Evol Ecol (2008) 22:273–277
DOI 10.1007/s10682-008-9250-8

EDITORIAL

Generality, specificity and diversity of clonal plant research

Marek Sammul · Tiiu Kull · Kalevi Kull · Ariel Novoplansky

When describing the structure and growth dynamics of the 'great Tree of Life', Charles Darwin writes:

> "As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever-branching and beautiful ramifications" (Darwin 1872, p. 100).

The principal feature of plant form underlying Darwin's metaphor for the Tree of Life captures the modularity of plant structure that allows it to readily develop and abort organs according to their performance, relative success and dynamic interactions with the external environment and other organs on the same plant (Sachs and Novoplansky 1995).

The concept of modularity in plants was further introduced to population ecology by John Harper (1977, 1985) and developed by others (e.g. Callaghan et al. 1990), but the fundamental concept goes all the way back to the late eighteenth century. According to the botanical studies of Goethe (1790), every plant and its shoots are comprised of similar elements, each made of a piece of a stem with a leaf at its end. Metamorphosis makes these elements different in size and shape, but the modular structure is universal.

Carl Schultz (1843) named these basic morphological elements 'anaphyts', and Charles Gaudichaud (1841)—'phytons'. The theory of anaphyt (or phyton) was further developed by Delpino (1883), Čelakovský (1901) and Velenovský (1905–1913). These ideas have been later used in developing the detailed classifications of plant growth forms (e.g. Serebryakov 1962). Thus, the conceptualization of clonal plants as modular structures can be seen as a variation on the early concept of the "anaphyt".

M. Sammul · T. Kull · K. Kull
Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Tartu, Estonia

A. Novoplansky (✉)
Mitrani Department of Desert Ecology, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede-Boqer Campus 84990, Israel
e-mail: anovopla@bgu.ac.il

Following the pioneering work of J. Harper, many studies dealt with the implications of plant modularity (e.g. Jackson et al. 1985). The idea was also used for the modelling of rhizome growth (e.g. Bell 1985). Since then, a more coordinated and extensive study of modular structures in plants and effects of modularity on growth and population dynamics has been developed (de Kroon and van Groenendael 1997). The research priorities formulated by Harper (1978) included the comparison of vegetative and sexual reproduction, studying the implications of fragmentation and integration of genets and ramets, comparison of rooting at nodes to creeping without rooting, and studying the adaptive aspects of spatial expansion and storage of assimilates in clonal structures (de Kroon and van Groenendael 1997). Later studies further diversified to include a wide spectrum of topics such as:

(a) Clonal growth and development in plants, including the ecophysiological regulation of clonal growth, signalling and communication;
(b) Plasticity of growth and foraging behaviour in situ and under controlled laboratory conditions;
(c) Integration and "division of labor" between different ramets on the same clone with an emphasis on the extent to which ramets are physiologically integrated, and the comparison of different integration strategies and their potential ecological and evolutionary implications;
(d) Inter- and intra-specific interactions at both the ramet and the genet levels, including the possible implications of self/non-self discrimination, and the relative roles of competitive and facilitative interactions within and between clones;
(e) Effects of clonality on community dynamics, in particular the extent to which different communities vary in the prevalence of sexual reproduction and vegetative propagation; the importance of the development and maintenance of bud banks to community dynamics; the environmental determinants of the relative importance of clonal growth and the extent to which vegetative propagation directs community dynamics at different ecosystems;
(f) The role of clonality in population genetics, including the implications of the ratio of asexual to sexual reproduction on genetic diversity; the effects of somatic mutations on the fitness of potentially eternal clonal genets;
(g) The evolution and evolutionary ecology of clonal plants with an emphasis on the adaptive significance of clonal growth.
(h) The effects of environmental variation on the relative importance of clonal vs. sexual recruitment;

Some of these fronts, e.g. the study of plastic attributes and foraging attributes of clonal growth and ramet mobility, have already yielded many important insights however the study on some of the other fronts still awaits detailed exploration.

Starting in 1988, regular international conferences on clonal plant research have been organized (Table 1). Proceedings of these meetings were usually dedicated to specific topics and accompanied by critical reviews (e.g. Eckert 1999). As such, they provided overviews on the development of clonal plant research through the last two decades.

The current Special Issue comprises a selection of papers that were presented at the Clonal Plant Workshop held in Pärnu Estonia in 2006. It includes review papers, case studies and discussion notes summarizing part of the leading research carried out on clonal plants in the last few years.

The Special Issue includes two *review papers*. Lonnie Aarssen proposes a hypothesis on the evolution and spread of clonality as a by-product of selection pressure on young individuals, offering an explanation to the rarity of clonality in taxa whose individuals are large.

Table 1 Clonal plant workshops

	Place	Year	Topic	Proceedings
1.	Schin op Geul, Netherlands	1988	Clonal growth in plants: regulation and function	van Groenendael and de Kroon 1990
2.	Abisko, Sweden	1990	Clonal plants and Environmental change	Callaghan et al. 1992
3.	Krkonoe Mountains, Czech Republic	1992	Plant clonality: biology and diversity	Soukupová et al. 1994
4.	Budapest–Visegrad, Hungary	1995	Clonality in plant communities	Oborny and Podani 1996
5.	Bangor, Wales, UK	1997	Clonal plants and environmental heterogeneity—space, time and scale	Price and Marshall 1999
6.	Obergurgl, Austria	2000	Ecology and evolutionary biology of clonal plants	Stuefer et al. 2001
7.	Kuusamo, Finland	2003	Reproductive strategies, biotic interactions and metapopulation dynamics	Tolvanen et al. 2004
8.	Pärnu, Estonia	2006	Generality, specificity and diversity of clonal growth	This volume

Honnay and Jacquemyn provide a review on the relationship between self-(in)compatibility and genotypic diversity. They demonstrate the counterintuitive potential of self-incompatibility to reduce rather than to increase genotypic diversity in natural populations.

A series of contributions provide *case studies* on various aspects of plant clonality that can be roughly divided into two groups. One group of studies deals with *plasticity of clonal growth*, including plant's abilities to perceive their environment and execute developmental decisions.

Herben and Novoplansky used spatially explicit modelling to explore the population- and community-level implications of self/non-self discrimination. According to the results, plants with significant self/non-self discrimination are able to pack their ramets more tightly, which in turn affects the spatial distribution and patterning of clones. Interestingly, self/non-self discrimination may also result in a decreased genet diversity which demonstrates a potential for emerging higher-order implications of basic physiological attributes.

The ramifications of plastic responses to changing environmental conditions were studied by Huber et al. They showed that petiole elongation in *Trifolium repens* enabled plants to avoid shade could be rather costly. Plasticity of cell number and flexural stiffness, but not of tissue rigidity provided a selective advantage. However, increasing the number of cells, decreasing the size of cells, or increasing the flexural stiffness was not associated with costs. Their data also suggested that selection on shade-induced changes in cell size and number differs among light environments.

Plasticity of clonal growth was also addressed by Hutchings and Wijesinghe who experimentally demonstrated that both the spatial extent and the quality of high-resource patches influenced plant growth. While this general phenomenon has been demonstrated before, the current study emphasized the observation that plant responses do not merely involve responses to local conditions, but are also based on integration between modules that develop under potentially contrasting conditions.

Thomas and Hay showed that stolon apical buds were able to perceive and plastically elongate their internodes in response to changes in the humidity in their immediate proximity. These responses increased plant performance and demonstrated an adaptive trade-off between explorative and exploitive ramet placement.

Macek and Lepš demonstrated that phenotypic plasticity enhanced the potential of *Potentilla palustris* to grow in a wide range of habitats thus increased plant performance at large spatial scales.

The second group of contributions focus on questions related to *physiological integration* and resource sharing in clonal plants.

In their study on clonal integration in patchy environments, Janeček et al. showed that multiple stresses might prohibit free exchange of limiting resources via clonal network. They used a three-link model system and found that the costs and benefits of resource sharing were equal in *Eriophorum angustifolium*. They also concluded that clone behaviour depended on its complexity.

The pattern of resource sharing between ramets of *Aegopodium podagraria* from contrasting habitats was explored by Nilsson and D'Hertefeldt. They demonstrated that forest genets of *A. podagraria* were more dependent on resource sharing than those from gardens. It is hard to evaluate if their results are caused by genetic drift or local adaptation to resource heterogeneity however their study provides further support to the notion that a high degree of resource sharing would be primarily beneficial in habitats where resources are distributed patchily.

Resource sharing can also have significant negative consequences, as demonstrated by a model by Koubek and Herben. Clonal integration may allow for a rapid spread of pathogens among physiologically integrated ramets. However, the model predicts that integration is expected to be selected against only under extremely high levels of pathogen infection.

Klimeš provided support for the hypothesis that species with prolonged physiological integration between ramets of a clonal fragment prevail in stressful environments, whereas "splitter" species dominate relatively benign habitats. However, the results also suggest that clonal integration is evolutionarily conservative as the relationships between clonal integration and environmental factors could be largely explained by phylogeny.

The Special Issue also gives a stage to a forum of short communications that are hoped to provoke discussions on a few debatable topics, in particular the regulation of growth and reproductive behaviour in clonal plants.

Over a decade ago, de Kroon and van Groenendael (1997) have noted that in clonal plant research "most of the new developments to date are defined at a single organization level, either the individual, the population or the community. One major challenge for the future will be to further explore the links between the concepts defined at each of these levels". About 11 years later we can only reiterate that statement and add that in spite of the great progress made on a few fronts, many phenomena related to clonal growth still beg for further research. In particular, we would like to stress the need for integrated multi-disciplinary efforts in studying emerging properties of lower hierarchical attributes and their scaled up implications at higher organizational levels of the population, community and the entire ecosystem.

Acknowledgements We would like to extend our thanks to all the participants of the Pärnu meeting. This is publication number 604 of the Mitrani Department of Desert Ecology.

References

Bell AD (1985) On the astogeny of six-cornered clones: an aspect of modular construction. In: White J (ed) Studies on plant demography: a festschrift for John L.Harper. London, Academic Press, pp 187–207

Callaghan TV, Svensson BM, Bowman H, Lindley DK, Carlsson BC (1990) Models of clonal plant growth based on population dynamics and architecture. Oikos 57:257–269

Callaghan TV, Svensson BM, Jónsdóttir IS, Carlsson BA (eds) (1992) Clonal plants and environmental change. Oikos 63:339–453

Čelakovský LJ (1901) Die Gliederung der Kaulome. Bot Ztg 59:79–114

Darwin C (1872) The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life, 6th edn. John Murray, London

de Kroon H, van Groenendael J (eds) (1997) The ecology and evolution of clonal plants. Backhuys Publishers, Leiden

Delpino F (1883) Teoria generale della fillotassi. Atti della Universita di Genova 4(2):1–345

Eckert CG (1999) Clonal plant research: proliferation, integration, but not much evolution. Am J Bot 86:1649–1654

Gaudichaud C (1841) Recherches générales sur l’organographie, la physiologie et l’organogénie des végéteaux. Imprimerie Royale, Paris

Goethe JW (1790) Versuch die Metamorphose der Pflanzen zu erklären. C. W. Ettinger, Gotha

Harper JL (1977) Population biology of plants. Academic Press, London

Harper JL (1978) The demography of plants with clonal growth. In: Freysen AHJ, Woldendorp JW (eds) Structure and functioning of plant populations. North-Holland, Amsterdam, pp 27–48

Harper JL (1985) Modules, branches, and the capture of resources. In: Jackson JBC, Buss LW, Cook RE (eds) Population biology and evolution of clonal organisms. Yale University Press, New Haven, pp 1–33

Jackson JBC, Buss LW, Cook RE (eds) (1985) Population biology and evolution of clonal organisms. Yale University Press

Oborny B, Podani J (eds) (1996) Clonality in plant communities. Opulus Press, Uppsala, Sweden

Price EAC, Marshall C (eds) (1999) Clonal plants and environmental heterogeneity—space, time and scale. Special Issue of Plant Ecology, 141:1–206

Sachs T, Novoplansky A (1995) Tree form: architecture models do not suffice. Isr J Plant Sci 43:203–212

Schultz CH (1843) Die Anaphytose oder Verjüngung der Pflanzen. Hirschwald, Berlin

Serebryakov IG (1962) Ekologicheskaya morfologiya rastenij: zhiznennye formy pokrytosemennyh i hvojnyh [Ecological morphology of plants]. Vysshaya Shkola, Moskva

Soukupová L, Marshall C, Hara T, Herben T (eds) (1994) Plant clonality: biology and diversity. Opulus Press, Uppsala, Sweden

Stuefer J, Erschbamer B, Huber H, Suzuki J-I (eds) (2001) Ecology and evolutionary biology of clonal plants. (Special issue of) Evol Ecol 15(4–6)

Tolvanen A, Siikamäki P, Mutikainen P (eds) (2004). Population biology of clonal plants. (Special issue of) Evol Ecol 18(5–6)

van Groenendael JM, de Kroon H (eds) (1990) Clonal growth in plants: regulation and function. SPB Academic Publishing, The Hague, The Netherlands

Velenovský J (1905–1913) Vergleichende Morphologie der Pflanzen. vols 1–4. Verlagsbuchhandlung von Fr. Rivnac, Prag