	2				
Independent variable	species	slope	intercept	R^2	P-value
Stipe diameter (cm)	A. marginata	0.963	0.599	0.01	0.4156
	E. menziesii	0.389	1.230	0.01	0.5038
	L. setchellii	0.147	1.128	0.28	0.0003
	M. pyrifera	0.871	1.660	0.89	< 0.0001
	N. luetkeana	0.302	1.448	0.23	0.0007
	P. californica	0.197	1.137	0.11	0.0304
Conduit packing (SE/ $\mu$ m <sup>2</sup> )	A. marginata	0.304	-1.953	0.06	0.1108
	E. menziesii	-0.550	-0.395	0.00	0.7414
	L. setchellii	0.749	3.156	0.00	0.8316
	M. pyrifera	-0.676	-0.955	0.95	< 0.0001
	N. luetkeana	-0.536	-0.554	0.04	0.1708
	P. californica	-0.800	-1.165	0.08	0.0751
Vascular fraction	A. marginata	0.346	1.346	0.40	< 0.0001
	E. menziesii	0.558	1.503	0.22	< 0.0001
	L. setchellii	0.526	1.517	0.32	0.0001
	M. pyrifera	1.597	2.608	0.68	< 0.0001
	N. luetkeana	0.735	1.991	0.46	< 0.0001
	P. californica	0.601	1.568	0.49	< 0.0001
Cumulative blade area $(cm^2)$	A. marginata	0.108	0.833	0.37	< 0.0001
	E. menziesii	-0.178	1.660	0.00	0.7740
	L. setchellii	0.229	0.366	0.46	< 0.0001
	M. pyrifera	0.193	0.803	0.88	< 0.0001
	N. luetkeana	0.182	0.777	0.03	0.2430
	P. californica	0.184	0.473	0.07	0.1072
Path length (m)	A. marginata	-0.168	1.064	0.01	0.5633
	E. menziesii	0.171	1.045	0.01	0.3867
	L. setchellii	-0.215	0.969	0.00	0.6835
	M. pyrifera	0.280	1.427	0.85	< 0.0001
	N. luetkeana	-0.278	1.542	0.05	0.1402
	P. californica	-0.335	0.958	0.01	0.4735
Cumulative biomass (g)	A. marginata	0.129	1.031	0.03	0.1985
	E. menziesii	0.121	0.861	0.00	0.8301
	L. setchellii	0.239	0.747	0.25	0.0006
	M. pyrifera	0.188	1.204	0.89	< 0.0001
	N. luetkeana	0.187	1.188	0.08	0.0569
	P. californica	0.167	0.819	0.03	0.2878

Table S1. Scaling parameters for the log-log relationship between average SE diameter and various functional anatomy traits.

## Supplemental Material Convergent evolution of vascular optimization in kelp (Laminariales)

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## I. MATHEMATICAL MODEL OF CARBOHYDRATE LOADING AND UNLOADING IN MACROALGAE

We model sugar transport by considering the movement of sap through collection of parallel conduits along the x-axis. We denote the flow velocity u(x) and the total conduit cross-section area A(x), while c is the total carbohydrate concentration. Phloem loading and unloading is included via a loading function  $\phi$  in the sap conservation equation [1]

$$c\frac{d}{dx}\left(Au\right) = \phi. \tag{1}$$

Here,  $\phi$  is amount of carbohydrate loaded into or unloaded from the phloem per unit time. We can express it as  $\phi = qc$ , where q is the sap volume entering or leaving the stipe phloem per unit length and time. Note that the sign of q reflects the direction of the sap flow leaving or entering the conduit system; q > 0 is used in a source while q < 0 applies in a sink organ. The coordinate x is measured from the start of the zone. For the unloading zone relevant to *M. pyrifera*, it is given by  $x = \ell + x^* - H$ , where  $x^*$  is the distance from the holdfast, H is the organism height, and  $\ell = 1$  m is the length of the unloading zone. Here we assume that  $\phi = qc$  is constant throughout either the loading or unloading zone. This assumption is supported by observations by Lobban, who found that the unloading rate reached a plateau near the apex in M. pyrifera [2]. Outside the transfer zones the loading factor  $\phi = 0$ . In that case (1) implies conservation of sugar mass flow cAu = const.

Equation (1) can be integrated to yield

$$Au = qx + c_1. \tag{2}$$

Imposing a no-flow boundary condition at the apex  $(Au = 0 \text{ at } x = \ell)$  leads to

$$Au = q(x - \ell). \tag{3}$$

We now use Darcy's law for the relationship between the velocity u and the pressure gradient dp/dx

$$\frac{dp}{dx} = -\frac{\eta u}{k},\tag{4}$$

where  $\eta$  is the viscosity of the phloem sap and k(x) is the permeability of a single phloem tube. For a cylindrical pipe, the permeability is given by

$$k = \frac{r(x)^2}{8} = \frac{a(x)}{8\pi},\tag{5}$$

where we have substituted the cross section area  $a(x) = \pi r(x)^2$  of a single conduit. Using the expression for velocity found in Eq. (3) in Eq. (4) leads to

$$\frac{dp}{dx} = -\frac{\eta q(x-\ell)}{k(x)A(x)} = -8\pi \frac{\eta q(x-\ell)}{a(x)^2 N(x)} \tag{6}$$

where we have written the total transport area as A(x) = a(x)N(x) where N(x) is the number of sieve elements at the position x. Experimental data suggest that the sieve tube number is approximately constant in the species we consider. For instance,  $N(x) \approx 500$  in M. pyrifera (Fig. 1). With these assumptions, Eq. (6) can be integrated to yield the pressure drop along the collection of conduits  $\Delta p = p(\ell) - p(0)$ 

$$\Delta p = 8\pi \frac{\eta q}{N} \int_0^\ell \frac{\ell - x}{a(x)^2} \,\mathrm{d}x \tag{7}$$

We now ask the question: what is the distribution of sieve tube area a(x) which minimizes the pressure drop  $\Delta p$ along the length  $\ell$  subject to the constraint that the total volume of conduits remains constant? In other words, we minimize

$$\frac{1}{8\pi} \frac{\Delta pN}{\eta q} = \int_0^\ell \frac{\ell - x}{a(x)^2} \,\mathrm{d}x \text{ subject to } N \int_0^\ell a(x) \,\mathrm{d}x = V_0.$$
(8)

A more convenient form of the equations are obtained when rescaling the axial coordinate by the apex distance to obtain the non-dimensional coordinate  $z = x/\ell$ . This leads to

min 
$$\int_0^1 \frac{1-z}{a(z)^2} dz$$
 subject to  $\int_0^1 a(z) dz = \text{const.}$  (9)

The Euler-Lagrange equation for this minimization problem is

$$\frac{\partial}{\partial a} \left( \frac{1-z}{a(z)^2} \right) = \lambda \tag{10}$$

where  $\lambda$  is a Lagrange multiplier to be determined from the boundary conditions. Equation (10) leads to

$$a(z) = \bar{a}(1-z)^{1/3} = \bar{a}\left(1-\frac{x}{\ell}\right)^{1/3}$$
(11)

where  $\bar{a} = a(0)$  is the area at x = 0. Equation (11) represents the optimized phloem tube cross section area distribution along the stipe. We can now compute the pressure drop (Eq. (7)) along the stipe



FIG. 1. The area of sieve elements vary along the stipe in *M. pyrifera*, while the number of conduits is approximately constant. (A) Number of sieve element conduits *N* and (B) sieve element cross-section area *a* plotted as a function of distance  $x^*$  from the holdfast. (C) Sieve tube area *a* plotted as a function of inverse distance  $1 - x/\ell$  using data from (B). Only data points within the unloading zone identified by Lobban of length  $\ell = 1$  m are used. The data are in reasonable agreement with the predicted optimum scaling  $(a(x) \sim (1 - x/\ell)^{1/3}$ , see Eq. (11)) indicated by solid black line.

$$\Delta p_{\rm opt} = 8\pi \frac{q\eta\ell}{N\bar{a}^2} \int_0^1 \frac{1-z}{(1-z)^{2/3}} \,\mathrm{d}z = 6\pi \frac{q\eta\ell}{N\bar{a}^2} \qquad (12)$$

We may contrast this pressure drop with that calculated assuming a uniform sieve element cross-section area  $a_0$ . Requiring that the two conduit populations have identical volumes leads to the identity

$$N\ell\bar{a}\int_0^1 (1-z)^{1/3} \,\mathrm{d}z = N\ell a_0.$$
 (13)

This can be conveniently expressed in the form

$$a_0 = \frac{3}{4}\bar{a}.\tag{14}$$

The pressure drop for a bundle uniform tubes is calculated from Eq. (7) by setting  $a(x) = a_0$ 

$$\Delta p_{\rm unif} = 8\pi \frac{\eta q \ell}{N a_0^2} \int_0^1 (1-z) \, \mathrm{d}z \tag{15}$$

$$=4\pi \frac{\eta q\ell}{Na_0^2} = \frac{64\pi}{9} \frac{\eta q\ell}{N\bar{a}^2} \tag{16}$$

Taking the ratio of the optimized to the uniform pressure drop leads to

$$\frac{\Delta p_{\text{unif}}}{\Delta p_{\text{opt}}} = \frac{32}{27} \approx 1.19 \tag{17}$$

This result shows that the optimal size distribution of sieve elements along the stipe reduces the required pressure drop by about 20%. We use size-invariant sieve elements as null hypotheses to test for optimality in M. pyrifera. To further elucidate the sensitivity of the pressure ratio in Eq. (17) to the value of the exponent n, we consider a general, power-law area dependence given by

$$a_n(x) = \bar{a}_n \left(1 - \frac{x}{\ell}\right)^n.$$
(18)

Here, n = 0 corresponds to the uniform area distribution and n = 1/3 is the optimal distribution found above. The general constant volume constraint is

$$\frac{3}{4}N\ell\bar{a} = N\ell\bar{a}_n\frac{1}{n+1}.$$
(19)

This gives a relationship between the individual conduit areas

$$\bar{a}_n = \frac{3(n+1)}{4}\bar{a},$$
 (20)

that allows us to compare the pressure drops required to drive flow given a constant conduit volume. The pressure drop is

$$\Delta p_n = 8\pi \frac{q\eta\ell}{N\bar{a}_n^2} \int_0^1 (1-z)^{1-2n} \,\mathrm{d}z, \qquad (21)$$

$$= 8\pi \frac{q\eta\ell}{N\bar{a}_n^2} \frac{1}{2(1-n)},$$
 (22)

$$= \frac{64\pi}{9} \frac{q\eta\ell}{N\bar{a}^2} \frac{1}{(1-n)(1+n)^2}.$$
 (23)

Finally, we find for the general pressure ratio

$$\frac{\Delta p_n}{\Delta p_{\rm opt}} = \frac{32}{27} \frac{1}{(n-1)(n+2)^2}.$$
(24)

The pressure ratio given in Eq. (24) is plotted in Fig. 2. While the required pressure increases substantially when  $n \rightarrow 0, 1$  a range of values around the optimum n =



FIG. 2. The energy efficiency of phloem transport depends on the tapering of conduit area. Pressure ratio (Eq. (24)) plotted as a function of power law exponent n (Eq. (18)). Exponents in the range 0.15 < n < 0.5 (shaded area) are within 5% of the efficiency of the optimum value n = 1/3.

1/3 require nearly the same pressure to drive flow. For instance, values in the range 0.15 < n < 0.5 are within 5% of the optimum, shown as the red shaded area in Fig. 2.

Figure 1(C) shows the sieve tube area *a* plotted as a function of inverse distance  $1 - x/\ell$ . The data are consistent with the predicted optimum scaling (Eq. (11)).

- Leonard Horwitz. Some simplified mathematical treatments of translocation in plants. *Plant physiology*, 33(2):81, 1958.
- [2] Christopher S. Lobban. Translocation of 14c in macrocystis pyrifera (giant kelp). *Plant physiology*, 61(4):585–589, 1978.



Figure S3. Log-log plot of average sieve element area vs. inverse relative plant height  $(1 - x^*/H)$  for (A) *Alaria* marginata; (B) *Laminaria setchellii*; (C) *Pterygophora californica*; (D) *Egregia menziesii*; (E) *Nereocystis luetkeana* (note larger y-axis); (F) *Macrocystis pyrifera*. Segments (points) from an individual sampled sporophyte are joined by lines; each individual is a different color. Error bars are one standard deviation.



Figure S4. Log-log plot of total estimated SE count (N) vs. inverse relative plant height (1 - x/l) for (A) *Alaria marginata*; (B) *Laminaria setchellii* (note larger y-axis); (C) *Pterygophora californica*; (D) *Egregia menziesii*; (E) *Nereocystis luetkeana*; (F) *Macrocystis pyrifera*. Segments (points) from an individual sampled sporophyte are joined by lines; each individual is a different color.



Figure S5. Illustrations of study species. (A,B,C,D) *Laminaria setchelli, Alaria marginata, Egregia menziesii, Pterygophora californica.* Scale bar = 1m. (E,F) *Nereocystis luetkeana, Macrocystis pyrifera.* Scale bar = 5m. Colored bars show approximate loading/unloading zones. Red zones are loading photoassimilate from the phloem, blue zones are unloading from the phloem, and purple zones are transporting bi-directionally.



Proportion of Sporophyte Height

Figure S6. Increase in normalized variation in sieve element (SE) area (coefficient of variation) with height in *M. pyrifera*. Variance in cell size increases in the distal segments of each sampled *M. pyrifera* frond (p<0.0001, R2 = 0.33); distal segments possess SE's that are an order of magnitude larger than the (~12  $\mu$ m diameter) mean.