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‘UC Golden Gate’ and ‘UC Keystone’: Fusarium Wilt—Resistant Day-Neutral Strawberry Cultivars with High Yields of Long-Shelf-Life Fruit

Glenn S. Cole, Dominique D.A. Pincot, Cindy M. Lòpez, Randi A. Famula, and Steven J. Knapp
Department of Plant Sciences, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA

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The emergence of perpetual flowering strawberry (*Fragaria* ×*ananassa*) cultivars at the University of California (UC), Davis, in the 1970s transformed strawberry production, first in California and later further afield (Ahmadi et al. 1990; Bringhurst and Voth 1976, 1989, 1990; Feldmann et al. 2024a; Hancock et al. 2008, 2018). Those cultivars were described as “day-neutral” by Bringhurst et al. (1989), a widely used descriptor that has been questioned because the long-day flowering characteristics of photoperiod-insensitive strawberry cultivars are temperature dependent (Bradford et al. 2010; Hancock et al. 2008; Sønsteby and Heide 2006). Although they are perhaps more accurately described as temperature-dependent perpetual flowering cultivars (Brukental et al. 2025; Sønsteby and Heide 2006), the day-neutral descriptor is widely understood to designate a market segment distinct from the short-day and summer-plant market segments. Arguments about categorical descriptors aside, the perpetual flowering cultivars that emerged in the 1970s and later at UC Davis were unique and game changing because they flowered and produced fruit in the open field from early spring through late fall without interruption (Ahmadi et al. 1990; Bringhurst and Voth 1980; Hancock et al. 2008). Until they were developed and their commercial promise was fully appreciated, strawberry cultivars that flowered as strongly and continuously as these under long days were unknown, which is why commercial production had previously been dominated by seasonal flowering, short-day cultivars, even though so-called “everbearing” cultivars had long been known (Darrow 1966; Feldmann et al. 2024a; Hancock et al. 2008, 2018).

‘UC Golden Gate’ and ‘UC Keystone’, the day-neutral cultivars described here, are part of a long line that trace back to ‘Wasatch’, a long-day flowering ecotype of *Fragaria virginiana* subsp. *glauca* native to a high-elevation mountain habitat (Bringhurst and Voth 1976, 1980; Hancock 2006, 2008; Pincot et al. 2021). The long-day flowering phenotype of ‘Wasatch’ was initially introduced into short-day (seasonal flowering) genetic backgrounds in the 1950s by phenotypic selection and backcross breeding, starting with the short-day cultivar Shasta and closely related short-day individuals as recurrent parents. The first day-neutral cultivars to emerge from that work, released by UC Davis in 1969–70, were ‘Hecker’, ‘Brighton’, and ‘Aptos’ (Bringhurst and Voth 1980). They did not immediately transform strawberry production in California but supplied the foundation on which UC Davis and many other day-neutral cultivars were built (Feldmann et al. 2024a; Hancock 2006, 2008). Ahmadi et al. (1990) showed that the perpetual flowering phenotypes of these cultivars were caused by *PERPETUAL FLOWERING* (*PF*), a dominant gene inherited from ‘Wasatch’ that abolishes temperature-dependent photoperiod-sensitive flowering and pleiotropically affects sexual and asexual reproduction (Brukental et al. 2025; Gaston et al. 2013; Sønsteby and Heide 2006).

Since 1970, a progressively improved series of day-neutral cultivars carrying the ‘Wasatch’ *PF* allele have been developed and released by UC Davis for the long-shelf-life market (Brukental et al. 2025; Feldmann et al. 2024a). ‘UC Golden Gate’ and ‘UC Keystone’—released by the College of Agriculture & Environmental Sciences at UC Davis in 2023—are the latest in that series. They are Fusarium wilt–resistant and were developed to replace ‘Monterey’ (Shaw and Larson 2008), a Fusarium wilt–susceptible cultivar with heavy runnering (runner and daughter plant growth); ‘San Andreas’ (Shaw and Larson 2009), a Fusarium wilt–resistant cultivar with normal runnering but significantly lower yields than ‘Monterey’ and ‘UCD Moxie’ (Knapp et al. 2019a), a high yielding, Fusarium wilt–resistant cultivar with reduced runnering (Brukental et al. 2025; Pincot et al. 2022). The reduced runnering phenotype of ‘UCD Moxie’ significantly decreases runner trimming costs for fruit growers but increases bare-root plant (clone) propagation costs for nursery growers (Brukental et al. 2025). At present, the added costs of propagating bare-root plants of reduced-runnering cultivars like UCD Moxie has slowed their adoption, despite clear downstream benefits. This reflects a broader misalignment of incentives between nursery and fruit production sectors rather than technical limitations of the cultivars themselves. Overcoming this barrier may simply require more coordinated cost-sharing or pricing models that account for downstream labor savings associated with runner trimming. ‘UC Golden Gate’ and ‘UC Keystone’ were selected to strike a balance between these opposing fruit and nursery production tradeoffs, with stolon (runner) and plantlet (daughter plant) growth and clone (bare-root plant) yields falling directly between ‘UCD Moxie’ (reduced runnering) and ‘Monterey’ (heavy runnering).

The development and deployment of cultivars resistant to Fusarium wilt, a devastating vascular disease of strawberry caused by the soilborne fungal pathogen *Fusarium oxysporum* f. sp. *fragariae,* has become critical in California (Gordon 2017; Henry et al. 2017, 2019; Winks and Williams 1965). This disease was first reported in California in 2006, shortly before ‘Monterey’ was released, and has since become one of the leading causes of plant death and yield losses among Fusarium wilt–susceptible cultivars in California (Gordon 2017; Koike et al. 2009; Koike and Gordon 2015). We initiated studies in 2015 to identify breeding solutions to the Fusarium wilt problem in California, identified multiple sources of resistance to California race 1 isolates of the pathogen, and discovered that resistance was conferred by dominant race-specific resistance genes, e.g., *FW1*, *FW2*, and others (Henry et al. 2021; Pincot et al. 2018, 2022). In this study, we show that ‘UC Golden Gate’ and ‘UC Keystone’ are heterozgyous for *FW1* and resistant to California race 1, the *F. oxysporum* f. sp. *fragariae* race most widely found in California (Dilla-Ermita et al. 2023; Henry et al. 2017; Pincot et al. 2022). Their development was facilitated by the discovery of *FW1* in elite genetic backgrounds and by the identification of highly predictive *FW1*-associated single-nucleotide polymorphisms (SNPs) for marker-assisted selection of *FW1* alleles (Pincot et al. 2018, 2022). Those factors accelerated the development of Fusarium wilt–resistant cultivars carrying *FW1*, including short-day and summer-plant cultivars (UC Monarch, UC Surfline, and UC Eclipse) developed and released in parallel with ‘UC Golden Gate’ and ‘UC Keystone’ (Cole et al. 2025; Knapp et al. 2023, 2025).

‘Monterey’ and other Fusarium wilt–susceptible cultivars are still widely grown in California, even though resistant cultivars have been identified (Gordon et al. 2016; Henry et al. 2017, 2019; Koike et al. 2009; Koike and Gordon 2015; Pincot et al. 2018, 2022). The adoption of resistant cultivars has progressed more slowly in the day-neutral

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S.J.K. is the corresponding author. E-mail: sjknapp@ucdavis.edu.

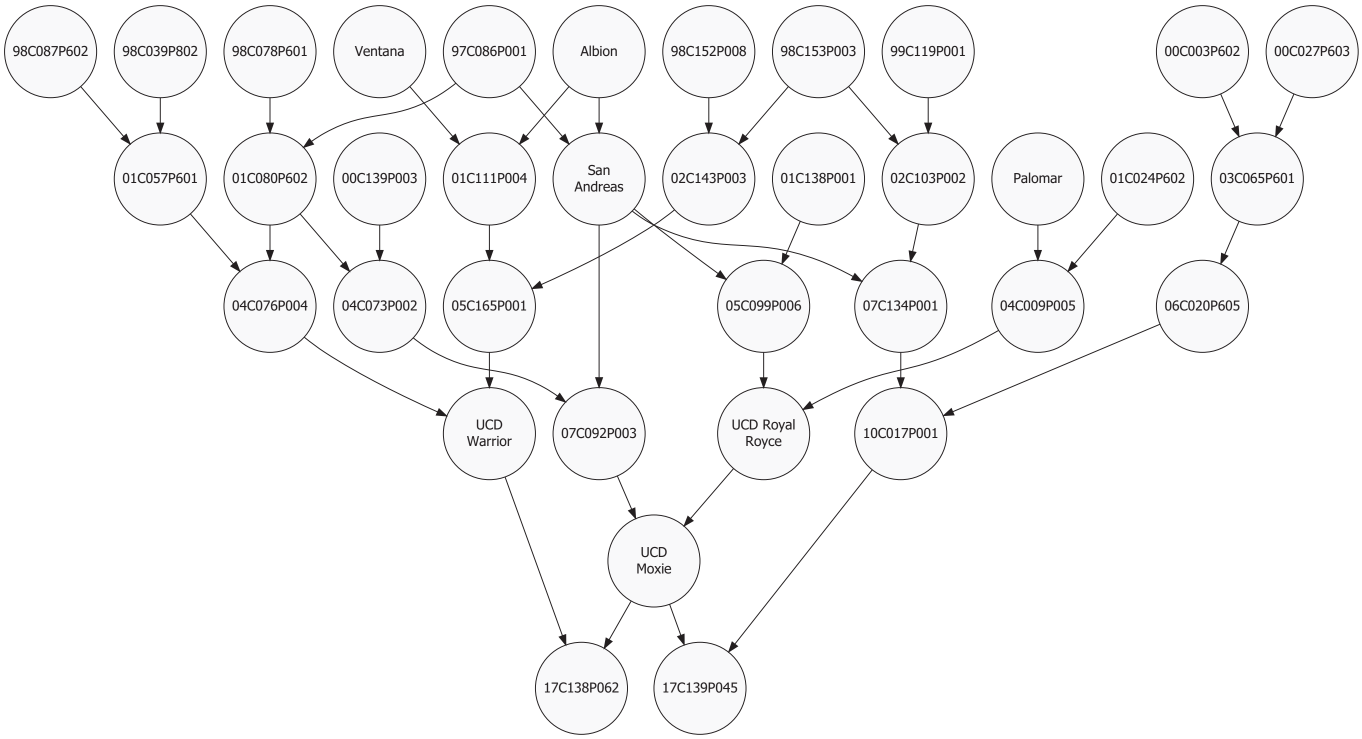

Fig. 1. Pedigrees for 'UC Golden Gate' (17C139P045) and 'UC Keystone' (17C138P062). UCD, University of California, Davis.

than the short-day and summer-plant segments because of the weaknesses of those previously available, e.g., 'San Andreas' and 'UCD Moxie'. In this study, we show that 'UC Golden Gate' and 'UC Keystone' overcome the weaknesses of those cultivars and deliver high yields of large, firm, long-shelf-life fruit. Importantly, we show that their fruit yields are greater than 'Monterey' and other high-yielding cultivars in the absence of Fusarium wilt.

Origin

'UC Golden Gate' (17C139P045) is a clonally propagated individual from a full-sib family (17C139) developed by hybridizing 'UCD Moxie' (11C141P001) and 10C017P001 (Fig. 1). 'UC Keystone' (17C138P062) is a clonally propagated individual from a full-sib family (17C138) developed by hybridizing 'UCD Moxie' and 'UCD Warrior' (08C138P003; Knapp et al. 2019b; Fig. 1). These parents were selected because they are high yielding, are large and firm fruited, and have long shelf life; were discovered to be resistant to Fusarium wilt (California race 1) and heterozygous for *FW1*; and were predicted to be sources of favorable alleles for improving clone yield, earliness, and resistance to Verticillium wilt and Phytophthora crown rot (PhCR). 'UCD Moxie' is a day-neutral (*PF*/*pf*) cultivar with reduced runnering and high marketable fruit yields, e.g., the fruit yields of 'UCD Moxie' surpassed 'Monterey' by 52% and 'San Andreas' by 64% in coastal California yield trials (Knapp et al. 2019a). Apart from 'UCD Moxie' (released in 2018), 'San Andreas' was the only Fusarium wilt–resistant day-neutral cultivar developed for the California market that was available when the breeding and cultivar development work described here got underway in 2015 (Pincot et al. 2022).

The parents of 'UC Golden Gate' and 'UC Keystone' were visually scored for runner and daughter plant growth (runnering) over three nursery growing seasons in Winters, CA, using an ordinal scale (1 to 5), where 1 = runnerless, 2 = reduced runnering, 3 = intermediate runnering, 4 = heavy

Table 1. Across-year estimated-marginal means (EMMs)[i] and *t* statistics for linear contrasts between EMMs[ii] for disease symptom ratings[iii] among test and check cultivars observed in 2019–20, 2020–21, and 2021–22 screening trials at Armstrong Farm, Davis, CA, USA.

			UC Golden Gate		UC Keystone	
Disease	Cultivar	EMM	t	Pr (>|t|)	t	Pr (>|t|)
Fusarium wilt	UC Golden Gate	1.17	—	—	0.19	0.85
	UC Keystone	1.25	−0.19	0.85	—	—
	San Andreas	1.15	0.04	0.97	0.19	0.85
	Monterey	3.36	−4.81	<0.0001	−4.67	<0.0001
	UCD Royal Royce	2.98	−4.28	0.0001	−4.12	0.0001
	UCD Valiant	2.88	−4.02	0.0001	−3.86	0.0003
Verticillium wilt	UC Golden Gate	1.97	—	—	0.34	0.74
	UC Keystone	2.12	−0.34	0.74	—	—
	San Andreas	1.29	0.99	0.33	1.19	0.24
	Monterey	2.36	−0.77	0.45	−0.46	0.64
	UCD Royal Royce	2.31	−0.81	0.42	−0.44	0.66
	UCD Valiant	1.93	0.09	0.93	0.43	0.67
PhCR[iv]	UC Golden Gate	2.25	—	—	0.34	0.73
	UC Keystone	2.44	−0.34	0.73	—	—
	San Andreas	1.83	0.59	0.56	0.85	0.4
	Monterey	3.07	−1.23	0.22	−0.92	0.36
	UCD Royal Royce	2.33	−0.16	0.87	0.21	0.84
	UCD Valiant	2.25	0.00	1.00	0.35	0.73

[i] EMMs were estimated from disease symptom ratings observed among four replications/entry/year over 3 years (12 observations/entry).
[ii] t statistics are displayed for tests of the null hypothesis of no difference between test and check cultivar EMMs (H_0: $EMM_1 = EMM_2$). Pr (> |t|) is the probability of observing a greater t statistic by chance for tests of the null hypothesis. Statistics for comparisons between 'UC Golden Gate' and check cultivar EMMs are displayed under the 'UC Golden Gate' subhead, whereas statistics for comparisons between 'UC Keystone' and check cultivar EMMs are displayed under the 'UC Keystone' subhead).
[iii] The ordinal scales used for rating disease symptoms were identical for each disease: 1 = highly resistant, 2 = moderately resistant, 3 = moderately susceptible, 4 = susceptible, and 5 = highly susceptible. Highly resistant individuals lacked symptoms, whereas highly susceptible individuals were killed by the disease.
[iv] Phytophthora crown rot (PhCR).

Table 2. Across-year estimated-marginal means (EMMs)[i] and t statistics for linear contrasts between EMMs[ii] for fruit quality traits among test and check cultivars grown on commercial farms in Nipomo and Prunedale, CA, USA, over three growing seasons (2019–20 to 2021–22).

			UC Golden Gate		UC Keystone	
Trait[iii]	Cultivar	EMM	t	Pr ($>\|t\|$)	t	Pr ($>\|t\|$)
Weight (g/fruit)	UC Golden Gate	28.7	—	—	1.2	0.23
	UC Keystone	28	−1.2	0.23	—	—
	Monterey	29.7	−1.88	0.06	−3.23	0.001
	UCD Royal Royce	28.8	−0.18	0.85	−1.39	0.16
	UCD Valiant	33	−7.41	<0.0001	−8.91	<0.0001
Firmness (*g*-force)	UC Golden Gate	303.7	—	—	3.25	0.002
	UC Keystone	260.6	−3.25	0.002	—	—
	Monterey	239.1	4.79	<0.0001	1.96	0.05
	UCD Royal Royce	349.9	−3.22	0.002	−7.18	<0.0001
	UCD Valiant	297.1	0.46	0.65	−2.93	0.005
TSS (%)	UC Golden Gate	7.84	—	—	−2.59	0.01
	UC Keystone	8.29	2.59	0.01	—	—
	Monterey	8.89	−5.92	<0.0001	−4.19	0.0001
	UCD Royal Royce	7.57	1.49	0.14	4.55	<0.0001
	UCD Valiant	7.37	2.55	0.01	5.78	<0.0001
TA (%)	UC Golden Gate	0.85	—	—	4.21	0.0001
	UC Keystone	0.77	−4.21	0.0001	—	—
	Monterey	0.76	3.73	0.0005	−0.39	0.7
	UCD Royal Royce	0.82	1.46	0.15	−2.87	0.006
	UCD Valiant	0.82	1.37	0.18	−2.97	0.005
TSS/TA	UC Golden Gate	9.45	—	—	−5.19	<0.0001
	UC Keystone	11.01	5.19	<0.0001	—	—
	Monterey	10.44	−7.5	<0.0001	2.69	0.01
	UCD Royal Royce	9.55	−0.34	0.73	5.12	<0.0001
	UCD Valiant	9.2	0.79	0.43	6.35	<0.0001

[i] EMMs were estimated from the phenotypes of fruit harvested at two time points from two 24-plant plots/entry (replications/entry) in each location over three growing seasons.

[ii] t statistics are displayed for tests of the null hypothesis of no difference between test and check cultivar EMMs (H_0: $EMM_1 = EMM_2$). Pr ($> |t|$) is the probability of observing a greater t statistic by chance for tests of the null hypothesis. Statistics for comparisons between 'UC Golden Gate' and check cultivar EMMs are displayed under the 'UC Golden Gate' subhead, whereas statistics for comparisons between 'UC Keystone' and check cultivar EMMs are displayed under the 'UC Keystone' subhead.

[iii] Fruit firmness, total soluble solids (TSS), and titratable acidity (TA) were measured as described by Petrasch et al. (2022) from multiple fruit per replication sampled at two time points in each environment (location × year).

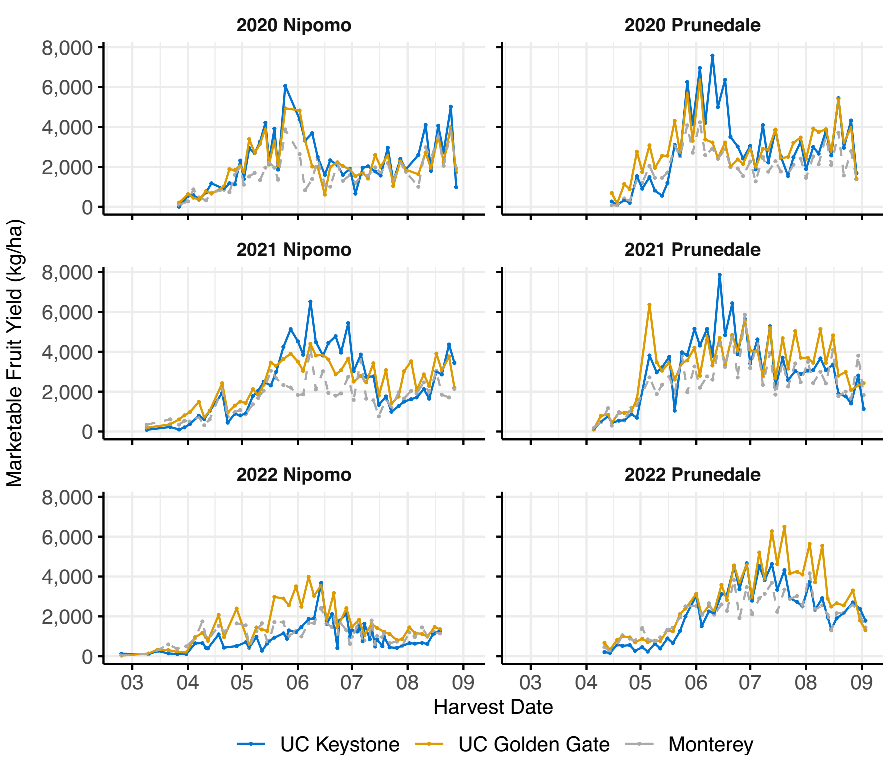

Fig. 2. Marketable fruit yield harvest-by-harvest. The figure shows harvest-by-harvest yields of marketable fruit for 'UC Golden Gate', 'UC Keystone', and the check cultivar Monterey grown on farms in Nipomo and Prunedale, CA, over three growing seasons (years). The number of harvests ranged from 40 to 61 per yield trial. Yield trials were grown on the same farms each year in Nipomo and Prunedale.

runnering, and 5 = excessive runnering (Brukental et al. 2025). The runner score means ($\bar{y}$) reported here were estimated from linear mixed model (LMM) analyses using the 'lme4' and 'emmeans' R packages with entry as a fixed effect and year and entry × year as random effects (Bates et al. 2015; Lenth 2019). 'UCD Moxie' was classified as reduced runnering ($\bar{y}$ = 2.0), whereas 'UCD Warrior' ($\bar{y}$ = 4.0), 10C017P001 ($\bar{y}$ = 4.0), and 'Monterey' ($\bar{y}$ = 4.0) were classified as heavy-runnering (Brukental et al. 2025). 'UCD Warrior' and 10C017P001 were selected as parents for hybridization with 'UC Moxie' to develop cultivars with stronger runnering than 'UCD Moxie' but weaker runnering than 'Monterey'.

The resistance of 'San Andreas' and susceptibility of 'Monterey' to Fusarium wilt, specifically to a California race 1 isolate of *F. oxysporum* f. sp. *fragariae* (AMP132), were unknown when those cultivars were released in 2008. Their resistance phenotypes and the resistance phenotypes of the parents of 'UC Golden Gate' and 'UC Keystone' were ascertained in parallel with the discovery of *FW1* in genetic studies conducted between 2015 and 2018 (Table 1; Pincot et al. 2018, 2022). Using Kompetitive allele-specific primer (KASP) and 50K array markers for SNPs associated with the *FW1* locus (Hardigan et al. 2020; Pincot et al. 2022), 'UCD Moxie', 'UCD Warrior', 10C017P001, and 'San Andreas' were predicted to be heterozygous (*FW1*/*fw1*), whereas 'Monterey', 'UCD Royal Royce', and 'UCD Valiant' were predicted to be homozygous for the recessive (susceptible) allele (*fw1*/*fw1*). Their DNA marker–predicted resistance phenotypes were confirmed by 3 years of screening clones artificially inoculated with AMP132 as described by Pincot et al. (2022). The KASP marker used for the initial analysis was FW1-K7 (A/C; bp 432,840). The 50K array SNP markers used for confirmatory analyses were AX-184326400 (T/C; bp 291,251), AX-184226354 (T/C; bp 414,365), and AX-184863196 (T/C; bp 1,012,042) (Hardigan et al. 2020). These SNPs flank the *FW1* locus on chromosome 2B (Pincot et al. 2022). The physical positions of these SNPs and others reported herein were ascertained in the haplotype-phased 'Royal Royal' genome (FaRR1; https://phytozome-next.jgi.doe.gov/info/FxananassaRoyalRoyce_v1_0; Hardigan et al. 2020).

'UC Golden Gate' and 'UC Keystone' were developed through a combination of phenotypic and marker-assisted selection between 2017 and 2022. They originated from two of 359 full-sib families (10,000 hybrid individuals) that were evaluated in the 2017–18 selection cycle, propagated from seed in the summer of 2017, and grown to maturity in Winters, CA, in 2017–18. Selected progenies were asexually propagated (cloned) in Winters, CA, in 2018–19 and Winters and Dorris, CA, each year thereafter until their official release in 2023. Clones (asexually propagated bare-root plants) for the first year of replicated testing (2019–20) were produced in Winters, CA. Clones for

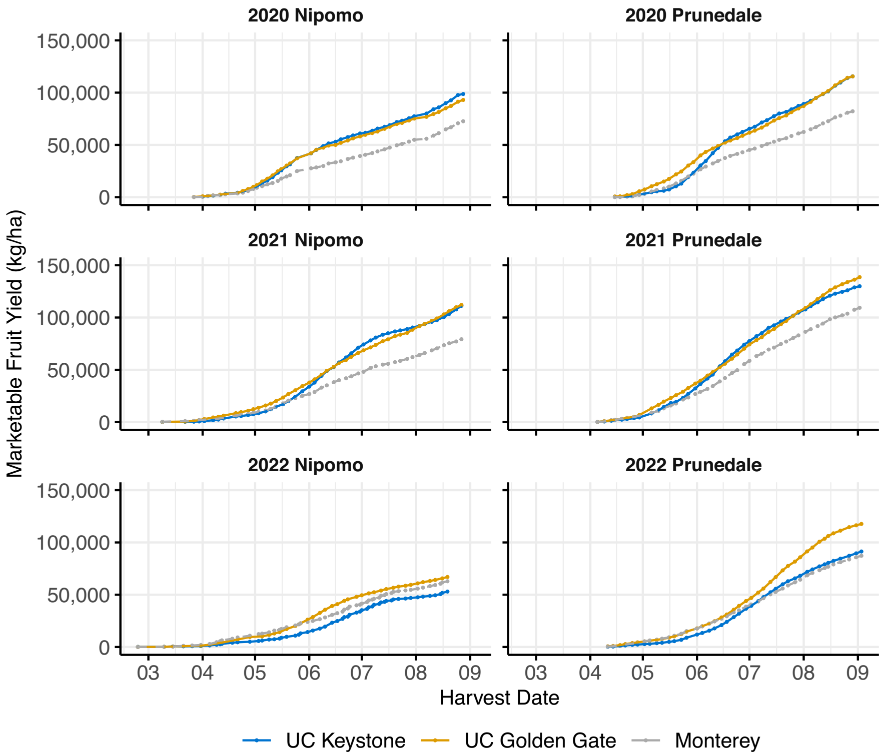

Fig. 3. Cumulative marketable fruit yield. Marketable fruit yields for 'UC Golden Gate', 'UC Keystone', and the check cultivar Monterey grown on California farms over three day-neutral growing seasons (years). The number of harvests ranged from 40 to 61 per yield trial. Yield trials were grown on the same farms each year in Nipomo and Prunedale.

subsequent years of replicated testing (2020–21 and later) were produced in high-elevation nurseries (Dorris, CA) using standard open-field plant propagation practices and postharvest chilling treatments optimized for the day-neutral market segment. The clones were harvested in late October, trimmed, and directly planted in late October and early November of each growing season on commercial farms in Nipomo, Santa Maria, and Prunedale, CA, and on the Armstrong Plant Pathology Farm in Davis, CA.

The first round of selection was applied to seed-propagated individuals phenotyped in the spring and summer of 2018 to identify perpetual flowering (day-neutral) individuals with outstanding fruit size, firmness, symmetry, color, gloss, and visual appeal; to eliminate individuals with fruit defects and deformities; to predict marketable fruit yields; and to evaluate and eliminate individuals with inadequate or excessive runnering. The entire population was genotyped with the FW1-K7 KASP marker in the spring of 2018 to identify and select individuals predicted to be heterozygous or homozygous for the *FW1* allele (*FW1_*). Collectively, 94 individuals with *FW1*/*FW1*- or *FW1*/*fw1*-predicted genotypes and runner scores in the $2.5 < y \leq 3.0$ range were selected for clonal multiplication and disease resistance screening in Davis, CA, and advanced testing on commercial farms in Nipomo, Santa Maria, and Prunedale, CA.

'UC Keystone' and 'UC Golden Gate', check cultivars, the 94 selected individuals, and 149 to 168 additional selected individuals were phenotyped for resistance to Fusarium wilt, Verticillium wilt, and PhCR over three disease-screening seasons (November to July) in Davis, CA. We collected and analyzed 31,404 resistance scores for these diseases to support statistical analyses, selection decisions, and disease resistance claims. These individuals were screened using bare-root plants (four clones/individual/year) that were artificially inoculated with a single isolate of a single pathogen, planted in chemically fumigated ground in November, and phenotyped for disease symptoms in late spring and early summer using previously described production practices, screening protocols, and pathogen isolates (Jiménez et al. 2023; Pincot et al. 2020, 2022). They were grown in soils that had been chemically fumigated to suppress soilborne pathogens and eliminate the confounding effects of diseases caused by nontarget soilborne pathogens within each pathogen-specific screen. Entries were arranged in randomized complete blocks experiment designs with four replications/entry (clones/entry). The R packages 'lme4' and 'emmeans' were used for LMM analyses of ordinal resistance scores with entry as a fixed effect and replicate, year, and entry × year as random effects (Bates et al. 2015; Lenth 2019). We used 'emmeans' to estimate entry estimated marginal means (EMMs). The EMMs of test cultivars ('UC Golden Gate' and 'UC Keystone') were compared with the EMMs of resistant and susceptible check cultivars using pairwise linear contrasts ($EMM_1 - EMM_2$), where EMM_1 is the mean for 'UC Golden Gate' or 'UC Keystone', and EMM_2 is the mean for one of the check cultivars. The null hypothesis (H_0:$EMM_1 = EMM_2$) was rejected when the *t* statistic for the linear contrast was greater than the critical value from a *t* distribution with a type I error probability <0.05.

The 94 individuals selected in the seed-propagated plant stage in 2017–18 were cloned for replicated testing over three growing seasons on commercial farms in Nipomo and Prunedale, CA. Selected individuals and check cultivars were grown in two 20-plant plots arranged in randomized complete blocks experiment designs. These yield trials were grown using the management practices, raised-bed configurations, plastic mulches, planting densities, planting dates, irrigation, fertilization and pesticide application practices and schedules, and harvest schedules of our cooperators. The number of harvests ranged from 40 to 61 across yield trials. The count and yield of marketable fruit per 20-plant plot were recorded at each harvest. To compare kg/ha yields across trials, the yield/plant was multiplied by the number of plants/ha within each location. We collected and analyzed 18,526 observations for these traits to support statistical analyses and selection decisions. Fruit from early and peak season harvests were sampled from every trial to phenotype individuals for firmness, total soluble solids (TSS%), and titratable acidity (TA%) using methods described by (Petrasch et al. 2022). Over three growing seasons, 2,273 phenotypic observations were collected for these traits to support statistical analyses and selection decisions. The R packages 'lme4' and 'emmeans' were used for LMM analyses with entry as a fixed effect and replicate, location, year, entry × location, entry × year, and entry × location × year as random effects (Bates et al. 2015; Lenth 2019). As before, pairwise linear contrasts were used to test for statistically significant differences between test and check cultivar EMMs for each trait.

To evaluate shelf life–associated fruit quality traits, early and peak season fruit were harvested from 100-plant plots on commercial farms in Santa Maria and Prunedale, CA, in 2021–22 (Table 2). Fruit samples were stored at 4 °C for 14 d postharvest (DPH) in 19-cm × 11.5-cm × 7-cm plastic clamshells designed to hold ∼454 g of freshly harvested fruit. Fruit samples were evaluated at 0, 7, and 14 d DPH for marketability; the incidence of molds caused by *Botrytis cinerea* or other fungal pathogens; and fruit weight, firmness, and TSS. The marketability of fruit was visually assessed using ordinal rating scale (1 to 10) comparable to the one proposed by do Nascimento Nunes (2015), where scores increase as marketability decreases (1 = fruit in perfect condition and 10 = unmarketable fruit). Fruit were stored undisturbed in one clamshell/cultivar for phenotyping fruit marketability and weight and in a second clamshell/cultivar for destructively phenotyping random samples of fruit for firmness and TSS at each time point. The statistical analyses of these data were identical to those described earlier with entry

Table 3. Within-environment estimated-marginal means (EMMs)[i] and t statistics for linear contrasts between EMMs[ii] for cumulative marketable fruit yield (kg/ha) among test and check cultivars tested on commercial farms in Nipomo and Prunedale, CA, USA, over three growing seasons (2019–20 to 2021–22).

				UC Golden Gate		UC Keystone	
Location	Season	Cultivar	EMM	t	Pr (>|t|)	t	Pr (>|t|)
Nipomo	2019–20	UC Golden Gate	92,998	—	—	−0.84	0.42
		UC Keystone	98,666	0.84	0.42	—	—
		Monterey	72,628	2.89	0.02	3.7	0.004
		UCD Royal Royce	89,248	0.41	0.69	1.03	0.33
		UCD Valiant	101,833	−1.26	0.24	−0.45	0.66
	2020–21	UC Golden Gate	112,012	—	—	0.08	0.94
		UC Keystone	111,204	−0.08	0.94	—	—
		Monterey	79,224	3.24	0.01	3.16	0.01
		UCD Royal Royce	104,398	0.75	0.47	0.67	0.52
		UCD Valiant	120,244	−0.81	0.44	−0.89	0.39
	2021–22	UC Golden Gate	66,960	—	—	0.97	0.34
		UC Keystone	63,542	−0.97	0.34	—	—
		Monterey	78,433	−3.25	0.004	−5.17	<0.0001
		UCD Royal Royce	43,983	5.64	<0.0001	5.54	<0.0001
		UCD Valiant	64,563	0.59	0.56	−0.29	0.78
Prunedale	2019–20	UC Golden Gate	115,521	—	—	−0.02	0.99
		UC Keystone	115,615	0.02	0.99	—	—
		Monterey	82,158	5.55	0.0002	5.56	0.0002
		UCD Royal Royce	113,370	0.36	0.73	0.37	0.72
		UCD Valiant	91,732	3.96	0.002	3.97	0.002
	2020–21	UC Golden Gate	138,615	—	—	1.23	0.24
		UC Keystone	129,916	−1.23	0.24	—	—
		Monterey	109,335	4.15	0.002	2.92	0.01
		UCD Royal Royce	144,413	−0.82	0.43	−2.05	0.06
		UCD Valiant	134,148	0.63	0.54	−0.6	0.56
	2021–22	UC Golden Gate	117,688	—	—	−8.08	<0.0001
		UC Keystone	178,119	8.08	<0.0001	—	—
		Monterey	170,512	−7.06	<0.0001	1.25	0.23
		UCD Royal Royce	104,154	1.57	0.13	9.89	<0.0001
		UCD Valiant	104,729	1.5	0.15	7.01	<0.0001
Combined	Combined	UC Golden Gate	107,299	—	—	−0.73	0.47
		UC Keystone	116,243	0.73	0.47	—	—
		Monterey	98,997	0.68	0.5	1.42	0.16
		UCD Royal Royce	99,805	0.61	0.54	1.35	0.18
		UCD Valiant	102,875	0.36	0.72	1.1	0.28

[i] EMMs were estimated from fruit harvested from two 24-plant plots/entry (replications/entry) once to twice weekly over the growing season on a commercial harvest schedule.
[ii] t statistics are displayed for tests of the null hypothesis of no difference between test and check cultivar EMMs (H_0: $EMM_1 = EMM_2$). Pr (>|t|) is the probability of observing a greater t statistic by chance for tests of the null hypothesis. Statistics for comparisons between 'UC Golden Gate' and check cultivar EMMs are displayed under the 'UC Golden Gate' subhead, whereas statistics for comparisons between 'UC Keystone' and check cultivar EMMs are displayed under the 'UC Keystone' subhead.

Fig. 4. Changes in the visual appearance of fruit of long-shelf-life cultivars in cold storage. 'UC Golden Gate', 'UC Keystone', and 'Monterey' fruit were stored in the dark at 4 °C for 0, 7, and 14 d post-harvest. The fruit were placed in 19-cm × 11.5-cm × 7-cm plastic clamshells and were not handled or disturbed.

and DPH as fixed effects and location, entry × DPH, and entry × location as random effects. We used the 'emmeans' R package to estimate the linear and quadratic effects of DPH on each trait and pairwise linear contrasts for comparison between test and check cultivar EMMs (Lenth 2019).

Description

'UC Golden Gate' and 'UC Keystone' are day-neutral. They produced an uninterrupted supply of fruit from the start of harvest near the vernal equinox through the spring and summer months on farms in Nipomo (35.0°N) and Prunedale (36.8°N), CA (Figs. 2 and 3). Their harvest-by-harvest and cumulative marketable fruit yields show that they flowered continuously under the temperature and photoperiod ranges normally encountered in coastal California locations where day-neutral cultivars are typically commercially grown (Figs. 2 and 3). Although we ended harvest by Sep 1, 'UC Golden Gate' and 'UC Keystone' continuously produced fruit and were commercially

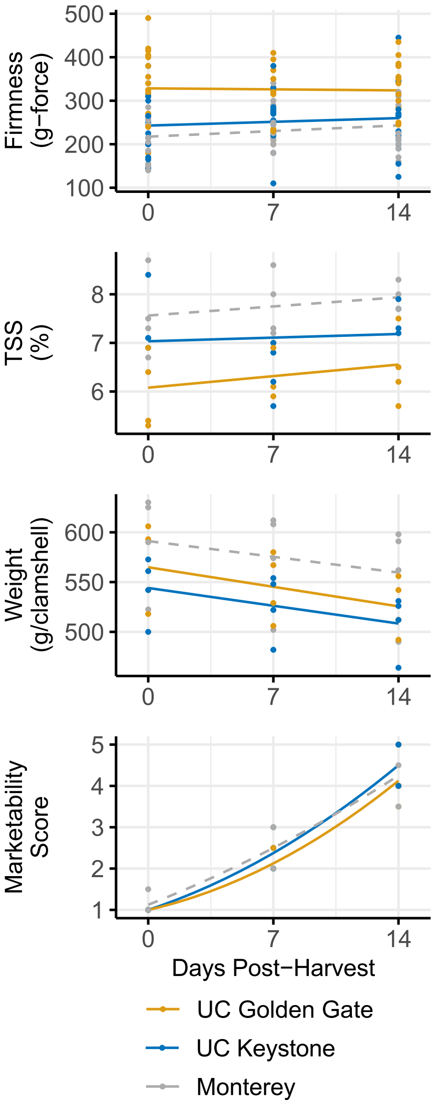

Fig. 5. Effect of postharvest cold storage on marketability and fruit quality traits of long-shelf-life cultivars. Weight, firmness, total soluble solids (TSS), and marketability of ‘UC Golden Gate’, ‘UC Keystone’, and ‘Monterey’ fruit stored in standard 19-cm × 11.5-cm × 7-cm plastic clamshells at 4 °C in the dark for 0, 7, and 14 d postharvest. Fruit were harvested on two dates in the 2021 to 2022 growing season on commercial farms in Santa Maria and Prunedale, CA. The marketability of fruit was scored using an ordinal scale (1 to 10), where marketability decreased as the score increased (1 = fruit in perfect condition and 10 = unmarketable fruit). Predicted values for linear regressions of TSS, firmness, and weight on d postharvest and quadratic regressions of marketability score on d postharvest are shown for each cultivar across locations.

harvested through late October or early November each year.

‘UC Golden Gate’ and ‘UC Keystone’ are Fusarium wilt resistant. This was substantiated by 3 years of screening plants artificially inoculated with AMP132, a California race 1 isolate of *F. oxysporum* f. sp. *fragariae* (Table 1). They were selected by screening DNA samples of seed-propagated full-sib progeny for the presence of the dominant *FW1* allele using the FW1-K7 KASP marker (Pincot et al. 2022). ‘UC Golden Gate’ and ‘UC Keystone’ were heterozygous for the KASP-SNP marker (A/C) and predicted to be heterozygous for *FW1* alleles. That prediction was confirmed using 50K array-genotyped SNPs in LD with *FW1* (Hardigan et al. 2020; Pincot et al. 2022). The 50K array SNPs used for this purpose bracket the *FW1* locus: AX-184326400 (T/C; bp 291,251), AX-184226354 (T/C; bp 414,365), and AX-184863196 (T/C; bp 1,012,042) (Pincot et al. 2022). Using these DNA markers, ‘Monterey’, ‘UCD Royal Royce’, and ‘UCD Valiant’ were predicted to be homozygous for the recessive (susceptible) allele (*fw1*/*fw1*). Consistent with these DNA marker predictions, ‘UC Golden Gate’, ‘UC Keystone’, and ‘San Andreas’ were confirmed to be resistant, whereas ‘Monterey’, ‘UCD Royal Royce’, and ‘UCD Valiant’ were confirmed to be susceptible to Fusarium wilt (Table 1). The mean symptom ratings for ‘UC Golden Gate’ ($\bar{y}$ = 1.17), ‘UC Keystone’ ($\bar{y}$ = 1.25), and ‘San Andreas’ ($\bar{y}$ = 1.15) were not significantly different from one another (Table 1). The replicates of these cultivars were mostly symptomless (y = 1). Conversely, we observed wilting, necrosis, and death among replicates of the susceptible check cultivars (Monterey, UCD Royal Royce, and UCD Valiant). The mean symptom ratings were significantly greater (more severe) for the susceptible checks than ‘UC Golden Gate’, ‘UC Keystone’, and the resistant check ‘San Andreas’ (Table 1).

‘UC Golden Gate’ and ‘UC Keystone’ are moderately resistant to Verticillium wilt and PhCR. This was substantiated by 3 years of field screening plants artificially inoculated with virulent isolates of the causal fungal pathogens (Table 1). Their resistance was found to be comparable to the most resistant modern cultivars identified to-date (Feldmann et al. 2024c; Jiménez et al. 2023; Mangandi et al. 2017; Pincot et al. 2020). Over 3 years of replicated testing, the mean symptom ratings were not significantly different among test and check cultivars for either disease (Table 1). The PhCR resistance of ‘UC Golden Gate’, ‘UC Keystone’, and the check cultivars was partly attributed to *RPc2*, a large-effect quantitative trait locus (QTL) on chromosome 7B (Jiménez et al. 2023; Mangandi et al. 2017). The favorable *RPc2* allele is dominant and increases PhCR resistance and, using screening protocols and experimental conditions identical to those reported here, the *RPc2* QTL was previously estimated to explain 28.7% to 39.7% of the additive genetic variance for PhCR resistance (Jiménez et al. 2023). Using a 50K array-genotyped SNP associated with the *RPc2* locus (AX-184109190; A/G; bp 22,332,550), we discovered that ‘UC Golden Gate’ and ‘UC Keystone’ are homozygous for the SNP allele (A) commonly associated with the favorable *RPc2* allele (Jiménez et al. 2023).

‘UC Golden Gate’ and ‘UC Keystone’ are among the highest yielding day-neutral cultivars documented to date (Feldmann et al. 2024b). The fruit yields for ‘UC Golden Gate’ and ‘UC Keystone’ were estimated from harvests over three growing seasons on farms where losses to diseases caused by soil-borne pathogens were negligible to nonexistent (Figs. 2 and 3; Table 3). Fruit were harvested from the start of the season (close to the vernal equinox) through the end of August each year following once or twice weekly commercial harvest schedules (the number of harvests per trial ranged from 40 to 61). Across years and locations, ‘UC Keystone’ produced the highest cumulative marketable fruit yields (116,243 kg/ha), followed by ‘UC Golden Gate’ (107,299 kg/ha), ‘UCD Valiant’ (102,875 kg/ha), ‘Monterey’ (98,997 kg/ha), and ‘UCD Royal Royce’ (99,805 kg/ha) across locations and years (Table 3; Fig. 3). Although these across-trial yield differences were not statistically significant, the yields of ‘UC Keystone’ were significantly greater than ‘Monterey’ within five of six trials, whereas the yields of ‘UC Golden Gate’ were significantly greater than ‘Monterey’ within four of six trials (Table 3; Fig. 3). ‘UC Golden Gate’ generally produced slightly higher early season yields than ‘UC Keystone’; however, their cumulative marketable yields were not significantly different in five of the six trials (Fig. 2). These data established that the intrinsic fruit yields of ‘UC Golden Gate’ and ‘UC Keystone’ are comparable to and often greater than ‘Monterey’, ‘UCD Royal Royce’, and ‘UCD Valiant’ in the absence of Fusarium wilt. The yield advantages of ‘UC Golden Gate’ and ‘UC Keystone’ over Fusarium wilt–susceptible cultivars are obviously bound to be much greater on farms infested with *F. oxysporum* f. sp. *fragariae*.

‘UC Golden Gate’ and ‘UC Keystone’ are long-shelf-life cultivars with the requisite fruit quality characteristics necessary for minimizing postharvest losses (Tables 2 and 4; Figs. 4 and 5). The fruit firmness, TSS, and TA percentage ranges were comparatively narrow among test and check cultivars; however, many of the differences were statistically significant (Table 2). TSS percentages were significantly greater for ‘UC Keystone’ (8.89) than ‘UC Golden Gate’ (7.84), whereas the TA percentages were greater for ‘UC Golden Gate’ (0.85) than ‘UC Keystone’ (0.77) and ‘Monterey (0.76) (Table 2). TSS was significantly lower for ‘UC Golden Gate’ and ‘UC Keystone’ than ‘Monterey’ (Table 2). The TSS/TA ratio (a perceived sweetness metric) was significantly greater for ‘UC Keystone’ (11.01) than ‘Monterey’ (10.44) and ‘UC Golden Gate’ (9.45).

‘UC Golden Gate’ and ‘UC Keystone’ are firm-fruited and among the most firmly fruited cultivars documented to date in strawberry (Tables 2 and 4; Jiménez et al. 2024). This trait is one of the most important determinants of shelf life—perishability increases and shelf life decreases as fruit firmness decreases (Harker et al. 2000; Cordenunsi et al. 2003; do Nascimento Nunes 2015; Jiménez et al. 2024; Petrasch et al. 2022; Watkins et al. 1999). The fruit of ‘UC Golden Gate’ (303.7 *g*-force) were significantly firmer than ‘UC Keystone’ (260.6 *g*-force), and the

Table 4. Effect of days postharvest (DPH) cold storage on fruit quality traits among test and check cultivars grown on commercial farms in Santa Maria and Prunedale, CA, USA in 2021–22[i].

Trait[ii]	Contrast[iii]	t	Pr (>|t|)
Marketability (score)	Linear	25.3	<0.0001
	Quadratic	3.0	0.0041
Fruit weight (g/clamshell)	Linear	−3.3	0.002
	Quadratic	0.1	0.93
Fruit firmness (*g*-force)	Linear	0.6	0.59
	Quadratic	0.1	0.90
Total soluble solids (%)	Linear	1.4	0.17
	Quadratic	−1.6	0.12

[i] Fruit were harvested from 100-plant plots of 'UC Golden Gate', 'UC Keystone', 'Monterey', and 11 additional long-shelf-life cultivars on two dates from each farm.
[ii] The marketability of fruit was visually scored using an ordinal scale (1 to 10) and rating system comparable to that proposed by do Nascimento Nunes (2015), where scores increase as marketability decreases (1 = fruit in perfect condition and 10 = unmarketable fruit). Fruit for weight measurements were stored undisturbed in a standard 19-cm × 11.5-cm × 7-cm plastic clamshell designed to hold ∼454 g of freshly harvested fruit. Fruit firmness and total soluble solids were measured as described by Petrasch et al. (2022).
[iii] t statistics are displayed for tests of the null hypothesis of no linear or quadratic effect of days postharvest storage. Effects were estimated using linear and quadratic contrasts for three equally spaced treatments (0, 7, and 14 DPH). Pr (> |t|) is the probability of observing a greater t statistic by chance.

fruit of 'UC Keystone' were significantly firmer than 'Monterey' (239.1 *g*-force). 'UC Golden Gate' fruit are especially resistant to physical damage caused by harvest and handling. The fruit firmness of 'UC Golden Gate' and 'UC Keystone' was partly attributed to the homozygosity of a favorable *POLYGALACTURONASE1* allele (*PG1-6A1*) that increases fruit firmness (Jiménez et al. 2024). Their *PG1-6A1* genotypes were predicted using 50K array-genotyped SNPs in LD with the *PG1-6A1* locus on chromosome 6A. The SNPs used for this purpose were AX-184953741 (T/G; bp 27,253,733), AX-184023221 (A/C; bp 27,593,175), AX-184726882 (T/G; bp 27,671,092), and AX-184210676 (T/G; bp 27,676,285), and AX-184242253 (T/C; bp 27,888,596).

There are other important but more subtle phenotypic differences between 'UC Golden Gate' and 'UC Keystone'. 'UC Golden Gate' has a more compact plant habit and slightly longer trusses than 'UC Keystone' but shorter trusses than 'UC Monarch' (Cole et al. 2025). 'UC Keystone' has heavier vegetative growth and a denser plant canopy than 'UC Golden Gate'. Consequently, 'UC Golden Gate' appears to be better adapted to tabletop, substrate, and tunnel production than 'UC Keystone', whereas 'UC Keystone' appears to be better adapted to organic production than 'UC Golden Gate'.

The long shelf life of 'UC Golden Gate' and 'UC Keystone' was substantiated by evaluating fruit for changes in marketability (visual appearance), mold incidence, and fruit firmness, TSS, and weight over 14 DPH of cold storage (Figs. 4 and 5; Table 4). We did not observe molds caused by *B. cinerea* or other fungal pathogens at 0 or 7 DPH among the fruit samples tested (Fig. 4). The mold incidence was <0.7% at 14 DPH. Statistically significant differences were observed among cultivars for TSS and firmness but not weight or marketability. Moreover, the cultivar × DPH interaction was not statistically significant for any trait. We did not observe statistically significant changes in fruit firmness and TSS as DPH increased (linear and quadratic regressions of fruit firmness and TSS on DPH were not statistically significant). Conversely, we observed a statistically significant linear decrease in fruit weight and quadratic decrease in marketability as DPH increased (Table 4; Figs. 4 and 5). Figure 5 shows that the marketability of 'UC Golden Gate', 'UC Keystone', and 'Monterey' decreased at an increasing rate as DPH increased (score increase as marketability decreases). The fruit of every cultivar became increasingly more desiccated, lighter, less glossy, and less marketable as storage time increased (Figs. 4 and 5). The marketability scores were perfect (1 on the ordinal scale) to near perfect for every cultivar at 0 DPH and increased to 4 or 5 by 14 DPH. Fruit with scores in the 4 to 5 range are marginally marketable (do Nascimento Nunes 2015). These data show that 'UC Golden Gate' and 'UC Keystone' have a shelf life approaching 2 weeks under generic cold storage conditions but become increasingly less visually appealing and less marketable the longer the fruit are stored (Fig. 4).

'UC Golden Gate' and 'UC Keystone' deliver strong yields of bare-root plants in nursery production. Using an ordinal scale for scoring runner and daughter plant growth, Brukental et al. 2025 showed that 'UC Golden Gate' ($\bar{y}$ = 3.0) and 'UC Keystone' ($\bar{y}$ = 3.2) runner less strongly than 'Monterey' ($\bar{y}$ = 4.0) and more strongly than 'UCD Moxie' ($\bar{y}$ = 2.0). The runner scores for 'UC Golden Gate' and 'UC Keystone' are typical of most day-neutral cultivars and were not significantly different from the population mean ($\bar{y}$ = 3.0) estimated from phenotypes observed in a study of several hundred elite and exotic generic resources, including heirloom and modern cultivars (Brukental et al. 2025). From a bare-root plant propagation perspective, they are an improvement over 'UCD Moxie' (reduced runnering). From a fruit production runner trimming perspective, they are an improvement over 'Monterey' (heavy runnering).

Availability

The release of 'UC Golden Gate' and 'UC Keystone' was approved by the College of Agricultural & Environmental Sciences at the University of California, Davis, in 2023. US Plant Patents have been granted for 'UC Keystone' and 'UC Golden Gate' (Knapp and Cole 2024a, 2024b). Plant breeder's rights are pending in territories outside the United States. Those interested in acquiring plants of 'UC Golden Gate' or 'UC Keystone' for commercial purposes should contact the Strawberry Licensing Program at Technology Transfer in the Office of Research at the University of California, Davis (https://research.ucdavis.edu/technology-transfer/plant-variety-licensing-program/strawberry-licensing-program/).

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