Proceedings of the 7th International Conference on Functional-Structural Plant Models, Saariselkä, Finland, 9 - 14 June 2013. Eds. Risto Sievänen, Eero Nikinmaa, Christophe Godin, Anna Lintunen & Pekka Nygren. http://www.metla.fi/fspm2013/proceedings. ISBN 978-951-651-408-9.

Plant structure in crop production: considerations on application of FSPM

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Highlights: Cereals, potato and glasshouse cut rose, representing monocot annuals, vegetative propagated dicot annual and woody perennials, have different structural development. 'Bud break', initiating tillering (monocots) and branching (dicots) is a key process determining plant structure. Plant population density is affecting bud break in each of these three species. The mechanisms explaining these observations and the application in models will be discussed, primarily carbon source : sink ratio and light quality (i.e. red : far red ratio.

Keywords: barley, maize, wheat, potato, cut rose, carbon source sink, red : far red ratio

INTRODUCTION

Growers apply crop management measures that modulate crop structure in order to influence the yield and properties of the produce, e.g. the size distribution. Examples of the latter are grain size distribution of malting barley, tuber size distribution in potato and length and diameter of flower shoots in glasshouse cut roses. Management starts already with decisions on planting density and plant configuration. In cereals, the desired degree of tillering has always been a subject of discussions on the preferred ideotype. Understanding plant structure, how it comes about, how it can be manipulated are therefore key questions in production-oriented plant sciences. Plants can modulate their structure by adaptation of sizes of individual organs, but more importantly by a variable degree of tillering (cereals, grasses) or branching (dicots). Insight in the mechanisms determining the degree of branching and tillering is a central issue for modelling plant structure. A special, but so far virtually neglected issue is the variation among individuals and if this degree of variation can be explained and perhaps managed.

The objectives of this paper include (i) to highlight the essential features of structural development of some different crop species, (ii) summarize the main factors determining the degree of tillering and branching, (iii) address the concepts used to model tillering and branching, using functional-structural plant models (FSPM). Endeavours to construct FSPMs reveal knowledge gaps on the one hand, and if solved or circumvented, provide the opportunity to analyze how organ properties evolve from ontogeny and plant plasticity and how management could make a difference in properties of organs, e.g. size distributions. FSPM can improve our understanding of the efficacy of management options.

This paper is limited to cereals, i.e. maize (*Zea mays*) and the small grain species barley (*Hordeum vulgare*), wheat (*Triticum aestivum*) and rice (*Oryza* spp.), as opposed to potato (*Solanum tuberosum*) and glasshouse cut rose (*Rosa hybrida*); cereals being representatives of monocotyledonous annual species, potato representing vegetatively propagated dicot annual species and cut rose representing dicot perennial species.

STRUCTURAL DEVELOPMENT OF CEREALS, POTATO AND CUT ROSE

Early work on the development of FSPM to field crops dealt with describing the structural development of maize in a model called ADELmaize (Fournier and Andrieu, 1999). Maize does not produce tillers under practical conditions, simplifying modelling of the structural development. The main issues were (i) quantifying the plastochron, the phyllochron, and the size distributions of the leaf blades, leaf sheaths and internodes (if extended).

Though temperature is the dominant driver of rate of development, it appeared that plant population density (Andrieu et al., 2006) and level of irradiance (Bos et al., 2000) affected the rate of development in maize. Andrieu and Fournier postulated that initiation, extension, and appearance of successive organs are highly coordinated processes, where environmental effects on rate and/or duration of one component process has consequences for the timing of all succeeding developmental events.

The structural analysis applied to maize was also applied to wheat (Fournier et al., 2003, Evers et al., 2005), barley (Buck-Sorlin et al., 2007) and rice (Xu et al., 2011). In these small grain cereals the degree of tillering is a prime mechanism to adapt plant structure to available resources. Fundamental insight in the regulation of tillering is key to adequate modelling of canopy structure and the consequences for issues such as grain size distribution.

The potato tuber can be regarded a stack of swollen phytomers, with axillary buds, called ‘eyes’, in phyllotactic arrangement on the tuber’s surface. Stems arising from a bud are called main stems. The structure of a potato plant is primarily determined by the number of main stems per plant. That number depends on many factors including number of eyes per planted tuber and fraction bud break. The second main determinant of the structure of the crop is branching. Buds in leaf axils just below and above the soil surface can break to produce basal lateral branches (Vos, 1995). The main stem apex produces a terminal inflorescence. Apical branching is of sympodial nature with apical branches commonly occurring from the axils of the second and third leaf below the flowers. Two primary apical branches can produce four secondary branches, which could produce eight tertiary branches, etc. The basal laterals can also produce inflorescences and apical laterals, adding to the complexity of the structure.

Rose crops commonly start from nodal cuttings. The primary shoot is commonly bent down near the time it would flower. It will branch in horizontal direction; any upright growth being re-bent or removed. The ‘bent canopy’ that develops in this way serves as a source of assimilates for vertically growing shoots which are harvested and sold. Axillary shoots emerging from the base of the primary shoot, called bottom breaks, form the basis of the woody structure from which vertically growing harvestable flower canes emerge continuously over 4-7 years. When a flower cane is harvested, commonly a shoot remainder is left with some nodes and axillary buds. Variable fractions of buds below the cut end may break and produce new shoots. When new shoots grow from shoot remainders of the preceding harvested shoot, each new generation of harvested flowers originates from a next higher level of branching. This is associated with intrinsically thinner shoots than the previous harvest. At ‘some stage’ the grower will decide to cut back the structure to stimulate branching from buds on lower orders of branching. Managing the crop so as to achieve continuous production of shoots of the desired dimensions is a complicated game involving management of woody structure, the number of shoots allowed to grow and glasshouse climate. There are practical experiences how to do this, but there is no solid theory explaining how a grower can achieve his/her objectives at minimum interference, i.e. at minimum cost.

MODELLING CROP STRUCTURE

The plant species considered, cereals, potato and cut rose, differ in many morphological and physiological respects. For cereals, concepts for modelling structural development are most advanced, allowing quite accurate prediction of the time when a next leaf or a next tiller will appear, *if* it is going to appear. For rose there is a prototype structural model (Buck-Sorlin et al., 2011) and for potato there is interest to develop it. Apart from simulating adaptation in organ sizes, the common challenge is to design concepts when buds will grow out to become a tiller or branch. In general, the number of tillers or branches declines with increase in plant population density. This is true in cereals (Darwinkel, 1978, Evers et al., 2006) and potato (Vos, 1995) and likely in rose (Wubs et al., in preparation). Ample availability of nitrogen (N) stimulates tillering (Longnecker et al., 1993) and branching (Vos, 1995). Soil N and P (phosphorus) as well as red : far red ratio of light in the canopy affect the plant’s hormonal signalling system controlling bud break (Domagalska and Leyser, 2011). Experimental evidence shows that the degree of tillering responds to the imposed red : far red ratio of the light regime (Casal et al., 1987, Skinner and Simmons, 1993). Literature search did not yield information on effects of red : far red ratio on (basal) branching of potato. In rose explants far-red illumination inhibited bud break, whereas red, blue and white light promoted bud break (Girault et al., 2008). When whole rose plants were illuminated with higher red:far-red ratios, more buds sprouted (Mor and Halevy, 1984). However, Wubs et al. (in preparation) did not find such effects of red and far-red on bud break in rose; higher irradiance on buds was associated with more bud break rather than spectral composition of light absorbed by the bud.

Information from ‘dose – response experiments’ on factors affecting bud break can generally not be used directly in mechanistic modelling. A mechanism explaining the observations has to be deduced using insights from physiology. Effects of plant population density fuelled the idea that trophic relations determine branching and tillering: with more plants growing per unit area, less light can be absorbed and fewer assimilates produced per plant. Too many sinks (growing organs) and associated low levels of available carbohydrate per sink would act as, or be translated into, signals precluding further bud break. The effect of nitrogen could fit in this picture, because N limitation feeds back on assimilate production per plant, i.e. source capacity. Many models use, with variable degree of conviction, carbon source-sink ratios as a regulator to simulate aspects of growth and development, e.g. the Greenlab series (Ma et al., 2008). Evers et al. (2007) used a reaction norm of bud growth to red : far red ratio to simulate cessation of tillering, but this descriptive approach needs mechanistic substantiation. Detailed models simulating bud break as emergent from internal hormonal interactions and external environmental cues may yield rules that can be implemented in plant and crop models (Evers et al., 2011). In rose, in spite of much effort (Girault et al., 2008), no consistent concept was found to model bud break in crop situations (Buck-Sorlin et al., 2011; Wubs et al., in preparation). Do we need paradigm shifts to make progress?

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