

Asymmetrical canopy architecture due to prevailing wind direction and row orientation creates an imbalance in irradiance at the fruiting zone of grapevines

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Abstract

Much effort is invested in trellising and training grapevines to maximize radiation interception by the canopy and to manage the radiation environment of the fruit clusters. Slope permitting, conventional wisdom among winegrape growers prompts many to adhere to north–south row orientations to balance between the two sides of the canopy both photosynthetic efficiency and the exposure of fruiting zones to solar radiation. In windy sites, thigmomorphogenesis in annually renewed shoots can reshape a bilaterally balanced canopy. We measured irradiance at the fruiting zone and shoot geometry in two contiguous vineyards differing only in row orientation. The prevailing west–southwest winds were roughly parallel to the rows of one vineyard and at an oblique angle to the rows of the second vineyard. Mean wind velocity in the prevailing direction was 3.3 m s^{-1} during the growing season. Shoots were grouped into four classes based on row orientation and shoot azimuth from the cordon. Windward shoots were significantly shorter (26–29%) than all other classes of shoots because of fewer nodes per shoot. Mean internode length per shoot ($\approx 5 \text{ cm}$) did not vary between shoot classes and was not related to row orientation. Regardless of row orientation or initial shoot azimuth, shoot tips tended to be displaced eastward (leeward). In rows oriented roughly parallel to the prevailing wind, shoots exhibited distinct down-row streamlining and vines had a bilaterally uniform canopy about the cordon. In rows at an oblique angle to the prevailing wind the vines did not form a uniform canopy about the cordon. Both row orientations resulted in similar differences between sides of the canopy in total irradiance at the fruiting zone ($+5.4 \text{ MJ m}^{-2} \text{ d}^{-1}$ on the west side of rows oriented at an oblique angle to the wind; $+6.0 \text{ MJ m}^{-2} \text{ d}^{-1}$ on the south side of rows oriented parallel to the wind); however, the timing of peak intensity on the side receiving higher irradiance differed by row orientation (11.9 LST at south-facing fruit; 13.7 LST at west-facing fruit). Wind-induced canopy asymmetry could result in unequal berry ripening in areas of high irradiance where peak insolation of the berries coincides with the highest temperatures of the day. Results indicate that in consistently windy locations, growers should establish row orientation based both on sun–earth geometry for maximizing radiation interception by the canopy, and on the consequences of radiation distribution at the fruiting zone due to wind-induced canopy asymmetry. In established vineyards, growers could compensate for non-uniform canopy architecture to some extent with modifications to the trellis system and standard training practices.

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1. Introduction

Jaffe is attributed widely with coining the term “thigmomorphogenesis” to describe the responses of plant development to mechanical perturbation,

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exemplified in his series of experiments on the responses of *Phaseolus vulgaris* L. and other plants to touching, shaking and air movement (Jaffe, 1973, 1976; Hunt and Jaffe, 1980). The range of observed responses of plants to mechanical stimuli, from gene expression to morphology, was reviewed recently (Braam, 2005). The effects of wind in particular have been investigated in crop science from the perspective of assessing windbreaks and shelterbelts (e.g., Rosenberg et al., 1983; Cleugh et al., 1998). The grapevine (*Vitis* spp.), a woody perennial, often is cultivated under annual pruning that results in a new set of herbaceous shoots emerging from buds on short woody spurs. The new shoots, upon which fruit is borne at proximal nodes, could be expected to exhibit thigmomorphogenesis. Wind-influenced canopy architecture can have implications for fruit quality, an attribute highly linked to the exposure of grape clusters to solar radiation (e.g., Morrison and Noble, 1990; Jackson and Lombard, 1993). Solar radiation is critical for the development of strong skin pigmentation and other phenolics associated with wine quality in red-fruited cultivars. By contrast, a combination of high irradiance and high fruit temperatures can compromise berry color and phenolic composition (Bergqvist et al., 2001) as we have found in the cultivar 'Merlot' (Spayd et al., 2002). Thus, vineyard managers typically seek to cultivate canopies that are spatially uniform about the axis of the trellis, with moderate irradiance at the fruiting zone. Many growers follow a conventional wisdom of orienting vine rows north–south to balance the total daily irradiance incident upon the fruit on both sides of the canopy and to maximize photosynthetic efficiency, or radiation interception by the canopy over the course of the day.

Vines in windy sites may develop asymmetrical canopy architecture depending upon the angle of attack of the prevailing wind. An asymmetrical canopy is potentially undesirable for less dense vine canopies (e.g., those under regulated deficit irrigation) in regions of high irradiance, should the fruit on one side of the vine be exposed to direct insolation under the highest temperatures of the day (e.g., Spayd et al., 2002). Wind-exposed vines (Hamilton, 1988; Bettiga et al., 1996) and the windward side of a vine canopy (Ewart et al., 1987) produced smaller clusters (i.e., fewer berries per cluster) and fewer clusters per vine, resulting in slightly lower yields than in sheltered vines and the leeward side of the canopy, respectively. Both direct and indirect mechanisms were proposed: wind-disrupted berry set, and later reductions in sugar accumulation by the maturing berries because of wind-induced stomatal closure limiting photosynthesis. Relevant to winemaking, fruit

from wind-exposed vines tended toward higher titratable acidity and lower pH than that from vines near windbreaks, although trained taste panelists could not detect differences among the finished wines (Bettiga et al., 1996).

There is a measure of consistency among results from the few studies in vineyards and controlled environments on the responses of grapevines to wind, or conversely, to the effects of shelter: exposure to wind decreased shoot growth (shorter internodes), decreased stomatal conductance and transpiration, but generally caused no detectable changes in leaf water potential (Freeman et al., 1982; Kobriger et al., 1984; Kliever and Gates, 1987; Hamilton, 1988; Bettiga et al., 1996). Where measured, trends in net photosynthesis were consistent with the proposal of a stomatal control mechanism. In field-grown vines, large decreases in stomatal conductance may not become apparent until wind speeds exceed 5 m s^{-1} (Campbell-Clause, 1998).

Field observations of canopy architecture in mature vines are valuable because of the difficulty of reproducing the radiation, temperature, humidity and turbulence of the field in wind tunnels and greenhouses, or of reproducing a field environment extensively enough to assess season-long growth and development. Wind exclusion is impractical and difficult to accomplish in the field without altering other environmental variables, including irradiance, a key contributor to grape and wine quality. The scale and layout of a tree nursery did facilitate extensive use of a wind generator to determine thigmomorphogenetic and phototropic responses of *Pinus* seedlings (Berthier and Stokes, 2005). However, such an approach would be unwieldy and cost-prohibitive in a mature vineyard. There is a notable body of work on the interaction of leaf area density and training/trellising systems with the radiation environment of the grapevine canopy (e.g., Smart, 1973; Smart et al., 1982, 1985; Schultz, 1995; Mabrouk et al., 1997a,b), but investigations are lacking on canopy architecture and the resulting irradiance at the fruiting zone as related to wind in the field environment.

Based on the evidence for wind-induced thigmomorphogenesis in plants, one might expect to observe shorter shoots on the windward side of vineyard rows. Shoots originating on the windward side of a vine are likely to be displaced leeward, regardless of their original azimuth, whereas shoots originating on the leeward side of a vine are more likely to maintain approximately their initial azimuth. Such expectations seem intuitive in vineyards along the Columbia River Gorge of Washington state and Oregon, USA, where vines exhibit an obviously windblown appearance that

resembles the “flag” trees found in naturally windy sites (e.g., Grace, 1977; Telewski and Jaffe, 1986) and that persists into the dormant season. The objective of this paper is to describe wind-induced morphogenesis in grapevine shoots and the effect of the resultant canopy architecture on exposure of the fruiting zone to solar radiation. Elsewhere we described effects of such exposure on quality-related attributes of the fruit in the same cultivar (Spayd et al., 2002). Our approach of assessing shoot geometry and the distribution of shoot attributes within individual vines is particularly relevant to viticulture because commercial growers regularly expend tremendous resources in training or manipulating shoots to offset perceived deleterious effects of the environment on vine growth, yield and fruit quality. The study was accomplished using contiguous vineyards whose rows were oriented either roughly parallel to, or at an oblique angle to the prevailing spring and summer winds at a site that could be described as consistently windy. As context, this area, the Columbia River Gorge, which includes the city of Hood River, OR, is a widely-acclaimed wind surfing center; the eastern end of the gorge has proven viable for producing electricity commercially with wind turbines.

2. Materials and methods

Measurements were recorded during and after the 2003 growing season in contiguous vineyards of *Vitis vinifera* L. ‘Merlot’ at a commercial site (45.88°N, 119.76°W; 255 m above m.s.l.) above the Columbia River, 17 km west of Paterson, WA, USA. The vines, planted in 1991, were own-rooted, double-trunked and trained to a bilateral cordon (permanent, horizontal extension of the grapevine trunk) at 1.1 m height on the bottom wire of a two-wire “sprawl” trellis system that allowed the generally upright shoots to bend without interference above a single catch wire at about 0.2 m above the cordon. Vines were spur-pruned annually to ≈ 28 buds per vine on two-bud spurs, resulting in an average of $26 (\pm 1.3)$ shoots per vine in vineyard I and $33 (\pm 1.2)$ shoots per vine in vineyard II. In this training system, growers remove downward pointing spurs. Shoots originating from the cordon rather than from spurs were removed by hand on Day of Year (DOY) 136 in vineyard I and on DOY 147 in vineyard II, a standard viticultural practice in the district. There were 1.8 m between vines and 2.7 m between rows, which were oriented northeast–southwest in vineyard I (4.65 ha), roughly parallel to the direction of the prevailing wind, and north–south in vineyard II (9.5 ha), at an oblique angle to the prevailing wind (Fig. 1). Vineyard I was

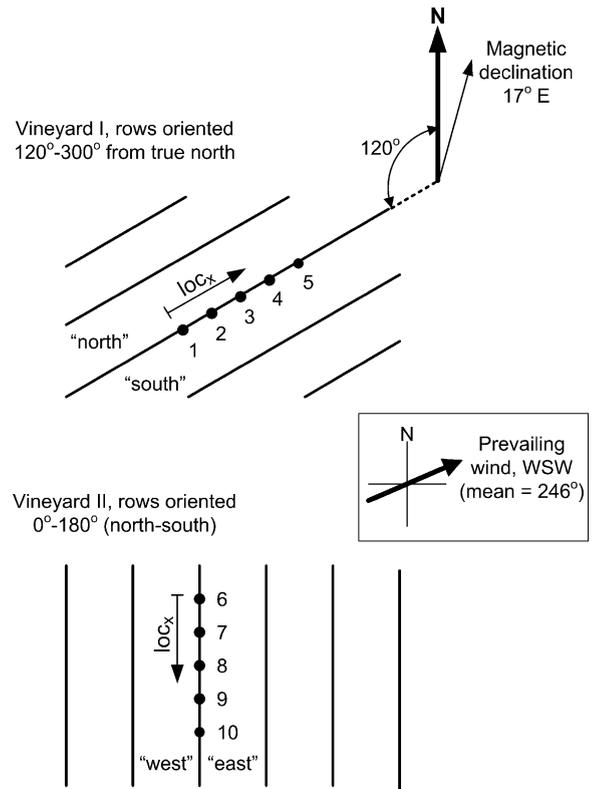


Fig. 1. Schematic diagram showing orientation of vineyard rows and the designation of shoot classes in the two contiguous vineyards west of Paterson, WA, USA.

bordered by other vineyards on all but its north side; vineyard II was bordered by other vineyards on all but its east side. All management practices including drip irrigation were identical for the two vineyards that were on a Quincy loamy sand (Mixed, mesic Xeric Torripsamment) with a 10% slope. Yield from each vineyard averaged 6.3 t ha^{-1} .

Shortly after veraison and after shoot growth had ceased, 1 m long tube solarimeters (model TSL, Delta-T Devices, Cambridge, UK) were mounted parallel to the cordon in a central row of each vineyard at the height of the fruit clusters (about 1.0–1.2 m) and within 0.2 m of the cordon. Solar radiation was measured simultaneously on both sides of the canopy in both vineyards for 24 h under clear skies, then the solarimeters were remounted sequentially down the row and the measurements repeated under clear skies until 6 m of row had been included in the sample ($n = 6$). The final dataset comprised values recorded between DOY 229 and 242. A reference pyranometer (model 8-48, Eppley Laboratories, Newport, RI, USA) was mounted above the canopy. Signals were scanned every 10 s and averaged every 12 min. Tube solarimeters had been calibrated

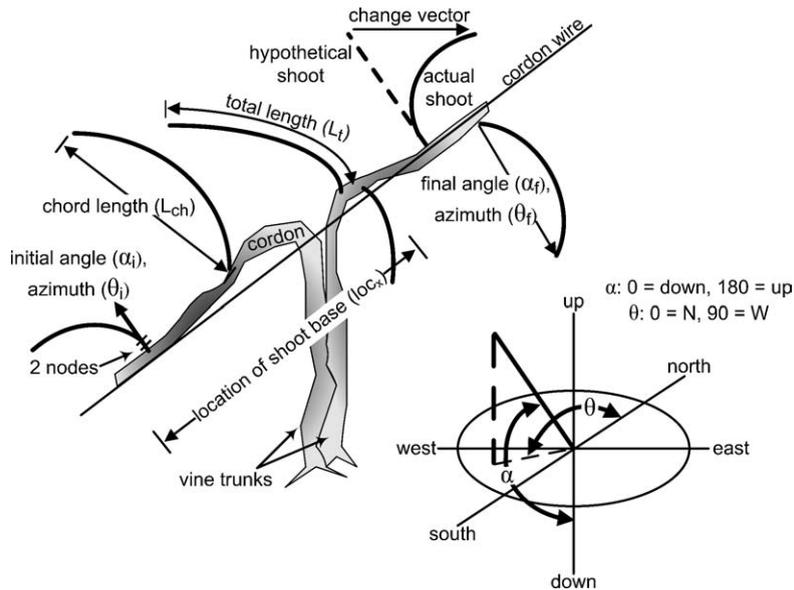


Fig. 2. Schematic diagram of a grapevine trained to a bilateral cordon, and the measured variables related to shoot geometry. The computed change vector can be considered an index of shoot curvature due to external forces and any tropisms. Inset defines circular coordinate system.

against the Eppley pyranometer for each row orientation. Prevailing winds for the district were characterized from publicly-available data recorded from a 3-cup anemometer and wind vane (Wind Sentry, R.M. Young, Traverse City, MI, USA) at 2 m height by the Public Agriculture Weather System (PAWS) station near Alderdale, WA (45.85°N, 119.88°W, 226 m above m.s.l.), one ridge west of the vineyard and overlooking the Columbia River. Signals were scanned every 10 s and averaged every 15 min. Within the experimental site, wind speed and direction also at 2 m height were measured by 3-cup anemometer and wind vane (Wind Sentry, R.M. Young) with 1 h averaging intervals as set by the vineyard manager.

A compass–protractor was constructed (Norman and Campbell, 1991) to measure both the angle of elevation (α) from the vertical ($0^\circ = \text{'down'}$ and $180^\circ = \text{'up'}$) and the azimuth (θ ; north = 0° ; $90^\circ = \text{west}$) of shoots at a resolution of 15° . For simplicity, the cordon and spurs collectively were considered a cylinder of infinitely small diameter from which the shoots originated. The cordon defined the origin of the y and z axes. The following variables (Fig. 2) were recorded after leaf fall to describe completely the three-dimensional geometry of every shoot on five vines in each vineyard that were selected from the center of each vineyard to minimize edge effects: location of the shoot base along the cordon (loc_x); initial shoot angle (α_i) measured between the shoot's origin at its spur and the shoot's second node; final shoot angle (α_f) measured between the shoot origin

and the shoot tip; initial shoot azimuth (θ_i) measured between the shoot origin at the spur and the shoot's second node; final shoot azimuth (θ_f) measured between the shoot origin and the shoot tip; total shoot length (L_t); chord length (L_{ch}), the shortest distance between shoot origin and shoot tip; and number of nodes (i.e., number of primary leaves). Average internode length per shoot was estimated from node density.

The exact location of each shoot origin and each shoot tip was defined in spherical coordinates governed by standard trigonometric equations (Fig. 2). A change vector was calculated in three dimensions as the difference between the hypothetical final location of the shoot tip had it grown in the absence of external forces (i.e., along the trajectory indicated by α_i and θ_i , and assuming $\alpha_i = \alpha_f$), and the actual final location of the shoot tip. The change vector can be thought of as an indicator of shoot curvature due to the combined external forces of gravity and wind, and any tropisms, including thigmotropism. Because gravitropic and shoot self-weighting effects primarily are in the vertical, further analysis was limited to the horizontal components of the change vector to improve the detection of shoot tip displacement by wind. The assumption of hypothetical shoot growth in the absence of external forces was made so that meaningful quantitative analysis could proceed despite the absence of a wind-free “control” vineyard for the practical constraints mentioned above.

Four classes of shoots were defined based on row orientation and θ_i (Fig. 1). Shoots designated “north” in

the northeast–southwest oriented rows (vineyard I) were defined by θ_i between 0 and 120° or between 300 and 360°. In the same rows, θ_i of “south” shoots was between 120 and 300°. In rows oriented north–south (vineyard II), θ_i of “west” shoots, loosely described as windward shoots, was between 0 and 180°. The θ_i of “east” shoots, loosely referred to as leeward shoots, was between 180 and 360°. The one or two shoots per vine originating on top of the cordon (i.e., $\alpha_i = 180 \pm 15^\circ$) were excluded from analysis.

Data were analyzed with SAS (v. 9.1.3, SAS Inc., Cary, NC). A one-way ANOVA was used to detect differences in shoot length, number of nodes and internode length per shoot between vineyards and between shoot classifications (i.e., north versus south, east versus west) within a vineyard. To stabilize normality and variance, the appropriate transformation of square root or log was used. Circular statistics were used to calculate mean wind direction and mean change vector direction (Batschelet, 1981). The magnitude of the change vector was square root transformed and analyzed with a *t*-test. Due to non-normality from a small sample size, non-parametric rank statistics with the Kruskal–Wallis test for significance were used to analyze differences in solar radiation incident at the four fruiting zones.

3. Results and discussion

The prevailing wind at the Alderdale PAWS station, indicative of the district, can be described as southwesterly with mean 15 min velocities ranging from 0 to 12 m s⁻¹. The general pattern of wind direction is quite consistent throughout the year, but data only between DOY 91 and 304 were used for this analysis. Budbreak in vines at this location typically occurs during the first week of April. Nearly two-thirds (63%) of the wind run during the growing season (Fig. 3) originated between 225 and 255° with an average velocity of 3.5 m s⁻¹; 78% of the wind run originated between 210 and 270°. Forty percent of all 15 min means were ≥ 3.0 m s⁻¹ and 14% were ≥ 5.0 m s⁻¹. Gusts to 20 m s⁻¹ at our site are not infrequent (Perez Peña, unpublished data). Wind speeds at the Alderdale PAWS site were not unlike those reported for some notably windy vineyard districts in coastal areas such as Salinas Valley, California (Bettiga et al., 1996) and Swan Valley, Western Australia (Campbell-Clause, 1998). At our experimental site, mean wind velocity was 3.3 m s⁻¹ with 54% of all hourly means ≥ 3.0 m s⁻¹ and 28% ≥ 5.0 m s⁻¹. Forty-one percent of the wind run during the growing season originated between 225 and 255°; nearly two-thirds (64%) originated between 210 and 270°.

Table 1

Grapevine shoot morphology and irradiance in vineyards with rows oriented parallel (vineyard I) and at an oblique angle (vineyard II) to the prevailing wind

Variable	Mean \pm S.E.M. ^a			<i>p</i> -Value			
	Vineyard I			Vineyard II			
Shoot length (L_i) (cm)	64.5 \pm 2.3			56.8 \pm 2.9			0.01 ^b
Number of nodes	12.9 \pm 0.5			11.6 \pm 0.6			0.02 ^b
Internode length/shoot (cm) ^c	5.1 \pm 0.1			5.0 \pm 0.1			0.45 ^b
Length of change vector (cm)	31.8 \pm 2.6			29.0 \pm 2.8			0.07 ^c
Daily irradiance at fruiting zone (MJ m ⁻²)	8.1 \pm 1.2			8.7 \pm 0.9			0.52 ^d
	Vineyard I, mean \pm S.E.M.			Vineyard II, mean \pm S.E.M.			
	North	South	<i>p</i> -Value	East	West	<i>p</i> -Value	
Shoot length (L_i) (cm)	64.2 \pm 3.2	64.8 \pm 3.4	0.98 ^b	66.8 \pm 4.7	47.6 \pm 3.2	0.01 ^b	
Number of nodes	13.0 \pm 0.6	12.7 \pm 0.7	0.71 ^b	13.5 \pm 1.0	9.8 \pm 0.7	0.004 ^b	
Internode length/shoot (cm) ^c	5.0 \pm 0.1	5.2 \pm 0.1	0.40 ^b	5.0 \pm 0.1	5.0 \pm 0.1	0.76 ^b	
Length of change vector (cm)	33.5 \pm 4.0	30.0 \pm 3.3	0.58 ^c	31.9 \pm 4.2	26.4 \pm 3.7	0.30 ^c	
Daily irradiance at fruiting zone (MJ m ⁻²)	5.1 \pm 0.5	11.1 \pm 1.6	0.01 ^d	6.0 \pm 0.4	11.4 \pm 0.6	0.004 ^d	
Time of day for maximum irradiance (h) ^f	13.00	11.00		10.30	13.70		

^a Standard error of the mean.

^b *Pr* > *F* tested with a general linear model, *p*-value based on transformation, while arithmetic mean is reported.

^c *Pr* > *t* tested with a *t*-test, *p*-value based on transformation, arithmetic mean displayed.

^d *Pr* > Chi-square tested with non-parametric rank statistics, significance is based on mean rank, arithmetic mean is reported.

^e Calculated from shoot length and number of nodes.

^f Local standard time.

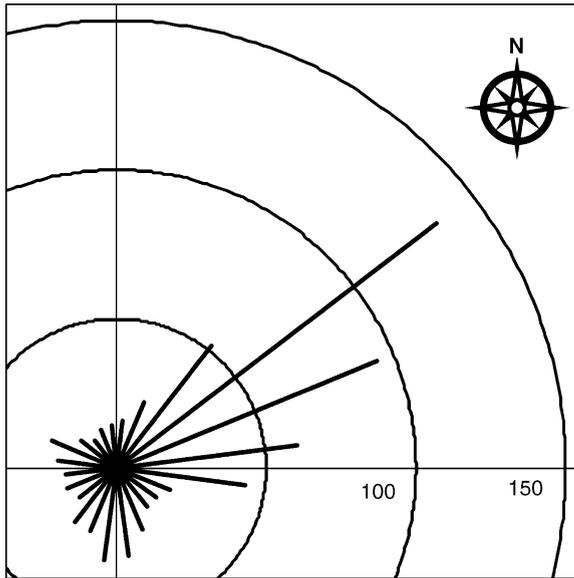


Fig. 3. Rose diagram of total wind run at the Alderdale, WA, Public Agriculture Weather System station during the 2003 growing season (DOY 91–304). Lines show wind moving from the center of the wind rose toward a compass direction to facilitate graphical comparison with canopy architecture. For graphical display, data were transformed by taking the square root of the total wind run (km) in 15° increments.

On average, shoots in the rows oriented parallel to the prevailing wind were longer than those in the rows oriented at an oblique angle to the wind, an outcome governed by less shoot growth on the windward (west) side of the north–south rows (Table 1). About half of shoots in the rows oriented at an oblique angle to the wind were ≤ 0.5 m long, whereas nearly two-thirds of shoots in the rows oriented parallel to the wind were > 0.5 m long (Fig. 4A). In rows oriented roughly parallel to the wind, average shoot length did not differ between sides of the vine (Table 1; Fig. 4B); however, in rows oriented at an oblique angle to the prevailing wind, windward shoots were on average 29% shorter than leeward shoots (Table 1). Approximately two-thirds of windward (west) shoots were ≤ 0.5 m long (Fig. 4C). Leeward shoots in the north–south rows were about the same length as those on either side of the vine in the rows oriented parallel to the wind, although shoots > 1.0 m were more likely to be found in the leeward, or “east” shoot class than any other.

There may have been more mechanical perturbation of windward shoots than of any other class of shoots because in a wide row configuration like a vineyard, cross-row air flow is more turbulent than down-row flow (Weiss and Allen, 1976). Little horizontal variation in wind speed was found for down-row flow, but for cross-row flow wind speed decreased from windward to

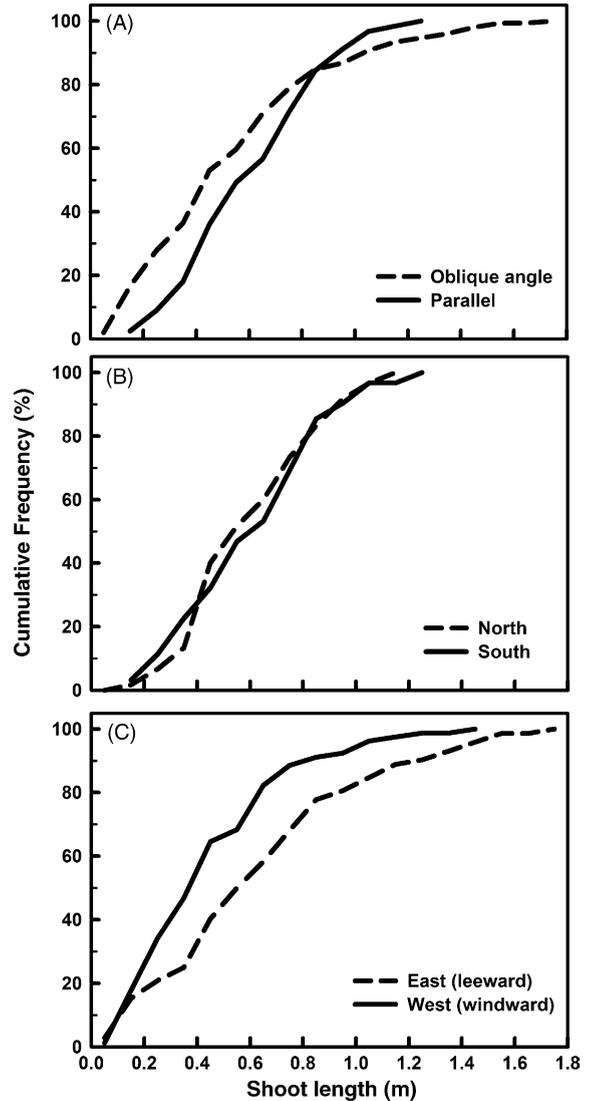


Fig. 4. Cumulative frequency of shoot length (m) for all shoots in vineyards I and II (A); the north and south shoot classes of vineyard I (B) and the east, or leeward, and west, or windward shoot classes of vineyard II (C). Rows were oriented roughly parallel to the direction of the prevailing wind in vineyard I and at an oblique angle to the prevailing wind in vineyard II. There was little difference in the distribution of shoot lengths between sides of the vine in vineyard I (B). Windward shoots tended to be shorter than leeward shoots in vineyard II (C).

leeward sides of the vine in a vineyard that was trained similarly and comprised comparable canopy dimensions to that in our experiment (Heilman et al., 1994). One might expect significant within-vineyard advection from bare soil between rows (McInnes et al., 1996), particularly at our site that was irrigated by drip and received only sparse rainfall during the growing season (60 mm, April 1–October 31, Alderdale PAWS). For

rows oriented at an oblique angle to the prevailing wind, it is conceivable that there may be biologically important differences in the temperature and water relations of shoot meristems between windward and leeward sides of the canopy. The small thermal mass of a shoot tip implies sensible heat transfer as a substantial component of its energy balance. Thereafter, shoot and leaf growth may be reduced via a direct effect of wind on leaf boundary layer and stomatal resistance. Given evidence in vineyards of greater turbulence with cross-row flow (Weiss and Allen, 1976), higher canopy wind speeds on the windward side of a canopy (Heilman et al., 1994), and a trend toward increasing stomatal resistance with increasing wind speed (Campbell-Clouse, 1998), it is not surprising that at the end of the growing season windward shoots comprised the dissimilar class and appeared stunted.

Mean internode length per shoot differed neither between vineyards (i.e., row orientations) nor between sides of the vine within a vineyard (Table 1), in contrast with previous observations of wind-related morphology in grapevine (e.g., Hamilton, 1988; Bettiga et al., 1996). In rows oriented at an oblique angle to the wind, there were about 27% fewer nodes per shoot on the windward

side of the vines (Table 1), consistent with the observed differences between sides of the canopy in mean shoot length and lack of detected differences in mean internode length per shoot. Consequently, one would expect a proportionately smaller canopy surface area on the windward side of the vine, independent of any canopy asymmetry that may have been caused by physical displacement of the shoots during growth. In the dense canopies common to well-watered vines, wind-induced asymmetry in canopy surface area may be of minor significance to the radiation environment of the fruiting zone if several leaf layers remain on the windward side of the vine, because grapevine leaves are known to absorb 85–90% of incident solar radiation (Smart, 1974). However, in the porous canopies maintained under regulated deficit irrigation, $\approx 30\%$ less leaf area on the windward side of a vine could result in the fruit being exposed to more intense solar radiation or for a longer duration than the fruit on the leeward side of the same vine, as discussed below. Sunscald in grapes was recognized as a consequence of canopy management several decades ago (Rhoads, 1924), prompting myriad investigations on training and trellising systems as well as more recent work that we pursued to separate

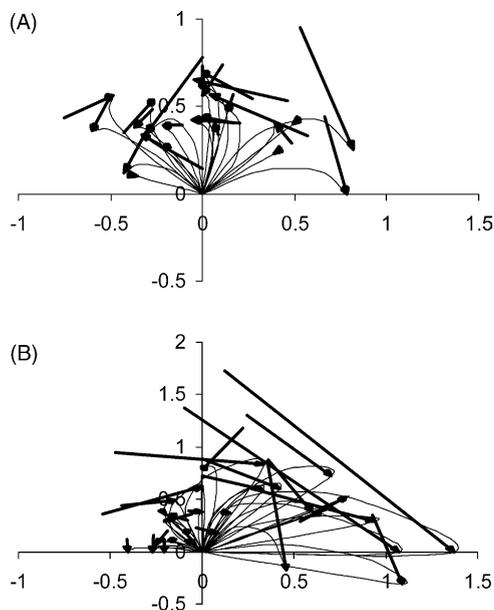


Fig. 5. Cross-sectional diagram of the canopy after leaf fall and the change vectors for all shoots of one exemplary vine (A) in the block whose rows were oriented parallel to the direction of the prevailing wind (vineyard I) and one exemplary vine (B) in the block whose rows were oriented at an oblique angle to the direction of the prevailing wind (vineyard II). In both panels, axis units are in meters (m) from the cordon, the origin of our spherical coordinate system. In panel A, the viewer is looking northeast and in panel B, the viewer is looking toward the north, down the cordon in both cases.

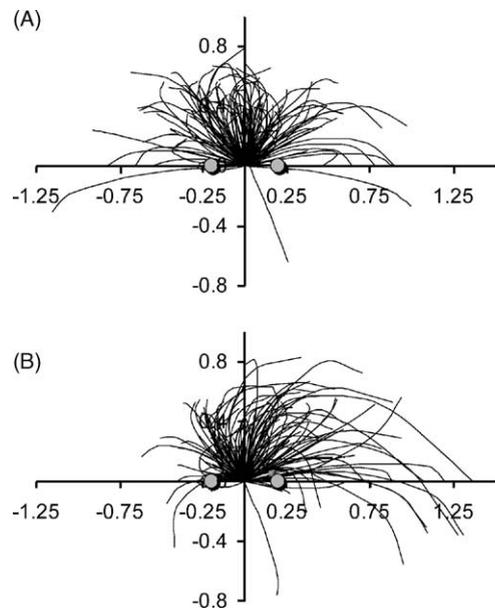


Fig. 6. Composite cross-sectional diagram of all measured shoots in the five-vine samples. In panel A the viewer is looking northeast down the cordon of a row oriented roughly parallel to direction of prevailing wind; in panel B the viewer is looking north down the cordon of a row oriented at an oblique angle to the prevailing wind. In both panels, axis units are in meters (m) from the cordon, the origin of our spherical coordinate system. Circles at the base of the shoots indicate the location of tube solarimeters.

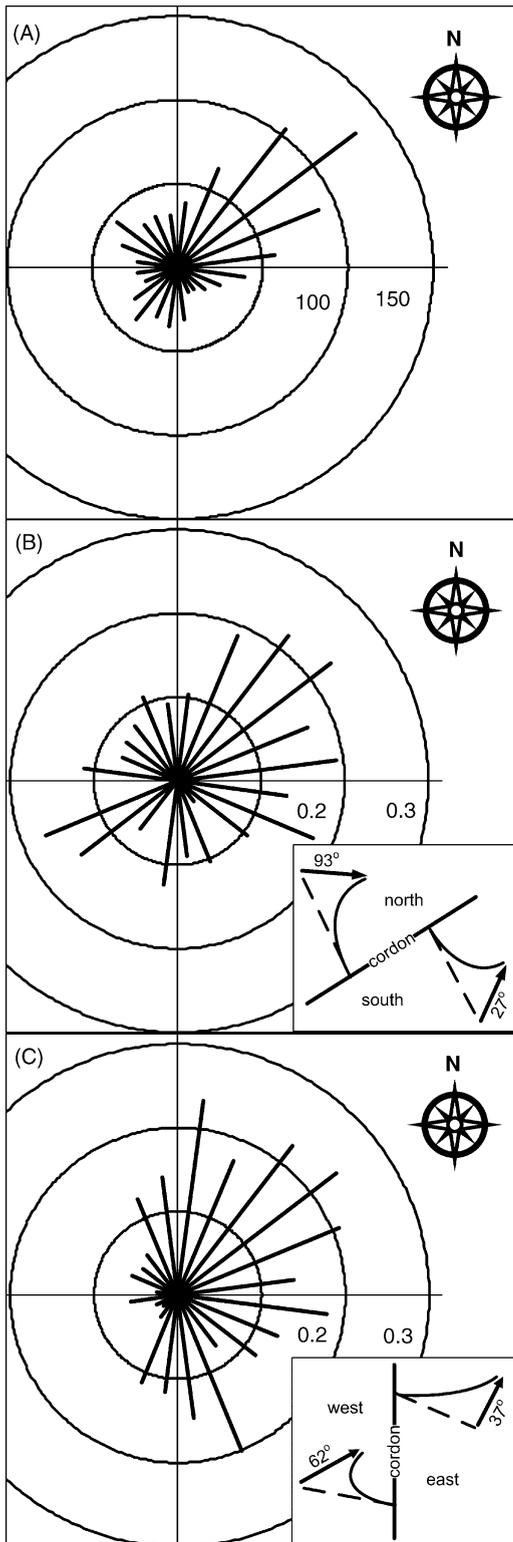


Fig. 7. Rose diagram of total wind run within the experimental vineyard (A) during the 2003 growing season (DOY 91–304). Lines show wind moving from the center of the wind rose toward a compass

in the field the effects of solar radiation from those of temperature on fruit quality (Tarara et al., 2000; Spayd et al., 2002).

In an effort to quantify the magnitude and direction of the wind’s effect on canopy geometry, from α_i , θ_i and total shoot length we calculated a hypothetical final location for each shoot tip (i.e., growth in the absence of external forces). The actual final locations of the shoot tips were displaced from their predicted locations (Fig. 5) regardless of row orientation or side of the canopy, not an unexpected outcome given the forces of gravity, wind and the influence of any tropisms. Downward deflection due to gravitational force was least apparent in windward (west) shoots, which were shorter than all others and had grown under consistent buffeting by wind (Fig. 6). The magnitude of the change vector quantifies the displacement of the shoot tips from their hypothetical to their actual final locations. There were no differences in the extent of displacement (vector length) between vineyards or between sides of the canopy within a vineyard (Table 1). However, the mean direction of the change vectors differed greatly among shoot classes (Fig. 7). In rows oriented parallel to the wind (vineyard I) vector directions differed by 66° between north and south shoots, yet the final locations of the shoot tips indicates down-row streamlining on both sides of the vine. In vineyard II, there was a smaller difference in vector direction (25°) between the two sides of the vine, but the mean change vector of the west (windward) shoots suggests upward and easterly displacement from their hypothetical final locations. By contrast, east (leeward) shoots were displaced away from the cordon with mild streamlining northward. The change vectors indicate that row orientation and canopy aspect in relation to the prevailing wind strongly determine shoot displacement over time and ultimately the shape of the canopy.

Roughly two-thirds of all shoot tips were displaced eastward of their hypothetical final locations, consistent

direction to facilitate graphical comparison with shoot tip displacement. Rose diagrams (B and C) of the horizontal components of the shoot tip change vectors summed for all shoots, in 15° increments. Insets show hypothetical mean shoot (growth in the absence of external forces; dashed line), actual mean shoot (solid line), the mean change vector, and the mean vector direction for each shoot class. Panel B represents vines in rows oriented roughly parallel to the direction of the prevailing wind (northeast–southwest). Panel C represents vines in rows oriented approximately due north–south, at an oblique angle to the prevailing wind. For graphical presentation, data in panel A were transformed by taking the square root of the total wind run (km), in 15° increments, and data in panels B and C were transformed by taking the square root of the total change vector (m).

Table 2

Displacement of shoot tips from different aspects (shoot classes) in vineyards with rows oriented parallel (vineyard I) and at an oblique angle (vineyard II) to the prevailing wind

Displacement, direction of	Vineyard I					Vineyard II				
	North ^a		South ^a		Total (%)	East ^a		West ^a		Total (%)
	Frequency	%	Frequency	%		Frequency	%	Frequency	%	
East	41	68	35	61	65	42	61	47	64	62
West	18	30	22	39	34	7	10	5	7	8
None	1	2	0	0	1	20	29	22	30	29

^a Shoot classes.

with the frequency and velocity of west–southwesterly wind (Table 2). Examination of mean change vector directions and change vector “roses” plotted analogously to wind roses in which lines show displacement *toward* a compass direction (Fig. 7) support our visual observations of cross-row streamlining in the rows oriented at an oblique angle to the prevailing wind (Fig. 8) and down-row streamlining in the rows oriented roughly parallel to the prevailing wind. However, most shoots did terminate on the same side of the canopy from which they had originated (75% of north shoots, 84% of south shoots, 96% of leeward or east shoots and 74% of windward or west shoots), suggesting less cross-row streamlining of the canopy than implied by visual observation. Thus, the majority



Fig. 8. Down-row view of one vineyard row oriented north–south (at an oblique angle to the prevailing wind). Viewer is looking north. The end post is in line with the cordon. Shoots on the west (windward) side of the canopy were significantly shorter than those on the east (leeward) side of the canopy; shoot tips were displaced leeward.

of shoot tips originating on the windward (west) side of the vine remained on that side of the canopy. This supports the hypothesis that stunting of the windward shoots had a greater effect on canopy asymmetry than leeward displacement by wind. Our data indicate that the canopy asymmetry, primarily due to wind-induced thigmomorphogenesis and manifested by shorter shoots, was greatest in windward shoots, and the natural direction of shoot displacement was a function of both row orientation and canopy aspect.

Aligning rows parallel to the direction of the prevailing wind potentially could be beneficial by promoting lower transpiration due to lower bulk transfer coefficients and the reduced surface roughness associated with down-row flow (Hicks, 1973), a relevant consideration in irrigated vineyards and semi-arid climates. Based on the Bowen ratio, Hicks (1973) estimated 10–20% lower transpiration with down-row flow than with cross-row flow. As a caveat, expected water savings as a result of lower stomatal and/or canopy conductance should not be considered independently of net CO₂ exchange, particularly in vines managed for relatively low ratios of leaf area-to-fruit mass, as may occur under regulated deficit irrigation. In less windy sites, orienting rows north–south balances the intensity and duration of radiation incident on the fruit between the two sides of the canopy and can be expected to maximize radiation interception by the canopy across the day (e.g., Smart, 1973), which was shown to result in higher daily water use efficiency (Intrieri et al., 1998).

By orienting vineyard rows parallel to prevailing winds, growers may achieve, without expensive trellis manipulation, a canopy symmetrical about the cordon (Fig. 6A). However, if prevailing winds indicate an east–west row orientation, non-uniform exposure to solar radiation will occur between fruiting zones with north and south aspects unless the grower undertakes some canopy manipulation by trellising or training. Because of the importance of irradiance to fruit quality,

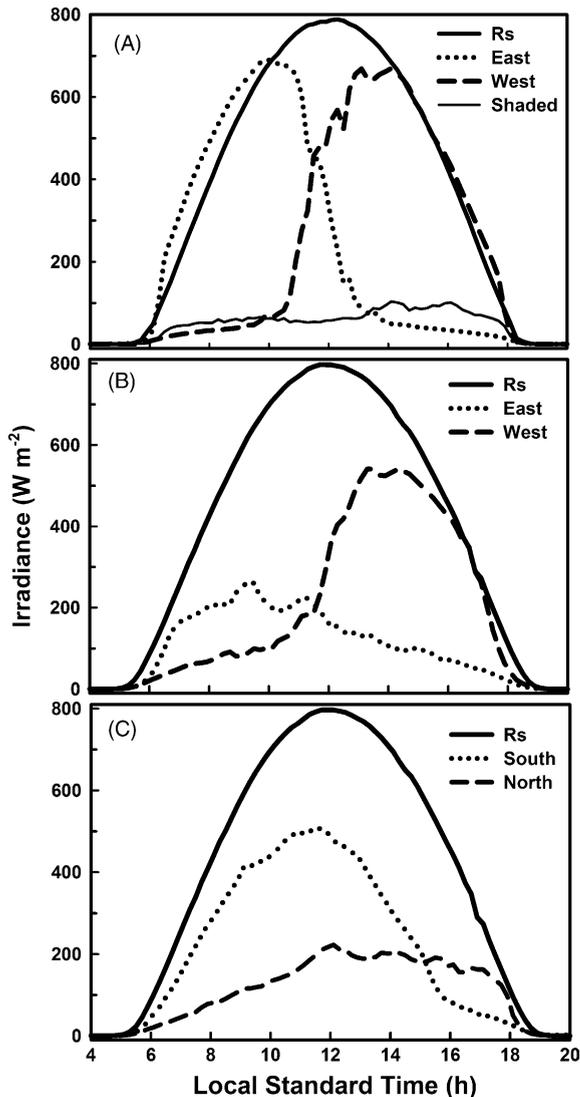


Fig. 9. Global irradiance and irradiance at fully-exposed fruit with east and west aspects (A) in *V. vinifera* L. 'Merlot' near Prosser, WA, USA. Rows were oriented approximately due north–south. Shoots had been trained to a single aspect (east or west) on each vine to allow the determination of maximum intensity, duration, and timing of fruit exposure, and resultant berry temperatures. Data were collected DOY 249, 1999. Global irradiance and irradiance at fruiting zones with east (leeward) and west (windward) aspects (B) in rows oriented at an oblique angle to the prevailing wind. Global irradiance and irradiance at fruiting zones with northwest and southeast aspects (C) in rows oriented roughly parallel to the direction of the prevailing wind. Data in panels (B) and (C) are mean values for 6 days with clear skies between DOY 229 and 242, 2003, in the vineyard west of Paterson, WA.

one should not consider canopy uniformity as a function of wind direction independently of compass direction. In north–south oriented vineyard rows one would expect daily maximum irradiance at the fruiting zone to be of equal intensity, and cumulative daily irradiance to be

approximately equal between east and west aspects of the vine, as demonstrated in 'Merlot' near Prosser, WA (46.30°N, 119.75°W; Fig. 9A), where the fruiting zone was allowed full exposure to incident radiation (Spayd et al., 2002).

In the commercial 'Merlot' vineyards of the current experiment, because of wind-induced canopy asymmetry, daily maximum irradiance at the fruiting zone with a west aspect (windward) averaged $\approx 550 \text{ W m}^{-2}$ and occurred at a mean time of 13.7 LST, about 300 W m^{-2} higher than the average daily maximum for an east (leeward) aspect, which occurred on average at 10.3 LST during our measurement period (Fig. 9B, Table 1). Of the several days with clear skies used for this analysis (between DOY 229 and 242), total global irradiance averaged $23.5 \text{ MJ m}^{-2} \text{ d}^{-1}$, with $11.4 \text{ MJ m}^{-2} \text{ d}^{-1}$ incident upon the fruiting zone with a west aspect and $6.0 \text{ MJ m}^{-2} \text{ d}^{-1}$ incident upon the fruiting zone with an east aspect. The windward (west) canopy intercepted 52% of total daily irradiance whereas the leeward (east) canopy intercepted 75%. In rows oriented roughly parallel to the wind, maximum irradiance at the fruiting zone with a southeast aspect ("south" shoot class) was $\approx 500 \text{ W m}^{-2}$ and occurred on average at 11.00 LST during our period of measurement, whereas at the fruiting zone with a northwest aspect ("north" shoot class) maximum irradiance was around 200 W m^{-2} and occurred on average at 13.00 LST (Fig. 9C), with the diurnal curve most closely resembling that of heavily shaded fruit (>3 leaf layers; Fig. 9A). On average, fruit with a northwest aspect ("north" shoot class) was exposed to less than half the total daily irradiance (5.1 MJ) as fruit with a southeast aspect ("south" shoot class; 11.1 MJ), not a unique result for the row orientation regardless of wind. For example, irradiance at mid-day peaked around 900 W m^{-2} for sun-exposed fruit with a south aspect (east–west row orientation) and around 450 W m^{-2} for sun-exposed fruit with a north aspect in the San Joaquin Valley of California (Bergqvist et al., 2001). What is important to draw from these results is that the maximum solar flux at a fruiting zone with a west aspect occurs around the same time of day as maximum ambient temperatures, creating the potential for fruit temperature to exceed optimum values for the biosynthesis of various secondary metabolites associated with fruit quality, or to exceed those values suspected of causing degradation of these compounds, visually recognized as 'sunscald' on the berry skins.

Radiation loading on grape berries has been shown to raise berry temperatures up to $7 \text{ }^\circ\text{C}$ (berry center) to $16 \text{ }^\circ\text{C}$ (berry skin) above ambient (Smart and Sinclair,

1976; Bergqvist et al., 2001; Spayd et al., 2002). In ‘Merlot’ and most other red-fruited *V. vinifera*, anthocyanins and other phenolics associated with wine quality reside primarily in the berry skin. Synthesis of anthocyanins appears to exhibit some light dependence but excessive berry temperatures may delay their formation, reduce their concentrations, and/or lead to an imbalance between the sugars and acids in the fruit that is critical to winemaking. Flavonol synthesis appears to be more strictly radiation-dependent than anthocyanin synthesis (e.g., Quercetin; Price et al., 1995; Spayd et al., 2002). In sunlit ‘Merlot’ berries, daily temperature maxima consistently were highest for fruit with a west aspect because peak irradiance at the fruiting zone coincided with the time of maximum ambient temperatures (Spayd et al., 2002). In locations where excessive exposure of fruit with a west aspect leads often to ‘sunscald,’ practical agricultural solutions for windy sites with prevailing west–southwest winds could lie in orienting an upper trellis member with a westward lean to counteract shoot tip displacement by the wind. By contrast, where prevailing easterlies promote westward shoot displacement and a greater likelihood of partially shading the fruit with a west aspect, wind-induced canopy asymmetry could confer an advantage and eliminate the need to retrofit trellises or invest in labor-intensive manipulation of the canopy. At windy sites where vines consistently exhibit shoot stunting or other thigmomorphogenetic responses, growers could consider counteracting expected shoot stunting by applying more ample irrigation early in the growing season. Alternatively, because grapevine shoots are renewed annually, wind-induced canopy asymmetry could be addressed relatively cost-effectively, for example, by aspect-specific pruning and catch wire installations. The occurrence of sunscald on exposed fruit with south and west aspects could be minimized with aspect-specific hand thinning, a labor-intensive though common practice in vineyards whose product is destined for the premium market.

4. Conclusion

Vineyard rows oriented at an oblique angle to the direction of the prevailing wind develop asymmetrical canopies about the central axis of the vine row, with a lower proportion of potential canopy surface area on the windward side of the vine. This asymmetry appears to be governed by wind-induced morphogenesis (i.e., stunted shoots and leeward displacement of shoot tips over time). Shoots originating on the windward side of the canopy were shorter than those originating on the

leeward side of the canopy because of fewer nodes per shoot. In rows oriented nearly parallel to the prevailing wind, down-row streamlining of shoots occurred, with some displacement of shoot tips leeward of their hypothetical final locations for growth in the absence of external forces. Wind-induced canopy asymmetry may in fact be desirable if the windward side of the vine has a northern aspect because it could improve the balance of total diurnal irradiance at the fruiting zone between sides of the canopy; however, it may be detrimental to fruit with a southern or western aspect because daily peak irradiance at the fruiting zone would occur nearer the time of ambient temperature maxima, inducing potentially deleterious temperatures in the berry skins for the synthesis of a number of secondary metabolites associated with fruit quality. Fruit on the windward side of a grapevine canopy may be exposed to more intense irradiance and for longer duration than would have occurred in the absence of wind-induced canopy asymmetry. In consistently windy sites growers may orient rows according to a combination of prevailing wind direction and vineyard topography, but with an understanding of the consequences of this layout on irradiance at the fruiting zone. For uniform fruit maturation and quality in existing vineyards growers could modify or adapt the trellis or training system to counteract the effects of wind-induced canopy asymmetry on fruit quality. Because row orientation should be considered both in terms of sun–earth geometry and in terms of other environmental perturbations like wind, there is not a single prescriptive solution for vineyard managers with consistently windy sites.

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