



Full Length Article

The Scaling Relationship of Below and Above-ground Biomass of Different Grain Crops during the Seedling Stage

Xiaoliang Qin^{1*}, Fengxia Zhang¹, Meiling Wang¹, Chengxiao Shi¹, Yuncheng Liao¹, Xiaoxia Wen^{1*} and Kadambot H.M. Siddique²

¹College of Agronomy, Northwest A and F University, Yangling, Shaanxi, 712100, China

²The UWA Institute of Agriculture, The University of Western Australia, Perth WA 6009, Australia

*For correspondences: xiaoliangqin2006@163.com; wenxiaoxia6811@163.com

Abstract

Allometric partitioning theory showed that root biomass (M_B) scales in a nearly isometric manner with respect to shoot biomass (M_A) for natural plants. Artificial selection has fundamentally transformed plants; for example, the biomass allocation pattern has changed in grain crops. This study investigated 32 genotypes from 20 grain crop species to test the effects of domestication and seed size on the scaling relationship of M_B vs. M_A for grain crops. The scaling exponent of M_B vs. M_A during 30 days of growth was 0.937 across the 32 grain crop genotypes, 0.999 for the dicotyledons and 1.034 for the monocotyledons. Based on the 95% CIs of the M_B vs. M_A scaling exponent (α_{RMA}) of the data sets for the 32 genotypes, eight values exceeded 1.0, nine values were less than 1.0 and the remaining 15 values were statistically indistinguishable from 1.0. Seed size was positively correlated with the scaling exponents of M_B vs. M_A for the 32 genotypes ($P < 0.05$), which means large-seeded species generally had more potential for allocating biomass to roots during the seedling stage. These findings suggest that a uniform isometric relationship exists in grain crop species and that artificial selection in crop species has not changed this relationship. In addition, larger seeds are an evolutionarily-stable strategy based on high grain yield per area. © 2016 Friends Science Publishers

Keywords: Allometry; Breeding; Domestication; Seed size; Grain crop; Scaling exponent

Introduction

Interspecific relationships between below-and above-ground biomass (M_B and M_A , respectively) are used widely in studies on climate change, ecology and evolution; many of these size-dependent trends are considered a consequence of natural selection and adaptive evolutionary change (Wardlaw, 1990; Niklas, 1994; Bazzaz and Grace, 1997; Charnov, 1997; Tilman *et al.*, 1997; Caspersen *et al.*, 2000; Robinson *et al.*, 2010). Allometric partitioning theory showed that M_B scales in a nearly isometric manner with respect to M_A across and within clades and different habitats (Enquist and Niklas, 2002; Niklas, 2005), and empirical statistical trends agree with this prediction (Niklas and Enquist, 2002; Enquist and Niklas, 2002; Niklas, 2004, 2005, 2006; Cheng and Niklas, 2007, Cheng *et al.*, 2015).

Crop plants, including monocotyledons and dicotyledons, undergo both natural and artificial selection. Long histories of domestication, selection and breeding have fundamentally transformed plants (Cronquist, 1988; Evans, 1993). A series of changes has taken place in seed plants: the increased allocation of biomass to reproductive organs accounts for much of the progress in breeding for high yield potential in wheat, oat, barley, maize and

sunflower (Slafer, 1994), along with more biomass being allocated to shoots in modern wheat genotypes (Siddique *et al.*, 1990; Zhang *et al.*, 1999, Qin *et al.*, 2012) and that wheat and barley crops have larger seeds than wild types (Dubcovsky and Dvorak, 2007). Whether artificial selection has changed the uniform isometric relationship in grain crop species is unclear.

Seed size is central to many aspects of plant ecology and evolution (Harper *et al.*, 1970; Leishman *et al.*, 2000; Moles *et al.*, 2005a, b; Sadras, 2007). Seed size may affect biomass allocation in an individual plant (Enquist and Niklas, 2002; Peng *et al.*, 2010). Seed size is particularly significant at the seedling stage since germination is an important factor affecting crop yield, such that lower seed germination rates cause production losses. After seed germination, seeds with larger endosperms and cotyledons are more likely to develop larger M_B/M_A ratios than those with smaller endosperms and cotyledons (Khurana and Singh, 2000; Niklas, 2005), and have a survival advantage during seedling establishment (Moles and Westoby, 2004).

To represent genetic variation in grain crops around the world, we selected 32 genotypes from 20 major grain crop species (oil, cereal and legume crops), 11 of which were dicotyledons and nine were monocotyledons. Seed

biomass of the 32 genotypes spanned two orders of magnitude (Fig. S1). We studied the allometric relationships of M_B vs. M_A during the seedling stage to test two hypotheses: (1) after long-term domestication by humans, M_B does not scale in an isometric manner with respect to M_A in grain crops, and (2) large-seeded genotypes allocate more biomass to roots during seedling growth.

Materials and Methods

Sixty grains of each genotype (Table 1) were selected, sterilized in 10% H_2O_2 for 30 min, repeatedly rinsed in distilled water until free of H_2O_2 , and then incubated at 25°C for 48 h. After accelerating germination, seedlings were transplanted to plastic pots (height, 25 cm; diameter, 20 cm) filled with moistened sand and vermiculite, and fertilized with half-strength modified Hoagland nutrient solution to prevent nutrient depletion (Hoagland and Arnon, 1950). Each pot contained three seedlings with 20 pots per genotype. The experiment was conducted in a growth chamber set at day/night temperatures of 25°C/18°C, relative humidity of 45/60±5%, photon flux density of 150 $\mu\text{M m}^{-2} \text{s}^{-1}$ and a light period of 12 h.

Ten individual plants of each genotype were harvested on each of six harvest dates (5, 10, 15, 20, 25 and 30 days after sowing). Seedlings were removed with care, and roots carefully rinsed with running water until free of sand and vermiculite. Root and shoot dry weights were determined after oven drying for 30 mins at 100°C followed by 48 h at 80°C.

Data for M_A and M_B were \log_{10} -transformed and Model Type II (reduced major axis, RMA) regression analysis was used to determine the scaling exponents (α_{RMA}) and allometric constants ($\log \beta_{\text{RMA}}$) (Niklas, 1994, 2005, 2006; Falster *et al.*, 2006; Warton *et al.*, 2006). The formula for the scaling equation is $\log M_B = \alpha_{\text{RMA}} \log M_A + \log \beta_{\text{RMA}}$. The Standardized Major Axis Tests and Routines (MATR) software package (Warton and Weber, 2002; Falster *et al.*, 2003) was used to determine if the numerical values of α_{RMA} for $\log M_A$ vs. $\log M_B$ differed between contrasting data subsets. The formula for the scaling equation is $\log M_B = \alpha_{\text{RMA}} \log M_A + \log \beta_{\text{RMA}}$. Heterogeneity in the numerical value of either regression parameter was rejected for each comparison if $P > 0.05$.

Results

The Scaling Relationship across Species

The scaling exponent of M_B vs. M_A during 30 days of growth was 0.937 (95% CIs = 0.918, 0.957; $N = 1890$; $r^2 = 0.793$) across the 32 grain crop genotypes, which was near to 1.0. The scaling exponent for the dicotyledons was 0.999 (95% CIs = 0.977, 1.020; $N = 940$; $r^2 = 0.883$) and the monocotyledons was 1.034 (95% CIs = 1.005, 1.063; $N = 950$; $r^2 = 0.816$) (Figs. 1, 2 and 3).

The Scaling Relationship within Genotypes

Based on the 95% CIs of the M_B vs. M_A scaling exponent (α_{RMA}) of the data sets for the 32 genotypes, eight values exceeded 1.0, nine values were less than 1.0 and the remaining 15 values were statistically indistinguishable from 1.0 (Table 2).

The Effect of Grain Size and Genotype on the Scaling Exponent of M_B vs. M_A

Tough points in Fig. 4 are slightly scattered, however seed size was positively correlated with the scaling exponent of M_B vs. M_A for the 32 grain crop genotypes ($P = 0.016$).

Discussion

A normal rule of thumb for plants is that M_B will scale in a nearly isometric manner with respect to M_A across and within clades and different habitats (Enquist and Niklas, 2002; Niklas, 2005). Niklas (2005) conducted a study using a large database (1406 data entries for 257 species) and found that the scaling exponent for non-woody plants and juvenile woody species agreed reasonably well with an isometric scaling relationship. Specific variation in biomass allocation is well known in response to differential selection pressure. However, in our study with seed biomass across two orders of magnitude, M_B scaled isometrically with M_A for the dicotyledons, monocotyledons and across the 32 grain crop genotypes. The intergenomic allometric across the 32 grain crop genotypes was slightly lower than 1.0 which may be a result of maternal effects. In other words, even though grain crop varieties have been selected for more than 10,000 years and a series of changes has taken place, the scaling allocation rules remain as per the natural plant.

Many of the intragenomic allometric scaling exponents (eight values exceeded 1.0, nine values were less than 1.0) were inconsistent with previous reports. However, the results do not conflict with an isometric relationship because roots are highly regulated by nutrient availability, and different crops may favor different soil conditions. In other words, the soil and nutrient levels proposed in the present study may be favored by some species, so the scaling exponent changed with species. Furthermore, at the seedling stage, the maternal effect of seed size is an important factor affecting biomass allocation in seedlings (Niklas, 2005). Our results showed that across two orders of magnitude for seed biomass, seed size and scaling exponent were positively correlated when 32 grain crop species were combined. This means that large-seeded species are more likely to allocate biomass to roots than small-seeded species during seedling growth, which is useful for the germinating seed to absorb nutrients from the soil environment, particularly in poor soil (Palta *et al.*, 2011).

Table 1: Details of the 32 genotypes of grain crop used in this study

Chinese genotype	Common name	Latin name	Application
<i>Dicotyledons</i>			
Baiyundou	Kidney bean	<i>Phaseolus vulgaris</i>	Legume
Hongyundou	Kidney bean	<i>Phaseolus vulgaris</i>	Legume
Bima	Castor	<i>Ricinus communis</i> L.	Oilseed
Zaoshu 6	Soybean	<i>Glycine max</i>	Legume
Zhonghuang 13	Soybean	<i>Glycine max</i>	Legume
Hongxiaodou	Adzuki bean	<i>Vigna angularis</i>	Legume
Lüdou	Green bean	<i>Vigna radiata</i> (Linn.) Wilczek.	Legume
Meikui	Sunflower	<i>Helianthus annuus</i>	Oilseed
Sandaomei	Sunflower	<i>Helianthus annuus</i>	Oilseed
Jiujiangkuqiao	Tartary buckwheat	<i>Fagopyrum tataricum</i> (L.) Gaertn	Cereal
Tianqiao	Common buckwheat	<i>Fagopyrum esculentum</i> Moench	Cereal
Yuzhi8	Sesame	<i>Sesamum indicum</i>	Oilseed
Yuzhi4	Sesame	<i>Sesamum indicum</i>	Oilseed
Biandou	Lentil	<i>Lens culinaris</i>	
Ganza 1	Rape	<i>Brassica campestris</i> L.	Oilseed
Jinyouza 2009	Rape	<i>Brassica campestris</i> L.	Oilseed
<i>Monocotyledons</i>			
Liao5236	Corn(inbred line)	<i>Zea mays</i>	Cereal
LG001	Corn(inbred line)	<i>Zea mays</i>	Cereal
Luoyanmai	Naked oat	<i>Avena nuda</i> L.	Cereal
Aiganyanmai	Husk oat	<i>Avena sativa</i>	Cereal
Mazhamai	Wheat	<i>Triticum aestivum</i> L.	Cereal
Xinong979	Wheat	<i>Triticum aestivum</i> L.	Cereal
Ganpi 1	Barely	<i>Hordeum vulgare</i> L.	Cereal
Heisileng	Barely	<i>Hordeum vulgare</i> L.	Cereal
Saozhougaoliang	Sorghum	<i>Sorghum bicolor</i> L.	Cereal
Shandonghonggaoliang	Sorghum	<i>Sorghum bicolor</i> L.	Cereal
Longmi 7	Broomcorn millet	<i>Panicum miliaceum</i> L.	Cereal
Yumi 3	Broomcorn millet	<i>Panicum miliaceum</i> L.	Cereal
Hongjiugu	Foxtail millet	<i>Setaria italica</i>	Cereal
Jingu 27	Foxtail millet	<i>Setaria italica</i>	Cereal
Ezao18	Rice	<i>Oryza sativa</i> L.	Cereal
Linhan1	Rice	<i>Oryza sativa</i> L.	Cereal

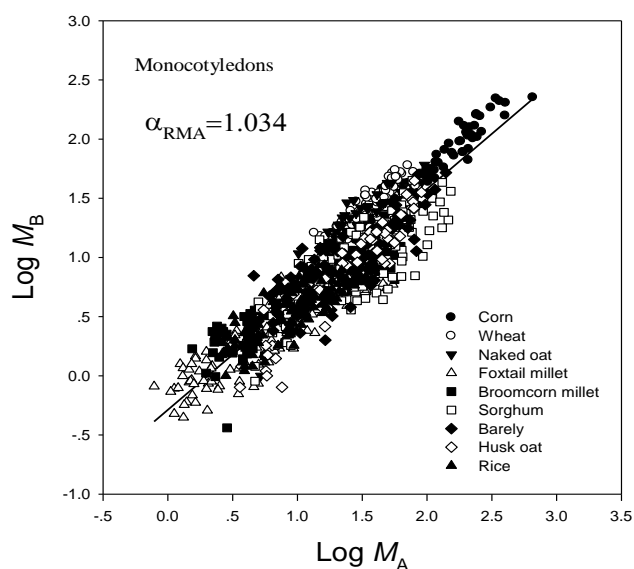


Fig. 1: Bivariate plots of log-transformed data for M_B and M_A for monocotyledons. The intergenomic scaling exponent was approximately isometric

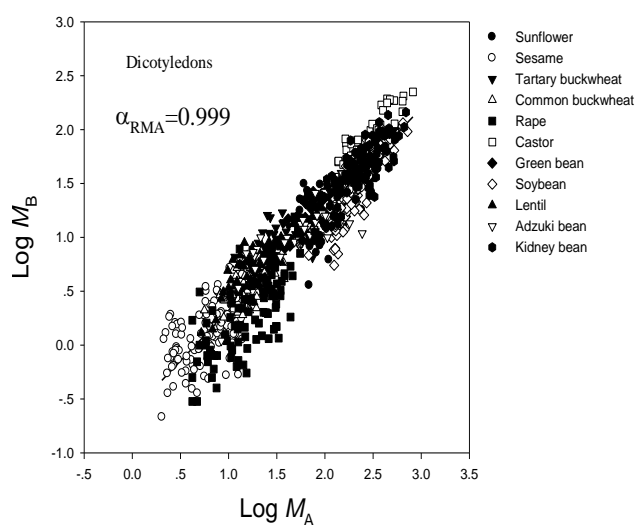


Fig. 2: Bivariate plots of log-transformed data for M_B and M_A for dicotyledons. The intergenomic scaling exponent was isometric

Table 2: Summary of SMA regression parameters for the scaling relationships between root and shoot biomass at the seedling stage for the 32 tested crop genotypes; all relationships were highly significant ($P < 0.001$)

Group	n	r ²	α_{RMA}	β_{RMA}
<i>Dicotyledons</i>				
Baiyundou	60	0.696	1.343 (1.161, 1.554)	-1.491
Hongyundou	60	0.358	1.119 (0.908, 1.379)	-1.037
Bima	50	0.79	1.128 (0.988, 1.287)	-0.838
Zaoshu 6	50	0.859	1.426 (1.279, 1.589)	-1.884
Zhonghuang 13	60	0.73	1.616 (1.410, 1.852)	-2.308
Hongxiaodou	60	0.812	0.875 (0.781, 0.981)	-0.470
Lidou	60	0.739	0.961 (0.840, 1.098)	-0.611
Meikui	60	0.615	1.124 (0.955, 1.322)	-1.090
Sandaomei	60	0.625	1.046 (0.891, 1.228)	-0.845
Jiujiangkuqiao	60	0.458	0.937 (0.773, 1.135)	-0.586
Tianqiao	60	0.519	0.804 (0.671, 0.964)	-0.295
Yuzhi8	60	0.363	0.993 (0.806, 1.223)	-0.588
Yuzhi4	60	0.431	1.122 (0.921, 1.366)	-0.837
Biandou	60	0.575	0.998 (0.842, 1.183)	-0.533
Ganza 1	60	0.701	1.210 (1.048, 1.396)	-1.194
Jinyouza 2009	60	0.614	1.362 (1.157, 1.602)	-1.320
<i>Monocotyledons</i>				
Liao5236	60	0.942	0.945 (0.865, 1.024)	-0.143
LG001	60	0.911	0.998 (0.890, 1.011)	-0.314
Luoyanmai	60	0.832	1.045 (0.938, 1.164)	-0.248
Aiganyanmai	60	0.885	1.143 (1.046, 1.250)	-0.694
Mazhamai	60	0.904	1.036 (0.955, 1.124)	-0.196
Xinong979	60	0.833	1.015 (0.912, 1.130)	-0.144
Ganpi 1	60	0.673	0.790 (0.680, 0.918)	-0.084
Heisileng	50	0.621	1.398 (1.172, 1.666)	-0.805
Saozhougaoliang	60	0.871	0.886 (0.807, 0.974)	-0.179
Shandonghonggaoliang	60	0.758	0.821 (0.722, 0.934)	-0.401
Longmi 7	60	0.837	0.734 (0.660, 0.816)	-0.084
Yumi 3	60	0.82	0.717 (0.642, 0.802)	-0.101
Hongjiugu	60	0.871	0.739 (0.672, 0.812)	-0.290
Jingu 27	60	0.792	0.655 (0.581, 0.738)	-0.125
Linhan1	60	0.715	0.874 (0.739, 1.010)	-0.171
Ezao18	60	0.600	0.847 (0.657, 1.037)	-0.135

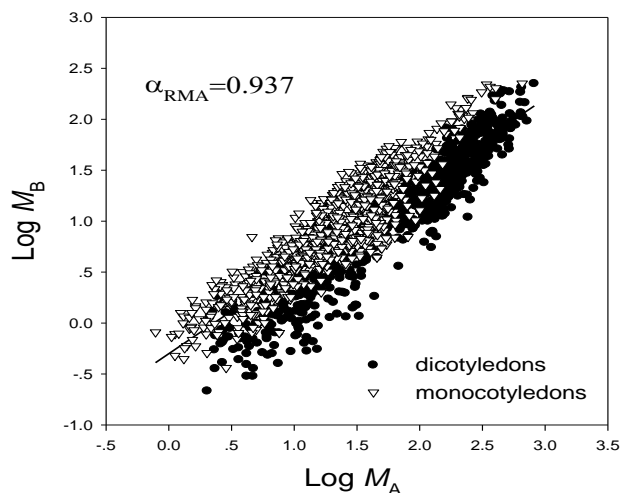


Fig. 3: Bivariate plots of log-transformed data for M_B and M_A of 20 grain crop species. The intergenomic scaling exponent was isometric

Our results are consistent with previous findings in *Albizia procera* and 257 different species where larger seeds had more potential to develop larger M_B/M_A ratios (Khurana and Singh, 2000; Niklas, 2005).

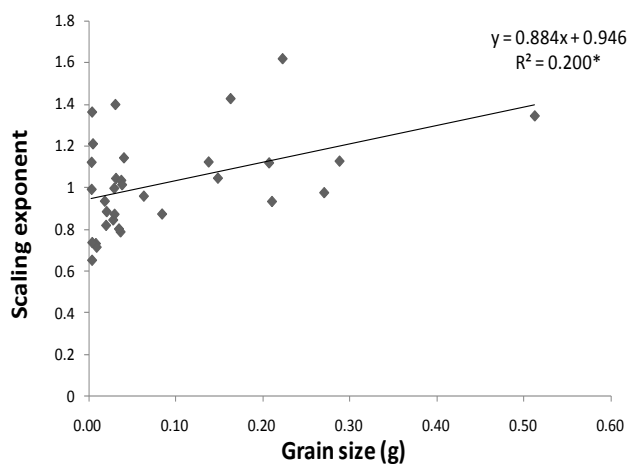


Fig. 4: Bivariate plots of log-transformed data for all 20 tested grain crop species ($P=0.016$)

Lower grain yields in the field often result from low survival and emergence rates. Large-seeded species, with larger embryos, suggest faster emergence and more competitive ability (Dalling and Hubbell, 2002; Moles and

Westoby, 2004, 2006). Our results showed that large seeds also allocate more root biomass to seedlings, which is useful during seed emergence to absorb water and nutrients from the soil environment, and implies better seedling establishment. So sowing larger seeds is an evolutionarily-stable strategy based on high grain yield per area.

Conclusion

Our results suggested that (1) the interspecific isometric relationship between roots and shoots is constant even in a small data set of seedlings, (2) artificial selection in crop species has not changed this uniform relationship, and (3) the scaling exponent of M_B vs. M_A for 32 grain crops is approximately isometric. Our results confirmed that seed size had a maternal effect on biomass allocation, with large-seeded grain crops generally have higher scaling exponents which may lead to better seedling establishment.

The purpose of crop breeding is to improve grain yields. After years of domestication, the most obvious changes to crop species are the increased investment of biomass to reproductive organs and the reduced investment of biomass to the root system (Siddique *et al.*, 1990). In future, it would be better to test our hypotheses over a whole growth period.

Acknowledgements

This work was supported by the National Key Technology Support Program (2015BAD22B03), the National Natural Science Foundation of China (Project No. 31401303) and the Special Fund for Agro-scientific Research in the Public Interest (201503121).

References

- Bazzaz, F.A. and J. Grace, 1997. *Plant Resource Allocation*. New York: Academic Press, London
- Caspersen, J.P., S.W. Pacala, J.C. Jenkins, G.C. Hurtt, P.R. Moorcroft and R.A. Birdsey, 2000. Contributions of land-use history to carbon accumulation in U.S. forests. *Science*, 290: 1148–1151
- Charnov, E.L., 1997. Trade-off-invariant rules for evolutionarily stable life histories. *Nature*, 387: 393–394
- Cheng, D.L. and K.J. Niklas, 2007. Above-and below-ground biomass relationships across 1534 forested communities. *Ann. Bot.*, 99: 95–102
- Cheng, D.L., Q.L. Zhong, K.J. Niklas, Y.Z. Ma, Y.S. Yang and J.H. Zhang, 2015. Isometric scaling of above-and below-ground biomass at the individual and community levels in the understorey of a sub-tropical forest. *Ann. Bot.*, 115: 303–313
- Cronquist, A., 1988. *The Evolution and Classification of Flowering Plants*, 2nd edition. New York Botanical Garden, Bronx, New York, USA
- Dalling, J.W. and S.P. Hubbell, 2002. Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *J. Ecol.*, 90: 557–568
- Dubcovsky, J. and J. Dvorak, 2007. Genome plasticity a key factor in the success of polyploid wheat under domestication. *Science*, 316: 1862–1865
- Enquist, B.J. and K.J. Niklas, 2002. Global allocation rules for patterns of biomass partitioning across seed plants. *Science*, 295: 1517–1520
- Evans, L.T., 1993. *Crop Evolution, Adaptation and Yield*, p. 500. Cambridge University Press, Cambridge, UK
- Falster, D.S., D.I. Warton and I.J. Wright, 2003. *(S)MATR: Standardised Major Axis Tests and Routines*. Version 1.0. <http://www.bio.mq.edu.au/ecology/SMATR>
- Falster, D.S., D.I. Warton and I.J. Wright, 2006. *User's Guide to SMATR: Standardised Major Axis Tests and Routines*. Version 2.0. <http://www.bio.mq.edu.au/ecology/SMATR/11> March 2006
- Harper, J.L., P.H. Lovell and K.G. Moore, 1970. The shapes and sizes of seeds. *Ann. Rev. Ecol. Syst.*, 1: 327–356
- Hoagland, D.R. and D.I. Arnon, 1950. The water culture method for growing plants without soil. *Calif. Agric. Exp. Station Circular*, 347: 1–32
- Khurana, E. and J.S. Singh, 2000. Influence of seed size on seedling growth of *Albizia procera* under different soil water levels. *Ann. Bot.*, 86: 1185–1192
- Leishman, M., A.J. Wright and A.T. Moles, 2000. The evolutionary ecology of seed size. In: *Seeds—the Ecology of Regeneration in Plant Communities*, pp: 31–57. Fenner, M. (ed.). CABI, Wallingford, UK
- Moles, A.T. and M. Westoby, 2004. Seedling survival and seed size: a synthesis of the literature. *J. Ecol.*, 92: 372–383
- Moles, A.T. and M. Westoby, 2006. Seed size and plant strategy across the whole life cycle. *Oikos*, 113: 91–105
- Moles, A.T., D.D. Ackerly and C.O. Webb, 2005a. Factors that shape seed mass evolution. *P. Nat. Acad. Sci. USA*, 102: 10540–10544
- Moles, A.T., D.D. Ackerly and C.O. Webb, 2005b. A brief history of seed size. *Science*, 307: 576–580
- Niklas, K.J., 1994. *Plant Allometry*. The scaling of form and process. Chicago: University of Chicago Press
- Niklas, K.J., 2004. Plant allometry: is there a grand unifying theory? *Biol. Rev.*, 79: 871–889
- Niklas, K.J., 2005. Modelling below- and above-ground biomass for nonwoody and woody plants. *Ann. Bot.*, 95: 315–321
- Niklas, K.J., 2006. A phyletic perspective on the allometry of plant biomass and functional organ-categories. (A Tansley Review.) *New Phytol.*, 171: 27–40
- Niklas, K.J. and B.J. Enquist, 2002. Canonical rules for plant organ biomass partitioning and growth allocation. *Am. J. Bot.*, 89: 812–819
- Palta, J.A., X. Chen, S.P. Milroy, G.J. Rebetzke, M.F. Dreczer and M. Watt, 2011. Large root systems: Are they useful in adapting wheat to dry environments? *Funct. Plant Biol.*, 38: 347–354
- Peng, Y.H., K.J. Niklas and P.B. Reich, 2010. Ontogenetic shift in the scaling of dark respiration with whole-plant mass in seven shrub species. *Funct. Ecol.*, 24: 502–512
- Qin, X.L., K.J. Niklas, L. Qi, Y.C. Xiong and F.M. Li, 2012. The effects of domestication on the scaling of below-vs. aboveground biomass in four selected wheat (*Triticum*; *Poaceae*) genotypes. *Am. J. Bot.*, 99: 1112–1117
- Robinson, D., H. Davidson, C. Trinder and R. Brooker, 2010. Root-shoot growth responses during interspecific competition quantified using allometric modeling. *Ann. Bot.*, doi:10.1093/aob/mcq186, available online at: www.aob.oxfordjournals.org
- Sadras, V.O., 2007. Evolutionary aspects of the trade-off between seed size and number in crops. *Field Crops Res.*, 100: 125–138
- Slafer, G.A., 1994. *Genetic Improvement of Field Crops*. Marcel Dekker, New York, USA
- Siddique, H.M., R.K. Belford and D. Tennant, 1990. Root:shoot ratios of old and modern, tall and semi-dwarf wheats in a Mediterranean environment. *Plant Soil*, 121: 89–98
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie and E. Siemann, 1997. The Influence of functional diversity and composition on ecosystem processes. *Science*, 277: 1300–1302
- Wardlaw, I.F., 1990. The control of carbon partitioning in plants. *New Phytol.*, 116: 341–381
- Warton, D.I. and N.C. Weber, 2002. Common slope tests for bivariate errors in-variable models. *Biometrical J.*, 44: 161–174
- Warton, D.I., I.J. Wright, D.S. Falster and M. Westoby, 2006. Bivariate line-fitting methods for allometry. *Biol. Rev.*, 81: 259–291
- Zhang, D.Y., G.J. Sun and X.H. Jiang, 1999. Donald's ideotype and growth redundancy: a game theoretical analysis. *Field Crops Res.*, 61: 179–187

(Received 18 April 2015; Accepted 07 December 2015)