# California processing tomatoes: Morphological, physiological and phenological traits associated with crop improvement during the last 80 years

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ABSTRACT

Breeding has greatly increased yields of many crops, but the contributions of particular morphological, phenological and physiological traits to these higher yields are rarely well understood. In the past 50 years, California processing tomato yields per hectare have more than doubled. This study evaluated a group of important processing tomato cultivars released over the past 80 years in California. The objective was to assess how a suite of traits might be associated with genetic improvement for yield gains. A wide array of morphological, physiological and phenological traits and relevant environmental variables was evaluated in the field for a discrete set of eight cultivars originating from a common ancestor. Multivariate statistics were used to analyze the set of 95 variables to understand how cultivars became adapted to a more mechanized agronomic management while also producing higher yields. No single trait seems to have driven yield increases. Instead, distinct assemblies of traits characterize the processing tomato cultivars in different eras. For instance, certain phenological traits (early flowering and concentrated fruit set) were associated with a set of morphological traits (smaller canopies and low vegetative biomass), along with gains in physiological traits (biomass N concentration and photosynthetic rates) in modern varieties. These results provide a platform to examine new suites of traits that could be relevant for future breeding and crop improvement.

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## 1. Introduction

For most crops, breeding has played an important role in increasing yields, but the mechanisms by which particular morphological, phenological and physiological traits contribute to these higher yields are not well understood (Sinclair and Purcell, 2005). Large yield increases are often the result of an interaction between crop improvement and new agronomic practices, *e.g.*, introduction of dwarfing genes and higher nitrogen (N) inputs in wheat, or more determinate growth and mechanized harvest in processing tomatoes (Evans and Fischer, 1999; Stevens and Rick, 1986). More emphasis is needed on how trait associations have contributed to yield gains, in order to overcome future potential environmental constraints, *e.g.*, diminishing water supply (Fischer, 2007; Passioura, 2002; Sadras and Lawson, 2013).

The processing tomato industry in California accounts for >90% of production in the USA, and ~35% worldwide (UCCE, 2008; USDA, 2009). According to the existing USDA (2009) records, crop yields per hectare (ha) have more than doubled in the past 50 years. The evaluation of a suite of traits could provide clues on how genetic improvement has contributed to these yield gains (Grandillo et al., 1999). Deeper understanding of plant phenology and other trait interactions with the environment is becoming more important for increasing yields (Fischer, 2007; Giunta et al., 2007), and trait associations are increasingly recognized as important for improving plant response to agricultural management, and thus for crop breeding in future uncertain climate scenarios.

In processing tomato, crop performance has usually been evaluated based on yield and fruit quality, but little is known about other traits that contribute to gains in these two complex traits. Selecting for a specific trait can inadvertently lead to breeding for trait associations that can have a positive or negative effect on a desired trait (Barrios-Masias et al., 2013; de Meijer and Keizer, 1996). One benchmark in the 1960s was the switch from hand-picked, indeterminate growth habit plants to cultivars with a determinate growth habit for machine-harvest (Stevens and Rick, 1986). Since then, yields have increased from 40 Mg to 90 Mg ha$^{-1}$, with most of the gain in crop productivity occurring after 1975 (Grandillo et al., 1999; Hanson and May, 2006). New introduction of genes for pest and disease resistance (such as nematode, *Fusarium* and *Verticillium* wilt) has occurred throughout this period (Hajjar and

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Hodgkin, 2007; Thomas, 1980). Between 1977 and 1994, the genetic improvement for California tomatoes was 1.5% per year in yield but without a significant gain in fruit total soluble solids (Grandillo et al., 1999). In addition, <30% of the annual genetic gain was associated with the adoption of hybrid cultivars in the 1990s (Grandillo et al., 1999).

Morphological changes that affect growth habit and biomass allocation have increased yields of major crops (Sinclair, 1998) such as dwarfing genes in wheat (Evans and Fischer, 1999), or in bush-type chickpea (Rubio et al., 2004). Changes in canopy architecture can help improve light use efficiency and provide an advantage for C assimilation when N uptake is optimal (Long et al., 2006; Rascher et al., 2011; Tei et al., 2002). Phenological traits such as the onset of flowering are influenced by plant growth habit, *e.g.*, soybean (Egli, 2005) and can also affect yields, *e.g.*, chickpea (Rubio et al., 2004). Physiological gains in C assimilation by higher photosynthetic rates ($P_n$) have sometimes been observed in modern cultivars of wheat (Evans, 1993; Fischer et al., 1998; Watanabe et al., 1994). Interestingly, changes in C assimilation potential have been associated with changes in growth habit in wheat (Morgan et al., 1990) and soybean (Tanaka et al., 2008). Gains in $P_n$ are usually accompanied by higher stomatal conductance ($g_s$), and as a result, intrinsic water use efficiency (WUE$_i$; $P_n/g_s$) tends to decrease (Barrios-Masias et al., 2013; Gilbert et al., 2011). Higher $P_n$ is also related to higher leaf-N concentration in particular to investment in Rubisco for higher C assimilation (Poorter and Evans, 1998; Watanabe et al., 1994). When C allocation to shoots is reduced, the number of fruits or grains per plant can increase, *e.g.*, wheat (Fischer and Stockman, 1986). Usually an increase in fruit number has a strong negative correlation with fruit weight, *e.g.*, tomato (Griffing, 1990). Carbon allocation, total plant biomass and fruit biomass can affect the harvest index (HI; yield per total biomass), which has increased in most field crops along with yield gains (Evans, 1993; Higashide and Heuvelink, 2009). Thus, evaluating plant performance for increasing crop yield may most effectively involve a complex interplay of traits and environment through the growing season.

This study evaluated a group of important processing tomato cultivars released over the past 80 years in California. The objective was to assess how a suite of traits might be associated with genetic improvement for yield gains in processing tomatoes. The approach was to evaluate a wide array of morphological, physiological and phenological traits and relevant environmental variables for a discrete set of cultivars originating from a common ancestor, then to use multivariate analyses to understand how changes adapted cultivars for more mechanized agronomic management, following statistical approaches by other studies that focused on germplasm evaluation (de Meijer and Keizer, 1996; Escribano and Lazaro, 2009; Perry and McIntosh, 1991; Yada et al., 2010). These results provide a platform to examine specific traits that could be relevant for future breeding and crop improvement.

## 2. Materials and methods

### 2.1. Plant material

A total of eight tomato cultivars representing different eras of the California processing tomato industry in the past 80 years were used in field and greenhouse studies.

- Pearson, mid 1930s release (LA0012)
- VF36, late 1950s release (LA0490)
- VF145 78-79, early 1960s release (LA1222)
- Heinz 1706-BG, early 1970s release (LA4345)
- M82, mid 1970s release (LA3475)
- Apex 1000, early 1980s release (LA3527)

- UC-204C, early 1990s release (LA3130)
- AB2, early 2000s release (AB Seeds)

All seeds but AB2 were obtained from the C. M. Rick Tomato Genetics Resource Center (TGRC) at UC Davis (LA numbered accessions). All cultivars were open pollinated, except AB2 which is a hybrid. Seeds were surface sterilized, germinated in trays, and seedlings maintained under day/night length of 16/8 h in greenhouses at the University of California at Davis (UC Davis). Seedlings were transplanted to either the field or in pots when they had at least 3 true leaves, *i.e.*, 6-week-old plants.

### 2.2. Field study

A field study was conducted during summer of 2007 at the UC Davis Plant Sciences Research Station in Davis, California. The soil was mapped as a Reiff very fine sandy loam, a coarse-loamy, mixed, nonacid, thermic Mollic Xerofluvent. During the experiment, from June 7 to September 24, the minimum and maximum average temperatures were 12.6 °C and 31.5 °C, respectively, with a minimum of 7.2 °C and a maximum of 40.6 °C, and no rainfall (CIMIS, 2010).

The field had been in wheat during the winter, and beds were prepared (1.52 m from furrow to furrow) for transplanting in spring of 2007. A total of 16 beds were divided in three blocks of four beds and one buffer bed on each side. Plots were 7.2-m long, and each block had a total of eight plots assigned to the eight cultivars in a randomized complete block design (RCBD; 24 plots total in the experiment). On June 7, 6-week-old seedlings were hand-transplanted in the center of the bed at a spacing of 0.6 m between plants (total of 12 plants per plot-length per bed and 48 plants per plot). In order to evaluate plant performance under minimal resource competition between neighboring plants, plant density was about half of what is currently used in modern commercial production. This density was intended to provide similar access to resources (fertilizer, water and light) even among cultivars with bigger canopies. Plants were sprinkler-irrigated after transplanting and two more times within the first 2 weeks to assure good establishment. Seven furrow irrigations followed until September 7 (92 days after transplanting, DAP) at intervals of ~11 days, and a total estimate of 620 mm of water applied for the entire growing season.

To monitor soil moisture content with a neutron probe, two PVC tubes of 5.4 cm in diameter were placed in each plot (one 2-m long and one 3-m long tube per plot; 48 tubes total). Tubes were placed in bed 2 and 3 between the edge and center of the bed, *i.e.*, 25 cm away from bed center, and toward the shared furrow. A Giddings machine was used to core the soil and place the tubes (Giddings Machine Company, Colorado, USA). Measurements were taken at every 30 cm interval with a count duration of no less than 16 s. Measurements were taken immediately before an irrigation event, and three days after to prevent furrow damage and soil compaction. Changes in soil moisture indicated the amount of water evapotranspired, but the first furrow irrigation (25 DAP) was not included because the disturbed soil was still settling around the tubes, assuring good contact for better neutron probe measurements later on.

A total of 95 variables were collected in the 109 days of the field experiment (Table 1). These variables included one-time measurements such as number of flowers per inflorescence; frequent measurements of the same variable, *e.g.*, soil canopy cover; and indexes derived from other variables, *e.g.*, HI (harvestable fruit/total aboveground biomass). Variables were grouped in three trait categories: morphological, physiological and phenological for which 51, 31 and 13 variables were obtained, respectively. These three categories were used based on traits associated with yield improvement in other crops (Fischer and Stockman, 1986; Gilbert et al.,