

The cover features a vibrant photograph of a field of red thistles. The thistles have bright red, spiky flower heads on tall, green stems. A bumblebee is visible on one of the flowers in the center. The background is filled with more thistles and green foliage.

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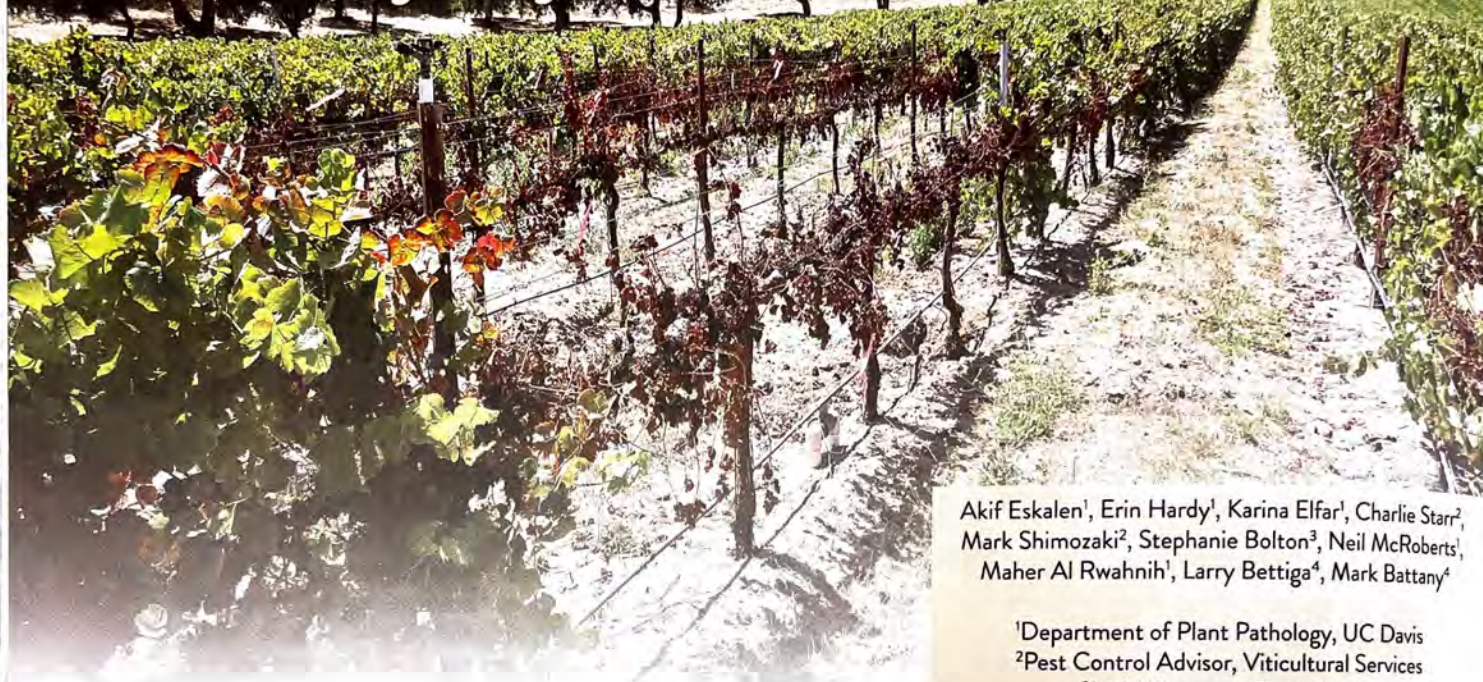
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Sudden (mystery) vine collapse



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Background

Since 2011, grape growers in the San Joaquin Delta, Central Valley, and Coastal counties of California have reported Sudden Vine Collapse (SVC), in which patches of vines within the vineyard, especially the ones on virus-sensitive rootstocks (Freedom, 039-16 and 101-14, among others), quickly die with no apparent cause (Fig. 1A). In some cases, patches are so large that can be seen via satellite images on Google Earth, with levels of loss that have caused growers to remove entire vineyards (Fig. 1B). The affected vines were mostly older vines (>5 year-old) grafted on Freedom rootstock, although different varieties have experienced the collapse in various locations including San Joaquin, Stanislaus and coastal grape growing counties in CA. In 2018, the disease has reached an economic threshold of destruction where it was affecting increasing number of grape growers economically to gain greater attention.

Symptoms

Early in the season, stunted shoot growth or dead arms (Fig 2A). Later, during the summer, entire vines start dying quickly in circular patches within the vineyard. In some cases, death is so fast that leaves remain dry on the plant (Fig 2B). Examined vines show a clear lack of feeder roots (Fig 3A), with grayish-purple lesions in the bark of scaffold roots. At the graft union level, the scion portion often appear swollen, with a necrotic line (Fig 3B). In many cases, rootstocks showed internal wedge-shaped cankers which were absent in the scion (Fig 3CD). Furthermore, mealybugs and common grapevine trunk disease (GTD) symptoms were observed in all affected vines (Fig 4B).

Mealybugs

Mealybugs are pests of grapevines that spread between vines and vineyards through animals, farm workers, equipment, ants, and other means. They are phloem feeders, which enables them to effectively infect plants with viruses when their stylets penetrate the plant tissue. Two of the viruses that they vector are Grapevine leafroll-associated viruses and vitiviruses (Selvarajan et al. 2016). These insects are found in moist and warm environments, including areas of California where SVC has been reported.

Synergy between grapevine viruses

Vines infected with a single viral species usually show mild to strong symptoms, and the yield is significantly reduced but usually the vine will not collapse. However, mixed infections with grapevine leafroll viruses (e.g. *Grapevine leafroll-associated virus 3*) and vitiviruses (e.g. *Grapevine virus A*, *Grapevine virus F*) can exacerbate symptoms and lead to vine decline (Golino et al., 1993; Rieger, 2019).

Grapevine Trunk Diseases: Grapevine trunk diseases (GTD) are currently one of the most important challenges for viticulture worldwide. These destructive diseases are caused by a broad range of wood-colonizing fungal pathogens, which primarily infect grapevines through wounds resulting from pruning, freezing, sunburn, and insects. In most occasions, a single vine is infected with more than one of these fungal pathogens. Characteristic GTD symptoms include poor vigor, distorted leaves and shoots, shoot and tendril dieback and berry specks caused by fungal toxins produced by some of these pathogens. SVC-symptomatic vines had characteristic GTD symptoms including esca diseases but these

FIGURE 1: (A) Sudden Vine Collapse in Paso Robles, California; (B) Patches of collapsed vines during summer 2019, Lodi, California

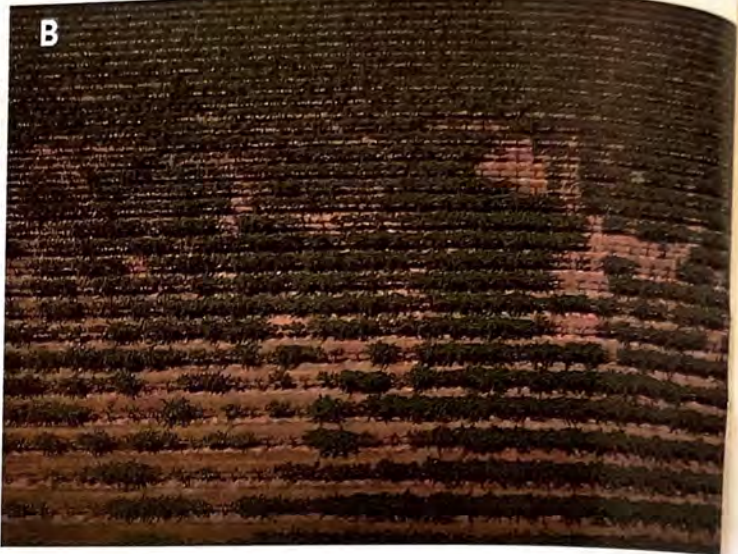


FIGURE 2: (A) Stunted shoot growth and dead arms early in the season; (B) Quick death of vines during the summer



FIGURE 3: (A) Lack of feeder roots; (B) Swelling and cracking on graft union bark; (C) Rootstock cut with cankered wood; (D) Presence of *Neofusicoccum parvum* pycnidia, a common grapevine trunk pathogen that causes Bot canker and dieback



symptoms were not consistently observed in each vine sampled in this study. Perennial cankers produced by fungi on grapevines may cause spur, cordon and trunk dieback and the eventual death of the entire vine. Previous studies have also shown that fungal pathogens in the Nectriaceae family cause grapevine black foot diseases and can cause severe root rot on plants predisposed by stress, poor root development, poor vine nutrition and heavy cropping.

Hypothesis and Study

Four vineyards exhibiting SVC in the Lodi American Viticulture Area were sampled in July 2019 (Table 1). Samples were collected from the roots, rootstock, scion, cordon, spurs, and leaves of the selected vines. From each vineyard, three vines of varying conditions were selected. One healthy-looking, one declining, and one advanced decline vine were sampled. Samples from each tissue were plated and cultured on media that selected for fungal growth. Isolated fungi were then identified using PCR. For the leaf

and rootstock samples, high-throughput sequencing was done to characterize the entire microbial profile of the vines. Additionally, to assess the extent of girdling at the graft union, an iodine starch test was performed by spraying iodine onto each of the root samples and evaluating the starch content. Iodine turns dark blue in the presence of starch, allowing us to estimate the amount of starch being transported from the leaves to the roots.

The results from this testing showed that, in each of the vines with moderate to severe decline symptoms, both Grapevine leafroll-associated virus 3 and a vitivirus, Grapevine virus A or Grapevine Virus F, were present. In some of the healthy-looking vines, only Grapevine leafroll-associated virus 3 was present, but the vitivirus was not. A myriad of Grapevine Trunk Disease (GTD) pathogens were isolated from the vines sample, both healthy-looking and symptomatic. These included *Fusarium* sp., *Diplodia seriata*, and *Diaporthe* sp. among others. However, no single fungal pathogen was consistently found in affected grapevines (Table 2).

TABLE 1: Age, grape variety, and rootstock of vineyards used in this study

Site	Planted	Grape Variety	Rootstock
Vineyard 1	1993	Cabernet Sauvignon	Freedom
Vineyard 2	1992	Chardonnay	Freedom
Vineyard 3	2013	Pinot Noir	Freedom
Vineyard 4	mid 1990s	Chardonnay	Freedom

Research shows that, while these leafroll-associated viruses and vitiviruses cause mild symptoms individually, they are capable of causing more severe disease when both are involved (Al Rwahnih et al. 2009, Rowhani et al. 2018). Vitiviruses can cause problems in certain rootstocks individually, and co-infection with a leaf-roll associated virus raises the titer of vitivirus, thus increasing pathogenicity. Freedom rootstock is most susceptible to co-infection by Grapevine leafroll-associated viruses and vitiviruses (Rowhani et al. 2017). Furthermore, the stress exerted on the

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vines by the viral infection likely renders the affected vines more susceptible to infection by fungal pathogens including the ones that causes GTD. Moreover, previous studies have shown that viral infection can cause graft incompatibility in certain rootstock (Golino 1993). In this case, the efforts of the rootstock to reject the scion following infection causes girdling at the graft union, preventing the flow of water and nutrients throughout the vine. The inability for the plant to transport starch leads to starch depletion in the roots and a subsequent lack of feeder roots, further preventing the vine from acquiring necessary nutrients from the soil. All of these factors contribute to the collapse of the vine.

In conclusion, we hypothesize that SVC is not caused by a single pathogen, but the result of a disease complex in which vines are predisposed to root stress due to co-infection by a leafroll virus (GLRaV-3), vitiviruses (GVA, GVF) and possibly others. Consequently, infected vines rapidly die by an additional infestation of fungal pathogens associated with grapevine trunk diseases and black foot disease.

Management

- Effective vector (vine mealybug) control.
- Remove collapsed vines from the vineyard.
- Transition to less susceptible rootstocks when replanting. ■

FIGURE 4: (A) SVC on vines grafted on Freedom but not on 5C rootstocks; **(B)** Large colonies of mealybugs under the bark of rootstock present in all collapsed vines



TABLE 2. Preliminary ranking of vines based on external disease symptoms

Vineyard	Vine	Ranking ¹	Vine Condition	Mealybug Present	Viral Pathogens			Feeder Roots Present	Fungal pathogens			Iodine Starch
					GLRaV-3	GVA	GVF		Grapevine Trunk Diseases	Fusarium spp.	Oomycetes	
1	1	4	Advanced Decline	+	+	-	+	-	+	+	-	-
	2	3	Declining	+	+	-	-	some	+	-	-	+
	3	1	Healthy Looking	+	+	-	-	Present	-	-	-	++
2	1	4.5	Advanced Decline	+	+	+	+	-	+	+	-	-
	2	3	Declining	+	+	-	-	some	+	+	-	+
	3	1	Healthy Looking	+	+	-	-	Present	-	-	-	++
3	1	3	Advanced Declining	+	+	+	-	-	+	+	-	++
	2	3	Declining	+	+	+	-	some	+	+	-	-
	3	1	Healthy Looking	+	-	-	-	Present	-	-	-	+++
4	1	4	Advanced Decline	+	+	+	-	-	+	+	+	-
	2	3	Declining	+	+	+	-	some	+	+	-	+
	3	1	Healthy Looking	+	+	+	-	some	-	-	-	++

¹Ranking on a scale of 1-5. 1: Healthy looking 2: Beginning Decline 3: Declining 4: Advanced Decline 5: Dead

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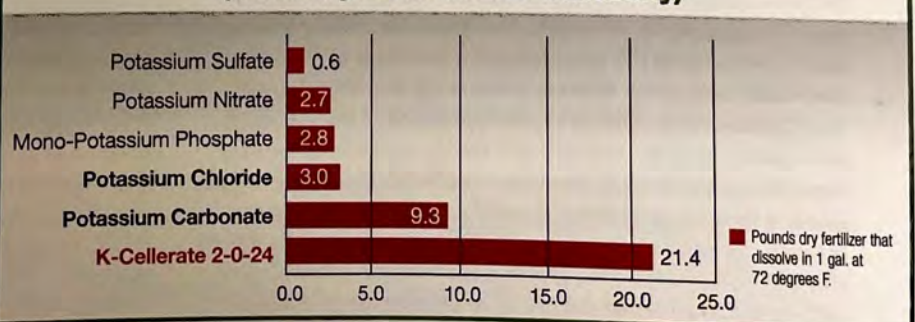
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