

SEED PRODUCTION AND SEEDLING ESTABLISHMENT OF A SOUTHWEST RIPARIAN TREE, ARIZONA WALNUT (*JUGLANS MAJOR*)

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ABSTRACT.—A four-year study of five populations has revealed influences on seed production and seedling establishment of the Southwest riparian tree *Juglans major*. Germination is abundant after production of large seed crops (masts), but masts are produced infrequently. Within years, germination is stimulated by summer rains, enabling seedlings to establish on riparian terraces as well as streambanks. Traits such as capacity for dormancy during summer drought allow some seedlings to survive on terraces, but abundant rainfall is essential for high rates of seedling success. Ranges of moisture tolerance vary among seeds collected from different populations, suggesting that ecotypes may exist between riparian sites with dissimilar moisture regimes. Population-based differences are associated, in part, with differences in seed size.

Arizona walnut (*Juglans major* [Torr.] Heller) is a member of the “Interior riparian deciduous forest,” an assemblage of trees that grow along streams in the Interior Southwest (Brown 1982). Walnut sometimes dominates this community (Szaro 1989), but more often it occurs at relatively low densities and frequencies. This distribution pattern, while indicating that establishment occurs infrequently, does not reveal the stage where regeneration is limited. Sudworth (1934) suggested low rates of seed production and high rates of seed predation by tree squirrels as possible natural causes of infrequent establishment; seedling mortality from cattle grazing also may play a role (Rucks 1984).

Lack of suitable germination and establishment sites may limit recruitment, but little is known regarding the relationship between these requirements and *J. major*. Certain generalizations have been made about the distribution of walnut trees, but the habitat characteristics of trees may differ from those in which the seedlings established. A study that specifically addressed riparian seedlings revealed that seedlings of *J. major*, a facultative riparian species, establish in many microsites throughout the riparian zone. This is in contrast to seedlings of obligate riparian trees such as Arizona alder (*Alnus oblongifolia* Torr.) that occur only immediately adjacent to the stream (Larkin 1987). Larkin conducted her study, however, in a wet, montane area of

central Arizona; germination “safe sites” for walnut may be more restricted in drier riparian sites such as along ephemeral streams. For example, seed burial may become a prerequisite of germination as soil moisture decreases, as is true for certain oaks (Barrett 1931).

Germination and establishment of walnut or other riparian species may also vary as a function of genetic differences between populations. The existence of riparian ecotypes is not a new idea (e.g., Hook and Stubbs 1967), and riparian populations may differ between isolated Southwest watersheds with different hydrologic characteristics. Other studies in this series on walnut reproduction have identified differences between populations in floral ratios and seed weight (Stromberg 1988), indicating that *J. major* shows either plastic responses or genetically based responses to environmental differences within and between riparian sites. The objectives of this study were to: (1) identify factors that limit seed production and seedling recruitment of *J. major* between sites and between years; (2) determine how germination requirements vary between microsites; and (3) determine how seedling growth response to soil moisture differs between populations.

METHODS

Seed production, germination, and seedling survival of *J. major* were studied through

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field and greenhouse experiments and field observations. Five sites were selected in central Arizona: Hitt Wash, an ephemeral stream near Prescott National Forest; Rock Creek, an intermittent stream in the Mazatzal Mountains; and perennial streams (South Fork Walnut Creek in Prescott National Forest and two sites along Workman Creek in the Sierra Ancha Mountains) (Stromberg 1988). Elevations vary from 1,100 m at Rock Creek to 2,100 m at Aztec Peak.

Field Observations

Twenty trees were selected at each site, and samples of 20 shoots per tree were selected for monitoring of seed production from 1983 to 1986. Average values per tree were calculated for seed production per shoot and for flower production, flower abortion, seed weight, and seed viability (Stromberg 1988). A mast (large seed crop) is operationally defined in this study as a crop 33% larger than average for the study.

Demography of natural seedlings was studied to determine when, where, and how many seeds germinate, and to compare survival rates between microsites. One walnut tree near the stream and one on the adjacent terrace with nearby seedlings were selected at each site. Each marked the center of an 8-m-radius circular plot. All seedlings in the plots were tagged and scored monthly from May to October of 1983, 1984, and 1985 for stem height, leaf length and number, and mortality. Twenty seedlings in a plot at Hitt Wash were excavated to measure depth of the nut in the soil profile.

Field Experiments

Seeds were sown in field exclosures in fall 1982 and 1983 to test for influence of microsite (soil moisture and canopy cover) and burial depth on germination and survival. Exclosures protected seedlings from trampling and predation. Four microsites (streamside, open canopy; terrace, open canopy; streamside, closed canopy; terrace, closed canopy) were selected per site, with three replicate exclosures per microsite. Exclosures were constructed from 1.3-cm hardware cloth, and were $0.6 \times 0.6 \times 1$ m high, with 15 cm of mesh below ground. Seeds were planted 36 per exclosure in 6 rows in 3 planting treatments: surface sown, partially buried, or

buried 2 cm deep. Sites were planted with their own seeds (except for Workman Creek and Rock Creek), and seedling size and survival were recorded through 1985. Microsite soil moisture was recorded monthly with a dew-point psychrometer, and canopy cover was estimated visually (Stromberg 1988). Influences on germination and seedling survival were analyzed through multiple regression analysis of germination and survival percentages with average seasonal values for microsite moisture level, canopy cover, and herbaceous cover.

Greenhouse Experiments

Nuts were collected in 1983 from trees at Rock Creek, Hitt Wash, and Walnut Creek to test for influence of seed weight and seed source on germination and seedling growth. Nuts were sown in the greenhouse in loam soil in polyethylene-lined pots under four watering regimes. One regime was watered every other day to maintain saturated conditions. Others were watered at less-frequent intervals, producing average soil moisture contents by dry weight of 80%, 40%, and 20%. Seeds were sown on the surface and buried 2 cm deep. Seven nuts from each of 24 parent trees were sown per treatment. Germination percent and speed and seedling survival were monitored. Eight weeks after emergence, plants were harvested for measurement of dry weight, stem height, and root length. At each soil moisture level, regression analysis was used to test for influence of seed weight, a continuous variable. Duncan's multiple range test was used to test for effects of seed source on germination and seedling growth rates.

RESULTS

Seed Production

Seed production differed substantially between sites and years. All sites had large annual variation in seed production, with annual coefficients of variation ranging from 100 to 140 among sites. Masts were produced in one or two of the four years among sites (Fig. 1). Large crops of seeds, irrespective of viability, were produced more frequently. Some exceptional trees produced four consecutive, large seed crops. Number of large flower crops also varied substantially between sites, ranging from one at Walnut Creek to three at Hitt Wash.

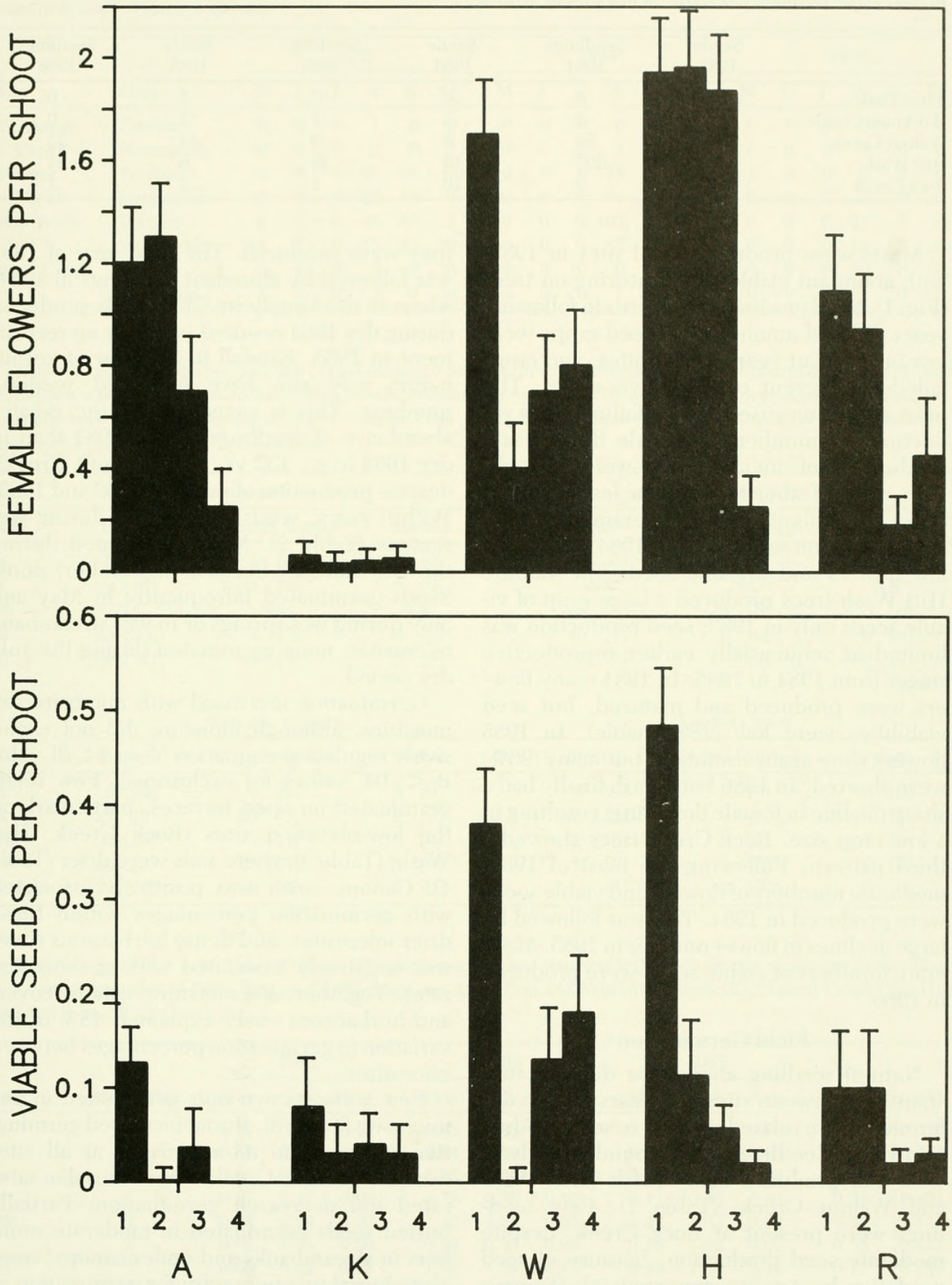


Fig. 1. Site means for female flowers and viable nuts produced per shoot for *Juglans major* from 1983 through 1986 at Aztec Peak (A), Workman Creek (K), Walnut Creek (W), Hitt Wash (H), and Rock Creek (R).

TABLE 1. Average rates of seed production (expressed as viable seeds produced per 100 shoots) and abundance of *Juglans major* seedlings per 200 m² at five sites in Arizona.

	Seeds 1983	Seedlings 1984	Seeds 1984	Seedlings 1985	Seeds 1985	Seedlings 1986
Aztec Peak	11	0	0	0	2	0
Workman Creek	9	2	3	1	3	0
Walnut Creek	38	52	0	0	14	23
Hitt Wash	46	207	10	48	6	24
Rock Creek	10	3	10	1	2	1

Masts were produced at all sites in 1983, with abundant viable nuts maturing on trees (Fig. 1). Seed production patterns in following years differed among sites. Seed crops were low in different years among sites, and crops failed at different reproductive stages. The most common causes of crop failure were reductions in numbers of female flowers and production of inviable, low-weight seeds; high rates of abortion were a less frequent cause. At Walnut Creek, for example, viable nut production was lowest in 1984, a result of few flowers and inviable seeds (3% viable). Hitt Wash trees produced a large crop of viable seeds only in 1983; seed production was limited at sequentially earlier reproductive stages from 1984 to 1986. In 1984 many flowers were produced and matured, but seed viabilities were low (28% viable). In 1985 flowers were again abundant, but many (96%) were aborted. In 1986 Hitt Wash finally had a sharp decline in female flowering, resulting in a low crop size. Rock Creek trees showed a third pattern. Following the mast of 1983, moderate numbers of flowers and viable seeds were produced in 1984. This was followed by large declines in flower number in 1985. Moderate numbers of viable seeds were produced in 1986.

Field Germination

Natural seedling abundance differed substantially between sites and years. These differences were related, in part, to seed production rates. Seedlings were abundant only at sites that produced many seeds (Hitt Wash and Walnut Creek) (Table 1). Few seedlings were present at Rock Creek, despite moderate seed production, because of seed predation by Arizona gray squirrels (*Sciurus arizonensis*; see Stromberg 1988). Annual seedling abundance was influenced by size of the prior year's crop of viable seeds, since seeds generally germinated the year after

they were produced. The mast year of 1983 was followed by abundant seedlings in 1984, whereas the largely inviable seeds produced during dry 1984 resulted in low or no recruitment in 1985. Rainfall in the year of germination may also have increased seedling numbers. This is suggested by the greater abundance of seedlings in wet 1983 than in dry 1984 (e.g., 132 vs. 52 at Walnut Creek), despite production of masts in 1982 and 1983. Within years, seeds germinated during wet seasons (Table 2). Most germinated during the late summer (August–September) rains. Seeds germinated infrequently in May and only during wet springs or in wet streambank microsites; none germinated during the July dry period.

Germination increased with microsite soil moisture, although moisture did not exclusively regulate germination ($r^2 = .24$, $df = 14$, $P < .04$; values for exclosures). Few seeds germinated on open terraces, particularly at the low-elevation sites (Rock Creek, Hitt Wash) (Table 3) where soils were drier (Table 4). Canopy cover was positively associated with germination percentages within these drier microsites, and dense herbaceous cover was negatively associated with germination rates. Together, soil moisture, canopy cover, and herbaceous cover explained 45% of the variation in germination percentages between microsites.

Few surface-sown nuts germinated in any microsite (Table 3). Burial increased germination rates within all microsites at all sites except Workman Creek, where burial in saturated soil decreased germination. Partially buried seeds germinated in moderate numbers in streambanks and under canopy; complete burial was necessary for germination in open terraces. Lack of burial limited germination of natural seed populations. For example, many seeds were ungerminated on the soil surface at Hitt Wash terrace. Excavation of

TABLE 2. *Juglans major* seedling recruitment by month (May through October) in streamside and terrace plots at sites in Arizona. Plots are 200 m².

Site	Plots	1983						1984						1985					
		M	J	J	A	S	O	M	J	J	A	S	O	M	J	J	A	S	O
Workman Creek	Terrace	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Streamside	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Walnut Creek	Terrace	0	0	0	53	44	0	0	0	0	18	12	0	0	0	0	0	0	0
	Streamside	0	0	0	22	13	0	0	0	0	14	8	0	0	0	0	0	0	0
Hitt Wash	Terrace	6	3	0	92	43	2	0	0	0	105	48	1	0	0	0	21	7	0
	Streamside	14	5	0	35	13	0	0	0	0	47	25	1	2	0	0	13	5	0
Rock Creek	Terrace	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Streamside	0	0	0	3	0	0	0	0	0	1	0	0	0	0	0	1	0	0

TABLE 3. Germination percentages of *Juglans major* sown at three planting depths in four microsites. Average seed viability was 60%. Values are means and standard deviations for 3 groups of 12 nuts. Planting depths are: buried at 2 cm, partially buried, and surface sown. Sites are: Aztec Peak (A), Workman Creek (K), Walnut Creek (W), Hitt Wash (H), and Rock Creek (R). NA = not available.

Site	Streambank, canopy			Streambank, open		
	Buried	Partially buried	Surface	Buried	Partially buried	Surface
A	0 [0]	0 [0]	0 [0]	0 [0]	0 [0]	0 [0]
K	4 [6]	25 [0]	8 [0]	NA	NA	NA
W	NA	NA	NA	29 [6]	13 [6]	8 [0]
H	45 [30]	3 [5]	0 [0]	46 [6]	0 [0]	0 [0]
R	50 [18]	5 [5]	0 [0]	50 [15]	0 [0]	0 [0]

Site	Terrace, canopy			Terrace, open		
	Buried	Partially buried	Surface	Buried	Partially buried	Surface
A	0 [0]	0 [0]	0 [0]	0 [0]	0 [0]	0 [0]
K	21 [6]	25 [0]	8 [0]	50 [33]	0 [0]	0 [0]
W	35 [19]	16 [11]	3 [5]	28 [16]	0 [0]	0 [0]
H	53 [5]	25 [14]	8 [9]	0 [0]	0 [0]	0 [0]
R	21 [12]	0 [0]	0 [0]	4 [8]	0 [0]	0 [0]

TABLE 4. Soil water potential at 30 cm (–MPa) for terrace (T) and streamside (S) open canopy microsites during May, July, and September of 1983, 1984, and 1985. Sites are: Aztec Peak (A), Workman Creek (K), Walnut Creek (W), Hitt Wash (H), and Rock Creek (R).

Site	Microsite	1983			1984			1985			Mean [± SD]	
		May	Jul	Sep	May	Jul	Sep	May	Jul	Sep		
A	T	0.02	0.15	0.01	0.68	0.83	0.06	0.11	0.79	0.06	0.30	[0.33]
	S	0.01	0.16	0.00	0.54	0.63	0.03	0.06	0.54	0.03	0.22	[0.25]
K	T	0.03	0.19	0.01	1.03	1.36	0.06	0.24	1.16	0.06	0.46	[0.52]
	S	0.01	0.17	0.00	0.78	0.96	0.02	0.12	0.93	0.04	0.34	[0.40]
W	T	0.03	0.24	0.02	1.18	1.26	0.05	0.42	1.33	0.04	0.51	[0.54]
	S	0.02	0.18	0.00	0.84	0.96	0.02	0.18	1.02	0.02	0.36	[0.42]
H	T	0.03	0.32	0.01	1.65	1.84	0.15	0.48	1.80	0.12	0.71	[0.76]
	S	0.03	0.22	0.02	1.45	1.63	0.05	0.26	1.58	0.06	0.59	[0.69]
R	T	0.04	0.43	0.20	1.86	2.04	0.13	0.64	1.83	0.14	0.81	[0.80]
	S	0.03	0.32	0.02	1.45	1.63	0.05	0.26	1.58	0.06	0.60	[0.68]
Mean		0.03	0.26	0.04	1.27	1.44	0.07	0.32	1.39	0.07		
± SD		0.01	0.09	0.06	0.38	0.39	0.04	0.16	0.35	0.04		

TABLE 5. Germination percentages for *Juglans major* buried in soil or sown on the surface at three soil water contents (by weight) in the greenhouse. No seeds germinated at 20% soil moisture. Seeds are from streambanks (S) or terraces (T) from Walnut Creek (W), Hitt Wash (H), or Rock Creek (R). Values are means and standard deviations.

Seed source		Saturated		80% moisture		40% moisture	
		Buried	Surface	Buried	Surface	Buried	Surface
W	S	21 [21]	50 [7]	50 [7]	0 [0]	7 [7]	0 [0]
	T	0 [0]	50 [29]	42 [18]	0 [0]	21 [21]	0 [0]
H	S	5 [6]	28 [31]	63 [29]	0 [0]	24 [33]	0 [0]
	T	0 [0]	18 [12]	61 [16]	0 [0]	19 [27]	0 [0]
R	S	0 [0]	22 [9]	39 [11]	0 [0]	13 [0]	0 [0]
	T	0 [0]	14 [7]	48 [15]	0 [0]	16 [5]	0 [0]

seedlings revealed that only 5% of the seedlings were from surface nuts, whereas 75% were from partially buried nuts and 20% were buried at depths of 9 to 15 cm in pocket gopher (*Thomomys* spp.) caches.

Greenhouse Germination

Juglans major germinated abundantly in soil with a moisture content of 80–100% by weight (Table 5). Few seeds germinated in the dry soil or saturated soil. Planting depth influenced germination at all soil moisture contents. In the saturated soil, surface-sown seeds germinated in substantially higher percentages than buried seeds. In contrast, seeds required burial for germination at all other moisture contents.

Germination rates in saturated soil varied between populations and with seed weight. Seeds collected from trees along the banks of perennial Walnut Creek germinated in higher percentages than seeds from sites with ephemeral (Hitt Wash) or intermittent (Rock Creek) stream flow (Table 5). Many cohorts from these latter sites did not germinate in saturated soil. Germination percentage in saturated soil also tended to increase as seed weight (g) per cohort decreased ($y = 31.8 - 5.3x$, $r^2 = .15$, $df = 22$, $P < .05$). Seed weight was not related to germination in dry or moist soil.

Speed of germination varied with soil moisture level and with seed weight. Seeds in moist soil (80–100%) germinated rapidly (16 ± 10 days), whereas seeds in drier soil (40% by weight) germinated 28 ± 12 days after planting. Although variance in germination speed was high within a cohort, median germination speed increased significantly with seed weight for a cohort ($y = -0.5 + 5.5x$, $r^2 = .34$, $df = 22$, $P < .01$, in 80% moisture). For

example, seeds weighing 3 g germinated in 16 days, compared with 38 days for those weighing 7 g.

Seedling Survival in the Field

Seedling mortality had a major role in limiting regeneration of *J. major*. Only 1 of 374 natural 1983 seedlings among the study sites was alive as of fall 1985. Mortality was high in the year of germination and in the two years following (Fig. 2). Most seedlings died in June, typically a dry month, or in winter. Precipitation was sparse in early 1984 (Table 6), and seedlings that germinated in 1983 had high winter mortality: only 7% of Hitt Wash and 9% of Walnut Creek 1983 natural fall cohorts survived until spring 1984. Many that did survive remained dormant through the spring and summer drought of 1984, withholding leaf-out until the late summer rains. In contrast, more than 20% of 1984 cohorts at both sites survived to spring of 1985.

Seedling survivorship varied between microsites (Table 7) as well as between years. A large part of the variation between microsites was attributable to soil moisture. Survivorship after two years increased with soil moisture between exclosures ($r^2 = .31$, $df = 14$, $P < .05$), with seedlings on open streambanks having highest survival. Seedlings that did survive in dry microsites had high mortality of buds and shoots during their first and second winters, and grew slowly. On terraces, 42% of year-old survivors originated new spring growth from basal buds, 49% from lateral buds, and only 9% from the terminal bud. On streambanks, in contrast, 15% regrew from basal buds, 58% from lateral, and 31% from terminal buds. Second-year seedlings on the open terrace that regenerated from a basal bud had average stem height of 2.5 cm, with

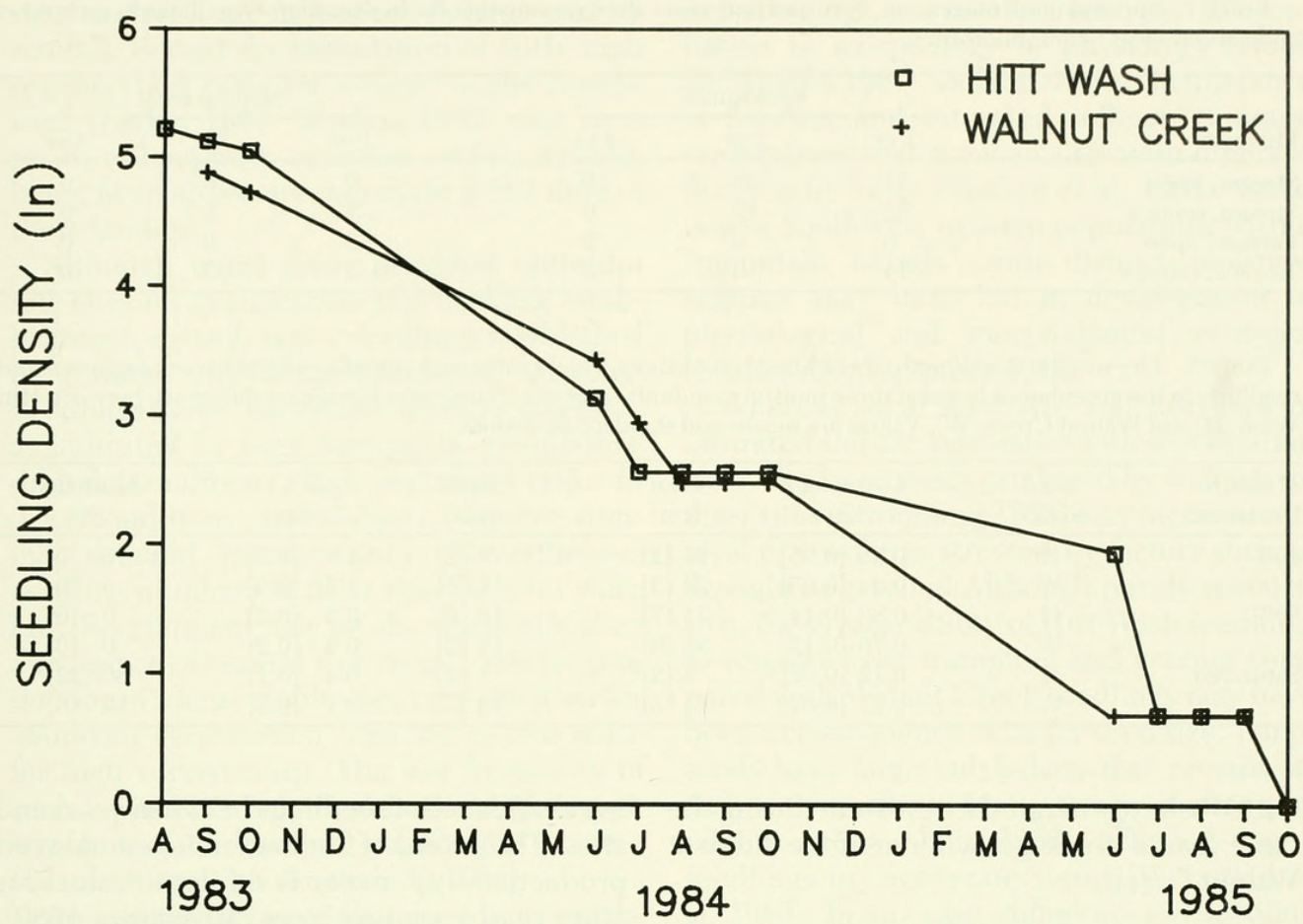


Fig. 2. Seedling survivorship for *Juglans major* that germinated in fall 1983 at Hitt Wash (HW) and Walnut Creek (WC). Values are log_e of seedlings remaining each month.

TABLE 6. Precipitation (cm) from 1982 to 1986 at a climatic station near the Walnut Creek study site. Average annual precipitation is 39 cm.

	1982	1983	1984	1985	1986
January–June	21	22	3	14	16
July–December	19	31	37	31	30
Total	40	53	40	44	46

as few as two leaves 1 cm long. These seedlings did not markedly increase in size from 1983 to 1985. Seedlings in moist, open areas grew rapidly, as evidenced by a two-year streambank seedling in full sun that reached 44 cm tall.

Flooding killed some streambank seedlings but did not impact terrace seedlings. Fall floods killed 10% of Walnut Creek and 5% of Hitt Wash 1983 streambank seedlings; mortality rates from winter/spring floods were not quantified. Physical impacts of floods included stem breakage, coverage with debris, and scouring of seedlings. Several seedlings resprouted after stem topping.

Herbivory damage from insects also con-

tributed to seedling mortality. Interestingly, seedlings did not have greatest herbivory at sites where adult herbivory was high (see Renaud 1986). Rather, seedlings in specific microsites had greatest leaf loss from herbivores. Seedlings on terraces, under canopy, had greatest herbivory damage; leaf area consumed by October 1983 was $33\% \pm 15$, compared to $< 9\%$ for all other microsites.

Effects of cattle grazing were included in the study out of necessity because of the almost ubiquitous presence of cattle in Southwest riparian areas. Two sites, Hitt Wash and Walnut Creek, had heavy to moderate cattle grazing. Seedlings in exclosures at both sites had substantially higher survival rates than those in similar unprotected areas; however, this was also true for the ungrazed sites (Table 7). Adverse impacts of cattle on seedlings included trampling and grazing. At Hitt Wash, 22% of 213 natural seedlings had broken or eaten stems, as did 13% of 130 seedlings at Walnut Creek. Ability of seedlings to recover from trampling and grazing varied between sites; 40% of all stem-damaged seedlings at

TABLE 7. Survival percentages one, two, and four years after germination for *Juglans major* seedlings in exclosures and natural areas in four microsites.

Microsite	Exclosures			Natural areas		
	1 yr	2 yr	4 yr	1 yr	2 yr	4 yr
Stream, open	51	28	16	0	0	0
Stream, canopy	22	15	0	7	0	0
Terrace, open	6	0	0	5	0	0
Terrace, canopy	14	0	0	3	0	0

TABLE 8. Dry weight, root length, shoot height, root:shoot weight ratio, and mortality of eight-week *Juglans major* seedlings in the greenhouse in soil at three moisture contents. Asterisk (*) indicates significant difference between Hitt Wash (H) and Walnut Creek (W). Values are means and standard deviations.

Moisture treatment	Seed source	Dry weight (g)	Root (cm)	Shoot (cm)	R:S ratio	Mortality (%)
40%	H	0.35 [0.05]	25 [2]	9 [2]	1.4 [0.3]	0 [0]
	W	0.44 [0.05]	29 [3]	11 [2]	1.1 [0.3]	0 [0]
80%	H	0.83 [0.14]	34 [7]	16 [2]	0.9 [0.2]	0 [0]
	W	0.76 [0.12]	34 [6]	15 [2]	0.9 [0.2]	0 [0]
Saturated	H	0.12 [0.02]*	4 [2]*	7 [2]*	0.4 [0.1]*	80 [22]*
	W	0.27 [0.04]	13 [3]	10 [3]	0.7 [0.2]	13 [6]

Hitt Wash regenerated a new stem during the same year of breakage, whereas none did so at Walnut Creek.

Greenhouse Seedling Survival

All seedling cohorts had greatest growth in intermediate soil moistures and poorest in saturated soil (Table 8). Root growth in particular was low in saturated soil, and root-to-shoot ratios were low compared to drier soils. Some cohorts, however, grew better than others in saturated soil. Similar to results for germination rates, seedling growth and survival in saturated soil were related to seed weight and seed source. Size and weight of seedlings in saturated soil increased significantly with decreasing seed weight among cohorts (e.g., seed weight in g = 26.5 – 4.5 * root length in cm, $r^2 = .49$, $df = 11$, $P < .01$). With regard to seed source, cohorts from the perennially saturated streambanks of Walnut Creek had greater root development and survivorship in saturated soil than did cohorts from drier Hitt Wash.

DISCUSSION

Although a survey of five populations is not representative of a species as a whole, this study has highlighted factors influencing recruitment of *J. major*. Low and fluctuating availability of seeds plays a large role in limit-

ing abundance of seedlings between years and sites. The extent of fluctuation in annual seed production by *J. major* is similar to values for other mast-cropping trees (Silvertown 1980), and frequency of mast production is similar to other Juglandaceae (Nixon et al. 1980, Sork 1983, Waller 1979). Seedlings were abundant only after mast years, substantiating the view that infrequent production of viable crops limits regeneration (Sudworth 1934). Rainfall, which varies considerably between years in the Southwest, appears to have an important influence on mast production. The evidence for this, although based on a limited number of years of observation, comes from associations detected between rainfall and the reproductive stages that are critical to production of successful masts—flower production, associated with abundant prior and present year rainfall, and seed weight, which increases with abundant spring rainfall (Stromberg 1988). Seed number between sites is limited variously by low soil moisture and high pre-dispersal seed predation (e.g., Rock Creek) and insect herbivory (e.g., Workman Creek) (Stromberg 1988).

Low rates of germination also limit recruitment to some degree. Whereas moisture for germination and establishment of some obligate riparian trees is provided by stream flow (Fenner et al. 1985), these processes in *J. major*, and perhaps other facultative

riparian trees, are influenced in large part by rainfall. Recent documentation of fairly high regeneration rates for walnut in the Southwest (Larkin 1987, Medina 1986) may be a result of long-term moisture cycles, Arizona being in an above-average cycle at the time of these studies.

Although moist areas provided optimum safe sites for germination and seedling establishment, some *J. major* seedlings established on terraces and along ephemeral streams. Seedlings were somewhat drought-tolerant, as indicated by high survival in greenhouse drought conditions, high root:shoot ratios in drier conditions, and ability to survive summer drought via dormancy. Nevertheless, seedling numbers in drier riparian sites were low. Recruitment may be abundant only after a sequence of several wet years—two for production of a large viable seed crop, another for abundant germination, and one or two more for high survivorship. The low frequency of such a sequence may explain the uniform age structure of adult walnut populations at some low-elevation sites (Stromberg 1988).

An additional factor that may limit establishment of seedlings in dry sites is lack of burial. Processes that bury seeds include deposition of flood debris (rare on terraces), caching by pocket gophers (rare except in sandy soils), trampling by large animals, and possibly caching by squirrels. Although tree squirrels commonly cache walnuts (Stapanian and Smith 1978), there is conflicting evidence about the frequency at which they cache nuts of *J. major*. In parts of their range where winters are mild, squirrels immediately consume gathered nuts (Brown 1984). This behavior may contribute to the decline in abundance of walnut at low elevations.

This study suggests that germination and establishment requirements of *J. major* differ between populations, as well as between microsites. Specifically, populations from perennial stream sites appear to be more tolerant of saturated soil at the seed and seedling stages; this should be verified on a larger sample of populations. The greater germination and seedling survival in saturated soil for seeds from such sites may be a consequence of lower oxygen demands of their smaller seeds (Stromberg 1988) or of physiological adaptations (Hook and Crawford 1978). Tolerance of moisture level is known to vary among seeds

and seedlings as a result of ecotypic differentiation in morphology or physiology (Hook and Stubbs 1967), and differences in tolerance of flooding and saturated soil are common among trees that grow on sites with different flooding histories (McGee et al. 1981). Isolation of Southwest riparian populations within "mountain islands" with distinct moisture regimes may have led to development of physiological and morphological ecotypes (Little 1950, Thornber 1915).

Whereas small seed size and tolerance of saturated soil are associated with wet riparian sites, the large seeds produced by walnuts on drier sites (Stromberg 1988) may increase survival of seedlings stressed by factors such as drought or grazing. Although purely speculative, the greater ability of Hitt Wash seedlings to recover from trampling and grazing compared with Walnut Creek seedlings may have been a consequence of larger seed size. Large seeds have large cotyledons that remain attached to seedlings for up to a year after germination (Stromberg 1988), allowing young seedlings to regenerate stems (Wetzstein et al. 1983). In any case, differences in seedling responses between walnut populations highlight the need for study of many populations to thoroughly understand reproductive dynamics of any riparian species.

ACKNOWLEDGMENTS

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