

traits considered here, the parent trees must be close to a random sample.

The main statistical consideration of the data resulting from these chemical analyses has been through standard analysis of variance for a set of diallel families. From this, and from further analysis based on parent/offspring regressions, the strongest feature to emerge has been the preponderance of highly significant additive control of all the traits measured. Evidence of non-additive variation was significant in three instances and was consistently so for α -pinene. In main stem oleoresin the proportion of additive variance for α -pinene was the lowest in a range of 13.8—23.4% whilst in branch apical shoot oleoresin it was highest in a range of 12.2—34.4%. This means that the presence of non-additive variation in some instances was not generally associated with a diminution of additive variation. Where significant non-additive variation was present, the ratio of additive to non-additive variance components varied from 1.4 to 3.9 whereas for the remainder of the terpenes considered it lay between 6.1 and 16.8.

It should be pointed out that, in the light of a critique by BIRKS and KANOWSKI (1988) of the methods of treatment of percentage data which are generally used in coniferous resin analysis, the numerical aspects of the present analysis should be viewed with caution. Nevertheless, we feel that our general conclusions are valid, particularly as a mere visual inspection of the raw percentage data suffices to demonstrate the close relationship between parental and progeny resin composition. Moreover, it is not apparent that any more rigorous means of treatment of such data is at present available.

This general evidence on the mechanism of control of inheritance of the monoterpene constituents of oleoresin in this species can provide the basis of any programme of selection in relation to these traits. Should it become necessary, through for example the establishment of any relationships between terpenes and traits of economic importance, to select for an increase or decrease in any one of the terpenes considered here, the fairly high levels of ad-

ditive variation found would ensure a good response to selection under any selection scheme designed to exploit such variation. In addition, there could be further gains from the incorporation of schemes to exploit the non-additive variation in those instances where it is present.

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Juvenile Performance in a Range-Wide Provenance Test of *Fraxinus pennsylvanica* Marsh.¹⁾

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Summary

Height growth, winter injury, and incidence of flowering through age six from seed are described for 60 provenances of *Fraxinus pennsylvanica* planted at ten locations in Iowa, Maine, Michigan, Nebraska, New Hampshire, New York, Pennsylvania, Vermont, and West Virginia.

With few exceptions, the tallest trees at age six originated in two areas: southern Ontario and a "central prairie" region extending from eastern Nebraska to central Illinois. There was no consistent growth advantage in trees originating south of planting sites, and near-local provenances were in general only marginally taller than plantation means.

Provenance \times plantation and provenance \times age interactions were largely attributable to the effects of differential winter injury on net height growth. A notable exception occurred in the Pennsylvania plantation, where provenance \times age interactions were caused by declining relative growth increments in southern provenances despite the absence of visible winter injury in the plantation over the period in question. Except at two plantations, 95 percent or more of all winter injury was confined to trees originating from latitudes at least 2° south of each respective planting site.

The "central prairie" and southern Ontario regions promise to be useful sources of fast-growing, winter-hardy trees for upland sites in the region represented by the test plantations. Several of the "central prairie" provenances had both generally fast growth and stable performance across all plantations that contained them. However, early sexual maturity could presage a decline in growth rate for these trees. A disproportionate number of trees from the "central prairie" region, and in fact from throughout the Great Plains, had begun flowering by age 6.

Key words: *Fraxinus pennsylvanica*, provenance test, height growth, winter injury, G \times E interaction.

Zusammenfassung

Für 60 Provenienzen von *Fraxinus pennsylvanica* auf 10 Standorten in Iowa, Maine, Michigan, Nebraska, New Hampshire, New York, Pennsylvania, Vermont und West Virginia werden Höhenwachstum, Winterschäden und das Auftreten von Blüten von der Aussaat bis zum Alter von sechs Jahren beschrieben.

Die im Alter von sechs Jahren höchsten Bäume stammten mit wenigen Ausnahmen aus Süd-Ontario und einer als

„Central Prairie“ bezeichneten Region zwischen Ost-Nebraska und Zentral-Illinois. Bäume südlicherer Herkunft hatten auf den Versuchsstandorten keinen deutlichen Wachstumsvorteil, und Provenienzen aus der Umgebung der Versuchsstandorte waren nur geringfügig größer als das Versuchsmittel.

Interaktionen zwischen Provenienzen und Versuchsorten sowie zwischen Provenienzen und Baumalter waren zum größten Teil erklärt durch den Einfluß der Winterschäden auf das Höhenwachstum. Eine bemerkenswerte Ausnahme zeigte sich auf der Versuchsfläche in Pennsylvania, auf der die Provenienz \times Alter-Interaktion verursacht wurde durch einen Zuwachsrückgang bei den südlichen Provenienzen, obwohl auf dieser Versuchsfläche während der Versuchsdauer keine erkennbaren Winterschäden auftraten.

Mit Ausnahme von zwei Versuchsflächen traten mindestens 95% aller Winterschäden bei Bäumen auf, deren Herkunft um mindestens zwei Breitengrade südlich von dem Versuchsstandort lag. „Central Prairie“ und das südliche Ontario sind vielversprechende Herkunftsgebiete für schnellwachsende und winterharte Bäume, anbaueeignet für Hochlagen in den Regionen, die durch die Versuchsflächen repräsentiert sind.

Einige Provenienzen aus der „Central Prairie“ waren sowohl generell schnellwüchsig als auch ökologisch stabil über alle Versuchsstandorte, auf denen sie vertreten waren. Der frühe Blühbeginn könnte jedoch ein Anzeichen für nachlassende Wuchsleistung bei diesen Bäumen sein. Eine unverhältnismäßig große Zahl von Bäumen aus dem Herkunftsgebiet „Central Prairie“ und sogar aus dem gesamten Gebiet der „Great Plains“ begann im Alter von sechs Jahren zu blühen.

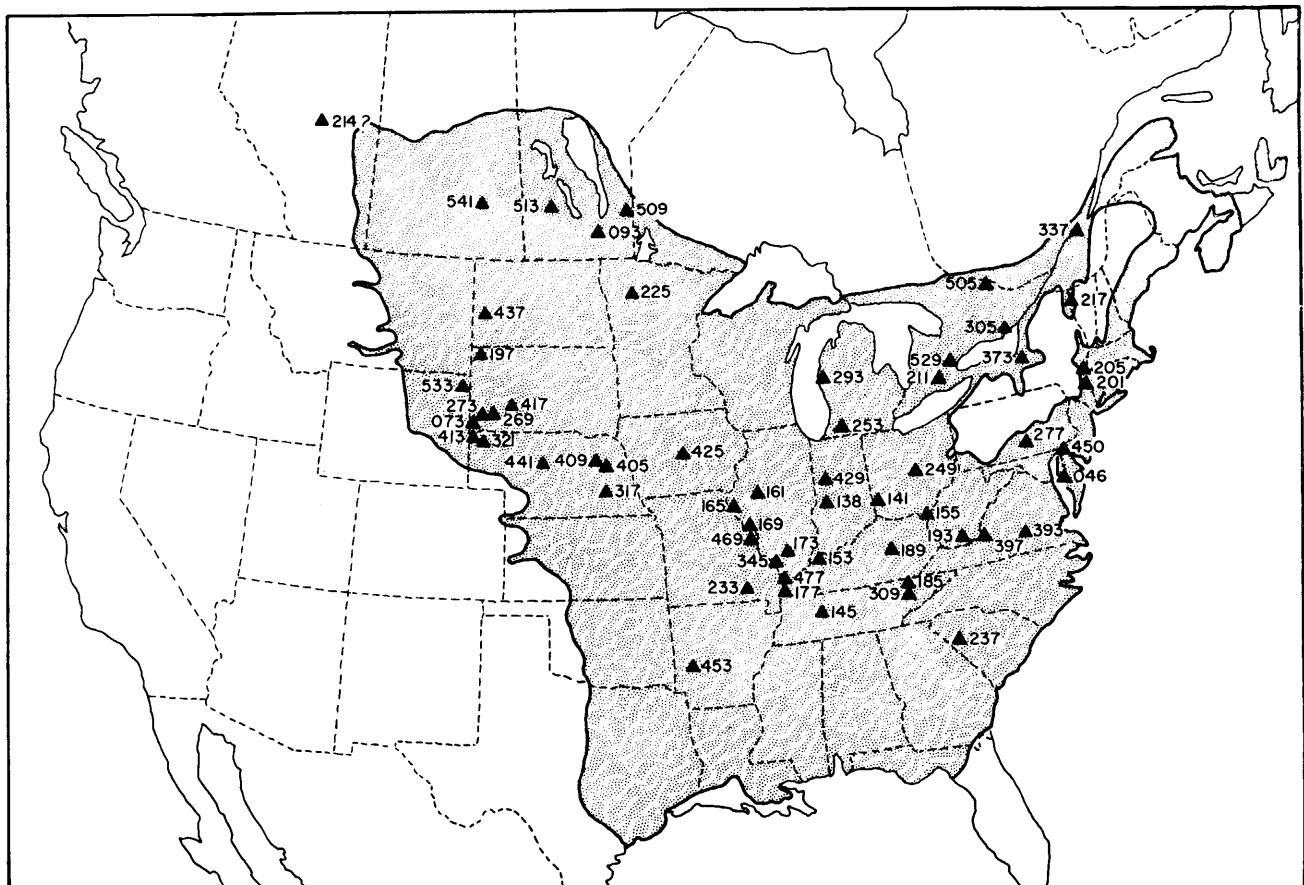


Figure 1. — Natural distribution of green ash and the geographic location of provenances represented in the study.

1. Introduction

Green ash (*Fraxinus pennsylvanica* MARSH.) occurs naturally over a large portion of North America (Figure 1) under nearly as wide a variety of environmental conditions as any native American tree species. Although the species typically grows on soils subject to occasional inundation, it appears as capable as the more mesophytic white ash (*Fraxinus americana* L.) of invading well-drained, upland fields (TAYLOR 1972). In the western portion of its range, green ash occurs near streams, but under conditions that are very droughty for most of the year. The ecological variability of green ash suggests considerable genetic variation and potential for improvement through selection.

The species is planted to a limited extent for timber, but widely for such purposes as shelterbelts, street and shade trees, and mine spoil reclamation. Even within its native range, green ash is used as an "exotic" in the sense that it is usually planted on sites to which it is not native. Thus, provenance testing is a useful approach to genetic improvement in the species (NIENSTÄEDT, 1979). Several studies have examined the performance of provenances from portions of the range (MEULI and SHIRLEY, 1937; SANTAMOUR, 1963; VAN DEUSEN and CUNNINGHAM, 1982; WRIGHT, 1944; YING and BAGLEY, 1976; YING *et al.*, 1974). In this paper we describe winter injury, flowering, and juvenile growth in ten plantations of a nearly range-wide provenance test of green ash.

2. Material and Methods

Seeds for this study were collected in the autumn of 1975 from two to four trees in each of 60 stand locations throughout the range of green ash (Figure 1). The seed parents at a location were separated from one another by a minimum distance of 90 m, but all grew within an arbitrarily defined area of no more than 26 km². Most parents were about average in growth rate and form compared to nearby trees. All parents were apparently native to their sites except those for three stands, which were probably of cultivated origin.

Seedlings from each provenance collection were grown in replicated arrangement in a Pennsylvania nursery and transplanted as 1:1 stock to ten experimental plantations in May 1978 (Table 1). Plantations follow randomized complete block designs with 15 to 60 provenances in each of 3 to 8 blocks, depending upon the plantation. Plots contain four trees except in two plantations in which they contain eight and 16 trees, respectively. Provenance origins, nursery practice, and plantations are described in more detail by STEINER (1983).

Table 1. — Composition and locations of experimental plantations examined in this study.

Plantation	Latitude	Longitude	Number of:	
			Blocks	Provenances
IA (Iowa)	41°55'	93°15'	3	38
ME (Maine)	44°18'	69°45'	4	32
MK (Michigan-Kellogg)	42°22'	85°21'	5	39
MR (Michigan-Russ)	42°06'	85°50'	5	39
NE (Nebraska)	40°30'	98°18'	4	18
NH (New Hampshire)	43°08'	70°56'	4	32
NY (New York)	41°46'	73°35'	3	17
PA (Pennsylvania)	40°48'	77°52'	8	60
VT (Vermont)	44°29'	73°12'	4	27
WV (West Virginia)	39°39'	79°48'	4	15

Survival by provenance was tallied at most plantations in most of the four years following planting. The most complete and informative set of survival data is that for age 6, after four growing seasons in the field. These data were recorded in late summer 1981 or spring 1982 at all plantations except Michigan-Russ.

Plot mean heights were measured at age 4 from seed at all plantations except Michigan-Kellogg and Michigan-Russ, and at age 6 at all plantations. Incidence of flowering was recorded for the Pennsylvania plantation at age 5, and for the Pennsylvania, Iowa, and Michigan-Russ plantation at age 6.

Stem dieback during the 1980–81 winter was measured in spring 1981 at all plantations except Nebraska and West Virginia. Data were recorded as the percentage of the 1980 (fifth-year) increment killed per tree in 20 percent classes (0 = none, 1 = 20 percent, . . . , 5 = 100 percent). This apparent cold injury always occurred with progressive severity from the apical bud downward, and it was nearly always confined to the 1980 growth increment.

For each plantation, an analysis of variance was performed on age 6 heights; and for each of the 8 plantations in which age 4 heights had been measured, an analysis of variance was performed using growth interval as a classification variable (*i.e.*, net increment in years 1 through 4 combined and net increment in years 5 and 6 combined). These analyses provided estimates of provenance and provenance × age interaction effects. An analysis of variance across all plantations was not made because of the very uneven representation of provenances at different plantations.

To examine provenance × plantation interaction effects we used WRICKE's "ecovalence" statistic as described by SHELBORNE (1972). Provenance mean heights at age 6 were standardized (by subtracting the plantation mean and dividing by the standard deviation of provenance means), and provenance contributions to provenance × plantation sum-of-squares were calculated as follows for every pair of plantations:

$$SS_i = \sum_{j=1}^2 (x_{ij} - \bar{x}_i)^2,$$

where x_{ij} is the mean of provenance "i" in plantation "j" and \bar{x}_i is the mean of provenance "i" across both plantations. This is identical to WRICKE's "ecovalence" formula, but simplified because plantation means using standardized data are 0. The use of standardized provenance means eliminates contributions to the interaction that are purely a function of scale as a result of provenances being more variable in some plantations than in others. It also enables the valid comparison of contributions for a given provenance across plantation-plantation combinations. A similar analysis was performed for age 4 heights *versus* combined fifth- and sixth-year height increments to further study the source of provenance × age interaction effects.

Examination of provenance differences in winter injury was made difficult by the uneven representation of provenances at the various plantations and by plantation differences in overall severity of injury. To obtain an approximate measure of provenance mean injury over all plantations, we calculated least-square provenance means from a general linear model ANOVA using "Type III" sums-of-squares (GLM Procedure, Statistical Analysis System, SAS Institute Inc., Cary, North Carolina). This procedure avoids confounding biases by fitting each effect in turn to the

residuals that are unexplained by all other effects in the model; the least-square means thus estimate what would have been the marginal means had the data set been balanced. Least-square means were calculated for only the 48 provenances of native origin represented in more than two plantations. The Pennsylvania and Michigan-Russ plantations were not included in this analysis because they sustained no injury. Also, as already mentioned, there were no winter injury data for Nebraska and West Virginia.

3. Results and Discussion

3.1. Survival

Overall plantation survival following the first growing season in the field (age 3) was high (91 to 99 percent) at all locations. Most mortality occurred gradually over subsequent years. By age 6, average survival varied from 71 percent at Nebraska to 97 percent at Maine and New Hampshire. All but three plantations (Nebraska, New York, and West Virginia) had an overall survival of about 90 percent or greater.

Provenance survival through age 6 varied from about 80 to 100 percent in most plantations. Only in the Iowa, Nebraska, and New York plantations did the range of percentages suggest real differences among provenances. Most provenances with high mortality in these plantations were native to locations that were considerably south of where the trees were planted (*e.g.*, 233, 185, 453, and 237, *Figure 1*). These probably succumbed to the effects of repeated cold injury. However, there is no obvious explanation for other instances of poor survival, such as several Canadian provenances in the Iowa and Nebraska plantations.

3.2. Winter Injury

Mean winter injury in the eight plantations measured in spring 1981 varied from zero at Pennsylvania and Michigan-Russ to 20–24 percent of the 1980 height increment at Iowa, Michigan-Kellogg, and New York. Plantation means were confounded to some extent according to which provenances they contained. Although we did not attempt to obtain unbiased estimates of plantation effects, there was no obvious relationship between overall plantation injury and geographic locations. In fact, the two Michigan plantations were among the most and least injured, respectively.

The lack of injury in the Pennsylvania and Michigan-Russ plantations was particularly striking in view of the fact that the Arkansas provenance (453), native 675 km or more to the south, sustained no injury in either plantation but 98–100 percent injury in all four of the other plantations where it was represented. These two plantations did not have exceptionally mild weather in the winter of 1980–81; indeed, minimum temperatures there were within 2° C of those at Iowa and Maine. We have no satisfactory explanation for the difference, except perhaps that the vigor of the trees at Michigan-Russ and Pennsylvania contributed to their hardiness. Those two plantations are the fastest growing.

Least-square mean winter injury differed greatly among provenances and generally increased as latitude of origin decreased (*Table 2*). Means ranged from 0 to 99 percent, but about half were less than 5 percent. Many Canadian provenances had no injury at any location, and all provenances from south of latitude 37° had 60 percent or more injury everywhere except Michigan-Russ and Pennsylvania. Regression of winter injury on a linear function of latitude

and normal mean minimum daily January temperature at provenance origins accounted for 78 percent of the variation among provenance means.

Although injury was greatest on southern provenances, many of the northern provenances sustained small amounts of apparent winter injury at one plantation or another. This was especially true at New York and Maine, where some provenances that were native north of the plantation sites had as much as 13 percent injury. The winter injury scores at Maine may have been confounded by injuries caused by the oviposition of tree crickets (*Oecanthus sp.*), which were present in the plantation in large numbers the previous summer.

At plantations other than Maine and New York, practically all injury was confined to provenances that were native south of the planting sites. Between 95 and 98 percent of the injury at Iowa, Michigan-Kellogg, New Hampshire, and Vermont occurred on provenances native at least 225 km (2° latitude) south of the plantations. In the Pennsylvania plantation, where record temperatures as low as –28° C have occurred since planting, winter injury in *all* years has been virtually confined to trees native more than 400 km to the south.

3.3. Height Growth

The ten plantations differed substantially in mean height at age 6 (*Table 2*). Growth of green ash is very sensitive to soil fertility (HANSEN and McCOMB, 1958), and good to excellent growth was achieved only at the exceptionally fertile Michigan-Russ location (the land had been used previously to grow soybeans). Differences in fertility and in weed control practices probably account for most of the differences among plantations. However, height growth in West Virginia was severely retarded by excessive deer browsing, and almost all trees in the Iowa plantation were killed to the ground by rodents in the first winter (they subsequently resprouted).

Provenance variation in net height growth was large: the tallest provenance was 1.5 (Michigan-Russ) to 4.3 (Vermont) times as tall as the shortest, depending upon the plantation. Provenance differences were statistically significant ($P < 0.001$) at all locations.

Relative performance of provenances tended to vary somewhat from plantation to plantation (*Table 2*), but several important generalizations about provenance performance apply to most or all locations. For convenience, provenances in *Table 2* are grouped into three regions: 1) Northeastern Region (northeastern U.S. and southeastern Canada), 2) Great Plains Region (former prairie regions of Canada and the Midwest), and 3) Southern Region (southern U.S. below approximately latitude 38°30'). Within regions, the provenances are arranged by increasing least-square mean winter injury.

Within the Great Plains Region, provenance mean heights tended to decrease with increasing latitude of origin. This pattern was evident in all plantations ($r = -0.46$ to -0.85), and it is attributable to the generally outstanding growth of the most southern provenances — those from eastern Nebraska to central Illinois (*Figure 1, Table 2*). We shall call this group the “central prairie” provenances in subsequent discussion. YING and BAGLEY (1976) observed a similar tendency, in several Midwest plantations, for southern provenances of this region to grow faster than northern provenances. Since Great Plains trees largely escaped winter injury at all locations, their growth

Table 2. — Least-square mean winter injury (percentage of fifth year height increment) and mean heights at age 6 in ten plantations (percentages of plantation means) for 48 provenances of green ash¹.

Provenance number	State or province ²	Winter injury	Relative height in plantation ² :									
			IA	ME	MK	MR	NE	NH	NY	PA	VT	WV
			<u>Northeastern Region</u>									
337	QUE	0	--	86	79	98	--	--	--	99	--	--
505	ONT	1	95	101	108	96	--	99	--	99	110	--
217	VT	1	--	--	--	--	--	106	103	85	103	107
253	MI	1	--	--	106	98	75	--	128	104	--	--
211	ONT	2	98	101	103	116	--	117	--	116	108	--
205	NY	3	--	--	98	98	--	124	119	91	--	127
305	ONT	5	129	112	122	116	77	99	121	97	122	141
529	ONT	5	--	--	127	102	--	94	--	105	123	--
293	MI	6	117	96	108	98	--	--	--	101	--	90
201	NY	8	--	99	96	95	--	--	110	91	82	--
249	OH	15	84	87	94	100	--	73	--	91	85	--
277	PA	23	--	--	--	--	92	--	111	107	--	156
429	IN	24	--	--	--	--	--	77	114	93	96	--
138	IN	27	81	95	95	115	--	--	--	96	105	--
			<u>Great Plains Region</u>									
513	MAN	0	--	86	106	86	89	84	--	87	--	64
509	MAN	0	114	102	118	86	--	--	--	88	--	--
533	WY	0	105	--	104	85	111	--	91	86	--	--
413	NE	0	110	110	120	95	110	--	--	103	--	--
093	MAN	0	91	--	96	86	--	95	--	92	--	85
273	SD	0	107	--	97	84	--	112	--	104	--	97
441	NE	1	121	109	--	--	111	109	112	90	--	--
321	NE	1	--	111	98	82	--	96	--	80	102	90
437	ND	2	106	--	94	85	96	--	90	79	--	--
425	IA	2	141	127	--	--	139	141	--	119	131	--
409	NE	2	146	121	131	102	126	120	--	109	--	--
073	SD	2	101	--	119	96	--	--	91	89	108	--
225	MN	3	110	87	--	--	--	96	105	86	109	--
405	NE	3	--	99	122	98	--	119	--	108	116	--
197	SD	3	106	106	117	79	--	--	--	90	--	89
469	MO	5	126	134	--	--	--	139	--	127	134	--
317	NE	5	122	106	112	101	111	123	--	93	123	--
269	SD	5	113	95	95	90	--	--	92	--	--	--
541	SAS	5	76	73	--	--	70	83	--	75	--	--
169	IL	11	116	110	129	120	--	--	--	123	121	--
165	IL	15	119	107	122	108	--	116	--	114	114	--
161	IL	17	--	--	117	117	116	144	107	125	--	100
			<u>Southern Region</u>									
193	WV	20	105	115	109	111	--	93	--	110	84	--
397	VA	48	84	--	78	97	--	--	--	82	--	--
189	KY	50	89	--	--	--	--	69	86	91	71	--
046	MD	51	--	--	123	120	--	--	--	124	--	--
309	TN	58	--	--	84	110	--	--	--	110	--	80
173	IL	65	70	123	--	--	--	--	--	118	93	--
345	IL	77	70	93	82	119	--	71	--	105	74	--
477	IL	86	62	--	62	112	--	--	--	110	59	89
145	TN	90	63	--	63	115	--	--	--	116	62	--
233	MO	92	54	--	50	105	78	70	58	108	--	--
177	MO	95	--	56	--	--	--	116	--	113	--	--
453	AR	99	61	--	39	93	87	--	40	94	31	--
\bar{x} (m) =			1.53	0.83	1.25	2.56	0.88	0.67	1.34	1.66	1.58	0.47
s_x =			0.18	0.09	0.16	0.18	0.09	0.05	0.12	0.10	0.13	0.05

¹) Cultivated sources and provenances represented in fewer than three plantations are not shown.

²) See Table 1 for explanation of plantation and some state abbreviations. Also: AR = Arkansas, IL = Illinois, KY = Kentucky, MAN = Manitoba, MD = Maryland, MI = Michigan, MN = Minnesota, MO = Missouri, ND = North Dakota, OH = Ohio, ONT = Ontario, QUE = Quebec, SAS = Saskatchewan, SD = South Dakota, TN = Tennessee, VA = Virginia, WY = Wyoming.

rates are not appreciably confounded by differences in cold hardiness.

A similar latitudinal pattern of variation did not occur in the Northeastern or Southern Regions, where if anything there was a tendency for provenance mean heights to increase with latitude of origin. For the Southern Region this

result was undoubtedly caused by differences in cold hardiness: the more northern provenances in the region sustained less winter injury and consequently exhibited larger net increments in height growth. In general, provenances from the Southern Region were above-average in height only at Pennsylvania and Michigan-Russ, where winter injury was minimal.

The Northeastern Region appeared to contain two groups of provenances with regard to height growth. Southern Ontario provenances were usually above-average, and northeastern U.S. provenances were usually below-average. The mean for all northeastern U.S. provenances was equal to or less than the plantation mean everywhere except New York and West Virginia, both of which happened to contain almost none of the provenances that excelled at other locations.

Winter injury does not account for the generally below-average performance of northeastern U.S. provenances. They had modest height growth even where they were not injured, and "central prairie" provenances with similar amounts of injury were almost invariably taller. This mediocrity in height growth of northeastern U.S. provenances, compared to Great Plains stock, shows also in SANTAMOUR'S (1963) data from a 13-year-old progeny test of green ash planted in Massachusetts.

The general features of variation in height as outlined above are further illustrated by examining the origins of the tallest 10 percent of the provenances at each plantation. These are tabulated below with "X" designating the tallest provenances at each location and "-" indicating provenances represented at a plantation but not among the tallest. Cultivated sources are ignored.

	IA	ME	MK	MR	NE	NH	NY	PA	VT	WV
Northeastern Region										
305 (ONT)	X	-	-	-	-	-	X	-	-	X
529 (ONT)			X	-	-	-	-	-	X	
253 (MI)			-	-	-		X	-		
277 (PA)							-	-		X
Great Plains Region										
409 (NE)	X	-	X	-	X	-		-		
317 (NE)	-	-	-	-	-	-		-	X	
425 (IA)	X	X			X	X		X	X	
161 (IL)			-	X	-	X	-	X		-
169 (IL)	-	-	X	X				X		-
469 (MO)	X	X				X		X	X	
Southern Region										
046 (MD)			X	X				X		
173 (IL)	-	X						-	-	
345 (IL)	-	-	-	X				-	-	

If provenance 173 and 345 (*Figure 1*) are grouped with the geographically contiguous "central prairie" provenances, this group plus southern Ontario accounts for 28 of the 33 entries. One or another of the "central prairie" provenances (especially 409, 425, and 469) was the tallest provenance at every location except New York and West Virginia, where they were not well represented. Maryland provenance 046 accounts for three of the remaining five entries. Its performance appears geographically anomalous compared to others in the mid-Atlantic region, but our collection records suggest that the parents may have been of planted origin.

In this study there was no consistent growth advantage in provenances from some distance south of the planting site, a tendency that has often occurred in provenance studies of other species in North America (WRIGHT, 1976). There was also no obvious height growth superiority in "local" provenances. Five plantations contained progenies from nearby stands. These "local" provenances always performed above-average, but only provenance 425 (Iowa) planted in the Iowa plantation was clearly superior, and it grew very well in all plantations where it was represented, as the above tabulation shows. The others grew only 3 to 10

percent faster than the respective plantation means, and "central prairie" provenances almost always grew faster.

3.4. Provenance \times Plantation Interactions in Height Growth

Provenance \times plantation interactions may be examined by reference to *Figure 2*, which graphically depicts contributions to provenance \times plantation interaction sums-of-squares for every plantation-plantation combination. Provenances are ordered from top to bottom in *Figure 2* in order of increasing least-square mean winter injury. Contributions are plotted for provenances common to all 45 possible pairs of the 10 plantations, but for simplicity we have provided plantation labels for only those contributions larger than the arbitrary figure of 1.30.

Most of the larger interactions involved Pennsylvania or Michigan-Russ and one or another of the remaining plantations, and they appear related to the lack of winter injury at those two locations. Provenances in the upper 60 percent of *Figure 2* (mean winter injury less than 10 percent) tended to be relatively taller at plantations *other* than Pennsylvania and Michigan-Russ, *i. e.*, locations where their cold hardiness gave them a relative height advantage over injured trees. Provenances in the lower portion of *Figure 2* tended to be relatively taller at Pennsylvania and Michigan-Russ, where the lack of injury permitted more southern provenances to perform better than elsewhere. This comparison alone accounts for 65 percent of all interaction sums-of-squares depicted in *Figure 2*.

One other comparison also explains an appreciable portion of the total interaction sum-of-squares. Provenances of the Northeastern Region generally were relatively shorter in Nebraska (the westernmost plantation) and relatively taller in New York and West Virginia than they were in other plantations. Instances where this was true account for 10 percent of the interaction sums-of-squares in addition to the 65 percent mentioned above. Thus, one can say that 75 percent of the inconsistency in provenance performance between plantations can be described with just two comparisons.

Several provenances (considering only those planted at more than half of the plantations) were notably stable in performance across locations (*Table 2*). Some of these were consistently average or below in height (*e. g.*, 093, 249, 513), and others were consistently superior. The latter group is composed of 165, 169, 409, and 425, all "central prairie" sources.

3.5. Provenance \times Year Interactions in Height Growth

Provenance \times age interactions were significant ($P < 0.05$) at seven of the eight plantations for which age 4 data were available, the exception being Maine. Provenance main effects were significant ($P < 0.05$) at only four plantations: Pennsylvania, Vermont, New York, and Maine.

To discover the sources of provenance \times age interactions, we examined individual provenance contributions to the interaction sum-of-squares at each plantation. Winter injury appeared to account for the major inconsistencies, as it did for provenance \times plantation interactions. In every plantation but one, the interaction variance component would have been nil without the large contributions to interaction sum-of-squares by several southern provenances that declined in relative net height increment in years 5 and 6.

The only exception was the Nebraska plantation, where provenance \times age interaction was caused primarily by a relative gain in fifth- and sixth-year increments on the

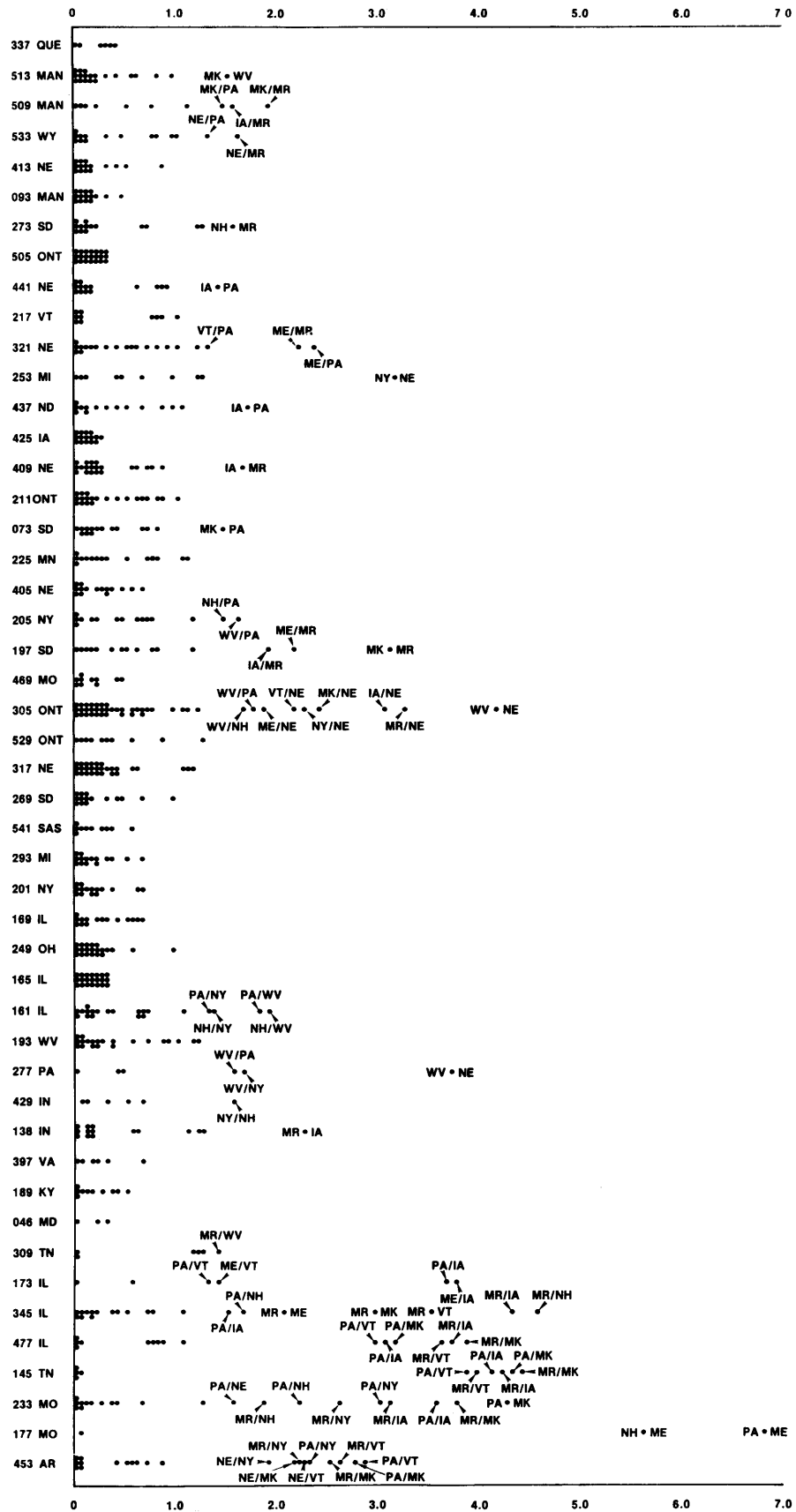


Figure 2. — Provenance contributions to provenance × plantation interaction sums-of-squares for age 6 height in paired plantation comparisons. Contributions larger than 1.3 are labelled by plantation-plantation pair, the first-named being the one in which the provenance was relatively taller. Provenances are ranked from top to bottom in order of increasing 1980–1981 winter injury. See Tables 1 and 2 for explanation of abbreviations. Data for cultivated sources and provenances represented in fewer than three plantations are not shown.

part of two very southern provenances (237 and 453). Injury occurred in Nebraska in the winter of 1978–79, prior to age 4 measurements, but injury was negligible in that plantation in the two subsequent years.

It is rather surprising that in Pennsylvania the same trend was evident as in other plantations with regard to declining height increments of southern trees. The pattern is quite consistent: 84 percent of the interaction sum-of-squares in that plantation is explained by the fact that provenances native south of the plantation site decreased in growth rate relative to other provenances in their fifth and sixth growing seasons. We have no good explanation for this result since this plantation suffered no visible winter injury during those years (some minor injury occurred prior to age 3). Perhaps injury had indeed occurred but without visible shoot dieback.

3.6. Flowering

The first flowering in the Pennsylvania plantation was observed at age 5 when 15 male trees and one female tree bore flowers. Although the total number of flowering trees amounted to less than one percent of the plantation, they were distributed among 10 of the 60 provenances. The same provenances plus 11 others flowered in Pennsylvania at age 6, in the spring of 1982. In the same spring, provenances with flowers were tallied also in the Iowa and Michigan-Russ plantations.

Trees that had begun flowering by age 6 represented 85 percent of the Great Plains Region provenances, 33 percent of the Northeastern provenances, and 6 percent of the Southern provenances. The only provenances flowering in all three plantations were from the Great Plains Region, and 27 percent of them were doing so. Thus, these trees were especially precocious at all three widely separated locations. There was no clear relationship between provenance flowering and provenance mean height: some of those flowering were relatively short (e. g., 269, 453, and 513) and some were relatively tall (e. g., 409, 425, and 469). Some relatively tall provenances had not begun flowering (e. g., 046, 161, and 305).

Green ash flowers are borne in axillary inflorescences, so precocious flowering should have no appreciable effect on form. However, early and abundant flowering can conceivably affect growth rates. Since most of the tallest provenances in this study come from the Great Plains and most have begun to flower, further changes in relative growth rates could occur over the next few years.

4. Conclusions

The fastest growing provenances in the five tallest plantations exhibited average annual height increments of 0.4 to 0.7 m. CLAUSEN (1979) predicted that annual increments of 1 to 2 m are possible for genetically superior green ash on excellent sites with optimum culture. Most of the plantation sites in our study are not excellent for green ash, but they are probably typical of the conditions under which most green ash in the Northeastern U.S. and Midwest is planted.

In the plantations that had winter injury in 1981, the injury amounted to a fairly uniform 14 to 24 percent of the total plantation growth increments for the previous year and showed no apparent relationship with plantation locations. Winter injury was a significant factor in net height

growth at most plantations. It may have been responsible for some instances of low provenance survival in plantations, and it accounted in large measure for provenance \times plantation and provenance \times age interactions in height. In general, winter injury was confined to provenances native more than 2° latitude south of a planting site.

Provenances from immediately south of a planting site were not necessarily the fastest growing or even above average. The tallest provenances usually originated in the relatively small "central prairie" region of the Great Plains extending from eastern Nebraska to central Illinois. Other provenances that exhibited good growth in most plantations originated in southern Ontario.

For white ash in the eastern U.S., CLAUSEN *et al.* (1981) found apparently clinal variation in growth, with the tallest provenances originating south of planting locations. Our results for growth of green ash suggest a racial pattern of variation that is more-or-less independent of latitude, particularly in the contrast between "central prairie" and Northeastern Region provenances. This contrast is strengthened by the generally earlier sexual maturity of "central prairie" and other Great Plains provenances compared to eastern provenances of similar latitudes. More intensive sampling of populations in Illinois and Indiana would probably have removed any apparent discontinuities in variation between "central prairie" and Northeastern Region provenances. However, "central prairie" provenances appear to have a combination of characteristics, perhaps including drought resistance (MEULI and SHIRLEY, 1937) as well as cold hardiness and general vigor, that resulted in a geographic pattern of height variation on these sites that conforms to no pattern known for any other North American species. On other sites, such as bottomlands in the South, a different pattern of variation would perhaps occur.

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