CHAPTER 20

FUNCTIONAL-STRUCTURAL MODELLING AS A POTENTIAL TOOL TO ASSESS THE IMPACT OF RESOURCE COMPETITION ON ARABLE COMMUNITIES

A. KARLEY AND B. MARSHALL

Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, United Kingdom

Abstract. Sustainable farming systems that maintain the diversity of arable plant communities and associated invertebrates are a key objective for European agriculture. Plant structure–function analysis and modelling are potentially important tools for studying these arable communities, and for understanding the impact of crop–weed interactions on crop productivity and on diversity in arable food webs. To understand the role of plant structure in trophic interactions and community composition, we need knowledge of the 'rules' governing plant structure, and how variation in structure affects the way that plants compete for and acquire resources, both above- and belowground.

As a first step to a structural-modelling approach, we have used a sonic digitizer to capture basic information on aboveground plant architecture for several weed species common to UK arable systems. The structural patterns that occurred in plants grown without resource limitation are presented and analysed for *Chenopodium album*, *Polygonum aviculare* and *Tripleurospermum inodorum*. For each species, the importance of these architectural rules for plant response to resource competition is inferred from plant growth habit in the field. The plant structural data gathered here will be used to construct models to explore the interaction between plant architecture and environmental variables, including the impact of resource availability (e.g., due to light competition) on growth and resource partitioning. This study is the initial stage of future work to model the interactions between adjacent plants of differing architectures and resource utilization strategies. The utility of a structure–function approach to observe the evolution of communities of interacting plants under different levels of resource competition is discussed.

INTRODUCTION

Sustainable farming systems that will protect and enhance the diversity of arable plants and their associated microbial and animal communities are the focus of new initiatives in European agriculture. Reforms to the Common Agricultural Policy (CAP) for Europe have introduced payments to farmers for farming in more environmentally sustainable ways that will promote biodiversity. To investigate the impact of farming practices, we need to develop methods to characterize the form

J. Vos, L.F.M. Marcelis, P.H.B. de Visser, P.C. Struik and J.B. Evers (eds.), Functional-Structural Plant Modelling in Crop Production, 231-241.

and function of different plant types as a basis for understanding the contribution of plant–plant interactions to the diversity of the arable system. This study aims to provide basic information on shoot architecture that will inform a structure–function approach to investigating arable-plant interactions.

Crop simulation modelling has a long history of dealing with uniform stands of genetically identical individuals. In reality, however, arable plant communities are composed of a diverse array of crop and weed individuals that vary in architecture and function. Plant structure–function analysis and modelling are potentially important tools for studying these arable communities, and for understanding the impact of crop–weed interactions on productivity, weed diversity and food webs. Knowledge of the 'rules' governing plant structure is an essential first step in understanding plant function and, by providing data for model parameterization, should enable the development of a formal structure–function-modelling approach to investigate how arable plants interact. Differences in structure between individuals affect the way in which plants acquire resources such as light, carbon, nutrients and water; and the degree of plasticity in plant architecture, and therefore in resource capture, could be essential to the survival of individuals under competition. Thus, analysis of the patterns of architecture exhibited by different types of arable plants should allow us to infer and assess plant responses to resource competition in the field.

As an initial step to developing a structure–function approach for characterizing arable plant communities, a range of arable weed species has been selected, based on the large data sets collected in UK Farm Scale Evaluation trials (Hawes et al. 2005), for detailed quantification of aboveground plant architecture in the absence of resource competition. The selected species are common in UK arable fields, but contrast in growth habit, architecture, competitive strength, phenotypic variability and the trophic groups they support (Marshall et al. 2003). Architectural measurements are reported for three of the selected species: *Chenopodium album*, which has an upright habit and reportedly limited phenotypic variability; the ground-spreading *Polygonum aviculare*; and *Tripleurospermum inodorum*, which produces finely divided leaves and whose form varies from compact bushy to upright with extended internodes, depending on the degree of competition.

METHODS

Plant material

Seeds of *Chenopodium album*, *Polygonum aviculare*, *Tripleurospermum inodorum* and *Viola arvensis*, collected in 2003 from arable sites across the UK (Burke 2003), were treated with gibberellic acid (0.02% w/v) overnight, then rinsed and surface-sterilized (1% [v/v] sodium hypochlorite and 0.1% [v/v] Triton-X-100) and sown in Murashige and Skoog medium solidified with 0.8% agar in a sterile Petri™ dish. Seeds were stratified at 4°C for 48 h and then transferred to 21°C in constant light to induce germination. When seedlings were large enough to handle (after approximately 10–14 days growth) they were transferred to Jiffys (Jiffy™, Jiffy Products International AS, Norway) and maintained under glass (18 h light, 20°C).

At day 38, the established seedlings were transferred to two-litre pots of standard compost (peat–sand–perlite mix containing 17N:10P:15K and Intercept^{TM} systemic insecticide) and transferred to a Tygan tunnel. A randomized block design was implemented, with four blocks arranged in a 2×2 structure, and each block was composed of a 3×4 array of plants; up to 3 individuals of each species were allocated randomly within each block. Plant pots were inserted through holes, spaced at 0.5-m intervals, cut into black polythene sheeting stretched over a frame surrounding each block such that the rim of the pot was flush with the sheeting. An under-pot watering system was established by daily irrigation of a sand/capillary matting (LS Systems, UK) substrate below each pot. Only a restricted set of architectural data were collected on *V. arvensis* and are not reported here.

Measurements

Temperatures were recorded every minute with Chromel-Alumel thermocouples using a Campbell Scientific CR23X micrologger. Hourly and daily averages, maxima and minima were saved to long-term output. Air temperatures in the Tygan tunnel were recorded at 1m above the ground at four locations. The sensors were shaded from direct sunlight and freely ventilated. Tissue surface temperatures of 16 plants were measured by placing thermocouples adjacent to the stem (1 sensor per species per block). Air temperatures recorded at the Institute's meteorological station, 100 m distant, showed that average air temperatures in the Tygan tunnel were within 0.1 K of that recorded at the meteorological station. Tissue temperatures were not significantly different from each other nor from the ambient air temperature. A global average of all tissue temperatures was used to calculate thermal time (K day) by accumulating above an assumed base temperature of 0^{o}C.

Leaf and flowering-stem appearances were monitored twice weekly. Plants were transferred to the laboratory for digitization using a FREEPOINT 3D sonic digitizer (GeoInstrument, Arnhem, Netherlands) in conjunction with Floradig software (CPAI, University of Queensland) for visualization and export of digitized data. The sonic digitizer recorded the X, Y and Z co-ordinates of objects relative to reference axes and a calibration reference accounted for variations in the speed of sound. Information on phyllotaxy, and on dimensions and orientation of main-stem leaves, petioles and flowering stems, was gathered at three time points between 39 and 72 days of growth, by which time all the plants had flowered. Data for the final digitization time point, which was restricted to the main-stem structures, are presented here.

Data and statistical analysis

Digitized data were exported to MS Excel for data handling. Parametric statistical tests were applied to datasets confirmed to be normally distributed (Ryan-Joiner one-sample test) with homogeneous variance (Bartlett's test). When the assumptions of normality and homogeneous variance could not be met, the non-parametric analysis used was the Kruskal-Wallis test.

RESULTS

Germination was generally low and particularly poor for *P. aviculare*, hence only 8 plants were available for digitization. However, once established in compost, all seedlings grew into mature plants (Figure 1), with a rapid increase in leaf production

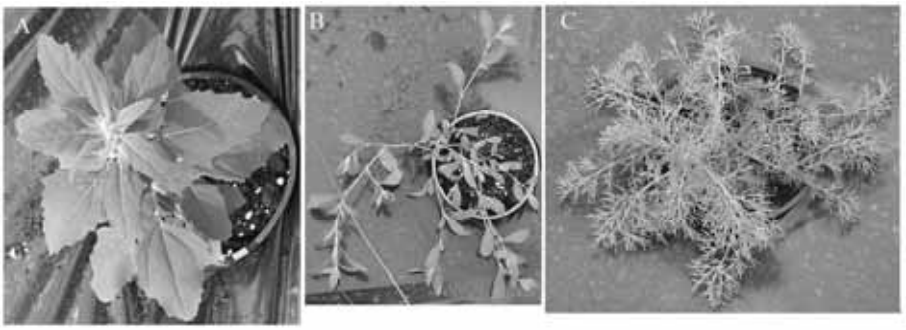

Figure 1. *Images of plants at 60 days after sowing. (A)* Chenopodium album, *(B)* Polygonum aviculare *and (C)* Tripleurospermum inodorum*. For scaling, note that pot diameter in each image was 150 mm*

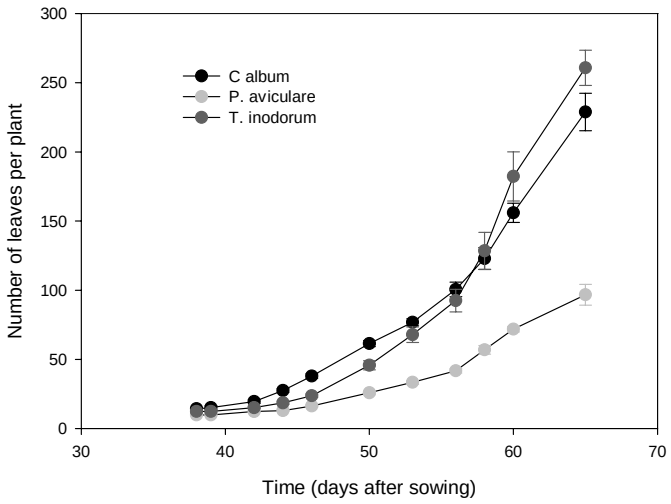

Figure 2. *Total leaf number on main stem and branches recorded for each plant during the experimental period. Values are the mean±s.e. of 12 plants except for P. aviculare (8 plants)*

at approximately 45-50 days after sowing (Figure 2). Total leaf numbers were highest in *C. album* and *T. inodorum*, while *C. album* and *P. aviculare* tended to

produce the longest main stems with higher numbers of phytomers (Table 1, Figure 3A).

Table 1. *Plastochron production rate and total phytomer number along the main stem in three arable weeds. Rates were calculated from phytomer production and accumulated thermal time above 0 °C, over the first and second half of the experimental period. Values represent the mean ±s.e. plastochron number per K day*

Time period	*C. album*	*P. aviculare*	*T. inodorum*
Weeks 1–2	0.044 ±0.003 (11)	0.034 ±0.004 (8)	0.024 ±0.008 (7)
Weeks 3–4	0.028 ±0.004 (12)	0.047 ±0.002 (8)	0.008 ±0.002 (12)
Total number of nodes	28.4 ±1.3 (12)	23.5 ±1.8 (8)	16.7 ±1.0 (12)

Data in brackets are numbers of plants.

Thermally-driven plastochron production during the experimental period (Table 1) varied significantly between species and between the two halves of the experimental period (GLM ANOVA: Species $F_{2,57}$=21.43, P<0.001; Time $F_{1,57}$=4.60, P<0.05; Interaction $F_{2,57}$=8.66, P<0.001). Rates of plastochron development were generally highest in the first half of the experimental period, with highest values achieved by *C. album*. Low values for *T. inodorum* in the second part of the experimental period reflected the determinate nature of growth in this species, as the appearance of a terminal inflorescence prevented the production of further

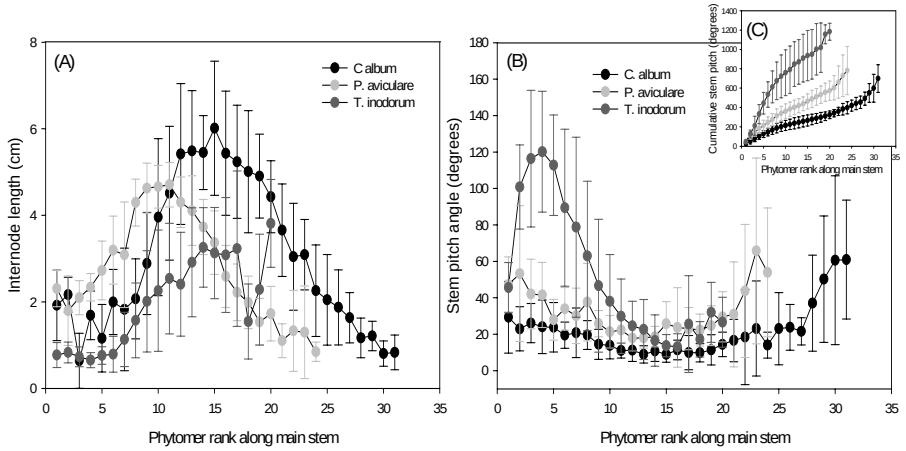

Figure 3. *Structural data for the main stem acquired by digitization of mature plants. (A) Internode length and (B) pitch angle of each internode relative to the previous internode axis; inset (C) represents cumulative pitch along the main stem. Values are the mean±s.d. of n=3-12 values per phytomer for 12 plants, except for* P. aviculare *(8 plants)*

plastochrons on the main stem. In contrast, *C. album* and *P. aviculare* continued to produce plastochrons at relatively high rates in the second half of the experimental period, indicating the indeterminate nature of their growth and flowering.

Digitization data are presented for mature flowering plants towards the end of their growth. Internode length tended to be greatest at mid-stem, although flower spike formation in *T. inodorum* was accompanied by an increase in internode length at the final two phytomers (Figure 3A). Stem pitch angle, which indicated changes in stem direction between adjacent internodes, varied significantly between species (Kruskal-Wallis analysis of average values per plant: H_2=25.49, P<0.001) and along the main stem (Figure 3B). Changes in stem direction were small at mid-stem (approx. phytomer rank 10-20), reflecting a relatively straight growth habit in this part of the stem; large changes in stem direction were observed at low phytomer rank for *T. inodorum* (Figure 3B). The degree to which stem direction varied was summarized in the cumulative pitch curve (Figure 3C), which represents the sum of pitch angle changes along the stem. The steep slope at low phytomer rank in the curve for *T. inodorum* indicated an accumulation of large changes in internode direction lower down the stem (Figure 3B, C), while flattening of the curve at high phytomer rank indicated a straight growth habit higher up the stem. *C. album* stems showed least deviation from the main axis of growth (Figure 3C).

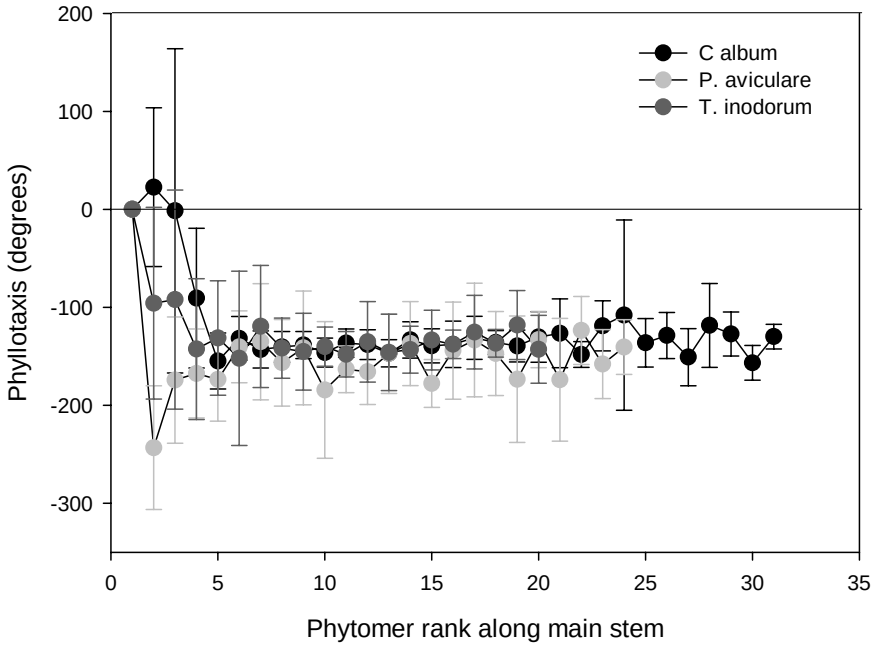

Figure 4. *Phyllotaxy or angle of rotation between consecutive phytomers of the main stem acquired by digitization of mature plants. Values are the mean±s.d. of n=3-12 values per phytomer for 12 plants except for* P. aviculare *(8 plants)*

Phyllotaxy, or the angle of rotation between consecutive nodes, differed significantly amongst the three species (Figure 4; ANOVA: $F_{2,31}$=14.89, P<0.001), with mean±s.e. values per plant of -124.1±2.5° (n=12, *C. album*), -160.8±5.7° (n=8, *P. aviculare*) and -140.1±5.3° (n=12, *T. inodorum*). There were also significant differences between the species in phyllotaxy when mean values at each node were analysed (Kruskal-Wallis test: H_2=19.27, P<0.001). Phyllotaxy was mainly anti-clockwise along the main stem (giving negative values), but a number of plants showing clockwise phyllotaxy were identified (1 *C. album*, 2 *P. aviculare* and 5 *T. inodorum* plants); note that clockwise values were converted to anti-clockwise values to allow comparison across plants. For *C. album* and *T. inodorum*, angle of node rotation was small for the first 3-4 nodes, after which a consistent pattern of rotation was observed along the stem; the greater degree of variability at high phytomer rank in *C. album* might reflect a change in architecture at the growing tip, but is also likely to reflect increased error in digitizing the much smaller structures occurring at these nodes (see also Figure 3B). Node-to-node variation in phyllotaxy was also observed for *P. aviculare* plants (Figure 4), and this might indicate that the direction of node development was influenced by contact with the ground in these low-growing plants.

The three species differed in leaf shape (Figure 1) and, therefore, in absolute length and width of the lamina (Figure 5A, C). Expressing the data relative to the length and width of, respectively, the longest or widest leaf on each plant allowed comparison of leaf shape patterns between species (Figure 5B, D). Both *P. aviculare* and *T. inodorum* showed a gradual decrease in leaf length along the main stem, but the longest *C. album* leaves developed at mid-stem regions (Figure 5B). The pattern in leaf width along the main stem was similar to leaf length in all species except *T. inodorum*, which developed wider leaves at mid-stem regions (Figure 5D). Note that at the time of digitization, leaf senescence and abscission had occurred at lower nodes. Thus, leaf shape was relatively constant along the stem of *P. aviculare*, as demonstrated by the absence of a consistent trend in length-to-width ratio (values varied from 3 to 4.5; Figure 5E), and between phytomer ranks 4 and 16 in *C. album* (ratio of <2), although leaves were increasingly elongate at high phytomer rank in the latter species (Figure 5E). In contrast, leaves of *T. inodorum* tended to be more oblate at high phytomer rank as the length-to-width ratio declined from approximately 3 to 1 (Figure 5E). The angle at which leaves were positioned relative to the stem axis is indicated by the petiole pitch angle or, in *T. inodorum* where there was no apparent petiole, by the leaf pitch angle (Figure 5F). In *C. album* and *P. aviculare*, leaves at low phytomer rank were positioned approximately at right angles to the main stem, while leaves at high rank numbers tended to be aligned closer to the stem axis, indicated by the decrease in petiole pitch angle. The leaf pitch angle in *T. inodorum* was large (approximately 90-120°: Figure 5F), except for leaves positioned at the lowest and highest phytomers, reflecting the fact that these leaves tended to droop downwards from the nodal point of emergence.

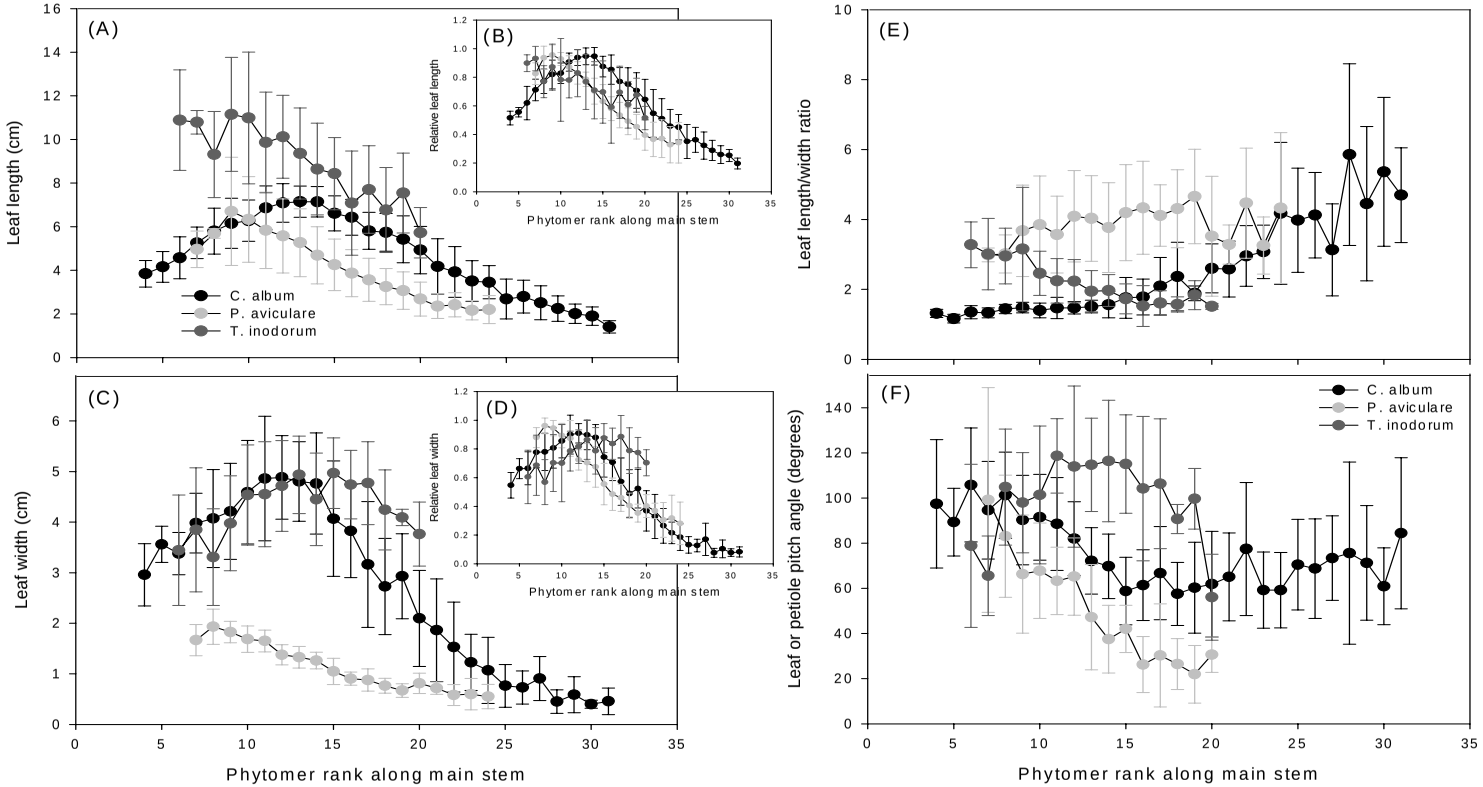

Figure 5. *Leaf shape parameters acquired by digitization of mature plants. (A) Leaf length, inset (B) leaf length relative to the longest leaf, (C) leaf width, inset (D) leaf width relative to the widest leaf, (E) leaf length-to-width ratio and (F) angle at which the petiole (or leaf) emerged from the main stem. Values are the mean±s.d. of n=3-12 values per phytomer for 12 plants except P. aviculare (8 plants)*

DISCUSSION

Comparison between species of shoot-architectural data, acquired by plant digitization, has provided detailed information on the growth and form of three different arable weed types that will form the basis of future architectural models. In this study, we have focused on analysis of the architectural data in order to make general predictions about the ability of different arable weeds to respond to environmental variables, particularly irradiance intensity. For example, despite experiencing the same thermal and light environment, rates of plastochron production varied significantly between the three arable weed species (Table 1). Plastochron production rates were maximal in the first half of the experimental period for *C. album* and *T. inodorum*, with faster development in *C. album*, reflecting the larger total number of nodes per plant in this species. In the same time period, intermediate rates of plastochron production were observed for *P. aviculare*. However, this rate could not have been sufficient to sustain the emergence of the majority of nodes, and plastochron production was maintained at a high rate in the second part of the experiment when development of the other two species had decelerated. High rates of plastochron production early in plant development might indicate a greater ability to respond to competition in a mixed stand, allowing rapid growth to avoid shading and maintain photosynthetic organs at the canopy surface.

Plant growth form and strategies to avoid self-shading can be summarized and postulated from the architectural data in Figures 2-5. For *T. inodorum*, which supported a high density of leaves per main stem node (compare Figure 2 and Table 1), possession of finely dissected leaves (Figure 1), is likely to be the major strategy to avoid self-shading. A phyllotaxis angle of 140^{o} also ensured that successive leaves on the main stem did not directly overshadow the previous leaf. In addition, leaves at high phytomer rank tended to be relatively short and would not overshadow the lower leaves. The tall, relatively open structure of *C. album* plants supported an intermediate density of leaves per main-stem node, and the mean phyllotaxis angle of 125^{o} suggested that there was potential for leaf overlap. However, the potential for overshadowing was mitigated by a relative decrease in leaf width and in petiole angle in leaves at high phytomer rank, which were oriented closer to vertical. The spreading growth habit of *P. aviculare* plants, representing an alternative strategy to avoid self-shading, might have been responsible for the variation in phyllotaxy along the main stem, indicating an effect of ground contact on the direction of node development.

The potential response of weed species to competition for light in the crop canopy can only be speculated at this stage of the research. A spreading growth habit in *P. aviculare* is likely to facilitate growth towards light at the edge of the stand of plants. This response might also be possible for *T. inodorum*, which exhibited large changes in stem pitch angle, and hence in growth direction, at low phytomer rank along the main stem. Alternatively, a reduction in stem pitch angle at these nodes would ensure that stem growth of shaded *T. inodorum* plants is directed up towards the top of the canopy. Increased allocation to stem elongation, in terms of internode and petiole extension, at the expense of branch production, is a typical

response to the reduction in the ratio of red/far-red wavelengths that accompanies canopy shading, and has been demonstrated in arable weed species like *C. album* (Smith 2000) and *Capsella bursa-pastoris* (Karley et al. in prep.). Depending on the plant developmental stage at which shading is imposed, this could alter the distribution of internode lengths along the main stem (Figure 3A). In addition, changes in resource allocation to shaded leaves are frequently observed, for example an increase in leaf dry-matter allocation when shading is imposed on *Polygonum* species (Griffith and Sultan 2005) and *C. bursa-pastoris* (Karley et al. in prep.). Other anatomical and biochemical changes are known to occur in shaded (compared to full sun) leaves (e.g. Eichelmann et al. 2005) which, in combination with reduced irradiance and altered spectral composition as light passes through the canopy, will impact on the rate and efficiency of photosynthetic carbon fixation. Changes in resource acquisition will have knock-on effects for allocation to reproduction (Smith 2000), root growth (Ryser and Eek 2000), and for organisms that shelter, feed or reproduce on the plant.

Thus, measuring the variability or plasticity of plant architecture is important for understanding how plants interact with their environment at biochemical, physiological and ecological scales. Differences between individuals in plant structure and the plasticity of their response to environmental variables affects the way in which plants compete for and acquire resources, and thus will influence the species composition of the plant canopy. This has important implications at the community scale, because arable-weed abundance, even when only a few percent of the total field biomass, can strongly influence the composition and diversity of other trophic groups (Hawes et al. 2003; Bohan et al. 2005), for example through variation in provision of food for herbivores or of suitable microclimates as refugia for invertebrates and their eggs or offspring. The ability to quantify plant architecture in three dimensions is therefore crucial for plant structure–function analysis in agro-ecology.

This study has demonstrated the utility of quantifying and analysing plant architecture to understand plant growth habit in relation to the arable environment. Our ultimate aim, to characterize the structure of arable-plant assemblages and explore functional responses to crop management, is ambitious and will require development and validation of new and existing plant structure–function models. Measurements gathered from digitized arable plants will enable models of plant growth and structure to be constructed and parameterized (e.g. Prusinkiewicz 1998; Mündermann et al. 2005). Modelling of plant structure in three-dimensional space will be a tool for hypothesis generation and is a critical step towards exploring the interaction between plant architecture and environmental variables, both in terms of plant–plant competition for resources and as a basis for understanding plant interactions with other trophic groups. The aim is not to model the entire agro-ecosystem but to explore small virtual assemblages to identify key interactions and sets of traits to which system behaviour is sensitive. Developing individual-based ecosystem models necessitates gross approximations to the structure of individuals, typically a 2-dimensional space occupancy or 3-dimensional bubble. More detailed functional-structural models of small assemblages can be used to test and inform the validity of these inevitable approximations. Is architecture important? Over what

scales and for what functions? For example, plant–plant interactions are likely to operate over different scales to plant–herbivore interactions. An L-systems approach to modelling plant architecture will be employed, along with experimental work to investigate the degree of within-species variation in architecture and test hypotheses about architectural plasticity in response to resource competition among plants. Ultimately, this approach will improve our understanding of the architectural diversity of the arable weed flora and the importance or otherwise of this diversity for weed–crop interactions and the arable food web.

ACKNOWLEDGEMENTS

We are grateful to Dr Dave Skirvin of HRI Warwick for the kind loan of digitizing equipment in the initial stages of the project. Thanks also to Gladys Wright and Mark Young for assistance with experiment design and to Sophie Holroyde for plant maintenance and monitoring, and assistance with plant digitization.

REFERENCES

Bohan, D.A., Boffey, C.W.H., Brooks, D.R., et al., 2005. Effects on weed and invertebrate abundance and diversity of herbicide management in genetically modified herbicide-tolerant winter-sown oilseed rape. *Proceedings of the Royal Society of London Series B, Biological Sciences*, 272 (1562), 463-474.

Burke, M., 2003. *Managing GM crops with herbicides: effects on farmland wildlife*. DEFRA, London. Farm Scale Evaluations. [http://www.defra.gov.uk/environment/gm/fse/results/fse-summary-05.pdf]

Eichelmann, H., Oja, V., Rasulov, B., et al., 2005. Adjustment of leaf photosynthesis to shade in a natural canopy: reallocation of nitrogen. *Plant, Cell and Environment*, 28 (3), 389-401.

Griffith, T.M. and Sultan, S.E., 2005. Shade tolerance plasticity in response to neutral vs green shade cues in *Polygonum* species of contrasting ecological breadth. *New Phytologist*, 166 (1), 141-148.

Hawes, C., Begg, G.S., Squire, G.R., et al., 2005. Individuals as the basic accounting unit in studies of ecosystem function: functional diversity in shepherd's purse, *Capsella*. *Oikos*, 109 (3), 521-534.

Hawes, C., Haughton, A.J., Osborne, J.L., et al., 2003. Responses of plants and invertebrate trophic groups to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 358 (1439), 1899-1913.

Karley, A.J., Holroyde, S., Wright, G.M., et al., in prep. *Response of above-ground architecture to shading and artificial herbivory in an arable weed, Capsella bursa-pastoris*.

Marshall, E.J.P., Brown, V.K., Boatman, N.D., et al., 2003. The role of weeds in supporting biological diversity within crop fields. *Weed Research Oxford*, 43 (2), 77-89.

Mündermann, L., Erasmus, Y., Lane, B., et al., 2005. Quantitative modeling of Arabidopsis development. *Plant Physiology*, 139 (2), 960-968.

Prusinkiewicz, P., 1998. Modeling of spatial structure and development of plants: a review. *Scientia Horticulturae*, 74 (1/2), 113-149.

Ryser, P. and Eek, L., 2000. Consequences of phenotypic plasticity vs. interspecific differences in leaf and root traits for acquisition of aboveground and belowground resources. *American Journal of Botany*, 87 (3), 402-411.

Smith, H., 2000. Plant architecture and light signals. *In:* Marshall, B. and Roberts, J.A. eds. *Leaf development and canopy growth*. Sheffield Academic Press, Sheffield, 118-144.