. acuminata*), Kachwekano2, and Kachwekano3 were 1.8, 5.6, 2.7, 1.2 respectively. Thus indicating a general increase in the ratio of chewing insects to sap suckers with maturity of *A. acuminata* stand (see Table 1 for age of stands). Overall, the intensity (number of individuals per 1m branch length) of herbivo-

Table 2. Total arthropod abundance and number of insect species sampled monthly from *Alnus acuminata* and *A. nepalensis* through 15 months at four sites in Kabale district, Uganda.

Arthropod group	Buhara	Kachwekano1		Kachwekano2	Kachwekano3	Total
		A. acuminata	*A. nepalensis*			
Insect herbivores						
Apionidae	148 (1)	421 (1)	1199 (1)	40 (1)	54 (1)	1862
Dominant species	*A. globulipenne*	*A. globulipenne*	*A. globulipenne*	*A. globulipenne*	*A. globulipenne*	
	D = 1.00	D = 1.00	D = 1.00	D = 1.00	D = 1.00	
Chrysomelidae	922 (10)	1158 (12)	810 (12)	974 (10)	555 (15)	4419
Dominant species	*Haltica pyritosa*	Coleopt. 27	Coleopt. 27	Coleopt. 27	Coleopt. 27	
	D = 0.36	D = 0.61	D = 0.65	D = 0.57	D = 0.34	
Other Coleoptera	187 (19)	1344 (30)	2547 (26)	742 (33)	215 (27)	5035
Dominant species	*Lobotrachelus* sp.	Coleopt. 2	Coleopt. 2	Coleopt. 2	Coleopt. 2	
	D = 0.41	D = 0.50	D = 0.61	D = 0.24	D = 0.13	
Total Coleoptera	1257 (30)	2923 (43)	4556 (39)	1756 (44)	824 (43)	11316
Dominant species	*Haltica pyritosa*	Coleopt. 27	*A. globulipenne*	Coleopt. 27	Coleopt. 27	
	D = 0.27	D = 0.24	D = 0.26	D = 0.32	D = 0.23	
Lepidoptera	76 (6)	73 (6)	103 (7)	114 (8)	119 (7)	485
Dominant species	Lepidopt. 2	Lepidopt. 2	Lepidopt. 1	Lepidopt. 5	Lepidopt. 2	
	D = 0.32	D = 0.29	D = 0.34	D = 0.46	D = 0.42	
Orthoptera	53 (7)	22 (7)	13 (7)	40 (7)	191 (13)	319
Dominant species	Orthopt. 10	Orthopt. 3	Orthopt. 8	*A. ruficornis*	*P. viridipes*	
	D = 0.40	D = 0.27	D = 0.31	D = 0.35	D = 0.20	
Psocoptera	996 (2)	299 (2)	244 (2)	1306 (2)	144 (2)	2989
Dominant species	Psocopt. 1	Psocopt. 1	Psocopt. 1	Psocopt. 1	Psocopt. 1	
	D = 0.53	D = 0.65	D = 0.72	D = 0.75	D = 0.63	
Hemiptera	77 (12)	258 (10)	206 (11)	236 (17)	140 (16)	917
Dominant species	Hemipt. 12	Hemipt. 2	Hemipt. 2	Hemipt. 2	Hemipt. 4	
	D = 0.29	D = 0.44	D = 0.46	D = 0.33	D = 0.50	
Homoptera	856 (13)	182 (9)	167 (9)	742 (9)	671 (14)	2618
Dominant species	*C. corticina*	*C. corticina*	*C. corticina*	*C. corticina*	*Cacopsylla* sp.	
	D = 0.53	D = 0.72	D = 0.64	D = 0.82	D = 0.43	
Other sucking insects	350 (13)	149 (5)	138 (7)	203 (9)	279 (10)	1119
Dominant order	Thysanoptera	Thysanoptera	Thysanoptera	Thysanoptera	Thysanoptera	
	0.71	0.82	0.85	0.73	0.75	
Natural enemies						
Hymenoptera	431 (25)	807 (20)	598 (18)	457 (18)	671 (14)	2964
Dominant species	Hymenopt. 3	Hymenopt. 3	Hymenopt. 3	Hymenopt. 3	Hymenopt. 3	
	D = 0.70	D = 0.71	D = 0.75	D = 0.56	D = 0.80	
Spiders	1556	1214	1141	1207	1328	6446
Other natural enemies	36 (7)	56 (6)	69 (9)	250 (9)	192 (10)	603
Dominant order	Mantodea	Coleoptera	Coleoptera	Coleoptera	Coleoptera	
	D = 0.47	D = 0.83	D = 0.83	D = 0.90	D = 0.60	

Number in brackets denote number of species in each insect group; sp., species; D, proportion of total catch due to the dominant insect species or order; species codes are used for unidentified dominant species held at the Faculty of Forestry and Nature conservation, Makerere University, Kampala, Uganda; *A. globulipenne*, *Apion globulipenne*; *A. ruficornis, Acanthacris ruficornis; P. viridipes*, *Phymateus viridipes*; *C. corticina*, *Coloborrtics corticina*.

rous insects on *A. acuminata* varied significantly ($P < 0.001$) among sites with the greatest number exhibited at Kachwekano1 (Table 3). This site had a significantly higher intensity of total chewing insects, but a lower intensity of total sucking insects than the other sites. In particular, the intensity of Apionidae, Chrysomelidae and other herbivorous Coleoptera on *A. acuminata* was greatest at Kachwekano1, resulting in more than double the intensity of total herbivorous Coleoptera collected from the species at any other site (Table 3).

When considered across all sites, Coleopterans were more abundant in the wet months from August–November 1999 and March–May 2000 (Table 3). However, patterns of Coleoptera abundance varied significantly among sites and families within the Order (Figure 2). Chrysomelidae, which constituted 39% of total herbivorous Coleoptera sampled, showed distinct peak populations in September 1999 (Kachwekano2), and February and August 2000 (Kachwekano1). An Apionidae species, *Apion globulipenne*, largely occurred at Kachwekano1 (Table 3) with a rapid population build up from May–August (Figure 2). Up to 65% of the total individuals of this species encountered were on *A. nepalensis* (Table 2), with distinct population peaks evident in August 1999 and 2000 (Figure 2). Whereas the dominant Coleoptera species sampled at Buhara was *Haltica pyritosa*, an unidentified Chrysomelidae (Coleopt. 27) dominated the Coleoptera sampled from *A. acuminata* at Kachwekano1, Kachwekano2, and Kachwekano3 (Table 2). Unlike Coleoptera, Psocoptera were more abundant in Kachwekano2 and Buhara but were relatively rare at Kachwekano1 and Kachwekano3. This order was dominated by only one species, an unidentified Polypsocidae (Psocopt.1), at all study sites (Table 2). The highest intensity of this order, across all sites, was observed in the short dry spell from December 1999 to January 2000 (Table 3). Prominent peaks of Psocoptera population were particularly evident at Kachwekano2 and Buhara in October and December 1999, and January, April and June 2000 (Figure 2).

Lepidoptera and Orthoptera generally occurred at low intensities, at less than one individual per branch, as were Hemiptera (Tables 3 and 4). However, Lepidoptera was the only insect order that showed statistically similar abundance ($P > 0.05$) on *A. acuminata* among all sites (Table 3). Kachwekano3 differed from other sites in Orthoptera abundance, particularly from February to May 2000 (Figure 2, Table 3). This was mainly attributed to an increase in the population of one species, *Phymateus viridipes* that was largely confined to the site.

Hemiptera intensity was highest at Kachwekano1, but this site exhibited a significantly lower intensity ($P < 0.05$) of total sucking insects than Buhara, Kachwekano2 and Kachwekano3 that showed statistically similar intensities of total sucking insects (Table 3). Homoptera dominated the total sucking insect encountered (56%) and generally showed lower intensity at Kachwekano1 than at all other sites throughout the study period (Figure 2). Distinct population peaks of Homoptera were evident in October 1999 (Kachwekano2) and June 2000 (Buhara). The peak Homoptera population at Buhara in June 2000 was largely due to an increase in the number of black bean aphid, *Aphis fabae*. Overall, *Coloborrtics corticina* dominated the Homoptera encountered at all sites except Kachwekano3 that was dominated by a *Cacopsylla* species (Table 3). The latter species possibly moved from adjacent *Prunus africana* plot at Kachwekano3 where it was observed to cause serious damage on the species, particularly between June and August.

The abundance of total natural enemies varied significantly between study sites ($P < 0.001$) and seasons ($P < 0.01$) (Table 3). Overall, high numbers of total natural enemies were evident in the first and third dry seasons (Table 3), perhaps in response to fluctuating host insect populations (Figures 2 and 3). Peaks of parasitiod Hymenoptera populations were evident in August 1999, and May and July 2000, particularly at Kachwekano1. On the other hand, there was no obvious peak in spider populations (Figure 2), possibly because of their ability to feed on a variety of hosts. At Kachwekano3, total natural enemies were more abundant than total insect herbivores in the first and second dry season (Figure 3). Overall, however, total insect herbivores were more abundant than natural enemies at all sites (Figure 3, Tables 3 and 4).

Of the two *Alnus* species that coexisted at Kachwekano1, *A. nepalensis* exhibited a substantially higher chewing/sucking insect ratio (9.6) than *A. acuminata* (5.6). Apionidae, total herbivorous Coleoptera, chewing insects and overall insect herbivores were significantly more abundant ($P < 0.001$) on *A. nepalensis* than on *A. acuminata* (Table 4). In contrast, sap sucking insects and natural enemies were generally more abundant on *A. acuminata* than *A. nepalensis*, albeit not significantly ($P > 0.05$). Similarly, no significant difference ($P > 0.05$) was evident

Table 3. Intensities of herbivorous insects and natural enemies on *Alnus acuminata* at four sites in Kabale district, Uganda during June 1999–August 2000.

Factors	Arthropod intensity (mean number per 1-m branch length)													
	Apionidae	Chryso-melidae	Total Coleop-tera	Lepidop-tera	Orthop-tera	Psocop-tera	Total chewing insects	Hemip-tera	Homop-tera	Total sucking insects	Total insect herbivores	Parasitic Hymenop-tera	Spiders	Total natural enemies
Site														
Buhara	0.23^{a}	1.37^{a}	1.94^{a}	0.120	0.09^{a}	1.37^{a}	3.67^{a}	0.13^{a}	1.28^{a}	2.00^{a}	5.76^{a}	0.70^{a}	2.51^{a}	3.29^{a}
Kachwekano1	0.83^{b}	2.09^{b}	6.09^{b}	0.160	0.05^{a}	0.57^{b}	6.99^{b}	0.49^{b}	0.43^{b}	1.30^{b}	8.51^{b}	1.56^{b}	2.82^{b}	4.65^{b}
Kachwekano2	0.07^{c}	1.48^{a}	2.62^{c}	0.179	0.07^{a}	1.64^{a}	4.90^{c}	0.39^{b}	1.17^{a}	1.99^{a}	7.61^{b}	0.80^{ac}	2.18^{c}	3.40^{a}
Kachwekano3	0.08^{c}	0.81^{c}	1.28^{d}	0.190	0.29^{b}	0.21^{c}	1.99^{d}	0.18^{a}	1.07^{a}	1.72^{a}	3.81^{c}	1.00^{c}	2.06^{c}	3.42^{a}
Season														
Dry1 (Jun.–Jul. 1999)	0.34^{d}	0.68^{d}	1.59^{e}	0.130^{a}	0.08^{c}	0.57^{d}	2.45^{e}	0.21	1.11^{e}	2.01^{c}	4.60^{d}	1.41^{d}	2.35^{d}	4.11^{e}
Wet1 (Aug.–Nov. 1999)	0.36^{d}	1.97^{e}	3.40^{f}	0.112^{ab}	0.08^{c}	0.72^{df}	4.50^{f}	0.28	0.50^{d}	1.32^{d}	6.14^{e}	0.97^{f}	2.20^{d}	3.59^{e}
Dry2 (Dec. 1999–Jan. 2000)	0.17^{e}	1.64^{e}	2.51^{g}	0.209^{ac}	0.13^{d}	1.89^{e}	5.38^{g}	0.26	0.65^{de}	1.27^{d}	6.87^{ef}	0.73^{f}	2.12^{d}	2.99^{de}
Wet2 (Feb.–May 2000)	0.11^{f}	1.69^{e}	3.20^{hf}	0.234^{c}	0.17^{d}	0.92^{f}	4.87^{fg}	0.26	0.86^{ce}	1.46^{d}	6.51^{ef}	0.97^{f}	2.40^{d}	3.49^{ce}
Dry3 (June–Aug. 2000)	0.39^{g}	1.22^{f}	2.70^{hg}	0.130^{ac}	0.14^{d}	0.49^{d}	3.70^{h}	0.45	1.93^{f}	2.93^{e}	7.10^{f}	0.92^{f}	2.88^{e}	4.22^{ef}

For each factor (site and season), means followed by different letters within a column differed significantly at 5% probability. t-test was performed on $\log_{10}(x + 1)$ transformed data.

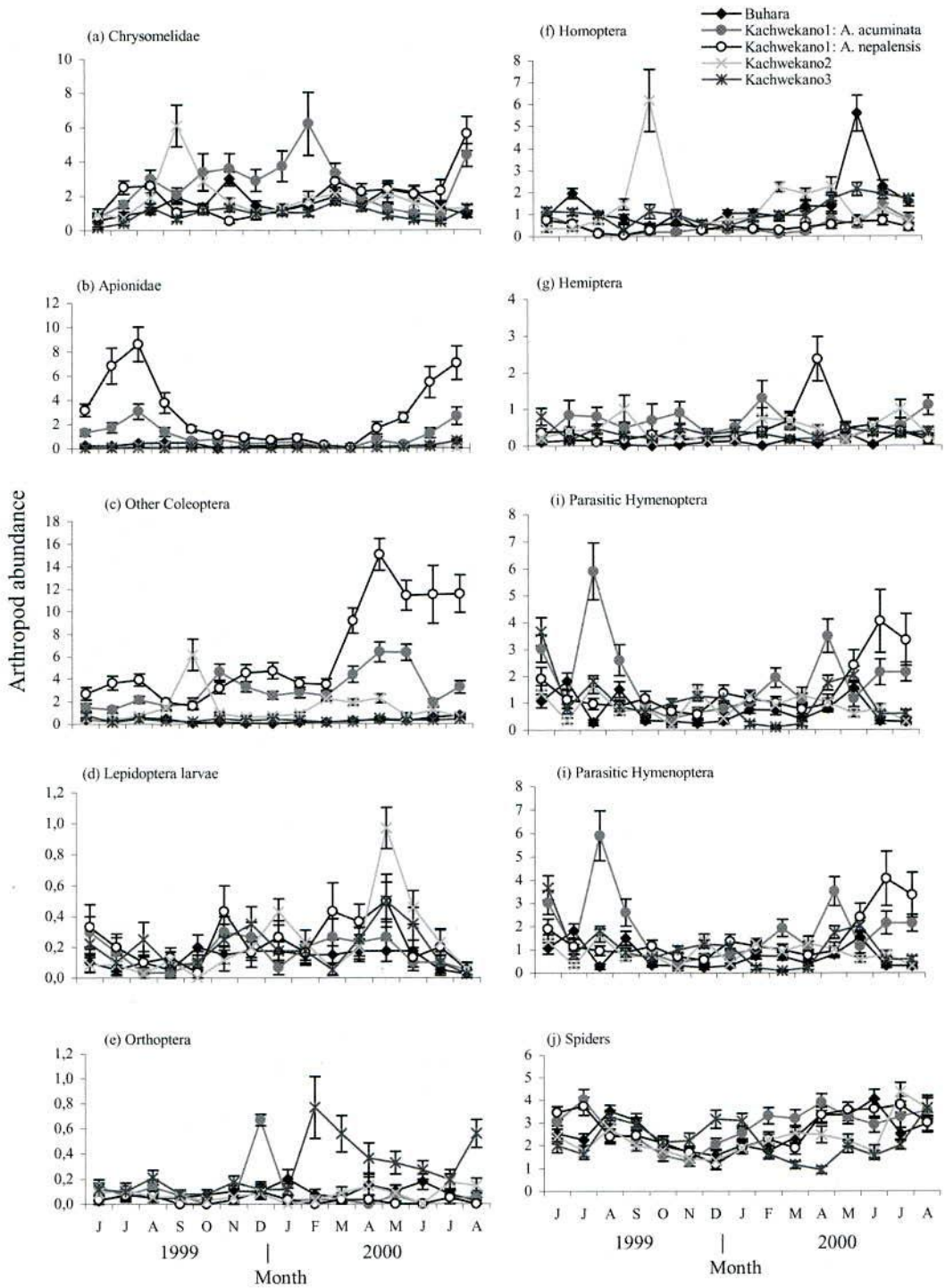

Figure 2. Trends over 15 months in abundance of herbivorous insects and natural enemies on *Alnus* species at four farmland sites in Kabale district, Uganda. Note the variability in scales on y-axis

between the two *Alnus* species in the abundance of other arthropod groups (Table 4). *A. nepalensis* harboured higher populations of chewing insects than natural enemies throughout the period of study, but

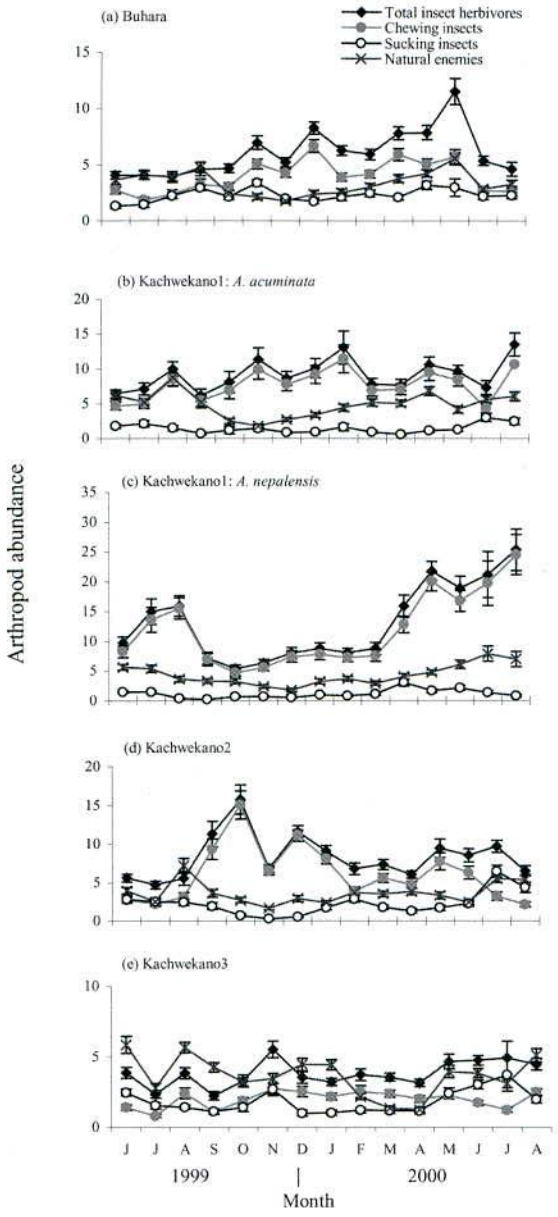

Figure 3. Patterns in abundance (number per branch) of arthropod groups on *Alnus* species at four farmland sites in Kabale district, Uganda.

sap sucking insects were consistently less abundant on the species than natural enemies (Figure 3). There were significant differences ($P < 0.05$) in seasonal abundance of most arthropod groups at Kachwekano1 (Table 4). The Coleopterans and parasitic Hymenoptera showed highest intensities in the third dry season (June–August 2000). On the other hand, Lepidoptera and Hemiptera were most abundant in the second wet season (February–May 2000). Orthoptera, Homoptera and spiders were most abundant in the first dry season. Psocoptera was the only order most abundant in the second dry season (December–January 2000).

Discussion

Significant site to site variability in arthropod abundance was observed in all arthropod groups examined in this study, except Lepidoptera larvae. This variation could be attributed to several factors including intersite distance, site to site differences in vegetation and/or microclimate (Kitching et al. 1993), and age and management of trees. For instance, total insect herbivores, in particular Coleoptera, and total natural enemies were most abundant on *A. acuminata* at Kachwekano1, a site that consisted of several multipurpose tree species with dense weedy vegetation. This concurs with the findings of Sileshi et al. (2000) that higher population of *Mesoplatys ochroptera* Stål., *Brachyplatys testudonigro* F. and predators of *M. ochroptera* occurred on *Sesbania* in unweeded than weed-free plots. Schowalter (1994) noted that dense vegetation such as forests with closed canopies maintain more stable temperatures, higher humidities, and low wind speeds that may permit survival of many arthropods that are intolerant to extreme temperatures or desiccation. Possibly, then, the higher abundance of total insect herbivores and natural enemies observed at Kachwekano1 was related to favourable niches created by the array of plant species at the site. In addition, this result suggests that most of the arthropods were not specific to *Alnus* but also attacked other plant species. Furthermore, it suggests that associating *Alnus* with other plant species as in agroforestry does not protect it from pest damage, as might be suspected, but may increase the danger of pest damage. If this is so, there are consequences for agroforestry (as compared to single-species plantations) in general.

When sites are considered according to stand age, there was a general increase in the chewing/sucking insect ratio with increasing stand age. This trend lends support to the findings of other authors (Ohmart et al. 1983; Schowalter and Crossley 1987; Sileshi et al. 2000) who observed that whereas sucking insects tend to be more abundant in young trees, chewing insects become more abundant as trees age. A clear cut example in this study was the abundance of total Coleoptera herbivores in the old *A. acuminata* stands at

Table 4. Intensities of herbivorous insects and natural enemies on *Alnus acuminata* and *A. nepalensis* at Kachwekano1, Kabale district, Uganda during June 1999–August 2000.

Factors	Arthropod intensity (mean number per 1m branch length)													
	Apionidae	Chryso-melidae	Total Coleop-tera	Lepidop-tera	Orthop-tera	Psocop-tera	Total chewing insects	Hemip-tera	Homop-tera	Total sucking insects	Total insect herbivores	Parasitic Hymenop-tera	Spiders	Total natural enemies
Alnus species														
A. acuminata	0.83[a]	2.09	6.09[a]	0.16	0.05	0.57	6.99[a]	0.49	0.43	1.30	8.51[a]	1.56	2.82	4.65
A. nepalensis	2.14[b]	1.73	9.70[b]	0.22	0.03	0.53	10.71[b]	0.40	0.39	1.10	11.92[b]	1.33	2.62	4.18
Season														
Dry1 (Jun.–Jul. 1999)	2.65[c]	1.25[a]	6.08[c]	0.23[a]	0.07	0.54[a]	7.08[c]	0.38	0.67	1.62[a]	8.96[c]	1.59[a]	3.52[a]	5.54[a]
Wet1 (Aug.–Nov. 1999)	1.92[d]	1.84[b]	6.69[c]	0.13[b]	0.04	0.26[b]	7.19[c]	0.37	0.13	0.74[b]	8.06[c]	1.29[a]	1.96[b]	3.43[b]
Dry2 (Dec. 1999–Jan. 2000)	0.59[e]	2.14[b]	6.66[c]	0.18[ab]	0.04	1.20[c]	8.19[c]	0.41	0.32	0.88[c]	9.09[c]	0.86[b]	2.08[b]	3.08[b]
Wet2 (Feb.–May 2000)	0.37[e]	2.20[b]	8.64[d]	0.32[c]	0.03	0.60[a]	9.72[d]	0.60	0.35	1.28[c]	11.03[d]	1.36[a]	3.06[c]	4.64[c]
Dry3 (June–Aug. 2000)	2.39[cd]	2.22[b]	11.47[e]	0.10[b]	0.02	0.32[b]	12.00[e]	0.48	0.64	1.62[a]	14.28[e]	2.33[c]	3.28[ac]	5.96[a]

For each factor (site and season), means followed by different letters within a column differed significantly at 5% probability. t-test was performed on $\log_{10}(x + 1)$ transformed data.

Kachwekano1 and Kachwekano2 that were more than double the total Coleoptera herbivores sampled from the young stands at Buhara and Kachwekano3. This insect order may therefore not be a serious problem during field establishment of *Alnus* seedlings.

Distinct peaks of abundance were evident among most arthropod groups, but the period of peak abundance differed between the various groups (Figures 2 and 3, Tables 3 and 4). This is indicative that one particular season is not universally unsatisfactory for all major insect groups (Denlinger 1980). For example, whereas most insect groups showed population build up in the wet season, *A. globulipenne* (Apionidae) were nearly absent in wet seasons but showed a rapid population increase in the dry season, particularly between May and August (Figure 2). Peak population of *A. globulipenne* occurred in August of both 1999 and 2000 despite a substantial difference (96.9 mm) in the amount of rainfall received in this month in the 2 years (Figure 1). It would appear, then, that the population of this insect species builds up during the dry season and then reaches high levels in August independently of whether August is dry or wet. Moreover, *A. globulipenne* exhibited significantly higher populations on *A. nepalensis* than on *A. acuminata* especially in the long dry season (June–August). There is need to take advantage of such significant variations between *Alnus* species. Damage assessment should be developed to identify resistance at several genetic levels, including *Alnus* species, provenances, families and individual trees.

When pooled across sites, the number of chewing insects generally tended to increase from dry to wet seasons while sucking insects were more abundant in the dry seasons. All arthropod groups, except Homoptera, showed the least abundance in the exceptionally dry season of 1999 (dry season 1) with no rainfall recorded in June and July. Decline in emergence of *Alnus* leaves in the dry season (Nyeko 2001) may have, in turn, initiated declines in most arthropod abundance (Fensham 1994). However, restricted periods of abundance may as well be dictated by advantages in predator avoidance and enhancement of mating success (Denlinger 1980).

The greater abundance of Homoptera in the dry seasons is contrary to the findings of Wolda (1978), but concurs with Fensham (1994) who reported an increase in Hemiptera in early dry season, after depressed abundance in the wet season. Possibly the Homoptera migrated from other host plants that became unsuitable or dried up during the dry season. This is particularly true for pests of seasonal crops and weeds that are capable of colonizing alternative hosts in the absence of the main host plant. An example in this study was *Aphis fabae* observed on beans and *Alnus*. Migration into suitable environments offers a viable strategy for maintaining a continuous active population, but seasonal occurrence of a species in a particular area also could be achieved by coordinating periods of dormancy and development with appropriate environmental signals (Denlinger 1980).

In conclusion, higher populations of arthropods occurred on mature *Alnus* stands than on saplings although the latter had a higher ratio of sap-sucking/chewing insects. Dominant and potentially serious pests of *Alnus* included *Apion globulipenne*, an unidentified Chrysomelidae (Coleopt. 27), *Phymateus viridipes*, *Coloborrtics corticina* and a *Cacopsylla* species (Homoptera: Psyllidae). There is an urgent need to quantify the impact of the potential pests on *Alnus* species in order to obtain cost/benefit analyses of possible control strategies. Spiders and Hymenoptera were the dominant natural enemies, which are potentially important in regulating pest populations on *Alnus*.

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