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Periclinal Chimeral Status of New Brunswick 'Russet Burbank' Potato

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Abstract The widely grown and important 'Russet Burbank' potato has now been almost 100 years under cultivation. 'Russet Burbank', derived from 'Burbank', is described as the classic example of a periclinal chimeral cultivar that is (by definition) a stable entity. This research investigated the chimeral status of the New Brunswick (NB) clone of 'Russet Burbank'. This was done through regeneration of somatic embryos from specific tuber tissues representing the three histogenic layers of the shoot meristem from microtubers and field tubers. Intraclones were evaluated for tuber periderm characteristics in two field seasons. Most intraclones had tubers with russet periderm regardless of tuber source tissues. The frequency of up to 4% for non-russet (wild-type) and up to 21% for patchy periderm suggests that one or more types of gene expression modification should be investigated for these phenotypic changes. Clearly, NB 'Russet Burbank' is not presently organized in a periclinal chimeral arrangement.

Resumen La ampliamente cultivada e importante papa 'Russet Burbank' tiene ahora casi 100 años bajo cultivo. 'Russet Burbank', derivada de 'Burbank', es descrita como el clásico ejemplo de cultivar de quimera periclinal que es (por definición) una entidad estable. Se investigó la condición quimérica del clon de Nueva Brunswick (NB) de 'Russet Burbank'. Esto se hizo a través de la regeneración de embriones somáticos provenientes de tejidos específicos del tubérculo que representan las tres capas histogénicas del meristemo de brotes de micro-tubérculos y de tubérculos provenientes del campo. Los intraclones fueron evaluados para características del peridermo del tubérculo en dos temporadas de campo. La mayoría de los intraclones tuvieron tubérculos con peridermo rugoso independientemente de la procedencia del tejido del tubérculo. La frecuencia de hasta el 4% para peridermo no-rugoso (tipo silvestre) y hasta 21% para peridermo rugoso sugiere el estudio de uno o más tipos de modificaciones en la expresión génica para determinar estos cambios fenotípicos. Claramente, el NB 'Russet Burbank' no está organizado en un arreglo de quimera periclinal.

Keywords 'Burbank' · *Solanum tuberosum* · Somatic embryogenesis · Histogenic layers

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Introduction

Solanum tuberosum L. 'Russet Burbank' has many synonyms, including: 'California Russet', 'Golden Russet', 'Idaho Baker', 'Idaho Russet', and 'Netted Gem' (Clark and Lombard 1946; Hardenburg 1949; Stevenson 1949; Darling 1968). It is the most important cultivar in North America, grown extensively in the USA (primarily in Idaho, Montana, Oregon, and Washington, but also other north-central and mid-western states) and right across Canada (Darling 1968; Atkinson et al. 2003; PAA 2008). Its enduring popularity is a tribute to its excellent storage and cooking qualities. It is favored for table use as a baking potato and for commercial processing, primarily for French fries (Clark and Lombard 1946; Darling 1968; CFIA 2008; PAA 2008).

'Burbank', was a seedling selection made by Luther Burbank in the 1870s from a rare chance fruit of 'Early Rose' (Davis 1992). Potato lore suggests that 'Russet Burbank' originated as a mutation from 'Burbank' and was discovered in 1914 by Lou D. Sweet, a farmer in Denver, Colorado, USA. It was assumed (but not rigidly tested) to have considerable resistance to potato scab (*Streptomyces scabies*) and late blight (*Phytophthora infestans*) compared with other cultivars of that time (Davis 1992). The popularity of 'Russet Burbank' supplanted that of 'Burbank' immediately and has continued to this day; almost 100 years under cultivation. The release date for 'Russet Burbank' is often confused with that of 'Burbank' and generalized ("around 1880", Canadian registration 1923, CFIA 2008) or listed for both cultivars as 1876 (Thornton and Sieczka 1980).

The tubers of 'Russet Burbank' have a periderm (skin) that is russet (reddish brown) with a heavily netted (raised "fish net") pattern, in contrast to the white skin of 'Burbank', while the inner flesh (cortex and pith) was apparently unaffected by the mutation and remained white (Davis 1992). A plant chimera is defined as a plant that contains two or more genetically dissimilar tissues as a result of mutation (Norris et al. 1983; Tilney-Bassett 1986). Chimeras usually arise from spontaneous or induced early-stage somatic mutations of the shoot meristem. If a mutant cell lineage stabilizes in any of the histogenic layers, this mutant condition is perpetuated in all lateral shoot outgrowth from the chimeral meristem (Stewart et al. 1972; Tilney-Bassett 1986; Poethig 1989; Marcotrigiano 1990; Marcotrigiano and Gradziel 1997; Burge et al. 2002; Hartmann et al. 2002). During shoot and tuber differentiation from the shoot meristem, the epidermis (and periderm) are derived from the outer tunica layer (L_1), the cortex and germ cells from the inner tunica layer (L_2), and the vascular ring and pith from the corpus (L_3; Dermen 1960). Plants with mutated outer and/or inner tunica layer (s) (L_1 and/or L_2), with the corpus wild-type, are called periclinal or "hand-in-glove" chimeras (Asseyeva 1931; Dermen 1960; Howard 1961; Marcotrigiano and Gradziel 1997; Hartmann et al. 2002).

The concept of periclinal chimerism is relevant to current horticultural research, where separation of chimeral plants into pure types is a common and recurring theme in the development of improved plants, including thornless blackberry and other *Rubus* spp. (reviewed by Skirvin et al. 1994), thornless roses (Canli 2003), and wine grapes (Franks et al. 2002; Hocquigny et al. 2004; Bertsch et al. 2005). Periclinal chimerism in two *Vitis vinifera* '*Pinot gris*' clones were recently confirmed through analysis of 50 microsatellite loci (Hocquigny et al. 2004).

Periclinal chimerism is characteristic of mutations of potato (Asseyeva 1931; Howard 1961), and was believed to be true of 'Russet Burbank'. Asseyeva (1931), Hardenburg (1949), Krantz (1951) Idaho Potatoes (2008) assumed (but did not prove) that 'Russet Burbank' is a periclinal chimera. Miller (1954) and Brown (1993) referred to 'Russet Burbank' as a somatic mutant of 'Burbank'. It was listed by Klopfer (1965) and Tilney-Basset (1986; adapted from Klopfer 1965) among many russet sports of potato that are periclinal for mutated (russet) L_1 and wild type for L_2 and L_3. The only experimental evaluation of 'Russet Burbank' chimeral status found by the authors was conducted by Clark (1930, 1933) using an "eye excision" method developed by Asseyeva (1927) and a crossing trial with the white-skinned cv. Katahdin. Thirty cut tubers of 'Russet Burbank' yielded plants with tubers that were all russet (Clark 1930). This work was repeated with 100 cut tubers in 1931. At the end of the season small tubers, from which periderm features were not distinct, were collected from each hill and replanted in 1932, yielding tubers that were 85% russet, and 15% patchy russet (Clark 1933). Results of crossing experiments were limited in number but not as expected for a periclinal chimeral arrangement; some seedlings had russet tubers and some had white tubers. Clark concluded that 'Russet Burbank' was probably a seedling and not a periclinal chimera of 'Burbank'. Clark's experimental work generated confusing results that were disparaged (Howard 1959) or overlooked. A sequence of repeated "hearsay" has contributed to the present day assumption that 'Russet Burbank' is a periclinal chimera.

Somatic cell technology provides a more precise tool for investigation of chimeral structure than the early-mid twentieth century technique of eye-excision as suggested, but not realized, by Van Harten (1972). We hypothesized that 'Russet Burbank' intraclones produced from tissues derived from L_1, L_2, and L_3 (periderm, cortex, and pith, respectively) would produce non-chimeral plants and tubers. We predicted that if 'Russet Burbank' was an L_1 periclinal chimera, periderm explants would produce intraclones with russet tubers like 'Russet Burbank' while cortex- and pith-derived explants would produce intraclones with non-russet tubers like 'Burbank' (Fig. 1 schematically represents this hypothesis).

The objective of this study was to investigate the current periclinal chimeral status of an important eastern North American accession, the New Brunswick (NB) 'Russet Burbank' through: (a) regeneration of plants called somatic regenerants first generation (SR_1 or intraclones) dissected from specific tuber tissues (periderm, cortex, and pith) derived from the L_1, L_2, and L_3, respectively, of the shoot meristem, and (b) examination of tuber periderm from these non-chimeral field-grown plants to determine whether the source tissue phenotype was mutated (russet) or 'Burbank'-type (smooth and white).

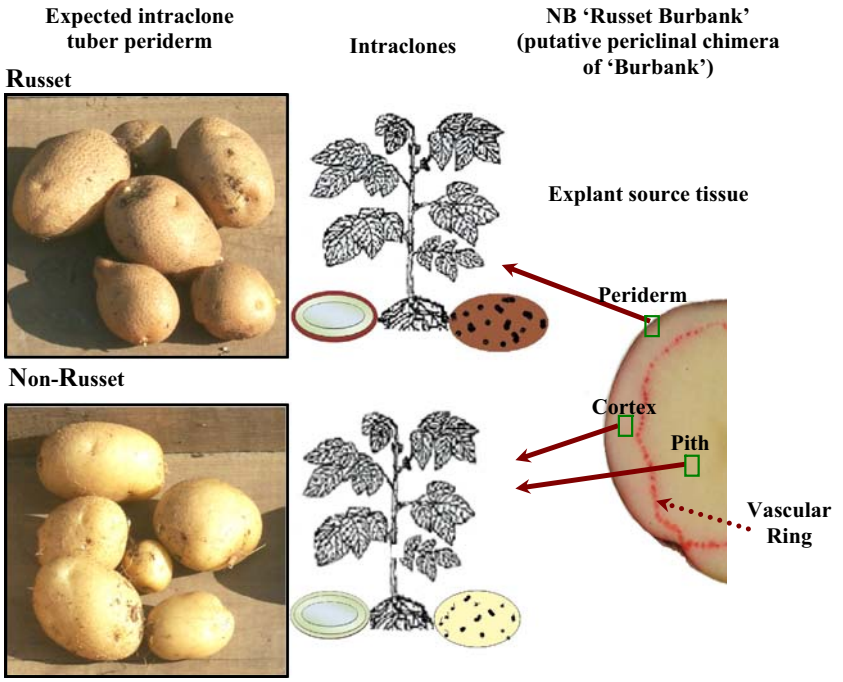

Fig. 1 Schematic representation of the hypothesis of this study. If NB `Russet Burbank` is an L_1 periclinal chimera, periderm-derived intraclones will have tubers with russet periderm like 'Russet Burbank', while cortex- and pith-derived intraclones will have tubers with non-russet periderm like 'Burbank'. Reference pictures of USDA 'Russet Burbank' and USDA 'Burbank' minitubers are from Bamberg and Martin 2004. US Potato Genebank, Sturgeon Bay, WI, USA

Materials and Methods

Source of Cultivars Russet Burbank and Burbank

Seed tubers of NB 'Russet Burbank' were obtained from the Bon Accord Elite Seed Potato Centre (Bon Accord, NB). In vitro plantlets of this clone (#179) were obtained from the Plant Propagation Center, New Brunswick Department of Agriculture, Fisheries and Aquaculture (Fredericton, NB). In vitro plantlets of 'Burbank' and reference photographs of 'Russet Burbank' and 'Burbank' minituber periderm were obtained from the United States Department of Agriculture (USDA) Research Service, Inter-Regional Potato Introduction Station (Sturgeon Bay, WI).

Intraclone Production

NB 'Russet Burbank' intraclones were produced through somatic embryogenesis, using a two-step procedure modified from Seabrook and Douglass (2001) in McGill University's Micropropagation Facility. This is a method that regenerates new plants from individual cells (Pedroso and Pais 1995; Sharma and Millam 2004). Tissue-specific (periderm, cortex, and pith) explants were aseptically removed from fresh field-grown NB 'Russet Burbank' tubers obtained from Bon Accord and from microtubers produced in our laboratory (Leclerc et al. 1994). After 2 weeks, callused explants were transferred onto somatic embryo regeneration medium. The first somatic plantlets were collected after 4–5 weeks and assigned an intraclone number, then micropropagated using single-node cuttings on MS basal salt medium (Murashige and Skoog 1962).

In preliminary experiments, a relatively small number of intraclones were regenerated from a few source tubers and transferred to pots for minituber production in the greenhouse (Ortiz-Medina 2006). This preliminary greenhouse trial was followed by a large field trial replicated over 2 years. Intraclones were regenerated from tissue-specific explants of two sources, field tubers and microtubers, during the winters of 2004 and 2005. Micropropagated control plantlets and intraclones were hardened-off in plug trays over a 3-week interval then trucked to McCain Foods Canada Ltd. research farm (Greenfield, NB). Plants of each intraclone, represented as a single plant in 2005 and as two plants in 2006, were transferred into irrigated plots in a completely randomized design (CRD) and harvested after 111 days (2005) or 119 days (2006). The number of intraclones that were grown in the field are shown in Table 1.

Classification of Tubers

At maturity, plants were individually dug, the tubers bagged, tagged, and graded. Tubers were then washed and digitally photographed. These photographs were used to classify tuber periderm into: R (russet) = the entire surface was russet; P (patchy) = the surface showed patches of russet, russet and non-russet tubers were mixed, or (2006 only) two plants representing one intraclone showed

Table 1 Field plants were established from micropropagated control plantlets of NB 'Russet Burbank' and USDA 'Burbank', or intraclones of NB 'Russet Burbank' derived from specific tissue (periderm, cortex, or pith) from two sources (microtubers or field tubers)

Field season	Source		Explant	Total no. of plantlets or intraclones	Number of intraclones		
	Cultivar	Plantlets/tubers			R	P	NR
2005[a]	NB 'R. Burbank'	Plantlets		10	8	2	0
	USDA 'Burbank'	Plantlets		6	0	1	5
	NB 'R. Burbank'	Microtubers	Cortex	101	85	15	1
			Pith	171	151	15	5
		Field tubers	Pith	96	83	13	0
2006	NB 'R. Burbank'	Plantlets		10	10	0	0
		Field tubers		6	6	0	0
	USDA 'Burbank'	Plantlets		9	0	0	9
	NB 'R. Burbank'	Microtubers	Periderm	54	49	5	0
			Cortex	51	42	8	1
			Pith	14	11	3	0
	NB 'R. Burbank'	Field Tubers	Cortex	53	47	4	2
			Pith	87	79	8	0

Intraclones were represented by one plant in 2005 and two plants in 2006. Tuber periderm phenotype [R (russet) = the entire surface was russet; P (patchy) = the surface showed patches of russet, russet and non-russet tubers were mixed, or two plants representing one intraclone (2006) showed inconsistent periderm characters; NR (non-russet) = the entire surface was smooth and white].

[a] Within each year, data were normally distributed. No significant differences occurred in periderm phenotype between intraclones regenerated from the different source tissues ($P \leq 0.05$).

inconsistent periderm characters; NR (non-russet) = the entire surface was smooth and white. Each designation was based on a picture that included all graded tubers (at least four tubers) and consensus by three of the authors.

Statistical Analysis

Data were tested for normality using the univariate procedure of the Statistical Analysis System (SAS 2003) and statistically analyzed using the general linear model (GLM) procedure to compare freshly harvested tuber periderm phenotypes (R, P, and NR) from different tissues ($P \leq 0.05$).

Results

Preliminary Greenhouse Trial

Periderm features on minitubers were recorded (data not shown). NB 'Russet Burbank' control minitubers all had russet periderm. All cortex-derived and some pith-derived intraclones produced minitubers with smooth white periderm similar to our USDA photographic reference for 'Burbank' periderm. However, some pith-derived intraclones produced minitubers with periderm that was clearly russet like NB 'Russet Burbank', in direct contrast to expected periderm characteristics.

Field Trials

Control plant tubers of NB 'Russet Burbank' usually had periderm that was russet (Table 1) but occasionally russet with some patchy areas. Control plant tubers of 'Burbank' usually had periderm that was non-russet; smooth, shiny, and white. Only one tuber, from one 'Burbank' control plant was non-russet with patches of russet. The incidence of NB 'Russet Burbank' intraclones with russet or patchy periderm was 84–88% and 9–14% (2005) and 79–91% and 8–21% (2006), respectively, with no significant difference related to explant source tissues. Only 0–4% of all intraclones showed non-russet periderm. Among periderm-derived intraclones, where 100% of the intraclones were expected to have tubers with russet periderm, 91% of intraclones had tubers that were russet while 9% were patchy and 0% were non-russet.

Discussion

A periclinal chimera is believed to be a stable arrangement consistent with evolutionary advantage to retention of mutations in stratified apices of angiosperms (Kletkowski et al. 1985). Results from a preliminary greenhouse trial with minitubers and 2 years of field trials consistently showed that NB 'Russet Burbank' does not fit the classic definition of a periclinal chimera. The field data show that

most intraclones produced tubers with russet periderm, regardless of source tissue origin (Table 1). We interpret this to mean that the genes for russet are currently present with similar incidence in all tissues of this clone regardless of the histogenic layer from which they are derived. From our data we cannot conclude that 'Russet Burbank' was never a periclinal chimera. However, our results support experimental observations of Clark (1930, 1933) who did not find evidence of periclinal chimeral structure in 'Russet Burbank' only 15 years or so following its discovery.

Russet periderm is proposed to be governed by three complementary genes, and the loss of any of the three genes can result in non-russet periderm (De Jong 1981). Somatic recombination can occur and cause somatic instability (Hu et al. 1998). Tissue culture is known to enhance genetic variation at both phenotypic and chromosomal levels (Larkin and Scowcroft 1981; Lee and Phillips 1988). Tissue culture can also cause DNA methylation changes and cause phenotypic modifications (Kaeppler and Phillips 1993). Potential sources of intraclones with non-russet periderm can be cell mix-up between histogenic layers, DNA somatic recombination, or gene expression changes of russet-involved genes. The occurrence of intraclones with non-russet and patchy periderm suggest that one or more types of gene expression modification is the most suspected cause to be investigated for these phenotypic changes.

Conclusions

We tested the current periclinal chimeral status of the NB 'Russet Burbank' over two field seasons with populations of intraclones produced in culture through somatic embryogenesis. The tubers of intraclones derived from all histogenic layers were almost always russet. Clearly, NB 'Russet Burbank' is not organized in a periclinal chimeral arrangement for an L_1 and/or L_2, mutation of 'Burbank'.

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