New Forests **25:** 211–225, 2003.
© 2003 *Kluwer Academic Publishers. Printed in the Netherlands.*

Walnut demonstrates strong genetic variability for adaptive and wood quality traits in a network of juvenile field tests across Europe

B. FADY[1,*], F. DUCCI[2], N. ALETA[3], J. BECQUEY[4], R. DIAZ VAZQUEZ[5], F. FERNANDEZ LOPEZ[5], C. JAY-ALLEMAND[6], F. LEFÈVRE[1], A. NINOT[3], K. PANETSOS[7], P. PARIS[8], A. PISANELLI[8] and H. RUMPF[9]
[1]Recherches Forestières Méditerranéennes, Institut National de la Recherche Agronomique, Avenue Vivaldi, Avignon 84000, France; [2]Istituto Sperimentale per la Selvicoltura, Arezzo, Italy; [3]Institut de Recerca i Technologia Agroalimentàries, Reus, Spain; [4]Institut pour le Développement Forestier, Lyon, France; [5]Centro de Investigaciones Forestales, Pontevedra, Spain; [6]Amélioration Génétique et Physiologie Forestières, INRA, Ardon, France; [7]Aristotelian University of Thessaloniki, Greece; [8]Consiglio Nazionale delle Ricerche, Porano, Italy; [9]Niedersächsische Forstliche Versuchsansalt, Staufenberg/Escherode, Germany; [*]Author for correspondence (e-mail: fady@avignon.inra.fr; phone: +33 4 90 13 59 10; fax: +33 4 90 13 59 59)

Received 10 September 2001; accepted in revised form 4 September 2002

Key words: Adaptation, Geographic pattern, *Juglans*, Selected material, Timber quality

Abstract. Adaptive and wood quality trait data were collected and analyzed on commercially available *Juglans regia* and *J. regia* × *J. nigra* provenances and progenies planted across Europe in a multi-site network. A total of 19 seed sources, replicated 35 times per site, were planted at 13 sites from 5 European countries, encompassing the potential distribution area of timber production plantation sites. The following traits were evaluated: survival, height, diameter at breast height, stem form, apical dominance, vegetative budbreak, along with biotic and abiotic damage. Mean values were significantly different both among provenances/progenies and sites. Most common damage was late spring and early autumn frost. Bud break ranking was significantly correlated with provenance and progeny origin. Although *J. regia* is fast growing, southern European early budbreak plant material should not be planted under most middle European conditions where late spring frost can be expected, as it has a significant negative impact on architectural (and thus wood quality) traits. Hybrid *J. regia* × *J. nigra* progeny performed better than *J. regia* provenances/progenies for most traits measured. Differences were significantly in favor of hybrids at sites with medium to low fertility, although some locally selected seed sources tended to perform as well as hybrids on high fertility sites.

Introduction

The naturalized European walnut tree, *Juglans regia* L., or common walnut, is traditionally cultivated for fruit production. It is also highly valued for its wood (e.g. fine quality cabinet making) which can command very high prices (mean European market value is 600 euros per m^3). This species is well suited for small-scale agroforestry type systems (typically less than 10 ha) where water availability is good and soil pH close to neutral (Jay-Allemand et al. 1996; Germain and Fady 1998). Under the current European Agricultural policy, such conditions are often found in

areas of extensive agriculture and the demand for wood producing walnut material is high. As a result, walnut has been over-exploited in the recent past and the current rate of planting is trying to compensate for this (e.g. 1000 ha/year in France, 5000 ha/year in Italy). As no breeding has yet been initiated for timber quality related traits in Europe, plant material available for timber production plantations in local nurseries comes from progeny of fruit producing cultivars or groups of naturalized trees known for some outstanding adaptive, growth or architectural trait (e.g. trees of the Lozeronne region in France and the Sorrento region in Italy). Notable exceptions are 2 interspecific hybrid progenies between the European walnut and the American black walnut (*J. nigra* L.) produced in French nurseries from open-pollinated seed orchards, and planted specifically for timber production (Jay-Allemand et al. 1996).

To offset this general lack of proper plant material for wood production in Europe, and because substantial adaptive trait phenotypic variability can be expected (e.g. results from black walnut provenance tests, Bresnan et al. (1994)), a European multi-site experimental network was implemented in 1994 to evaluate the adaptive and wood quality potentials of the most commonly available *Juglans* plant material in European nurseries. This European Walnut Experimental Network is the first of its kind on this scale and it is expected to provide guidelines in terms of plant material to be used for timber production plantations across Europe.

In this study, a) we provide the ecological database of the European Walnut Experimental Network and the database of the plant material used and b) we evaluate traits related to adaptation and wood quality in the *Juglans* plant material found in the network, emphasizing the potentials of *Juglans* provenances and progenies in comparison with two French interspecific hybrid *J. regia* x *J. nigra* progenies.

Material and methods

Plant material and experimental design

A selection of 19 seed sources were chosen from 5 European countries (Table 1). They were either provenances, single-cultivar open pollinated progenies or single-cultivar controlled pollinated progenies. Seeds were collected in 1993 and sown in two different nurseries (Lalanne nurseries, near Bordeaux and Payre nurseries, near Grenoble, France) in 1994. Seedling lots were made as homogeneous as possible prior to planting to avoid within site heterogeneity (Becquey 1994). Seedlings were planted at 13 different experimental sites in 5 European countries (Figure 1) during the winters of 1995 (one-year-old seedlings) and 1996 (two-year-old seedlings), depending on site availability. At each site, soil was plowed in rows and weeds were controlled mechanically each year. The main characteristics of the experimental network are found in Table 2. The experimental design was as follows: 35 complete blocks per site, 9 to 19 seed sources per block, of which 8 were common to all sites (Table 1), 5 $\times$ 5 m tree spacing. Unequal distribution of seed sources within

Table 1. Seed sources of *Juglans* sampled by the European Walnut Experimental Network. An 'x' indicates that the provenance or progeny is present and was studied at the chosen site. Latitude and longitude coordinates refer to the origin of the plant material.

Seed source code	Seed source name	Seed source origin (latitude, longitude)	Type of material	Number of progeny collected	Number of seedlings raised	Sites included in the European Walnut Experimental Network												
						S01-F	S02-F	S03-F	S04-F	S05-F	S06-D	S07-G	S08-I	S09-I	S10-I	S11-E	S12-E	S13-E
AL1	Ascheberg	51° 47′ N; 7° 37′ E	progeny (O)	1	41				x						x			
AL2	Colbitz	52° 20′ N; 11° 36′ E	progeny (O)	1	51				x									
ES1	MBT122	41° 00′ N; 0° 30′ E	progeny (O)	1	456	x		x	x	x	x	x	x		x		x	x
ES2	MBT231	40° 45′ N; 0° 30′ E	progeny (O)	1	115				x								x	
FR1	MJ209 × RA	45° 10′ N; 5° 20′ E	progeny (C)	1	842	x	x	x	x	x	x	x	x	x	x	x	x	x
FR2	NG23 × RA	45° 05′ N; 1° 40′ E	progeny (C)	1	867	x	x	x	x	x	x	x	x	x	x	x	x	x
FR3	Lozeronne	44° 40′ N; 5° 20′ E	provenance	25	1063	x	x	x	x	x	x	x	x	x	x	x	x	x
FR4	Charentes	45° 30′ N; 0° 10′ W	provenance	10	932	x	x	x	x	x	x		x	x		x	x	x
GR1	Arcadia	37° 20′ N; 22° 20′ E	provenance	10	530	x		x	x	x	x	x	x	x	x	x	x	x
GR2	West Crete	35° 20′ N; 24° 00′ E	provenance	15	665	x	x	x	x	x	x	x	x	x	x	x	x	x
GR3	Vamvaku	37° 19′ N; 22° 47′ E	progeny (O)	1	85				x			x			x			
GR4	Alonistaena	37° 37′ N; 22° 10′ E	progeny (O)	1	298			x	x		x	x		x	x		x	
GR5	Kato-klitoria	37° 53′ N; 22° 07′ E	progeny (O)	1	43				x	x								
IT1	Sorrento	40° 55′ N; 14° 48′ E	provenance	25	250				x		x	x	x		x		x	
IT2	Malizia	40° 55′ N; 14° 48′ E	provenance	25	1091	x	x	x	x	x	x	x	x	x	x	x	x	x
IT3	Feltrina	46° 01′ N; 11° 53′ E	provenance	25	1185	x	x	x	x	x	x	x	x	x	x	x	x	x
IT4	Bleggiana	46° 01′ N; 10° 50′ E	provenance	25	3014	x	x	x	x	x	x	x	x	x	x	x	x	x
IT5	Boschi MG	43° 46′ N; 11° 48′ E	progeny (O)	1	538	x		x	x		x	x	x	x	x	x	x	x
IT6	Pian del Ponte	43° 48′ N; 11° 52′ E	progeny (O)	1	1024	x	x	x	x	x	x	x	x	x	x	x	x	x
		Number of seed sources per site				12	9	13	19	12	14	14	13	12	15	11	15	12

Progeny (C): controlled pollinated progeny of a single cultivar (1 or 2 pollinating clones).
Progeny (O): open-pollinated progeny of a single cultivar.
Provenance: seeds collected from several trees in a single stand or locality.

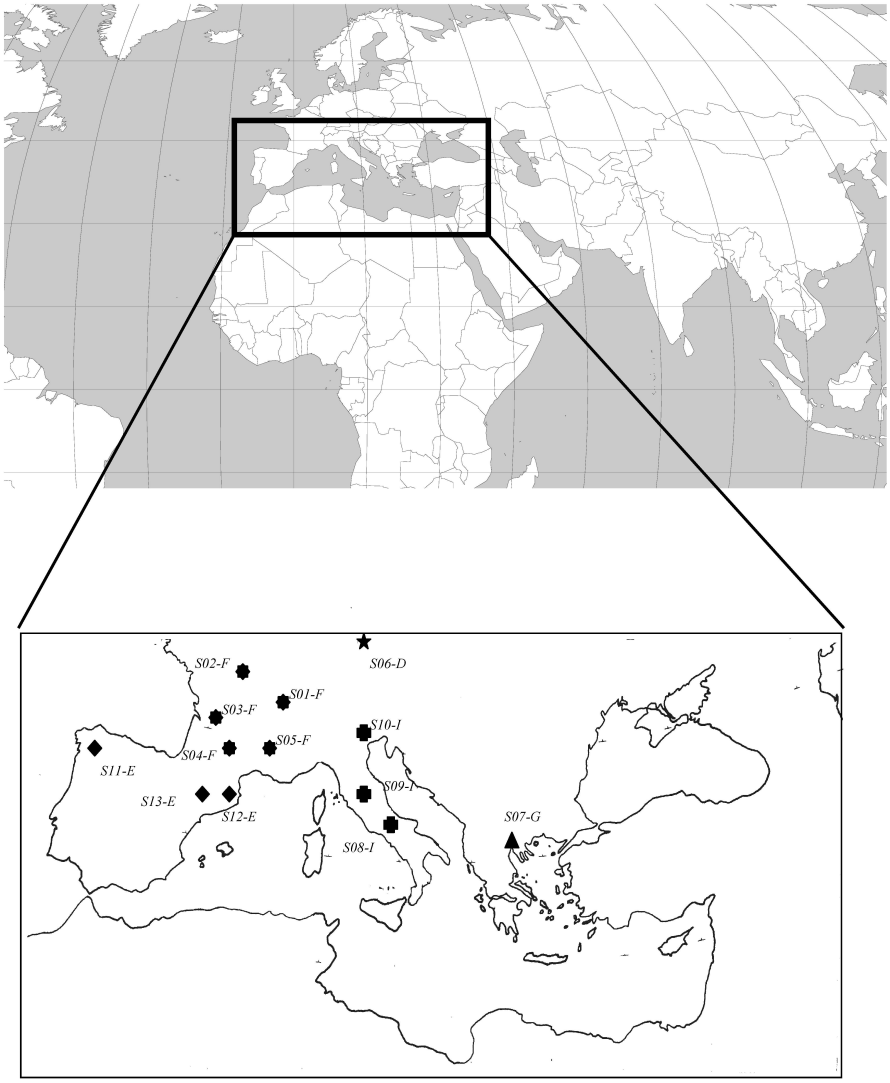

Figure 1. Geographic distribution of *Juglans* sites within the European Walnut Experimental Network.

experimental sites was related both to unequal seed availability at collection time and unequal seed germination potential per seed source (Becquey 1994).

Traits evaluated

A total of 10 different traits were measured: 1) survival in 1999; 2) initial total height after planting; 3) total height; 4) diameter at breast height (DBH); 5) stem form; 6) apical dominance; 7) vegetative flushing (budbreak) and a series of biotic

Table 2. Ecological conditions for the *Juglans* experimental sites established by the European Walnut Experimental Network.

Site code	Country	Site and region name	Latitude	Longitude	Altitude in m	Plantation year*	Climate zone	Date of latest frost	Date of earliest frost	Mean annual rainfall in mm	Summer rainfall (J+J+A) in mm	Mean annual temp. in °C	Mean minimum temp. in °C	Mean maximum temp. in °C	De Martonne drought index ***	Soil fertility ****
S01-F	France	Saint Antoine, Aquitaine	44° 50′ N	0° 10′ E	15	1995	Oceanic	April 23**	Oct. 30	802	188	13.4	7.9	18.9	57.6	high
S02-F	France	Pouzay, Centre	47° 05′ N	0° 35′ E	48	1996	Oceanic	April 24**	Oct. 29	606	115	12.2	7.2	17.1	51	medium
S03-F	France	Moriat, Auvergne	45° 24′ N	3° 15′ E	435	1995	Continental/Oceanic	May 7**	Oct. 30	561	171	11.2	4.9	17.4	50.5	low
S04-F	France	Bonrepos, Midi-Pyrénées	43° 40′ N	1° 32′ E	232	1996	Oceanic/Continental	April 22	Oct. 23	660	151.9	13.1	8.3	17.9	46.8	medium
S05-F	France	Les Mages, Languedoc	44° 12′ N	4° 10′ E	146	1996	Mediterranean	May**	Oct.	1052	170	13	7.7	18.3	61.3	low
S06-D	Germany	Grohnde, Nieder Sachsen	51° 58′ N	9° 25′E	250	1995	Continental	NA	NA	854	397	8.2	NA	NA	524.9	medium
S07-G	Greece	Axios, North Greece	40° 42′ N	22° 41′ E	35	1996	Mediterranean	April 17	Nov. 19	463	8.4	14.8	9.1	20.4	27.2	high
S08-I	Italy	Biagio, Umbria	42° 43′ N	12° 02′ E	540	1995	Mediterranean	April 19**	Nov. 20	879	140	12,15	8.05	16.72	50.1	high
S09-I	Italy	Chiusi, Tuscania	43° 09′ N	11° 50′ E	200	1995	Mediterranean	April 19**	Nov. 20	517	75.4	13.0	7.4	20.2	46.15	high
S10-I	Italy	Tapoglliano, Friuli Venezia	45° 58′ N	13° 27′ E	30	1996	Mediterranean/Continental	April 24	Nov. 21	1340	269.2	12.4	6.9	18.2	72.2	medium
S11-E	Spain	Ortigueira, Galicia	46° 36′ N	7° 48′ W	400	1995	Oceanic	NA	NA	1559	141	9.98	7.9	11.7	100.6	medium
S12-E	Spain	Massanes, Catalunya	41° 25′ N	4° 07′ E	164	1995	Mediterranean	April 14**	Nov. 7	680	116	13.9	7.7	20.3	36.6	high
S13-E	Spain	Prades, Catalunya	41° 40′ N	3° 20′ E	950	1995	Mediterranean	April 20**	Nov. 7	735.4	120.8	10.46	5.5	15.7	61.1	medium

NA: not available.

* one-year-old seedlings planted in 1995, two-year-old seedlings planted in 1996.

** frost of 1997.

*** drought index from De Martonne (1926): $i = [(P/T+10) + (12p/t+10)]/2$ where P = annual rainfall, T = mean annual temperature, p = rainfall of warmest month, t = mean temperature of warmest month.

**** extimated by depth, soil description and vegetation type.

Table 3. Description of measured traits, scoring methods and planting sites for *Juglans regia* and hybrids in the European Walnut Experimental Network.

Trait measured	Date of measurement	Scoring method	Unit of measurement	Sites where measured*
Survival	Spring 1999	Direct counting	Percent	All sites
Total initial height	Spring 1995 or 1996**	Height pole	Centimeter	All sites except ISSA1 and 2
Total height 1998	Spring 1999	Height pole	Centimeter	All sites
Diameter at breast height	Spring 1999	Caliper rule	Millimeter	All sites except NFV1
Stem form	Spring 1999	3 level scale	7: straight tree 4: curved tree 1: crooked tree	All sites
Apical dominance	Spring 1999	3 level scale	7: tree has one leader 4: tree has two leaders 1: tree has more than two leaders	All sites
Vegetative flushing	April 1999	5 level scale (Germain et al. 1999)	From 5 (expanding shoot) to 1 (dormant bud)	All sites
Late spring frost damage	April 1999	Direct observation	1: apical bud lost 0: apical bud present	CNR1, IDF1, IDF2, IDF3, IRTA, IRTA2
Early autumn frost damage	Autumn 1998 or 1999	Direct observation	1: blackened frozen shoot 0: normal shoot	IDF1, IDF2, IDF3, IRTA, IRTA2
Insect damage	April 1999	Direct observation	1: presence or trace of larvae on shoot 0: shoot intact	AUTH1, CNR1, INRA1, INRA2, IRTA1

* site CIF1 is not included in this table.
** depending on planting year.

and abiotic damage: 8) late spring frost damage; 9) early autumn frost damage and 10) insect damage. An additional trait, height growth increment between total height and initial height, was generated by subtracting measurement 3) from measurement 2), and averaging it over the number of years considered. Measurement methods were kept as simple as possible to maintain homogeneity and to be easily transferable into forest practice. For example, the scoring method used for apical dominance is directly related to the intensity of pruning needed to regain apical dominance. Measured traits, scoring methods and sites where observations were performed are listed in Table 3. Very few measurements were made at S11-E because it was partially destroyed by uncontrolled grazing in 1997, and were not included in this study. Traits 1 and 7 to 10 can be considered as good indicators of adaptation, traits 2 to 4 of both adaptation and wood quantity, and traits 5 and 6 of wood quality.

All traits except damage and survival were considered to be quantitative and were analyzed keeping each site separate and using three consecutive one-way analyses of variance (ANOVAs). The ANOVA model used allows for unbalanced designs and missing values. The first ANOVA was used to adjust mean provenance and progeny values to block effects. The second one was used to adjust mean provenance and progeny values to initial height effect (nursery effect) when necessary. The third ANOVA was used to analyze seed source effect. Mean provenance and progeny values were ranked using the Newman and Keuls method. Seed source and site survival variability was analyzed using chi-square tests. Damage data were not statistically analyzed due to incomplete data sets.

Ecological data

Table 2 summarizes ecological data for each experimental site. Latitudes ranged from almost 52° N in Germany to less than 41° N in Greece. Longitudes ranged from almost 08° W in Spain to more than 22° E in Greece. Altitudes varied from 15 m to 950 m above sea level. Within this geographical range, the experimental sites were located in 3 main climate zones: Mediterranean, semi-Continental and Oceanic climate zones, with intermediate variations. Rainfall ranged from 1559 mm (S11-E) to 561 mm (S03-F) in the Oceanic zone, from 1052 mm (S05-F) to 464 mm (S07-G) in the Mediterranean zone and from 1340 mm (S10-I) to 854 mm (S06-D) in the semi-Continental zone. Summer rainfalls varied from 397 mm (S06-D) to 8.4 mm (S07-G). Mean Annual temperatures were from 14.8 °C. (S07-G) to 8.9 °C. (S06-D). Frosts were recorded on average from October 30 to April 20. Soil fertility ranged from low to high.

Results

Qualitative traits

Damage data were not recorded at all sites. However, the sites analyzed sample a large ecological range. Early autumn frost damage ranged from loss of apical

Table 4. Annual increments in cm (and standard deviations), mean total heights (in cm) and mean survival (in %) for selected *Juglans seed* sources and sites.

Seed source	Sites										Mean accross sites**		
	S01-F	S02-F	S03-F	S04-F	S05-F	S06-D	S07-G	S08-I	S12-E	S13-E	incr.	ht98	survival
ES1	102.55 (4.24)	NT	45.01 (4.52)	17.58 (2.47)	8.11 (2.40)	17.30 (2.21)	98.90 (5.99)	103.64 (4.59)	102.28 (6.02)	86.85 (4.20)	64.69	191.62	88.20
FR1	103.77 (4.24)	46.18 (3.30)	40.92 (3.20)	19.65 (2.44)	10.12 (2.33)	26.79 (2.00)	88.56 (5.87)	94.08 (4.66)	128.58 (6.11)	92.54 (4.07)	65.12	242.83	95.82
FR2	128.94 (4.24)	52.93 (3.30)	44.24 (3.52)	15.06 (2.40)	19.7 (2.33)	31.68 (2.05)	74.58 (5.87)	103.48 (4.73)	101.94 (6.02)	89.94 (4.07)	66.25	239.13	95.38
FR3	97.38 (4.37)	4.62 (3.45)	33.31 (5.64)	16.30 (2.44)	10.75 (2.29)	16.76 (2.07)	76.84 (6.36)	91.58 (4.59)	72.08 (6.91)	44.70 (4.56)	46.43	166.06	81.49
GR2	94.72 (4.24)	7.02 (3.93)	13.17 (4.23)	16.57 (2.44)	−6.67* (2.33)	15.48 (2.04)	90.04 (5.87)	91.84 (4.66)	97.49 (6.41)	76.19 (4.14)	49.59	199.19	87.25
IT2	82.94 (4.44)	8.45 (3.63)	6.642 (3.69)	20.23 (2.40)	5.00 (2.40)	14.49 (2.04)	90.99 (6.11)	76.99 (4.59)	96.40 (6.02)	82.91 (4.14)	48.50	193.54	89.75
IT3	96.99 (4.24)	23.69 (3.45)	45.61 (4.52)	18.93 (2.40)	11.98 (2.30)	18.88 (2.07)	80.90 (5.99)	108.91 (4.59)	105.42 (6.41)	85.03 (4.20)	59.64	190.54	88.95
IT4	104.40 (4.24)	14.93 (3.30)	8.35 (4.23)	14.42 (2.40)	7.12 (2.33)	20.01 (2.17)	86.34 (5.87)	94.74 (4.59)	85.94 (6.31)	72.05 (4.26)	50.83	199.78	90.55
IT6	92.76 (8.31)	25.45 (3.57)	33.70 (4.69)	15.16 (2.36)	5.84 (2.30)	19.74 (2.07)	91.52 (5.87)	88.79 (4.59)	92.76 (6.31)	67.62 (4.08)	53.33	185.70	90.33
mean incr.	100.49	22.91	30.11	17.10	8.00	20.13	86.52	94.89	98.10	77.54	56.04		
mean ht98	293.97	145.07	133.41	135.58	96.31	121.01	266.66	232.65	229.20	181.14		200.93	
mean survival	98.10	87.30	49.67	97.74	96.19	90.82	96.83	97.58	85.90	94.29			88.78

NT: not tested.

* a minus indicates a loss of apical dominance.

** mean Ht98 and mean survival values were calculated accross all 12 measured sites.

dominance (and the emergence of shoots from lateral buds) to death of tree. Differences among seed sources were not significant in the 5 sites studied except at S03-F (chi-square test, $p = 0.0001$). The hybrid progenies FR1 and FR2 were the least affected by autumn frost at all sites. At S03-F, the chi-square test became non significant when both progenies were removed from the analysis. Late spring frost tended to result in loss of apical dominance following apical bud destruction in all 6 sites studied. Differences among seed sources were highly significant (chi-square test, $p = 0.0001$). French plant material had late frost damage frequency below 5% while it was over 65% for Greek material. Other seed sources had variable damage frequencies, from 17% to 100% depending on the site. The most common insect damage noted at all 5 sites studied was due to the larvae of the butterfly *Zeuzera pyrina*. Bacterial blight (*Xanthomonas campestris* pv *juglandis*) was noted at sites S04-F and S05-F.

Mean mortality across seed sources and sites was 11.2%. Survival of provenances and progenies at different sites is summarized in Table 4. A chi-square test performed on mean site mortality indicated significant differences among sites ($p = 0.0001$). Survival at site S03-F was lower than in others. Another chi-square test performed within the site with the highest mean mortality (S03-F) indicated that mortality was significantly different among seed sources ($p = 0.0001$). Across sites, survival was consistently lower than average for provenances IT1, FR3 and FR4, while survival was consistently higher than average for progenies FR1 and FR2. There tended to be provenance/progeny × site interaction for other seed sources.

Quantitative traits

Significant initial height (nursery) effects were observed on total height and DBH of 7 sites. However, there were no significant nursery effects on budbreak and apical dominance. In addition, nursery effects were significant on tree form at only three sites. After adjustment to initial height effect, seed sources were found to be statistically different for most traits analyzed. Total height at plantation time (i.e. total height in nursery) was variable according to sites and was related to plantation year and the nursery seedling lots that were sent to the different experimental sites. However, total height of progenies FR1 and FR2 was consistently (and sometimes significantly) higher than other seed sources at plantation time.

Total height 1998 and mean increment (Table 4) showed a different site ranking than total height at plantation time. Site ranking according to mean height increment (calculated using seed sources common to all sites) was considered to reflect site potentials (also referred to as fertility in this study). All low fertility sites (S05-F, S04-F, S06-D, S02-F and S03-F) had mean provenance/progeny height increments below the 56 cm mean site average and their mean total height was less than 140 cm after 4 growing seasons. Progenies FR1 and/or FR2 ranked highest in all sites and were statistically superior in growth to all other seed sources in experimental sites with the lowest fertility, where their mean total height was between 168 and 218 cm after 4 growing seasons. Although this trend remained true for height increment,

there were no more significant differences for the poorest growing sites (S05-F and S04-F). In S07-G (a high fertility site), there were also no significant differences between seed sources. In high fertility sites, differences between FR1 and FR2 were sometimes high. Some seed sources performed as well as the hybrids at those sites, usually with strong genotype × site interaction. These fast growing seed sources were sometimes selections from the country or region where the site was located (e.g. FR4 in S01-F, IT4 in S09-I) or selections from other countries (e.g. IT3 in S12-E). Progeny ES1 had a high height increment in most high fertility sites and FR3 performed poorly at all sites. Mean total height in high fertility sites was between 181 and 294 cm after 4 growing seasons.

DBH values were significantly higher for hybrids FR1 and FR2 in lowest and mid fertility sites except S05-F. This trait must be considered with caution as sample size was very low in the lowest fertility sites where many trees had a total height less than 1.30 m. This trait was also significantly higher for FR1 and FR2 in high fertility sites S01-F, S12-E and S13-E.

The architectural trait stem form did not reveal clear differences between high and low fertility sites. Progenies FR1 and FR2 generally had a better stem form than others. In S05-F, this difference was very significant. Provenance FR3 had generally good stem form. The other architectural trait, apical dominance, showed a general site fertility gradient, with lowest fertility sites having very significantly higher apical dominance for progenies FR1 and FR2 and highest fertility sites showing no significant differences among seed sources.

Site ranking for budbreak was significantly correlated with site longitude ($r = 0.655$, p-value $= 0.021$), but not with latitude, nor with time of observation. Absence of correlation with latitude was due to sites S08-I and S13-E, which had late budbreak dates although they are in the southernmost part of the geographic range tested. Without these two sites, the correlation between budbreak and latitude was $r = -0.670$ and p-value $= 0.0341$. Seed source ranking for budbreak using all 19 French, Italian, Greek and Spanish provenances/progenies was significantly correlated to latitudinal coordinates ($r = -0.720$ and p-value < 0.001). Southern seed sources open their vegetative buds earlier in the spring than northern ones. Correlation with longitudinal coordinates was also significant for the same plant material ($r = 0.680$ and p-value $= 0.002$), probably because the earliest seed sources (from Greece) were both the southernmost and easternmost ones. Seed sources were separated into 3 groups (Figure 2). The first group was characterized by early budbreak dates and included all Greek, Spanish and Italian material except IT4. This provenance belongs to an intermediate flushing group which clustered with progeny AL2 at the only site where it was present. The last group was composed of late budbreak seed sources and contained all French material (including interspecific hybrid progenies) and progeny AL1 at the only site where it was present.

Correlation among traits

Total height was positively and significantly correlated with initial height, except at

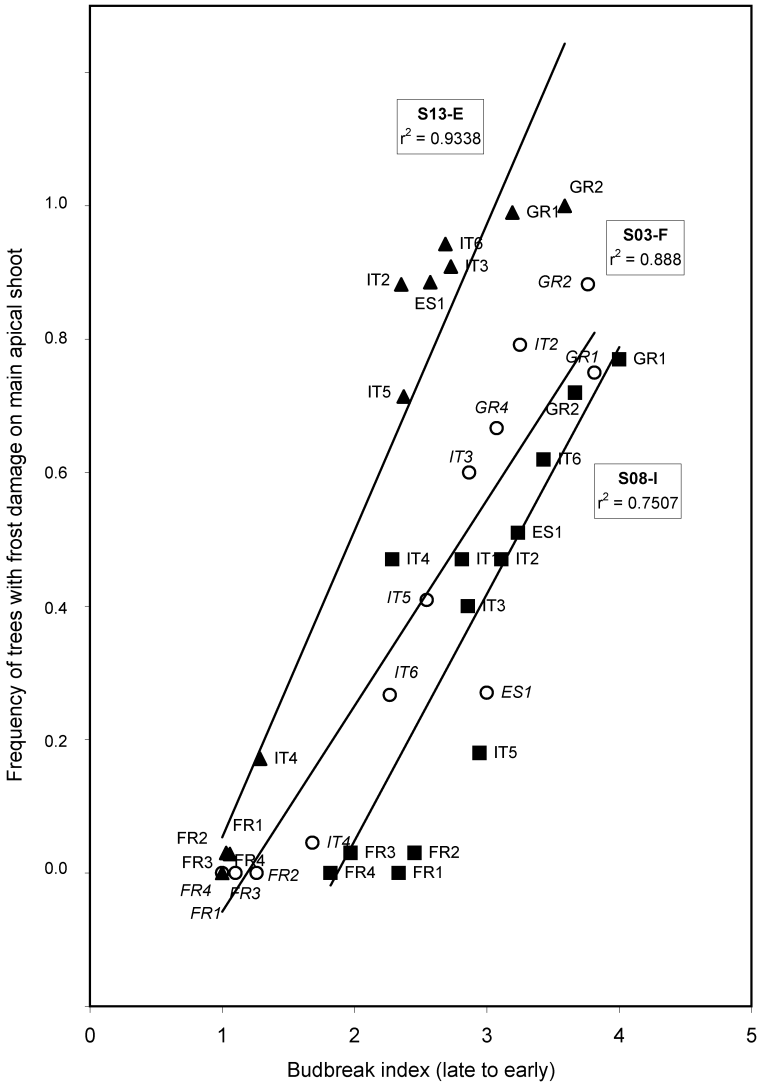

Figure 2. Correlation between budbreak index and susceptibility of *Juglans regia* and hybrid seed sources to early frost damage at 3 sites in the European Walnut Experimental Network. ▲ = S13-E; ○ = S03-F; ■ = S08-I.

site S03-F and S08-I (no correlation). At sites S05-F, S02-F and S03-F, total height was positively and significantly correlated to apical dominance and to tree form at site S05-F. Budbreak index was never correlated to height performances. It was negatively and significantly correlated to architectural traits at all sites except S02-F (Table 5, r^2 between 0.40 and 0.73). When it was correlated to both stem form and apical dominance, these two traits were then positively and significantly correlated

Table 5. Correlation between seed source budbreak index and architectural traits for *Juglans regia* and hybrids at 12 sites of the European Walnut Experimental Network.

Site	Traits			
	Tree form		Dominance	
	r	p-value	r	p-value
S01-F	0.770	0.0034	NS	
S02-F	NS		NS	
S03-F	NS		0.736	0.0041
S04-F	0.638	0.0033	0.510	0.0258
S05-F	0.697	0.0118	0.915	0.0001
S06-D	0.852	0.0001	0.757	0.0017
S07-G	0.787	0.0008	0.822	0.0006
S08-I	0.854	0.0002	0.685	0.0098
S09-I	0.806	0.0016	NS	
S10-I	0.761	0.0016	NS	
S12-E	0.847	0.0001	0.668	0.0065
S13-E	0.674	0.0162	0.926	0.0001

NS: non significant

(at 7 sites). Late spring frost damage data collected from 3 sites (S08-I, S03-F and S13-E, i.e. sampling a large ecological range) indicated a strong correlation with budbreak index (Figure 2). Between 75 and 93% of spring frost apical bud damage could be explained by budbreak index.

Discussion

A large range of climate and soil conditions were sampled in this experimental network. More than half the sites were under Mediterranean climate conditions, but overall the collection is a good representation of walnut in Europe (Jay-Allemand et al. 1996).

There was a generally good correlation between observed fertility (ecological assessment) and measured fertility (height increment). Some sites of the experimental network were clearly marginal. Survival was very low at S03-F and growth was very limited at S05-F. These types of sites probably represent the lowest fertility limit for walnut wood cultivation. The site ecological database summarized in this work can be used as guidelines for determining which plantation site conditions should be avoided. Other sites could be called medium potential sites in our sample. S04-F, S06-D and S02-F were characterized by height growths, increments and/or DBH values below average. In these sites, hybrid progenies performed significantly better than common walnut provenances and progenies. Again, the experimental site database found in this work can be used as guidelines to determine plantation sites that can be suitable, although having medium potentials for walnut wood cultivation. The remaining sites (S01-F, S07-G, S08-I, S09-I, S10-I, S12-E, S13-E) could be considered as high to very high fertility sites, with a mean total height of 181 to

294 cm after 4 growing seasons. As a comparison, *J. nigra* selected progenies reached total heights from 55 cm on the poorest site to 240 cm on the richest site after 5 years of plantation in the US (Williams et al. 1985). On the most fertile sites, hybrids did not always perform significantly better for height growth traits than some locally selected common walnut provenances and progenies (e.g. ES1 for Spain, IT4 for Italy). The trait apical dominance confirmed this trend as no significant differences were noted among seed sources in high fertility sites. Our findings confirmed, at the European level, what is usually recommended for walnut plantations in France, for example, in terms of appropriate sites (Becquey 1990a) and plant material (Becquey 1990b).

When assessing seed source adaptive potentials for plantation purposes, height growth traits must be adjusted for climate related traits. Because bud dormancy and spring budbreak in trees are strongly controlled by climatic factors (Mauget 1987) and by genetic factors (heritability of bud break date $> 90\%$ in *J. regia*, Germain (1992)), budbreak date is a very efficient trait for assessing general adaptation to local conditions, especially in relation to late spring frost (e.g. Steiner (1987)). Mean earlier bud-break of southernmost seed sources could be interpreted as a lesser need of cold days to break winter bud dormancy (milder winters in southernmost regions, see Table 2) and thus a shorter time for degree-day accumulation to trigger budbreak in the spring (Mauget 1983). As shown for sites S03-F, S08-I and S13-E, early budbreak can lead to significant frost damage during late spring frost years. As there was no overall significant north-south gradient for mean site budbreak index (although the trend is that southern sites have an earlier budbreak), local climate conditions must be carefully inventoried before selecting plant material. Budbreak index can also be considered as an efficient marker for predicting architectural (wood quality related) traits, both in medium and high fertility sites. Early budbreak leads to loss of apical dominance and/or defective stem form when late spring frosts occur. In low fertility sites, loss of apical dominance was directly connected to reduced total height. In this study, all southern seed sources open their vegetative buds earliest. Under these climates, growing seasons start earlier and late spring frost damage is not to be expected. The length of the growing season in high fertility southern sites is in favor of early budbreak seed sources. They can perform as well as hybrids whose highest growth potential was clearly demonstrated in medium fertility sites. Locally or regionally selected fast-growing seed sources could thus be economically valuable in highest fertility sites. On the contrary, planting early budbreak seed sources in northern Italy, France, Germany or wherever late spring frost is expected, should be completely avoided. Although sometimes very vigorous, these seed sources tended to produce trees with low apical dominance and/or poor stem form. Under such temperate climate conditions where late spring frost can be expected (large areas in Europe but also on other continents), the interspecific hybrids tested here represent a valuable plant material.

A lack of clear geographic variation pattern has been noted for isozyme markers on comparable populations and attributed to the existence of possible European refugia during the last Ice Age, as opposed to the theory of recolonization from an Asian refugium (Fornari et al. 1999). In our study, an absence of clear geographic

variation pattern was noted for all traits except budbreak and all seed sources except interspecific hybrid progenies. Our data do not contradict the European refugia hypothesis, although transfer of selected cultivars for human use across long distances could also be expected to lead to a lack of clear geographic variation pattern. Our data may also indicate a lack of strong selection pressure during the period investigated. In addition, the traits investigated may not be fully expressed in the material used which was selected for fruit production. However, the fact that progenies FR1 and FR2 (which were bred for timber production) were generally better for all measured traits indicates that a selection strategy is possible for these traits. Heritability and genetic gain figures estimated on *J. nigra* can be used to sustain this hypothesis. *J. regia* (for which no data was found in the literature) is a relatively close relative of *J. nigra* (the two species can intercross) and *J. nigra* is typically bred for timber production. Narrow sense heritability estimates ranged from 0.33 to 0.45 for height and 0.25 to 0.40 for diameter in 5 year old *J. nigra* trees (Beineke 1983). Other heritability estimates for height ranged from 0.18 to 0.55 for 5 year old *J. nigra* trees (Rink and Clausen 1989). An architectural trait such as straightness showed considerable variation and its narrow sense heritability estimates ranged from 0.32 to 0.70 (Beineke 1983). Clonal breeding strategies demonstrated that, for example, a 10% gain in height and 16% gain for straightness was possible for black walnut (Beineke 1983). Expected genetic gain in height can be up to 25% using family selection strategies (Rink 1984). If the same levels of genetic variation were confirmed on the material tested in the studied sites, breeding for timber production using these seed sources, and notably interspecific hybrids, could be a viable option in Europe, and an especially valuable one for medium fertility sites.

All tested seed sources were no more than 4 years of age at measurement time. At that age, nursery effects were demonstrated to be less significant than genotype and site effects on height growth for *J. nigra* (Williams et al. 1985). Selection for height growth was also demonstrated to be efficient at that age for *J. nigra* (Rink 1984). In our study, nursery effects are still significant at 7 sites. However, earliest expected rotation time could be 30 years in most fertile sites and much longer in low fertility sites. Even though first growing years are very important and early fast growing plant material can lead to reduced silvicultural work, more data should be taken in the following years to confirm the observed trends. Among these data, biotic damage related traits such as late spring frost and early autumn frost should be systematically taken into account.

Acknowledgements

Many thanks to D. Vauthier, H. Duval, and G. Olimpieri for their technical assistance. This work was made possible through the financial support of two consecutive European projects: AIR3-CT92-0142 ''*European development of walnut for wood and fruit production as an alternative extensive system to agricultural crops*'' (1993 – 1996) and FAIR-CT96-1887 ''*W-BRAINS: Walnut, production of*

high quality timber in Europe; up-to-date tools for tree adaptation, wood standards and management'' (1997 – 2000).

References

Becquey J. 1990a. Où peut on planter des noyers? Quelques principes de base. Forêt Entreprise 72: 15–16.

Becquey J. 1990b. Quel noyer choisir? Les facteurs déterminants. Forêt Entreprise 72: 17–19.

Becquey J. 1994. Synthèse des travaux, groupe D. Third report, contract AIR3-CT92-0142. European development of walnut for wood and fruit production as an alternative extensive system to agricultural crops. 11 pp.

Beineke W.F. 1983. The genetic improvement of black walnut for timber production. In: Janick J. (ed.), Plant Breeding Reviews Vol. I. AVI Publishing Co. Inc., Westport Conn., USA, pp. 236–266.

Bresnan D.F., Rink G., Diebel K.E. and Geyer W.A. 1994. Black walnut provenance performance in seven 22-year-old plantations. Silvae Genetica 43: 246–252.

De Martonne E. 1926. L'indice d'aridité. Bull. Assoc. Géog. Fr 9: 3–5.

Fornari B., Cannata F., Spada M. and Malvolti M.E. 1999. Allozyme analysis of genetic diversity and differentiation in European and Asiatic walnut (*Juglans regia* L.) populations. Forest Genetics 6: 115–127.

Germain E. 1992. Le noyer. In: Gallais A. and Bannerot H. (eds), Amélioration des espèces végétales cultivées, objectifs t critères de sélection. INRA éditions, Paris, France, pp. 620–632.

Germain E. and Fady B. 1998. *Juglans* et hybrides interspécifiques – noyer. In: Arbez M. and Lacaze J.F. (eds), ≪ Les ressources génétiques forestières en France. Tome 2 : les feuillus ≫. BRG and INRA éditions, Paris, pp. 109–136.

Germain E., Prunet J.P. and Garcin A. 1999. Le noyer. CTIFL, Paris, 279 p.

Jay-Allemand C., Fady B. and Becquey J. 1996. Walnut trees for woodland use in Mediterranean countries: current situation and prospects. Nucis 5: 10–13.

Mauget J-C. 1987. Dormance des bourgeons chez les arbres frutiers de climat tempéré. In: Le Guyader H. (ed.), Le dévéloppement des végétaux, aspects théoriques et synthétiques. Masson, Paris, pp. 133–150.

Mauget J-C. 1983. Etude de la levée de dormance et du débourrement des bourgeons de noyer (*Juglans regia* L., cv. ''Franquette'') soumis à des températures supérieures à 15 °C au cours de leur période de repos apparent. Agronomie 3: 745–750.

Rink G. 1984. Trends in genetic control of juvenile black walnut height growth. For. Sci. 30: 821–827.

Rink G. and Clausen K.E. 1989. Site and age effects on genotypic control of juvenile *Juglans nigra L.* tree height. Silvae Genetica 38: 17–21.

Steiner K.C. 1979. Patterns of variation in bud burst timing among populations in several*Pinus* species. Silvae Genetica 28: 185–194.

Williams R.D., Rink G. and Funk D.T. 1985. Planting site and genotype affect black walnut seedling development more than nursery environment. Can. J. For. Res. 15: 14–17.