## INFLUENCE OF *PHYTOLYMA LATA* (HOMOPTERA: PSYLLIDAE) ON SEEDLING GROWTH OF *MILICIA EXCELSA*

<sup>1</sup>V. K. Agyeman, <sup>1</sup>D. A. Ofori, <sup>1</sup>J. R. Cobbinah and <sup>2</sup>M. R. Wagner

<sup>1</sup> Forestry Research Institute of Ghana, Council for Scientific and Industrial Research KNUST P. O. Box 63, Kumasi, Ghana
<sup>2</sup> School of Forestry, Northern Arizona University, Flagstaff, AZ 86011

#### ABSTRACT

Milicia excelsa (Iroko) is a valuable timber species occurring naturally in the humid forests of Africa. The high quality and great demand of wood obtained from M. excelsa has resulted in its overexploitation. Attempts at establishing large scale plantations to ensure sustained production have been hampered by the gall forming psyllid **Phytolyma lata**. In spite of the economic importance of **P. lata** little research has been conducted on the impact of the psyllid on the establishment of M. excelsa plantations. The effect of **P.** lata on growth, dry matter accumulation and allocation of **M. excelsa** seedlings is assessed in this study. Seedling growth in infested plots was significantly reduced. Plants infested had lower height, stem diameter and biomass growth. Mean yield losses of stem, branches, and leaves of infested plants were 68.9%, 48.3% and 64% respectively of matched uninfested plants. Infested plants also had smaller, fewer and highly chlorotic leaves. There were no significant differences (P > 0.05) in yield, specific leaf area, leaf area ratio and leaf weight ratio of plants growing in the open screen house and open plot without screening (infested plots) even though irradiance incident in the open screen house was 70% of that in the open plot without screening. It is concluded that **P. lata** infestation has significant effect on growth and biomass accumulation in the early development of Iroko and that such information would improve integrated pest management (IPM) programme for P. lata. Secondly, biomass allocation of M. excelsa seedlings is not significantly different probably at irradiances greater than 70% ambient full sun.

Keywords: Milicia excelsa, Phytolyma lata, seedling growth, pest infestation, biomass

#### **INTRODUCTION**

The Iroko gall fly, *Phytolyma lata* is the most important limiting factor to the establishment of Iroko plantations (Cobbinah and Wagner, 1992;

Cobbinah and Appiah-Kwarteng, 1996). *P. lata* attacks buds and young leaves of *Milicia excelsa* 

plants resulting in the formation of galls which burst to release adults after 3-4 weeks. The mechanism of gall formation is quite complex. *P. lata* lays eggs

*Ghana J. Forestry*, Vol. 25, 2009 28

in large numbers on young stems, leaves and shoots of the host tree (Nichols *et al.*, 1997). First-

instar nymphs, hatching at eight days, puncture plant surfaces and induce gall formation. The galls continue to increase in size even when the insect appears to have been killed by the application of systemic insecticide after the initiation of gall formation (White, 1968). This indicates that the nymph triggers growth that does not cease immediately on the death of *P. lata.* This is probably because the growth mechanism of galls is not related to viral or fungal attack but rather to a toxicogenic effect (White, 1968). Generally, gall formation is followed by saprophytic fungi attack on the apical region of the infested plant leading to dieback.

Earlier studies have concentrated on the biology, ecology and the epidemiology of P. lata (White, 1968; Orr and Osei-Nkrumah, 1978; Cobbinah, 1986; 1990). In recent years, efforts have focused on natural regeneration (Nichols et al., 1997) and progeny evaluation for resistant lines (Cobbinah and Wagner, 1995) of M. excelsa. Numerous studies have been conducted on the impact of insect injury on the yield of agricultural crops, but few studies have addressed the effect of pest infestation on the growth and yield of forest tree species. Quantification of plant response to insect injury is critical to the development of decision rules and pest management strategies. The study reported here was conducted to study the effect of P. lata induced injury during Iroko early development on dry matter accumulation and partitioning.

## MATERIALS AND METHODS

#### **Experimental Site and Screen Houses**

Field trials were conducted in 1995 at the Forestry Research Institute of Ghana's central nursery at Mesewam in the Moist Semi-deciduous Forest Type. The rainfall pattern at the site is bimodal with mean annual rainfall ranging between 1250 and 1500 mm. Two walk-in screen houses supported by wooden framework and enclosed by mosquito netting were constructed to preclude P. lata from attacking M. excelsa seedlings. The size of each screen house was 20 m long, 6 m wide and 3 m high. The screen houses had incident irradiance of 70% ambient full sun. Ceptometers were used in measuring irradiance in the screen houses. The shading effect of the screen houses was also monitored because Wagner et al. (1996) have shown positive influence of shading on early development and growth of M. excelsa seedlings.

## **Experimental Design**

Seventy-five *M. excelsa* seedlings (5 rows x 15 plants per row) spaced 1 m apart were planted in each of the two screen houses and on the open plot in between the two screen houses. All seedlings used were raised from one half-sib family (AA 24) because of small inherent growth differences within half-sib families (Cobbinah and Wagner, 1995). Seedlings were transplanted at the two leaf stage into polythene bags and conditioned under shade (irradiance 20% ambient full sun) for 8 weeks before planting. Seedlings were selected for uniform growth stage and size before planting.

Three treatments were used, namely; screen house with door always closed (SHC), screen house with

door always open (SHO) and plot without a screen house (NSH) to serve as a second control. The open screen house allowed pest entry and infestation in order to test whether shading resulting from screening had an effect on extent of pest infestation and subsequent growth of seedlings. Natural infestation of exposed plots was from a 3 year old Iroko stand situated about 30 m away from the trial plot.

## **Growth Measurements**

The influence of P. lata infestation on M. excelsa development and biomass accumulation and partitioning was examined by measuring seedling height (height from base of plant to the tip of shoot), stem diameter (at 10 cm from soil level) and number of leaves of five randomly chosen plants in each of the three plots. The area of four leaves from each of the 15 plants chosen for all the plots was determined by measuring the length and width of individual leaves. Leaf area estimates of 20 leaves using the length and width method were cross-checked by drawing the leaves on a graph sheet and counting the number of squares. A regression equation between the two area methods was determined using SYSTAT V.5. The best fit equation was as follows:  $Area_1 = 8.466 + 0.676 Area_2$ 

Where  $Area_2 = Area$  derived from length and width. Area<sub>1</sub> = Area determined using graph sheets.

Subsequent estimates of leaf area using the length and breadth method were made by application of the equation. Seedling height and stem diameter were measured using a metre rule and vernier calipers respectively.

Biomass measurements were determined when the first plant hit the roof of the screen house (about 18 months after planting). Fifteen plants were randomly chosen from each of the three treatment plots for the determination of biomass accumulation and partitioning. Plants were severed at the soil line and separated into leaves, branches and stems. Fresh weight of the different plant parts were recorded in the field using a battery operated Ohaus balance. Thereafter each plant part was placed within individual drying bags and labelled according to treatment. The drying bags carrying the different plant parts were oven dried at 75°C for 48 hours and reweighed.

Leaf area ratio (LAR), specific leaf area (SLA) and leaf weight ratio (LWR) were derived from oven dry weights of leaves, branches and stem (above-ground assessment). Instantaneous measures of LAR, SLA and LWR using the formulae in Hunt (1990) were used. The relationships were

$$\label{eq:LAR} \begin{split} LAR &= L_A \! / W \\ SLA &= L_A \! / L_W \quad \text{and} \qquad LWR \\ &= L_W \! / W \end{split}$$

where:

Yield loss was estimated as the difference in weight between plants growing on infested and control plots. Moisture content (%) was determined using the formula in Beadle *et al.* (1993).

 $MC = ((W_f - W_d) / W_d) \times 100\%$ 

where:

 $W_f =$  Fresh weight at time of sampling

 $W_d$  = Oven dry weight The number galls on infested plants in all the three plots were recorded at monthly intervals in-situ.

#### **Statistical Analysis**

Regression analysis was conducted to determine the relationship between gall numbers and plant yield. Analysis of variance (ANOVA) and Tukey's HSD test were done to determine whether seedling growth varied significantly between the various treatments. Pairwise comparison was done using least significant difference (LSD). Analyses were done using SYSTAT V5 statistical software (SYSTAT, 1990). Alpha for rejection of the null hypothesis was set at  $\alpha$ =0.05.

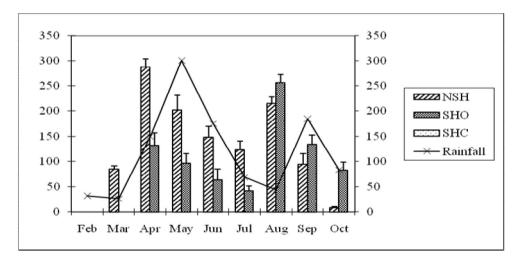


Figure 1: The relationship between rainfall (mm) and mean monthly number of *Phytolyma lata* induced galls in the unscreened plot (NSH), opened screen house (SHO) and closed screen house (SHC). There was zero galling for SHC.

*Ghana J. Forestry*, Vol. 25, 2009 31

Generally, foliage production was higher in the rainy season than the dry season.

## RESULTS AND DISCUSSION RESULTS Pest Infestation

*Phytolyma lata* density in the infested plots was highest in the months preceding the major (April) and minor (August) rainy seasons (Figure 1). Gall density was low during the peak of the rainy and dry seasons. However, generally there is a decline in gall numbers from the rainy to the dry season. Based on years of field observation we concluded that the pattern of Insect activity is consistent with the trend of gall density on *Milicia excelsa*.

Height growth of *M. excelsa* seedlings growing in protected (SHC) and unprotected (NSH and SHO)

plots was similar in the dry season i.e. February to April (Figure 2). However, seedling height growth was higher in the protected compared to unprotected plots in the wet season (Figure 2). This suggests that the influence of pest activity on seedling growth is reduced during the dry season.

The trend of foliage production resulting from pest infestation was similar to that of height growth. Production of leaves was similar for plants growing in the protected and unprotected environments during the dry season (Figure 3). However, leaf production was higher in the protected compared to unprotected environments during the rainy season. Influence of *Phytolyma lata* on seedling growth of *Milicia excelsa al.* 

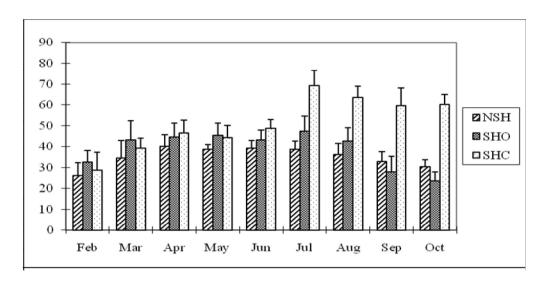
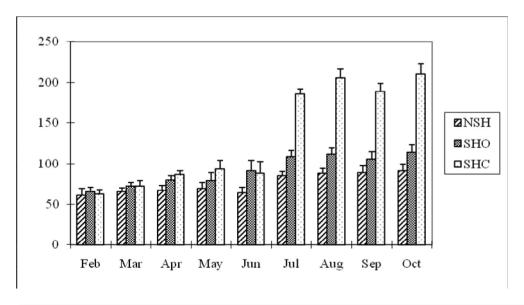


Figure 2: Mean seedling height (cm) of *Milicia excelsa* following pest infestation at different periods of the year.



*Ghana J. Forestry*, Vol. 25, 2009 32

Figure 3: Foliage production (number of leaves) of *Milicia excelsa* seedlings following infestation at different periods of the year.

Table 1: Mean number of leaves, leaf area  $(cm^2)$ , stem diameter (cm) and height (cm) of *M. excels* seedlings after 18 months growth in unprotected plot (NSH), open screen house (SHO) and closed screen house (SHC) following *P. lata* infestation.

Treatment	Mean Number of Leaves	Mean Leaf Area (cm <sup>2</sup> )	Mean Stem Diameter (cm)	Mean Height (cm)
NSH	$35.8^{a} \pm 4.6$	$147.0^{a} \pm 5.2$	$1.53^{a} \pm 0.12$	$98.4^{a} \pm 6.09$
SHO	$34.0^{a} \pm 5.4$	$174.0^{b} \pm 9.1$	$1.33^{a} \pm 0.13$	$100.9^{a} \pm 7.0$
SHC	$57.6^{b} \pm 9.8$	$253.9^{\circ} \pm 8.3$	$2.06^{b} \pm 0.18$	$208.7^{b} \pm 11.1$

Values with the same letter in a column are not significantly different at P=0.05

#### Height, Stem Diameter and Biomass Accumulation

Mean height of plants growing in the screen house with closed door (SHC) protected from *Phytolyma lata* infestation was about twice that of seedlings growing in the screen house with door open and in the plot without a screen house (Table 1). Tukey's HSD test indicates that height growth in SHC was significantly higher than that in SHO and NSH. There were however no significant differences in height between plants growing in SHO and NSH (Table 1). Mean stem diameter of plants growing in SHC was also significantly higher than those in SHO and NSH (Table 1).

Mean leaf area of plants growing in SHO and NSH were significantly lower ( $p \le 0.05$ ) than those growing in SHC (Table 1). However, there was no significant difference between mean leaf area of plants growing in SHO and NSH.

Differences in all the 3 component parts of the total dry biomass (leaves, branches, stem) of the infested and uninfested plots were significant (Table 2). The cumulative effect of these was a significant reduction in yield in the infested plots. Dry biomass yield loss of plants growing in NSH and SHO were 65.9% and 64.9% respectively when compared to SHC after 18 months growth (Table 3). Biomass allocation to leaves, branches and stem was however not different among treatments (P > 0.93).

Table 2: Mean and total dry matter production (leaves, branches and stem) of *M. excelsa* seedlings after 18 months growth in unprotected plot (NSH), open screen house (SHO) and closed screen house (SHC) following *P. lata* infestation.

Mean Dry Matter (g)						
Treatment	Leaves	Branches	Stem	Total Biomass (g)		
NSH	$17.3^{a} \pm 3.0$	$7.3^{a} \pm 1.6$	$39.87^{a} \pm 6.1$	66.43 <sup>a</sup>		
SHO	$25.3^{\rm a}\pm5.3$	$16.4^{\rm b}\pm4.6$	$43.0^{a} \pm 8.2$	84.73 <sup>a</sup>		
SHC	$59.3^{b} \pm 10.2$	$22.9^{c} \pm 6.0$	$133.6^{b} \pm 24.6$	215.85 <sup>b</sup>		

Values with the same letter in a column are not significantly different at P=0.05

Table 3: Percent mean loss of some plant morphometric variables of *M. excelsa* seedlings after 18 months

growth in unscreened plot (NSH) and open screen house (SHO) compared with the closed screen house (SHC)

	Percent (%) Mean Loss		
Variable	NSH	SHO	
Height (cm)	50.97	49.72	
Stem Diameter (cm)	30.73	35.43	

Influence of *Phytolyma lata* on seedling growth of *Milicia excelsa al.* 

Foliage	37.84	4.97	
Leaf Area (cm <sup>2</sup> )	68.49	69.21	
Dry Biomass (g)	65.93	64.97	

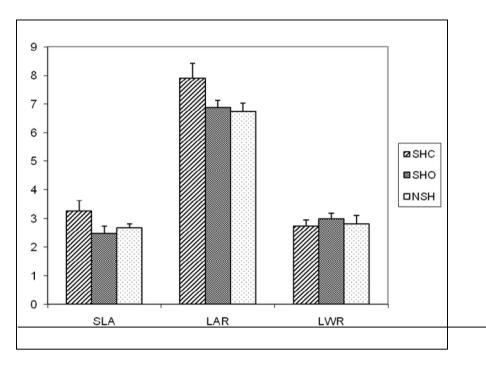


Figure 4: Specific leaf area (SLA( $10^{-1} \text{ m}^2 \text{ kg}^{-1}$ )), leaf area ratio (LAR( $m^2 \text{ kg}^{-1}$ )) and leaf weight ratio (LWR( $10^{-1} \text{ g} \text{ g}^{-1}$ )) of *Milicia excelsa* seedlings growing in the unscreened plot (NSH), open screen house (SHO) and closed screen house SHC).

*Ghana J. Forestry, Vol. 25, 2009* 36

## Leaf Area Ratio, Specific Leaf Area and Leaf Weight Ratio

Leaf area ratio (LAR), which is a morphological index of the leafiness of the plant, was significantly higher in SHC compared to SHO and NSH (Figure 4). This indicates that plants growing in the protected environment invests more in leaf area (photosynthetic component) relative to total dry biomass (respiratory burden) compared to those growing in unprotected environments. This may probably explain why relative growth rate of plants was higher in SHC compared to the others.

Specific leaf area (SLA) which is defined as the amount of leaf area per unit leaf weight was also significantly higher in SHC than SHO and NSH (Figure 4). The relatively low SLA of infested plants may be due to physical and chemical changes in leaf structure resulting from accumulation of secondary defence compounds. Leaf weight ratio (LWR), which is an index of the leafiness of the plant on a dry weight basis, was however, not significantly different among treatments (Figure 4).

## DISCUSSION

# Effect of Pest Infestation on Seedling Growth and Yield

*Phytolyma lata* infestation was first recorded in NSH about 2 months after transferring the seedlings into the experimental plots. All the seedlings growing in NSH were attacked three months after the first recorded infestation of seedlings in the plot. After all the seedlings in NSH were attacked, *P. lata* infestation shifted onto seedlings in SHO probably

because of the relatively better physiological state of the leaves in this plot compared to that of NSH.

*P. lata* infestation was greatest during the rainy season. The level of infestation declined progressively after August reaching its lowest level in October. This pattern of increase in the pest population from the raining season towards the dry season and subsequent decline at the outset of the dry season is typical of the population dynamics of *P. lata* (Cobbinah, 1986). Reduced activity of *P. lata* during the dry season can be attributed to leaf morphological changes and reduced availability of leaf substrate.

Generally, no linear relationship was found between pest density and growth parameters (height, number of leaves, stem diameter and total biomass). This is in part explained by the fact that the greatest effect on Iroko growth is the damage by the saprophytic fungi responsible for dieback (Cobbinah, 1990, Karadzic and Milijasevic, 2008). Whilst initial innoculum may be influenced by intensity of attack or pest density, subsequent growth of the pathogen may be influenced by environmental factors such as humidity, rainfall, temperature as well as plant vigour. Generally, the period of attack is a more relevant factor than psyllid intensity where seedling growth is concerned. It may therefore be important to protect Milicia excelsa from pest activity during periods when conditions for growth of saprophytic fungi are optimal. The lower relative growth rate of infested plants may be due to the high costs associated with the accumulation of anti-herbivore compounds (c.f. Lambers and Poorter, 1992). Generally, the photosynthetic return per unit weight of a well protected leaf is less than that of a leaf which allocates less carbon to quantitative defence compounds (Lambers and Poorter, 1992, Durand and Goldstein, 2001).

The results show that about 60 to 65% of the net photosynthate was channelled into the stem. This greater partitioning of the photosynthate to stem formation underscores the importance of Iroko for timber production. Stem growth is usually related to foliage quality and quantity. Feeding by *P. lata* removes plant nutrients (Cobbinah, 1986). Such losses would lower foliage quality and affect stem growth. This contributed to the significant loss in total biomass accumulation in the infested plots. The significant variation in the number of leaves of the two infested plots may be a manifestation of the extent to which the pest influences the physiological processes of *M. excelsa*.

## Effect of Pest Infestation on Leaf Morphology and Biomass Allocation

Earlier infestation of the unscreened plot accelerated the senescence process resulting in early yellowing and shedding of leaves. Chlorosis of leaves reduce the photosynthetic area leading to a drastic reduction of carbohydrate synthesis resulting in poor growth. However, the similarities in the growth parameters of the two infested plots (NSH and SHO) despite early yellowing and shedding of leaves in the unscreened plot (NSH) shows that yellowing of leaves alone is not the primary cause of seedling growth reduction. Other factors influencing seedling growth in infested plants include die-back due to fungal attack, formation of secondary defence chemicals and development of morphological defence structures against pest infestation

Plants growing in the protected plot had more leaves and higher leaf area ratios compared to the unprotected environment. Generally, under optimum conditions, a high investment in leaves (i.e. a high leaf area ratio) leads to greater competitive ability. The higher leaf area ratio of plants growing in the protected environment may probably be linked to their higher relative growth rate. This is probably because leaf area ratio is the predominant factor explaining inherent variation in relative growth rate (Poorter, 1989).

Infested plants also had relatively low specific leaf area (thicker leaves). Low specific leaf area may probably be attributed to the lower carbohydrate and a higher lignin content of infested leaves of M. excelsa (Djabletey, 1994). Plants under stress and pest infested plants tend to invest relatively more in compounds such as tannins and lignin which reduce the palatability of the leaves (Coley, 1986). Leaves of infested plants of M. excelsa were slightly thicker and coarser than that of uninfested plants. Pest infestation is relatively reduced by leaf toughness or coarseness (Grubb, 1986) and can be the primary mechanism responsible for differential susceptibility of trees to insects in the field (Wagner and Zhang, 1993). The coarse nature of the leaves may be due to the presence of more support tissue. According to Baruch et al. (1985) the presence of more support tissue usually results in lower specific leaf area and relative growth rate. Generally, changes in specific leaf area of plants growing under different conditions are influenced by the anatomy (Lambers and Poorter, 1992), morphology (Young and Smith,

1980) or chemical composition (Waring *et al.*, 1985; Rufty *et al.*, 1988) of leaves.

Leaf weight ratio which is a measure of the protective investment of the plant (Hunt, 1990) was not significantly different between infested and uninfested plants. Seedling growth between infested and unifested plants of *M. excelsa* was not related to LWR probably because current information shows that leaf weight ratio is less important than LAR and SLA in explaining inherent variation in relative growth rate (Lambers and Poorter, 1992).

# Effect of Different Irradiances on Yield and Pest Infestation

The differences in yield (above ground biomass), leaf area ratio, specific leaf area and leaf weight ratio of the two infested plots (SHO, NSH) was not significant even though irradiance incident in the open screen house was 70% of that of the unprotected plot. The similarities in values of the infested plots suggest that the differences in irradiance reaching plants in these plots did not influence growth rates. Agyeman (1994) also observed that whereas optimum growth of *Milicia excelsa* occurred at 42% ambient full sun there was no significant difference in relative growth rates of *M. excelsa* in high irradiance (greater than 60%).

Generally, plants growing in high irradiance increase their allocation to leaves leading to more photosynthate being invested in the energy capture system (Ledig and Perry, 1969) resulting in higher relative growth rate. However, it is evident from this study that biomass allocation in plants may not be significantly different above a certain threshold (probably greater than 70% ambient full sun). This is probably because light is not a limiting factor under conditions of high irradiance.

#### REFERENCES

Agyeman, V. K. (1994) Environmental influences on tropical tree seedling growth. PhD. Thesis. University of Aberdeen.

**Baruch, Z., Ludlow, M. M. and Davis, R.** (1985) Photosynthetic responses of native and introduced  $C_4$  grasses from Venezuelan savannas. *Oecologia* 67:388-393.

**Beadle, C. L., Ludlow, M. M. and Honeysett, J. L.** (1993) Water relations. *In: Photosynthesis and production in a changing environment: A field and laboratory manual.* 

Hall, D. O., Scurlock, J. M. O., Bolhar-Nordenkampf, H. R., Leegood, R. C. and Long, S. P. (eds.) pp. 113-128. Chapman and Hall.

**Cobbinah J. R.** (1986) Factors affecting the distribution and abundance of *Phytolyma lata* (Homoptera: Psyllidae). *Insect Science and Application* 7:111-115.

**Cobbinah J. R.** (1990) The biology, seasonal activity and control of *Phytolyma lata* (Homoptera: Psyllidae), pp. 180-185. *In*: Hutacharern, C., MacDicken, K.G., Ivory M.H. and Nair, K.S.S. (eds). *Proceedings IUFRO Workshop. Pests and Diseases of forest Plantation*. RAPA Publication 1990. FAO, Bangkok.

**Cobbinah J. R. and Wagner M. R.** (1995) Phenotypic variation in *Milicia excelsa* to attack by *Phytolyma lata* (Psyllidae). *Forest Ecology Management* 75: 147-153.

**Cobbinah, J. R. and Appiah-Kwarteng, J.** (1996) The impact of *Phytolyma lata* injury on growth and biomass accumulation of Iroko (*Milicia excelsa*). *Proceedings XX International Congress of Entomology*, Firenze, Italy, August 25-31, 1996.

**Cobbinah, J. R. and Wagner M. R.** (1992) Population dynamics of a gall forming psyllid on the tropical timber tree species, *Milicia excelsa*. *Proceedings XIX International Congress of Entomology*, Beijing, China. pp 428.

**Coley, P. D.** (1986) Costs and benefits of defense by tannins in a neotropical tree. *Oecologia* 70:238-241.

**Djabletey, G. D.** (1994) Comparative leaf anatomy of resistance and susceptible leaves of Milicia spp. to Phytolyma lata. B.Sc Dissertation, Institute of Renewable Natural Resources, University of Science and Technology.

**Durand, L. Z. and Goldstein, G.** (2001) Growth, leaf characteristics and spore production in native and invasive tree ferns in Hawaii. *American Fern Journal 91 (1): 25-35.* 

**Grubb, P. J.** (1986) Sclerophylls, pachyphylls and pycnophylls: The nature and significance of hard leaf surfaces. In: *Insects and Plant Surface* Juniper, B. and Southwood, R. (eds.). pp. 137-150. Edward Arnold, London. Hunt, R. (1990) Basic growth analysis. Unwin Hyman, London.

**Karadzic, D. and Milijasevic, T.** (2008) The most important parasitic and saprophytic fungi in Austrian Pine and Scots Pine plantations in Serbia. *Bulletin of the Faculty of Forestry 97: 147-170* 

Lambers, H. and Poorter, H. (1992) Inherent variation in growth rate between higher plants. A search for physiological causes and ecological consequences. <u>In</u>: *Advances in Ecological Research* 23. Begon, M. and Fitter, A.H (eds.). pp 187-261.

**Ledig, F. T. and Perry, T. O.** (1969) Net assimilation rate and growth in Loblolly Pine seedlings. *Forest Science* 15:431-438.

Nichols, J. D., Wagner, M. R., Agyeman, V. K., Bosu, P. and Cobbinah, J. R. (1997) Influence of artificial gaps in tropical forests on survival, growth and *Phytolyma lata* attack on *Milicia excelsa. Forest Ecology and Management* (in review).

**Orr, R. L. and Osei-Nkrumah, A.** (1978) Progress report on *Phytolyma lata* Homoptera: Psyllidae. Forest Products Research Institute, Kumasi, Ghana.

**Poorter, H.** (1989) Interspecific variation in relative growth rate: On ecological causes and physiological consequences. <u>In</u>: *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants.* Lambers, H.,

Cambridge, M. L., Konings, H. and Pons, T. L. (eds.). pp 45-68. SPB Academic Publishing, The Hague.

**Rufty, T. W., Huber, S. C. and Volk, R. J.** (1988) Alterations in leaf carbohydrate metabolism in response to nitrogen stress. *Plant Physiology* 88:725-730.

**SYSTAT** (1990) *SYSTAT: The System for Statistics*. Evanston, I.L. SYSTAT, Inc.

Wagner, M. R., Atuahene, S. K. N. and Cobbinah, J. R. (1991) Forest Entomology in West Tropical Africa: Forest Insects of Ghana. Kluwer, Dordrecht, 210 pp.

Wagner, M. R. and Zhang, Z. Y. (1993) Host plant traits associated with resistance of ponderosa pine to the sawfly *Neodiprion fulviceps. Canadian Journal of Forest Research* 23(5):839-845.

Wagner, M. R., Cobbinah, J. R. and Ofori, D. A. (1996) Companion planting of the nitrogen fixing *Gliricidia sepium* with the tropical timber species *Milicia excelsa* and its impact on the gallforming insect *Phytolyma lata*. Pp 264-271. *In: Dynamics of Forest Herbivory: Quest for Pattern and Principle*. Mattson, W.J., Niemela, P. And Rousi, M. (Eds.). USDA Forest Service General Technical Report. NC-183. North Central Forest Experiment Station, St. Paul, MN. 286 pp.

Waring, R. H., McDonald, A. J. S., Larsson, S., Ericsson, T., Wiren, A. and Arwidsson, E. (1985) Differences in chemical composition of plants grown at constant relative growth rates with stable mineral nutrition. *Oecologia* 66:157-160.

White M. G. (1968) Research in Nigeria on the Iroko gall bug (*Phytolyma* spp.) *Nigerian Forestry Information Bulletin* (New Series) No. 18, 72pp.

Young, D. R. and Smith, W. K. (1980) Influence of sunlight on photosynthesis, water relations and leaf structure in the understorey species *Arnica cordifolia*. *Ecology* 61: 1380-1390.