

**MANUSCRIPT 3**

**Allometry in Quackgrass (Elytrigia repens)  
Infesting Spring Wheat (Triticum aestivum)**

**Abstract.** Growth of natural infestations of quackgrass in spring wheat fields was monitored during the 1988 and 1989 growing seasons at six locations in southern Manitoba. At each site quackgrass was systematically sampled at 30, 60 and 93 days after planting (DAP<sup>8</sup>) to wheat. Rhizome bud weight, rhizome bud length and rhizome to shoot ratio 93 DAP were not significantly correlated with the corresponding variable values at 30 and 60 DAP. Allometric relationships between selected vegetative variables and reproductive variables were determined for each sampling date. Correlation coefficients for the strength of the allometric relationships generally increased with sampling time and varied significantly from harvest to harvest. For any specific vegetative variable, allometric relationships with rhizome variables were usually stronger than those with head variables. Linking the allometric models with a wheat yield-loss model was determined to give accurate estimates when compared to data from the pooled dynamic stratified random sampling design used to develop the models. The allometric relationships from this design differed significantly from those from an independently collected dataset, thereby indicating that such models are not "universally" applicable.

---

<sup>8</sup>Abbreviations: DAP, days after planting; Variate abbreviations are listed in Table 15.

Nomenclature: Quackgrass, Elytrigia repens L. Nevski #<sup>9</sup> AGGRE; wheat, Triticum aestivum L. 'Katepwa';

Additional index words. Agropyron repens L. Beauv., growth, competition, modelling, AGGRE, survey.

## INTRODUCTION

Weed scientists want to determine the relation between crop yield and weed infestation easily, accurately, and with a minimum of observations. Although both crop yield loss and weed population dynamics are important components in any assessment of the long-term impact of a weed, most crop yield-loss models do not include corresponding weed growth/population models. If practical application of yield loss models to assessment of long-term weed impact is desired then more sophisticated approaches will be required.

One approach is to link simple yield-loss models with weed population dynamics through regression and allometry. Allometry refers to the growth relationship that exists among the different parts of an organism. Although many mathematical expressions could be used the most common model for describing an allometric relationship is the simple empirical power function provided by Pearsall (1927):

---

<sup>9</sup>Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Weed Sci. 32, Suppl. 2. Available from WSSA, 309 West Clark Street, Champaign, IL 61820.

$$\Theta_i = \beta \Theta_p^\alpha.$$

The allometric coefficient,  $\beta$ , is the value of  $\Theta_i$  when  $\Theta_p = 1.0$  and is a scalar parameter.

The allometric exponent,  $\alpha$ , is a measure of the relative growth rates of  $\Theta_i$  and  $\Theta_p$  (Whitehead and Myerscough, 1962). Although originally developed to relate growth of a part to the whole, the equation is commonly applied to relate the growth between various parts of an organism. Huxley (1932) has even suggested that this allometric equation is a true biological law for relating growth of parts of an organism.

The allometric relationship is usually utilized in its  $\ln$ -transformed form:

$$\ln(\Theta_i) = \ln(\beta) + \alpha \ln(\Theta_p) (+ \ln(\epsilon)).$$

The term  $\ln(\epsilon)$  is added to account for residual variation not accounted for through allometry itself. The error parameter is usually ignored but should not be forgotten as its presence can limit the utilization of this allometric equation. Even though the methodology involved in determining allometric relations is relatively standardized, the interpretation of results requires certain precautions (Niklas, 1994; Seim and Saether, 1983; Smith, 1980) and can be aided using techniques which attribute part of the residual variation to treatment effects (Jolliffe *et al.*, 1983). An excellent overview of plant allometry is presented in the text of Niklas (1994).

The growth of quackgrass, both in crop and in isolation, has been extensively analyzed. However, only a few studies have provided any information on the allometric relationship between quackgrass variables (Cussans and Wilson, 1975; Neuteboom, 1975; 1980; Reekie and Bazzaz, 1987a; 1987b; 1987c; Rioux, 1982). Neuteboom (1975) listed correlations as

determined from earlier sampling.

## MATERIALS AND METHODS

### Survey Data

In south central Manitoba, six commercial fields of spring wheat (cv. Katepwa) infested with quackgrass were surveyed using a dynamic stratified random sampling design. Of the six fields, four were surveyed in 1988 and two in 1989. Sites were sampled three times throughout the growing season using 0.25 m<sup>2</sup> quadrats. The three sampling times were approximately 30, 60 and 93 days after planting (DAP). Details of the sites and sampling techniques are presented elsewhere (Manuscript 2).

For the purposes of this paper the variables selected for discussion can be categorized as measures of vegetative size and dispersion and measures of reproductive effort and fecundity. The relative quackgrass ratio and culm number were categorized as indicators of vegetative plant dispersion. Height, shoot density, total density, and shoot dry matter were categorized as indicators of plant size. Rhizome length and head dry matter were categorized as measures of reproductive effort. Head number and rhizome bud number were considered measures of reproductive fecundity. Complete descriptions of the measured and derived variables and their abbreviations are listed in Table 16.

To assist in assessing the cross-site utility of the stratified random sampled results independent data was collected over 1987 to 1989. Areas of approximately 20 m<sup>2</sup> were

**Table 16. Description of quackgrass variable abbreviations.**

Abbreviation <sup>a</sup>	Description	Units
$Bl_i$	rhizome bud length ( $R_{li} / R_{Bi}$ ) x 100	cm bud <sup>-1</sup>
$BW_i$	rhizome bud dry matter ( $R_{Wi} / R_{Bi}$ ) x 1000	mg bud <sup>-1</sup>
$H_i$	head number	# m <sup>-2</sup>
$H_{Wi}$	head dry matter	g m <sup>-2</sup>
$HR_i$	reproductive partitioning ( $H_{Wi} / R_{Wi}$ ) x 100	%
$l_i$	plant height (extended)	m
$R_{Bi}$	rhizome bud number	# m <sup>-2</sup>
$R_{li}$	cumulative rhizome length	m m <sup>-2</sup>
$R_{Wi}$	rhizome dry matter	g m <sup>-2</sup>
$RS_i$	rhizome to shoot ratio ( $R_{Wi} / (S_{Wi} + H_{Wi})$ )	unitless
$S_{Di}$	shoot density ( $(S_{Wi} + H_{Wi}) / l_i$ )	g m <sup>-3</sup>
$S_i$	shoot number	# m <sup>-2</sup>
$S_{Wi}$	shoot dry matter	g m <sup>-2</sup>
$S_{\%i}$	relative quackgrass ratio ( $S_i / (S_i + WS_i^b)$ )	unitless
$W_i$	total dry matter	g m <sup>-2</sup>
$W_{Di}$	total density ( $W_i / l_i$ )	g m <sup>-3</sup>
Others		
$\Theta$	any variable	varies
$\beta_k$	model parameter	varies

<sup>a</sup> The subscript "i" denotes harvest number. 1 ≈ 30 DAP, 2 ≈ 60 DAP, 3 at wheat harvest (≈ 93 DAP).

<sup>b</sup>  $WS_i$  is the wheat shoot number m<sup>-2</sup>

selected in each of six commercial fields of spring wheat (cv. Katepwa) soon after each emerged. Two fields were sampled in 1987, three fields in 1988, and one field in 1989. All fields were located in south central Manitoba. At wheat maturity these sites were sampled using approximately thirty 1 m<sup>2</sup> quadrats whose sampling positions were determined using baseline stratified random sampling (Knight, 1978). Further details of the sampling techniques have been reported elsewhere (Manuscript 2).

## **Model Development and Selection**

### **Auto-Regressions**

The results from each dynamic stratified random sampled survey were converted to a 1.0 m<sup>2</sup> basis and the results from each stratum pooled and averaged to simulate the type of data one would expect farm operators to collect. The surveys were pooled and linear regression<sup>10</sup> used to relate quackgrass variable values at the 30 or 60 DAP to the values at 93 DAP. In this manuscript these regressions are referred to as auto-regressions.

To facilitate comparisons between harvests and treatments, linear regression was used. Linear regressions were usually significant ( $P=0.05$ ), and any improvement of fit by quadratic or higher order relationships was frequently not significant.

The auto-regression models were of the form

$$\Theta_3 = \beta_0 + \beta_1 ( \Theta_i ).$$

---

<sup>10</sup> PROC REG, SAS V5., SAS Institute, Cary, NC.

Where  $\Theta_3$  is the predicted value of the variable at the third harvest and  $\Theta_i$  the variable values at harvests  $i = 1$  or  $2$ .  $\beta_0$  and  $\beta_1$  are the regression line intercept and slope, respectively. The comparative strengths of the regressions were determined using coefficients of determinations ( $R^2$ ) calculated as described by Kvalseth (1985). Individual models for each variable were compared to a pooled model to determine if the individual models were significantly different from one another according to a parameter invariance testing procedure (Ratkowsky, 1983).

### **Allometric Relationships**

The allometric models discussed in this manuscript are limited to allometry between vegetative components and reproductive components as these relationships were considered most important in terms of relating field measurements to long-term quackgrass population dynamics. Additionally, the relationship between a derived variable and any of its components was not determined because of the expected autocorrelation.

The allometric relations were developed using simple regression. It was felt that for the comparative and predictive purposes, for which this data would be used within this manuscript, that simple regression analysis would be satisfactory. However, for cross species or other confounded comparisons, particularly when there are weak allometric correlations, major axis analysis or reduced major axis analysis (Seim and Saether, 1983) would be a more appropriate form of analysis.

At each harvest an allometric model for each variable pair was determined using linear

regression on *ln*-transformed variable values. The relative strength of the derived allometric relationships was assessed by comparing the coefficients of determinations ( $R^2$ ) calculated as described by Kvalseth (1983). For an allometric model to be considered useful its  $R^2$  value had to be significant ( $P=0.05$ ). Individual models derived for each variable were compared to a pooled model to determine if the models were significantly different according to a parameter invariance testing procedure (Ratkowsky, 1983).

Cross utility of the models was evaluated by comparing the allometric relationships derived for variables at 93 DAP to similarly derived relationships from the baseline stratified random sampling surveys (validation survey). The independent models were compared to a pooled model using a parameter invariance testing procedure (Ratkowsky, 1983). If the models were significantly ( $P=0.05$ ) different then the allometric relationships were considered to not have cross-utility.

## RESULTS AND DISCUSSION

### Auto-Regressions

Linear regression relationships between quackgrass variable values at 30 and 60 days after planting (DAP) and variable values at wheat harvest (93 DAP) were determined for all variables listed in Table 16. Six of the variables had non-significant coefficients of determination ( $R^2$ ) values for one or more of the harvests. Using the 30 DAP data these

variables were  $l$ ,  $H_W$ ,  $B_W$ ,  $B_l$ ,  $RS$ , and  $HR$ , whereas using 60 DAP values these variables were  $B_W$ ,  $B_l$ , and  $RS$ . Values for  $B_W$ ,  $B_l$  and  $RS$  at 30 and 60 DAP were consistently independent of final harvest values, and were of no predictive value.

Except for  $B_W$ ,  $B_l$  and  $RS$ , the estimated parameter values and associated  $R^2$  values for the auto-regression relationships are listed in Table 17.

Except for  $HW_1$  and  $l_1$ , all models had significant  $R^2$  values. Significant  $R^2$  values ranged from 0.24 for  $H_1$  to 0.84 for  $W_2$ . Often, but not in every instance,  $R^2$  values for auto-regressions from 60 DAP were superior to auto-regressions from 30 DAP. Sixty DAP variable values are closer temporally to 93 DAP harvest values relative to 30 DAP values and would be expected to have stronger relationship to final values.

Sampling time was important in determining both the strength of fit and the model structure. The 30 DAP and 60 DAP auto-regressions differed significantly for every variable. There was always a significant difference in slope (parameter  $\beta_1$ ) and the slope for 60 DAP auto-regressions was usually less than 30 DAP auto-regressions. Intercepts (parameter  $\beta_0$ ) in the auto-regression models were often poorly estimated and as a result often did not differ significantly between sample dates.

### **Allometric Relationships**

The allometric relationships for determining reproductive variables at the 30, 60, and 93 DAP sample dates are presented in Tables 18, 19, and 20, respectively. Head production

**Table 17. Parameter estimates and associated R<sup>2</sup> values for selected temporal autoregressions for quackgrass variables in the pooled stratified random surveys.**

Variable <sup>b</sup>	Harvest <sup>c</sup>	Parameter <sup>a</sup>		R <sup>2</sup> <sup>d</sup>
		$\beta_0$	$\beta_1$	
<i>H</i>	1	7.052 (4.5289)	13.401 (2.5294)	0.36**
	2	2.109 (2.2624)	0.939 (0.0612)	0.83**
<i>H<sub>w</sub></i>	1	1.421 (0.7042)	22.695 (7.5648)	0.14 <sup>ns</sup>
	2	0.265 (0.2876)	1.294 (0.0794)	0.84**
<i>I</i>	1	0.150 (0.1020)	2.458 (0.6118)	0.24**
	2	0.122 (0.0489)	0.922 (0.0998)	0.63**
<i>R<sub>B</sub></i>	1	336.520 (97.2979)	1.656 (0.1490)	0.72**
	2	197.965 (112.7521)	1.209 (0.1226)	0.66**
<i>R<sub>I</sub></i>	1	10.384 (3.2375)	1.431 (0.1575)	0.63**
	2	3.667 (2.8440)	1.201 (0.0989)	0.75**
<i>R<sub>w</sub></i>	1	7.194 (4.2312)	1.565 (0.1509)	0.69**
	2	19.669 (4.9467)	1.624 (0.2715)	0.41**
<i>S</i>	1	6.227 (17.7374)	2.479 (0.1946)	0.77**
	2	3.129 (15.7047)	1.4952 (0.1040)	0.80**
<i>S<sub>D</sub></i>	1	9.000 (12.2819)	2.482 (0.1849)	0.79**
	2	5.198 (14.7751)	1.409 (0.1308)	0.70**
<i>S<sub>w</sub></i>	1	-7.207 (11.3599)	11.705 (0.9018)	0.77**
	2	-0.667 (10.5517)	2.032 (0.1529)	0.78**
<i>S<sub>%</sub></i>	1	0.051 (0.0168)	1.212 (0.0953)	0.77**
	2	0.021 (0.0187)	1.096 (0.0900)	0.75**
<i>W</i>	1	3.447 (19.2444)	4.556 (0.4889)	0.64**
	2	13.545 (11.0751)	2.040 (0.1239)	0.84**
<i>W<sub>D</sub></i>	1	28.508 (20.1612)	0.981 (0.0952)	0.69**
	2	23.975 (18.9844)	1.464 (0.1342)	0.70**

<sup>a</sup> From the regression model  $\Theta_3 = \beta_0 + \beta_1 (\Theta_i)$ . Standard errors for the parameter estimates are enclosed in brackets beside the estimate.

<sup>b</sup> Descriptions of variable abbreviations are found in Table 16.

<sup>c</sup> Harvest number: 1 = 30 DAP, 2 = 60 DAP, 3 at wheat harvest ( $\approx$  93 DAP).

<sup>d</sup> \*, \*\* and <sup>ns</sup> indicate significant at P=0.05, P=0.01, and not-significant, respectively.

was minimal at 30 DAP and consequently the strength, as indicated by the  $R^2$  value, of the allometric relationships for the dependent variables  $H_{W1}$  and  $H_1$  are relatively poor or not significant (Table 18). At later sample dates, the strength of the allometric relationships involving the dependent variables  $H_W$  and  $H$  increased as head production increased. However, even at 93 DAP, the strength of the allometric relationships involving the dependent head variables was comparatively weak relative to those involving rhizome variables. In contrast Neuteboom (1980) determined that the correlations from reproductive variables  $R_W$  and  $H$  regressed against  $S$  and  $S_W$  were of similar strengths. The contrasting results may be attributed to Neuteboom's relationships having been determined on plants grown in the absence of interference whereas quackgrass in this study was competing with wheat.

In general, the strength of the allometric relationships between vegetative and reproductive variables increased over time. The mean  $R^2$  values were 0.50, 0.58, and 0.73, at the 30, 60 and 93 DAP sample dates, respectively (Tables 18,19 and 20). The lower  $R^2$  value for the 30 and 60 DAP allometric relationships compared to 93 DAP relationships can be attributed to the smaller range in variable size of the two variables at earlier sample dates.

An increase in size will result in a change of form. For the quackgrass variables this was reflected in significantly different allometric relationships for every variable from one sample date to the next (Tables 18, 19 and 20). Differences in the allometric relationships were as much to do with parameter  $\alpha$  as parameter  $\beta$ .

In the allometric equation, parameter  $\beta$  is of little interest. As a scalar  $\beta$  lacks

**Table 18. Parameter estimates and associated  $R^2$  values for selected quackgrass allometric relationships at approximately 30 days after planting wheat.**

Variable <sup>a</sup>		Parameter <sup>b</sup>		
Indep.	Depend.	$\beta$	$\alpha$	$R^2$ <sup>c</sup>
----- <i>(ln)</i> -----				
I	$R_W$	6.481 (0.8738)	2.233 (0.4517)	0.34**
	$R_l$	5.867 (0.6886)	2.152 (0.3559)	0.43**
	$H_W$	1.216 (4.5051)	6.628 (2.3291)	0.13 $ns$
	$H$	4.827 (5.4874)	7.986 (2.8370)	0.13 $ns$
	$R_B$	9.134 (0.6677)	2.058 (0.3452)	0.42**
S	$R_W$	-0.447 (0.4537)	0.782 (0.1237)	0.45**
	$R_l$	-1.441 (0.1605)	0.936 (0.0438)	0.90**
	$H_W$	-22.135 (2.2376)	3.128 (0.6101)	0.35**
	$H$	-23.528 (2.7094)	3.833 (0.7387)	0.35**
	$R_B$	2.145 (0.1662)	0.895 (0.0453)	0.89**
$S_D$	$R_W$	-0.248 (0.4759)	0.770 (0.1379)	0.39**
	$R_l$	-1.151 (0.2563)	0.906 (0.0743)	0.76**
	$H$	2.442 (0.2581)	0.861 (0.0748)	0.73**
	$R_B$	-22.657 (2.7838)	3.809 (0.8068)	0.31**
$S_W$	$R_W$	1.281 (0.2104)	0.721 (0.1088)	0.47**
	$R_l$	0.696 (0.0891)	0.813 (0.0507)	0.84**
	$H_W$	-14.999 (1.0817)	2.720 (0.5589)	0.32**
	$H$	-23.528 (2.7093)	3.833 (0.7387)	0.35**
	$R_B$	4.194 (0.1010)	0.774 (0.0522)	0.82**
$S_{\%}$	$R_W$	4.375 (0.3595)	0.760 (0.1163)	0.47**
	$R_l$	4.260 (0.1422)	0.884 (0.0460)	0.89**
	$H_W$	-3.287 (1.8357)	2.884 (0.5938)	0.32**
	$H$	-0.416 (2.2220)	3.539 (0.7188)	0.33**
	$R_B$	7.568 (0.1570)	0.835 (0.0508)	0.85**
W	$R_l$	-0.507 (0.2417)	0.847 (0.0814)	0.69**
	$H$	-20.262 (2.3494)	3.673 (0.7916)	0.30**
	$R_B$	3.079 (0.2466)	0.794 (0.0831)	0.65**
$W_D$	$R_l$	-2.491 (0.5482)	0.929 (0.1163)	0.57**
	$H$	-29.744 (4.5996)	4.218 (0.9757)	0.27**
	$R_B$	1.243 (0.5510)	0.866 (0.1169)	0.59**

<sup>a</sup> Descriptions of the variable abbreviations can be found in Table 16.

<sup>b</sup> From the allometric model  $\Theta_j = \beta \Theta_p^\alpha$ . Standard errors for the parameter estimates are enclosed in brackets beside the estimate.

<sup>c</sup> \*, \*\* and  $ns$  indicate significant at  $P=0.05$ ,  $P=0.01$ , and not-significant, respectively.

**Table 19. Parameter estimates and associated  $R^2$  values for selected quackgrass allometric relationships at approximately 60 days after planting wheat.**

Variable <sup>a</sup>		Parameter <sup>b</sup>		
Independ.	Depend.	$\beta$	$\alpha$	$R^2$ <sup>c</sup>
		-----( <i>ln</i> )-----		
I	$R_W$	2.266 (0.3058)	0.773 (0.2682)	0.13 $ns$
	$R_I$	3.866 (0.2457)	1.716 (0.2155)	0.57**
	$H_W$	3.289 (1.0706)	7.123 (0.9389)	0.54**
	$H$	6.232 (1.2367)	8.110 (1.0847)	0.53**
	$R_B$	7.206 (0.2318)	1.556 (0.2034)	0.55**
S	$R_W$	-0.896 (0.5041)	0.608 (0.1199)	0.34**
	$R_I$	-2.016 (0.2821)	1.066 (0.0672)	0.84**
	$H_W$	-18.380 (1.9633)	3.737 (0.4673)	0.57**
	$H$	-18.157 (2.3189)	4.184 (0.5519)	0.54**
	$R_B$	1.799 (0.2589)	0.985 (0.0616)	0.84**
$S_D$	$R_W$	-1.783 (0.5361)	0.842 (0.1313)	0.46**
	$R_I$	-2.666 (0.3776)	1.247 (0.0825)	0.79**
	$H$	1.131 (0.3260)	1.170 (0.0799)	0.82**
	$R_B$	-18.537 (3.1132)	4.347 (0.7628)	0.40**
$S_W$	$R_W$	-0.056 (0.3227)	0.535 (0.0964)	0.38**
	$R_I$	-0.428 (0.1708)	0.899 (0.0510)	0.87**
	$H_W$	-12.761 (1.2824)	3.137 (0.3833)	0.58**
	$H$	-11.827 (1.5238)	3.499 (0.4554)	0.55**
	$R_B$	3.258 (0.1529)	0.834 (0.0457)	0.87**
$S_{\%}$	$R_W$	2.898 (0.3362)	0.579 (0.1269)	0.29**
	$R_I$	4.840 (0.1691)	1.102 (0.0638)	0.86**
	$H_W$	5.288 (1.3145)	3.705 (0.4959)	0.53**
	$H$	8.384 (1.5395)	4.166 (0.5801)	0.51**
	$R_B$	8.112 (0.1637)	1.009 (0.0618)	0.85**
W	$R_I$	-1.388 (0.2663)	1.089 (0.0749)	0.81**
	$H$	-14.712 (2.2240)	3.985 (0.6251)	0.45**
	$R_B$	2.327 (0.2265)	1.022 (0.0637)	0.84**
$W_D$	$R_I$	-2.714 (0.7655)	1.160 (0.1750)	0.47**
	$H$	-15.322 (4.7398)	3.253 (1.0842)	0.14 $ns$
	$R_B$	0.957 (0.6762)	1.118 (0.1545)	0.52**

<sup>a</sup> Descriptions of the variable abbreviations can be found in Table 16.

<sup>b</sup> From the allometric model  $\Theta_j = \beta \Theta_p^\alpha$ . Standard errors for the parameter estimates are enclosed in brackets beside the estimate.

<sup>c</sup> \*, \*\* and  $ns$  indicate significant at  $P=0.05$ ,  $P=0.01$ , and not-significant, respectively.

**Table 20. Parameter estimates and associated  $R^2$  values for selected quackgrass allometric relationships at approximately 93 days after planting wheat (wheat harvest).**

Variable <sup>a</sup>		Parameter <sup>b</sup>		
Indep.	Depend.	$\beta$	$\alpha$	$R^2$ <sup>c</sup>
		-----( <i>b</i> )-----		
I	$R_W$	4.567 (0.1882)	2.258 (0.2064)	0.71**
	$R_I$	4.330 (0.1717)	2.399 (0.1884)	0.77**
	$H_W$	2.481 (1.1832)	8.299 (1.2981)	0.45**
	$H$	4.465 (1.4397)	9.131 (1.5795)	0.40**
	$R_B$	7.859 (0.1623)	2.369 (0.1780)	0.79**
S	$R_W$	-1.454 (0.3184)	1.006 (0.0704)	0.81**
	$R_I$	-2.084 (0.2569)	1.073 (0.0568)	0.88**
	$H_W$	-20.031 (2.2484)	3.789 (0.4977)	0.55**
	$H$	-20.583 (2.7408)	4.230 (0.6067)	0.50**
	$R_B$	1.458 (0.1985)	1.075 (0.0439)	0.93**
$S_D$	$R_W$	-2.149 (0.4658)	1.169 (0.1048)	0.72**
	$R_I$	-2.774 (0.4320)	1.235 (0.0972)	0.77**
	$H$	0.746 (0.3781)	1.242 (0.0851)	0.82**
	$R_B$	-25.651 (3.1700)	5.413 (0.7132)	0.54**
$S_W$	$R_W$	-0.202 (0.2356)	0.869 (0.0609)	0.81**
	$R_I$	-0.723 (0.2008)	0.920 (0.0519)	0.87**
	$H_W$	-15.915 (1.5531)	3.439 (0.4017)	0.60**
	$H$	-15.985 (1.9152)	3.843 (0.4953)	0.55**
	$R_B$	2.830 (0.1649)	0.920 (0.0426)	0.91**
$S_{96}$	$R_W$	5.414 (0.1666)	1.191 (0.0699)	0.86**
	$R_I$	5.211 (0.1322)	1.256 (0.0555)	0.91**
	$H_W$	5.489 (1.3752)	4.329 (0.5770)	0.54**
	$H$	7.731 (1.7069)	4.742 (0.7166)	0.47**
	$R_B$	8.733 (0.1123)	1.243 (0.0471)	0.94**
W	$R_I$	-1.405 (0.1474)	0.982 (0.0343)	0.94**
	$H$	-17.698 (2.2547)	3.821 (0.5250)	0.52**
	$R_B$	2.197 (0.1186)	0.969 (0.0276)	0.96**
$W_D$	$R_I$	-3.988 (0.3668)	1.137 (0.0751)	0.87**
	$H$	-28.062 (3.8205)	5.401 (0.7822)	0.50**
	$R_B$	-0.352 (0.3342)	1.354 (0.0684)	0.89**

<sup>a</sup> Descriptions of the variable abbreviations can be found in Table 16.

<sup>b</sup> From the allometric model  $\Theta_i = \beta \Theta_p^\alpha$ . Standard errors for the parameter estimates are enclosed in brackets beside the estimate.

<sup>c</sup> \*, \*\* and ns indicate significant at P=0.05, P=0.01, and not-significant, respectively.

biological significance and its accuracy is weak because it incorporates the measurement error ignored in the model determination.

Parameter  $\alpha$  is related to relative growth rates of  $\Theta_i$  in respect to  $\Theta_p$  ( $R\Theta_i/R\Theta_p$ ) (Whitehead and Myerscough, 1962). For all variables parameter  $\alpha$  differed significantly from sample date to sample date indicating change in relative growth rates during plant development (Tables 18,19 and 20). There was no *a priori* reason to suppose that the relative growth rates should remain proportional to one another. Similar variations in relative growth rate proportions in other species have been reported by others (Jolliffe *et al*, 1988; Stanhill, 1977a).

When  $\alpha=1$  the relative growth rates of the two variables are equal. Positive allometry is where  $\alpha>1$  and negative allometry is where  $\alpha<1$  (Richards, 1969). All three types of allometry were present and not all variables were consistent from sample date to sample date in any particular type. The lowest negative allometry  $\alpha$  value was 0.579 and occurred at 60 DAP with the independent variable  $S_{\%}$  and dependent variable  $R_W$  (Table 19). The highest positive allometry  $\alpha$  value was 9.131 and occurred at 93 DAP with the independent variable  $l$  and dependent variable  $H$  (Table 20). The greatest change in  $\alpha$  was a 2.9 fold difference for the independent variable  $l$  and the dependent variable  $R_W$  from 0.773, at 60 DAP to 2.258 at 93 DAP (Tables 19 and 20).

The allometric relationships for quackgrass in the pooled baseline stratified random sampling survey (validation data) are presented in Table 21. The  $R^2$  values for the allometric relationships ranged from 0.00 for the independent variable  $S_{\%}$  and dependent variables  $H_W$

**Table 21. Parameter estimates and associated R<sup>2</sup> values for selected quackgrass allometric relationships at wheat harvest from the pooled baseline stratified random surveys.**

Variable <sup>a</sup>		Parameter <sup>b</sup>		
Indep.	Depend.	$\beta$	$\alpha$	R <sup>2</sup> <sup>c</sup>
----- <i>(ln)</i> -----				
I	R <sub>W</sub>	3.586 (0.1739)	2.071 (0.4363)	0.11*
	R <sub>I</sub>	3.155 (0.1549)	1.911 (0.3887)	0.11*
	H <sub>W</sub>	-1.674 (0.7400)	15.022 (1.8571)	0.26**
	H	0.243 (0.8493)	16.609 (2.1313)	0.25**
	R <sub>B</sub>	6.717 (0.1478)	2.003 (0.3708)	0.13**
S	R <sub>W</sub>	-1.178 (0.1701)	1.035 (0.0402)	0.78**
	R <sub>I</sub>	-1.157 (0.1472)	0.935 (0.0347)	0.80**
	H <sub>W</sub>	-11.169 (1.6718)	1.242 (0.3952)	0.05**
	H	-9.954 (1.9084)	1.297 (0.4511)	0.04**
	R <sub>B</sub>	2.407 (0.1253)	0.927 (0.0296)	0.84**
S <sub>D</sub>	R <sub>W</sub>	2.761 (0.1661)	0.076 (0.0440)	0.01 <sub>ns</sub>
	R <sub>I</sub>	2.368 (0.1481)	0.080 (0.0392)	0.02 <sub>ns</sub>
	H	-7.883 (0.8269)	1.188 (0.2193)	0.13**
	R <sub>B</sub>	5.829 (0.1414)	0.108 (0.0375)	0.04**
	S <sub>W</sub>	R <sub>W</sub>	-0.307 (0.1239)	0.935 (0.0323)
R <sub>I</sub>		-0.339 (0.1118)	0.835 (0.0291)	0.05**
H <sub>W</sub>		-10.271 (1.3321)	1.163 (0.3476)	0.05**
H		-8.981 (1.5221)	1.205 (0.3972)	0.04**
R <sub>B</sub>		3.257 (0.1011)	0.817 (0.0263)	0.84**
S <sub>%</sub>	R <sub>W</sub>	3.760 (0.1395)	0.273 (0.0325)	0.28**
	R <sub>I</sub>	3.293 (0.1248)	0.245 (0.0291)	0.28**
	H <sub>W</sub>	-5.972 (0.7693)	0.080 (0.1794)	0.00 <sub>ns</sub>
	H	-4.622 (0.8749)	0.050 (0.2039)	0.00 <sub>ns</sub>
	R <sub>B</sub>	6.788 (0.1215)	0.231 (0.0283)	0.26**
W	R <sub>I</sub>	-1.106 (0.0817)	0.916 (0.0190)	0.93**
	H	-8.347 (1.7821)	0.890 (0.4144)	0.02 <sub>ns</sub>
	R <sub>B</sub>	2.551 (0.0775)	0.886 (0.0186)	0.93**
W <sub>D</sub>	R <sub>I</sub>	2.272 (0.1664)	0.097 (0.0407)	0.03 <sub>ns</sub>
	H	-8.404 (0.9426)	1.155 (0.2308)	0.12*
	R <sub>B</sub>	5.724 (0.1588)	0.123 (0.0389)	0.05*

<sup>a</sup> Descriptions of the variable abbreviations can be found in Table 16.

<sup>b</sup> From the allometric model  $\Theta_i = \beta \Theta_p^\alpha$ . Standard errors for the parameter estimates are enclosed in brackets beside the estimate.

<sup>c</sup> \*, \*\* and <sub>ns</sub> indicate significant at P=0.05, P=0.01, and not-significant, respectively.

and  $H$ , to 0.93 for independent variable  $W$  and dependent variable  $R_B$ . The mean  $R^2$  for the allometric relationships from the validation data was 0.28 and is much less than the mean  $R^2$  of 0.73 from Table 20. The difference either reflects true differences in the quackgrass populations sampled or may be an artifact of the validation data using actual quadrat values, whereas the data in Table 20 was fit to the stratum averages.

The allometric relationships presented have practical value. If a farm operator determines a quackgrass infestation of 55 shoots  $m^{-2}$  then this paper presents the equations required to determine the infestation that might be present at harvest. Substitution into the equation  $S_3 = 6.227 + 2.479 ( S_1 )$  from Table 17 predicts that at harvest 143 shoots could be present. Further substituting this estimated harvest culm density of 143 shoots  $m^{-2}$  into the allometric equation  $R_B = 4.297 ( S_3 )^{1.075}$  indicates that there could be 892 rhizome buds associated with this infestation.

The example value of 55 shoots  $m^{-2}$  is the actual mean value for the 30 DAP in the dataset used to develop these allometric relationships. In addition the actual mean 93 DAP variable values for  $S$  and  $R_B$  were 144 and 890  $m^{-2}$ , respectively. Clearly, the models work well in estimating variable values from which the models were derived.

The allometric relationships can be linked to yield loss models presented elsewhere (Manuscript 2). For example substituting the harvest 3 quackgrass infestation of 143 shoots  $m^{-2}$  into the equation :

$$WY_{\%} = 96.4 \times (1 - ((0.113 \times S_3) / (100 \times (1 + ((0.113 \times S_3) / 203.4))))$$

results in an estimated wheat yield ( $WY_{\%}$ ) of 82 per cent of what would occur in a weed

free situation. The actual mean  $WY_{\%}$  in these surveys was 83 per cent.

It is important that allometric relationships be linked in stepwise fashion rather than merged with the yield-loss model into some unified equation. The mathematically unsound nature of such a merged allometric yield-loss model in most situations has been discussed by Jolliffe *et al* (1988).

The cross-utility of the allometric relationships was tested using the models based on the 93 DAP data (Table 20) and comparing to the independent validation survey allometric relationships (Table 21). For all variables, the models and model parameter  $\alpha$  differed significantly between the two datasets. The allometric relationships were specific to the specific environment from which they were derived. Other researchers have demonstrated the dependence of allometry on environmental conditions including population density, temperature and soil nutrients (Jolliffe *et al*, 1988; Stanhill, 1977b). The implication of this finding is that there is no "universal" allometric equation at any particular time for quackgrass growing with wheat. Until allometric models can account for environmental variation they will be unable to provide information on the underlying biology.

The following example will illustrate the scale of the errors that might result in using an allometric model developed for one dataset on a different dataset. The mean  $S$  at 93 DAP in the pooled dynamic stratified random sampled was 144 m<sup>2</sup>. Substituting into the equation

$$R_B = 11.101 ( S )^{0.927}$$

gives an estimated  $R_B$  of 1,011 m<sup>2</sup>. The actual mean  $R_B$  value was 890 m<sup>2</sup>. The allometric

model from the different dataset overestimated the rhizome buds present by 14 per cent. However, given that the standard error of means for the mean quackgrass variable values were often around 18 per cent (Manuscript 2), then an allometric model that is "off" by 14 per cent might be considered satisfactory for many practical applications.

The damage caused in wheat due to quackgrass may be assessed in relation to existing and future crops. Estimation of impact on the current crop is dependent on wheat yield response to quackgrass and has been addressed elsewhere (Manuscript 2). The damage to future cropping cycles is related to quackgrass carryover into future cycles and simple models for estimating this potential have been expressed in this manuscript. However, the conventional allometric model utilized in this manuscript is inherently limited in applicability due to time dependence and restricted applicability to the specific environmental and biological conditions for which it was derived. To avoid such limitations and be universal in applicability allometric models for quackgrass will have to be more sophisticated accounting for environmental and temporal variation.