

A COMPARISON OF LEAF APPEARANCE RATES AMONG TEOSINTE, MAIZE LANDRACES AND MODERN MAIZE

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ABSTRACT - The rate at which successive new leaves emerge at the stem apex in gramineae (phyllochron) is largely controlled by temperature. Utilizing genetic variation for the phyllochron may be a way to alter plants' responses to the environment or to manipulate time to maturity. Little is known about possible genetic variation in the phyllochron among maize landraces, its ancestor teosinte and modern maize. Controlled environment (phytotron) and field studies were conducted to investigate possible genetic variation for the phyllochron among seven maize (*Zea mays*) landraces (Apachito, Chapalote, Cónico, Tabloncillo, Tehua, Tuxpeño, and Zapalote Chico) sampled from the center of maize diversity in Mexico, a modern US maize hybrid (B73 x Mo17), and two teosintes (*Zea diploperennis* and *Z. mays* ssp. *parviglumis*). In the phytotron the phyllochron was determined for three day/night temperature regimes (22/18, 27/21 and 33/25°C) under a 12 h photoperiod. Genetic variation for the phyllochron among the genotypes was observed in the phytotron and field, however, it was small with extreme values of about +/-15% of the mean. A generally similar phyllochron for modern maize and its wild relatives suggested that this trait has been conserved despite thousands of years of human and natural selection. A similar leaf development rate among genotypes which varied widely for final leaf numbers (14-24) indicated that early flowering in some landraces was almost exclusively due to earlier floral initiation.

KEY WORDS: Teosinte; Maize; Phyllochron; Leaf appearance.

INTRODUCTION

Vegetative development in gramineae is characterized by the regular initiation and appearance of successive leaves. The rate of leaf initiation on the

apical meristem and the rate of leaf appearance above the pseudostem or whorl are primarily controlled by temperature (WILHELM and McMASTER, 1995). Over a wide temperature range the relationship between leaf appearance and temperature is curvilinear (TOLLENAAR *et al.*, 1979; WARRINGTON and KANEMASU, 1983), however between about 15 and 25°C the relationship for maize is nearly linear (YAN and HUNT, 1999). In field studies, where temperatures vary from day to day, leaf appearance is often expressed as the phyllochron. The phyllochron is defined as the duration (in accumulated temperature) between the appearance of two successive leaves (WILHELM and McMASTER, 1995). Accumulated temperature is typically expressed as growing degree days (GDD) which is defined as the accumulated temperature above a base at which growth is assumed to begin.

Under normal growing conditions with adequate nutrients and moisture the phyllochron of maize (*Zea mays*) remains stable throughout the life of the plant and values are similar among a wide variety of genotypes and environments (KINIRY and BONHOMME, 1991; RITCHIE and NE SMITH, 1991). For field-grown hybrid maize, the phyllochron ranges between 36 and 52 degree days (base 8°C) per leaf tip (see BIRCH *et al.*, 1998; VINO CUR and RICHIE, 2001), however values between 37 and 42 GDD are most frequent. Some of the variation among studies may be due to whether soil or air temperature was used (VINO CUR and RITCHIE, 2001). Shading or low light levels may also increase the phyllochron (BIRCH *et al.*, 1998; TOLLENAAR, 1999). Moreover, the phyllochron may be different when constant versus alternating day/night temperatures are used, despite similar mean temperatures, especially when part of the day is at extreme high or low temperature (WARRINGTON and KANEMASU, 1983).

A high degree of genetic control of the phyl-

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TABLE 1 - Origin and characteristics of maize and teosinte genotypes.

Genotype	Collection	Seed Source ^a	Group ^b	Characteristics
Apachito	CHIH177	CIMMYT	6	Mexican early northern highland
B73		NCSU		USA Stiff Stalk inbred line
B73 x Mo17		NCSU		USA Corn Belt Dent hybrid
Chapalote	SIN 2		5	Mexican popcorn, northwest lowland
Cónico	PUE 116	INIA	6	Mexican early north-central highland
Mo17		NCSU		USA Lancaster inbred line
Tabloncillo	JAL 100	INIA	7	Mexican eight-rowed western
Tehuá	CHIS 29	CIMMYT	3	Mexican late maturity southern lowland
Tuxpeño	OAX 9	INIA	1	Mexican late tropical southern lowland
Zapolote Chico	OAX 50	INIA	1	Mexican early tropical southern dent
<i>Zea diploperennis</i>	bulk of PI 441932 and PI 441931			Mexican perennial diploid teosinte, western
<i>Zea mays</i> ssp. <i>parviglumis</i>	seed from original Beadle collection	M.M. Goodman		Mexican annual teosinte southern, mid elevation

^a CIMMYT - Centro Internacional de Mejoramiento de Maíz y Trigo; NCSU - North Carolina State University, Raleigh NC, USA; INIA - Instituto Nacional de Investigaciones Agrícolas (Mexico).

^b SANCHEZ and GOODMAN (1992).

lochron is indicated by high broad-sense heritabilities reported in other Gramineae species: 71% to 91% in barley (*Hordeum vulgare*; DOFING, 1999) and 83 to 91% in rice (*Oryza sativa* ssp. *japonica* x *O. indica*; MORITA *et al.*, 2005). A single gene mutation resulted in reducing the phyllochron of rice in half (MIYOSHI *et al.*, 2004), but other studies indicated that the phyllochron is controlled by a polygenic system (DONG *et al.*, 2004; MIYAMOTO *et al.*, 2004; MORITA *et al.*, 2005). In maize, the *terminal ear 1* mutation increases the rate of leaf initiation by nearly 40% compared to wild type maize, but this mutation also dramatically alters plant morphology, in which the tassel is replaced with an ear-like inflorescence, alternate phyllotaxy is disrupted, and leaves manifest other abnormalities (VEIT *et al.*, 1998).

Maize was domesticated from teosinte in Mexico about 9000 years ago and is most closely related to *Z. mays* ssp. *parviglumis* (MATSUOKA *et al.*, 2002). Subsequently, maize evolved separately in many regions with landraces now showing adaptation to specific temperature regimes (DUNCAN and HESKETH, 1968; RUIZ *et al.*, 2008) and growing season durations (SANCHEZ and GOODMAN, 1992). The phyllochron, along with timing of floral initiation may influence time to flowering, as all unmerged leaves present at time of floral initiation must fully develop before flowering can occur. Identifying genetic variation within maize for the phyllochron may improve its response to its environment (PADILLA and OTEGUI,

2005) or help identify genes associated with maturity time. Little is known about the possible genetic variation for the phyllochron among maize landraces or their ancestors. The objective of this study was to examine leaf development among maize landraces, modern maize and teosinte in order to test for genetic variation for phyllochron in a diverse sample of the *Zea* genus.

MATERIALS AND METHODS

Leaf development of a modern maize hybrid, Mexican maize landraces and two teosinte species were studied in the field and in a controlled environment (the North Carolina State University phytotron). For the phytotron treatments, seven maize landraces, a modern maize F₁ hybrid (B73 x Mo17), *Z. diploperennis*, and *Z. mays* ssp. *parviglumis* (Table 1) were grown in three growth chambers, each having a unique day/night temperature regime (22/18, 27/21, or 33/25°C) and a common 12 h photoperiod. Temperature was recorded in a light-shielded aspirated housing by a copper-constantan thermocouple located 1 m above the chamber floor. Light was provided by a mixture of 1500 ma cool-white fluorescent and 100 W incandescent lamps. Lamps were separated from the chamber by a plexiglass barrier. The light levels measured about 1 m above the chamber floor were 500 (+/- 15) $\mu\text{mol m}^{-2} \text{s}^{-1}$. The typical red:far red light ratio for these lamps is 0.838. Relative humidities in the chambers were typically above 70%. More detailed environmental specifications are available at <http://www.ncsu.edu/phytotron/manual.pdf>, see description of "B chambers".

Within each chamber, the experimental design was a randomized complete block with three replications (one pot per genotype per replicate). The experimental unit was a 9000 ml

pot containing 1/3 peat-lite and 2/3 gravel into which five seeds of a single genotype were planted. After emergence, pots were thinned to one plant per pot. Plants received water and a nutrient solution twice daily.

Maize seeds contain 5-6 preformed leaves (WARRINGTON and KANEMASU, 1983; PADILLA and OTEGUI, 2005) with early growth dependent on seed reserves (i.e., autotrophic). To avoid confounding environmental effects with autotrophic seedling growth, data collection commenced when plants had about five visible leaves. The fifth and tenth leaves of each plant were marked to facilitate leaf counts of the latest developed leaves. At approximately 3-5 day intervals, the numbers of visible leaf-tips and ligules were recorded for each plant. The total number of visible leaf-tips on each plant at the time the tassel or ear emerged was also recorded. The number of leaf tips and leaf ligules were regressed against time (d) for each plant to estimate the phyllochron.

In the field trial, the same 10 genotypes studied in the phytotron along with inbred lines B73 and Mo17 were established in plots on 25 April 2007, at the Central Crops Research Station (Clayton NC, USA). Plots consisted of single rows (3m length with 1m row spacing), arranged in a randomized complete block of three replications. Within-row plant spacing was about 0.2 m. Fertilizer applications along with weed and insect control were typical for commercial corn production in the region (HEINIGER *et al.*, 2000). Plots were irrigated at least once a week if rainfall was considered to be limiting. When all genotypes had attained at least five visible leaves, seven plants per row were tagged. The number of leaf-tips and ligulated leaves were recorded every 3 to 5 days on all tagged plants until the tassel was visible in the whorl or 7 July.

Daily mean air temperatures at a 2m height (average of temperature recorded every minute) were obtained from an automated weather station located about 1 km from the plots. Growing degree days (GDD's) were calculated as the summation of mean daily temperature less a base of 8°C. The base temperature for these and other genotypes may vary (RUIZ *et al.*, 1998; PADILLA and OTEGUI, 2005), but we used a common base of 8°C to facilitate comparisons with previous reports (BIRCH *et al.*, 1998; VINO CUR and RICHIE, 2001; PADILLA and OTEGUI, 2005).

Data from individual chambers were subjected to an analysis of variance with genotypes treated as fixed effects and replicates treated as random using SAS Version 9.1 Proc GLM (SAS INSTITUTE, 2004). The least significant difference (LSD) was used to differentiate among the means when the genotype effect was significant at $p < 0.05$. Data were also analyzed across chambers, using the chamber-by-genotype interaction mean square to test the effect of genotypic differences averaged across chambers.

RESULTS AND DISCUSSION

In the phytotron, all plants emerged within 3-5 days after planting at all temperatures. Emergence times were similar for maize and teosinte (data not shown) however, when data collection commenced, the maize genotypes had on average 1.7 more leaves than teosinte (data not shown). Presumably this was the result of greater seed size in maize compared to teosinte and possibly a larger number of embryonic leaves in maize than teosinte.

In the phytotron, leaf appearance data were restricted to the first 14-15 visible leaf-tips. After that stage, the earliest genotypes had visible tassels and some plants of the later maturing genotypes reached the chamber ceiling, which potentially could have affected later leaf emergence. Slower plant growth at lower temperatures resulted in 18, 14, and 13 sampling days for the 22/18, 27/21, and 35/27°C temperature regimes, respectively. Some plants that were clearly unhealthy or suffered mechanical damage were discarded, such that unequal sample sizes resulted.

In the field, some genotypes failed to emerge, such that data were collected from five of the ten genotypes used in the phytotron plus the inbred lines B73 and Mo17. Leaf counts commenced on 5 May when the maize genotypes had an average of 6.3 leaves and teosinte had 4.4. Temperatures in the field during the period from sowing to the end of data collection averaged 23.9°C, however, average temperature varied slightly among genotypes because the flowering time varied among genotypes. Photoperiod (civil sunrise to civil twilight) during this period was 14.5 to 15.5 h. *Z. mays* ssp. *parviglumis* and *Z. diploperennis* did not flower under the long-day field conditions as they require shorter days to initiate floral development (RODGERS, 1950).

The relationship of leaf-tip and ligule number with time (d) was linear for all genotypes and temperatures. A typical example is given for B73 x Mo17 and *Z. mays* ssp. *parviglumis* at the 21/27°C phytotron treatment (Fig. 1). A constant or near constant phyllochron for a given genotype over time is common for maize and typical of many grasses. This pattern occurs even as leaf length changes. A common explanation is that the developmental sub-processes of leaf initiation, leaf expansion, and cessation of growth are coordinated. Typically as leaves become longer or shorter, the distance a leaf must expand to emerge from the whorl changes, however, this is compensated with a change in the dynamics of leaf extension, such that there is no change in leaf appearance rate (FOURNIER *et al.*, 2005).

Our values for leaf appearance rate (Table 2) were similar to other growth room studies with modern maize hybrids. For example, at the 27/21°C temperature regime, our mean rates (0.40 leaf-tips and 0.30 ligules per day) were very close to the 0.43 leaf-tips per day predicted by the equation of TOLLENAAR *et al.* (1979) and 0.28 ligules per day predicted by WARRINGTON and KANEMASU (1983). Converting our leaf appearance rate at the intermediate

TABLE 2 - Leaf appearance rate (leaves per day) for leaf-tips and ligules of maize genotypes at three temperature regimes.

Genotype	Temperature (day/night)							
	22/18°C		27/21°C		33/25°C		Mean	
	tips	ligules	tips	ligules	tips	ligules	tips	ligules
	leaves day ⁻¹							
Apachito	0.31	0.23	0.39	0.30	0.48	0.38	0.39	0.30
B73 x Mo17	0.29	0.19	0.41	0.28	0.48	0.34	0.39	0.27
Chapalote	0.35	0.24	0.47	0.31	0.53	0.40	0.45	0.32
Cónico	0.33	0.21	0.38	0.25	0.45	0.38	0.38	0.28
Tabloncillo	0.35	0.23	0.43	0.32	0.49	0.38	0.42	0.31
Tehua	0.31	0.20	0.39	0.29	0.45	0.36	0.38	0.28
Tuxpeño	0.31	0.21	0.38	0.29	0.49	0.37	0.39	0.29
Zapolote Chico	0.35	0.25	0.46	0.34	0.51	0.37	0.44	0.32
<i>Z. diploperennis</i>	0.31	0.22	0.38	0.30	0.49	0.36	0.39	0.29
<i>Z. mays</i> ssp. <i>parviglumis</i>	0.27	0.21	0.36	0.30	0.45	0.37	0.36	0.29
Mean	0.32	0.22	0.40	0.30	0.48	0.37	0.40	0.30
LSD(0.05)	0.05 ^a	0.05 ^a	0.05	0.04	ns	ns	0.03	0.02

^a LSD values are not same for each comparison due to unequal sample numbers. The value given is the largest possible value.

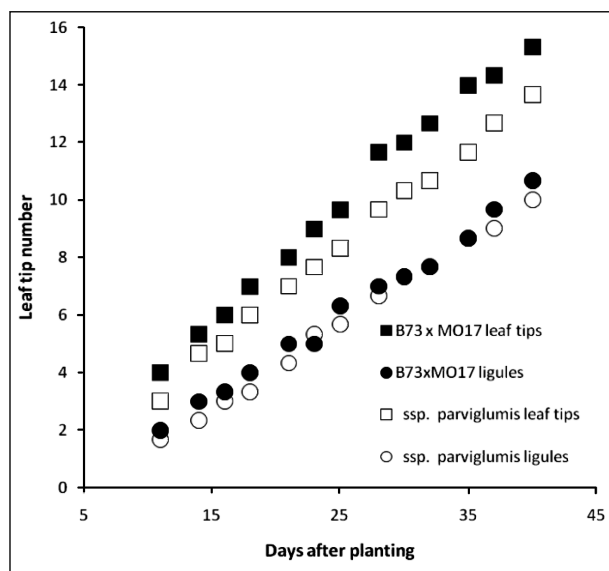


FIGURE 1 - Relationship between leaf-tips and ligules with time (d) for maize hybrid B73 x Mo17 and *Zea mays* ssp. *parviglumis*. Plants were grown in the phytotron at a 27/21°C day/night temperature regime.

temperature (0.40) to a degree day basis gives 45, 40, and 35 GDD per leaf tip for base temperatures of 6, 8, and 10°C, respectively.

In the field, the phyllochron ranged from 37 to 46 GDD (base 8°C) with an overall average of 40 GDD (Table 3). This value was comparable to our data ob-

served in the phytotron and was similar to previous studies under temperate field conditions where the phyllochron is most often in the 37 to 42 GDD range (BIRCH *et al.*, 1998; VINOUCUR and RICHIE, 2001).

In the phytotron, the genotype effect was significant ($p < 0.05$) for leaf-tip and ligule appearance rate at the 22/18 and 27/21°C treatments (Table 2). The genetic variation among genotypes was small, however; extreme values were only about 15% from the mean. In the field, significant differences ($p < 0.05$) among genotypes of about the same magnitude were observed for leaf-tip and ligule phyllochron (Table 3). There was no obvious relationship between phylogenetic relationships and phyllochron; although the teosintes tended to have lower phyllochron, the differences between them and most maize entries were not significant (Tables 2 and 3). There was evidence for dominance for smaller phyllochron, as B73 x Mo17 had significantly lower phyllochron than Mo17 (Table 3), although this may be related to hybrid vigor *per se* rather than to dominance at specific phyllochron genes. TOLLENAAR *et al.* (2004) also observed a lower phyllochron (higher leaf appearance rate) in hybrids than their inbred parents. They reported that the leaf appearance rate of twelve hybrids was on average 18.5% greater than that of their inbred parents. These findings suggest that some of our observed genetic variation in the phyllochron among geno-

types could have resulted from varying levels of heterozygosity within the landraces.

Our results are in general agreement with previous studies showing limited genetic variation for the phyllochron in maize. TOLLENAAR *et al.* (1984) and PADILLA and OTEGUI (2005) reported variation among genotypes in field studies, however, WARRINGTON and KANEMASU (1983) did not find any in a controlled environment study with an early and late temperate hybrid. BIRCH *et al.* (1998) found differences in the 10% range among a variety of hybrids under tropical and temperate conditions. They also observed that when tropically adapted maize was moved to temperate regions its phyllochron was similar to locally adapted lines. KINIRY and BONHOMME (1991), did not find differences for leaf-tip phyllochron among Mexican Sinaloa, Amarillo Salvadoreño and a commercial hybrid (Pioneer 3780) in the field in Texas.

This study differed from previous studies examining the phyllochron in maize, in that it examined a wider range of genotypes as well as wild relatives. Our sample of genotypes included highland types adapted to short seasons and cool temperatures as well as tropical lowland types. These results confirm earlier work indicating limited genetic variability for the phyllochron in maize and expand this finding to include wild relatives of maize.

Limited genetic variability for phyllochron within maize contrasts it with other Gramineae species which exhibit more variation for leaf development rates. For example, in rice (*O. sativa*), MORITA *et al.*

TABLE 3 - *Phyllochron (GDD base 8°C) for leaf-tips and ligules of maize genotypes under field conditions.*

Genotype	tips	ligules
	GDD leaf ⁻¹	
Apachito	44	58
B73 x Mo17	37	51
B73	39	52
Mo17	46	59
Chapalote	37	48
<i>Zea diploperennis</i>	37	44
<i>Zea mays</i> ssp. <i>parviglumis</i>	41	47
Mean	40	51
LSD (0.05)	3	7

(2005) reported genetic variation in the phyllochron of about 25% between an indica and japonica cultivar. In switchgrass (*Panicum virgatum*) the phyllochron was almost double for some early-maturing northern cultivars than for late-maturing cultivars from southern locations and appeared to play an important role in regulating maturity time (VAN ESBROECK *et al.*, 1997). Genetic variation among cultivars for the phyllochron was also reported in wheat, barley and forage grasses, however it was often small (5-10%) (FRANK and BAUER, 1995). Although the maize *terminal ear 1* mutation causes a major change in the phyllochron of maize, it pleiotropically results in a host of other abnormalities (VEIT *et al.*, 1998), indicat-

TABLE 4 - *Final leaf number for maize genotypes grown at three temperature regimes in a phytotron.*

Race	Temperature (day/night)			Mean
	22/18°C	27/21°C	33/25°C	
	leaves plant ⁻¹			
Apachito	14.0	15.5	14.7	14.7
B73 x Mo17	17.0	17.0	17.0	17.0
Chapalote	16.7	18.0	20.3	18.3
Conico	14.0	15.0	16.0	15.0
Tabloncillo	14.7	16.7	18.0	14.5
Tehua	23.7	24.0	23.5	23.7
Tuxpeño	20.3	21.0	22.0	21.1
Zapolote Chico	16.3	18.0	18.3	17.5
<i>Zea diploperennis</i>	15.3	15.0	18.7	16.3
<i>Zea mays</i> ssp. <i>parviglumis</i>	16.0	16.0	18.3	16.8
Mean	17.0	17.7	18.6	17.7
LSD(0.05)	2.6 ^a	1.2 ^a	2.1 ^a	1.5

^a LSD values are not same for each comparison due to unequal sample numbers. The values given are the largest possible value.

ing that this mutation does not contribute to the standing natural variation of phyllochron in maize.

A result similar to this study was reported by BULTYNCK *et al.* (2004), who found that the phyllochron of wheat (*Triticum aestivum* and *T. durum*) was similar to three of its wild relatives (*Aegilops umbellulata*, *A. caudata* and *A. tauschii*). Moreover, in barley (*H. vulgare*) and oats (*Avena sativa*), phyllochron values of modern cultivars are very similar to those of cultivars developed over 50 years ago (ABELED0 *et al.*, 2004; PELTONEN-SAINIO and RAJALA, 2007). Maize also appears similar to sorghum, which shows limited genetic variation for the phyllochron despite a large number of geographically distinct accessions (CRAUFORD *et al.*, 1998; CLERGET *et al.*, 2008).

In contrast to the phyllochron, we observed considerable genetic variation in the final number of leaves produced. Final leaf number in the phytotron ranged 14 to 24 leaves (Table 4). Lowest values were for highland types (Apachito and Cónico) and highest values for Tehua. We observed generally higher final leaf numbers at higher temperatures. With Mexican landraces, DUNCAN and HESKETH (1968) reported an increase of 0 to 5.4 more leaves per 10°C temperature increase whereas STEVENSON and GOODMAN (1972) show about 1.88 to 2.75 more leaves per 10°C at short and long photoperiods, respectively (comparing the 18/14 and 34/30°C values). The common explanation for more final leaves at higher temperatures is a delay in tassel initiation (i.e., tassel initiation at later leaf stage; TOLLENAAR and HUNTER, 1983; ELLIS *et al.*, 1992).

As leaf appearance rates were generally similar among genotypes, the low final leaf number of the highland lines inferred floral initiation at an earlier leaf stage. This excludes the rate of leaf emergence (under the moderate temperatures in our study) from playing a major role in maturity time. Others have observed similar results. PADILLA and OTEGUI (2005) did not find a relationship of final leaf number with phyllochron and found greatest genetic variation in phyllochron among hybrids of similar final leaf numbers and maturity times.

A characteristic of all genotypes in this study was that leaf-tips emerged at a faster rate than leaf ligules (Table 1) such that un-ligulated leaves accumulated in the whorl. This pattern of leaf development contrasts maize with sorghum (CLERGET *et al.*, 2008), rice, and wheat, where leaf appearance and ligule formation occur at a near constant rate (SKINNER and NELSON, 1995). One general difference between modern maize and teosinte was in the extent to which the

rates of leaf-tip emergence exceeded that of ligule emergence. For example, (using the 27/21°C values for B73 x Mo17 and the teosinte genotypes in Table 2) in teosinte leaf appearance rate exceeded ligule appearance rate by an average of 23%, whereas the value was 46% for B73 x Mo17. This difference implies genetic variation in the dynamics of leaf development between maize and teosinte. Given that leaf blade extension ceases around the time the ligules forms (FOURNIER *et al.*, 2005), a delay in ligule formation in maize suggests that maize had more visibly elongating leaves. However, it is not clear whether the total number of elongating leaves varied between maize and teosinte, as we did not account for leaves hidden within the whorl.

To our knowledge, this is the first report of the phyllochron for teosinte. In both a field (long photoperiod) and controlled environment study at several temperatures, there were only small differences for the phyllochron among maize land races, modern maize and teosinte. We found this surprising, given the fact that the study included maize of contrasting climatic regimes. Moreover, this shows that selection for agronomic traits in modern maize has had little indirect effect on the phyllochron. Surprisingly, there was more variation within maize genotypes for the phyllochron than between maize and its wild ancestors. The similarity between the phyllochron in modern maize and its wild ancestors despite separation by 9,000 years of natural and human selection, suggests that this trait is not easily altered. If alterations in maturity are the desired goal of breeding programs, then targeting variation final leaf number (i.e., the timing of floral initiation) will be more fruitful than attempting to exploit genetic variation in the phyllochron.

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