The Influence of Spacing on Seed Production

Its Application to Forest Tree Improvement

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Introduction

The rapid depletion of the native hoop pine stands in Queensland has been largely responsible for the establishment of plantations of exotic and native coniferous species. The management practices adopted in these plantations are designed to produce a high proportion of quality wood to satisfy a demand for this type of material.

Silvicultural treatment can influence the quality of the timber produced through its effect on rate of growth. branch size, and form factor; however the inherent characteristics of the stem, such as straightness, branching habit, wood density, fibre length, and figure in wood, can be controlled and improved only by careful attention to seed selection.

Since 1939, the seed for the exotic species in Queensland has been collected as far as possible from specially selected trees, and in the case of hoop pine (Araucaria cunninghamii), all seed for plantation purposes has been obtained from selected natural grown trees. These practices will continue, and will be supplemented in future with seed collected from plus stands, until such time as seed orchards are producing sufficient seed for these purposes.

A tree improvement Programme has been under way in Queensland for a number of years; the emphasis at present being on the production of clonal material (grafts) from specially selected "plus" trees. This stock is being used to establish seed orchards for the production of high quality seed. The bulk of this work to date has been carried out with slash pine *(Pinus* elliottii var. *elliottii*), the major exotic plantation species in Southeast Queensland.

The study described in this report was undertaken in an effort to determine the influence of spacing on the seed production of plantation grown trees. The main species studied was slash pine (Pinus elliottii), and it was considered that the information would be helpful in determining the optimum spacing for maximum seed production in plus stands and seed orchards.

Experimental Details

The material used for this study represented "free growth" plots in the following plantation species — slash pine Pinus elliottii var. elliottii, loblolly pine Pinus taeda, and hoop pine Araucaria cunninghamii. The ages of the respective plots at the commencement of the study in March 1953 were as follows: —

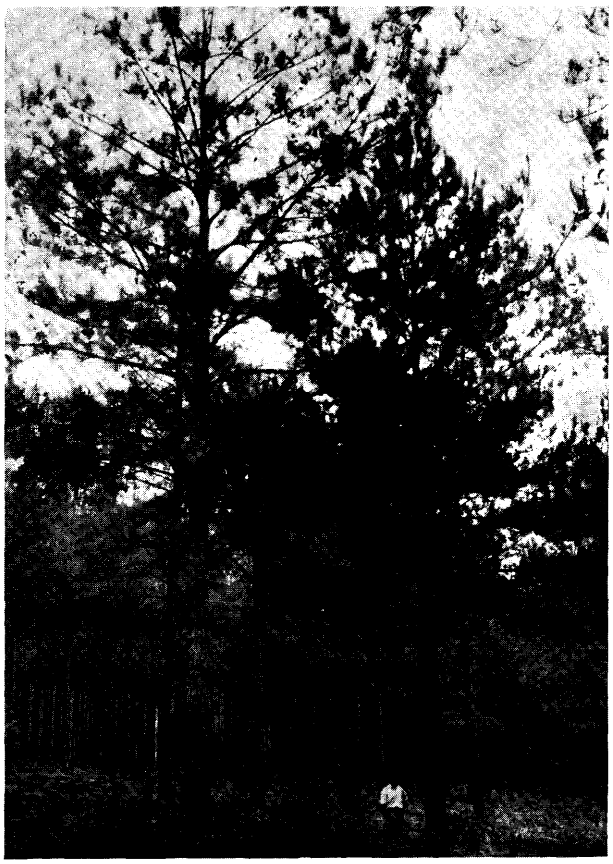

Fig. 1. — Loblolly pine, — widest spaced plot (52 treeslacre). — Note the wide deep crowns and abundand cones. (Age 16 years.)

Fig. 2 .— Loblolly pine plot unthinned (770 treeslacre). — Note the small crowns and scarcity of cones. (Age 16 years.)

P. elliottii 13½ years Loc. Beerwah,
P. taeda 12½ years Loc. Beerwah,
A. cunninghamii 16 years Loc. Imbil,
A. *cunninghamii* 18 years Loc. Yarraman.

The free growth plots were used as they provided a range of stockings from 50 to 800 stems per acre. The treatments which involved thinning in advance of competition, have had the same effect as planting initially at the respective stockings, and as a result, the trees in the wider spacings have developed deep wide healthy crowns.

The area of the net plots was approximately 0.15 of an acre, and the layout consisted of a randomised block with two replications.

Enumeration Procedure:

In all cases cone counts were conducted by climbing, as ground observations have not proved reliable. The counts were made just prior to seed fall in the years 1953, 1954 and 1955.

(1) Slash pine:

Complete enumerations were made on the duplicated plots at the wider spacings. No counts were made on plots with a stocking of over 400 trees per acre. The five largest trees (on a girth basis) in each plot were marked, and the cone counts on these recorded separately. Cones collected from these trees were used for the study on seed production per cone for the various spacings.

(2) Loblolly pine:

The cone counts on this species were restricted to the five largest trees in each plot. From this limited enumeration only the influence of spacing on cone production per tree can be gauged.

(3) Hoop pine:

A random sample was taken from each plot to calculate cone production for this species. Cone counts were possible only in 1953, as no cones were produced in the year prior to, and subsequent to this date.

Table 1. — The influence of spacing on cone production of slash pine

Average Stems/acre	*Cone Production per Tree*		
	1953	1954	1955
57	40	120	85
83	32	85	60
183	8	45	25
320	2	20	14
Average Stems/acre	*Cone Production per Acre*		
	1953	1954	1955
57	2210	6690	4800
83	2610	7140	4880
183	1450	8400	4470
320	670	6580	4410

I. The influence of spacing on cone production

The existence of marked seed years is evident from the wide variation in cone production over the three years; production in 1954 was consistently the highest for all stockings.

Over the three year period, cone production per tree was greatest at the widest spacing, and progressively declined with closer spacings; this is graphically illustrated in Fig. 3a.

The trend of cone production per acre is essentially the same each year, increasing with closer spacing, until a stage is reached where further increases in stocking produce a decrease in cone production (Fig. 4a). This trend is not so evident in 1954 owing to the fact that the heavier production was sustained over a greater range of stockings.

Table 2. — Influence of spacing on cone production of loblolly pine

Average Stems/acre	*Cone Production per Tree*		
	1953	1954	1955
52	191	163	210
66	112	161	150
77	112	150	146
106	65	140	94
135	65	125	149
163	116	148	147
246	45	59	60
390	28	72	33
770	5	14	13

There is no strong evidence of a marked variation in cone production over the three year period. There is, however, a decrease in cone production per tree with increasing stocking, (Fig. 3b). The overall cone production for loblolly pine is greater than that of slash pine.

Table 3. — Influence of spacing on cone production of hoop pine

Cone Production per Tree			
Yarraman		Imbil	
Averge Stems/acre	1953	Average Stems/acre	1953
100	85	100	54
180	65	160	32
280	44	250	11
380	18	350	11
576	8	600	5
Cone Production per Acre			
Yarraman		Imbil	
Average Stems/acre	1953	Average Stems/acre	1953
100	8540	100	5360
180	11690	160	4910
280	12170	250	2740
380	6980	350	3790
576	4360	600	2160

Figure 3c shows the decline in cone production with increased stocking for both areas. The cone production at Yarraman was generally better than that at Imbil for all plots, and this can be attributed possibly to site differences.

The pattern of cone production per acre is not the same for both localities; on the uniform site at Yarraman there is a build up to a maximum around 250 stems/acre (Fig. 4b), whereas at Imbil, on a less uniform site, there is a decline from the widest spacing at 100 stems/acre.

Discussion:

The stocking producing maximum cone production per tree is much lower than that giving maximum cone production per acre.

For the material studied the maximum cone production per individual tree will be obtained most likely when the tree is within the zone of free growth. This point, below which further increase in spacing will yield no further increase in cone production, has not been established, as in only one case with the plots at the widest spacing were the cone primordia laid down when the trees were still in the zone of free growth. In this instance, the plot inside the zone of free growth produced more cones than the comparable plot just outside. Thus for slash and

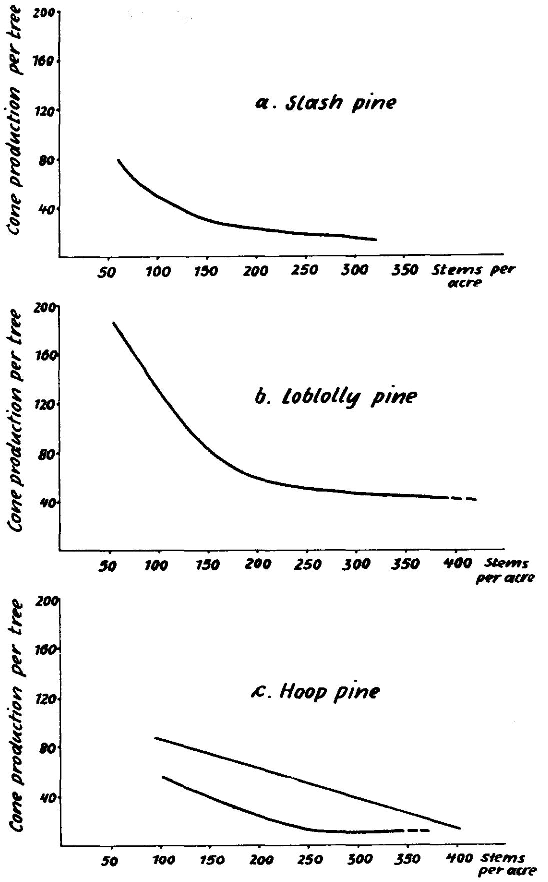

Fig. 3. — Effect of the number of stems per acre on the cone production of the individual tree of *(a) slash, (b) loblolly,* and *(c) hoop* pines.

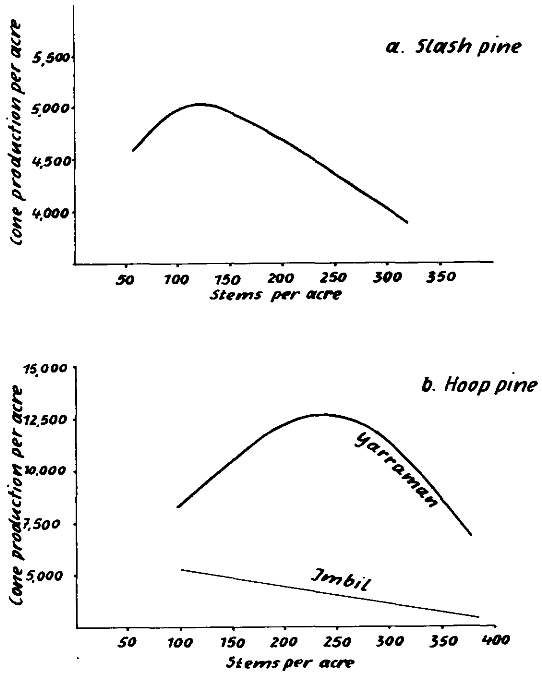

Fig. 4. — Effect of the number of stems per acre on the number of cones produced per acre, in stands of *(a) slash,* and *(b) hoop* pines.

loblolly pines at a height of approximately 50', for maximum cone production per tree, the stand should be growing at a stocking of no greater than 50 stems per acre (30' × 30').

For hoop pine of comparable size, the stocking giving maximum production per tree has not been established; however it is reasonable to assume that this figure will be well below 100 trees per acre, and this is confirmed by observation on younger material.

To produce maximum cones per acre, a closer spacing is necessary. For slash pine stands at this stage of development, a stocking of approximately 120 trees per acre is indicated (Fig. 4a). For hoop pine the position is not clear; however, a spacing in the region of 200 stems per acre appears desirable.

These results apply to stands under 20 years of age, and will have to be modified when applied to older stands if the production is to be maintained at or near maximum.

II. The Influence of Spacing on Seed Production

(1) The Effect of Spacing on Cone Sice

In the only study conducted on hoop pine, the widest spacings produced the largest cones. In 1953 a similar correlation was established for the Southern pines. However, this has not been substantiated by subsequent measurements.

(2) The Effect of Spacing on Number of Seed per Cone

The seed production per cone in 1953 is considerably lower than that in the two succeeding years; also the trend of decreasing seed production per cone with increasing stocking has only been apparent in this year. The annual variation in seed production per cone appears to be dependent on the availability of pollen and this will be discussed in Section III.

(3) The Effect of Spacing on Viability

Seed samples of loblolly and slash pine from each spacing were subjected to laboratory germination tests. No correlation was found between spacing and seed viability, all lots falling within the range 75—80% viability.

Table 4. — Slash pine

Average Stems/acre	Seed/cone [1])		
	1953	1954	1955
57	54	142	103
83	63	125	122
183	60	135	108
320	39	127	91

[1]) Based on 100 cones/spacing

Table 5. — Loblolly pine

Average Stems/acre	Seed/cone [1])		
	1953	1954	1955
52	106	137	138
66	109	140	135
112	76	134	133
157	73	134	115
246	64	148	94
390	68	104	127
770	46	140	121

[1]) Based on 100 cones/spacing.

In hoop pine considerable variation was found in seed viability at the various spacings. In this study the percentage of filled seed with healthy embryos has been taken as an indication of seed viability.

The reduction in the percentage of filled seed over the closer spacings is most marked, and it is felt that the most likely contributing factor is the shortage of pollen at the closer spacings. This is discussed more fully in Sektion III.

III. The Influence of Spacing on Pollen Production

An investigation was carried out on the loblolly pine plots in 1954 to determine whether spacing had any effect on the production of pollen. Sampling counts of the production of male amenta were taken in each of the duplicated plots at the various spacings.

Table 6. — Seed viability of hoop pine at various spacings.

Stems/acre	% of Filled Seed	
	Imbil	Yarraman
100	12	18
160	6	—
180	—	6
250	3	—
280	—	2
350	2	—
380	—	5
Unthinned	0	0

Table 7. — Influence of spacing on pollen production of loblolly pine

Average Stems/acre	Male Amenta per tree	Male Amenta per acre
52	60,500	315×10^4
66	57,000	376×10^4
106	50,500	536×10^4
163	24,000	385×10^4
246	3,200	78×10^4
770	2,200	172×10^4

The pattern of pollen production over the range of spacings is very similar to findings for cone production and no doubt has an important bearing on the production of viable seed per cone. In years of low pollen production such as 1951 (and 1954), the supply of pollen in the closer spacings is possibly limiting, and this would explain the variation in the number of seed per cone in 1953 (Tables 4 and 5). The years of heavy pollen production in 1952 and 1953 have resulted in an almost two-fold increase in seed yield per cone in 1954 and 1955, and there was little variation over the range of spacings in these years.

Pollen production expressed on a per acre basis has built up to a maximum around 100—120 stems per acre. This again follows fairly closely the trend in cone production for this species.

Hoop pine is a species which is very slow to produce pollen under plantation conditions, and cannot be relied upon to produce a reasonable quantity until 25 years of age or thereabouts.

Any fertilised seed found in young plantations has probably resulted from an outside pollen source, (e. g. virgin hoop pine in scrub fire breaks) or from the occasional precocious tree in the plantations.

Assuming that the distribution of extraneous pollen in free growth plots was uniform over the plots, then the increase in the number of fertilised seeds in wider spacings (Table 6) must have resulted from pollen produced within the plot. On this assumption, the widest spacing have produced the most pollen, and this could be an important consideration in planning seed orchards of this species.

IV. The Influence of Site Quality on Cone and Pollen Production

Cone Production

All previous results in this report have been based on the average figures of the duplicated plots at each spacing, which at times have varied considerably.

Initially in locating the plots in the loblolly pine free growth experiment, for each spacing the best and worst plots were progressively paired. As a result one plot at each spacing lies across the upper section of the slope and the other across the lower moister section of the slope.

From these results it can be seen that the better site had an advantage in cone production which has been borne out consistently over all plots with the exception of the plots at the stocking of 246 stems per acre. No explanation can be given for this except that the cone production on the better plot at this spacing seems unusually low.

This influence of the site on cone production is also evident on the hoop pine plots at Imbil; however this could not be found on the Yarraman plots which were established on a much more even site.

Table 8. — Influence of site quality on cone production of loblolly pine

Average Stems/acre	Cone Production per Tree	
	Better Site Lower Slope	Poorer Site Upper Slope
52	194	182
66	154	128
106	130	68
163	152	121
246	48	60
390	60	28
770	12	8
	750	595

$SE = 6.3 \quad t = 3.5$
For 40 degrees of freedom, $t\ 5\% = 2.021$
$t\ 1\% = 2.704$
Difference is highly significant.

Table 9. — Influence of site quality on cone production of hoop pine — Imbil

Average Stems/acre	Cone Production per Tree	
	Better Sheltered Site Lower Slope	Poorer Exposed Site Upper Slope
100	59	49
160	48	16
250	9 [1])	13
350	15	7
600	7	2
	138	87

[1]) Least sheltered plot on the lower slope.

Excluding plots at 250, $SE = 5.4 \quad t = 2.7$
For 6 degress of free $t_5 = 2.45$
$t_1 = 3.71$
The difference is a significant one.

Pollen Production

From the results of the study on the effect of spacing on cone production, figures were taken out to gauge the influence of site on the production of pollen.

Although growth figures for the two series of plots do not show big differences, the plots on the lower moister sites have produced up to five times the quantity of pollen. From the evidence of the previous section, pollen production on poor sites could be a limiting factor in seed production in poor years.

Table 10. — Influence of site quality on pollen production of loblolly pine

Average Stems/acre	Male Amenta per Acre	
	Better Site Lower Slope	Poorer Site Upper Slope
52	529×10^4	100×10^4
66	625×10^4	128×10^4
106	824×10^4	249×10^4
163	676×10^4	93×10^4
246	101×10^4	55×10^4
770	252×10^4	93×10^4
	3007×10^4	718×10^4

Conclusions

The findings of this study are summarised below, however it must be kept in mind that the figures apply to young stands in S. E. Queensland and therefore can be used only as a guide when applied to other stands grown under different conditions.

Southern Pines:

Slash pine stands between 13 and 16 years of age and approximately 50' in height, if grown initially at wide spacing, can be expected to produce, on the average, 27 pounds[1]) of viable seed per acre when grown at optimum spacing of 19' × 19' (i. e. 120 stems per acre).

Maximum seed production on single trees of slash and loblolly pine at this same stage of development can be expected at a spacing of 30' × 30' or wider, (50 trees per acre), and the yields will be in the region of 0.44 and 0.78 pounds[2]) of viable seed per tree respectively.

For hoop pine, no definite figure can be given, but it is evident that in stands from 15 to 20 years old, viable seed will be produced only at wider spacings. For the production of maximum seed per acre a spacing in the vicinity of 20' × 20', (100 trees per acre), is recommended, and for the maximum production on single trees a wider spacing, 30' × 30', (50 trees per acre), should be adopted.

In all cases the best sites have produced more cones and pollen than the corresponding poorer sites, and this should be taken into consideration when selecting sites for seed orchards.

The effect of the early wide spacing on the trees in this experiment has had an important bearing on the good cone yields obtained, as it has resulted in the trees having good deep healty crowns, similar to the type one would expect to find in a seed orchard. No data is available on stands thinned only a few years prior to seed collection, but it is doubtful if the yield would approach that from trees grown initially at wide spacing.

The concept of spacing associated with maximum seed production is a dynamic one, changing with the age and development of the stand, and therefore these figures are limited in their application, and will no doubt require modification for use in older stands. They do however shed some light on the possible yields from well managed seed orchards and plus stands of these species.

[1]) Based on 5,000 cones/acre—100 seeds/cone—75% viability—14,000 seeds/pound.

[2]) Based on 188 and 82 cones per tree respectively—100 seeds per cone (conservative for loblolly)—75% viabilitiy—18,000 and 14,000 seed/pound respectively.

Practical Application

Based on the results of this study the following recommendations can be made in relation to the establishment of seed orchards and plus stands under Queensland conditions.

Seed Orchards:

A spacing of 24' × 24' is suggested in establishing seed orchards of both slash pine and hoop pine. This figure is a compromise between that giving maximum cone production per acre, and maximum cone production per tree, and it will also allow for the removal of undesirable clones, and possible thinning towards the end of the seed orchard rotation.

Good quality sites should be chosen, in moist, well sheltered positions, and if necessary they should be fertilised to bring the fertility up to the level required.

Based on the yields obtained in this experiment, a slash pine seed orchard of 15 acres will produce all the seed required for the State's planting programme with that species of 3,000 acres a year. This is probably an over estimate, as it is expected that grafted trees will cone more heavily than seedling progeny, and with the methods available for inducing heavier flowering, the cone production per tree may be increased. An estimate of this nature can not be given for hoop pine, but if pollen supplies were adequate, considering the relatively greater number of seed per cone, an area similar to that for slash pine would be sufficient to produce the seed requirements of this species.

Plus Stands:

In this case the area available for the establishment of high quality plus stands is often limiting, and rather than strive for maximum cone production per tree e. g. 30' × 30' for slash pine, it is recommended that a closer spacing be adopted, so that the greatest possible production can be maintained from these areas. It is the quality of the stems in the stand that is the ultimate deciding factor on spacing, and it is usually not possible to leave more than 70—80 stems per acre if a good standard is to be maintained. For the age and size of the species covered in this report, a spacing of 24' × 24' is recommended when establishing plus stands, and where possible the thinning should be made as early as possible in the life of the stand, and if necessary in stages to prevent wind damage.

The following is a guide to the yields of viable seed that can be expected from plus stands at about age 20 years, thinned to this intensity:

Slash Pine . . . . . 25 pounds/acre,
Loblolly Pine . . . . 43 pounds/acre,
Hoop Pine . . . 1000 pounds/acre (total seed),

(slash pine based on 62 cones/tree, loblolly on 136 cones/tree, hoop pine 70 cones/tree; 5 dry cones = 1 lb. seed).

These yields will appear high as they are based on trees that have grown up under conditions of wide spacing; however they are an indication of the quantity that trees with well developed crowns are capable of producing.

Acknowledgements

This study was carried out as a part of the research programme of the *Queensland Forest Service*, and the assistance and facilities offered are gratefully acknowledged.

Summary

The study was designed to determine the influence of spacing on cone production, and ultimately, seed production of plantation conifers. The three species investigated were slash pine *Pinus elliotti* var. *elliottii,* loblolly pine *Pinus taeda,* and hoop pine *Araucaria cunninghamii.*

The influence of spacing on cone production per acre, and on a per tree basis is discussed, and the stocking for maximum production in each case is given. Figures relating to the effect of spacing on cone size, number of seed per cone, and seed viability are tabled and some theories presented. The effect of site quality on cone and pollen production is brought out, and the implications discussed.

In summarising the finding of this study, estimates of seed production are given, both for single trees and stands at optimum spacing; and the importance of good sites and early thinning is discussed. In referring to the practical aspects of this study, recommendations are given for the establishment of seed orchards and plus stands, including the optimum spacing, and area required to supply Queensland's future seed requirements.

Résumé

Titre de l'article: *L'influence de l'espacement sur la production de graines. — Application à l'amélioration des arbres forestiers.* —

Cette étude a été entreprise dans le but de déterminer l'influence de l'espacement sur la production de cônes et de graines d'une plantation résineuse. Les recherches ont porté sur trois espèces: "Slash pine" *(Pinus elliotti* var. *elliottii),* "loblolly pine" *(Pinus taeda)* et "hoop pine" *(Araucaria cunninghamii).*

L'étude de l'influence de l'espacement sur la production de cones à l'hectare, et par arbre, permet d'établir dans chaque cas la valeur optimum du matériel pour une production maximum. Des tableaux de chiffres traduisent l'effet de l'espacement sur la dimension des cones, le nombre de graines par cone, et la faculté germinative des graines. Quelques théories explicatives sont proposées. L'effet des conditions de la station sur la production de cones et de pollen entre également dans la discussion.

En conclusion, on donne des estimations de la production de graines, à la fois pour des arbres pris isolément et pour des peuplements à l'espacement optimum; l'importance de bonnes conditions de station et de l'éclaircie précoce est mise en évidence. En ce qui concerne les applications pratiques de cette étude, on envisage l'établissement de vergers à graines et le choix de peuplements plus, à l'espacement optimum, ainsi que les surfaces nécessaires pour subvenir aux futurs besoins en graines du Queensland.

Zusammenfassung

Titel der Arbeit: *Der Einfluß der Standweite auf die Samenproduktion. — Ihre Bedeutung für die Forstpflanzenzüchtung.* —

Die Untersuchung hatte den Zweck, den Einfluß der Standweite auf die Zapfenproduktion und damit auf die Samenproduktion bei Koniferen-Pflanzungen zu studieren. Folgende Holzarten sind untersucht worden: *Pinus elliotti* var. *elliottii* (slash), *P. taeda* (loblolly) und *Araucaria cunninghamii* (hoop pine).

1. Allgemein war die Zapfenproduktion je Einzelbaum bei den größten Standweiten am größten und nahm fortlaufend mit kleiner werdenden Standweiten ab. Die Zapfenproduktion je Flächeneinheit *(acre)* stieg mit enger werdenden Standweiten an bis zu der Stufe, bei der weitere Bestockungszunahme eine Abnahme in der Zapfenproduktion bewirkte.

2. Bei der Untersuchung der Araukarie ließ sich eine Korrelation zwischen Standweite und Zapfengröße feststellen. Eine ähnliche Korrelation war, allerdings nur im Jahre 1953, auch für die südlichen Kiefern zu finden. Im gleichen Jahr wurde ferner ein Trend sichtbar zwischen abnehmender Samenproduktion je Zapfen und steigendem Bestockungsgrad. Allerdings lag in diesem Jahre überhaupt die Samenproduktion je Zapfen beträchtlich niedriger als in den zwei vorhergehenden Jahren. Es wird angenommen, daß die jährliche Schwankung der Samenproduktion je Zapfen von der verfügbaren Pollenmenge abhängig ist.

3. Zwischen der Qualität des erzeugten Saatgutes und der Standweite konnte bei den südlichen Kiefern keine Korrelation ermittelt werden. Bei einer Untersuchung an der Araukarie zeigte sich allerdings eine ausgeprägte Reduktion des Prozentsatzes an vollen Samen bei dichteren Standweiten.

4. Untersuchungen an der Loblolly-Kiefer ergaben, daß die Pollenproduktion ansteigt, bis zur Standweite 100 bis 120 Stämme je acre. Sie folgt damit eng dem Trend für die Zapfenproduktion bei dieser Holzart.

5. Eine signifikante Korrelation zwischen Standortqualität und der Zapfen- und der Pollenproduktion wurde ermittelt: Je besser der Standort, desto größer werden die Zapfen- und die Pollenmengen.

6. Zwecks Zusammenfassung der Befunde aus diesen Untersuchungen werden Saatgut-Produktionsschätzungen für Einzelbäume und für Bestände bei optimaler Standweite wiedergegeben. Auf die Bedeutung des guten Standortes und der frühen Durchforstung wird eingegangen. Unter Hinweis auf die praktischen Aspekte der Untersuchungen werden Vorschläge für die Einrichtung von Samenplantagen und für den Aufbau von Plus-Beständen gemacht, einschließlich ihrer optimalen Standweiten, und außerdem Flächen gefordert, die Queenslands künftigen Saatgut-Bedarf zu decken vermögen.