



# Evidence of Local Adaptation in the Demographic Response of American Ginseng to Interannual Temperature Variation

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**Abstract:** *Bioclimatic envelope models of species' responses to climate change are used to predict how species will respond to increasing temperatures. These models are frequently based on the assumption that the northern and southern boundaries of a species' range define its thermal niche. However, this assumption may be violated if populations are adapted to local temperature regimes and have evolved population-specific thermal optima. Considering the prevalence of local adaptation, the assumption of a species-wide thermal optimum may be violated for many species. We used spatially and temporally extensive demographic data for American ginseng (*Panax quinquefolius* L.) to examine range-wide variation in response of population growth rate ( $\lambda$ ) to climatic factors. Our results suggest adaptation to local temperature, but not precipitation. For each population,  $\lambda$  was maximized when annual temperatures were similar to site-specific, long-term mean temperatures. Populations from disparate climatic zones responded differently to temperature variation, and there was a linear relation between population-level thermal optima and the 30-year mean temperature at each site. For species that are locally adapted to temperature, bioclimatic envelope models may underestimate the extent to which increasing temperatures will decrease population growth rate. Because any directional change from long-term mean temperatures will decrease population growth rates, all populations throughout a species' range will be adversely affected by temperature increase, not just populations at southern and low-elevation boundaries. Additionally, when a species' local thermal niche is narrower than its range-wide thermal niche, a smaller temperature increase than would be predicted by bioclimatic envelope approaches may be sufficient to decrease population growth.*

**Keywords:** climate change, geographic range, local adaptation, *Panax*, plant demography

Evidencias de Adaptación Local en la Respuesta Demográfica del Ginseng Americano a la Variación de Temperatura Interanual

**Resumen:** *Los modelos bioclimáticos de las respuestas de especies al cambio climático son utilizados para predecir cómo responderán las especies al incremento de temperatura. Estos modelos frecuentemente se basan en la suposición de que los límites norteños y sureños del rango de una especie definen su nicho térmico. Sin embargo, esta suposición puede ser violada si las poblaciones están adaptadas a regímenes de temperatura locales y han evolucionado un óptimo térmico específico de cada población. Considerando la prevalencia de la adaptación local, la suposición de un óptimo térmico para la especie puede ser violada para muchas especies. Utilizamos datos extensivos, espacial y temporalmente, del ginseng americano (*Panax quinquefolius* L.) para examinar la variación en el rango de distribución como respuesta de la tasa de crecimiento poblacional ( $\lambda$ ) a factores climáticos. Nuestros resultados sugieren la adaptación a la temperatura local, pero no a la precipitación. Para cada población,  $\lambda$  fue maximizada cuando las temperaturas anuales fueron similares a las temperaturas promedio a largo plazo, específicas de cada sitio. Las poblaciones en distintas zonas*

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climáticas respondieron de manera diferente a la variación en la temperatura, y hubo una relación lineal entre el óptimo térmico a nivel poblacional y la temperatura promedio de 30 años en cada sitio. Para especies que están adaptadas localmente a la temperatura, los modelos bioclimáticos pueden subestimar el grado en que el incremento de la temperatura disminuya la tasa de crecimiento poblacional. Debido a que cualquier cambio direccional de las temperaturas promedio a largo plazo disminuirá las tasas de crecimiento poblacional, todas las poblaciones en el rango de distribución de la especie serán afectadas adversamente por el incremento en la temperatura, no solo las poblaciones en los límites sureños y con baja elevación. Adicionalmente, cuando el nicho térmico local de una especie es más angosto que su nicho termal amplio, se podría pronosticar un pequeño incremento de la temperatura mediante métodos bioclimáticos que sea suficiente para disminuir el crecimiento poblacional.

**Palabras Clave:** adaptación local, cambio climático, demografía de plantas, *Panax*, rango geográfico

## Introduction

The net effect of the climate change on a given species will be a function of its demographic, evolutionary, and spatial responses (Walther et al. 2002; Parmesan 2006; Aitken et al. 2008). Despite the known importance of population-level demographic and evolutionary processes in determining long-term species persistence (Lande 1988, 1998), a popular paradigm of species' response to the climate change is rooted in bioclimatic envelope models (Jeltsch et al. 2008), which do not incorporate mechanistic, population-level information. Instead, these models use the relation between a species' distribution and climatic factors to define a realized climatic niche and thus are based on the assumption that there is a range-wide relation between fitness and climate. Unless temperatures increase beyond the breadth of the thermal range defined by the current species' distribution, fitness theoretically increases in high-elevation and high-latitude populations within the range as temperatures in these regions shift closer to the species-wide thermal optimum. However, the assumption of a species-wide thermal optimum may be incorrect if past selection has led populations to adapt to current local climate (Davis & Shaw 2001). If this is the case, the population-level thermal niche may be considerably narrower than the thermal niche as defined by the species' range. Fitness may be optimized to local climate, precluding, in the absence of gene flow, an increase in fitness of northern or high-elevation populations in response to the climate change (Holt & Gaines 1992; Holt 2003, 2009).

Local adaptation refers to the genetic differentiation of populations within a species' range, such that, where a population occurs, local genotypes have greater fitness relative to non-local genotypes (Clausen et al. 1947; Kawecki & Ebert 2004; Hereford 2009). Populations may be adapted to diverse environmental factors, including heavy metals, availability of nutrients and light, interactions with other species (Linhart & Grant 1996), and climate (Turesson 1930; Linhart & Grant 1996; Etterson 2004). Within a heterogeneous environment, adaptive genetic differentiation of populations occurs when gene

flow and genetic drift are too weak to counteract selection and when the effect of alleles on fitness depends on environment, such that no single genotype has the greatest fitness in all environments (Primack & Kang 1989; Kawecki & Ebert 2004). Specialization of populations is adaptive in a stable environment, but may incur a fitness cost in a dynamic environment (Davis & Shaw 2001). For populations adapted to local climate, rapid increases in air temperature may exceed the limits of a narrow specialized niche, precipitating population decline. Local adaptation has been demonstrated hundreds of times for many species (Taylor 1991; Linhart & Grant 1996; Kaltz & Shykoff 1998).

We examined whether American ginseng (*Panax quinquefolius* L.) is adapted to local climate by investigating range-wide trends in demographic response to annual climatic variation. We evaluated whether demographic responses to climatic variables suggest a single, range-wide climatic optimum or, as would be expected if populations were adapted to local climate, population-specific, local optima. We also tested whether there was a direct, linear relation between populations' climatic optima and the long-term (30-year) mean climate at each site.

## Methods

### Study Species

American ginseng is a medicinal plant that is harvested in the wild and cultivated with a range of techniques that vary in intensity (Robbins 2000). In the United States, regulation of ginseng harvest from the wild was placed under management of the U.S. Fish and Wildlife Service when ginseng was added to Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) list in 1975. Ginseng is a widespread, herbaceous perennial found in the understory of deciduous forests of the eastern United States and southern Canada (McGraw et al. 2003). Ginseng has hermaphroditic flowers and can reproduce by outcrossing or self-pollination. Pollinators of ginseng include

syrrhid flies and halictid bees, both generalist pollinators (Lewis & Zenger 1983). Ginseng plants can live for over 50 years (Mooney & McGraw 2009). High levels of genetic differentiation have been detected among ginseng populations (Cruse-Sanders & Hamrick 2004; Grubbs & Case 2004).

### Census

Over 6 years (1998–2004), we located 12 natural ginseng populations in 6 states (Indiana, Kentucky, New York, Pennsylvania, Virginia, and West Virginia). The size of the areas occupied by populations varied from approximately 0.2–4.0 ha. The closest 2 populations were 0.85 km apart, a distance sufficient to genetically isolate them (Hackney 1999). Although populations were not randomly selected for census, we considered them representative of the range of aspects, elevations, and land-use types occupied by the species. We withheld exact population locations to prevent harvest of the populations. Each population was censused twice per year for 6–12 years, depending on when censusing was initiated.

All plants within a population were cryptically and uniquely marked with a numbered aluminum tag. To relocate plants, we used a “photo-trail” method in which photographs paired with written directions guided researchers to plants. This method of relocating plants reduced the likelihood of drawing plants to the attention of harvesters and minimized trampling. The first census in each year occurred after the aerial parts of the plants (leaves, sympodia) stopped growing for the season (mid-May to mid-June). At that time, we measured sympodium height and length and width of the longest leaflet per leaf. We used a previously derived multiple-regression equation (Souther & McGraw 2011) to estimate the leaf area from these field measurements of leaflet length and width. During the first yearly census, we searched for new seedlings in a 2-m radius around each plant. This search radius was based on a previous experiment that tracked the movement of approximately 16,000 seeds and showed that 90% of seeds germinated <2 m from where they were deposited (Van der Voort 2006). At the end of the growing season (early to mid-August), we conducted a second census, during which we measured seed production and assessed the status (e.g., senesced, diseased, browsed) of each plant. Ginseng berries have a distinct morphology depending on the number of seeds (between 1 and 3) they contain, which allowed us to directly count seeds.

We conducted a seed-cage experiment for each population to determine seed-bank dynamics and germination rates. In August 2006, we obtained approximately 7200 seeds from a wild-simulated ginseng grower in West Virginia. Wild simulated refers to a method of ginseng cultivation in which plants are derived from wild stock and grown in wooded areas to simulate natural conditions.

During the winter, seeds were held in large, sand-filled mesh bags under leaf litter at a forested site (i.e., stratified) that had a natural ginseng population. The following spring we deployed 12 seed cages 1 at each site. Cages were formed from segments of polyvinyl-chloride tubing (diameter 8.5 cm, length 8 cm) with plastic screen mesh affixed to the base. We placed 50 stratified seeds into each of 12 seed cages containing soil collected from the site. We topped seed cages with coarse plastic-mesh cloth to allow precipitation but not herbivores to enter the cage. The seed cages were set into the soil in 3 groups of 4, evenly distributed across each site with an average distance between groups of 15 m. Within the 3 groups, seed cages were placed 25 cm apart. Each year for 4 years, we counted germinants and tested the viability of the seeds from 3 randomly selected cages (1 cage per group) with tetrazolium staining ( $n = 3$ ) (Baskin & Baskin 1998). We used these data to calculate the probability of survival and germination of seeds in each age cohort. For populations in which a prior seed-cage experiment had been carried out (McGraw & Furedi 2005), age-related seed survival within the seed bank and germination, determined as described above, were averaged across the 2 experiments. Although use of the common seed source and resulting seed-cage data to parameterize seed-bank transition probabilities eliminated the influence of local genetic variation in germination rates, we believed that it was important to incorporate the age structure of the seed bank and thus capture natural lags in germination caused by site-to-site variation in the soil.

### Population Projections

Data from the censuses and seed-cage experiments were used to parameterize population projection matrices with 8 stages (Fig. 1 & Supporting Information). Within a projection matrix, transition elements ( $a_{ij}$ ) represent the number of individuals of size  $i$  (at time  $t+1$ ) per individual size  $j$  (at time  $t$ ) (Caswell 2001). The number of individuals in each stage consisted of the individuals present during the first census of each year. Stages 1–4 consisted of seeds within the seed bank that were, respectively, 9, 21, 33, and 45 months old (Supporting Information). We calculated the age of these seed cohorts as the number of months between seed maturation and the census. The probability of seeds surviving and transitioning to the following age from year  $t$  to year  $t+1$  (transitions  $a_{21}$ ,  $a_{32}$ ,  $a_{43}$ ) was estimated directly from postgermination viability tests of seeds remaining in the seed cages at each site and was calculated as

$$a_{ij} = \frac{S_i}{S_j}, \quad (1)$$

where  $a_{ij}$  is the probability of seed survival from stage  $j$  to stage  $i$  within 1 year ( $i < 5$ ,  $j = i - 1$ ) and  $S$  is the mean number of viable seeds in seed cages.

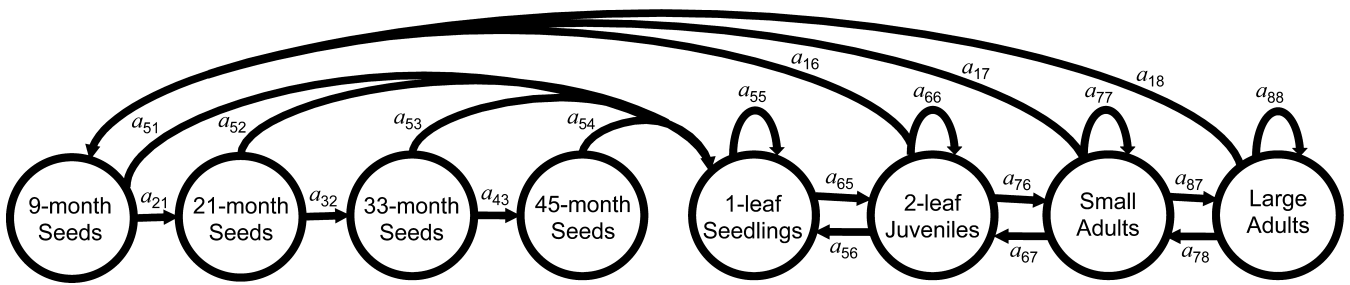


Figure 1. Life-cycle stages used for demographic modeling of ginseng populations. The seed bank is divided into 4 age-based stages (9-, 21-, 33-, and 45-month-old seeds), and the plant population is categorized by size-based metrics (1-leaf, 2-leaf, small-adult, and large-adult plants). Arrows and  $a_{ij}$  elements, which represent the number of individuals of size  $i$  (at time  $t+1$ ) per individual size  $j$  (at time  $t$ ), indicate possible transitions for individuals within ginseng populations.

Stage 5 consisted of 1 leaf seedlings. Probabilities of germination (i.e., the transition to stage 5 for stages 1 through 4;  $a_{5j}$ , where  $j = 1, 2, 3, 4$ ) were calculated as

$$a_{5j} = \frac{G_i}{S_j}, \tag{2}$$

where  $G$  is the mean number of germinants. Death of seeds was inferred as the proportion that did not either survive or germinate. In this species, germination does not occur in the first spring, so there is no direct adult to seedling transition; all recruits come from the seed class.

We established the postgermination life-cycle stages to divide the population into groups with similar survival and reproduction rates and to keep parameter-estimation error low. We delineated the first 2 stages on the basis of the number of leaves (1-leaf seedlings, stage 5, and 2-leaf juveniles, stage 6). Using analysis of covariance (ANCOVA), we found that after plants reached the adult size (3 or 4 leaves), the leaf area explained more variation in seed production than the number of leaves. Therefore, we created 2 equal-size groups that we based on the median adult leaf area of the population: small adults (stage 7) and large adults (stage 8). Possible transitions among stages 5–8 for above ground plants included stasis ( $a_{ij}$  where  $i = j$ ), shrinkage ( $a_{ij}$  where  $i < j$ ), or growth ( $a_{ij}$  where  $i > j$ ). We calculated these stage transitions as the proportion of individuals in stage  $j$  that transitioned to stage  $i$  the following year. In the case of plants that were absent at the spring census (e.g., due to browse, damage, or death), the absent individual was assigned to its stage prior to disappearance. Because long-term vegetative dormancy was rare, undetected plants were retroactively assigned to stage 9 (dead) if no aboveground parts were observed for 2 consecutive years.

Fertilities, the mean contribution per plant stages 6, 7, and 8 to stage 1 seeds ( $a_{1j}$ , where  $j = 6, 7, 8$ ), were calculated as follows:

$$a_{1j} = v \frac{\sum S_j}{n_j}, \tag{3}$$

where  $\sum S_j$  is the number of seeds produced by each individual in stage  $j$  summed over all individuals in the stage, and  $n_j$  is the total number of individuals in stage  $j$  ( $j = 6, 7, 8$ ). The constant  $v$  equals 0.94 and is the proportion of seeds remaining viable from the time of dispersal to the next census (9 months). This constant was derived from a replicated seed-cage study that showed no statistically significant variation among sites in initial 9-month seed survival (McGraw & Furedi 2005). The finite rate of increase of each population for each transition year was determined by calculating the dominant eigenvalue of the transition matrix (**A**) (Caswell 2001). Standard errors were calculated with a jackknife procedure (Supporting Information).

Over 12 years, 4 extreme, stochastic events dramatically affected ginseng population dynamics: a canopy defoliation due to an outbreak of a tent caterpillar, a major canopy loss following a storm, an outbreak of an unknown herbivore that nearly defoliated one population ( $n \approx 400$ ), and an outbreak of a seed predator that rendered ginseng seeds uncountable. We excluded the 4 years in which these events occurred a priori from our analyses. In addition, due to the delayed determination of fates of absent plants, the last census transition (2009–2010) was excluded. A total of 60 transition years was used in analyses.

Daily maximum temperature explains more variation in population growth rate ( $\lambda$ ) for ginseng than minimum or mean temperature; therefore, we used only maximum temperature in our analyses (K.R. Hunter-Cevera, S.S. and J.B.M., unpublished data). We calculated total precipitation at each site over the growing season (15 April–30 September) in each year by summing daily precipitation measurements from 10 climate stations located within 50 km of each population (for 2 pairs of populations, 1 of the 10 stations was the same). To measure site-specific temperatures, we deployed a HOBO pendant data logger (Onset Computer Corporation, Bourne, MA, USA) that recorded hourly temperature at each site in 2007. We created an equation to adjust climate-station

temperature data to reflect site-specific temperatures by regressing at least 1 year (in most cases 2 of daily maximum growing-season temperatures derived from HOBO data loggers on corresponding daily temperature data obtained from the 10 local climate stations (Supporting Information). In this regression, Tukey biweight was used to give outliers, principally caused by sunfleck effects on HOBO data, less weight (Motulsky & Christopolous 2004). Using data adjusted to reflect site-specific temperatures, we calculated the mean maximum growing-season temperature for each population.

### Analyses

To examine range-wide relations between ginseng demography and climatic variables, we calculated  $\lambda$  values for each set of transition years for each population ( $n = 60$  matrices). We then pooled  $\lambda$  values across populations and regressed  $\lambda$  on mean maximum growing-season temperature ( $T$ ) and on total growing season precipitation ( $P$ ). Although multiple  $\lambda$  estimates for each population were incorporated into these analyses, we treated each observation of  $\lambda$  as independent due to lack of among-population differences in mean  $\lambda$  values and absence of temporal covariation of  $\lambda$  within populations.

To compare ginseng response to climatic variables among sites with different mean climates, annual growing-season temperature and total growing-season precipitation were expressed in terms of deviation from site-specific means. Annual deviations from the mean for temperature ( $T_{SD}$ ) and precipitation ( $P_{SD}$ ) were expressed, respectively, in units of SD as

$$T_{SD} = \frac{T_i - \bar{T}}{SD}, \quad (4)$$

where  $T_i$  is the observed mean growing season temperature in a given study year at each site,  $\bar{T}$  is the mean temperature across study years at a site, SD is the standard deviation of annual temperatures from the mean temperature at each site and

$$P_{SD} = \frac{P_i - \bar{P}}{SD}, \quad (5)$$

where  $P_i$  is the observed total precipitation in a given growing season at each site,  $\bar{P}$  is the mean precipitation across study years at a site, and SD is the standard deviation of annual precipitation from the mean precipitation at each site. We regressed  $\lambda$  on  $T_{SD}$  and  $P_{SD}$ .

For each climatic variable, we tested 4 competing statistical models. These 4 models included linear and quadratic models of each climatic variable expressed first in standard units and second in terms of SD. To objectively select the model that best fit our data while accounting for disparity in the number of parameters for linear versus second-order polynomial models, we calculated the Akaike information criterion (AIC) (Akaike

1974; Anderson et al. 2000) for each model for each climatic variable separately

$$AIC = n \cdot \log_e(\hat{\sigma}^2) + 2K, \quad (6)$$

where  $n$  is the sample size,  $\hat{\sigma}^2$  is the residual sum of squares given by the regression model divided by  $n$ , and  $K$  is the number of parameters in the model. Weight of support for each model ( $w_i$ ) was calculated as

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{i=1}^R \exp\left(-\frac{1}{2}\Delta_i\right)}, \quad (7)$$

for  $i = 1, 2, \dots, R$  models, where  $\Delta_i = AIC_i - AIC_{\min}$ .

The mean population-level thermal niche across ginseng populations was defined as the number of SDs from the mean temperature at which  $\lambda \geq 1$ . We calculated this range with the second-order polynomial fit to the regression of  $\lambda$  on  $T_{SD}$ . We used a mean SD among all populations, weighted by the number of annual temperature observations, to express SD in terms of temperature.

Although the sample of years and populations was limiting for models with a greater number of effects, we explored whether the effects of temperature on  $\lambda$  depended on precipitation and whether the results from single climate-variable models were consistent with results of models that considered both temperature and precipitation. We created a second-degree polynomial response surface with  $T$  and  $P$  as explanatory variables (model =  $T, P, T^2, P^2, T^*P$ ) for the dependent variable  $\lambda$ . We repeated this procedure with  $T_{SD}$  and  $P_{SD}$ .

To calculate climatic optima for each population, we determined the relation between  $\lambda$  and climate at the population level. We did not want to assume a particular shape of the response of  $\lambda$  to model parameters. Therefore, we used 3 ANCOVA models to test for a population\* $T$  or a population\* $T^2$  interaction (SAS 2009). Effects in the 3 statistical models were (1) population,  $T$ , and population\* $T$ , (2) population,  $T$ , population\* $T$ , and  $T^2$ , and (3) population,  $T$ , population\* $T$ ,  $T^2$ , and population\* $T^2$ . The same 3 models were evaluated with precipitation instead of temperature. The model with the highest adjusted  $r^2$  was selected as the model that best explained variation in  $\lambda$  (Gotelli & Ellison 2004) and was used to calculate population  $T$  and  $P$  optima.

When the model fit curves with optima (not minima), we calculated the temperature or precipitation corresponding to the optima by setting  $\frac{\partial y}{\partial x}$  equal to zero and solving for  $x$ . We then regressed these optimum values on the 30-year (1971–2000) means for each climatic variable obtained from the adjusted climate station data. These 30 years corresponded roughly to the time when adult reproductive plants within the censused populations were established (Mooney & McGraw 2009). We performed a  $t$  test to determine whether the slope of the regression

of temperature optima on long-term temperature means differed from one. To determine whether the population temperature optima differed from 30-year mean temperatures or instead tracked current temperature means, we tested pairwise differences between temperature optima, mean maximum temperature during the study period, and 30-year mean temperature with 2 way analysis of variance without replication.

## Results

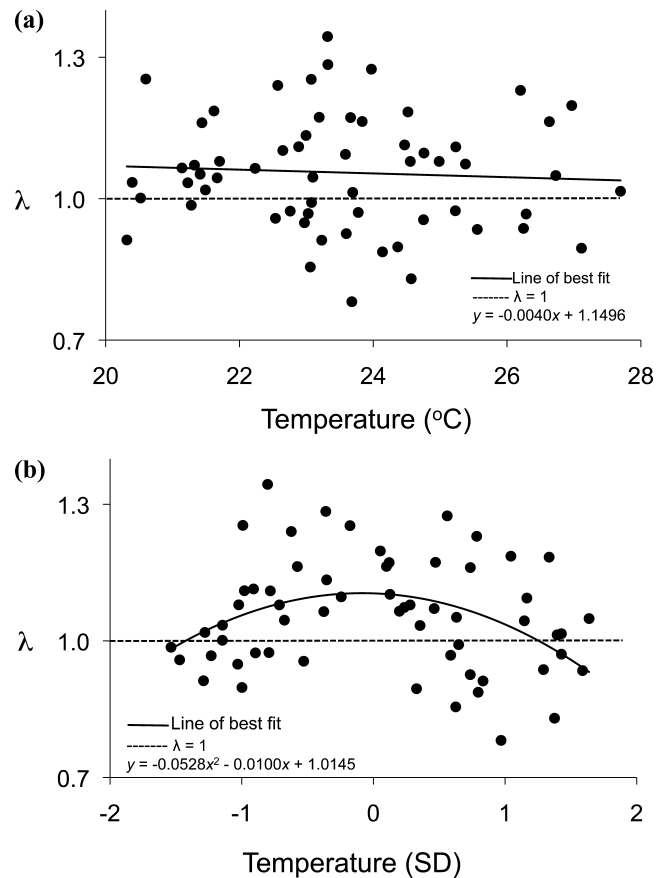
### Range-Wide Relation to Temperature and Precipitation

A range-wide relation of  $\lambda$  values across all populations of ginseng to temperature expressed in degrees Celsius would be consistent with a uniform thermal niche. However, variation in  $\lambda$  was not explained by mean maximum growing-season temperature ( $T$ ) when either a linear model ( $p = 0.65$ ,  $r^2 < 0.01$ ; Fig. 2a) or a second-order polynomial model ( $p = 0.87$ ,  $r^2 < 0.01$ ) was fit to the data. When temperature was expressed in terms of SD from mean  $T$  ( $T_{SD}$ ), there was no linear relation ( $p = 0.35$ ,  $r^2 = 0.02$ ). However, consistent with expectations of local climatic adaptation, a second-order polynomial model explained a significant amount of variation in  $\lambda$  ( $p < 0.01$ ,  $r^2 = 0.14$ ; Fig. 2b). The polynomial response was convex, such that temperatures that were either higher or lower than the mean reduced  $\lambda$ .

The response of  $\lambda$  to precipitation contrasted with the response to temperature. When  $\lambda$  was regressed on total growing-season precipitation ( $P$ ) across all populations, a linear model again did not explain significant variation in  $\lambda$  ( $p = 0.12$ ,  $r^2 = 0.04$ ); however, a second-order polynomial fit explained significant variation in  $\lambda$  ( $p < 0.05$ ,  $r^2 = 0.11$ ; Fig. 3a). When  $P$  was expressed in terms of SD from the mean ( $P_{SD}$ ), neither a linear model ( $p = 0.20$ ,  $r^2 = 0.03$ ; Fig. 3b) nor a second-order polynomial ( $p = 0.38$ ,  $r^2 = 0.04$ ) explained a statistically significant amount of the variation in  $\lambda$ .

Comparing among single climate-variable regression models with temperature ( $T$  and  $T_{SD}$ ) as the explanatory variable, the weight of support ( $w_i$ ) for the second-order polynomial model of  $T_{SD}$  was 0.90 (Table 1). Weight of support for a polynomial fit of  $P$  was 0.64 (Table 1). An estimate of the thermal niche breadth of the average ginseng population can be derived from the regression of  $\lambda$  on temperature expressed in SD and is defined as range of  $T_{SD}$  for which  $\lambda \geq 1$ . For these populations, the mean, population-level thermal niche breadth was approximately 1.62 °C.

For tests that incorporated both climatic variables as explanatory variables, when  $T$  and  $P$  were not expressed in units of variance,  $P$  explained a significant portion of the variation in  $\lambda$  ( $p < 0.05$ ,  $r^2 = 0.07$ ). However, when climatic variables were expressed in terms of deviation

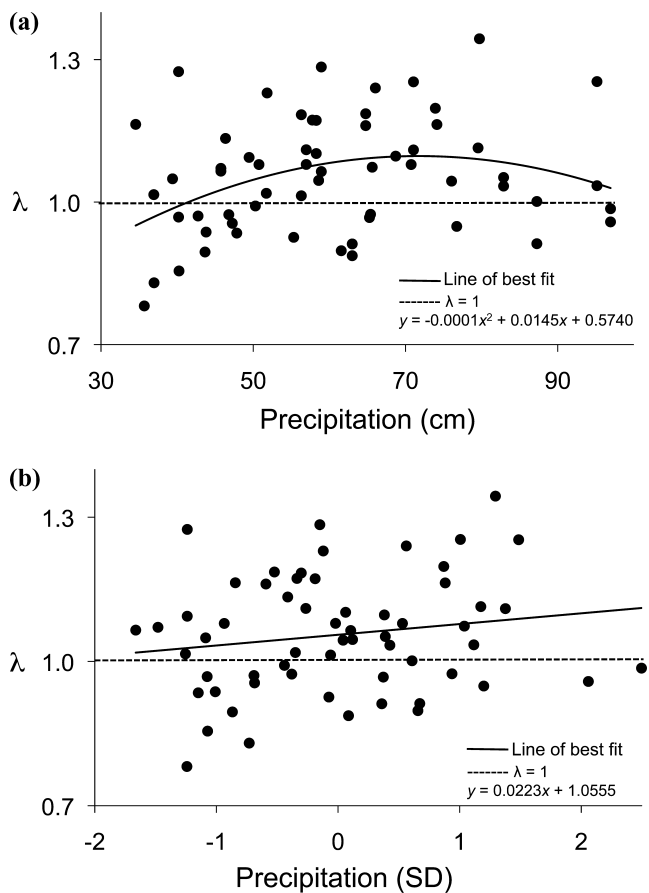


**Figure 2.** Response of population growth rate ( $\lambda$ ) to (a) mean maximum growing-season temperature and to (b) mean maximum growing-season temperature expressed in terms of deviation (SD) from site-specific means. Among all temperature models, (b) a polynomial fit of  $\lambda$  regressed on temperature expressed in SD was the best supported model ( $w_i = 0.90$ ,  $p < 0.01$ ,  $r^2 = 0.14$ ).

from the mean,  $T_{SD}$  explained significant variation in  $\lambda$  ( $p < 0.05$ ,  $r^2 = 0.06$ ). The effect of  $T$  on  $\lambda$  did not depend on  $P$  in either case ( $p = 0.47$ ,  $r^2 < 0.01$ ;  $p = 0.92$ ,  $r^2 < 0.01$ ; respectively).

### Climatic Optima versus Local Climate

We evaluated 3 statistical models per climatic variable to produce the equations to calculate climatic optima. For temperature, the model that best described the data contained all first- and second-order terms, but did not include the population\* $T^2$  interaction (adjusted  $r^2 = 0.29$ ,  $r^2 = 0.58$ ,  $F = 2.02$ ,  $p < 0.05$ ). This model showed that the effect of temperature on  $\lambda$  varied among populations and produced a series of convex polynomial fits (Fig. 4a). For precipitation the complete model, including all first- and second-order terms and the population\* $T^2$  interaction, produced the best fit (adjusted  $r^2 = 0.36$ ,



**Figure 3.** Response of population growth rate ( $\lambda$ ) to (a) total growing-season precipitation and to (b) total growing-season precipitation expressed in terms of deviation (SD) from site-specific means. Among all precipitation models, (a) a polynomial fit of  $\lambda$  regressed on precipitation (cm), was the best-supported model ( $w_i = 0.64$ ,  $p < 0.05$ ,  $r^2 = 0.11$ ).

$r^2 = 0.74$ ,  $F = 1.93$ ,  $p < 0.05$ ). In this analysis, the effect of precipitation on  $\lambda$  also depended on population. However, the polynomial fits were highly variable, and although most were convex, a few were concave

(Fig. 4b). The overall shape of the relations did not conform to one of local adaptation.

Contrary to expectations of a range-wide temperature optimum, response-curve optima did not converge to a single value when the temperature optima of the populations were regressed on the 30-year mean maximum temperature ( $T_{30}$ ). Instead, there was a direct linear relation between temperature optima and  $T_{30}$ , with  $T_{30}$  explaining a large and statistically significant portion of the variation in temperature optima ( $F = 96.68$ ,  $p < 0.001$ ,  $r^2 = 0.91$ ) (Fig. 5a). Temperature optima fell between  $T_{30}$  and mean temperatures during the study period, but did not differ significantly from either ( $F = 0.24$ ,  $p = 0.63$ ;  $F = 1.77$ ,  $p = 0.21$ ; respectively) (Fig. 6). In contrast to the results for temperature, the 30-year mean total growing season precipitation ( $P_{30}$ ) did not explain a statistically significant portion of variation in precipitation optima ( $F = 2.58$ ,  $p = 0.16$ ,  $r^2 = 0.30$ ) (Fig. 5b).

## Discussion

Results were consistent with expectations of adaptation to local temperature regimes in the form of a convex response curve when  $\lambda$  was regressed on temperature expressed in terms of SD from local means. Deviation from site-specific mean temperatures in either direction reduced  $\lambda$ . These results were observed despite the numerous other biotic and abiotic factors that affect ginseng population growth (McGraw & Furedi 2005; Van der Voort & McGraw 2006; Souther & McGraw 2011). Additionally, there was a direct linear relation between each population's local temperature regime and the temperature at which population growth rate was optimized, indicating specialization of populations to local temperatures. There was little evidence to suggest local adaptation to precipitation. In contrast, a range-wide, parabolic relation of  $\lambda$  regressed on precipitation indicates precipitation may constrain the overall distribution of ginseng.

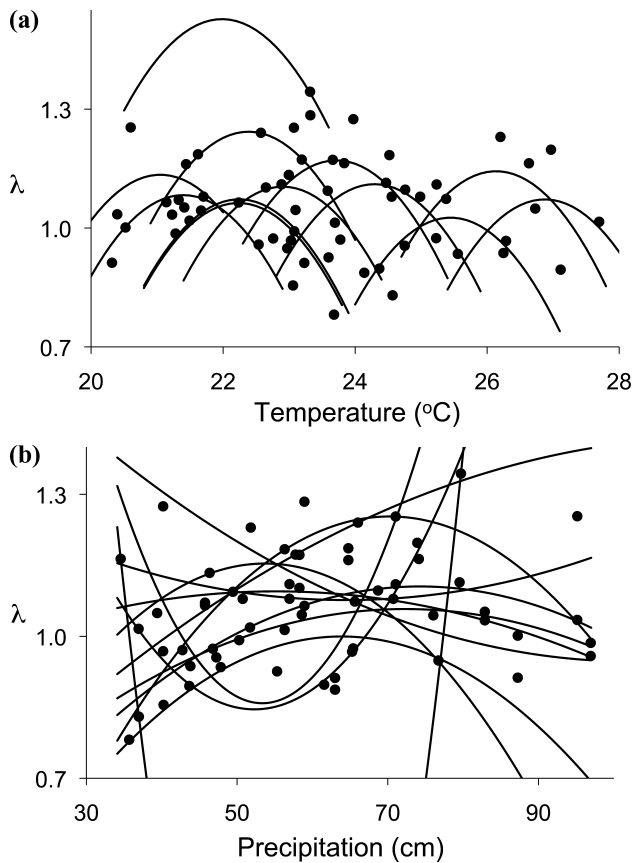
**Table 1.** Weight of support ( $w_i$ ) for competing statistical models of ginseng population growth rate ( $\lambda$ ) regressed on temperature or precipitation expressed in standard units or in terms of SD for linear and second-order polynomial fits.

| Variable                      | Model      | AIC <sup>a</sup> | D <sub>AIC</sub> <sup>b</sup> | Likelihood | w <sub>i</sub> |
|-------------------------------|------------|------------------|-------------------------------|------------|----------------|
| Temperature                   | Linear     | -247.46          | 6.49                          | 0.04       | 0.04           |
|                               | Polynomial | -245.49          | 8.46                          | 0.01       | 0.01           |
| Temperature SD <sup>c</sup>   | Linear     | -248.17          | 5.78                          | 0.06       | 0.05           |
|                               | Polynomial | -253.95          | 0.00                          | 1.00       | 0.90           |
| Precipitation                 | Linear     | -249.73          | 2.55                          | 0.28       | 0.18           |
|                               | Polynomial | -252.28          | 0.00                          | 1.00       | 0.64           |
| Precipitation SD <sup>c</sup> | Linear     | -248.96          | 3.32                          | 0.19       | 0.12           |
|                               | Polynomial | -247.79          | 4.49                          | 0.11       | 0.07           |

<sup>a</sup>Akaike information criterion. Lowest AIC values correspond to the model with best fit.

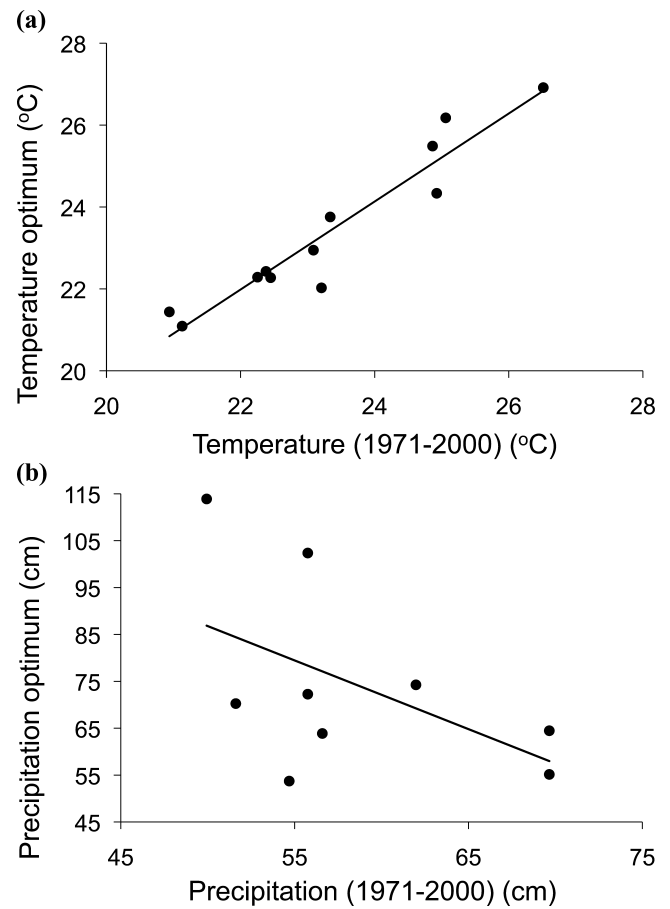
<sup>b</sup>Difference in AIC value from the best model.

<sup>c</sup>Expressed in terms of SD from the mean.



**Figure 4.** Response of population growth rate ( $\lambda$ ) to annual variation in (a) temperature and (b) precipitation by population. Curves were derived from the statistical model that best described the response of  $\lambda$  to temperature by population. Several populations were censused just 4 years; hence, the actual temperature variation over the study period was insufficient to define the shape of the temperature response curves for all populations. For clearer visualization of response curves in (a), values corresponding to temperatures  $\pm 1.5^\circ\text{C}$  from each population's temperature optimum are plotted.

Experimental tests of local climatic adaptation are necessary to establish definitively a genetic basis. However, 2 lines of evidence strongly suggest the observed response of  $\lambda$  to temperature variation has an underlying genetic component. First, ginseng plants are deciduous; thus, multiyear acclimation of the photosynthetically active plant parts is not possible. A long-term acclimation response would have to be explained by carryover effects from the previous year's temperature on the structure and physiology of the root and rhizome. If such long-term acclimation caused the observed response to temperature, we would expect that  $\lambda$  values would be temporally correlated, such that in 2 consecutive warm years, one would anticipate a higher population growth

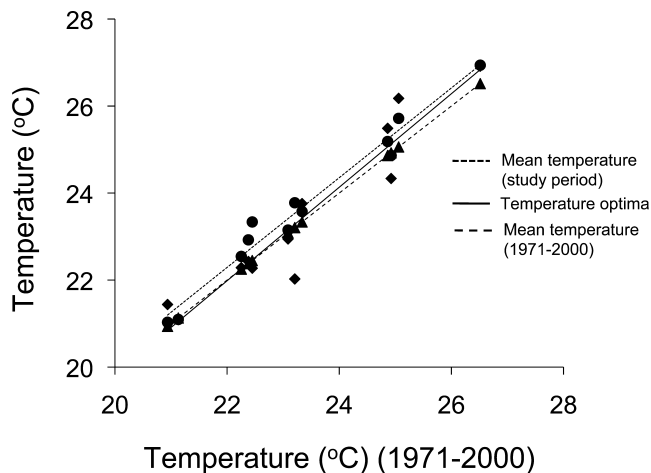


**Figure 5.** Linear regression of (a) site-specific temperature optima on 30-year mean maximum growing-season temperature and (b) precipitation optima on 30-year mean total precipitation. Only the model that included temperature as the independent variable explained a statistically significant proportion of the variation in  $y$  ( $p < 0.001$ ,  $r^2 = 0.91$ ). For this model, the slope of the line of best fit did not statistically differ from 1 ( $t = 0.68$ ,  $p = 0.51$ ).

rate in the second year. However, we detected no temporal correlation of  $\lambda$  values. Rather,  $\lambda$  appears to respond independently to each year's temperature. Although experimental manipulations of temperature could provide a stronger empirical test of local climatic adaptation, such studies have confounding variables. For example, growth chambers allow control of temperature but cannot replicate field conditions, and field manipulations of temperature are likely to confound effects such as precipitation alteration and herbivore exclusion.

For species composed of many locally adapted populations, the population-level thermal niche is narrow compared with the thermal niche defined by the spatial distribution of the species. Consequently, the increase in





**Figure 6.** The relation between mean temperature during the study period, site-specific temperature optima, and 30-year (1971–2000) mean temperatures at each site. Mean temperatures over the duration of the study were on average  $0.33\text{ }^{\circ}\text{C}$  higher than the 30-year mean maximum temperature ( $F = 15.40$ ,  $p < 0.01$ ). Temperature optima fell between mean temperatures during the study period and 30-year mean temperatures, but did not statistically differ from either ( $F = 1.77$ ,  $p = 0.21$ ;  $F = 0.24$ ,  $p = 0.63$ ; respectively).

temperature associated with a decrease in the probability of persistence of the species may be substantially smaller than would be predicted by models that define a species' thermal niche on the basis of its geographic range. For ginseng we estimated a mean niche breadth of approximately  $1.62\text{ }^{\circ}\text{C}$ . On average, a further mean temperature increase of approximately  $0.73\text{ }^{\circ}\text{C}$  would be necessary for  $\lambda$  values to decrease below replacement across all populations in ginseng's range. Projections of climate models estimate an increase in global temperature of  $1.1\text{--}6.4\text{ }^{\circ}\text{C}$  by 2100 (IPCC 2007). Therefore, projected increases in temperature exceed ginseng's population-level thermal niche. The difference in mean temperature across study sites is approximately  $5.9\text{ }^{\circ}\text{C}$ . Use of a climatic-envelope approach to model ginseng response to the climate change would erroneously predict the persistence or growth of ginseng populations at high latitudes and elevations in most scenarios.

In general, local adaptation of plants is expected (Linhart & Grant 1996; Kawecki & Ebert 2004; Savolainen et al. 2007). Climate change may have direct effects on demography of species with local climatic adaptations or indirect effects propagated across trophic levels. Local adaptation is promoted by low gene flow (Kawecki & Ebert 2004; Savolainen et al. 2007), which suggests that dispersal may be low within genetically differentiated populations. Habitat fragmentation may further preclude dispersal that enables persistence as climate changes.

When spatial response is not possible, the persistence of locally adapted populations will rely on rapid in situ adaptation to novel climatic conditions (Davis & Shaw 2001; Bradshaw & Holzapfel 2006) or possibly human-assisted relocation (Richardson et al. 2009).

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## Supporting Information

Mean transition probabilities for fertility and size-related matrix elements by population (Appendix S1), transition probabilities quantifying seed-bank dynamics (Appendix S2), annual  $\lambda$  values and associated standard errors by population (Appendix S3), and the regression of daily maximum temperature from a data logger on corresponding climate-station temperature data for one representative population (Appendix S4) are available online. The authors are responsible for the content and functionality of these materials. Queries (other than the absence of the material) should be directed to the corresponding author.

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