

How does In-season Heat Affect Postharvest Physiology & Quality...?

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Introduction

This presentation summarizes and integrates many of the results from our research on the effects of heat stress on tuber physiology, performance and quality, starting with seed production and extending to maincrop potatoes for frozen processing. Heat stress (high tuber pulp temperature) during production of seed can accelerate physiological aging during storage, which in turn affects stem numbers, tuber set and size distribution the following season. Heat stress during production of potatoes for frozen processing can affect sugar-related disorders and retention of process quality during storage. Soil heating cables (Fig. 1A) were used to manipulate tuber pulp temperatures at key points during tuber development to study the effects of temperature on quality retention for seed and frozen processing potatoes. Soil temperatures were increased by approximately 10°F above ambient during tuber bulking (114-155 DAP) and 10 and 20°F above ambient during maturation (155-179 DAP) (Fig. 1B).

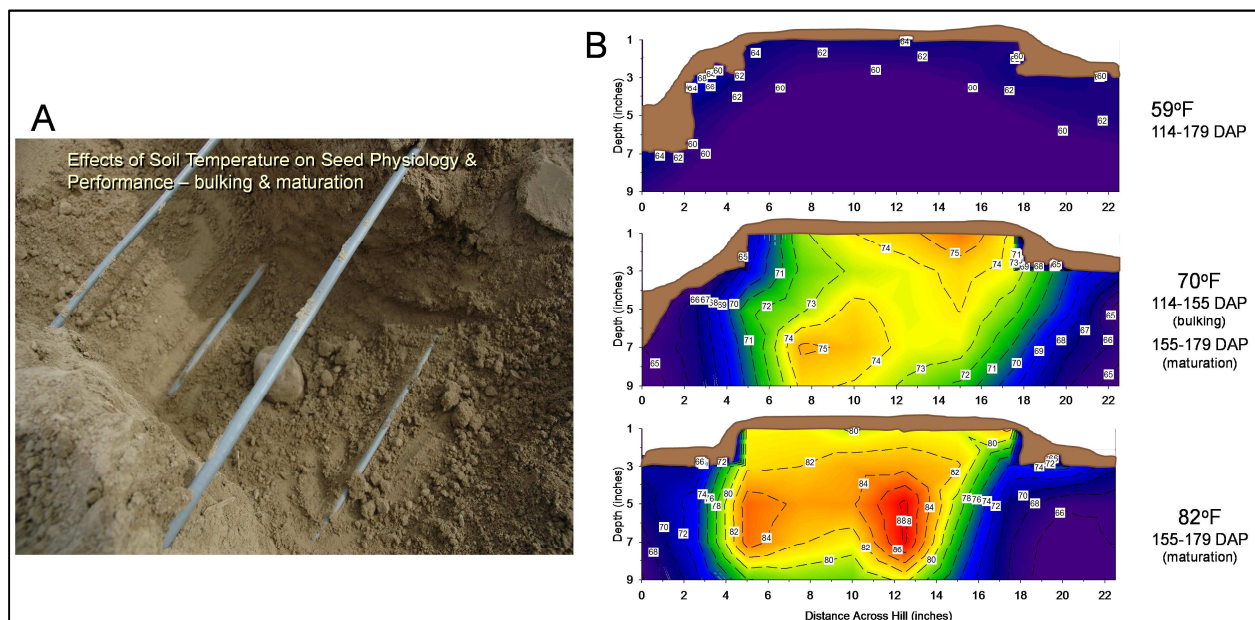


Fig. 1. The effects of temperature during growth on quality of seed and processing potatoes were evaluated for Ranger Russet, Premier Russet and AO02183-2. (A) Soil temperatures (and thus tuber temperatures) were manipulated with heating cables installed in-furrow at planting. Treatments in 2012 consisted of one soil temperature during bulking (70°F; +11°F above ambient; 114-155 DAP; Aug. 8 to Sept. 18) and two soil temperatures during maturation (70°F and 82°F; +11°F and +23°F above ambient; 155-179 DAP; Sept. 18 to Oct. 12). The soil temperature profiles (B) were measured October 4, 2012 during maturation. Non-heated control plots averaged 59°F (ambient).

Seed Physiology & Performance

The quality of a seed crop is dictated by tuber size at harvest, dormancy length, physiological age at planting, and ability to produce high yields of optimum size maincrop potatoes. Symptoms of advanced physiological age include more rapid plant emergence and establishment, reduced apical dominance (increased stems), increased tuber set per plant, and shift in tuber size distribution. These parameters were assessed during the 2013 growing season for seed-tubers (Ranger Russet, Premier

Russet, AO02183-2) grown at elevated temperature in the heat cable plots in 2012. The seed-tubers were stored for ~200 days at 39°F (95% RH) prior to planting.

Seed-tubers from the heat cable plots were morphologically indistinguishable at harvest; however, the elevated soil temperatures during bulking and maturation in 2012 produced tubers of advanced physiological age at planting in 2013. Plants emerged sooner from the seed grown at higher temperatures and this led to quicker plant establishment. Stem numbers per seedpiece increased by an average of 0.5 stems for seed grown at 70°F during bulking (114-155 DAP) and 0.4 and 1.1 stems when soil temperatures averaged 70 and 82°F, respectively, during maturation (155-179 DAP), compared with the control seed grown at ambient (59°F) temperature (Fig. 2 insets). Overall marketable yields produced in 2013 from heat-stressed and control seed were equal, though tuber number per plant was higher and average tuber weight lower from seed grown at elevated temperatures during bulking and maturation. The net result was a significant shift in tuber size distributions toward higher yields of 10-oz and under tubers at the expense of tubers greater than 10 oz, as a proportion of total marketable (U.S. #1 + <4-oz) yields for each cultivar/clone (e.g., Ranger Russet, Fig. 2). These results are the first direct demonstration that tuber temperature during bulking and maturation can affect seed age and subsequent performance the following season and help to explain some of the variation in productivity and performance of seed grown in different regions and used for production in the Columbia Basin.

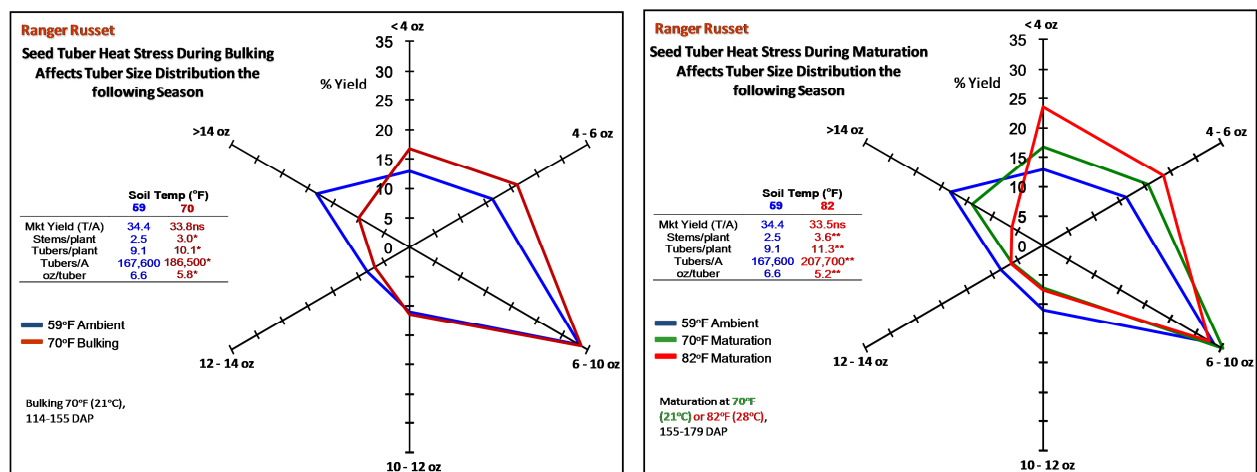


Fig. 2. Effects of heat stress during production of Ranger Russet seed on tuber size distribution the following season. Seed-tubers were grown at 59 (ambient) or 70°F during bulking (114-155 DAP, left) or 59, 70 and 82°F during maturation (155-179 DAP, right) in the heat cable plots (see Fig. 1) in 2012. Following harvest, the seed-tubers were stored at 39°F until planting in April 2013. Seed subjected to high soil temperatures (70 or 82°F) during bulking and maturation the previous season produced more stems resulting in higher tuber set and a significant shift in tuber size distribution toward smaller tubers. Effects of temperature on yield, stem numbers, tuber set and average tuber size are summarized in the inset tables (***) $P < 0.05$ and 0.01 , respectively).

In addition to in-season heat, exposure of seed-tubers to elevated temperature during storage also accelerates physiological aging to alter plant emergence, apical dominance and tuber size distribution the following season. Recent work has suggested that tuber respiration is the ‘pacemaker’ of aging (Blauer et al., 2013). Aging is an oxidative process that affects the hormonal regulation of apical dominance (Kumar and Knowles 1996a; 1996b; 1993) and temperature has both direct and indirect effects on the process. Tuber respiration increases when tubers are exposed to elevated temperature (direct effect) thus accelerating the aging process. Moreover, seed tubers exposed to a relatively brief period of high temperature (e.g. 21 days at 90°F) initially in storage (heat priming), followed by holding at 39°F for the remainder of a ~200-day storage interval, maintain a higher basal metabolic (respiration) rate throughout storage compared with non heat-stressed tubers stored the entire season at 39°F (Fig. 3). In essence,

tubers ‘remembered’ the heat priming treatment, which permanently altered their metabolic rate as reflected by higher respiration even after the heat stress was removed (indirect effect of temperature). The longer the metabolic (respiration) rate of tubers remains elevated the more advanced the physiological age. Temperature thus interacts with time to determine the ultimate physiological age of seed at planting. Higher temperatures during bulking and/or maturation (Fig. 1) may affect the rate of aging by a mechanism similar to the heat priming treatments administered early in storage (Fig. 3) or may simply advance the maturity and thus age of tubers via a direct effect of temperature without inducing a residual (indirect) effect on respiratory metabolism.

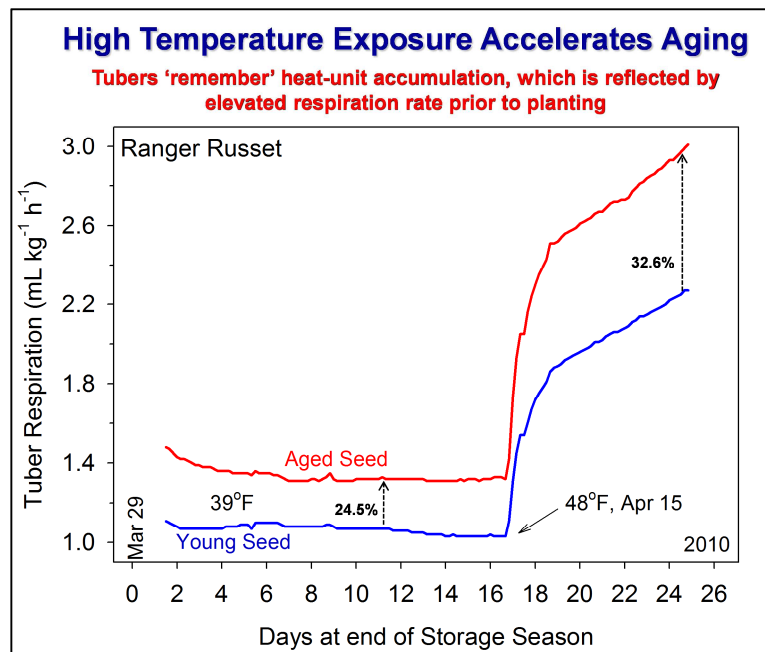


Fig. 3. Effect of a high temperature, age-priming treatment (21 days at 90°F) at the beginning of a 200-day storage period on the basal respiration rates of seed-tubers prior to planting. ‘Ranger Russet’ seed-tubers were acquired at harvest, wound-healed at 54°F (95% RH) for 10 days and then stored at 39°F, except for the 3-week age-priming treatment administered after wound healing (aged seed). The non-age-primed control (young) seed was stored the entire season at 39°F. Tuber respiration rates were compared over the final 16 days of storage at 39°F. The storage temperature was then raised to 48°F on April 15 to induce sprouting (from ~16-25 days). Heat primed tubers had a significantly ($P < 0.01$) higher rate of respiration than control tubers at the end of storage and during early sprouting, indicating a permanent effect of the high temperature treatment on tuber metabolism.

If high temperature-induced accelerated aging (heat priming) depends on permanently elevating the basal metabolic rates of tubers, and respiration is the pacemaker of aging, the efficacy of a heat priming treatment in advancing the age of seed tubers should change depending on when the priming treatment is applied during the storage season (early vs late). Indeed, the efficacy of a high temperature age-priming treatment for hastening plant emergence, increasing stems and altering tuber set and size distribution (i.e. advancing the physiological age) decreased as the treatment was moved from vine kill through storage to planting (Fig. 4). However, the respiration response induced by the high temperature priming treatment was the same regardless of when it was administered during the storage season (Fig. 5). These results underscore the importance of time in the aging process. Exposure of seed to a high temperature age priming treatment at the beginning or end of storage elevates respiration (the pacemaker of aging) to the same degree but the timing of these treatments results in vastly different physiological ages (Blauer et al., 2013). The only difference between these treatments was the time interval from treatment to planting. Again, the longer the respiration rate of tubers remains at an elevated level the greater their physiological age at planting. These results are fundamental to our understanding of the aging process and have practical implications for end-of-season handling and storage of both seed and processing potatoes.

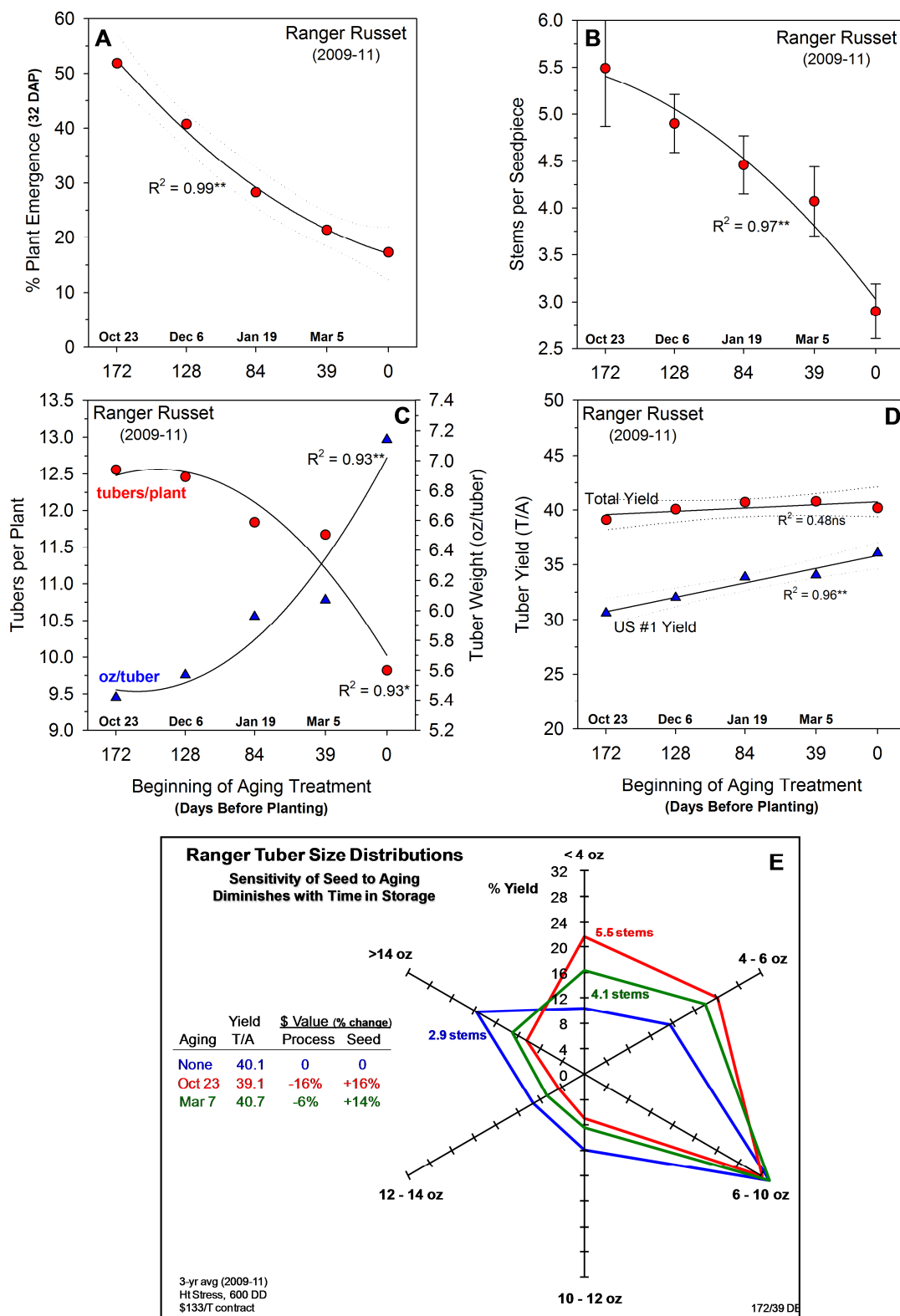
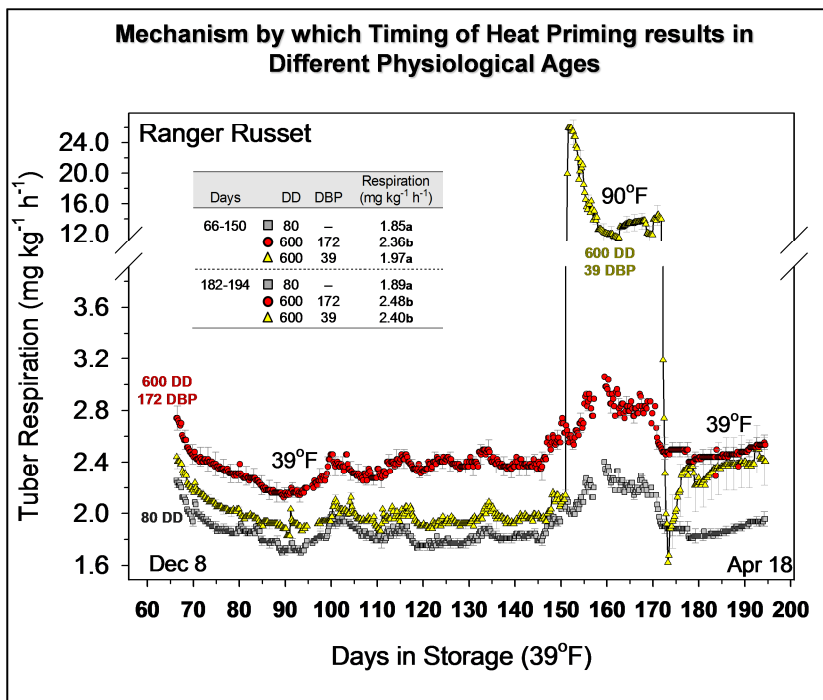


Fig. 4. Timing of a seed aging treatment affects plant emergence (A) stem number per seedpiece (B), tuber set and average size (C), total and U.S. # 1 yields (D), tuber size distribution and crop value (E). The consequences of high-temperature induced accelerated aging are greatest at harvest and become progressively less with time in storage. For these studies, seed-tubers were acquired at harvest (early Oct.) and wound-healed at 54°F (95% RH) for 10 days. The seed was then stored at 39°F except for brief age priming treatments (21 days at 90°F, 95% RH) on Oct. 23 (172 days before planting, DBP), Dec. 6 (128 DBP), Jan 19 (84 DBP), and Mar. 5 (39 DBP). Control (non-aged) seed was stored the entire season at 39°F. The four aged seed lots thus accumulated 600 degree days (4°C base) at

different times over the 200-day storage interval. The greatest effects of the aging treatment on physiological age occurred when given early (172 DBP). Effects on emergence, stems number, tuber set and tuber size distribution diminished progressively as the age priming treatment moved later in the storage season. The age priming treatment likely sets the ‘pacemaker’ of aging (tuber respiration) at a high rate. The longer respiration is maintained at a high rate before planting, the greater the physiological age.

Fig. 5. Effects of aging seed-tubers at the beginning or end of a 194-day storage season on the basal respiration rates of tubers during storage. ‘Ranger Russet’ seed-tubers were acquired at harvest, wound-healed at 54°F (95% RH) for 10 days (80 DD), then stored at 39°F, except for a brief (21-day) age priming treatment at 90°F (95% RH) on Oct. 23 (172 days before planting, DBP) or Mar. 5 (39 DBP) to produce 600-DD seed. The non-age-primed control seed was stored the entire season at 39°F (80 DD). Tuber respiration rates were compared from Dec. 8 to April 18. The 600-DD tubers primed 172 DBP had a higher respiration rate than non-aged tubers over the entire 131-day assessment period ($P < 0.01$). Average respiration rates at 39°F before and after the 39-DBP priming treatment are given in the inset table. Letters indicate mean separation by LSD at $P < 0.01$ and 0.05 for the 66-150 and 182-194 day storage periods, respectively. Developmental, yield and tuber size distribution data are presented in Fig. 4.



Maincrop Potatoes for Frozen Processing

In addition to affecting seed age and thus quality, field heat also affected a multitude of quality parameters in maincrop potatoes destined for frozen processing. Low specific gravity, shortened dormancy, sugar end development, early loss of process (fry) color, loss of resistance to low temperature sweetening (LTS), and early onset of senescent (irreversible) sweetening were induced by elevated temperatures during bulking and maturation of tubers in the heat cable plots (Zommick et al., 2014). Tubers appear to be particularly sensitive to heat-induced accelerated aging during the maturation period under dead vines at season end.

The maturation period extends from physiological maturity (PM) to harvest. For best quality and longest storage life, tubers should be harvested within 7-10 days of PM, which is defined as the average days after planting to reach maximum yield, maximum specific gravity, minimum sucrose and reducing sugars (glucose + fructose) in tubers. For most late season russet cultivars in the Columbia Basin, PM will be reached approximately 145 to 155 DAP when grown with optimum fertility and water. Delaying harvest well beyond PM exposes tubers to prolonged periods of daily temperature fluctuation (e.g. Fig. 6). We believe this exposure accelerates physiological aging even more so than if tubers were to remain at a constant average temperature over the same maturation period. The longer the maturation period at fluctuating temperatures the more advanced the physiological age of tubers at harvest and this can compromise retention of process quality during storage.

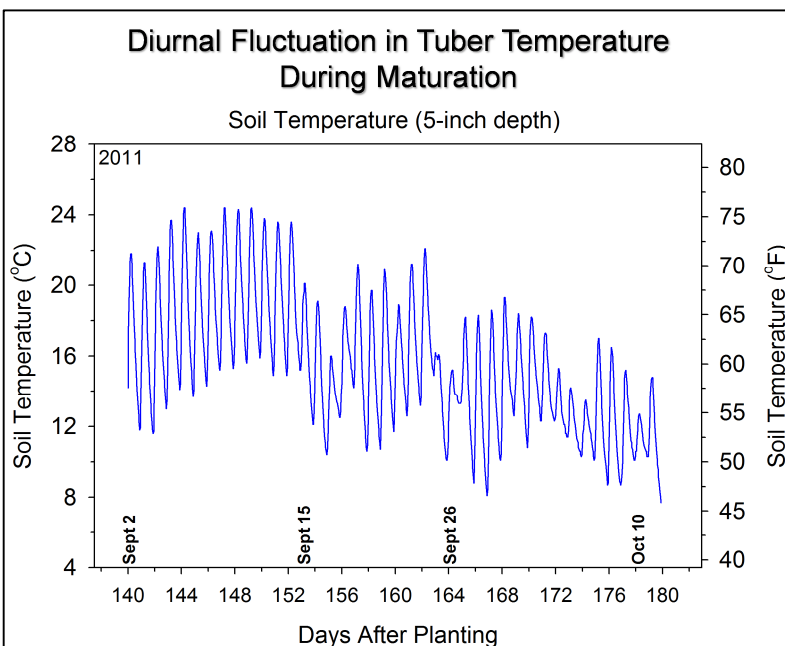
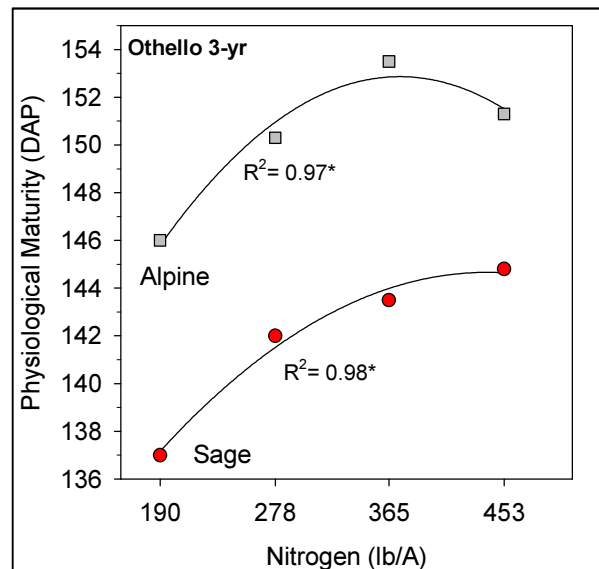


Fig. 6. Typical diurnal fluctuation in soil and thus tuber temperature (5-inch depth) during maturation of tubers under dead vines from 140 to 180 DAP at Othello, WA (2011 growing season). Tuber respiration rate will parallel these changes in temperature, which no doubt contributes to the physiological age of tubers at harvest.

Fertility management can affect the timing of PM and thus potentially the retention of process quality during storage. For example, PM is delayed as N rate increases (Fig. 7). High rates of N prolong vine and tuber growth late into the season. Figure 8 shows the effect of low and high rates of N on specific gravity, tuber reducing sugar content and the timing of PM for Alpine Russet. Regardless of N rate, tubers were harvested 181 DAP. The maturation period was thus longer for tubers grown with low N than high N. The low-N tubers were exposed to a longer period of fluctuating temperatures during maturation and were therefore likely physiologically older than the tubers from the high N crop. At harvest, the low-N tubers contained higher concentrations of reducing sugars in the stem and bud ends than the high N tubers (Fig. 8), which were physiologically younger and able to retain process quality longer over a 230-day storage period at 44 and 48°F (Fig. 9). In-season fertility management can therefore affect retention of process quality through influencing the extent and rate of aging of tubers during maturation and subsequent storage.

Fig. 7. Three year average (2011-13) effects of N rate on days after planting to physiological maturity (PM) for Alpine and Sage Russet tubers. Planting dates were April 19 (2011), April 9 (2012) and April 18 (2013). Vines were mowed 157 (2011), 162 (2012) and 161 DAP (2013). PM is the average of DAP to reach max yield, max specific gravity, minimum sucrose, and minimum reducing sugars in tubers (e.g. see Fig. 8). Sage reached PM earlier than Alpine. Tubers should be harvested soon after PM to minimize exposure to fluctuating temperatures during maturation (Fig. 6), which accelerates physiological aging and can potentially compromise retention of process quality (see Figs. 8 & 9).



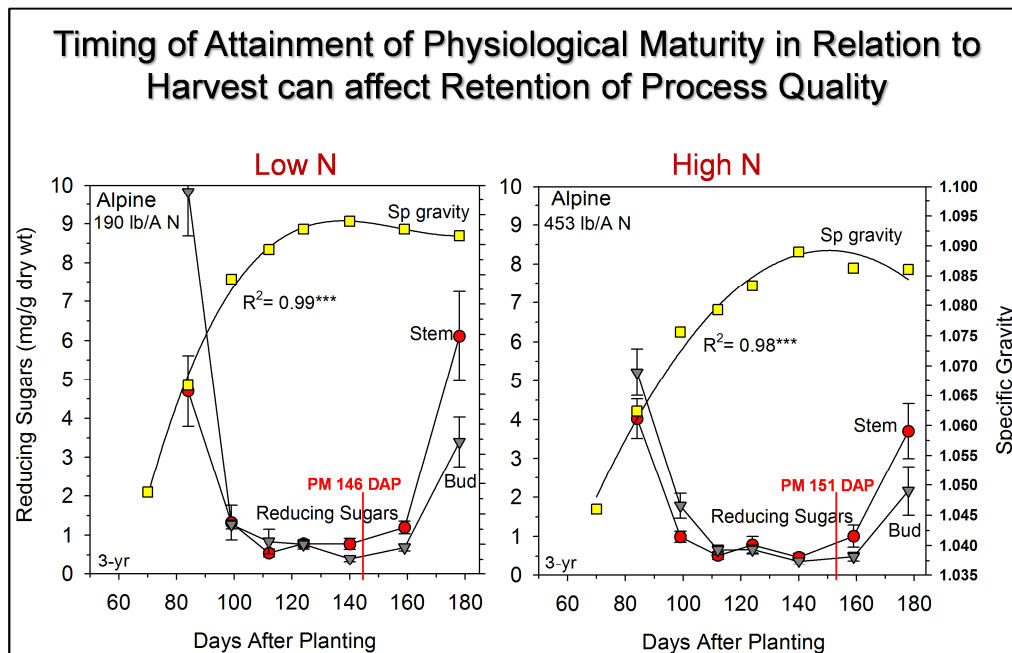


Fig. 8. Changes in reducing sugars (glucose + fructose), specific gravity and physiological maturity (PM) as affected by low (190 lb/A) and high (453 lb/A) rates of N (average over 3 seasons, 2011-13). PM of tubers was estimated at 146 and 151 DAP for the low- and high-N crops, respectively. **Tubers grown with low N matured earlier, resulting in physiologically older tubers at harvest (181 DAP).** The reducing sugar content increases following PM (especially in the stem end), which can lead to sugar ends at harvest. The extent of sugar accumulation depends on length of the maturation period (from PM to harvest). High N delayed PM, resulting in a shorter maturation period. **High N tubers were physiologically younger than low N tubers at harvest and maintained lighter fry color throughout most of a 230-day storage period (see Fig. 9).** Fertility management can thus affect tuber PM, which in turn can influence retention of process quality during storage.

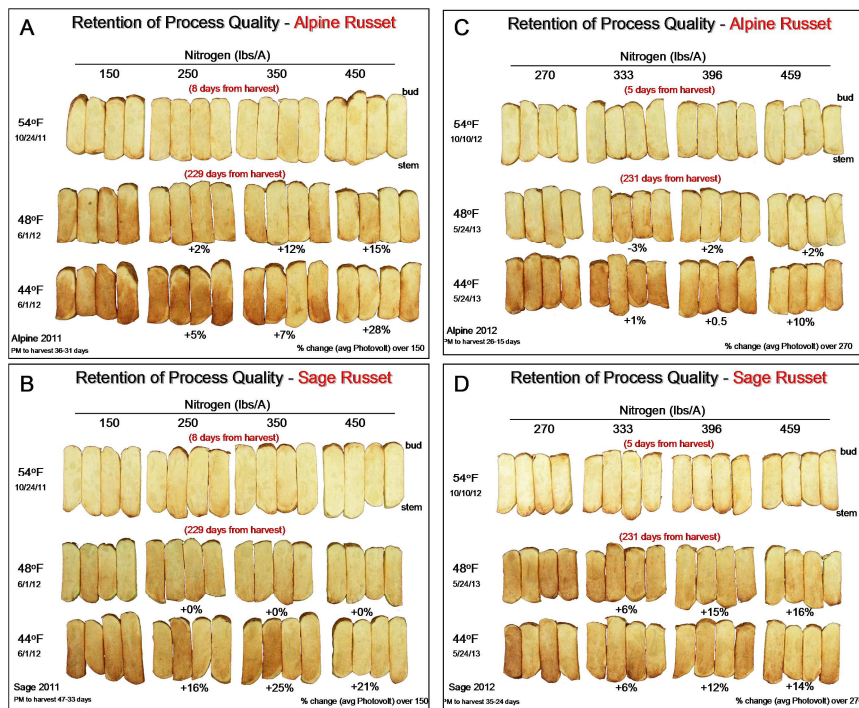


Fig. 9. Effects of N rate and storage temperature on retention of process quality of **Alpine Russet** (A,C) and **Sage Russet** (B,D) tubers following wound healing at 54°F and storage at 48 and 44°F in 2011 (A,B) and 2012 (C,D) (~230 days storage). Fry color was light and uniform after wound healing regardless of N rate. Process quality deteriorated noticeably by ~230 days of storage for both cultivars at both temperatures. Tubers grown with higher N rates retained lighter fry color, especially when stored at 44°F. For Alpine Russet grown with the lowest levels of N, the average intervals between tuber PM and harvest were 36 (2011) and 31 days (2012). At the highest levels of N, these intervals shortened to 31 (2011) and 15 days (2012). For Sage Russet grown with the lowest levels of N, the average intervals between tuber PM and harvest were 47 (2011) and 35 days (2012). At the highest levels of N, these intervals shortened to 33 (2011) and 24 days (2012).

In summary:

- High tuber temperatures during bulking and/or maturation can result in physiologically older tubers.
- Heat stress has both a direct and indirect (latent) effect on tuber physiology.
- Exposure to high temperature can induce a higher respiration rate that is sustained even after the temperature has been lowered (indirect effect), which reflects an elevated metabolic rate that accelerates the aging process...respiration is the pacemaker of aging. The longer respiration remains high the older the seed at planting.
- The impact of heat-induced accelerated aging diminishes when tubers are exposed to high temperature later in storage. Seed can tolerate more heat-unit accumulation toward the end of storage just prior to planting.
- Heat stress during bulking and/or maturation also affects at-harvest quality and storability of processing potatoes – low gravity, sugar ends, shorter dormancy, premature loss of process quality, loss of LTS resistance.
- Tubers have the best quality and longest storage life if harvested at physiological maturity (PM).
- A prolonged interval between PM and harvest (i.e. maturation period) exposes tubers to potential heat stress and fluctuation in temperature, which accelerates aging.
- Management (e.g., N fertility) can affect retention of postharvest quality by influencing the timing of PM in relation to harvest.
- For a particular cultivar and production area, physiological maturity can be gauged collectively by DAP, cumulative degree days from planting, and the extent of foliar senescence. Most healthy late-season russet cultivars in the central Columbia Basin will reach PM 145-155 DAP when grown with optimum fertility and irrigation.

References

- Blauer, J.M., L.O. Knowles, and N.R. Knowles. 2013. Evidence that tuber respiration is the pacemaker of physiological aging in seed potatoes (*Solanum tuberosum* L.). **J Plant Growth Regul** 32:708-720.
- Driskill, E.P. Jr., L.O. Knowles, and N.R. Knowles. 2007. Temperature-induced changes in potato processing quality during storage are modulated by tuber maturity. **Amer J Potato Res** 84:367-383.
- Knowles, N.R., E.P. Driskill, Jr., and L.O. Knowles. 2009. Sweetening responses of potato tubers of different maturity to conventional and non-conventional storage temperature regimes. **Postharvest Biol Tech.** 52:49-61.
- Knowles, N.R., M.J. Pavek, L.O. Knowles, and Z. Holden. 2008. Developmental profiles and postharvest behavior of long-season processing cultivars. Proceedings of the 47th Annual Washington State Potato Conference, Feb. 5-7, Moses Lake, WA, pp. 45-65.
- Knowles, N.R., E.P. Driskill Jr., L.O. Knowles, M.J. Pavek, and M.E. Martin. 2006. Physiological maturity of Ranger Russet tubers affects storability and processing quality. **Potato Progress** 6(3):1-4.
- Kumar, G.N.M. and N.R. Knowles. 1996a. Oxidative stress results in increased sinks for metabolic energy during aging and sprouting of potato seed-tubers. **Plant Physiol.** 112:1301-1313.
- Kumar, G.N.M. and N.R. Knowles. 1996b. Nature of enhanced respiration during sprouting of aged potato seed-tubers. **Physiol Plant** 97:228-236.
- Kumar, G.N.M. and N.R. Knowles. 1993. Involvement of auxin in the loss of apical dominance and plant growth potential accompanying aging of potato seed-tubers. **Can J Bot** 71:541-550.
- Whitworth J.L., R.G. Novy, J.C. Stark, J.J.Pavek,D.L. Corsini, S.L. Love, N. Olsen, S.K. Gupta, T. Brandt, M.I. Vales, A.R. Mosley, S. Yilma, S.R. James, D.C. Hane, B.A. Charlton, C.C. Shock, N.R. Knowles, M.J. Pavek, J.S. Miller, and C.R. Brown. 2011. **Alpine Russet:** A potato cultivar having

long tuber dormancy making it suitable for processing from long-term storage. **Amer J Pot Res.** 88:256-268.

Zommick, D.H., G.N.M. Kumar, L.O. Knowles and N.R. Knowles. 2013. Translucent tissue defect in potato (*Solanum tuberosum* L.) tubers is associated with oxidative stress accompanying an accelerated aging phenotype. **Planta** 238:1125-1145.

Zommick, D.H., L.O. Knowles, M.J. Pavek and N.R. Knowles. 2014. In-season heat stress compromises postharvest quality and low temperature sweetening resistance in potato (*Solanum tuberosum* L.). **Planta** DOI 10.1007/s00425-014-2048-8 (*Online First*).