



Plasticity of winter wheat modulated by sowing date, plant population density and nitrogen fertilisation: Dimensions and size of leaf blades, sheaths and internodes in relation to their position on a stem

Tino Dornbusch^{a,b}, Rim Bacchar^{a,b}, Jillian Watt^c, Jonathan Hillier^d, Jessica Bertheloot^e, Christian Fournier^{f,g}, Bruno Andrieu^{a,b,*}

^a INRA, UMR 1091 EGC, F-78850 Thiverval-Grignon, France

^b AgroParisTech, UMR 1091 EGC, F-78850 Thiverval-Grignon, France

^c University College London, Department of Geography, London WC1E 6BT, UK

^d University of Aberdeen, School of Biological Sciences, Aberdeen, AB24 3UU Scotland, UK

^e INRA, UMR 462 SAGAH, IFR 149 QUASAV, F-49071 Beaucouzé, France

^f INRA, UMR 759 LEPSE, F-34060 Montpellier, France

^g SupAgro, UMR 759 LEPSE, F-34060 Montpellier, France

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ABSTRACT

Mathematical models to describe crop–environment interaction on organ scale need to take crop or plant architecture into account. Up to now, architectural plant models are largely descriptive and parameters need to be estimated for each species, cultivar and environment. Required measurements are extensive and time-consuming. Hence investigating morphological patterns and their modulation as a response to environmental conditions may help to reduce measurement efforts and to predict plant architecture in crop models. In this paper, we describe the plasticity of winter wheat – expressed as the dimensions and sizes of leaf blades, sheaths and internodes in relation to their position on a stem – under the climatic conditions of the Paris region. Results are discussed with respect to: (i) genotypic variability, (ii) inter-annual variability, (iii) sowing date and plant population density, (iv) Nitrogen fertilisation and (v) tiller rank.

Eight wheat cultivars grown in the same season showed similar patterns of leaf and internodes dimensions in relation to their position on the stem. For the cultivar 'Soissons', main stem architecture at flowering was remarkably stable when similar growth conditions were reproduced in the different seasons. Increased plant population density yielded longer juvenile, but shorter adult leaf blades and sheaths. Earlier sowing led to an increase in the number of juvenile phytomers – growing before the onset of stem elongation – on the main stem, whereas the number of adult phytomers was almost identical. Further there were little differences in the size of leaf blades, sheaths and internodes between the main stem and axillary tillers. We found remarkable differences in the size of adult leaf blades and sheaths in different growing seasons, with different timing of nitrogen fertilisation and we discuss decreased availability of nitrogen in the soil in spring as a likely cause.

Data presented here can be used to enlarge the understanding of wheat plasticity regarding the regulation of organ size by temperature, light, plant-available nitrogen and size-mediated effects towards a mechanistic modelling of these responses.

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1. Introduction

The structure of crop canopies is an essential component to describe the interactions between crops and their environment

* Corresponding author at: INRA, UMR 1091 EGC, F-78850 Thiverval-Grignon, France.

E-mail address: bruno.andrieu@grignon.inra.fr (B. Andrieu).

with mathematical models. A simple description of structure is used in classical crop models taking only a small number of compartments – typically roots, stems and leaves – into account. Detailed representation of plant architecture at organ scale allows to investigate, e.g. radiation transfer (Chelle and Andrieu, 1998), movement of liquid water (Bassette and Bussi ere, 2008), or interception of pesticides (Dorr et al., 2008) by individual plants and organs. Development of functional–structural plant models and the use of descriptive architectural models to simulate physical trans-

fers aim at addressing new questions such as competition of plants with weeds, analysis of epidemics, and design of new ideotypes (for review see Vos et al., 2010).

The plasticity of architecture in response to environmental conditions, which is an essential component of plant fitness and productivity, is however not fully understood. This arises from the number of processes involved in the regulation of the amount of plant modules (organs) produced, their size, geometry and lifespan. Leaf size, for example, is regulated by the availability of water, carbon (C) and nitrogen (N), physical factors (e.g. temperature, water vapour pressure deficit), phytohormones and other metabolites mediating responses to developmental (e.g. floral transition) and environmental signals (e.g. red: far red light).

In cereals, few quantitative studies on plasticity have been carried out so far, which take dimensions of phytomers (mainly: leaf blades, sheaths and internodes) on all tillers into account. Evers et al. (2005), Fournier et al. (2003) and Tivet et al. (2001) presented relationships of phytomer dimensions between main stem and axillary tillers for one cultivar. Other work encompass only data for the first juvenile leaves or for the main stem alone (Equiza and Tognetti, 2002; Kirby et al., 1982; Friend, 1965; Gallagher, 1979). Assuming non-limiting nutrient and water supply, temperature and incoming photosynthetically active radiation were identified as the most relevant external environmental factors to influence leaf dimensions. Further, Abbe et al. (1941) and Kirby (1977) proposed a direct relationship between size of the shoot apical meristem (SAM) and leaf blade width. Casey et al. (1999) pointed out that the length of the sheath tube a leaf blade grows in, largely determines its final length. In other words, the length of a cereal leaf (more precisely the whorl) influences the length of the consecutive one. This phenomenon was denoted as a size-mediated effect by Louarn et al. (2010). Size-mediated effects interplay with growth responses to environmental conditions. Hence a range of sometimes interconnected regulatory mechanisms – some of which have been indicated above – need to be taken into account to develop mechanistic models that are able to describe cereal plasticity.

As a consequence, existing models of plant architecture are largely descriptive. To a large extent they rely on the identification and formalisation of patterns found in the architectural traits of organs according to their age and topological position within a plant. The regulatory mechanisms that lead to the observed patterns are not fully understood, so that identifying these patterns – as stable relationships of organ dimensions with topological position that are conserved in a range of environments – is essential to build and parameterise architectural models. More generally, this would provide the framework for an efficient description of plasticity as a genotype–environment interaction ($G \times E$).

Wheat (*Triticum aestivum* L.) is one cereal species for which architectural models are actively being developed and applied. For instance ADEL-wheat has been parameterised to model winter wheat architecture for one set of environmental conditions (Fournier et al., 2003). The model parameterisation has further been adapted for spring wheat and a different set of environmental conditions including various plant population densities (Evers et al., 2005). ADEL-wheat coupled to process-based models was used to investigate the conditions of axillary tiller bud outgrowth (Evers et al., 2007a) and disease epidemics (Robert et al., 2008). Recent works have partly elucidated functional aspects such as the translocation of nitrogen (Bertheloot et al., 2008) or the role of source–sink relationships in bud outgrowth (Evers et al., 2010), but modelling of organ size still remain empirical and hence dimensions need to be measured for each genotype and environment.

As a substitute for the lack of the availability of mechanistic models to predict organ size and as a step towards developing such models, this study explores the plasticity of the dimensions and size of winter wheat leaf blades, sheaths and internodes in relation

to their position on the stem. Here we present the impact of: (i) genotypic variability, (ii) inter-annual variability, (iii) sowing date and plant population density, (iv) N fertilisation and (v) tiller rank, on the dimensions and size of leaf blades, sheaths and internodes based on datasets obtained during five years of field experiments.

2. Materials and methods

2.1. Field experiments

Experiments were located at the INRA research unit of Thiverval-Grignon, near Paris (48°51'N, 1°58'E, 70 m) with a maritime influenced climate (Köppen climate classification Cfb; Köppen, 1931) that permits high yields for winter annual crops. Winter wheat (*Triticum aestivum* L.) was grown on a deep loamy soil (typic *Eutrochrept*; US soil taxonomy) under non-limiting availability of water (irrigation when needed) and nutrients. The standard regional agronomic practices for winter wheat are: (i) sowing at mid to late October (ii) plant population density of 200–300 plants per m², (iii) N fertilisation of 150–200 kg ha⁻¹ split into two doses, the first usually given late February to early March and the second at the onset of stem elongation, early to mid April and (iv) fungicide, herbicide and growth retardant applications if required. Our experiments comprised eight wheat cultivars (Y03/04), three plant population densities ('Soissons' in Y98/99, Y07/08, Y08/09), three sowing dates ('Soissons' in different seasons) and two N fertilisation treatments ('Soissons' in Y05/06). Plots consisted of nine planting rows with an inter-row distance of 0.175 m. Plant population density is referred to as low density (D_1), normal density (D_2), and high density (D_3). Sowing dates are divided into early sowing late September (S_1), normal sowing mid to late October (S_2) and late sowing mid November (S_3). N fertilisation followed the standard scheme (two doses) except in the N_0 treatment in Y05/06, where no N was supplied during the whole season. Major experimental conditions for the different growing seasons (abbreviated as e.g. Y08/09) are summarised in Table 1.

2.2. Sampling procedures and measurements

In all experiments, we aimed at a faithful estimation of the dimensions and size of mature (fully extended) leaf blades, sheaths and internodes using median plants, thus avoiding consideration of the plant-to-plant variability at crop level. To select median plants, we used two simple criteria: (i) similar number of tillers per plant, (ii) similar developmental stage of the main stem using the Haun stage (H; after Haun, 1973). Based on these criteria, leaf blades of tillers were regularly tagged during growth. The main stem is denoted as MS and the axillary tillers as Tk ($k=0, 1, 2, \dots$) T1 being the tiller that emerges from the axil of the first true leaf blade. The coleoptile tiller T0 rarely emerged and was not considered in data processing.

In Y98/99, Y03/04, Y05/06, the architectural traits length (l_{bl}) and width (w_{bl}) of leaf blades, and length of sheaths (l_{sh}) and of internodes (l_{in}) were measured with a ruler. The distance of the leaf collar from the shoot base (in short: collar height h_{col}) was measured for each phytomer. The distance of the ear collar (sum of internodes + peduncle) is referred to as stem height. Leaf blade area (A_{bl}) was derived as $A_{bl} = l_{bl} \cdot w_{bl} \cdot f_t$, where mean values for the shape factor f_t for each phytomer rank were taken from measured data given by Dornbusch et al. (2011).

In Y07/08 and Y08/09, at two to eight occasions during crop growth depending on the experiment, 15–45 tagged median plants were collected and l_{bl} , w_{bl} and A_{bl} were computed from images obtained with a flat-bed scanner that were processed using the program Lamina2Shape (Dornbusch and Andrieu, 2010). In addi-

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