PERENNIAL CROPS FOR FOOD SECURITY PROCEEDINGS OF THE FAO EXPERT WORKSHOP

POLICY, ECONOMICS AND WAY FORWARD

24 PERENNIAL POLYCULTURES: HOW DO WE ASSEMBLE A TRULY SUSTAINABLE AGRICULTURAL SYSTEM?

Douglas J. Cattani

Department of Plant Science, University of Manitoba, Winnipeg, MB Canada R3T 2N2 Email: Douglas.Cattani@ad.umanitoba.ca



ABSTRACT

Population growth and demand for food continues to place pressure upon agriculture to provide for mankind. Primary staple production is currently from annual crop species. Herbaceous perennial species for grain and other food products have not been rigorously pursued. Current interest and research into the development of herbaceous perennial species for food is providing new options for food production systems. Development of perennial species will provide the cornerstones for perennial polyculture development. Production challenges including weed competition and fertility requirements may addressed by perennial polyculture. Utilization of multiple species has been demonstrated to provide greater DM productivity by utilizing the entire growing season. Issues concerning synchronization of production and harvest however may not be easily resolved. Historically selection of perennial grasses species for seed production has most often failed to translate into consistent enhanced productivity at the field scale. Current selection methodology and nursery design are most likely inadequate to address field level productivity issues. Competitive nurseries are suggested to provide field level gains at both the mono and polyculture levels. Landscape-wide utilization of narrow genetic cultivars will lead to divergent communities and reduce reliability of production. Initial development and deployment of perennial grains and oilseeds would be enhanced by the utilization of greater diversity within the crop species. Utilization of companion species will aid in many issues related to sustainability, e.g. N_2 fixation, weediness. Initial economic utilization of perennial grains and oilseeds and perennial polyculture are linked to animal production.

Keywords: perennial grain and oilseeds, selection, competition, diversity, companion species

Greater demands for food production, for efficiencies in food production and for sustainability of food production systems are required to meet the needs of an ever-growing population.

Herbaceous perennial species are only recently receiving favourable consideration for grain and oilseed production. Whether owing to the size of the seed, or the ease of establishment and combined with relatively quick production, annuals have been preferred and therefore have garnered almost all of the effort and resources for improvement. Breeding and selection of herbaceous perennials for their seed crops has also received very little effort over the millennia of agriculture. Where improvement in seed productivity has been attempted, seed yield improvement of herbaceous perennials has frequently not experienced great success.

NATURALIZED PRODUCTION

"Production agriculture with its ecosystems simplification, pesticide and fertilizer use, and emphasis on yield, often appears to be at odds with conservation biology." (Banks, 2004). Potential for perennial polyculture to bring agriculture and conservation biology closer may be demonstrated in the ecology of natural production systems such as prairies (Glover *et al.* 2010).

Inputs for controlling environmental factors such as water stress via irrigation have negative impacts at the landscape level (Pataki *et al.* 2011). Reduction in anthropogenic impacts of agriculture may be accomplished through the use of perennials for bioenergy (Georgescu *et al.* 2011) and therefore, by extension, herbaceous perennials as grain, oilseed and potentially as other types of crops. Perennial monocultures for bioenergy are still subject to yield fluctuations owing to environmental conditions, despite adequate agronomic practices (Tulbure *et al.* 2012). Grasslands, nature's polycultures, however are seen as important for carbon sequestration (O'Mara, 2012).

(325)

Monoculture seed production of herbaceous perennials, while allowing for many environmental benefits (depending upon inputs), has some shortcomings. Shortcomings include added fertility, weed control, insect control and a single, defined growth period. All of the above may be addressed through polyculture.

POLYCULTURE

Hunter-gatherer societies in North America had long been passive participants in natural polycultures with their infrequent harvests across wide areas (Kuhnlein and Turner, 1991). However no active polycultures of desirable species are reported, although some groups practiced monoculture agriculture (Kuhnlein and Turner, 1991). We currently practice polyculture in home vegetable, herb and ornamental gardens and in our production of forages for animal feed (e.g. Picasso *et al.* 2008; Wiltshire *et al.* 2010). Pastures and rangelands provide resource conservation, biodiversity enhancement and ecosystem preservation (Wiltshire *et al.* 2010). Polyculture establishment of herbaceous perennial species for large-scale food or feed production will be a new endeavour for humans. Perennial polycultures, where coupled with animal production, are envisioned to require little if any outside applications of nutrients or pest management materials (Glover *et al.* 2010) and the benefits to sustainability should surpass those which have been attributed to organic systems (Lammerts Van Bueren *et al.* 2002) owing to the potential to resist short- and long-term variations in the growth environment.

The Land Institute with its concept of natural systems agriculture has been the recent champion of perennial crop breeding (Jackson, 2002; DeHaan *et al.* 2005; Cox *et al.* 2006, 2010). Once perennial grain and oilseed crops have been developed, a logical next step will be polyculture. Polyculture proposes the annual harvest of potentially several crop species cropped together in each year (Jackson, 2002) and emphasizes sustainability. No single species predominates across the landscape (MacDougall *et al.* 2013) (Figure 1). Even areas predominated by invasive species allow niches for native species to persist (Gilbert and Levine, 2013).

Many herbaceous perennial forage crop species are produced under bi- or polyculture conditions. In experiments where up to sixteen and twenty-four species were seeded (Tilman *et al.* 2001, 1996, respectively), as the number of plant species seeded increased, higher above-ground biomass productivity was realized and soil nitrogen use by the plant community was more complete. DeHaan *et al.* (2009) however showed that if perennial biomass productivity is the sole aim, bi-cultures of a grass and legume are as productive. Seed productivity of perennials, where species maturity and reproductive productivity are major concerns was not addressed. Mixtures of grasses and legumes were found to provide increased DM production over a number of years (Sturludóttir *et al.* 2013). Similar efforts will be required for both bi- and polyculture for food.

Monoculture production of either annual or perennial species, is subject to appearance of non-intended plants (weeds) (Cattani *et al.* 2009; Sturludóttir *et al.* 2013) (Figure 2).



FIGURE 1. VARIABILITY IN STAND IN A HERBACEOUS FI

FIGURE 2. COMPETITION IN AN HERBACEOUS PERENNIAL SEED PRODUCTION FIELD WITH UNSEEDED SPECIES OCCURRING



Picasso *et al.* (2008) found that as the number of seeded species increased above-ground DM production by weeds decreased. Weeds status however can be an arbitrary assignment to a species. Fletcher (1897) defines weed as: "There are many definitions of the word weed ... from a farmer's standpoint ..., 'any troublesome or unsightly plant that is at the same time useless or comparatively so'." This statement implies recognition that there are plants whose impacts are either neutral or beneficial, indicating that multispecies communities were known and accepted. Perennial polycultures with their growing- season long growth potential should lead to reduced weed growth and reduced potential yield loss due to reduced weed competition as seen in many annual crops (e.g. Zhao *et al.* 2006). In many perennial seed increase operations, manual removal of troublesome species is required owing to either the lack of an adequate control chemical and/or timing of appearance of the troublesome species with respect to reproductive growth of the desired crop species.

Weinberg's (1975) systems complexity theory hypothesizes that organized complexity (systems) are less random than unorganized complexity (aggregates). Extending Weinberg's (1975) systems complexity theory to monocultures versus polycultures, with the lack of system complexity in monocultures (e.g. relative genetic uniformity, single species), random events or factors entering the system and not under the control of the producer (e.g. climate, insects, weeds, disease) may have major impacts on the system (e.g. year to year variation in yields).

Human intervention in ecosystems may lead to the loss of redundancy in native species diversity (MacDougall *et al.* 2013). Polyculture systems should provide sufficient system plasticity to adapt to variability in growth environment and allow for adequate production. Components of total productivity will vary from year to year and from location to location (see Picasso *et al.* 2008). Included in this complexity and potential interactions, is the reduced ability to quantify effects of individuals due to the interactions (Weinberg, 1975). These interactions are the most critical components of multispecies (polyculture) systems (Chen and Welter, 2005; Dray *et al.* 2012).

(327)

Construction of a community that enhances the productive capacity of crop species or several crop species is possible. Companion species however, should not restrict crop production, or if a reduction occurs, the companion species contribution should be to a future year's productivity or to sustainability. Therefore, productivity must be evaluated over the life-span of plantings and include benefits accrued to the land unit (e.g. N₂ fixation, soil organic matter, weed control) and include ecosystem benefits and not be measured solely by crop yield and market value. Selection of proper species and selection potentially within of all component species will be required to ensure growing-season-long growth for greater sustainability and productivity. Selection within companion species may need to be against uniformity.

A properly designed perennial system should greatly reduce inputs demands, nutrient losses and the associated environmental impacts (Crews, 2005). Species coexistence depends in part upon temporal variation and therefore polyculture may also buffer impacts of climate volatility (Adler *et al.* 2006). For example, alfalfa (*Medicago sativa*) and stinkweed (*Thlapsi arvense*) are frequently found together in alfalfa seed production fields (perennial seed crop) in Manitoba, Canada (Cattani *et al.* 2009). Overlapping of the reproductive growth and development phases of these species does not occur whereas Canada thistle (*Cirsium arvense*) is relatively synchronized with alfalfa with respect to flowering (Cattani *et al.* 2009) (Figure 2). Canada thistle directly competes with alfalfa during its flowering and pod fill periods and is considered one of the major weed species in alfalfa seed production. The former may be an example of coexistence or concurrence while the latter exemplifies yield competition.

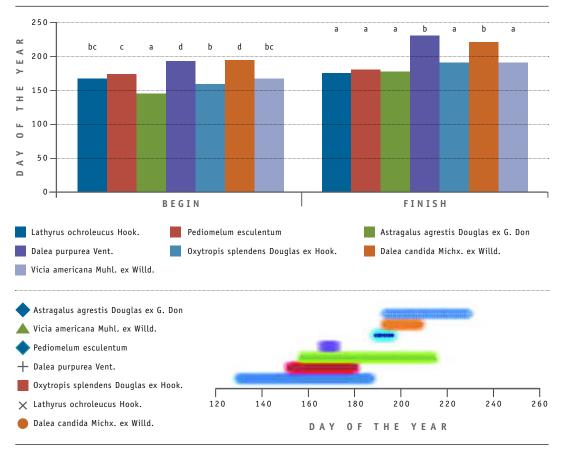
If Weinberg's (1975) theory holds, genetic diversity within a given species must also be broad (greater complexity) in order for that species to be able to appear across a wide swath of the landscape. Vellend (2006) predicts this and Picasso *et al.* (2008) found that the end result of polycultures in both different systems and locations can lead to different production communities. Picasso *et al.* (2008) however, used cultivars or composites for all of their seed sources which may have been too narrow genetically but only if the desired result was a similar species composition across diverse environments. Species diversity has been found in restored grasslands (Helsen *et al.* 2012) and this is most likely due to the occurrence of niches within an ecosystem (MacDougall *et al.* 2013). Selection should aid in the utility of crop and component species. Other factors that have the potential to impact plant biodiversity and persistence include herbivory (Chen and Welter, 2005; Dyer *et al.* 2010; Stein *et al.* 2010), foliar pathogens (Allan *et al.* 2010) and system management (MacDougall *et al.* 2013). Once established, plant recruitment is primarily from vegetative reproductive structures, with seedling establishment contributing very little (Jonsdottir, 1991; Benson and Hartnett, 2006).

Plant systems do not occur in isolation. An estimated 87.5 percent of angiosperms interact with pollinators (Ollerton *et al.* 2011). Cane (2006) reported that *Dalea purpurea* attracted a wide array of pollinating insects throughout its flowering period while Clement *et al.* (2006) list a number of species visiting *Astragalus* and *Onobrychis sp.* Facilitation by common species may

allow for pollination success of rare species (Bizecki Robson, 2013). This indicates that selection of a few species that attract diverse pollinators and that have a somewhat overlapping flowering period may be used to provide adequate sustenance for pollinating species and to perpetuate pollinator species across years (Hajjar *et al.* 2008).

We have been monitoring flowering periods of native species for the past four growing seasons at sites around Manitoba. Looking at native legumes, flowering times are relatively consistent across years with respect to their order (Figure 3a). Selection of which species to include that would ensure an overlapping of flowering periods could result in dual purpose species, i.e. species that attract pollinators and are N_2 fixing. Other considerations such as potential toxicity to animals, if post-harvest biomass is to be grazed or fed, must also be considered (e.g. *Oxytropis splendens*, Macdonald, 1974).

FIGURE 3. A) MEAN BEGINNING AND FINISHING OF FLOWERING TIMES OF SEVEN NATIVE LEGUME SPECIES AT SETON, MB, FROM 2010-2013; B) MEAN OVERLAP OF FLOWERING PERIODS OF NATIVE LEGUMES AT SETON, MB, FOR 2010-2013



329

Breeding of perennial species for use in polyculture will be dependent upon the individual species involved as crop species. If, for example, *Helianthus maximiliani* is bred for uniculm production, yield will likely be dependent upon pollinator availability. Companion species' that can attract pollinators and flower near and/or across the period of *H. maximiliani* flowering will aid in productivity. Companion plant density will need to be weighed against crop plant density to determine the appropriate balance. Pollinators may be brought in from outside the area of production however sustainability is decreased in favour of profit and potentially at the expense of the surrounding ecosystem.

SELECTION

Selection for perennial herbaceous species has primarily been for forage production (Casler and Brummer, 2008). Cultivar development can often be outside of the country of use (e.g. Acharya *et al.* 2013).

Performance in agricultural settings is often very specific. Harlan and Martini (1938) found that few barley varieties were adapted across wide swaths of the landscape. Selection pressure with respect to the genetic uniformity of the crop species requires that it be determined prior to system development. Cultivar development dictates relative morphological uniformity within the resultant cultivar for identification purposes.

One approach for landscape-wide polyculture plantings requires multiple cultivars being developed to the current regulations only to utilize a number of cultivars in an individual planting to increase diversity of the crop species' with the aim of enhancing the crop's ability to withstand stresses (e.g. disease, moisture extremes) across the landscape. Limited selection within a species on important traits (e.g. seed yield and synchronous flowering) yet maintaining genetic diversity could benefit this system by providing adequate plasticity within each species (e.g. Ecovar[™], Ducks Unlimited Canada). Utilization of the entire growing season could be achieved by selecting for maturity differences especially within the supporting species. Increasing diversity within component species should allow for greater adaptability, reducing the variation in the composition among communities established at different sites (Vellend, 2006).

How then should selections for perennial species be made? Will plant nursery type impact the utility of the end product in a different system (e.g. monoculture versus polyculture)? Can progress be made and maintained?

If productivity is to be realized from more than a single species, harvest timing must be such that (e.g. in a two crop species system) either one species is harvested prior to the reproductive growth of the second or both species mature simultaneously and/or are harvested simultaneously. Harvestable species may dictate the system utilized as inherent qualities of the species (e.g. shattering) could determine the approach taken. Companion species benefits must be quantified, possibly their contributions via N, fixation, attraction of pollinators (e.g.

Dalea purpurea (Cane, 2006)) or the ability to suppress other plant growth that would have a greater negative impact on the harvestable species. Ground cover provision in spring or autumn when the crop species may be relatively non-competitive may be beneficial. If a crop assembly is desired, testing will be required to identify ranges of reproductive effort of the potential member species and then combinations of complimentary maturation timings for sustainability of the system.

Elgersma *et al.* (1994) found that selection in space planted nurseries did not correlate to seed yield in progeny seed rows in perennial ryegrass (*Lolium perenne* L.) while Hayward and Vivero (1984) found similar results for forage yield in perennial ryegrass. Burton and DeVane (1953) inferred that advancement under selection under space planted conditions does not translate to similar increases in forage or seed yield in competitive stands. Genetic improvement for forage yield in perennial forage crops has been relatively poor (Casler and Brummer, 2008) due to the lack of a readily apparent traits and selection against 'quality' traits. Conversely, selection for harvest index in annual crops has allowed for genetic gain for yield, but possibly at the cost of overall fitness (Chen and Welter, 2005).

Seed yield component compensation may be impacting plant reproductive efforts under competitive conditions. Yield component compensation is likely environmental and not genetic and that the sequence of developing traits is important (Adams, 1967). Dofing and Knight (1992) based their proposed model for path coefficient analysis on this premise. Species ability to compensate for yield components (plasticity) will in part be dictated by the reproductive requirements of the species as well as reproductive morphology. For example, requirements for dual induction (Heide, 1994) may limit a plant's ability to recover from a poor autumn regrowth period in the spring if reproductive tiller number is fixed by autumn regrowth (e.g. Cattani *et al.* 1997) or by spikelets consisting of a single perfect floret (Cattani *et al.* 2004).

Stand duration prior to selection will also impact adaptation and persistence. Local adaptation is important and may take up to three years to become evident in a perennial species (Hufford and Mazer, 2012). Selection for harvest index in perennial species may decrease overall stand duration via allocation to sexual reproduction versus perenniating structures and tissues (parent-offspring conflict, e.g. Zhang and Jiang, 2000) given the importance of vegetative reproduction in perennial grasslands (Jonsdottir, 1991; Benson and Hartnett, 2006). A positive correlation between storage (corms) and seed production in *Amphibromus scabrivalvis* was reported indicating that increasing harvest index may not necessarily reduce long-term fitness and survival (Cheplick, 1995). In two *Geranium sp.* it was found that flowering had different effects on the following year's flower production (Ågren and Willson, 1994). Fitness reduction may increase with greater pollination success (Ågren and Willson, 1994) therefore selection for increased fertility and increased harvest index may negatively impact long-term survival of the crop in the field. Therefore, species differences may be such that seed yield progress under selection may impact life history in some species but not others.

"The potential seed yield of forage species is high, whereas realized seed yields are generally low and unpredictable." (Elgersma and van Wijk, 1997), due in part to the lack of importance placed upon seed versus forage production of these species and domestication traits such as shattering resistance. The Fecundity Allocation Premium hypothesis indicates that larger (by mass) species can have a greater range of variation of seed sizes (by mass), however species with larger seeds are more likely to have lower lifetime fecundity (Aarssen, 2005). Simply put larger but fewer seeds. Therefore, selection for larger seeds may reduce seed number per plant. In order to increase seed size and/or number for production purposes, selection for larger plant size should then be required. Or selection for greater allocation to seed mass or increased seed number may be at the expense of perenniating structures. The challenge, at least until adaptation to the growing environment is complete, will be to select for increased seed size and/or seed set and retain sufficient tolerance to "normally expected stress levels" and acknowledge the risk of extreme stresses adversely affecting stand longevity. Selection for increased seed productivity however may reduce the competitive ability of the individual within the community and enhance the diversity.

Schaaf and Rogler (1962) found seed weight highly heritable but not yield in crested wheatgrass. Christie and Kalton (1960) indicated that recurrent selection over inbreeding in *Bromus inermis* and seed weight selection on space plants was effective. Selections for seed yield in tall fescue based on clone materials were correlated to single cross progeny tests however, each parent was cloned 40 times (Thomas and Frakes, 1967). This methodology will greatly increase resources required for a selection programme. Knowles (1977) was successful using space-planted nurseries with intermediate wheatgrass, however the author noted that the moderate creep of the plants and the use of two and three year-old plant stands for selection purposes may have approximated production field conditions.

Selection in space planted nurseries therefore may be successful in perennial crops for both end use and seed production characteristics if related to identifiable characteristics. In creeping bentgrass selection for reduced plant spread resulted in greater tiller density in the intended end use, golf course turf (Cattani *et al.* 1996). These selections were also based upon higher reproductive tiller density for seed production purposes and resulted in higher harvest index values across production years in field studies (Cattani *et al.* 2004). Increased tillering was shown to be related to leaf appearance rates and reduced internode lengths (Cattani *et al.* 2002). Therefore improvements in perennial species for seed production can be made, however fitness traits may be reduced, (e.g. dwarf phenotypes). Three important caveats to the success of the above are: 1) the production region was identified prior to selection; 2) the product was for a monoculture seed production system; and 3) species plasticity may compensate for changes within the growth environment and reduce or nullify selection efficacy.

SELECTION NURSERIES

Plant competition can impact performance, and with polyculture the plant-to-plant interactions may be most important to overall stand performance. Weiner *et al.* (2010) argue for selection under high density and with group selection to increase characteristics for the good of the collective stand. The typical yield improvement approach is to improve an individual's fitness.

Annual species are better suited to the theory that individual fitness is what has been under natural selection, while perennial species have evolved other mechanisms of fitness (i.e. perenniating structures). Therefore selection for individual reproductive fitness may lead to increased productivity in perennials at the cost of perenniating vegetative structures. Care is then needed to balance reproductive methods to ensure long-term persistence of a plant within a stand.

A plant's performance may be dependent upon its neighbours and selection without this competition may impact not only the performance of the species in polyculture but also the overall performance of the polyculture. Selection in competitive nurseries should provide greater performance from all component species. Differences in access to resources as described by Smith *et al.* (2009) (Resource Pool Diversity Hypothesis) could account for differential performance under competitive versus non-competitive selection environments. Callaway and Aschehoug (2000) provide an example of differential impact of root exudates from *Centaurea diffusa* and competition for phosphorus on grasses dependent upon whether *C. diffusa* was from it its' area or origin versus its area of introduction. This is important in that competition for phosphorus was not reduced and may be explained by RPDH, and that selection for reducing allelopathic effects is possible.

A number of factors will impact a community including competition, facilitation and evolutionary processes (Brooker, 2006). The example of *C. diffusa* above illustrates evolutionary processes. *Helianthus maximiliani* (perennial sunflower) is a potential perennial oilseed crop and there are reports that it can be allelopathic (Leather, 1983). If true, selection in competition with *H. maximiliani* will be needed to provide maximization of reproductive effort for co-crop species and supporting species in polyculture.

Selection for monoculture cropping does not translate into optimum production in mixtures and selection under production environment conditions is needed (Wright, 1985). Similarly, Lammerts Van Bueren *et al.* (2002) argue that in order to make progress in developing adapted varieties for organic production selection and evaluation must take place under organic conditions, i.e. the conditions of production environments.

Perennial crop cultivars have lasted long after introduction, (e.g. Kentucky 31 tall fescue released in 1943, Climax timothy in 1947) are still in demand in 2013. Based on current regulations, intermediate wheatgrass (*Thinopyrum intermedium*) could therefore be produced for up to six years as a certified seed crop if seeded with foundation seed (CSGA, 2011). Additional

years of seed production would then be considered common seed. Seed (grain) for human or animal consumption does not have to meet seed certification quality standards (for genetic make-up) but would be subject however to end-use quality parameters.

Adoption of new germplasm and the ability maintain desired seedstocks can be dependent upon socio-economic issues as well as agronomic performance (Sperling and Loevinsohn, 1993). Perennial crop species may reduce this through the need to only establish the crop once and make repeated harvests from the area, minimizing the risk of successive poor harvests reducing seedstocks. Additionally, land races may be developed over time, reducing the requirement for breeding for specific regions within the landscape.

CONCLUSIONS

Selection within herbaceous perennials for grain and oilseed production has historically not received great interest. Perennial grain and oilseed crops can be achieved however long-term resources must be available to allow for development. Once individual species have been developed, polyculture will be a logical next step. As development of individual species for enhanced forage production has not shown good correlation to production in bi- or polycultures for forage, breeding for polyculture production then will involve selection under different conditions than we currently employ for individual species improvement. Companion species will be required to contribute to sustainability of the system. Profitability of the crop stand will need to be measured by parameters other than simply crop market value to ensure fair comparison of systems and crops.

REFERENCES

Aarssen, L.W. 2005. Why don't larger plants have proportionately bigger seeds? OIKOS. 111: 199- 207.

- Acharya, S.E., Sottie, B., Coulman, A., Iwaasa, T., McAllister, Y.I., Wang, & Liu, J. 2013. New sainfoin populations for bloat-free alfalfa pasture mixtures in western Canada. *Crop Science*. 53: 2283-2293.
- Adams, M.W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean. *Crop Science*. 7: 505-510.
- Adler, P.B., HilleRisLambers, J., Kyriakidis, B.C., Guan, Q. & Levine, J.M. 2006. Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proceedings of the National Academy of Sciences.* 103: 12793-12798.
- Ågren, J. & Willson, M.J. 1994. Cost of seed production in the perennial herbs *Geranium maculatum* and *G. syvaticum*: an experimental field study. *OIKOS*. 70: 35-42
- Allan, E. van Ruijven, J. & Crawley, M.J. 2010. Foliar fungal pathogens and grassland biodiversity. *Ecology*. 91: 2572-2582.
- **Banks, J.E.** 2004. Divided culture: integrating agriculture and conservation biology. *Frontiers in Ecology and the Environment.* 2: 537-545.
- Benson, E.J. & Hartnett, D.C. 2006. The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. *Plant Ecology*. 187: 163-177.
- **Bizecki Robson, D.** 2013. An assessment of the potential for pollination facilitation of a rare plant by common plants: *Symphyotichum sericium* (Asteraceae) as a case study. *Botany*. 91: 43-42.
- Brooker, R.W. 2006. Plant-plant interactions and environmental change. New Phytologist. 171: 271-284.
- Burton, G.W. & DeVane, E.H. 1953. Estimating heritability in tall fescue (*Festuca arundinacea*) from replicated clonal material. *Agronomy Journal*. 45: 478-481.
- Callaway, R.M. & Aschehoug, E.T. 2000. Invasive plants versus their neighbours: A mechanism for exotic invasion. *Science*. 290: 521-523.
- Cane, J.H. 2006. An evaluation of pollination mechanisms for purple prairie-clover, *Dalea purpurea* (Fabaceae: Amorpheae). *American Midland Naturalist*. 156: 193-197, DOI: 10. 1674/0003-031(2006)156[193:AE 0PMF]2.0.C0;2.
- **Casler, M.D. & Brummer, E.C.** 2008. Theoretical expected genetic gains for among-and-within-family selection methods in perennial forage crops. *Crop Science*. 48: 890-902.
- Cattani, D.J., Elliott, B., Ostermann, D. & Northover, P. 2009. Summary of the Manitoba forage seed reports for 2009. (Available at: www.umanitoba.ca/afs/agronomists_conf/2009/Posters/Cattani_ poster_forage_seed.pdf).
- **Cattani**, **D.J.**, **Miller**, **P.R. & Smith Jr**, **S.R.** 1996. Relationship of shoot morphology between seedlings and established turf in creeping bentgrass. *Canadian Journal of Plant Science*. 76: 283-289.
- Cattani, D.J., Gjuric, R., Feindel, D.E., Miller, P.R. & Smith Jr, S.R. 1997. Management requirements for dryland creeping bentgrass seed production. In *Proceedings of the XVIII International Grassland Congress*. 25: 25-52.
- Cattani, D.J., Smith Jr, S.R., Miller, P.R., Feindel, E.E. & Gjuric, R. 2004. Seed yield of creeping bentgrass entries in Manitoba. *Canadian Journal of Plant Science*. 84: 117-124.
- **Cattani, D.J., Struik, P.C. & Nowak, J.N.** 2002. Comparative morphological development of divergent flowering types of annual bluegrass and tillering types of creeping bentgrass. *Crop Science*. 42: 754-762.
- **Chen, Y.H. & Welter, S.C.** 2005. Crop domestication disrupts a native tritrophic interaction associated with the sunflower, *Helianthus annuus* (Asterales: Asteraceae). *Ecological Engineering*. 30: 673-683.

(335)

- **Cheplick, G.P.** 1995. Life history trade-offs *in Amphibromus scabrivalvis* (Poaceae): Allocation to clonal growth, storage, and cleistogamous reproduction. *American Journal of Botany.* 82: 621-629.
- Clement, S.L., Griswold, T.L., Rust, R.W., Hellier, B.C. & Stout, D.M. 2006. Bee associates of flowering Astragalus and Onobrychis genebank accessions at a Snake River site in eastern Washington. Journal of the Kansas Entomological Society. 79(3): 254-260.
- Christie, B.R. & Kalton, R.R. 1960. Recurrent selection for seed weight in bromegrass, *Bromus inermis* Leyss. *Agronomy Journal*. 52: 575-578.
- Cox, T.S., Glover, J.R., Van Tassel, D.L., Cox, C.M. & DeHaan, L.R. 2006. Prospects for developing perennial grain crops. *BioScience*. 56: 649-659.
- Cox, T.S., Van Tassel, D.L Cox, C.M. & DeHaan, L.R. 2010. Progress in breeding perennial grains. Crop and Pasture Science. 61: 513-521.
- **Crews, T.E.** 2005. Perennial crops and endogenous nutrient supplies. *Renewable Agriculture and Food Systems*. 20: 25-37.
- **CSGA.** 2011. Section 6: Foundation, Registered and Certified Production of Grasses. (Available at www. seedgrowers.ca/pdfs/Circular%2062010/Circ6-SECTION%2006-ENGLISHRev01-6_20110122.pdf).
- DeHaan, L.R., Van Tassel, D.L. & Cox, T.S. 2005. Perennial grain crops: A synthesis of ecology and plant breeding. *Renewable Agriculture and Food Systems*. 20: 5-14.
- DeHaan, L.R., Weisberg, S., Tilman, D. & Fornara, D. 2010. Agricultural and biofuel implications of a species diversity experiment with native perennial grassland plants. *Agriculture, Ecosystems and Environment*. 137: 33-38.
- **Dofing, S.M. & Knight, C.W.** 1992. Alternative model for path analysis of small grain yield. *Crop Science*. 32: 487-489.
- Dray, S., Pélissier, R., Couteron, P., Fortin, M-J., Legendre, P., Peres-Neto, P.R., Bellier, E., Bivand, R., Blanchet, F.G., De Cáceres, M., Dufour, A-B., Heegaard, H., Jombart, T., Munoz, F., Oksanen, J., Thoulouse, J. & Wagner, H.H. 2012. Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs*. 82: 257-275.
- Dyer, L.A., Letourneau, D.K., Chavarria, G.V. & Amoretti, D.S. 2010. Herbivores on a dominant understory shrub increase local plant diversity in rain forest communities. *Ecology*. 91: 3707-3718.
- Elgersma, A., Winkelhorst, G.D. & den Nijs, A.P.M. 1994. The relationship between progeny seed yield in drilled plots and maternal spaced-plant traits in perennial ryegrass. *Plant Breeding*. 112: 209-214.
- **Elgersma, A. & van Wijk, A.J.P.** 1997. Breeding for higher seed yields in grasses and forage legumes. *Forage Seed Production: I. Temperate Species,* D.T. Fairey and J.G. Hampton eds. CAB International, UK 1997.
- Fletcher, J. 1897. Weeds. Dept. of Agriculture, Central Experimental Farm. *Ottawa Canada Bulletin*. 28: pp.43 and index.
- Georgescu, M., Lobell, D.B. & Field, C.B. 2011. Direct climate effects of perennial bioenergy crops in the United States. *Proceedings of the National Academy of Sciences*. 108: 4307-4312.
- Gilbert, B. & Levine, J.M. 2013. Plant invasions and extinction debts. *Proceedings of the National Academy* of Science. 110: 1744-1749.
- Glover, J.D., Culman, S.W., DuPont, S.T., Broussard, W., Young, L., Mangan, M.E., Mai, J.G., Crews, T.E., DeHaan, L.R., Buckley, D.H., Ferris, H., Turner, R.G., Reynolds, H.L. & Wyse, D.L. 2010. Harvested perennial grasslands provide ecological benchmarks for agricultural sustainability. *Agriculture, Ecosystems and Environment*. 137: 3-12.
- Hajjar, R., Jarvis, D.I. & Gemmill-Herren, B. 2008. The utility of cropgenetic diversity in maintaining ecosystem services. Agriculture, Ecosystems and Environment. 123: 261-270.
- Hayward, M.D. & Vivero, J.L. 1984. Selection for yield in *Lolium perenne*. II. Performance of space plant selections under competitive conditions. *Euphytica*. 33: 787-800.

(336)

- Heide, O.M. 1994. Control of flowering and reproduction in temperate grasses. *New Phytologist*. 128: 347-362.
- Helsen, K., Hermy, N. & Honnay, O. 2012. Trait but not species convergence during plant community assembly in restored semi-natural grasslands. *OIKOS*. 121: 2121-2130.
- Hufford, K.M. & Mazer, S.J. 2012. Local adaptation and the effects of grazing on the performance of *Nassella pulchra*: Implications for seed sourcing in restoration. *Restoration Ecology*. 20: 688-695.
- Jackson, W. 2002. Natural systems agriculture: a truly radical alternative. *Agriculture, Ecosystems and Environment.* 88: 111-117.
- **Jonsdottir, G.A.** 1991. Tiller demography in seashore populations of *Agrostis stolonifera, Festuca rubra* and *Poa irrigata. Journal of Vegetation Science.* 2: 89-94.
- Kuhnlein, H.V. & N.J. Turner. 1991. Food and Tradition in History and Anthropology. Volume 8. Traditional Plant Foods of Canadian Indigenous Peoples: Nutrition, Botany and Use. Solomon H. Katz, Editor. Gordon and Breach Publishers. (Available at www.fao.org/wairdocs/other/ai215e/AI215E05.htm).
- Lammerts van Bueren, E.T., Struik, P.C. & Jacobsen, E. 2002. Ecological concepts in organic farming and their consequences for an organic crop ideotype. Netherlands Journal of Agricultural Science. 50: 1-26.
- Macdonald, H. 1974. *Native Manitoba plants in bog, bush and prairie*. Publication No. 452, Manitoba Department of Agriculture, May 1974.
- MacDougall, A.S., McCann, K.S., Gellner, G. & Turkington, R. 2013. Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature*. 494: 86-89.
- **Ollerton, J., Winfree, R. & Tarrant, S.** 2011. How many flowering plants are pollinated by animals? *OIKOS*. 120: 321-326.
- O'Mara, F.P. 2012. The role of grasslands in food security and climate change. *Annals of Botany*. 110: 1263-1270.
- Pataki, D.E., Carreiro, M.M. Cherrier, J., Grulke, N.E., Jennings, V., Pincetl, S., Pouyat, R.V. Whitlow, T.H. & Zipperer, C. 2011. Coupling biogeochemical cycles in urban environment: ecosystem services, green solutions, and misconceptions. *Frontiers of Ecology and the Environment*. 9: 27-26.
- Picasso, V.D., Brummer, E.C., Liebman, M., Dixon, P.M. & Wilsey, B.J. 2008. Crop species diversity affects productivity and weed suppression in perennial polycultures under two management strategies. *Crop Science*. 48: 331-342.
- Schaaf, H.M. & Rogler, G.A. 1962. Breeding crested wheatgrass for seed size and yield. Crop Science. 2: 347-351.
- Smith, R.G., Mortensen, D.A. & Ryan, M.R. 2009. A new hypothesis for the functional role of diversity in mediating resource pools and weed-crop competition in agroecosystems. Weed Research. 50: 37-48.
- Sperling, L. & Loevinsohn, M.E. 1993. The dynamics of adoption: distribution and mortality of bean varieties among small farmers in Rwanda. *Agricultural Systems*. 41: 441-453.
- Stein, C. Unsicker, S.B., Kahmen, A., Wagner, M., Audorff, V., Auge, H., Prati, D. & Weisser, W.W. 2010. Impact of invertebrate herbivory in grasslands depends on plant species diversity. *Ecology*. 91: 1639-1650.
- Sturludóttir, E., Brophy, C. Bélanger G., Gustavsson, A.M., Jørgensena, M., Lunnan, T. & Helgadóttir, Á. 2013. Benefits of mixing grasses and legumes for herbage yield and nutritive value in northern Europe and Canada. *Grass and Forage Science*. doi:10.1111/gfs.12037.
- Thomas, J.R. & Frakes, R.V. 1967. Clonal and progeny evaluations in two populations of tall fescue (*Festuca arundinacea* Schreb.). Crop Science. 7: 55-58.
- Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. 2001. Diversity and productivity in a long-term grassland experiment. *Science*. 294: 843-845.

(337)

(338)

- Tilman, D., Wedin, D. & Knops, J. 1996. Productivity and sustainability influenced by biodiversity in grassland systems. *Nature*. 379: 718-720.
- Tulbure, M.G., Wimberly, M.C., Boe, A. & Owens, V.N. 2012. Climatic and genetic controls of yields of switchgrass, a model bioenergy species. *Agriculture, Ecosystems and Environment*. 146: 121-129.
- **Vellend**, M. 2006. The consequences of genetic diversity in competitive communities. *Ecology*. 87: 304-311.

Weinberg, G.M. 1975. An introduction to general systems thinking. John Wiley & Sons, New York. 17-19.

- Weiner, J., Andersen, S.B., Wille, W.K-M., Griepentrog, H. & Olsen, J.M. 2010. Evolutionary agroecology: the potential for cooperative, high density, weed-suppressing cereals. *Evolutionary Applications*. 3: 473-479.
- Wiltshire, K., Delate, K., Wiedenhoeft, M. & Flora, J. 2010. Incorporating native plants into multifunctional prairie pastures for organic cow-calf operations. *Renewable Agriculture and Food Systems*. doi: 10.1017/S174217051000044X 13pp.
- Wright, A.J. 1985. Selection for improved yield in inter-specific mixtures or intercrops. *Theoretical and Applied Genetics*. 69: 399-407.
- Zhang, D.Y. & Jiang, X.H. 2000. Costly solicitation, timing of offspring conflict, and resource allocation in plants. Annals of Botany. 86: 123-131.
- Zhao, D.L., Atlin, G.N., Bastiaans, L. & Spiertz, J.H.J. 2006. Cultivar weed-competitiveness in aerobic rice: Heritability, correlated traits and potential for indirect selection in weed –free environments. Crop Science. 46: 372-380.